

**FEEDING, RANGING AND SOCIAL ORGANISATION OF THE
GUINEA BABOON**

Martin John Sharman

**A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews**



1982

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Martin John Sharman



Thesis submitted to the Department of Psychology, University of St. Andrews

SUMMARY

Before this study, the Guinea or Western baboon, Papio papio, was almost unknown in its natural environment. This thesis reports a nineteen-month field study of two troops of P. papio carried out in south-eastern Senegal. The monkeys were followed on foot, and aspects of their feeding, ranging and social behaviour were recorded.

The troops were censused whenever possible. Both study troops, and other troops in the area, were found to be unusually large by comparison with other known troops in the genus, and although their age-sex compositions were not exceptional, there was some indication that recruitment into the adult population was low.

The activity budgets of both troops were similar, and members of both troops spent more time moving and feeding in the dry season than they did in the wet, when they spent more time in social behaviour. These differences were probably related to seasonal changes in productivity, which were large, since no rain fell in six months of the year.

The home range of one of the study troops covered about 45 to 50 square kilometres, while the other troop, whose home range was less well known, ranged over about 18 to 20 square kilometres. There were no seasonal differences in the mean distance travelled per day by either troop, although there was great daily variation about the mean of roughly 8 kilometres. This distance was greater than that travelled by most other troops of baboons, and was ascribed to low productivity in the dry season and large troops in the wet. The troops visited some habitats more frequently than they did others, and moved more slowly through those that they visited frequently than through those that they visited less frequently. In the dry season both troops visited areas in which there was relatively dense shade more frequently than they did areas with little shade. In the wet season they avoided areas

in which visibility was poor.

Sleeping sites were found to have a profound influence on the ranging patterns of the baboons, with usage of the home ranges being inversely proportional to the square of the distance from the nearest sleeping site. The baboons apparently chose to sleep in trees which afforded them protection against predation. The sleeping sites were restricted to places in which there was permanent water.

The baboons were largely frugivorous. In this they resembled baboon troops studied in other areas. Their diet changed throughout the year, as various plants fruited or seeded, and was more diverse in the wet season, when a wider variety of foods was available. More than a hundred different food items were known to be eaten, and the number of known food types increased throughout the study. Animals in their diet were mostly invertebrates found beneath boulders, but some vertebrates were also eaten.

The social organisation and mating system of these baboons were compared with those of the other baboons, including Theropithecus gelada. It was unlikely that they lived in a society in which adult females were constrained to mate with only one male, as are females in two other species of baboon. Instead, there appeared to be competition for sexual partners, with the formation of consortships between adults during the time of the female's oestrus. Adult males groomed each other in this species, which is uncommon in baboons with competitive mating, except at times of stress.

DECLARATION

I alone wrote this thesis, it reports my own work and it has not been submitted in part or entirely in any previous application for a higher degree.

This disseration is submitted to the University of St. Andrews for the Degree of Doctor of Philosophy. I was admitted as a research student and as a candidate for the Degree of Doctor of Philosophy under the Ordinance General No. 12 in September 1976.

CERTIFICATE

I hereby certify that Martin John Sharman has completed nine terms of research under supervision after being admitted as a research student under Ordinance General No. 12. He has fulfilled the conditions of the resolution of the University Court, 1967, No. 1 and is qualified to submit the accompanying thesis in application for the Degree of Doctor of Philosophy.

A. Whiten

Research Supervisor.

August, 1981.

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The colour of the common baboon (Papio papio) is reddish-brown; his face and hands are black, and his upper eyelids white. The hair of his cheeks forms a considerable tuft on each side; and the under surface of his body is but sparingly covered. In bulk he is equal to a middle sized dog; his proportions are thickset and inelegant; but he is by no means dull or inactive.

From: Bennett E.T. The Tower Menagerie,
(quoted in Hill, 1970).

...amongst the mighty granite crags and boulders was a vast assembly of baboons, with their almost human eyes fixed on the invaders. Biggles abandoned all pretence at finesse. "Run for it!" he yelled.

From: Johns W.E.(1936) Biggles in Africa.

ACKNOWLEDGEMENTS

With great pleasure I take this opportunity of thanking all of the many people who have helped me while I was preparing this thesis.

My supervisor, Andy Whiten, gave me help and encouragement in my preparation for the field, and rekindled my enthusiasm in Senegal when I had begun to get discouraged. He and Suzie Whiten kindly welcomed me into their home during my readjustment to civilization. Andy has also given me valuable criticism of my written work, and I am very grateful for his help.

Without Bill McGrew and Caroline Tutin I would never have met the baboons who have occupied my life so fully for the last few years. For this opportunity and for the ease with which they and Pamela Baldwin accepted me into their small community in a remote corner of West Africa I am deeply grateful and indebted. Life in this isolated settlement was made enjoyable by them and by the companionship of all those who later shared it with us, especially Mike and Sarah Harrison, Byron Alexander and Jim Anderson. I am especially grateful to Stephanie Hall, who shared a year of her life with me in pursuit of baboons. I am even grateful to Jezebel, who taught me more about six cylinder Land Rovers than I thought I wanted to know.

Our camp was about 100 kilometers of hot and dusty road from Hotel Simenti, where cold Storks and colder Gazelles never tasted so good. To Patrice Marty and Michel Fernandes and Nigel Orbell I extend my warmest thanks for so many spiritually refreshing evenings. Without them, and their swimming pool, life "en brousse" would have been a great deal drier. They and Claude Lucazeau also gave freely of their advice and invaluable help in tending the ills of an ageing vehicle.

I am grateful to the Government of Senegal, and to the Director of National Parks, Andre Dupuy, for permission to work in the Niolcolo-Koba National Park and to the staffs of the Park and of the Hotel Simenti for all the help they provided in making that work possible.

On my return from Senegal I visited three baboon sites in Kenya. I am grateful to Joe Popp and Jeanne Altmann for introducing me to their baboons, and to Shirley Strum for inviting me to spend several weeks

getting to know the Pumphouse Gang.

This thesis was written up in Cambridge, where David Chivers welcomed me into his unit in the Department of Veterinary Anatomy, for which I am extremely grateful. I benefited greatly from the help of the members of the King's College Research Group, and especially from Richard Wrangham. Robin Dunbar encouraged me to see P. papio in relation to the other baboons, which perspective now permeates this thesis. When King's Research Group disbanded Tim Clutton-Brock invited me to join his Large Mammal Research Group at Storey's Way. The encouragement that I recieved from the dedicated and enthusiastic atmosphere generated by Tim, Steve Albon and Glen Iason boosted me through the bulk of my writing up. To them, and to Gabriel Horne for permission to work there, I extend my thanks.

It is with pleasure that I acknowledge the help, assistance, and encouragement of the friends I have found in Cambridge. I doubt that I will ever be able to repay Gareth Hawksworth for his hospitality and friendship during one of the least sociable years of my life. Duncan Mackinder has helped enormously in the preparation of this thesis, both with computing and with photography. Kathy Rasmussen has kindly read and commented on several chapters with painstaking thoroughness. Debbie Snelson undertook the tedium of checking the references. Phyllis Lee has given me both emotional support and practical advice, and has read, reread, commented on and critisised every chapter in this thesis. To all these people I am deeply grateful.

The University of Cambridge Computing Service gave me the means and the resources to carry out much of the analysis in chapters three and five. This thesis was edited and typeset using programs developed by Philip Hazel.

The research was funded initially by the Science Research Council of Great Britain. I am grateful for their generous support. Finally, I would like to thank my mother, who has supported me openhandedly since the SRC grant ended. It is to her that I dedicate this thesis.

CHAPTER 1: Introduction

Papio papio (Desmarest 1820) has seldom been studied in the wild, and little is known of its ecology or behaviour outside captivity. By contrast, the other species of the genus, and the single living species of the closely related genus Theropithecus (Geffroy 1843), are among the best known of all non-human primates.

The taxonomy of the baboons is not clear. Apart from serious problems of nomenclature (Booth 1956a, Freedman 1963, Tappen 1960) and priority (Delson 1975a, Hill 1970), there is considerable debate about which taxonomic level the recognised forms of the genus Papio should take (Buettner-Janusch 1966, and review in Hill 1970). Throughout this thesis I shall follow Napier and Napier (1967) and Hill (1970) and treat the genus Papio as though it was made up of five species, P. hamadryas (Linnaeus 1758), P. anubis (Lesson 1827), P. cynocephalus (Linnaeus 1766), P. ursinus (Kerr 1792), and P. papio. The genus Mandrillus (Linnaeus 1758), like Theropithecus, is closely related to Papio (Erxleben 1777). The taxonomy and evolutionary history of Papio, Theropithecus, and other cercopithecids are revised in Delson (1975b), Delson (1977), Delson and Andrews (1975) and Patterson (1954).

P. papio is distributed over a small area of West Africa, being found in restricted areas of Mauritania, Mali, Guinea and Guinea Bissau, but having most of its range in Senegal. The National Park in which this study took place lies in the centre of the distribution of the species.

Most previous studies of baboons have been conducted in Eastern and Southern Africa. T. gelada (Rüppell 1835) has been studied in several sites within its restricted distribution in central Ethiopia. P. hamadryas has been studied in the arid semi-desert east of these Ethiopian highlands. Both of these species live in large groups within which are subgroups in which the mating of females is restricted to a single adult male. In the case of P. hamadryas this social organisation is thought to be an adaptation to foraging in small, widely dispersed groups in their unproductive habitats (Kummer 1968a). The extinct

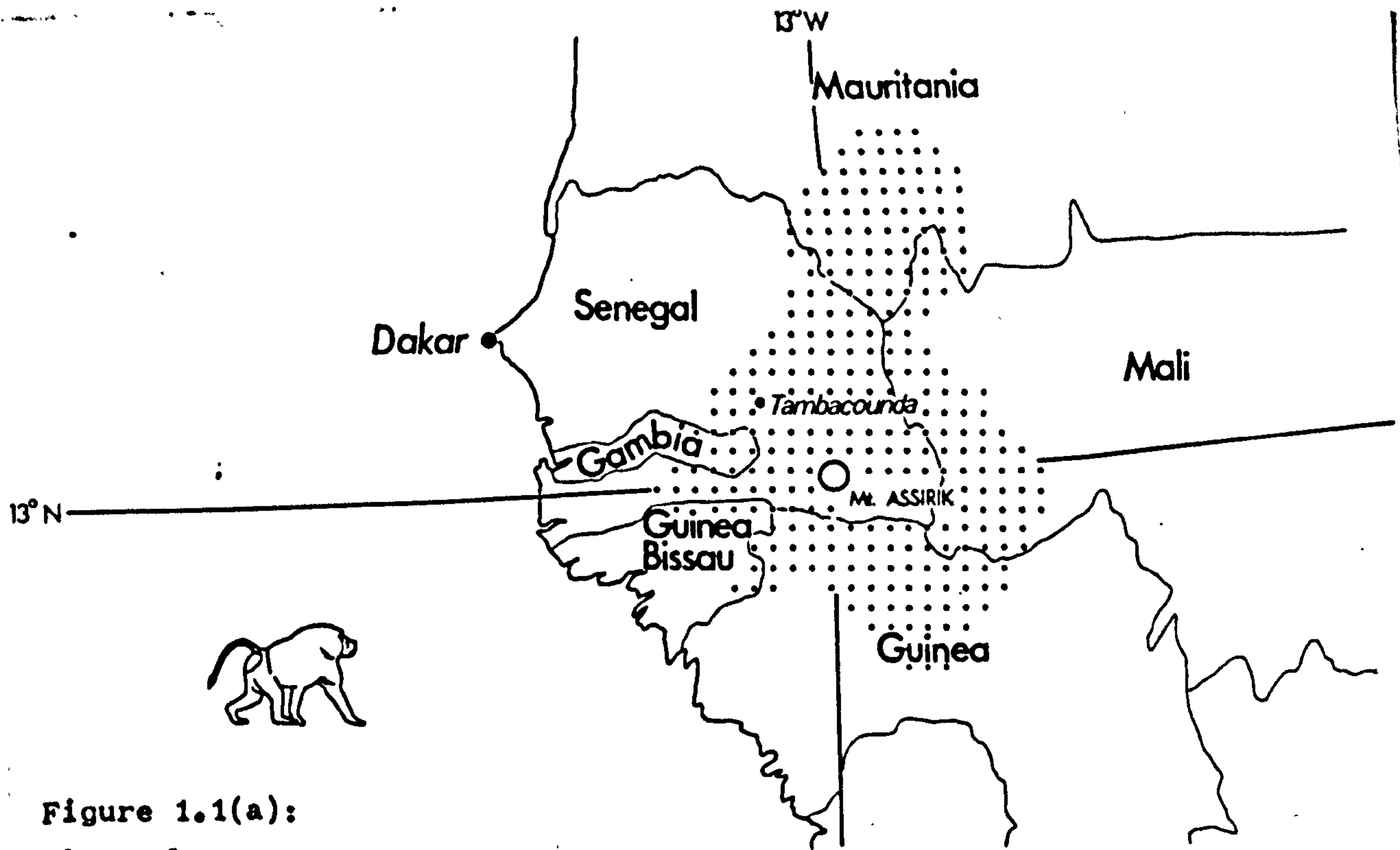


Figure 1.1(a):

distribution of *Papio papio*; location of field site (Mt. Assirik)

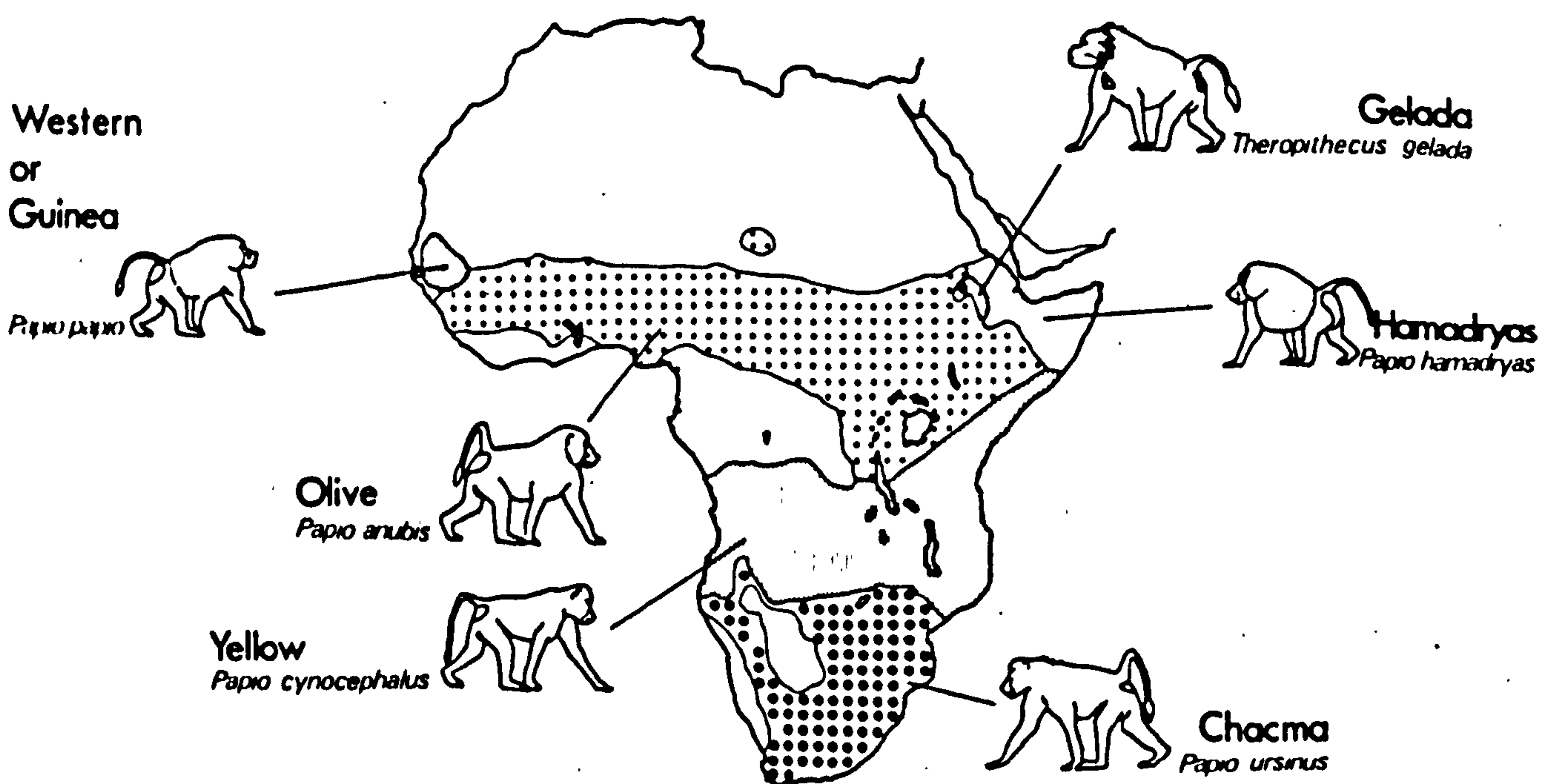


Figure 1.1(b):

approximate distribution of the long-tailed baboons

after Jolly and Brett 1973

T. oswaldi and perhaps other Theropithecus species are thought to have lived in one-male groups each with its own home range, as does Erythrocebus patas today (Dunbar 1981). This social organisation was probably also an adaptation to environments of low productivity. The one-male groups of T. gelada may be a relic of this adaptation.

The other well-known baboons have far more extensive distributions (Fig 1.1). P. anubis has been studied in thinly wooded gorges in Ethiopia, desert in Cameroon, coastal forest in Kenya, riparian forest in Uganda, and a lakeside forest in Tanzania. Most of the work that has been done on this species, however, has taken place in the thinly wooded grassland of central and southern Kenya. This species has always been found to live in groups in which adult males compete for sexually receptive females, who tend to associate with close female relatives. This social organisation is thought to arise from the need for females to compete for food with other females. To succeed in this competition they form coalitions with kin. These kin groups associate with other kin groups for mutual protection against predators. Adult males may form special relationships with certain females, but sexual consortships are often contested by other males in the troop.

Identical social organisations are found in the similar lightly wooded environments in Southern Kenya and in Tanzania in which P. cynocephalus has been studied. P. ursinus has been studied in coastal grassy plains with scattered trees, semi desert and desert in Namibia, and on the edges of the Okavangu swamp. In all of these study sites it lives in societies similar to those of P. anubis. In one locality in semidesert it lives in groups resembling those of P. hamadryas (Anderson 1980b). The reason advanced for this fragmentation into autonomous one-male groups is effectively identical to that proposed for P. hamadryas. Although most previous studies of Papio baboons have been in scrub desert, tree-studded grasslands, or on the edges of riparian forests, reconstructions of the Plio-pleistocene environment of baboons suggest woodland interspersed with grass swards (McGrew et al. 1981), an environment in which present-day baboons have not been studied, but which covers much of the range of P. papio. Our knowledge of the range of possible adaptations of the

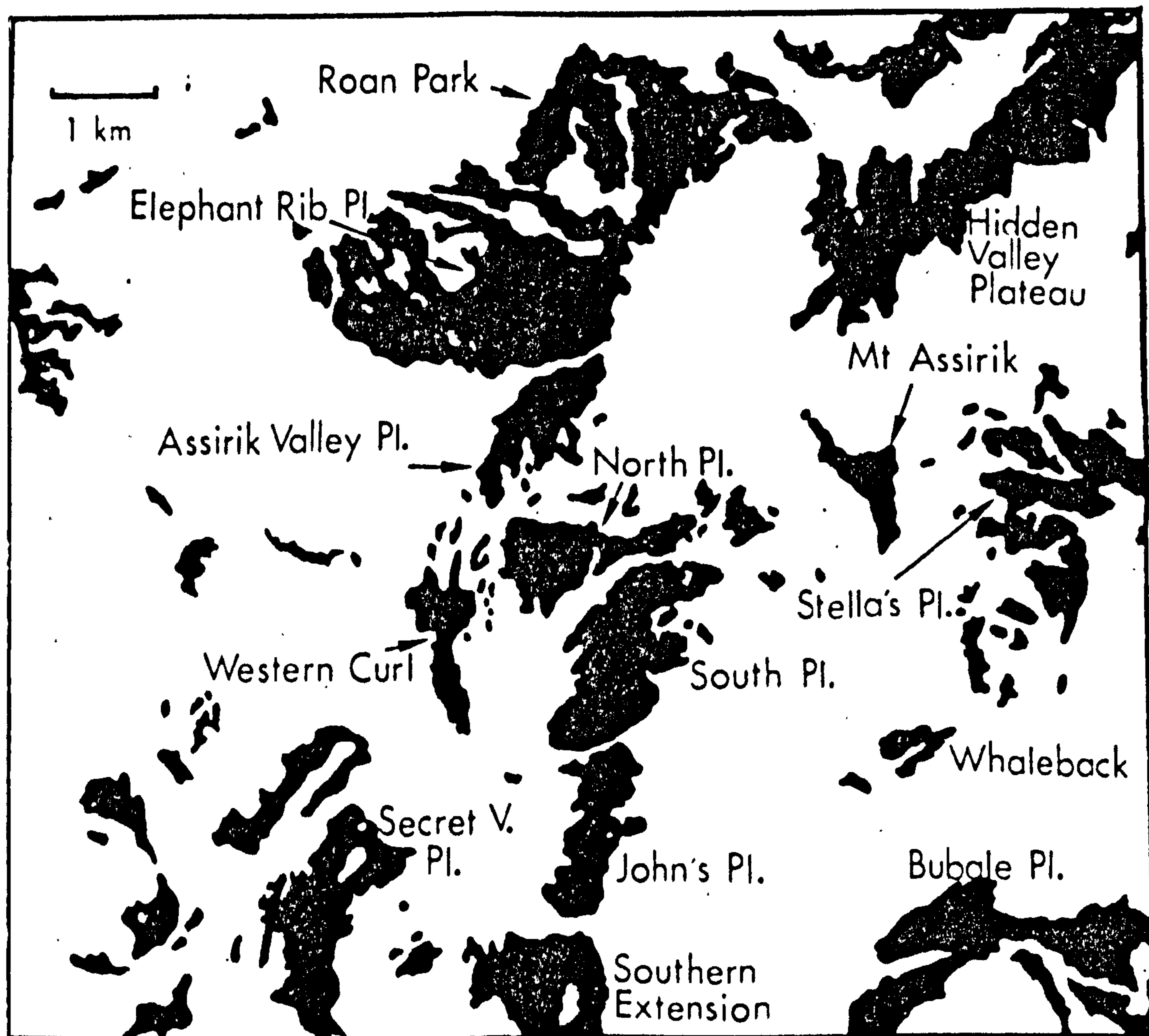
social organisation of baboons to various environments, and to this important environment in particular, has therefore been limited.

It has been suggested that males of P. papio have exclusive mating rights over females (Boese 1975). This would set the species apart from the promiscuous savanna baboons and place it with the two baboon species with one-male groups.

This study sets out to examine, in one population of P. papio, several aspects of ecology which are thought to influence social organisation in baboons. Since troop structure influences the number and nature of possible relationships between the members of the group, the demography of the population is examined in some detail. The activity budgets of individuals in a group are influenced by the ecology of the area in which the group lives and hence may provide clues to the extent to which the animals are affected by their environment. Environment influences the patterns of range use, which in turn influence social organisation. I have therefore examined the way in which ranging was influenced by various aspects of habitat, including vegetation, sleeping sites and water. Since diet is one of the major factors thought to influence social organisation in primates the diet of P. papio is discussed at length. Finally I examine the social organisation of, and mating system within, this one population.

For the sake of clarity no further review is given here, but each chapter is prefaced by a detailed introduction.

Figure 2.1:
Extent of lateritic plateaux in field area.
Camp was on the southern rim of North Plateau,
near its closest approach to South Plateau



CHAPTER 2: Site, Materials and Methods

INTRODUCTION

2.1: Geography

Senegal is the western-most country in Africa, bounded on the north by Mauritania, on the east by Mali, and on the south by Guinea and Guinea Bissau. The Grand Parc National du Niokolo-Koba (GPN du NK), 500km from the sea, covers about 8000 sq km (4%) of Senegal's 197,000 sq km. It lies in an area of drought-deciduous woodland, with Sudan savanna in the north of the park and Guinea savanna in the south (McGrew et al. 1981). Most of the park lies to seaward of the highest point in the park, Mt. Assirik, whose flat top, of about 0.5 sq km, is only 311m above sea level. Mt. Assirik and its surroundings represent the north-western limit of the foothills of the Fouta-Djalou massif, in which the River Gambia finds its source. The area in which this study took place occupied roughly 100 sq km, with Mt. Assirik lying within and to the east of its centre.

2.2: Geology, Topography and Vegetation

A 5 to 10m thick crust of laterite, a reddish, ferruginous product of chemical tropical weathering, formed the flat summit of Mt. Assirik. This surface was overlain by a cover of residual boulders. This low mesa was in the middle of a series of similar isolated laterite plateaux (Fig 2.1) which stretched in a 10km-wide band from the north to the south, overlying a broad ribbon of ancient metamorphic rock (Hebrard and Michel 1971). To the west of this raised ribbon lay a plain stretching to the Atlantic Ocean. In the field area this plain was underlain by an Upper Cambrian red sandstone. To the east of the ribbon of plateaux lay an area of low hills of Middle Cambrian pelites.

Almost no soil had formed on the laterite plateaux, and the plant communities that they supported were generally shallow-rooted grasses (eg Andropogon pseudopricus). In places these grass swards were interspersed with stunted bushes, principally Combretum etessei, but also including Boscia senegalensis and other species (Adam 1971). This habitat I have called "Combretum scrub" or "scrub on laterite plateau". Debris had

accumulated as boulder slopes beneath the cliffs at the edges of the plateaux. Many of these slopes were stabilised by bamboo (Oxytenanthera abyssinica) and large trees (eg Cola cordifolia, Khaya senegalensis, Afzelia africana, and Adansonia digitata). Canopies often touched, and these communities I called "dry forest" or "closed canopy woodland". Erosion on slopes was active and had led to the formation, both beneath the talus slopes and elsewhere, of a lithosol consisting of loose, variably-sized, unconsolidated, quartzitic, schistic, or granitic debris (Adam 1971, Bridges 1970). These areas were generally more or less lightly wooded, with most trees between about 3m and 4m tall. The community included Combretum spp., Pterocarpus erinaceus, Piliostigma thonningii, Grewia lasiodiscus, Hexalobus monopetalus, and Vitex madiensis. Many species of grasses grew beneath these trees, reaching to about 2m in the wet season. Genera included Andropogon, Schizachyrium, and Hyparrhenia (Adam 1971). In the lowest parts of the basins and in the plains to the west of the plateaux the soil was deeper, and highly porous, consisting of unconsolidated sand-sized particles. In most areas it lacked illuvial horizons, but there was a substantial superficial organic layer in places. Plant communities in the plains in areas distant from the larger gullies made up a habitat I described as "scrub-grassland" with scattered Grewia lasiodiscus among the tufts of Pobeguinea arrecta (Adam 1971). Along the sides of the riverbeds there were areas of elephant grass (Andropogon gayanus), bamboo (Oxytenanthera abyssinica), and strips of dry forest whose trees included Borassus aethiopum, Oncoba spinosa, and Zizyphus spp. The seasonally dry riverbeds were characteristically deeply incised, with vertical banks of up to 2m showing active erosion in the sandy soil.

Water draining from the sides of Mt. Assirik flowed into one of five catchment basins whose only outlets were ravines cut through the surrounding laterite plateaux. Permanent or near-permanent water flowed or rested in the bottom of these ravines, which were typically deep and narrow (sometimes as much as 30 m deep and only 30 m wide from rim to rim). This was the only permanent water in the area, and was not only vital to primates and to other obligate drinkers, but also nourished restricted strips of dense riverine gallery forest, with Ceiba pentandra,

Erythrophloeum suaveolens, Afzelia africana, Ficus spp., Diospyros mespiliformis, Adansonia digitata, and many species of liana, including Saba senegalensis, Nauclea latifolia, Landolphia heudelottii and several species of Combretum (Adam 1971). These riverine gallery forests allowed chimpanzees (Pan troglodytes verus) to survive (Baldwin 1979) in a field-area which also supported patas (Erythrocebus patas patas) (Henty in prep). They also provided green monkeys (Cercopithecus aethiops sabaeus) with productive territories (Harrison in prep), and were used by baboons (Papio papio) as sleeping sites. Further details of the vegetation are given in Baldwin (1979).

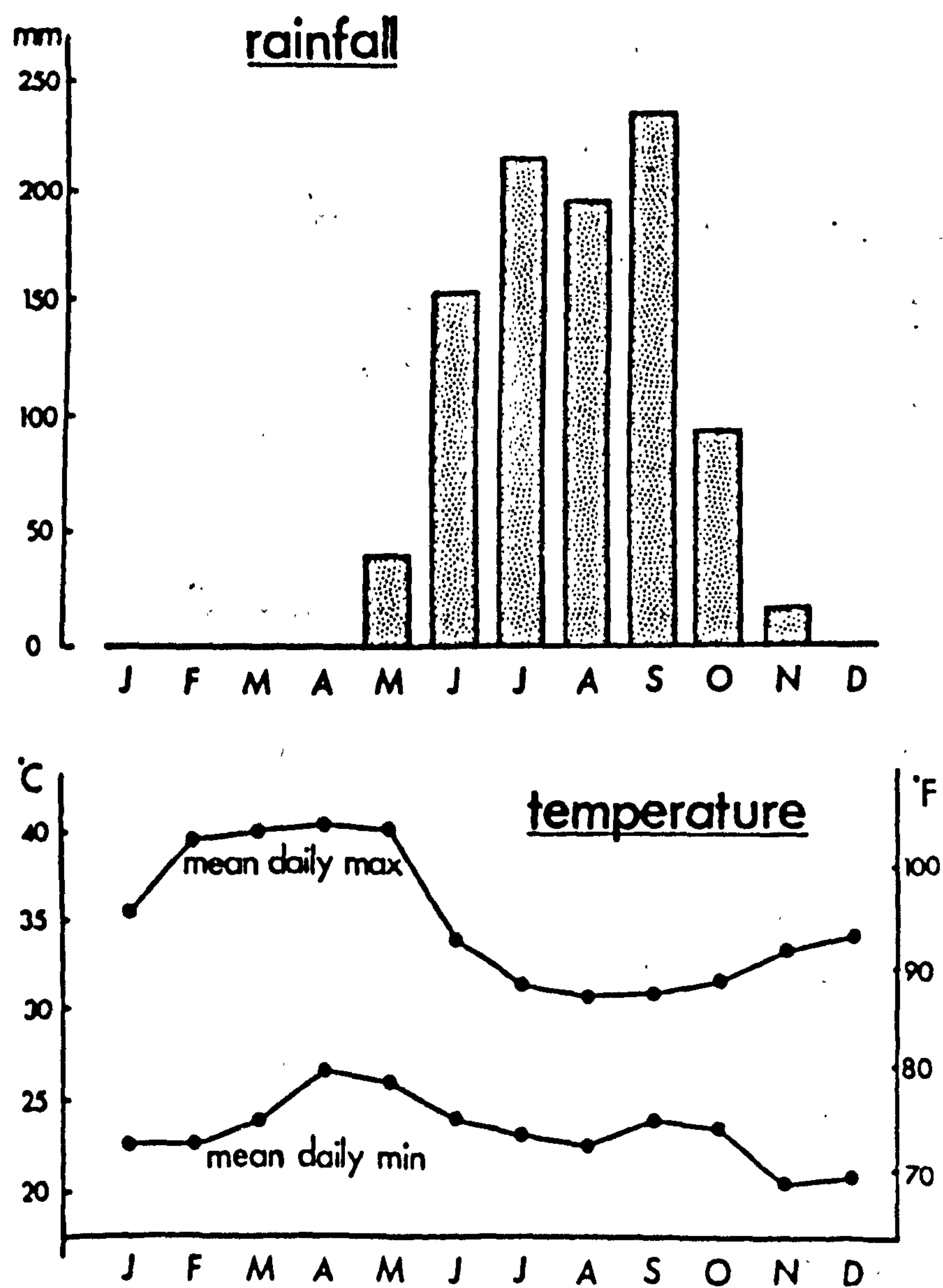
The geology of the area had another consequence of importance to the baboons. Laterite, chemically stable in the surface environment, is rich in partially hydrated oxides of iron and aluminium. In the wet season water is taken up by these oxides and the rock swells. In the dry season the rock gives up its water and shrinks. Repeated wetting and drying eventually causes the rock to split, forming a surface layer of boulders of various sizes (Weyman and Weyman 1977). These rough boulders provided shelter for small vertebrates such as lizards and snakes, and for many species of invertebrates. Baboons found what was possibly a major part of their diet by rolling these boulders over (chapter 7).

2.3: Climate

Adam (1971) gives a vivid description of the seasonality at the site. "The dry season is the season of implacable sun, white skies, colourless, indistinct horizons, the savanna scorched by fire, soil black with ash, skeletal trees, whirlwinds that lift dust high into the atmosphere, the overheated soil radiating like a furnace.... The vegetation awakens with the rains. The grass grows 2m tall, hiding everything...the dirt roads disappear beneath the grass, the animals vanish, the dry gullies become torrents, the baked mudflats become mires, the forests which had been shadeless are now a vault through which the sun barely glitters...everything disappears beneath the exuberant vegetation."

The methods used to obtain climatological data and the climate of the field area have been described in detail by Baldwin (1979). A summary and

Figure 2.2:
 Climate at Mt. Assirik
 (This figure is not referred to in the text)



some additional information follows. Rainfall data were collected daily. Air temperature, sun temperature, and relative humidity were assessed hourly between 07:00 and 20:00 hrs throughout the field study.

Annual rainfall was about 1000mm, but 5 or 6 months of the year (November or December to April) were dry, with no rain. The wettest month was July once (with 330mm) and September twice (198mm and 277mm). Most rain fell in storms, typically of 20-50mm, and most storms occurred at night. Relative humidity tended to be high in the wet season (about 85% at noon in September) and low in the dry season (about 15% at noon in April). Relative humidity was highest at dawn and lowest shortly after noon.

Mean daily maximum temperature, usually occurring at around 15:00-16:00hrs, varied between 29°C (August 1978) and 41°C (April 1978), while mean daily minimum temperature, usually occurring at around 07:00hrs, varied between 20°C (November 1977) and 27°C (April 1977). The mean daily range of shade temperature was $11^{\circ} \pm 3.8^{\circ}\text{C}$ and the range between the means of the hottest and coolest months was about 6.5°C.

Sun temperatures rose to roughly 10°C above air temperatures in the heat of the day. The following insolation data are taken from Thompson (1965). Sun temperatures in the dry season reached levels recorded at two other baboon field-sites - Badi (the site used by Dunbar and Nathan 1969, 1972, only 100km from Mt. Assirik), and Waza in the Cameroons (the site used by Struhsaker and Gartlan 1970) There were 6.6 ± 1.56 hours of bright sunlight per day on average. March had more hours of bright sunlight than any other month (an average of 9 per day) while August had the fewest (4).

The mean annual evapotranspiration at Mt. Assirik (640mm) was calculated from the annual rainfall and mean annual temperature, using the method developed by Holdridge (1962). The mean annual above-ground productivity ($996 \text{ gm m}^{-2} \text{ yr}^{-1}$) was then estimated from the regression line given in Rosenzweig (1968). The standard error on this estimate is large (Rosenzweig 1968).

2.4: Habitat Map

The area known to be used by the two study troops of baboons, together with about 15 sq km which was not known to be used, could be enclosed within a rectangle of 10 km north-south by 11 km east-west. A map of this area, showing 7 habitat types, was prepared from six aerial photos of the field area (scale 1:50,000) which were sufficiently detailed that when they were viewed in stereo they showed some canopies of individual trees, and allowed a resolution of habitat types finer than Baldwin (1979) attempted.

The correspondence between the zones on the photographs and the habitats that they depicted is given in Table 2.1.

Table 2.1:

Correspondence Between Zones on Aerial Photographs
and Habitat Types

Appearance on photo	Appearance of subdivisions		Habitat type
	density	grain	
Very pale	almost white;	little	Stands of grass, usually but not always on laterite pan
	pale grey;	slight	<u>Combretum</u> scrub with grass; usually on laterite pan
Pale grey	pale;	little	Grassland with scrub or trees
	darker;	grainy	Scrub with grassland
Dark grey	pale;	grainy	Open woodland with grass understory
	dark;	little	Woodland. Often with bamboo understory. Some areas closed- canopy dry forest
Nearly black	none used		Riverine gallery forest

To draw the map, acetate paper was placed over matched pairs of aerial photos. The lines of transition between zones of equal density and texture corresponding to each of the 7 habitats were traced, with a

Plate 2.1:
Habitat types in field area.
Scale roughly 1.3cms per km.



KEY:	black	riverine gallery forest
	pale yellow	grass on laterite plateau
	dark yellow	<u>Combretum</u> scrub on laterite plateau
	pale green	open woodland
	dark green	dry forest
	pale pink	scrub grassland
	dark pink	scrub

Rotring pen, onto separate sheets of acetate. The final map was made by overlaying these individual maps and enlarging the result to a scale of 5 cm to 1 km. Each zone was coloured and the result photographed (Plate 2.1).

It was normally easy to decide how to separate an area into zones of density and texture. Occasionally the border between two zones was indistinct, sometimes reflecting a gradation on the ground, sometimes poor resolution in the photos. An estimate of this error was made by constructing two versions of part of the map, each on a separate acetate sheet. Several "transect" lines were drawn across the overlain acetate sheets. The gap between the two versions of every mapped line that intersected a transect line was normally less than 1 mm. Since the map was to be used in association with ranging patterns of baboons whose position I could rarely determine with accuracy, this error was satisfactorily small.

The aerial photos slightly distorted the appearance of the terrain towards the edges. The effect of this distortion was estimated by comparing the distance between two outstanding features both of which occurred near the edge of one photo and centre of another, and which lay on a line perpendicular to the local edge of the photo. Features near the edge of the photo were a mean of $2.1 \pm 0.94\%$ ($n=40$) closer together than those near the centre.

When the map was enlarged all errors were also scaled up. The final error was probably less than about 40m on the ground in the position of most lines, but may have been more in certain portions of the map.

2.5: Estimating Habitat Composition

In order to calculate the area occupied by the various habitats I imposed on the map a grid of kilometre squares oriented north-south and east-west. Each 1 km square was then divided into 25 four-hectare quadrats, and each quadrat into 25 0.16 hectare (40m x 40m) "point" samples. The dimension of 40m was chosen because it represented, as explained above, the "grain" size of the map. I recorded the single

habitat type that I considered to occupy the greatest part of each point sample. The habitat of each 4 hectare quadrat could then be described in terms of 25 point samples, and the entire map in terms of 56,250 point samples. The final composition of the mapped area is shown in Table 2.2. The range given here assumes an error of $\pm 5\%$.

Table 2.2:

Habitat Composition of Field Area

Habitat	% of map	hectares	estimated error
Riverine Gallery Forest	0.4(11)	39.7	37.7- 41.7
Grassland (usu. on laterite)	6.2(12)	559.0	521.0- 587.0
Scrub Grassland	7.7(16)	694.4	659.7- 729.1
<u>Combretum</u> scrub (on laterite)	14.4(27)	1298.4	1233.5-1363.3
Dry Forest	21.2(35)	1915.7	1819.9-2011.5
Scrub	22.5(44)	2031.7	1930.1-2133.3
Open Woodland	27.3(46)	2461.1	2338.1-2584.2

2.6: Visibility

Visibility may play an important part in the foraging strategies of primates, and foraging strategies may in turn have consequences for social structure (Struhsaker and Leland 1979). In field sites where visibility is good, baboon troops apparently forage as a unit, seldom fragmenting into small foraging parties (Altmann and Altmann 1970, Harding 1976, Popp 1978). At other field sites baboons have apparently coped with poor visibility by adopting a foraging strategy which includes fragmentation into small groups (Aldrich-Blake et al. 1971, Crook and Aldrich-Blake 1968, Dunbar and Nathan 1972, Kummer 1968a, Tayler and Saayman 1972). There has been no quantification of the levels of visibility which promotes either of these foraging strategies. In an attempt to provide data which may later be used to correlate foraging strategies with visibility, I measured the distances over which a baboon on the ground and in a tree 170cm above the ground was likely to be able to see another baboon in various habitats.

The method used to determine these distances also enabled me to estimate the foliage density in a manner similar to that used by MacArthur and MacArthur (1961). If the probability of encountering the silhouette of an object large enough to obscure the view along an imaginary cylinder of cross sectional area 1 sq cm and length 1 m were p , then after d metres the probability that any such cylinder does not contain a silhouette would be given by

$$p = e^{-pd}$$

The distance at which half the area of a board was obscured by the vegetation would then be h where

$$e^{-ph} = 0.5$$

or

$$p = -1/h \times \ln 0.5$$

This relationship enables us to determine the cross-sectional area a of obscuring vegetation per cubic metre of space in each habitat. A "baboon-sized" target was constructed by pasting 13 white 10cm x 10cm squares onto a 50cm x 60cm piece of cardboard to provide a regular 50cm x 50cm chequerboard with a 10cm x 50cm margin at the bottom.

Random points were selected well within the vegetation zone to be sampled. At these points cairns were built so that the same points could be used again in subsequent seasons. From each point an observer watched while an assistant, holding the board vertical, with its chequered surface facing the observer, moved along each of the four cardinal points of the compass in turn, periodically placing the lower edge of the board in contact with the ground. In each of the four directions the distance from the observer to the board was recorded to the nearest metre when the observer with eyes at about (1) 60cm and (2) 170cm above the ground could see (a) just fewer than half of the squares and (b) none of the board. Distances over 100m were estimated to the nearest 5m; distances over 200m to the nearest 50m.

Scrub grassland was not sampled in the wet season. The results for visibility in this habitat were taken from a road-strip survey of the park described later.

In the wet season two baboons on the ground more than 20m apart were unlikely to be able to see each other in any habitat but Combretum scrub-covered plateau (Table 2.3). Visibility in the wet season was principally obscured by grass, which in many places grew to chest height or higher. In the dry season the grass was trampled down, burned off, or collapsed, leaving only fire-resistant shrubs and trees to obscure the view. The effect of grass in obscuring the view in the wet season can clearly be seen in the seasonal difference in the area of silhouette per cubic metre of habitat in the two seasons (Table 2.4).

As a result, Grass on Laterite and Open Woodland habitats were visually dense in the wet season because of the tall grasses in these areas, while in the dry season they were the habitats with the least obscuring vegetation.

Table 2.3:

Visibility in Various Habitats. Distance in metres over which observer could see specified amount of chequerboard.

Season	Habitat	Half Visible				Invisible			
		Height of Eyes				Height of Eyes			
		60cm		170cm		60cm		170cm	
		median	range	median	range	median	range	median	range
Wet	GP	3	1-10	4	1-12	7	3-11	8	4-15
	SP	28.5	13-44	30	15-20	31.5	21-49	35	20-60
	OW	2.5	1- 6	3	0- 7	4.5	2- 7	6	1- 9
	SG	-	-	-	-	-	-	-	-
	FB	8.5	0-18	10	1-17	9	4-13	11.5	7-16
	RG	12	1-23	13	3-34	11	3-19	11.5	0-48
Dry	GP	54	22-200	54.5	25-200	88	32-300	83	32-300
	SP	49	14-125	51	29-175	58	30-200	60	26-120
	OW	21	4-90	21.5	4-68	55.5	26-84	67.5	23-143
	SG	-	-	-	-	30	0-100	57.5	25-200
	FB	23.5	7-57	21	7-51	45.5	22-65	58.5	24-73
	RG	7	5-14	10	5-28	16	5-39	24	5-66

KEY to habitat types:

GP grass on laterite plateau SP scrub on laterite plateau
OW open woodland SG scrub grassland
FB dry forest, sometimes with bamboo understory
RG riverine gallery forest

note: Scrub grassland was not sampled in the wet season.

Riverine forest was the only habitat in which visibility was sometimes worse in the dry season than it was in the wet season (Table 2.3). In this habitat there was little change in the density of the undergrowth with the seasons, as growth was presumably limited by light and not by water. In some cases visibility near the streambed was improved in the wet season by water carrying off obstacles such as fallen trees.

Table 2.4:

Habitat	<u>Square Centimetres of Silhouette per</u> <u>Cubic Metre of Habitat</u>						
	Wet			Season 	Dry		
	Height above Ground				Height above Ground		
	60cm	170cm	mean		60cm	170cm	mean
Grass on laterite	2310	1733	2022		128	127	128
Scrub on laterite	243	231	237		141	136	139
Open woodland	2773	2310	2542		330	322	326
Dry forest	815	693	754		295	330	313
Riverine Gallery	587	533	555		990	693	842

2.7: Cover

Kummer (1968a) reported that P. hamadryas baboons sat down in shade whenever possible after 09:00. In an environment where sun temperatures sometimes topped 50°C and where shade temperatures were some 10°C lower, the relative amounts of shade in different habitats might have influenced the ranging of the baboons. The amount of shade in wet and dry seasons in four habitats was measured.

The same transects used for assessing visibility were used in the assessment of percent of cover. At every metre along the transect I noted the presence of foliage, apart from grass, vertically above the ground.

In order to estimate the effectiveness of this cover, a 50cm x 50cm chequerboard was marked with 100 5cm x 5cm squares, and placed at noon beneath areas on the transects assessed as having cover. The number of

squares in full sunlight, full shade, and in penumbra was recorded.

About 40% of the field area (I have included in this figure the unsurveyed scrub grassland) had less than 5% ground cover above grass level, while 20% had more than 75% (Table 2.6).

Table 2.5:

Percent of Cover in Various Habitats

Habitat	Wet Season		Dry Season	
	median %	range	median %	range
Grass on laterite plateau	3	1-7	2.5	1-4
Scrub on laterite plateau	3	1-9	3	0-7
Open Woodland	32.5	22-50	26	6-42
Scrub Grassland	-	-	-	-
Dry Forest (some bamboo)	84	75-98	80	65-93
Riverine Gallery Forest	96	92-100	93	88-99

The proportion of samples assessed as having cover changed little between the seasons. A more objective method, like that of Emlen (1967) might have shown greater seasonal differences, as was suggested by the different amounts of shade found beneath such "covered" points in the two seasons.

In every case shade increased in the wet season, as a direct consequence of greater area of foliage on plants (Table 2.5), although penumbra decreased in every case. In the dry season there were many naked branches whose shadows on the ground were principally penumbra, while in the wet season most branches bore leaves and cast deep shadows. The apparent decrease from wet to dry season in the median percentage of the ground lit directly by the sun on plateaux was not statistically significant (95% binomial confidence limits). In the dry season, shadow was densest in the riverine gallery forests and least dense in the drought-deciduous open woodland.

The proportion of the ground in deep shadow in each habitat in both seasons was calculated from data in Tables 2.5 and 2.6. The amount of shadow was not statistically correlated with the visibility (compare Table 2.6 with Table 2.4).

Table 2.6:

Percent of Ground in Various Intensities of Sunlight
Beneath Points Assessed as having Cover
in Various Habitats

Habitat	Illumination	Wet Season		Dry Season	
		median	range	median	range
Plateau	Full Sun	13.5	7-45	8.5	7-39
	Penumbra	25	6-35	27.5	19-49
	Shadow	57	24-76	54	12-67
Woodland	Full Sun	15.5	3-24	50.5	19-79
	Penumbra	12	2-29	34.5	6-81
	Shadow	73	51-95	10	0-33
Dry For.	Full Sun	9.5	2-46	33.5	17-42
	Penumbra	14	8-47	20.5	6-34
	Shadow	69.5	40-88	44.5	34-68
Riverine	Full Sun	6.5	2-15	9	8-13
	Penumbra	7	1-23	15	3-29
	Shadow	86.5	68-94	76	58-88

Table 2.7:

Percentage of the Ground in Shadow

Habitat	Percentage of Dense Shadow	
	Wet Season	Dry Season
Grass on laterite	1.7	1.4
Scrub on laterite	1.7	1.6
Open woodland	23.6	2.6
Dry forest	58.4	35.6
Riverine Gallery Forest	83.0	70.7

2.8: Topography

The field area included various natural features such as cliffs, ravines, ridges, and streams. I recorded which of 10 topographic features occurred in each quadrat in the field area. Two features, sleeping sites and dry season water, were chosen for their relevance to the baboons, while the others were chosen on the same criteria by which I constructed the relief map of the field area which was used to plot the ranging of the baboons. If two or more features occurred in the

same quadrat I characterised it by the topographic feature which was higher in a hierarchy determined by two principles. Firstly, relatively rare features generally had higher rank than relatively common features although this ordering was modified by my assessment of their importance to the baboons. Secondly, a quadrat was described as "undifferentiated" when none of the other 9 features appeared in the quadrat. The categories and their relative rank are given in Table 2.8.

Table 2.8:

<u>Topographic Types</u>			
Rank	Feature	No. of Quadrats in Field Area	% of Quadrats
1	Sleeping Site	19	0.8
2	Dry Season Water	21	0.8
3	Ravine	30	1.2
4	Cliff	364	14.7
5	Ridge	140	5.7
6	Catchment Stream	231	9.3
7	Drainage Stream	364	14.7
8	Marigot	52	2.1
9	Plateau	211	8.5
10	Undifferentiated	1043	42.1

Definitions of Features are given in the text.

2.8.1: Topographic Definitions

Sleeping Site: trees in which baboons were known to sleep.

Dry Season Water: a water course containing one or more pools in which water persisted for most or all of the dry season. These pools were usually in or downstream of the ravines.

Ravine: a narrow cleft in a laterite plateau. Nearly all the sleeping sites were found in ravines. All ravines held streams, and nearly all held permanent water in the dry season. Ravines usually contained riverine gallery forest.

Cliff: the laterite plateaux often ended in cliffs, occasionally up to 30m high, where the laterite crust had been eroded away. The vegetation at the base of these cliffs was typically dense, often

having large trees (eg Khaya senegalensis) and vines (eg Saba senegalensis) stabilising the talus slopes.

Ridges: ridges ran out from Mt. Assirik and other hills.

Catchment Streams: dendritic gullies which drained the catchment basins between Mt. Assirik and the fringing plateaux.

Drainage Streams: streams meandering across the plains between the ravines and one of three more major rivers.

Marigot: a French word meaning "backwater" or "creek", and used in Senegal to refer to any small watercourse. Here I use it to mean "watercourse across laterite plateau".

Plateau: called "bowal" in Senegal, these plateaux were extensive areas of more or less naked laterite.

Undifferentiated: a quadrat containing none of the other topographic features. This was normally an area of low-lying, flat sandy soil covered with poor vegetation. Most of these quadrats lay in the west of the field area.

2.9: Following the Baboons

Baboons were followed on foot. I tried to stay with them from the time that they left the sleeping site in the morning to the time that they reached their destination in the evening. Observations were made through 10x40 binoculars, and longhand notes were made in a notebook and later transcribed and catalogued. Data were collected according to several sampling methods which are described in detail in the relevant chapters. Samples of food were collected whenever possible for later identification, usually by other members of the Stirling African Primate Project (SAPP), but occasionally with reference to other sources, including Kew Gardens. S. Hall and A. Whiten accompanied me on several all-day follows.

The vegetation restricted the view of the baboons to such an extent that I was normally within their flight distance as soon as I could see them. Before I became used to following more by noise than by vision, and to judge their pace and to adjust mine accordingly, I repeatedly either startled them and caused them to flee, or lost contact with them

in the attempt not to "push" them. This became less common towards the end of the study. Habituation and individual recognition were also hampered by the observation conditions,^{and} since troops or subtroops shared sleeping sites, there was usually no way of knowing whether the baboons followed from one sleeping site on two successive days belonged to the same troop. As a result, it was not until the wet season at the end of the study that it became clear that two troops were using the field area, by which time I rarely came to the end of a day's follow without knowing which troop I had been following. These troops were named Anecdote's troop (after an adolescent male with a distinctive, short tail) and Fable's troop (after an adult male with an equally distinctive tail). Throughout the study I tried to detect characteristic marks on the animals. In some cases an individual with characteristic marks was seen more than once. If it was ever seen in a known troop I assumed that the troop in which it was previously and subsequently seen was the same troop, or a fragment of the same troop. This supposes, firstly, that animals did not change troops, and secondly, that re-identifications were certain. Both of these suppositions are questionable. Where I refer to one or other troop in the dry season, the identification was probable, not certain. In this thesis I have compared the behaviour and ecology of these two troops, though data has also been collected on the behaviour of baboons whose troop was unknown.

2.10: Nomenclature: Age-Sex Classes

Since individuals were for the most part not known, I have depended entirely on age-sex categorisation in this thesis. The terms "age-sex category" and "age-sex class" are used to refer to animals belonging to one of the groups whose description is given below.

Age-Sex Categories recognised at Mt. Assirik

<u>Code</u>	<u>Class</u>	<u>Description</u>
Male	adult male	Mane and canines fully developed (canines may be broken or worn). Massive appearance. Gives characteristic bass "wahoo".
(M)	young male	Mane developed, but not as large as mane of fully adult male. Body not quite as large as that of a fully adult male. Canines often well developed and sharp-looking. This class was pooled with adult males for analysis.
Oestrus	oestrus female	Adult female with swollen sex skin. Note that adolescent females in prefertile cycles were classified as oestrus under this criterion.
Pregnant	pregnant female	Adult female with pink to scarlet para-ischial callosities. Taken as sign of pregnancy (Altmann 1973b). In late pregnancy swelling of abdomen noticed in early morning (before foraging).
Ventral	female with ventral infant	Adult female carrying infant (often black) on ventrum.
Dorsal	female with dorsal infant	Adult female carrying infant (often brown) on dorsum.

Age-Sex Categories recognised at Mt. Assirik (cont)

<u>Code</u>	<u>Class</u>	<u>Description</u>
Female	female of unknown sexual status	Nipples button-like when nulliparous, pink and elongate when parous. Full adult size. Sexual status not recorded; in long grass an infant carried ventrally might be missed.
Subad M	subadult male	Mane and canines starting to appear. Larger, more muscular than adult females, but may be hard to distinguish sometimes.
Subad F	subadult female	Nipples like brown buttons, only visible when chest frontally exposed. Too large to be older juvenile class, but lacking full adult female build. Very hard class to distinguish.
Older J	older juvenile	Gangly. Active, but not as gratuitously active as younger juvenile. Play is rough.
Young J	young juvenile	Usually independent, but often unweaned. Small and active.
Brown I	brown infant	Hair (almost) completely brown. Skin black.
Trans I	transitional infant	Hair black on crown and spine, brown on flanks. Face black.

Age-Sex Categories recognised at Mt. Assirik (cont)

<u>Code</u>	<u>Class</u>	<u>Description</u>
Black I	black infant	Hair completely or mostly black. Skin pink or red.
Ventr I	infant carried ventrally	Infant riding on the ventrum of another animal usually an adult female
Dorsal I	infant carried dorsally	Infant riding on the back of another animal, often an adult female.
Unknown	animal of unknown class	Animal whose class could not be determined.
Juvenile	juvenile of unknown class	Juvenile which could not be classified more accurately.
Infant	infant of unknown class	Independent infant whose colouration could not be made out.

CHAPTER 3: Demography

INTRODUCTION

3.1: Group Size: Introduction

Dupuy and Verschuren (1977) claim that troops of P. papio in the GPN de NK often include more than 500 members. If this were true, these troops would probably be the largest unprovisioned primate troops known. Unfortunately Dupuy and Verschuren (1977) provide no data to support their assertion. Data is provided in this chapter on the sizes of 18 troops of P. papio in the park.

Group size is influenced by rates of birth, death, migration (Altmann and Altmann 1979, Cohen 1969, 1971, 1972), and long term fission (Altmann and Altmann 1970 Chepko-Sade and Olivier 1979, Cheverud et al. 1978, Dunbar and Dunbar 1974d, Furuya 1968, Hall 1963a, Nash 1976), and fusion (Altmann et al. 1977, Hall 1963a, Suzuki 1979), all of which are governed largely by ecological pressures (Altmann and Altmann 1970, Taylor and Taylor 1977); for example, individuals in large groups may be less likely to suffer predation but more likely to experience feeding competition.

Savanna baboon troops sometimes aggregate to form large groups, often at sleeping sites and waterholes (Altmann and Altmann 1970, Saayman 1971c, Washburn and DeVore 1961). The members of the groups may or may not mingle and interact. The size and age-sex composition of one such assemblage at Mt. Assirik is recorded here.

3.1.2: Nomenclature: Counts and Censuses

I distinguish between "counts", in which the number of individuals was counted but the age or sex of few or none of the individuals was recorded, and "censuses", in which the age-sex class of many or all of the individuals in some fragment of the troop was determined.

Frequently I was able to detect the presence of animals which were out of sight (by movement of the foliage, noises, and so on) so that the count or census was known to be incomplete. These I describe as "partial" counts or censuses. A partial census was also recorded when poor observation conditions reduced the certainty with which individuals could

be classified.

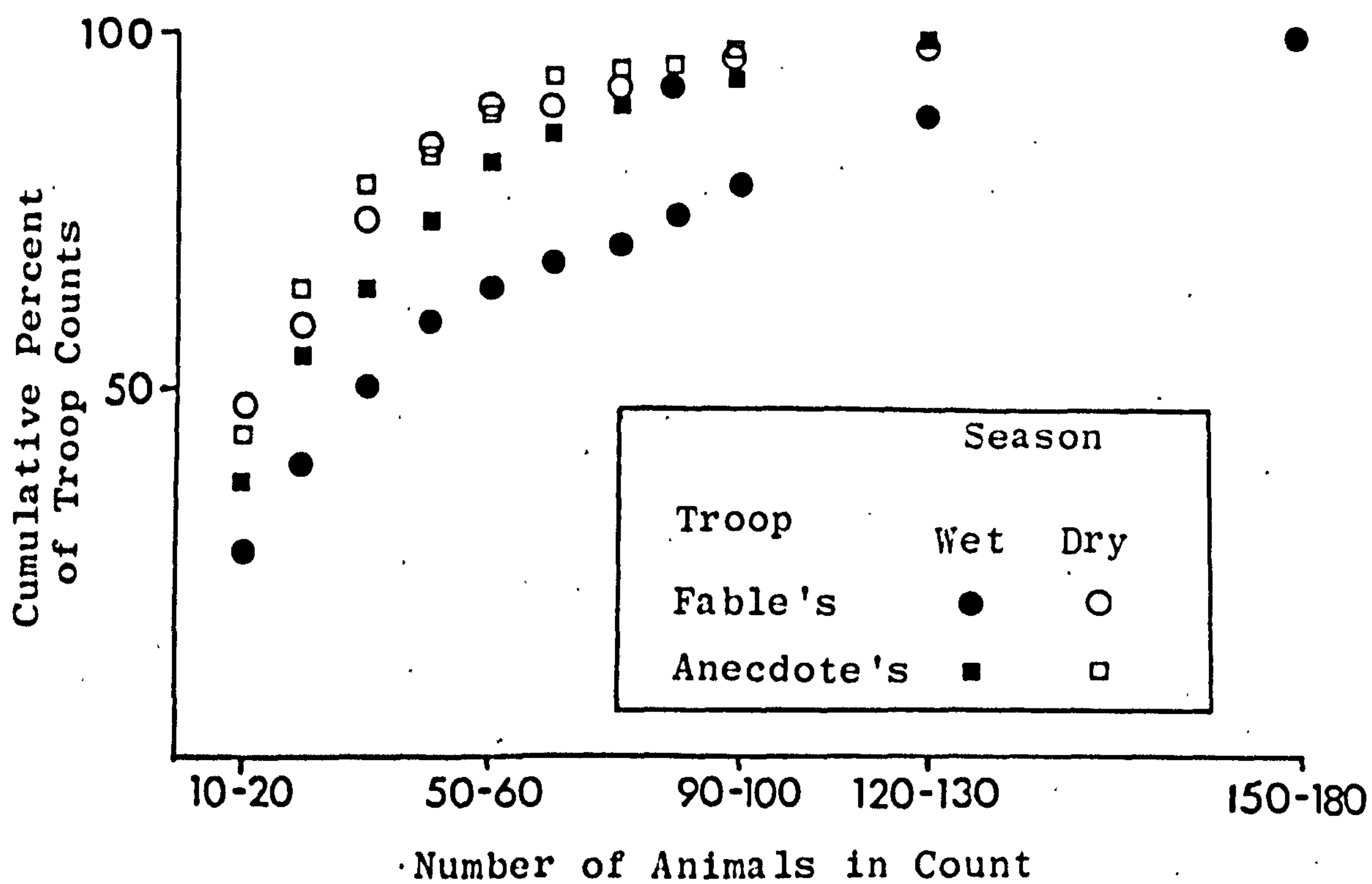
3.2: Group Size: Methods

Counts were made whenever the baboons were sighted under conditions which made censusing impractical. Most counts were incomplete, a problem not unique to this field site. For example, Hall (1962a) reported that no more than 52 of a group of 65 were ever seen at any one time by either of two observers in open, undulating country. Homewood (1976), Jones and Sabater Pi (1968), Maples (1969), Maxim and Buettner-Janusch (1963), Ransom (1971), Rowell (1966a) and Struhsaker (1969) all mention the problem of observing primate groups in dense vegetation, which, rather than topography, was the major difficulty at Mt. Assirik. Aldrich-Blake (1970) discusses further the relationship between visibility, group size, and duration of observation. At Mt. Assirik it was sometimes possible to count a complete troop as it crossed an open plateau. Repeated counts of this sort gave an indication of troop size. Counts made in thicker vegetation gave variable results. In this analysis I have excluded those counts or partial counts which contained 9 or fewer animals, and have constructed frequency distributions whose median counts were used as additional indicators of changes in troop size. Note that a "median count" of group size is necessarily smaller than the group size. Thus if fragments of a group of 100 were seen repeatedly, with 27, 30, 42, 63, 64, 70 and 87 counted on 7 occasions, the median count would have been 63. The relationship between median count and group size is not clear, but smaller groups will presumably tend to give smaller median counts.

3.3: Group Size: Results

Repeated counts of known groups showed that the number of animals in a troop in the wet season remained roughly constant for at least 4 weeks at a time. In the dry season no constancy of troop size could be detected. In the wet season, Fable's troop contained about 250 individuals (median count 35) while Anecdote's troop contained about 135 (median count 22). Counts of both troops were smaller in the dry season than they were in the wet season (Kolmogorov-Smirnov two-sample test; $p < 0.001$ for Fable's

Figure 3.1:
Cumulative frequency with which counts of increasing size were
made on two troops in two seasons.



troop, $p < 0.05$ for Anecdote's troop). The median count for both troops in the dry season was about 17, and the typical dry season troop probably contained between 50 and 90 individuals (Fig 3.1).

In both seasons, parties would frequently break away from the main troop and forage independently. These parties might include as few as 7 animals, but were occasionally made up of a third or more of the troop. Separated parties normally foraged within earshot of other members of the troop, but occasionally moved off completely on their own. For example, a large fragment (about 50) of the troop (of 135) was observed on 27/7/78 to set off from the sleeping site independently of the remainder of the troop. Both fragments were followed; they foraged independently for two hours and then rejoined each other having been separated by just over 2km. Occasionally the parties might spend the night at separate sleeping sites; for example, a party of 13 became separated from the main troop and did not rejoin them until the next day.

Fragments were also observed to coalesce, frequently but not always at sleeping sites, to form groups larger than the largest known troop. On 29/9/77 a group of 311 formed 200m from a sleeping site, engaged in social behaviour for roughly 30 min, and then moved to the sleeping site where they remained overnight. In the dry season a group of 275 formed in the late morning about 4km from the nearest known sleeping site. They remained together for about 2 hours, during which time they moved about 1.5km, and were seen foraging, feeding, resting and in social behaviour, before fragmenting again in the early afternoon.

The larger of the two troops (Fable's troop) was once seen in association with another troop (Lucky Break's troop). These two troops, with about 450-500 members between them, spent at least two hours together on the evening of 8/8/78 as they approached a sleeping site from about 2km away. During this time they were censused once (425 individuals censused), and counted twice (453,496). They shared a sleeping site with a third troop (Southern troop, of 137 individuals). In the morning, Southern troop moved off to the south-west, and the other two troops then spent two hours in social behaviour together, before moving off together to the west. At this point three observers at widely separated vantage points (Whiten,

Hall, Sharman) counted them (465,412,424). The mean count was 450 ± 33 ($n=5$). The composition of this group, according to the single census, is given later in this chapter (section 3.7.1).

3.3.1: Number and Population Density of Baboons at Mt. Assirik

A lower limit on the total population could be obtained from data collected on the night of 8/8/78, when about 630 individuals shared a single sleeping site at Secret Valley (Map 6.1). On the same night, about 140 individuals spent the night at Lion Valley, and S. Harrison (pers comm) heard baboons in Stella's Valley. The population at Mt. Assirik must therefore be greater than 770. An upper limit on the density of baboons in Fable's troop's home range can be calculated from data on home range area to be presented in chapter 6. This calculation gives between 5.5 and 7.2 baboons per sq km, without accounting for overlap between troops. If Fable's troop shared about half of its home range with other baboons at similar densities, then the mean occupation density of this home range was around 8.7 baboons per sq km.

3.3.2: Comparison of *P. papio* with other *Papio* species

Sixteen troops were counted elsewhere in the park. The median troop size was 55 ($n=16$; range 10-236)(Table 3.7). The typical dry season troops at Mt. Assirik and the study troops in the wet season were therefore larger than the median (dry season) troop size for troops elsewhere in the park but within the range of troop sizes known for *P. papio*. Troop sizes of baboons of the genus *Papio* are log-normally distributed ($n = 179$; skewness = 0.007 ns; kurtosis = 2.60 ns), with a transformed mean of 48.4 individuals (data from Dunbar and Sharman in prep). The distribution of troop sizes within each species is also log-normal. The mean log troop size of *P. papio* (data from this study and Boese et al. 1975) is significantly smaller than the mean log sleeping-group size of *P. hamadryas*, but larger than the mean log troop size of all other *Papio* species (Table 3.1). Variance in troop size for *P. papio* is larger than it is in any other *Papio* species, significantly so for all but *P. ursinus*.

Table 3.1:

Comparison of Mean Ln Troop Size of Papio species

Species	n	mean	sd	Significance level of difference between <u>P. papio</u> and other spp. (t and F tests)	
				mean	sd
<u>P. papio</u>	39	4.23	0.75	-	-
<u>P. anubis</u>	59	3.59	0.33	<0.001	<0.001
<u>P. cynocephalus</u>	47	3.89	0.52	<0.025	<0.025
<u>P. ursinus</u>	25	3.68	0.58	<0.005	ns
<u>P. hamadryas</u> sleep-group	9	4.59	0.34	<0.05	<0.025
<u>P. hamadryas</u> bands	8	4.06	0.21	ns	<0.001

Population densities of baboons of the genus Papio are highly variable, ranging from 1.8 km^{-2} (P. hamadryas, Kummer 1968) to 25.1 km^{-2} (P. anubis, Aldrich-Blake et al. 1971) (median density 10.3 km^{-2} ; $n = 13$). The population at Mt. Assirik was probably living at a population density slightly lower than the median for all population of baboons for which the figure is known.

3.4: The Social Group at Mt. Assirik: Discussion

In the remainder of this thesis I shall use "troop" to mean a group of animals which are seen together, and which apparently share social bonds. The term "social network" has not been used because it is not clear whether, for example, Fable's and Lucky Break's troops were part of the same social network, in that they were known to exchange members (Chapter 9), while it is more certain that individuals in one troop would have had at best tenuous social bonds with individuals in another. A troop moves in a cohesive unit for at least part of the day. Members of the troop forage at a relatively small distance from other troop members for most of the day.

This definition means that the social groups seen in both wet and dry seasons are called "troops". Dry season troops may be "group segments" of the wet season "group" (Carpenter and Nishimura 1969), or

they may be "clans" from the wet season "bands" (Abegglen 1976), but there is no advantage in making either assumption until the social organisation of the baboons at Mt. Assirik is better understood. The identity and nature of the social group is discussed further in Chapters 10 and 11.

3.4.1: Group Size: Discussion

Group size in groups of Papio baboons is partly a species characteristic; groups of P. papio tend to be larger than those of any species but P. hamadryas. The cause of such species differences is not yet known.

Baboons at Mt. Assirik live at densities which are well within the range of those at other sites. Since densities are probably related to resources (Hladik 1975), the habitat at Mt. Assirik is probably not unusually favourable for baboons. However, in the wet season, at least two troops of baboons at Mt. Assirik (Fable's and Lucky Break's) formed cohesive social groups that were among the largest known in any non-human primate and were larger than any other recorded troop of any savanna baboon species. The two troops at Mt. Assirik whose size is known were larger than 90% of all recorded troops of baboons, being exceeded in size by ten troops of P. papio, four of P. cynocephalus, three bands of P. hamadryas, and four herds of T. gelada (although bands of T. gelada are much smaller, and are more relevant to this comparison). (Data from Dunbar and Sharman in prep).

The largest herd of T. gelada known contained 519 individuals (Dunbar and Dunbar 1975), and the median herd size recorded in their study was 370. Herds are made up of bands, of which the largest was of about 350 individuals (Dunbar pers comm). Although the band is not a coherent social group in the sense that P. anubis troops and P. hamadryas bands are (Dunbar and Dunbar 1975), being assemblages of autonomous social units, they may be more coherent than the troops at Mt. Assirik, since they did not fragment for long periods in the dry season (Iwamoto 1975).

At the eastern end of Kummer's (1968a) broad survey, where mean group size was considerably larger than it was in other areas of the survey, the mean number of individuals in P. hamadryas parties encountered during the day was 227. The largest "moving party [of P. hamadryas]...observed at midday comprised 494 individuals" (Kummer 1968a). The equivalent figure for P. papio at Mt. Assirik was 275 in a "moving party" at midday. The sleeping aggregations of P. hamadryas may reach 750 (Kummer 1968a); the largest sleeping aggregation of P. papio seen at Mt. Assirik was of about 630 individuals. There seems no doubt that P. hamadryas sometimes live in cohesive social units that are far larger than those of P. papio. Like T. gelada, most social interactions in P. hamadryas bands take place within the one-male group.

Large troops are also known in savanna baboons. Altmann and Altmann (1970) recorded one of almost 200 animals, which remains the largest known troop of savanna baboons yet recorded. Casual assemblages of savanna baboons have been seen which are far larger; these are discussed below.

Seasonal changes in group size, though known in other primates, eg T. gelada (Crook 1966), Cercocebus galeritus (Homewood 1976), Ateles paniscus (van Roosmalen 1980), and Presbytis senex (Hladik 1975), have been described for only one other population of Papio baboons (Anderson 1980a,b). Troops of P. ursinus at Suikerbosrand, in South Africa, fragmented into smaller groups in the dry season. Some of these subgroups resembled the one-male groups described for P. hamadryas by Kummer (1968a). Anderson speculates that reproductive isolation has allowed this small population (350 individuals) rapidly to adopt new behaviours adapted to the exploitation of scattered resources in a predator-free environment. This explanation fails to account for the reassembly of the groups in the wet season, nor does it generalise to the population of baboons at Mt. Assirik. Firstly, the baboons in the study site at Mt. Assirik were probably part of a near-continuous distribution of baboons extending from the River Gambia, to the south, to the River Niokolo-Koba to the north (pers obs of baboons on the roads to the north and south of the field site). Even if the study

population was reproductively isolated, the deme (Mayr 1963) of which it was a part probably contained at least 1000 animals. Secondly, the environment was not predator-free; the effect of predation on group size is discussed later in this Chapter.

The observation that the troops at Mt. Assirik sometimes split and rejoined does not help to distinguish between the various social organisations known to be possessed by baboons. Since early reports of foraging parties of P. cynocephalus breaking off from the main body of the troop (DeVore and Hall 1965, Hall 1962a), troops of every species of baboon have been seen to fragment and reform in the space of a day (P. anubis, Aldrich-Blake et al. 1971; P. cynocephalus, Altmann and Altmann 1970 p 37; P. ursinus, Anderson 1980b; P. hamadryas, Kummer 1968a, Stolba 1979; P. papio, Dunbar and Nathan 1972, this study; T. gelada, Dunbar and Dunbar 1975), as have troops of hybrid P. hamadryas x P. anubis baboons (Sugawara 1979).

Two suggestions have been put forward to explain such temporary fragmentation of primate social groups. Poor visibility certainly makes it difficult for group members to keep in contact (Aldrich-Blake et al. 1971, Altmann and Altmann 1970, Byrne in press, Gautier-Hion 1970, Jones and Sabater Pi 1968, Kummer 1968a), and feeding competition may promote the formation of subgroups (Anderson 1980b, Hamilton and Watt 1970, Hall 1963a, King 1975, Rubenstein 1978, Williams 1974).

Unlike herds of T. gelada (Dunbar and Dunbar 1975), it is apparently rare for Papio troops to associate other than at waterholes or sleeping sites (P. anubis, Rowell 1964, 1966a; P. cynocephalus, Washburn and DeVore 1961, Altmann and Altmann 1970; P. ursinus, Stoltz and Saayman 1970; P. hamadryas, Kummer 1968a). In this respect P. papio at Mt. Assirik seems more like the other Papio baboons than it does T. gelada or some species of macaques (eg Macaca fuscata, Carpenter and Nishimura 1969, Macaca silvana, Deag and Crook 1971).

3.5: Age-sex Structure of Troops: Introduction

The demography of a troop influences the social environment in which individuals live (Altmann and Altmann 1979) and this in turn may lead to variations in social organisation (Kummer and Kurt 1963, Rowell 1979) and in social behaviour (Dunbar 1979). Social behaviour cannot in any case be correctly interpreted without a knowledge of the demographic structure of the troop (Rowell 1966a, Struhsaker and Leland 1979). Of particular interest to this study, the adult sex ratio will influence the amount of within-sex competition experienced by members of the group, and may lead to differences in mating strategies between populations of the same species (Dunbar and Dunbar 1976, Rowell 1967b).

If the troops at Mt. Assirik belonged to a rapidly expanding population (as is asserted by Dupuy and Verschuren 1977) we should expect a high immature to adult female ratio. Furthermore, the relative numbers in the three classes of infants may indicate whether or not the birth rate has been steady, increasing, or declining in recent years. The duration of any trend can be examined by consideration of data presented in an earlier census of the baboons in the park.

3.6: Age-Sex Structure of Troops: Method

The troops were censused whenever possible. Under ideal conditions the animals were moving diagonally away from the observer in single file across a grassless clearing, in such a way that I felt that all of the animals present were seen. This occurred rarely, and most of the censuses were partial censuses. Large groups of animals are difficult to census even in areas of good visibility (Crook 1966, Altmann and Altmann 1970). In many cases in this study bunching of the animals forced the observer to make rapid evaluations of age and sex. Whenever an evaluation was doubtful the individual was classified into a broader category (eg juvenile, rather than older juvenile male), and if it was not possible to classify at all, the individual was counted and scored as an "unknown".

The age-sex composition of troops were estimated from all censuses of more than 50 animals. The censuses were weighted by summing within

age-sex classes across censuses.

It was always possible to say whether an infant was riding dorsally or ventrally, but not always to decide into which of the three categories (black, transitional, or brown) the infant should be placed. To assess the proportions of infants in the three age categories I recorded whenever possible the position of the infant (ventral or dorsal) on the animal carrying it (nearly always an adult female) together with the colour of the infant's coat. The results were used to estimate the probable age category of an infant whose riding position but not coat colour could be recorded.

Altmann (1980) has provided data (p 34) which make it possible to calculate the relative proportions of infants in the three age-sex classes at Amboseli. By assuming that age-specific mortality at Mt. Assirik and Amboseli was roughly similar among infants, it is possible to compare the recent birth rate at Mt. Assirik with that of a stable population of baboons (Altmann 1980 p 19).

3.6.1: Comparison with Other Troops

Crook (1970a) and Rowell (1979) point out that the demographic structure observed at any one field site at any one time is unlikely to be a fixed species characteristic. Since it was possible that the baboons at Mt. Assirik lived in groups of abnormal size or structure, baboon troops elsewhere in the park were also censused.

Two people, Hall and myself, took part in a road-strip survey of the baboons in the Park. The survey was carried out between 3/4/78 and 9/4/78, 4 years after a similar survey by Boese et al. (1975). For one trip Baldwin accompanied us. One person drove the survey vehicle, a Land-Rover, at about 15kph, while the other person (the observer) sat on the roof scanning the vegetation for baboons. Every time baboons were seen the vehicle was stopped, if possible at a good vantage point, and the troop censused at least twice. To take the census the observer watched the troop, which was usually moving in a progression, through binoculars, and called out the age-sex categories of the animals to the driver, who noted them onto a checksheet. The driver was sometimes

able to watch the troop as a check on the classifications by the observer. Whenever possible the vehicle was then moved to a better vantage point for subsequent censuses, although we did not leave the road (since this was not permitted in the park). As many censuses as possible were taken on each group, and a record was made of the quality of each, on a 5-point scale. The results of the highest quality census of each series were used in the analysis.

The data collected during this field study were also compared with those collected by Boese et al. (1975) in an earlier census of the baboons in the park. This was used to examine changes in the age-sex structure of the population of baboons in the park over the previous 4 years, and to provide indications of population trends.

The proportion of adults to immatures, and of adult females to immatures, and the adult sex ratio have been described for many populations of baboons. The data from Mt. Assirik are compared with those from other studies of baboons, and especially with three populations of P. cynocephalus, one of which was declining and two increasing at the time of the censuses.

3.7: Age-Sex Structure of Troops: Results

The proportion of each age-sex class included in any census varied across censuses within troops. The mean and standard deviation for each age-sex class in the 14 largest censuses for both troops is given in Table 3.2. In no case was the mean proportion of any age-sex class different in one troop from its proportion in the other troop (t test, p always > 0.05).

The only differences in the variances within age-sex classes between the two troops were among younger juveniles, independent transitional and black infants, and infants carried ventrally (F test; $p < 0.025$ in every case), which were the classes subject to the greatest variability in difficulty in seeing them. As a result, I pooled the data from both troops for the analyses.

Table 3.2:
Proportion of various age-sex classes in the 14 most complete censuses for two troops

Class	<u>Fable</u> (n=14)			<u>Anecdote</u> (n=14)		
	Mean(%)	sd(%)	est	Mean(%)	sd(%)	est
Male	24.26	3.21	61±8	22.30	3.95	30±5
Oestrus	2.04	1.43		2.42	2.16	
Pregnant	1.02	1.12		1.59	1.52	
Female	29.20	5.70	81±14	28.41	6.33	43±9
Subad M	2.97	1.91	7±5	3.50	2.18	7±3
Older J	10.72	4.47	27±11	11.17	5.47	15±7
Young J	14.24	1.73	37±4	14.70	4.49	20±6
Brown I	6.02	3.78		6.11	4.83	
Trans I	0.37	0.69		0.86	1.24	
Black I	0.27	0.56	36±9	0.42	1.13	20±7
Ventr. I	2.76	1.37		3.79	2.93	
Dors. I	4.78	2.23		3.84	2.65	

KEY: for age-sex code see Chapter 2.
note that sum of mean % is not necessarily 100
est = estimated numbers of pooled age-sex class in troop

3.7.1: Age-Sex Structure in the Population

Out of 77 censuses of more than 20 animals, 35 (45%) included fewer than 50 animals (small censuses), and 42 (55%) included 50 or more animals (large censuses). The mean percentages of each age-sex class in these censuses are given in Table 3.3, together with the standard deviation of each percentage.

Variance in large censuses was smaller than in small censuses (two-tailed Wilcoxon signed-rank matched pairs, $p < 0.01$). There was therefore more internal self-consistency in censuses in which 50 or more animals were recorded than there was in censuses of fewer animals.

The mean proportion of the census made up by each age-sex class was not in general influenced by the number of animals in the census.

Table 3.3:
Censuses Containing More or Less than 50 Animals

Class	<u>small</u> (>20 but <50) n=35			<u>large</u> (>=50) n=42	
	%	sd		%	sd
Male	23.0	8.6		21.7	4.6
Oestrus	1.6	2.6		2.3	2.1
Pregnant	1.3	1.9		1.0	1.3
Female	30.4	9.5		29.3	5.9
Subad M	3.9	3.3		3.1	2.2
Subad F	0.3	1.2		0.1	0.4
Older J	10.8	6.6		11.7	5.0
Young J	15.3	6.2		16.9	6.6
Brown I	2.9	5.2		5.1	4.8
Trans I	0.1	0.5		0.5	0.9
Black I	0.1	0.6		0.2	0.7
Ventral	3.0	2.7		2.9	2.2
Dorsal	6.2	3.8		4.2	2.4

KEY: for age-sex code see Chapter 2.

There was one exception: fewer independent transitional infants were seen in small censuses than in large ones (t test, $p < 0.025$). For the following analysis I have pooled data from censuses of 50 animals or more.

The age-sex structure of the population is not accurately assessed by the proportions shown in Table 3.3, since smaller, perhaps more fragmentary, censuses of less than 100 animals are given the same weight as larger censuses. A better estimate is provided by pooling the results of censuses. The 42 censuses of more than 50 animals included between them 4977 animals. Of these, 32% were adult females in various reproductive states, and 23% were adult males. The adult sex ratio was 1:1.42. Subadults made up 3% of the censuses, juvenile animals 28%, and infants 14%. The adult female to immature ratio was 1:1.31. These data are shown in detail in Table 3.5, and are taken to represent the

approximate proportions of the age-sex classes in both troops at Mt. Assirik during the study.

Table 3.4: Summary of Censuses of 50 or more Animals

Specific Age-Sex Class	Total	%	binomial 95% cl		Summary Age-Sex Class	Total	%	binomial 95% cl	
Male	1130	22.7	20	26	Male	1130	22.7	20	26
Oestrus	113	2.3	1	3					
Pregnant	58	1.2	0	2					
Ventral	157	3.2	2	4					
Dorsal	234	4.7	4	7					
Female	1037	20.8	19	24	Female	1599	32.1	29	35
Subad M	151	3.0	2	4					
Subad F	5	0.1	0	1	Subadult	156	3.2	2	4
Older J	582	11.7	10	14					
Young J	759	15.3	13	17					
Juvenile	37	0.7	0	2	Juvenile	1378	27.7	25	31
Brown I	287	5.8	5	8					
Trans I	23	0.5	0	2					
Black I	13	0.3	0	2					
Ventr. I	157	3.2	2	4					
Dors. I	234	4.7	4	7	Infant	714	14.3	12	16

KEY: for age-sex code see Chapter 2.
In this table, V, D and F are listed separately.

A census of an exceptionally large group, made up of two troops, was made on 29/9/77 (reported on page 3.3). The composition of this group (98 adult males, 133 adult females, 18 subadult males, 100 juveniles and 76 infants) was similar to that of the population of censuses on the study groups (chi squared = 7.40; df = 4; ns).

From data presented in this Chapter, the probable composition of Fable's and Anecdote's groups, and a hypothetical 'standard' dry-season group can be calculated (Table 3.5).

Table 3.5:

Possible Composition of Troops at Mt. Assirik.

Troop	Adult		Subadult		Juveniles	Infants
	Males	Females	Males			
Fable	57	80	8		69	36
Anecdote	31	43	4		37	19
Dry Season	20	29	3		25	13

3.7.2: Infants

The age and position of 313 infants were recorded. Of these, the principal classes were brown infants riding dorsally (46%) and black infants riding ventrally (27%) (Table 3.6).

Table 3.6:

Infants Riding on Adults

Position on Adult	Age Class					
	Black		Transitional		Brown	
	No.	%	No.	%	No	%
Ventral	84	26.8	7	2.2	7	2.2
Dorsal	42	13.4	30	4.5	143	45.7
	126		37		150	
						313

The combined data from Tables 3.4 and 3.6 suggest that 27.0% of the infants were black, 9.4% transitional, and 63.5% brown. If infants are transitional for about two months, then the percentages are very close to the percentage of its life that a P. cynocephalus infant which survived throughout infancy might expect to spend in each of the categories (33.3%, 8.3% and 58.3%) (Altmann et al. 1977). Deaths in any category should have led to successively lower percentages being found

in the three categories, but since the numbers observed in each category tallied closely with the relative length of time infants were likely to spend in each category, there may have been low infant mortality at Mt. Assirik, or a falling birth rate over the last two years. It is possible, perhaps likely, that the numbers of black infants in the censuses were underestimated relative to the numbers of brown infants. However, Boese et al. (1975) provide similar data; 32.2%, 8.3%, and 59.9% of the 289 infants they observed were black, transitional and brown respectively. The two sets of data may be affected by a similar bias, but if the figures are unbiased, they suggest either that mortality of infants was also low in 1974, or that the recruitment rate of the population in the park has been falling since 1972, or both. At Amboseli, in a stable or slightly declining population, about 40%, 8%, and 52% fell into the three categories.

3.7.3: Censuses Elsewhere in the Park

Sixteen troops were censused in the road-strip survey of the Park (Table 3.7). The data from the road-strip survey were collected in the dry season, when, at Mt. Assirik at least, troops tended to be smaller than they were in the wet season. These data should therefore be taken to represent minimum troop sizes of P. papio in the GPN de NK. The 9 censuses of more than 50 animals included between them records of 990 animals. Of these, 22% were adult males and 34% were adult females, giving an adult sex ratio of 1:1.54. Subadults made up 4% of the population, juveniles 31%, and infants 9%. The adult female to immature ratio was 1:1.18.

The proportions of the censuses made up by each age-sex class were similar in these censuses to the corresponding figures from Mt. Assirik (Table 3.8) with the exception of infants, which appeared to make up a larger proportion of the population at Mt. Assirik than elsewhere (Cochran's adaptation of the Fisher-Bihren's t test $t' = -3.26$, $p < 0.01$).

Boese et al. (1975) counted 1723 individuals, of which .16% were adult males, 30% adult females, 9% subadults, 29% juveniles, and 17%

Table 3.7:
Best Censuses of Troops of Baboons Encountered During Road-Strip
Survey of the Grand Parc National du Niokolo-Koba

Census Number	Age-Sex Category							n
	M	F	S	O	Y	I	U	
1	24.2	32.2	4.2	13.6	19.5	6.4	0.0	236
2	20.2	37.6	2.2	18.0	12.4	9.6	0.0	178
3	22.8	36.1	5.1	9.5	15.8	7.6	3.2	158
4	19.2	36.7	5.8	12.5	10.8	15.0	0.0	120
5	16.7	27.8	3.3	23.3	20.0	8.9	0.0	90
6	29.0	30.6	1.6	6.5	6.5	8.1	17.7	62
7	16.1	32.1	1.8	17.9	21.4	10.7	0.0	56
8	32.1	17.9	5.4	17.9	19.6	0.0	0.0	56
9	13.0	38.9	1.9	14.8	20.4	11.1	0.0	54
10	34.0	8.5	4.3	8.5	10.6	2.1	0.0	47
11	15.0	37.5	7.5	17.5	10.0	12.5	0.0	40
12	21.1	23.7	7.9	26.3	18.4	2.6	0.0	38
13	23.5	26.5	5.9	26.5	17.6	0.0	0.0	34
14	17.2	20.7	3.4	17.2	37.9	3.4	0.0	29
15	46.7	13.3	0.0	13.3	13.3	6.7	6.7	15
16	10.0	40.0	0.0	40.0	0.0	10.0	0.0	10

Table 3.8:
Proportion of various age-sex classes in population
(estimated from censuses containing 50 or more individuals)

Age-Sex Class	At Mt. Assirik		Road-Strip		Boese et al.	
	%	95% cl	%	95% cl	%	95% cl
M	22.7	20 26	22.1	19 25	15.7	14 18
F	32.1	29 35	34.0	31 37	29.8	27 33
S	3.1	2 4	3.8	3 5	8.5	7 11
O	11.7	10 14	14.8	13 17	12.4	10 14
Y	15.3	13 17	16.4	14 18	16.9	15 19
I	14.3	12 16	8.8	7 11	16.8	15 19
n	4977		990		1723	

KEY: for age-sex code see Chapter 2.

infants. Their data are compared with the data from this study in

Table 3.8. They found significantly fewer adult males and significantly more subadult males. They also reported significantly more infants than were recorded in the road-strip survey, but the proportion of infants at Mt. Assirik corresponded with their figure.

Although the troops at Mt. Assirik lay well within the range of other troops of the genus Papio in the proportion of adult animals in the troop, the number of immature animals per adult female, and the number of adult males per adult female, they had a higher proportion of adult animals than did most other populations of baboons, with more adult males per adult female, and fewer immature animals per adult female (Table 3.9).

Table 3.9:
Demographic parameters of known populations
of baboons relative to the population at Mt. Assirik.

Demographic Parameter	mean for all baboons	mean for genus <u>Papio</u>	Mount Assirik	x(n)	p
Proportion of adult animals	0.46±0.08	0.47±0.08	0.54	28(33)	0.16
Number of immature animals per ad.fem.	1.69±0.58	1.66±0.57	1.31	26(35)	0.23
Number of adult males per ad.female	0.45±0.23	0.47±0.24	0.70	25(35)	0.17

KEY:
x number of known populations of baboons in genus Papio with a less extreme value than that found at Mt. Assirik.
(n) number of populations of baboons in genus Papio for which the value was known
p proportion of populations in genus Papio with a more extreme value than that seen at Mt. Assirik.

3.8: Age-Sex Structure of Troops: Discussion

The variance in the mean percentage of every age-sex class was lower in Fable's troop than in Anecdote's troop, presumably a consequence of the larger numbers included in censuses of Fable's troop. The only significant differences noted in the censuses of the two troops at Mt. Assirik was in the variance in four age-sex categories, three of which were classes of infant. Absolute numbers of infants in each of these categories were very low, and small fluctuations in numbers would have introduced large variance. Furthermore, Owens (1972) states that P. anubis infants started to ride dorsally at about 6 weeks, so that a much greater proportion of the infants at Mt. Assirik should have been riding dorsally than were observed. However, black, transitional, and even brown infants rode ventrally when the troops were alarmed (pers obs), while the proportion of baboon infants riding ventrally declines as troops become more habituated to the presence of humans (Lee pers comm). Infants riding ventrally were more likely than were infants riding dorsally to be missed in a census. Anecdote's troop seemed rather more timid than did Fable's troop, so that the high variance in infant numbers might have been the result of poor visibility and easily alarmed animals.

The censuses indicate a population with rather few juveniles per adult female or per adult animal by comparison with other known populations of baboons. Both Rasmussen (1980) and Lee (pers comm) felt that the populations that they were studying were expanding rapidly; at Mikumi, for each adult female in the population there were 1.9 immature animals, while at Ruaha the comparable figure was 2.3 (Lee and Oliver 1979). The population of baboons in Amboseli was declining rapidly (Western and van Praet 1973, Altmann 1980) at a time when for each adult female there were 1.4 immature animals (Altmann and Altmann 1970). The equivalent figure in the GPN de NK was 1.3. It is unlikely, therefore, that this population is still undergoing the rapid growth referred to by Dupuy and Verschuren (1977), and it may have started to decline.

The low proportion of immatures to females is difficult to interpret if infant mortality has indeed been low in the park for at

least 4 years. It seems possible that the age structure of infants in the study troops indicated that recruitment was higher about a year before the study started than it was during the year of the study. A similar pattern can be seen in the data on troops elsewhere in the park collected by Boese et al. (1975) four years previously. If this interpretation is correct, the depressed recruitment in these troops has apparently continued, so that the proportion of infants in them is now low.

The age-sex structure of the population elsewhere in the park was similar to that at Mt. Assirik, except that infants were less well represented in this wider sample. The ratio of adult females to immature animals indicated a population which, by comparison with ones known to have been declining, may be starting on a major crash.

Boese et al. recorded more subadult and fewer adult males in their study, but classified as "subadult" animals whose manes were developing; many of these animals would probably have been classified as adult in this study. Classification of subadult and adult males is notoriously variable between observers in other species of baboons as well (Strum pers comm, Altmann pers comm, Popp pers comm).

3.9: Predation and Size of Group: Introduction

If group size within a species is partly determined by ecology, some feature or features in the environment at Mt. Assirik should favour the individual living in a large group in the wet season.

There are two views on the relationship between visibility, predation and group size. Firstly, Cook and Martin (1974) argue that if each animal has a constant probability of being detected then large groups are more likely to be detected than are small groups, irrespective of visibility. Altmann and Altmann (1970) predicted that group size would be largest in areas where visibility was good, since poor visibility would lead to difficulty in the coordination of the troop, and hence to its fragmentation. With good visibility an individual may benefit by belonging to a group, ^{since} detection of predators is improved as the number of prey in the group gets larger (Bradbury and

Verencamp 1976b, Cushing and Harden-Jones 1968, Hamilton 1971, Lazarus 1972, Powell 1974, Pulliam 1973, Treisman 1975a).

The opposite prediction is supported by Olson (1964), who showed mathematically that detection of the group by the predator depends upon the size of the group when visibility is good. Large groups should be favoured under conditions of poor visibility because detection of the prey by the predator is probably independent of the size of the group (Brock and Riffenburgh 1960, Jarman 1974, Lazarus 1972), and the larger the group in which an animal finds itself the less chance it has of being selected by a predator in any one attack (Bradbury and Verencamp 1976b, Hamilton 1971, Lazarus 1972).

If the baboons at Mt. Assirik responded to changes in difficulty of coordination, group size should have varied seasonally, being largest in the dry season, when visibility was good. If on the other hand the baboons responded to changes in predation risk by changing group size, as groups of other mammals are known to do (Estes 1976, Jarman 1974), the groups should have been largest in the wet season.

At Mt. Assirik I kept in contact with the baboons largely by the noise made by the animals, not by vision. The effective detection radius of the troop was about 50m under normal conditions, but would occasionally increase to about 200m or more when adult males were "wahooing". Small troops were extremely difficult to follow, since there was generally too little noise, but there was no apparent difference in following a troop of 100 and 200 animals. As far as I am aware no theory has yet been developed for the case of predators that can detect their prey by noise, where the relationship between detectability and group size will depend on the relationship between group size and noise as well as on the acoustic properties of the environment.

3.10: Predation and Size of Group: Results

Baboons were frequently able to detect a hidden observer dressed in cryptic clothing well before the observer could detect the baboons (pers obs), and in the dry season, in which, by comparison with the wet season, visibility was generally good, might normally have been expected to detect predators in good time. However, there was evidence that in either season a predator could remain undetected until the troop was all around it. For example, on one occasion in the wet season I came within 5m of a hidden leopard near which many baboons had walked, while the same thing happened to Byrne (pers comm) in the dry season. Since visibility changed with season (Chapter 2) the ease with which a predator might have hidden itself from the troop probably also changed, and predation risk was almost certainly greater in the wet season than it was in the dry season.

No incidents of predation were observed in this study, although 12 bones and bone fragments from the pectoral girdle of an adult-sized baboon were discovered. The scapula had been perforated, possibly by the canine of a predator of about the size of a leopard. These bones and some baboon fur were found on the flat 3m x 0.5m top of a sheer-sided, 2m high boulder, a site possibly suitable for the cache of a leopard. On other occasions two skulls were found, with no hint of the cause of death. That few remains were found is not surprising since a baboon skeleton is rather fragile, and leopards are capable of eating a whole baboon, including the bones (but not the skull) (Brain 1970). The animals whose skulls were found might have died from causes other than predation. For example, the observed death of one animal was probably not the result of an attack by a predator. A dying adult female was found beneath a dormitory tree. She had slight contusions above her right eye and a trace of blood beneath her nostrils. She was unable to open her eyes and had great difficulty in sitting up. An autopsy revealed that her skull had been badly fractured. A triangular section of side 2cm of the right frontal above the orbit had broken away from the rest of the bone, the palate (maxilla) was split, and a crack ran from orbit to orbit near the sutures between the frontal, nasal and

maxilla. Her death was almost certainly the result of a fall from a branch about 10m above the ground onto her head on the boulders beneath. The cause of the fall is unknown, and apart from her injuries she seemed to have been in good health. She was helpless when she was found in mid-morning, and could have offered no resistance to a predator.

Baboons reacted noisily to the night-time calls of leopards (the noise of the baboons could be heard over 2km away), and were observed on two occasions (Hall and pers obs) to flee precipitately from close encounters with lions. They reacted to the presence of wild dogs by climbing trees and "wahooing". Spotted hyaena were also present in the area, but the reaction of the baboons to these predators was not seen. Until about 15 years ago man was a major predator of baboons in the area, with the local people, the Alien, hunting them for food with dogs (Rene Bonang, pers comm). The reactions of baboons to humans has already been described.

3.11: Predation and Size of Group: Discussion

DeVore and Hall's (1965) remark: "relations between baboons and the animals that can prey on them is the most important single factor in the interpretation of baboon ecology and social behaviour" is possibly overstated (Anderson 1980b), but predation may indeed have had a major influence on the social organisation of baboons. For example, it has clearly played some part in the roosting habits of baboons (T. gelada, Crook 1966; P. papio, Bert et al. 1967a, Bert and Pegrarn 1969, Dunbar and Nathan 1972, this study; P. anubis, Booth 1956a,b, Harding 1976; P. cynocephalus, Altmann and Altmann 1970; P. ursinus, Hall 1963a, 1965b). There are admittedly rather few records of animals preying on baboons. Baboons generally form a tiny part of the diet of large predators. Schaller (1972) saw no baboons eaten by lions anywhere in the Serengeti in a survey in which he recorded over 1000 food items. At Manyara he found 6 baboons in 100 food items. Fewer than one in 2000 lion kills in Kruger National park was of a baboon (Pienaar 1969, quoted in Schaller 1972). Leopards of the Serengeti have also been known to include baboons in their diets (1 of 164 kills, Schaller 1972,

2 of 55 kills, Kruuk and Turner 1967). Hadow (1952) saw baboons being killed by leopards. Nagel (1973) described one possible case of predation on an infant by a leopard. Altmann and Altmann (1970) recorded 3 kills and one probable kill of baboons mostly by leopards, and Altmann (1980) one more, by a hyaena. Rasmussen (1980) reported 3 kills by leopards at night. Cilliers (1963) described a lion eating a baboon that had been begging from a tourist's car, and Rhine (1975) mentions the "loss to lions of an adult female and her son". Ransom (1971) reported 24 attempted predations on baboons by chimpanzees in 2 years, and Rhine and Owens (1972) recorded 7 deaths in one troop in the same period, all due to chimpanzees. Above all, man has probably had an important evolutionary influence on primates through predation (Dittus 1975, Jolly 1972, Tappen 1960).

The baboons at Mt. Assirik were exposed to two species of cursorial predator (three in the recent past) and two of ambush predators. Most of the baboon's home range was wooded, so that escape up a tree from the wild dogs and hyaena would normally have been possible, thus reducing the threat presented by these species. Lions and especially leopards would have been less easy to avoid, while the combination of man and dog probably represented a formidable predator. Since predation pressure except from man probably came principally from ambush predators, seasonal changes in visibility would have led to a higher predation risk in the wet season.

Differential predation in the wet and dry season may in part account for changes in group size. Some support for this hypothesis is given by data from other troops living under conditions of equally bad, or worse, visibility, in areas of differing predation risks (Mikumi, Rasmussen 1980, Budongo, Paterson 1973, Gombe Stream, Ransom 1971). Baboons at Mikumi, especially those living in smaller troops, were said to suffer quite heavy predation (Rasmussen 1980), while those at Budongo almost certainly suffered less (Paterson 1973). Baboons did not treat chimpanzees as predators at Gombe Stream (Ransom 1971), and there were few other large predators in the Park, so that mean troop sizes (80.2, 63.5, and 38.0 respectively) at these sites apparently decreased

with decreasing risk of predation.

3.12: Food and Size of Group: Introduction

The relationship between the size of savanna baboon troops and the abundance of food in the habitat is unclear, especially since troops exploiting overlapping home ranges can have widely different troop sizes (DeVore and Hall 1965, review in Altmann and Altmann 1970). There is some evidence that abundance does influence troop size beyond the presumable limitation by scarce food (DeVore and Hall 1965). At one extreme, troop structure can disintegrate entirely under severe food stress (Hall 1963a), while at the other extreme, abundant food allows large herds of T. gelada to form (Dunbar and Dunbar 1975).

It is likely, however, that food abundance on its own is not sufficient to account for troop size. The degree to which the food is clumped, the interaction between predation risk and feeding competition, and the speed with which resources can renew themselves are all certainly important. Two opposed views emerge from these considerations.

Firstly, since baboons feed selectively from a wide variety of plant food sources, it is unlikely that the optimum group size is governed directly by the number of animals that can feed on or defend one clump, as it is, for example, for lions (Caraco and Wolf 1975, Lamprecht 1978). Thompson et al. (1974) suggest that if each individual monitors others and joins them should they find a source of food, then food which is not strongly clumped is best exploited by large groups, especially when such clumps as there are contain enough food for the whole group. Post et al. (1980) showed that animals gain access to food in rank order. This is well accepted in studies of captive primates and has been given further support from field work by both Dittus (1977) and Wrangham (1981), who showed that at a time of starvation subordinate animals died first, being denied access to, or being displaced from, food sources. Subordinate animals, suffering most from feeding competition, should be the first animals to leave the group; having done so they might benefit by forming groups of their own (Anderson 1980b,

Chepko-Sade and Sade 1979, Rubenstein 1978). We should expect that such fragmentation should occur at times of low abundance of food. Both Thompson et al. (1974) and Baker et al. (1981) felt that at times of reasonably abundant food, foraging in groups reduced the risk to the individual of doing badly, at the expense of increased feeding competition. In general, then, times of reduced feeding competition should allow the formation of larger groups, and group size should vary seasonally, with groups being smallest at times of low food abundance.

By contrast, Pulliam (1976) suggested, on theoretical grounds, that among animals in which there is both feeding competition and in which time is spent in watching for predators, groups will be largest when food is scarce. Hamilton and Watt (1970) expressed a similar idea by suggesting that if resources renew themselves more rapidly than the group can return to harvest them, then fragmentation of the group will permit more efficient exploitation of the area. However, Wrangham (1980) points out that if patches are shared by other troops or other species, there might be little advantage to regulating the time between successive visits to a food source in this way.

Cody (1971, 1974) showed that wintering finches did not form flocks where food was abundant, but did flock in areas where food was scarce. However, there was little feeding competition between the birds (Cody 1971) and there were "no predators of consequence" (Cody 1974) so that Pulliam's argument could not be applied. A modified form of Hamilton and Watt's idea was supported; Dunbar (1973) and Cody (1974) both suggested that a group exhausts a swath which is detected and avoided by the group in subsequent passes through the area. They suggested that if the same number of animals foraged as individuals they would slowly reduce the resources over the entire area, making foraging less efficient. Evidence that grazing primates are capable of detecting a swath which has previously been grazed is provided by Wrangham (1976). Small groups should therefore be found in areas or at times of high above-ground productivity.

3.13: Food and Size of Group: Results

The median number of animals seen feeding in any one plant of any species varied with the species (Table 3.10) but was always less than the median count of animals travelling together. An entire troop was thus never able to feed together from a single plant of any species. Stands of any one species were very unlikely to be large enough to support the whole troop in either season. Numerous displacements from feeding sites of one animal by another were seen. Feeding competition was therefore probable at almost every feeding site. This observation is discussed further in Chapter 7.

The annual above-ground productivity at Mt. Assirik was probably around $1 \text{ kg m}^{-2} \text{ yr}^{-1}$ (Chapter 2), but since no rain fell in the dry season, nearly all of this production was in the wet season. Food was probably at its least abundant in the dry season (other methods of determining food abundance are used in Chapter 7).

Table 3.10:

Feeding Group Size

Species	min	max	mode	median	n
<u>Acacia dudgeoni</u>	3	14	3=4	1.0	6
<u>Adansonia digitata</u>	1	17	1	4.6	111
<u>Afzelia africana</u>	1	14	1	2.3	17
<u>Alophylus africanus</u>	2	2	—	—	1
<u>Anona senegalensis</u>	1	2	1=2	1.5	6
<u>Bombax costatum</u>	1	1	1	1.0	2
<u>Borassus aethiopum</u> in	1	4	1	1.6	9
<u>Borassus aethiopum</u> below	1	30	1	1.0	21
<u>Cassia sieberiana</u>	2	2	—	—	1
<u>Cola cordifolia</u>	1	8	2	2.0	7
<u>Cola sp. unknown</u>	18	18	—	—	1
<u>Combretum spp.</u>	1	20	1	1.0	14
<u>Cordia myxa</u>	1	5	1=5	3.0	2
<u>Cordyla pinnata</u>	3	3	—	—	1
<u>Diospyros mespiliformis</u>	1	14	2	3.0	6
<u>Erythrophloeum suaveolens</u>	1	20	1=2=4	4.5	12
<u>Ficus spp.</u>	2	17	2	4.0	13
<u>Gardenia erubescens</u>	1	1	—	—	1
<u>Grewia lasiodiscus</u>	1	3	1=2=3	2.0	3
<u>Hexalobus monopetalus</u>	1	5	1	1.0	4
<u>Kaempferia aethiopica</u>	1	1	1	1.0	5
<u>Khaya senegalensis</u>	1	13	1=6	6.0	5

Species	min	max	mode	median	n
<u>Landolphia heudelottii</u>	1	3	1=3	2.0	2
<u>Lannea acida</u>	1	46	1	2.5	48
<u>Lannea microcarpa</u>	1	10	1	2.5	6
<u>Manilkara multinervis</u>	2	2	-	-	1
<u>Meliaceae sp.</u>	1	1	1	1.0	3
<u>Nauclea latifolia</u>	1	4	1	1.0	9
<u>Oncoba spinosa</u>	1	2	1	1.0	3
<u>Oxytenanthera abyssinica</u>	1	3	1	1.0	8
<u>Parkia biglobosa</u>	1	5	2	2.0	5
<u>Pericopsis laxifolia</u>	1	4	1	1.0	4
<u>Piliostigum thonningii</u>	1	10	1	1.0	6
<u>Pterocarpus erinaceus</u>	1	17	1	3.6	32
<u>Raphia sudanica</u>	1	1	-	-	1
<u>Saba senegalensis</u>	1	18	1	2.6	35
<u>Sorindea juglandifolia</u>	2	2	-	-	1
<u>Spondias mombin</u>	1	2	1	1.0	5
<u>Sterculia setigera</u>	7	7	-	-	1
<u>Strychnos spinosa</u>	1	1	1	1.0	6
<u>Tamarindus indica</u>	1	1	-	-	1
<u>Trichilia prieuriana</u>	1	1	1	1.0	3
<u>Urtica sp. unknown</u>	1	1	1	1.0	5
<u>Vitex madiensis</u>	1	4	1	1.0	6
<u>Zizyphus spinachristi</u>	1	5	1=2=3=5	2.5	4
grass	1	135	1	4.0	11
<u>Cissus spp.</u>	1	5	1	2.5	8
sp. unknown (1)	1	1	1	1.0	4
sp. unknown (2)	4	4	-	-	1
sp. unknown (3)	1	15	5	4	8

3.14: Food and Size of Group: Discussion

Feeding competition in troops of baboons and other primates has been observed or implied in many field studies (Chalmers 1968b, Dittus 1977 Hall 1965a, Hamilton et al. 1978 Homewood 1976, Ransom 1971, Smuts in prep, Struhsaker and Leland 1979, Wrangham 1976, 1981).

Pulliam's (1976) view that animals suffering both feeding competition and risk of predation should form large groups in times of reduced food availability was not supported by observations made in this study on P. papio (see page 3.3); nor was it in Homewood's (1976) study; nor by observations on mixed-sex herds of T. gelada, whose members may suffer feeding competition (Wrangham 1976), and whose adult males suffer

the threat of "predation" by all-male groups (Wrangham 1976). In these animals, herds are smaller in the times of scarce food (Crook 1966) and larger where swards of grass are more extensive (Dunbar 1973). At Mt. Assirik there was some risk of predation. As there was evidence for feeding competition amongst the baboons, Pulliam's (1976) conditions were satisfied, and we should have predicted that group size was largest in times of low food abundance.

3.15: General Discussion of Causes of Changes in Group Size

In human societies, predation on the group apparently plays little part in determining group size. However, seasonal changes in group size can often be related to changes in food abundance or concentration. For example, the Eskimo (Damas 1972, Maus 1906), the Shoshonean Indians (Steward 1955), the Walbiri Aborigines (Meggitt 1962), the G/wi bushmen (Silberbauer 1972), and the Murugin of Northern Australia (Warner 1937) congregated seasonally at concentrated food sources, and dispersed to forage on scattered resources at other times of year. In other human societies the seasonal dispersal and aggregation of groups may be related to the size of prey available (eg the Hadza, Woodburn 1975) or to the availability of water (eg the !Kung, Lee 1972), or may have social causes apparently unrelated to ecology (eg the Birhor, Sinha 1972, Williams 1974).

It seems unlikely that changes in the abundance of biting flies influenced the sizes of groups of baboons (as it may do in horses, Duncan and Vigne 1979), since tsetse flies (Glossina morsitans) were erratically abundant at all times of year.

In summary, it seems probable that seasonal changes in baboon group size (page 3.3) at Mt. Assirik came about as a result of increased risk of predation at a time of abundant food, and a decreased risk at a time of low food availability.

CHAPTER 4: Activity Budgets

INTRODUCTION

4.1: Ecological Constraints on Activity

Different groups of baboons apparently balance their activity budgets in different ways in response to ecological conditions. For example, an increase in time spent feeding may be achieved by feeding at less profitable times of day (Schoener 1971), or at a time of day which results in some loss in a "currency" other than food. Several studies have shown that in times of food shortage, baboons spend more time feeding (Nagel 1973, Oliver and Lee 1978, Iwamoto and Dunbar in prep). and either spend less time in social behaviour (Oliver and Lee 1978, Post 1981), or spend less time resting (Dunbar 1980, Iwamoto and Dunbar in prep., Nagel 1973).

Seasonal differences in food availability within one home range may be greater than the differences between the habitats of neighbouring home ranges, which may cause activity budgets to differ more between seasons than they do between neighbouring troops (Homewood 1976, Nagel 1973).

The time of day at which various activities are seen may change with environmental changes. When feeding competition is intense, the largely frugivorous baboons of Mt. Assirik (chapter 7) might attempt to arrive at renewing food sources such as fruiting trees earlier than competitors (eg frugivorous birds).

For a social animal, the environment consists not only of its physical surroundings but also its social companions. The number of animals in the group might well influence the time budget; for example in a larger group the larger number of competitors may lead to greater difficulty in finding food, and a greater proportion of the day given over to feeding. However, the larger the social group the greater the possible number of relationships within it. The increase is rapid; for Anecdote's troop, with 135 members, there are 9,045 possible dyads, while for Fable's troop, with about 250 members, there are over 31,000 dyads. In a larger social group each individual probably has to spend longer in social exchange, and hence the troop may spend a greater proportion of the day in

social interaction, perhaps at the expense of resting time.

Coalitions between two (or more) animals against another may alter an individual's competitive ability against a rival in conflicts over food (Varley and Symmes 1966) or sexual partners (Cheney 1977, Varley and Symmes 1966, de Waal 1977) and in reversing the probable outcome of an agonistic encounter (Kummer 1968b, Seyfarth 1980). Any individual that can rely on the support of one or more other baboons in agonistic encounters is likely to do better than one of equal rank that cannot. There are, of course, very many more possible triadic than there are dyadic relationships in each group; each member of Fable's troop can be involved in more than 30,000 different three-way associations. Adult females typically support other members of their matriline (review in Datta 1981), and troop size presumably would have little effect on this. However, we might expect coalitions, especially among adult males, but also between juveniles (Massey 1977, Watanabe 1979), to be formed more frequently in large groups than in small groups (Rasmussen 1980). Observation conditions at Mt. Assirik were not suitable for collecting data directly on coalitions, but in several species of monkeys, including baboons, animals which regularly support each other in coalitions also spend much time grooming one another (Dunbar and Dunbar 1975, Dunbar 1976, Seyfarth 1980, Strum 1976, Varley and Symmes 1966, and reviews in Goosen 1980 and Wrangham 1981). We should therefore predict that animals in larger troops spend more time grooming one another than do animals in smaller troops.

METHODS

4.2: Activity Budgets

Activity budgets were determined in two ways. (1) During times of social activity the animals often sat in open areas in which they were relatively easy to observe. At these times activities of all visible animals were recorded at intervals of 20 minutes. The principal activity categories included: sit, stand, walk, eat, self-groom, and watch observer

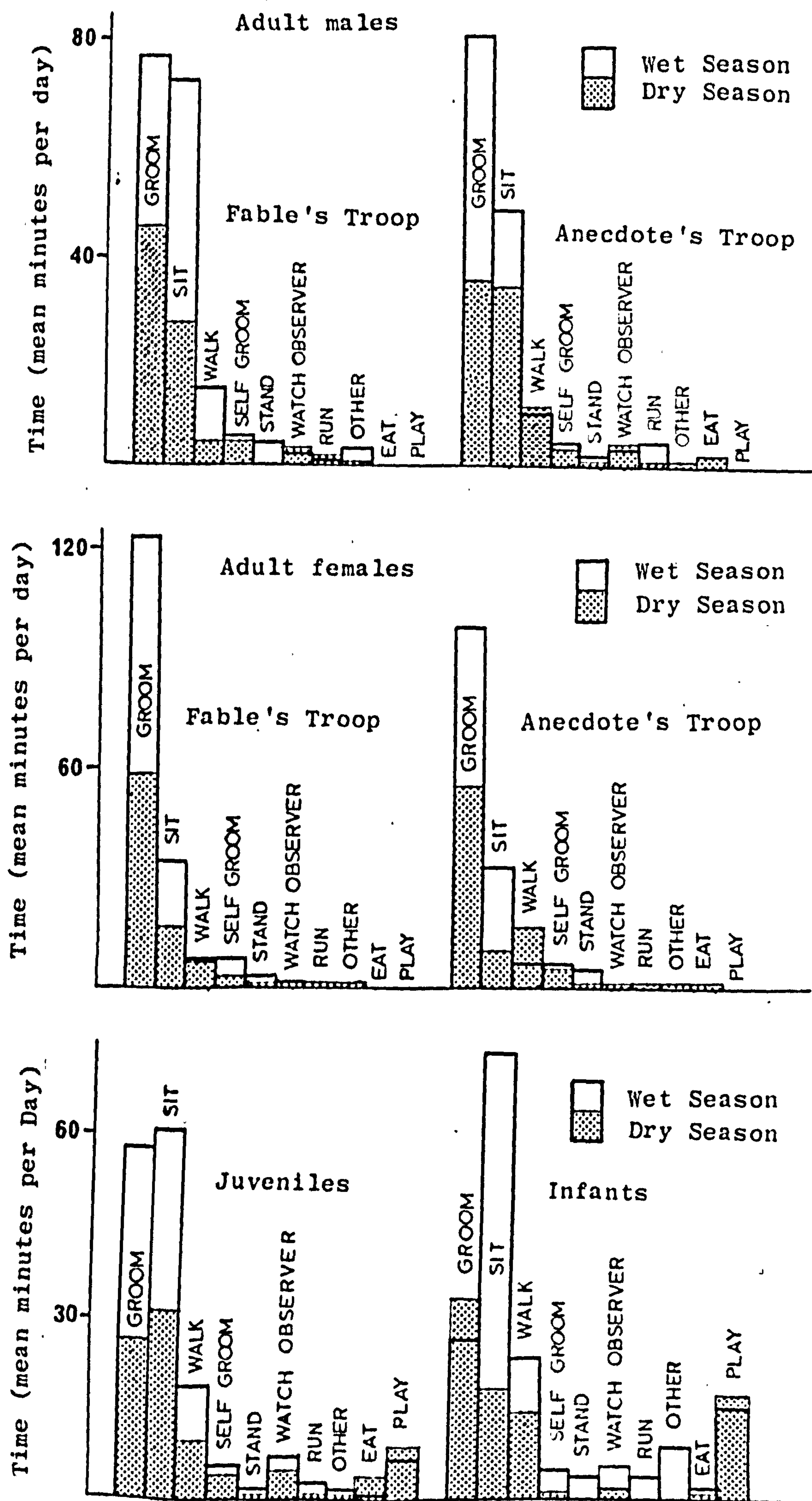
(all activities during which the animal was apparently not interacting with any other baboon), groom and be groomed (in the analysis both categories are included under "groom"), suckle, play, mount, copulate, and chase. Activities not on this list were also recorded, together with a full description of the behaviour if necessary. Focal animal sampling was not attempted because active animals tended to move out of sight within a short space of time, and sampling would have been biased towards sedentary activities, such as grooming. (2) When the animals were foraging or feeding they were usually difficult to observe, and regular scan samples were impossible. Instead, whenever I saw the animals I recorded the predominant activity (social, resting, feeding, or moving), together with the time at which the record was made. My appearance usually interrupted their behaviour and frequently caused the visible animals to move out of sight so that assessment of their behaviour was normally made in the first few seconds of each contact. In this my sampling resembled the instantaneous sampling of Clutton-Brock (1972) rather than the durational sampling of Struhsaker and Leland (1979). For the purposes of this analysis I extracted from my notes the activity recorded on the hour, or if there was no record on the hour, the activity mentioned in the first record after the hour. The data was extracted from all-day follows, together with records from part-day follows combined so that each hour of the day was equally represented within either troop in any one season. This method of data selection is not subject to any obvious bias apart from that of differential visibility of different activities. This problem is discussed by Clutton-Brock (1972) and by Homewood (1976). The total number of observations falling into each of the four activity categories were summed within seasons for both troops. The activity budgets of the two troops were then compared (using chi squared). The proportion of records concerning each activity were cumulated across the active day and results for each activity compared, using the Kolmogorov-Smirnov two-sample test, with the same activity in the same troop across seasons and with the same activity across troops in the same season.

RESULTS

4.3: Activity Budgets

The baboons left the trees earlier in the dry season (median time between 06:31 and 06:45) than they did in the wet season (median time between 06:46 and 07:00) (medians test; chi squared = 9.59; df = 1; $p < 0.005$). They then sat, either on laterite plateaux bordering the ravine or in the valley beneath the dormitory trees, and engaged in social behaviour. After stormy nights in the wet season they often sat dozing on the ground for an hour or more before gradually starting to interact socially. At the end of the social period troop-mobilising behaviour (Kummer 1968a, Stolba 1979) was sometimes seen, with a pseudopod forming which changed gradually into a general progression. Usually, however, the troop moved off abruptly although in these cases troop-mobilising might have taken place out of the observer's sight. The troop began its day's movement earlier in the dry season (median time between 07:46 and 08:00) than it did in the wet (median time between 08:16 and 08:30) (medians test; chi squared = 7.06; df = 1; $p < 0.02$). The troop stayed more or less together as it moved, until it entered the first foraging area of the day, whereupon it began to fragment and spread out, with some animals lagging behind at food sources while others moved on. The scattered troop might reform wholly or in part throughout the day, sometimes to rest and socialise, occasionally when moving together across apparently unproductive areas. At some time in the mid to late afternoon the troop would reach a sleeping site, often a different one from the one at which they spent the previous night. There was often some social behaviour before the baboons climbed into the trees. The baboons were always in the trees by nightfall and were never known to descend to the ground during the night.

Figure 4.1:
The estimated mean number of minutes per day spent by different age-sex classes in various activities during social times in both seasons.



4.3.2: Distribution of Sample

Each hour of the day between 07:00 and 17:00 was sampled the same number of times within seasons, but the sample size differed between troops and seasons. The hours of 06:00 and 18:00 were sampled a fewer number of times. Table 4.1 summarises these sample sizes.

Table 4.1:

<u>Sample size (number of samples of each hour)</u>					
Troop	Season	06:00	07:00-17:00	18:00	n
Fable	Wet	12	253	14	274
	Dry	0	143	26	177
Anecdote	Wet	20	220	20	262
	Dry	2	187	20	210

4.3.3: Absolute Frequency of Activities

Both troops were seen to feed less in the wet season than they were in the dry season (chi squared = 6.02; df = 1; $p < 0.02$ for Fable's troop; chi squared = 31.05; df = 1; $p < 0.001$ for Anecdote's troop).

No seasonal differences were found for the time spent moving or for time spent resting (Table 4.2).

Table 4.2:

<u>Frequency of Observation of Activities</u> <u>of Two troops throughout the day</u>						
Troop	Season	Activity				Total
		Moving	Social	Feeding	Resting	
Fable	Wet	102	68	42	62	274
	Dry	80	22	47	28	177
Anecdote	Wet	93	56	49	64	262
	Dry	66	27	81	36	210

No differences were found between the two troops within seasons, and data for the two troops were pooled for the comparison of activity

budgets in the wet and dry seasons.

Baboons at Mt. Assirik engaged in social behaviour more frequently in the wet season than they did in the dry season (chi squared = 11.38; $df = 1$; $p < 0.005$), and were seen feeding more frequently in the dry season than in the wet (chi squared = 22.84; $df = 1$; $p < 0.005$).

A total of 3093 observations of individual activities were made in the scan samples during social behaviour, of which 1841 were collected on Fable's troop (1102 in the wet and 739 in the dry season) and 1252 were collected on Anecdote's troop (655 in the wet and 619 in the dry season).

The most common activity recorded during social times was grooming, which occupied 44.0% of the scanned animals either as active or as passive partners. Activities not involving other baboons (sit, walk, stand, run, eat, self-groom, watch observer) occupied 49.4% of the animals recorded in the scans.

No age-sex category of Fable's troop groomed other animals from the same category more frequently than did those of Anecdote's troop (chi squared, p never < 0.05). In particular, adult males from both groups groomed other adult males at equivalent frequencies (chi squared = 0.02; $df = 1$; ns).

The proportion of time spent on various activities by each age-sex class was similar across the two troops within seasons (chi squared, p never < 0.05). The results from the two troops were therefore pooled within age-sex classes within seasons. The proportion of time spent by each age-sex class on the various activities was different between seasons (chi squared, p always < 0.025). Each age-sex class distributed its time differently among the various activities from those of other age-sex classes (chi squared, p always < 0.025).

From the known proportion of the day spent in social activity (Table 4.1) an estimate of the number of minutes per day spent on the various activities was calculated. The results are shown in Fig 4.1. In both troops adult and juvenile baboons spent about twice as much time grooming in the wet season as they did in the dry (two-tailed t test, $p < 0.01$ in each case) and almost all age-sex classes in both troops

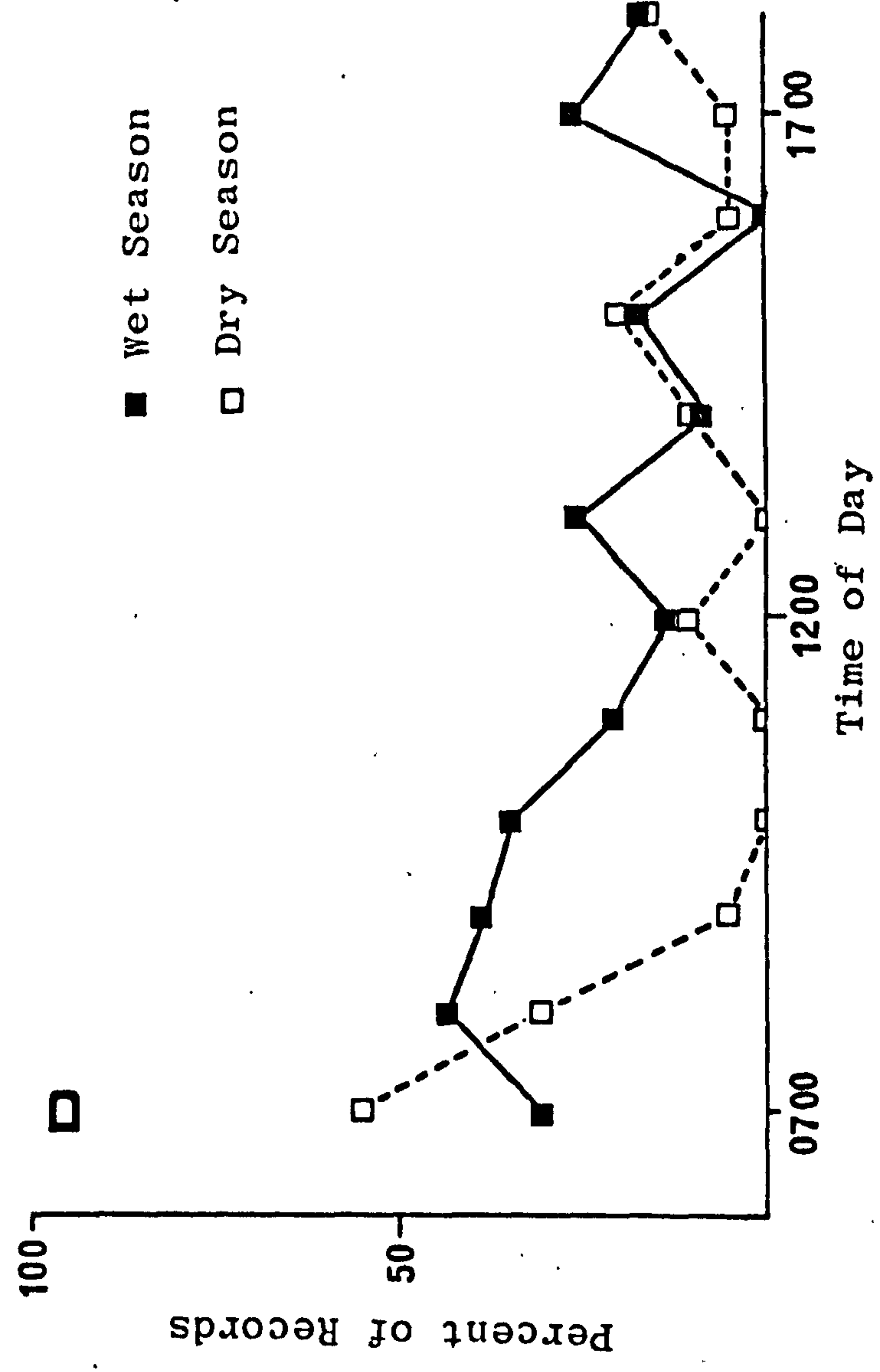
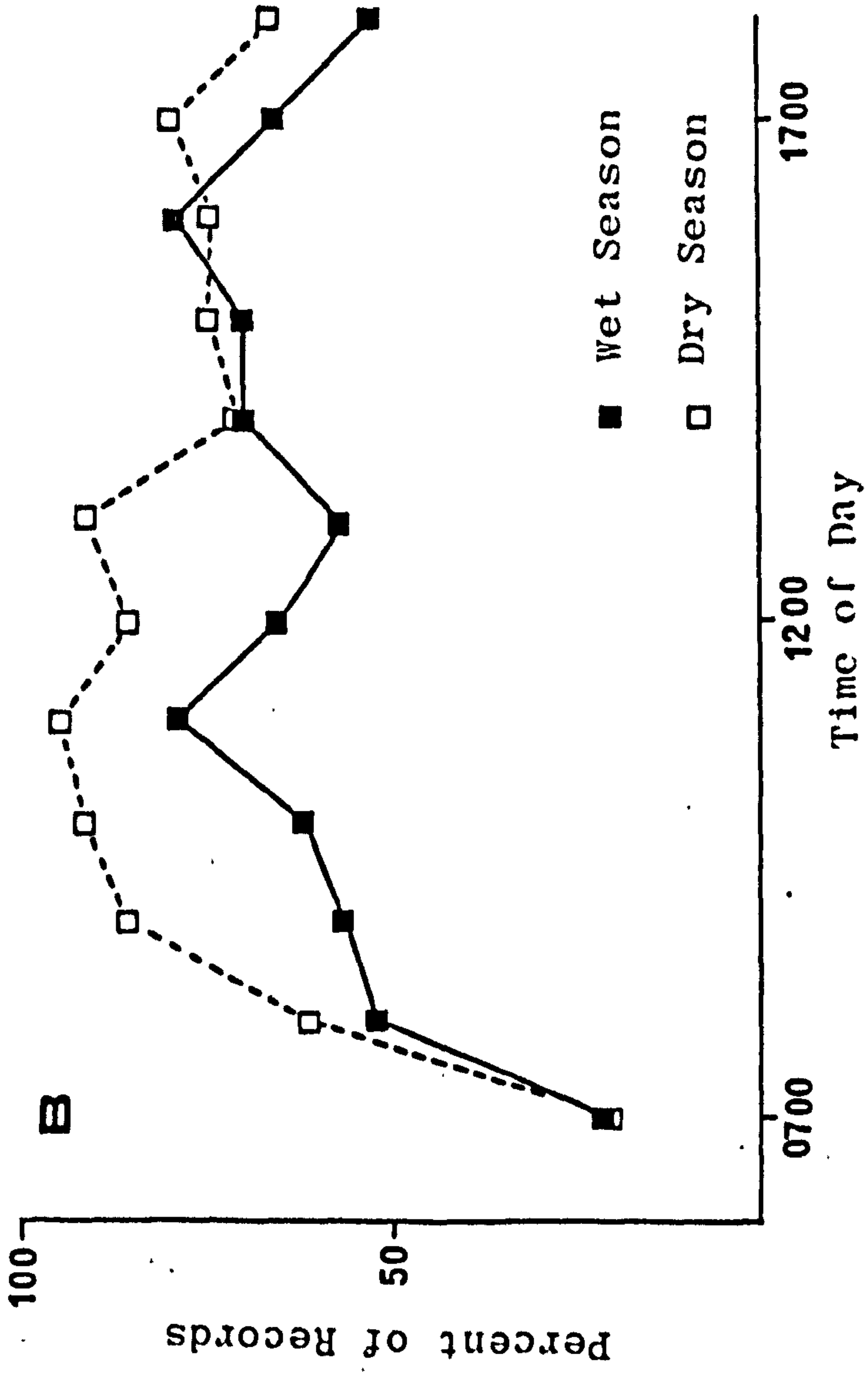
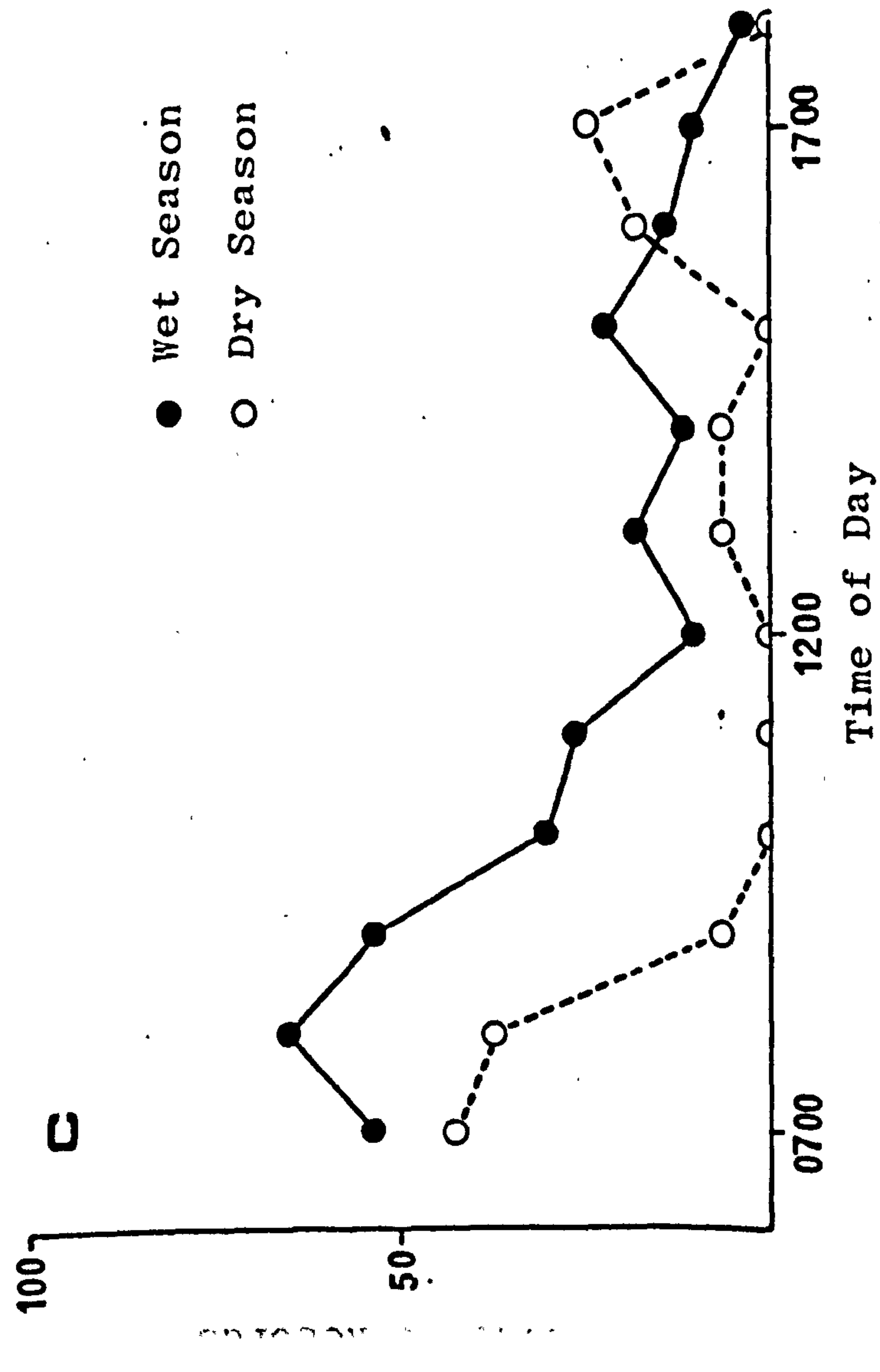
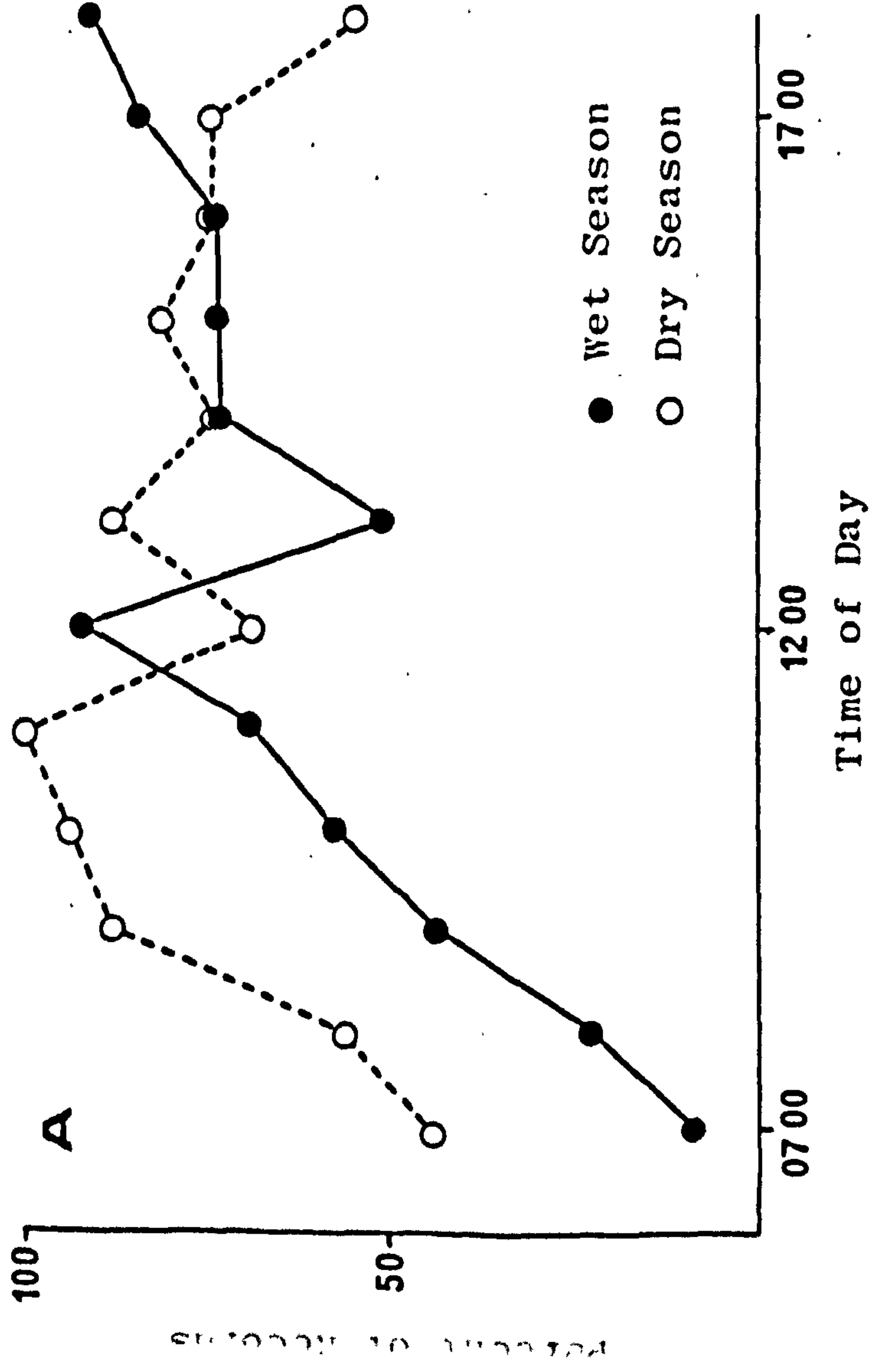


Figure 4.2:

Probability of finding members of two troops in social behaviour at various times of day.

- A Percentage of hourly records in which Fable's troop were feeding or moving in two seasons
- B Percentage of hourly records in which Anecdote's troop were feeding or moving in two seasons
- C Percentage of hourly record in which Fable's troop were engaged in social behaviour in two seasons
- D Percentage of hourly records in which Anecdote's troop were engaged in social behaviour in two seasons

Adult males

Adult females

spent more time sitting "doing nothing" in the wet season than they did in the dry season (t test, p always < 0.01). The exception was for adult males in Anecdote's troop, for whom there was no statistical difference in the amount of time sitting in the wet season. There was no difference in the amount of time spent in play by juveniles and infants in the two seasons (t test, p always > 0.05).

There may have been some correlation between the amount of time spent grooming by adults and juveniles and the size of group since the rank order of time spent grooming was the same as the rank order of median group size for the two troops in two seasons.

4.3.4: Distribution of Activities across the day

The two troops were likely to be engaged in social behaviour, or moving, feeding or resting at a similar time of day in the two seasons (Kolmogorov-Smirnov 2-sample test, ns). Results across troops within seasons, and within troops across seasons, were therefore pooled.

The probability of finding either troop in social behaviour stayed above about 30% until 10:00 in the wet season. In the dry season, however, a similar probability was only likely until about 08:00, and by 10:00 the probability of finding either troop in social behaviour was extremely low (Fig 4.2). About 10-20% of records after 10:00 in the wet season were of social behaviour, while in the dry season social behaviour occupied less than 10% of records until the mid to late afternoon, when, in Fable's troop, it climbed to about 25% by about 17:00. In the wet season both troops were increasingly likely to be seen moving or feeding from the time they left the trees until about 11:00 or 12:00, at which time about 80-90% of records were of feeding or moving. For the rest of the day between 50 and 90% of records were of feeding or moving. In the dry season both troops were either feeding or moving in about 60% of records by 08:00, and in over 90% by 10:00, after which these activities remained the principal ones, accounting for over 50% of records until 18:00.

In summary, the behaviour characterising the troops at different times of day differed with the season. In the wet season the baboons

socialised until mid-morning and began to move and feed later in the day. In the dry season social activity gave way to moving and feeding before 09:00.

4.3.5: Comparison With Other Troops

One other study (Dunbar and Nathan 1972) provides data on the activity budget of P. papio in the wet season. Their data show a different activity profile from that in this study (Table 4.3), with more resting and less moving. However, they state that they were unable to follow the baboons all day, so that their activity budget is biased towards periods when the baboons were not moving.

Table 4.3:
Comparison of Activity Budgets of two Populations of
P. papio.

Group	Activity			
	Moving	Social	Feeding	Resting
Dunbar and Nathan (1972)	9.1%	15.8%	26.1%	46.6%
Fable's troop	40.2%	20.5%	19.2%	20.2%
Anecdote's troop	33.7%	17.4%	27.8%	21.1%
Mt. Assirik	36.9%	18.9%	23.5%	20.7%

Troops from any given species of baboon may manage their time rather differently from troops of other species. In particular, 7 populations of P. anubis spent more time in social behaviour than did 3 populations of P. cynocephalus ($t = 4.10$; $df = 8$; $p < 0.005$) but less time than did 2 populations of T. gelada ($t = 3.01$; $df = 7$; $p < 0.025$). P. papio spent their time in the dry season rather like the troops of P. anubis in dry habitats (Harding 1976, Dunbar and Dunbar 1974c), although they spent more time moving and less time feeding than did either of those troops. (Aldrich-Blake et al. 1971, Dunbar and Dunbar

1974c, 1975, Hall 1965b, Hamilton et al. 1978, Iwamoto and Dunbar in prep, Nagel 1973, Oliver pers comm, Rasmussen pers comm, Van Citters et al. 1967).

DISCUSSION

4.4: Activity Budget within Social Period

The activity budgets of the baboons at Mt. Assirik were qualitatively similar to those of P. cynocephalus in Amboseli in Kenya (Post 1981).

The activity budgets of the two troops were similar, but differed within troops between seasons. Adults and juveniles groomed each other more in the wet season, when the troops were large, than they did in the dry season, as predicted. This may suggest that animals in larger groups spend more time grooming each other in order to maintain and strengthen social bonds, although there are other possible interpretations of this behaviour. In particular, both the troops spent more time feeding in the dry season, so that energetic constraints may have reduced the time the baboons could afford to spend in grooming.

Adult males in Fable's troop probably spent a little less time each day of the wet season (77 mins) in grooming or being groomed than did those of Anecdote's group (82 min), which goes against the predicted trend and accords with the observation that, on the basis of grooming frequencies, coalitions within age-sex classes may have been no more common in Fable's troop than they were in Anecdote's troop.

Juveniles and infants apparently did not play more in the wet season than in the dry, contrary to prediction. This observation may be due partly to the manner in which the data were collected. Since scans were not made throughout the day, play bouts while the baboons were moving or foraging probably went largely undetected. If such behaviour occurred more in the wet season than it did in the dry, bias would have been introduced into the results.

About half of the activities recorded during "social" periods were apparently solitary activities, often involving the animal sitting, either dozing or watching other animals, including the observer. It might seem artificial to separate the categories "social" and "resting" in this study, especially since the proportions of animals resting and socialising in a "resting" or "social" group probably varied continuously, with the majority of animals first in one category and then in the other. I felt however that it was more prudent to keep the categories separate since data on frequencies of behaviour in social times were collected largely in the early morning and were possibly not representative of the activities of the baboons in all "social" periods throughout the day and almost certainly not of "rest" periods.

Nagel (1973) suggested that since the baboons he observed spent more than 26% of their time resting in the dry season, the habitat, though marginal, did not overtax the baboons. Baboons at Mt. Assirik spent less of their time (about 16-17%) resting in the dry season, which suggests that the combination of habitat and troop sizes made their environment more taxing in the dry season than was the habitat at Awash.

CHAPTER 5: Ranging

INTRODUCTION

Without knowing the home range area of a troop we cannot estimate its biomass per unit area and hence the influence that it is likely to have on the ecology of the region. The gene pool of baboons in an area is determined in part by which troops have overlapping ranges, which share sleeping sites, and which exchange members. We do not yet have any means of estimating whether or not the baboons in the park are part of one or several demes because we do not yet know how large the home ranges of the baboons in the park are or with how many other troops each might overlap. Since ranging patterns determine which troops might meet (Deag 1973), the epidemiology of the area must include knowledge of the ranging of the baboons. This observation is perhaps especially relevant to the GPN de NK, since Dupuy (1971) remarks that plagues control the population of baboons in the park. Certainly, baboons are known or thought to suffer from many infectious diseases including: infectious mange (Nagel 1973), malaria (DeVore 1965a), schistosomiasis (DeVore 1965a, Douglas-Hamilton 1975, File pers comm to McGrew), respiratory infections (Dunbar 1980a, Dunbar and Dunbar 1975, pers obs) and intestinal parasites (Dunbar 1980a, Hausfater and Watson 1976, Kuntz and Moore 1973, File in prep). Finally, no management should be attempted until we understand how the animals exploit their environment, and what governs their movements.

5.2: Size of Home Range

The size of an animal's home range depends in part on its body weight (Brown 1975, Hunter 1964, Milton and May 1976) or metabolic rate (Harvey and Clutton-Brock 1981, McNab 1963, but see Turner et al. 1970 for a conflicting view) and partly upon the degree to which it is frugivorous, folivorous, or omnivorous (Clutton-Brock and Harvey 1977, McNab 1963, Milton and May 1976). Thus all troops of Papio baboons, being similar in size, terrestrial, and omnivorous, should have home range areas of roughly the same order of magnitude, depending partly on group size or weight (Clutton-Brock and Harvey 1977, 1979, DeVore and Hall 1965, Suzuki 1979),

local densities (Bernstein 1972, DeVore and Hall 1965), and possibly upon the social organisation of the troops (Bernstein 1972, McNab 1963, Hladik 1975, Milton and May 1976).

The location, as well as the size and shape of home ranges of many primates, and certainly baboons, are all influenced by the distribution in space and time of essential resources (Altmann 1974, Brown and Orians 1970), including water (Altmann and Altmann 1970, Gautier Hion 1971, Hamilton et al. 1976, Harding 1976, Stoltz and Keith 1973, Stoltz and Saayman 1970), sleeping sites (Altmann and Altmann 1970, Kummer 1968a) and food (Bernstein 1972, Casimir and Buetenandt 1973, Clutton-Brock 1974a, Clutton-Brock and Harvey 1977, 1979, DeVore and Hall 1965, Hladik 1975, Struhsaker 1967b, van Winkel 1975).

5.3: Movements of Baboons

Rasmussen (1979) showed that patterns of range use affect social behaviour and hence social organisation. The movements of many species of animals are well researched (review in Baker 1978), and we now understand to some extent how a baboon troop might plan and control its daily movements. Stolba (1979) and Sigg and Stolba (in press) demonstrated that the daily movements of one group of P. hamadryas baboons were largely decided at the start of the day's ranging. Byrne (in press) demonstrated that the baboons at Mt. Assirik coordinated their movements during the day's ranging by vocalisation. Troop spread has been shown to be affected by the presence of food and water and of other troops or humans, and by visibility (Harding 1976). This chapter complements these findings by considering how day range length, speed of movement of the troops, and the frequency with which they entered areas could be related to several independent variables, including group size, season, time of day, proximity to sleeping sites, land form, habitat, and climate.

5.3.1: Group Size

The length of the daily range of a group-living animal is partly determined by group weight (Clutton-Brock and Harvey 1977), so that within a species, large groups tend to have longer day ranges, and therefore move

faster on average than do smaller groups (Anderson 1980b, Iwamoto and Dunbar in prep). Fable's troop (with 250 members) should therefore have had longer day ranges and ^{have} moved faster than did Anecdote's troop (with 135 members).

5.3.2: Time of Day

Speed of movement is frequently affected by the time of day (Aldrich-Blake et al. 1971, Altmann and Altmann 1970, Clutton-Brock 1974b, Kummer 1968a, Sigg and Stolba in press, Stolba 1979). The activity patterns of the baboons (Chapter 4) suggest that the habitat in which the baboons were likely to be found should also have been influenced by time of day; specifically, that those habitats in which they tended to socialise should be entered earliest, followed at mid-morning by entry into habitats likely to contain food. There should have been no consistent daily pattern with habitats of slight importance to the baboons, so that the median time of first entry would presumably fall sometime in the middle of the day. Furthermore, the baboons would be unlikely to enter these habitats in the first few hours of the day, when social activity or feeding had high priority.

5.3.3: Season and Climate

Season affects speed of movement (Harding 1976, Stoltz and Saayman 1970), and frequency of entry into an area (Lindburg 1971, Waser 1976, Lee in prep). Times of low productivity are sometimes those in which day ranges are longest (Baldwin and Baldwin 1972, Struhsaker 1967b, van Roosmalen 1980), but the relationship between season and day range length in baboons is not clear. Although some groups of baboons show seasonal differences in day range (DeVore and Hall 1965, Hall 1962a, Oliver and Lee 1978), others do not, despite strong climatic differences between seasons (Stoltz and Saayman 1970, Sigg and Stolba in press).

In some studies the distance moved by a troop in the course of a day's ranging was apparently related to the maximum temperature reached by the air that day (Hall 1962a, Stoltz and Saayman 1970), although temperature seems to have little effect on the speed of movement of baboon troops (eg

Harding 1976). Climatic data from Mt. Assirik are excellent (McGrew et al. 1981), making it possible to examine in detail the relationships between speed of movement and temperature, humidity, and combinations of the two. For example, it might be that temperature interacted with humidity to influence speed of movement, and baboons, like humans, might tend to move less when both temperature and humidity were high. Because near-saturated hot air can absorb more moisture than can near-saturated cold air, the amount by which an animal can cool itself by sweating or panting is closely related to the vapour pressure deficit of the air (Moen 1973). At the end of the wet season at Mt. Assirik the mean vapour pressure deficit varied little, and was at its highest at 16:00 hrs (10.5 ± 2.4 mm Hg), while at the end of the dry season it varied from 9.9 ± 3.8 mm Hg at 07:00 hrs to 57.6 ± 7.6 mm Hg at 16:00 hrs. Sweating was therefore ineffective in the wet season, when human skin became moist after even slight exertion, but highly effective in the dry season. Since vapour pressure deficit changed little through the day in the wet season, speed of movement might have been more closely related to temperature in the wet season than it was in the dry season, when evaporative cooling would have ameliorated the effect of high temperatures in mid-afternoon.

5.3.4: Geography, Topography, and Variables associated with Habitat

The speed with which a troop of baboons moves and the frequency with which it enters certain areas are both apparently influenced by its physical environment (Sigg and Stolba in press, Stolba 1979). Sleeping sites exert a strong influence over the ranging of those animals, including baboons, which have few sleeping sites (Altmann and Altmann 1970, Gautier Hion 1971, Hall 1965a, Rowell 1972, Sigg and Stolba in press, Stoltz and Saayman 1970). Thus Harding (1976) found that baboons living in a home range of over 19 sq km spent more than half of their waking hours within 200m of a sleeping site. The simplest model to account for the ranging of baboons might be that the probability of their being found at any given distance from the nearest sleeping site fell off linearly. If this were true, then the probability of finding them in any given quadrat would be roughly proportional to the inverse of the square of their

distance from that site.

The frequency with which animals are found in various parts of their home range may be influenced by the distribution of the vegetation (Chalmers 1968a, Clutton-Brock 1973, 1975, Nagel 1973, Post 1976, Pyke et al. 1977), especially by that of fruiting trees (Glander 1975, Waser 1977). Thus we expect, and find, that baboons do not distribute their time evenly over the habitats available to them, but spend more time in the more productive habitats or in those which are preferred for social behaviour (eg Aldrich-Blake et al. 1971, Nagel 1973). Pyke et al. suggest that speed will be inversely related to the productivity of the area. As yet no correlations of speed of movement or frequency of entry into different areas with habitat type have been attempted. Aerial photographs allowed me to map the the habitat of the field area (Chapter 2). It was therefore possible to examine the effect of habitat on speed of movement and frequency of entry into different parts of the home range.

Since land form affects the exposure of the land to rain and sun and determines the rate of runoff and course of streams, and hence affects vegetation, it may be possible to predict ranging patterns from topography. This has not been attempted for primates before.

If shade were important to the baboons, as I suggested in Chapter 2, then its effects should have been most pronounced in the dry season when sun temperatures were frequently over 50°C. In this season baboons should have tended to be found in more shaded areas and to move rapidly through shadeless areas where this was compatible with the other needs of the troops.

In Chapter 3 I suggested that visual density in the wet season might have led to a higher risk of predation in that season. If this were true, baboons should have tended to avoid areas of poor visibility and to move rapidly through them if they entered them. In the dry season, however, the understory in large areas of the home ranges was burnt off, and baboons would probably have found little to encourage them to enter such desolate parts of their ranges. In the dry season the troops should have entered areas of relatively poor visibility more frequently and moved more slowly through them than they did areas of low visual density.

METHODS

5.4: Day Range Maps

The location of the troop was recorded on maps (Chapter 2) whenever possible. In many parts of the range geographical features or, sometimes, habitat borders (ecotones) visible on the ground and on an aerial photograph of the field area helped to locate the troop to within 200m or less of its true position. In areas of low or no relief and relatively homogeneous habitat intersecting compass bearings were taken on any visible landmarks, if necessary by climbing a tree to take the bearings. The position of the troop on the half hour throughout the day was estimated by interpolation between known locations, and these "half-hour points" recorded on the map. Occasionally the baboons were continuously out of sight for more than half an hour, and occasionally I was unable to estimate my position. In these cases the track between successive points was not known, and I assumed that the baboons moved in a straight line at constant velocity between known points. These plots formed the basis for the analysis in this chapter.

In order to establish that distances could be measured accurately from the maps made from aerial photographs, distances were estimated in three ways. Firstly they were calculated by pacing out a measured 0.5 km and then counting paces while following the baboons for 10 full day ranges and 5 part day ranges, secondly by the use of a pedometer calibrated to my stride length, and thirdly by summing the straight-line distances between known troop locations on the map. The three methods gave similar measures of distance travelled. The correlation between pacing and map measurement was very high ($r = 0.994$; $n = 15$; $p < 0.01$), with 4000 paces equivalent to 4.3km on the map (and 4.7km on the pedometer). The distances for all results used here were taken from map measurements.

5.4.2: Defining Home Range

Burt (1943) defined home range as "that area traversed by the individual in its normal activities of food-gathering, mating and caring for young", but excluded areas into which migrating or young animals might go and occasional sallies of individuals. This definition was reiterated by Brown (1975) and Brown and Orians (1970), although Jewell (1966) had earlier recommended that home range be defined either as the area over which an animal travelled "in pursuit of its routine activities" or as that area used by the animal in the course of its life. While this second alternative is presumably realistic for the animal concerned, it is of no practical use, except, perhaps, for very short-lived species or in very long-term, intensive studies. Furthermore, "routine activities" are hard to define for a primate group, and in practice field-workers have tended to define home range in terms of the area entered during the course of some specified time (eg monthly; Clutton-Brock 1972, Waser 1975, or seasonal; Hamilton et al. 1976, Harding 1976).

The way in which "the area entered" is defined further influences the meaning of "home range" in any given case. There are many comprehensive reviews of the methods used to estimate home range, including Hayne (1949), MacDonald et al. (1980), Mohr and Stumpf (1966) and Voigt and Tinline (1980). I defined home range in two ways. Firstly, in order to estimate the area which the troops probably exploited, the track of each full day's follow was enclosed as if by a taut string and all such areas superimposed. Although this method encloses areas into which the baboons were never followed, Sigg and Stolba (in press) have shown that with a large sample size there were no areas within the borders of the home range into which the troops were not known to go. Secondly, in order to examine the use of their home range by the baboons, all quadrats transected by the track of the troops were said to have been entered by the baboons and each entry into every quadrat was tallied. Lacunae were therefore excluded from this definition of home range.

5.4.3: Measuring Home Range Area

The accuracy with which home range area can be estimated depends on the number of full day ranges for which the troop was followed, the length of the day ranges, and the size of the home range. Normally estimates of home range area are based on small samples, especially with animals that travel several kilometres a day (exceptions are Amboseli, Post 1978, and Gilgil, Demment in prep). Home range area must usually be estimated from incomplete data. The normal method is to plot the cumulative new home range area against time for which the observation has been maintained. This curve tends to rise steeply at first, after which it levels off towards an asymptote. This shape of curve is given by the equation

$$y = k \times (1 - e^{-mt})$$

The value k of the asymptote is taken to be the home range area; thus at first glance it would seem possible to predict home range area on the basis of just enough full day ranges t to find the value of m that fits the data. This, in essence, is the rationale of the method of Metzgar and Sheldon (1974). Unfortunately the method is sensitive to the sequence in which the new areas are invaded. If three day ranges, A, B and C are arranged such that B and C barely enclose any common ground, but A happens to enclose almost all the ground enclosed by the other two, then the chance of whether the animals are seen to travel A, B, C or B, C, A or C, A, B will determine whether or not we believe that we have reached the asymptote to the curve.

Researchers normally construct the plot in the order in which the data were collected (eg Altmann and Altmann 1970), but there is no reason to suppose that this sequence arrives at a more accurate result than any arbitrary sequence would. The true home range area might lie somewhere between the area predicted by taking the day ranges in such an order that the asymptote is as low as possible and that order which gives as high an asymptote as possible.

The method adopted here was to use Metzgar and Sheldon's (1974) method to derive a straight line of known slope and intercept and to establish confidence limits for both parameters (Pollard 1977). These confidence limits were then treated as if they determined the smallest and

largest predicted home range area.

5.4.4: Confidence Ellipses and Home Range Area

The most statistically sophisticated method to have emerged so far from studies of the repeated trapping of animals (Brown 1975, Burt 1943, Gilmer et al. 1973, Harvey and Barbour 1965, Jorgensen 1968, Koepl et al. 1975, 1977, MacDonald et al. 1980, Mazurkewicz 1969, Metzgar 1972, Stickel 1954 and Trevor-Deutsch and Hackett 1980) has been the technique of drawing ellipses, around the points of capture, which account for a given proportion of the variance in the records (Mazurkewicz 1969). Trevor-Deutsch and Hackett (1980) showed that the surface area enclosed by the 70% confidence ellipses around the home ranges of chipmunks were similar to the home range area assessed by radio-tracking the animals.

Speed of movement was calculated for each half-hour point by assuming that the baboons moved between half-hour points along the known track at constant speed. The assumed speed of movement with which the baboons crossed each quadrat in their track was also recorded.

It was seldom possible to time the baboon's entry and exit from any habitat. In order to estimate the time spent in various habitats, the habitat type which covered the greatest area of each quadrat, the "principal habitat" of that quadrat, was recorded. The percentage of time for which the baboons were in each principal habitat was calculated from the position of the troops every hour after leaving the sleeping trees.

Principal habitats were also used to determine the median time by which the baboons first entered a habitat, and the probability that the baboons would have entered that habitat by the end of the first fifth of the day. If the baboons had left riverine gallery forest by the time that they had been out of the sleeping trees for half an hour they were said to enter riverine gallery forest for the first time when they moved back into it later in the day.

Temperature and humidity were recorded hourly at the camp in the centre of the field area by other members of SAPP while I was following the baboons. Speeds of movement could therefore be compared hour by hour with the prevailing air temperature, sun temperature, humidity and vapour

Figure 5.1:
Increase in known home range of Anecdote's troop with increasing
sample size.
(400 quadrats = 16 square kilometers)

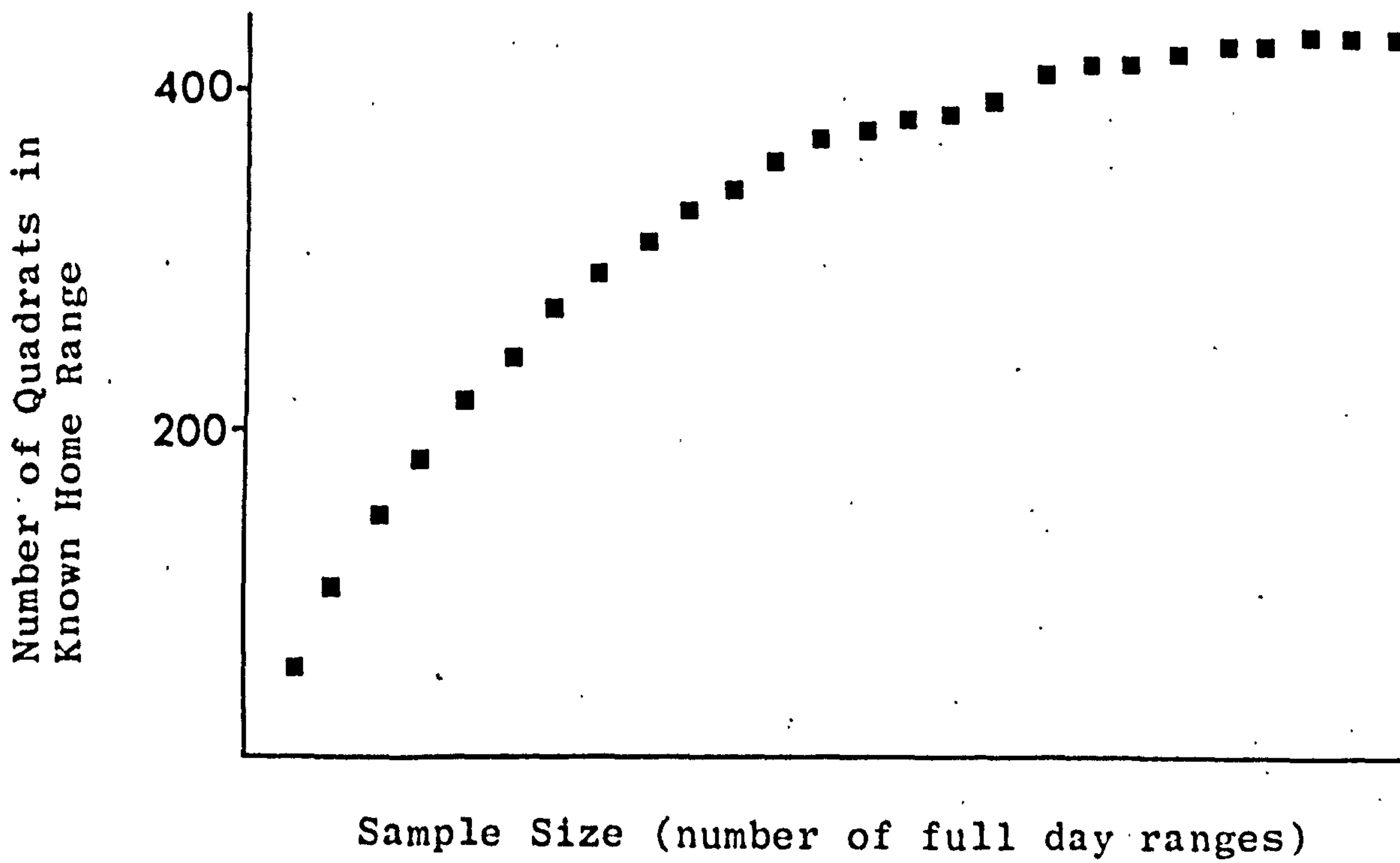
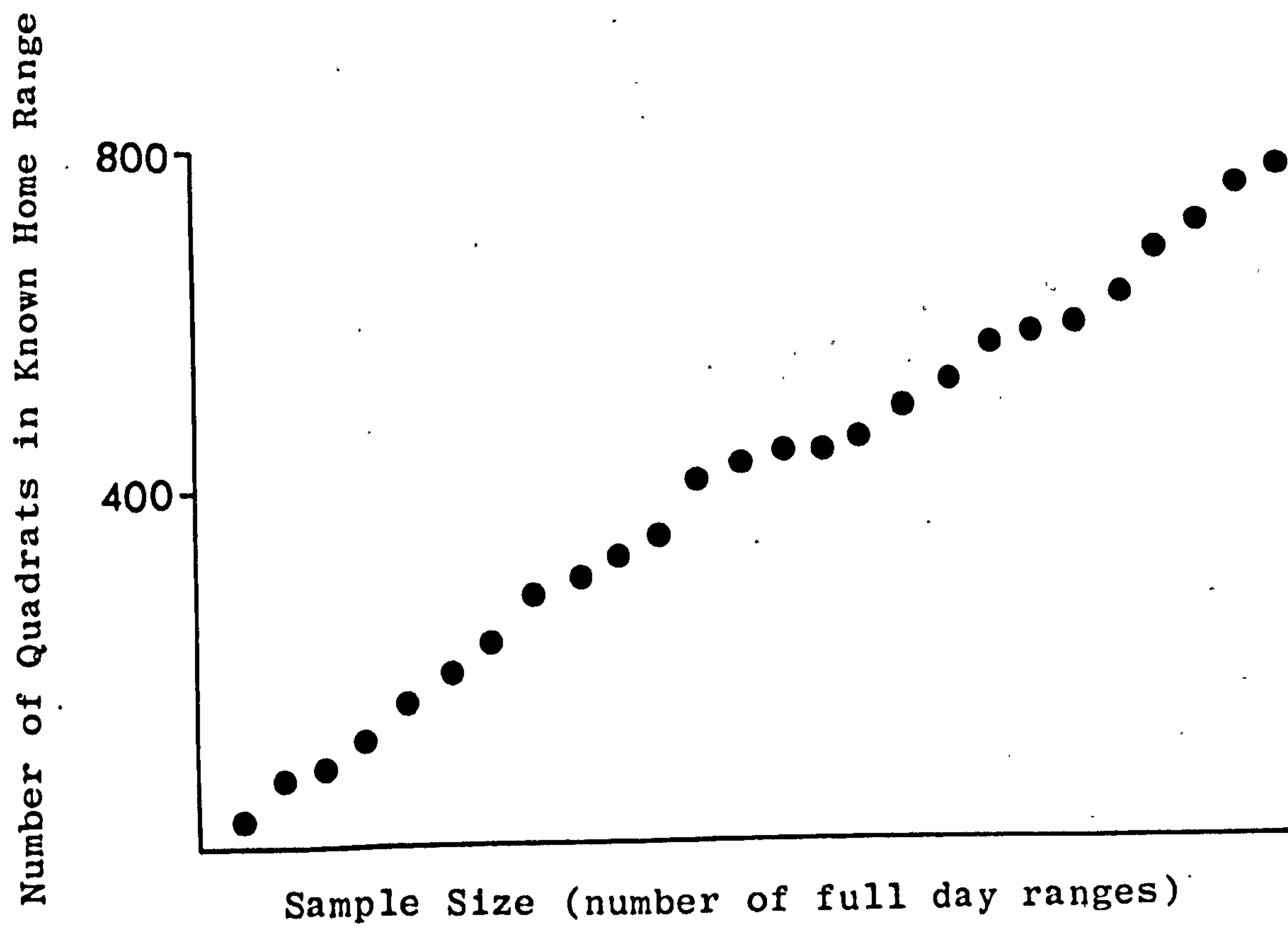


Figure 5.2:
Increase in known home range of Fable's troop with increasing
sample size.
(800' quadrats = 32 square kilometers)



pressure deficit.

Some of the more detailed methods used in the examination of ranging behaviour are given in the appropriate sections in the results.

RESULTS

5.5: Size of Home Range

For Anecdote's troop the plot of the number of quadrats in the known home range against the number of day ranges, taken chronologically, fits the curve

$$\text{Area} = 428 \times (1 - e^{-0.11t}) + 41$$

where t = number of day ranges (chi squared = 18.1; $df = 24$; ns) giving an estimated home range area of about 470 quadrats, or 18.8 sq km (Fig 5.1). Metzgar and Sheldon's (1974) method allows confidence limits to be set on this area (16.7 to 24.2 sq km). Superimposed full day ranges covered an area of 18.8 sq km. Thus for Anecdote's group both methods gave closely similar results. For Fable's troop, however, the plot of numbers of quadrats in the known home range against number of day ranges is a straight line (Fig 5.2)

$$\text{Area} = 28.0n + 45$$

$$(r = 0.96; n = 26; p < 0.01).$$

Increasing quadrat size up to 1 sq km made little difference to the tendency of the line to reach an asymptote. Metzgar and Sheldon's (1974) method shows that the smallest home range area possible on the basis of these data would be about 52.8 km sq, compared with the 42.7 sq km given by superimposing full day ranges. A final prediction of home range area was made by plotting the cumulative new area enclosed within full day ranges. The data tend towards an asymptote of about 40 sq km until the fourth-last day range, in which an increase of 22% in known home range area was made, which, together with small increases in the next three days caused the curve to tend towards an asymptote at about 68 sq km.

In summary, Anecdote's known home range covered an area of about 20 sq km, while Fable's covered at least 42 and probably more than 45 sq km

Figure 5.3(a):

Known home ranges of two troops of P. papio at Mt. Assirik.

Zone shared by both troops (roughly 9 sq km) is shaded.

Sleeping sites (shown as black dots) are numbered as follows:

- 1 Xanadu
- 2 Elephant Rib
- 3 Secret Valley
- 4 Assirik Valley
- 5 Flycatcher Falls
- 6 Old Camp
- 7 Amphitheatre (camp)
- 8 Cross Valley
- 9 Stella's Waterfall

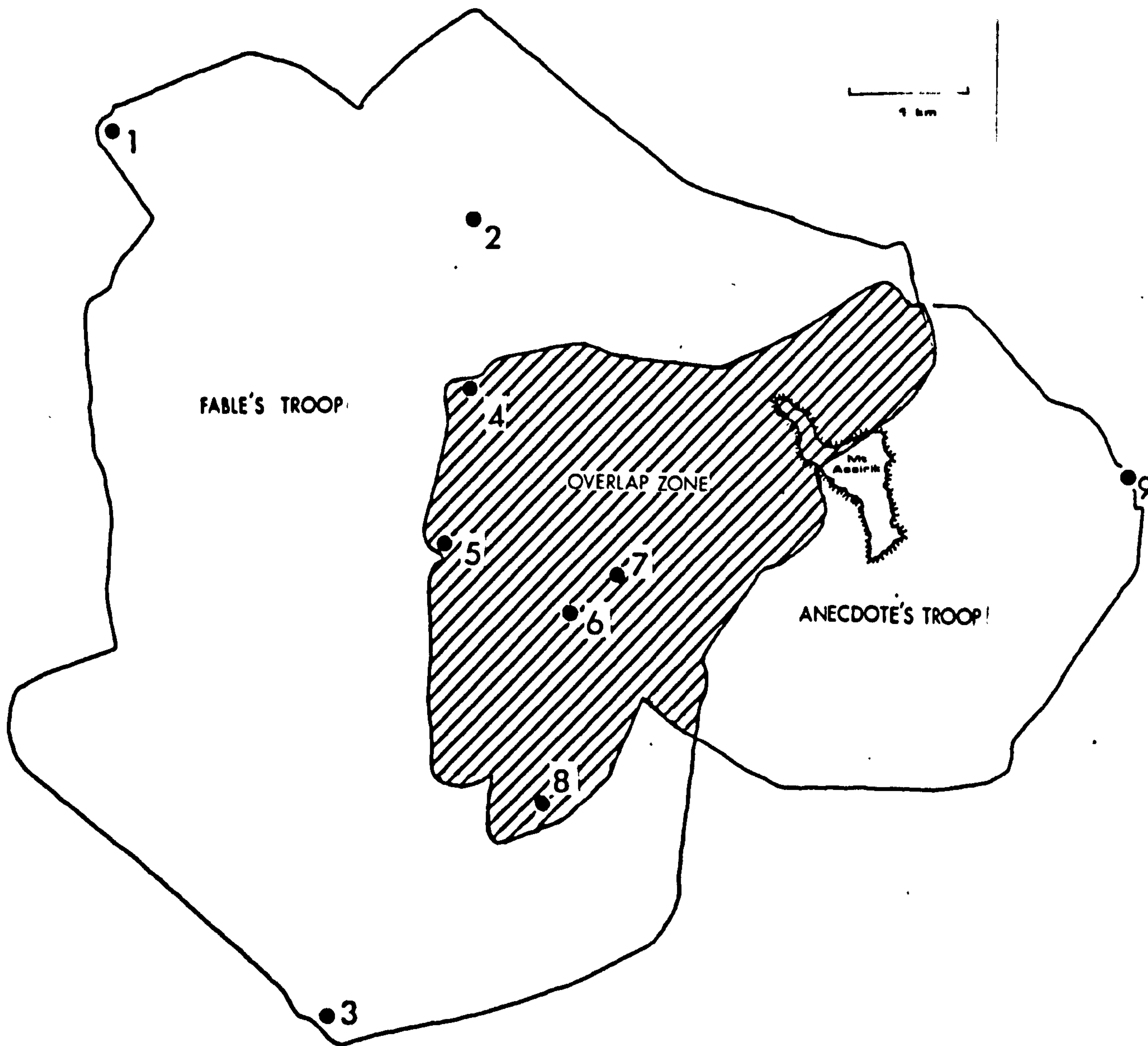
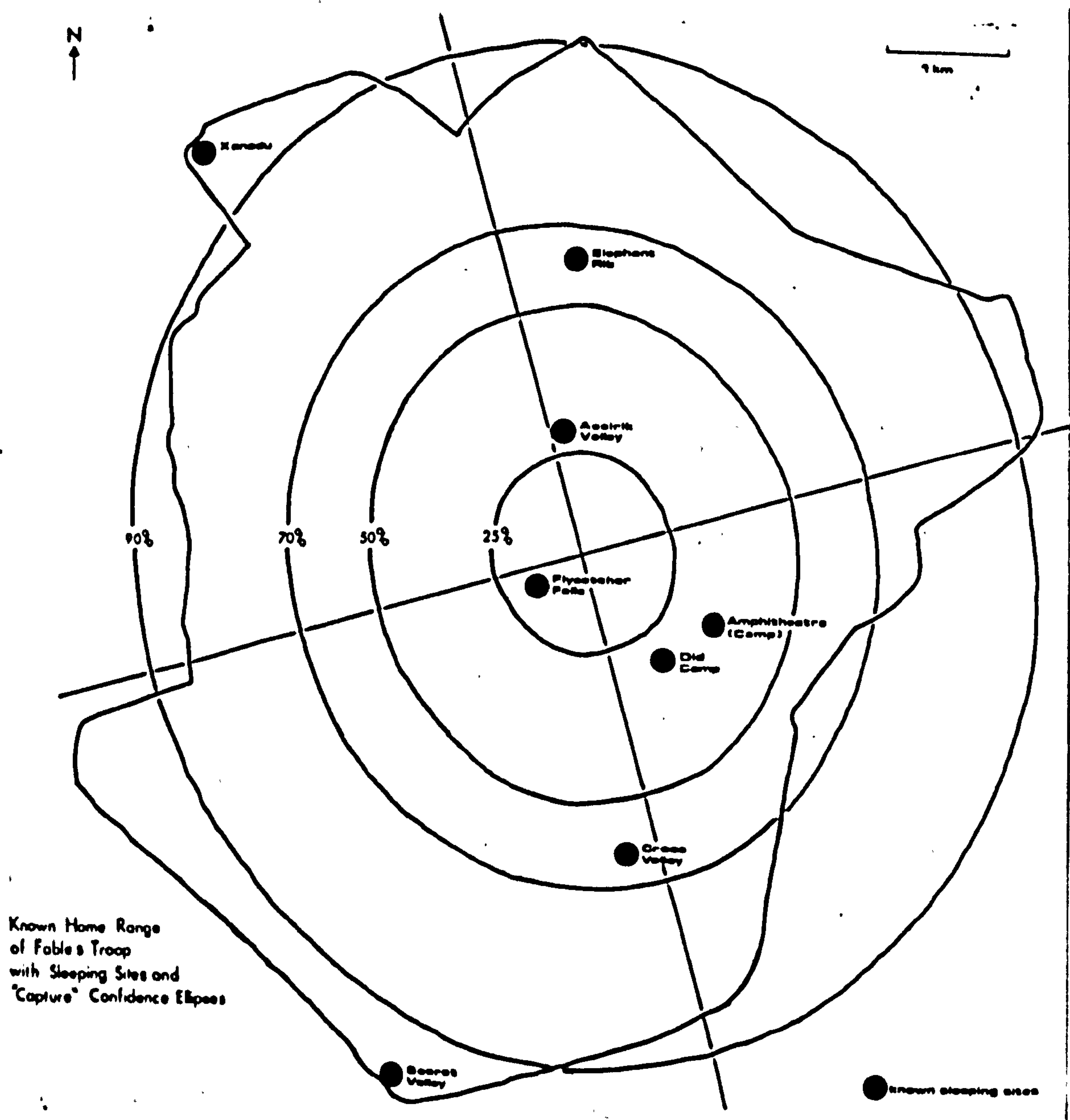


Figure 5.3(b):
Known home range of Fable's troop with sleeping sites and
"Capture" confidence ellipses. Area of home range is most
closely approximated by the 90% confidence ellipse.



The home range area of Fable's troop was not approximated by the 70% but by the 90% confidence ellipse (Fig 5.3).

Anecdote's troop's known home range was centred on Mt. Assirik, and hence included many laterite plateaux and marigots. Ridges were common and drainage streams rare. Fable's troop ranged largely to the west of Mt. Assirik, where there was little relief. Despite this, in the dry season Fable's troop's home range included a high proportion of quadrats containing cliffs, with their dense thickets of vegetation at their bases. Fable's troop extended its range in the wet season into the undifferentiated areas lying to the west of Mt. Assirik, while in the dry season its range, confined to the environs of Mt. Assirik, included more quadrats containing cliffs and ravines. The known home range of Anecdote's troop did not shift between the seasons.

5.5.2: Home Range Area: Comparison with other Studies

The home range area of Fable's troop was larger than all but 3 of the 30 troops of other species of baboon for which I have data (Table 5.1). Anecdote's troop, with its possibly fragmentary home range of 18.8 sq km, had the tenth largest home range of all known troops, including Fable's. There is a non-significant trend for larger troops to exploit larger home ranges (Kendall's tau; $p < 0.097$).

5.6: Movements of Troops

The baboons were followed for a total of 49 full day ranges (Fable's troop, 14 in the wet season, 9 in the dry; Anecdote's troop, 14 and 12 respectively). The distribution of day range lengths was normal (skew 0.13, ns; kurtosis 3.03, ns). The mean distance travelled in a day by Fable's troop was 8.1 ± 2.1 km, and by Anecdote's troop 7.6 ± 2.1 km (Table 5.2).

In neither Fable's nor Anecdote's troop was there a statistically significant difference between seasons, in either variance ($F = 2.0$ and 1.3 respectively) or mean distance travelled ($t = 0.8$ and 0.4 respectively). Similarly, there was no statistically significant difference between troops within seasons (wet season $F = 1.5$; $t = 0.8$;

Table 5.1:

Home Range Areas of Troops of Baboons

Square roots of home range areas are log-normal

Species	Area	Source
<hr/>		
<u>P. anubis</u>		
	0.9	Dunbar and Dunbar 1974c
	3.0	Ransom 1971
	3.2	Suzuki 1979
	3.9	Rowell 1966a
	4.3	Aldrich-Blake <u>et al.</u> 1971
	5.2	Rowell 1966a
	6.3	Maxim and Buettner-Janusch 1963
	6.0	Nagel 1973
	19.7	Harding 1976
	24.8	DeVore 1965a
	52.0	Popp 1978
	73.0	Bolwig 1959
<hr/>		
<u>P. cynocephalus</u>		
	16.7	Altmann and Altmann 1970
	40.0	Post 1981
	43.0	Rasmussen 1979
	61.0	Oliver pers comm
<hr/>		
<u>P. ursinus</u>		
	2.1	Hamilton <u>et al.</u> 1976, 1978
	4.0	"
	4.7	"
	4.8	"
	6.5	"
	9.1	Hall 1963a
	9.4	Hamilton <u>et al.</u> 1978
	10.7	Hall 1962a
	12.7	"
	13.0	Stoltz and Saayman 1970
	14.8	Hall 1963a
	33.7	"
<hr/>		
<u>P. hamadryas</u>		
	15.0	Nagel 1973
	29.0	Sigg and Stolba in press
<hr/>		
<u>P. papio</u>		
	18.8	This study (Anecdote's troop)
	42.7	This study (Fable's troop)
<hr/>		

dry season $F = 1.7$; $t = 0.3$), and none between troops with all day ranges included ($F = 1.0$; $t = 0.9$). In summary, the baboons at Mt. Assirik travelled about 7.8 ± 2.0 km per day irrespective of season or

Table 5.2:
Lengths of Day Ranges by Two Troops in Two Seasons

Rank	Troop			
	Fable		Anecdote	
	Wet	Dry	Wet	Dry
1	4.6	3.9	5.3	3.5
2	5.5	5.0	5.4	5.2
3	6.8	7.2	5.5	6.1
4	7.2	7.3	5.7	6.4
5	8.3	7.8	6.2	7.2
6	8.5	8.1	6.6	7.4
7	8.5	8.5	7.5	7.4
8	8.5	10.8	7.8	7.4
9	9.5	11.0	8.2	9.4
10	9.6		8.8	9.4
11	9.7		9.1	9.6
12	10.1		9.5	9.8
13	10.1		9.9	
14	10.5		13.1	
<hr/>				
x	8.38	7.68	7.75	7.40
sd	1.79	2.51	2.21	1.95

troop.

The distance travelled by the end of a day's ranging could be predicted from the distance travelled at any time after midday. In general, if l was the predicted day's range and d the distance travelled by time t ($t > 12:00$) then

$$l = (0.347 \times (t - 12) + 0.089) \times d + 0.3$$

The correlation between the prediction and the final distance travelled improved asymptotically with time of day so that where r is the correlation coefficient and t the time of day, for $n = 15$,

$$r = (1 - e^{-0.3 \times (t - 9)})$$

The population at Mt. Assirik apparently had a mean day range within one standard deviation of the mean day range (around 6.5 km) for the genus. P. anubis and P. cynocephalus tend to have shorter day ranges than did the baboons at Mt. Assirik (mean of 5 estimates = 4.3 ± 1.8 km; Aldrich-Blake et al. 1971, Altmann and Altmann 1970, Anderson 1980b, Dunbar and Dunbar 1974c, Harding 1976, Nagel 1971). Stoltz and Saayman (1970) reported that troops of one population of

P. ursinus ranged over a mean of 8.0 km per day, although other estimates for P. ursinus are lower (Hall 1962a, 1963a). Of all the baboons only P. hamadryas typically ranges further than P. papio, with a mean of estimates being 9.1 ± 2.1 km (Kummer 1968a, Nagel 1973, Stolba 1979, Sigg and Stolba in press). Mandrillus sphinx also ranges over about 8 km each day (Jouventin 1975). Mean day range length for single troops of other species of baboons varies from 0.6 km (T. gelada, Dunbar and Dunbar 1974c) to 11.1 km (P. hamadryas, with 10 day ranges included, Kummer 1968a).

5.6.1: Speed

There was no significant correlation in 19 of a sample of 24 full day ranges which was examined for autocorrelation between speeds of movement at successive half-hour intervals (Table 5.3). The common correlation coefficient (rho) was about 0.3.

Table 5.3:

Autocorrelation of Speed at Half-Hour Intervals

Sample	Fable's Troop		Anecdote's Troop	
Number	r	sig level	r	sig level
1	.489	5%	.680	1%
2	.197		.341	
3	.413		.342	
4	.637	1%	.209	
5	.355		.320	
6	.187		.307	
7	.455	5%	.241	
8	.214		.036	
9	.303		.298	
10	.179		.421	5%
11	.093		.164	
12	.298		-.187	

Over the whole year the median speed of movement of a moving troop recorded on the half-hour for was, for Fable's troop, 0.72 kph (range 0 - 2.8 kph) and for Anecdote's troop, 0.66 kph (range 0 - 2.8 kph). There was no difference in the median speeds with which the two troops

moved (medians test, chi squared = 2.51; df = 1; ns). In the wet season the median speed of movement of Fable's troop was 0.80 kph; in the dry season it was 0.64 kph (medians test, chi squared = 7.48; df = 1; $p < 0.01$). Anecdote's troop moved at a median speed of 0.67 kph in the wet season and 0.65 kph in the dry season (medians test, chi squared = 0.072; df = 1; ns).

These median speeds are higher than these reported by Altmann and Altmann (1970) for P. cynocephalus (median of about 0.44 kph, range 0 - 3.9 kph) but similar to those recorded for P. hamadryas (mean of 0.8 kph, range 0 - 4.0 kph, Stolba 1979; max speed over one hour 4.7 kph, Kummer 1968a).

Speeds recorded on the half hour represented the mean speed for 30 minutes travelling. Speeds of movement across quadrats were often estimated from sightings at shorter intervals, and hence were more variable. The fastest recorded movement of either troop across a quadrat was 3.9 kph, by Fable's troop in the wet season, while Anecdote's troop was seen to move across a quadrat at about 3.6 kph in the same season. The fastest speeds with which the troops were seen to move across quadrats in the dry season were 3.1 and 2.9 kph respectively. Median speeds across quadrats lay between about 1.1 and 1.3 kph. (Note that median speeds across quadrats are biased towards high speeds since in a given time interval more quadrats are crossed if the troop is moving fast.)

5.6.2: Time

The fastest speeds with which the baboons moved were not distributed randomly across the three periods 6:00-11:59, 12:00-15:59, and 16:00-19:59 (chi squared goodness-of-fit, chi squared = 4.08; df = 2; $p < 0.05$). Top speeds tended to occur in the last third but not in the middle of the day. Second fastest speeds tended to fall in the first third of the day (chi squared = 8.92; df = 2; $p < 0.025$), while periods for which the baboons were stationary on the half-hour fell more frequently than expected into the central third of the day (chi squared = 7.57; df = 2; $p < 0.01$).

Riverine gallery forest and the closely associated Combretum scrub on laterite tended to be first entered shortly after the baboons left the trees (Table 5.5). Once they had left the social areas the baboons tended to enter open woodland and dry forest earlier than any other habitat. The percentage of first visits to a given habitat which occurred in the first fifth of the day reflected the skewness of these distributions, and corresponded to the probability of the baboons getting to these habitats early in the day (Table 5.5). Roughly half of the first entries to open woodland and 2/5 of the entries to dry forest were made in the first fifth of the day, while scrub and scrub grassland were rarely or never entered in this period.

Table 5.4:

Median Time of First Visit
Whole Year; Both Groups
Data From All Full Day Ranges

Habitat	Median Time
Riverine Gallery Forest	07:00
<u>Combretum</u> scrub on laterite	08:15
Open Woodland	09:30
Dry Forest	09:30
Scrub Grassland	10:30
Scrub	11:30
Grass on laterite	12:30

Table 5.5:

Percentage of Observations on Which First Visit
To a Given Habitat was in First 1/5th of Day

Habitat	Troop		Season		Total
	Fable	Anecdote	Wet	Dry	
Riverine Gallery Forest	86	87	92	80	86
<u>Combretum</u> scrub on laterite	57	71	58	71	64
Open woodland	32	64	39	59	48
Dry Forest	56	40	32	50	39
Grass on laterite	20	11	16	16	16
Scrub	0	19	6	11	9
Scrub Grassland	0	0	0	0	0

5.6.3: Climate

There was no significant relationship between the distance travelled by the troops and the maximum air temperature of the day, either within seasons or across the year (r never > 0.3 ; p never < 0.05).

There were no correlations between hourly speed of movement by either troop in either season with air temperature, sun temperature, humidity, or vapour pressure deficit (correlation coefficients in no case significantly different from zero).

5.6.4: Sleeping Sites

The distance of the troop to the nearest sleeping site was recorded for 590 positions of the troops during full day ranges.

The probability p of finding the troop at a given distance d from a sleeping site was inversely proportional to their distance from that site, and was given by the linear equation

$$p = 0.06 \times d - 0.02$$

The median distance of the troop from a sleeping site was 0.78 km, while the median distance from any point in either of their seasonal home ranges to the nearest sleeping site was about 1.9 km. The baboons were normally to be found significantly closer to sleeping sites than they would be if they used their home ranges evenly (medians test, chi squared = 54.88; $df = 1$; $p < 0.001$). The frequency with which both troops in both seasons visited quadrats was also linearly correlated with the distance of the quadrat from the nearest sleeping site (p always $<< 0.001$), but the inverse square of the distance to the nearest sleeping site explained more much of the variance in the frequency with which the troops used any quadrat (Fable: wet 21%, dry 22%; Anecdote: wet 20%, dry 21%).

Both troops tended to move faster when they were further from sleeping sites in the wet season (Fable: slope 0.17 kph/km; $p << 0.001$; Anecdote: slope 0.1 kph/km, $p < 0.006$), but there was no effect of distance from the site on speed in the dry season.

5.6.5: Habitat

The estimation of habitat type is described in Chapter 2. Speed of movement across and frequency of entry into quadrats were regressed on the proportion of the various habitats present in the quadrat. These regression lines were then used to predict the speed of movement and frequency of entry into a quadrat entirely covered by each habitat.

The percentage of a given habitat affected the speed with which the troops moved across a quadrat in 13 out of 28 cases (two troops, two seasons, seven habitats) (regression lines, n between 660 and 2250, $p < 0.01$) (Table 5.6).

Table 5.6:

Speed (kph) Predicted from Regression Line
Across Quadrat Containing 100% of Habitat

* = $p < 0.01$
** = $p < 0.001$

Troop	Season	Habitat						
		Bush	Scrub	Combr	Woods	Forest	Grass	Gallery
F	W	2.05*	1.74**	1.26	1.18	1.08*	0.99*	[-0.3]**
	D	2.22**	1.61*	1.50	0.94**	1.54*	1.30	[-0.1]**
A	W	1.59	1.51	1.28	1.34	1.20	0.77**	[-0.2]**
	D	0.98	0.87	1.33	1.15	1.00	1.04	[-0.3]**
Mean Speed		1.71	1.43	1.34	1.15	1.21	1.03	[-0.2]

KEY: F = Fable's troop A = Anecdote's troop

W = Wet season D = Dry season

Bush = Scrub grassland

Scrub = Scrub

Combr = Combretum scrub on laterite

Woods = Open woodland

Forest = Dry forest

Grass = Grass on laterite

Gallery = Riverine Gallery Forest

In both seasons both troops tended to move slower the more riverine gallery forest was present in the quadrat. Fable's troop moved faster the more scrub and scrub grassland there was in the quadrat. In the dry season it moved faster the more dry forest was present in the quadrat, but in the wet season, the more dry forest was present, the slower the troop moved. Increasing proportion of grass on laterite plateau in a quadrat was negatively correlated with the speed of movement of both troops in the wet season. This trend was also

present, though not statistically significantly so, in the dry season. Scrub on laterite plateau was the only habitat for which the regression was never statistically significant.

It was possible to predict from the regression line the speed that the troop might be expected to have in a pure quadrat of each habitat (Table 5.6). The troops would have moved fastest in a quadrat of pure scrub grassland, and slowest in riverine gallery forest. The regression line predicted a negative speed in riverine gallery forest, and I have assumed that the baboons would have moved very slowly in a quadrat containing only this habitat.

Almost all the habitat effects were due to riverine gallery forest (two-way anovar F between habitats = 19.7; $p < 0.025$; Scheffe's multiple comparisons, all habitats significant at $p < 0.025$ with riverine gallery forest) but the speeds with which the troops moved through scrub grassland ("Bush" in the Tables) was significantly higher than the speeds with which they moved through grass on laterite (Scheffe's multiple comparisons, $p < 0.05$). Very little of the variance in the speeds of movement could be accounted for by any single habitat. Riverine gallery forest, with between 3 and 6.4%, and scrub, with between 1.0 and 5.0%, accounted for more variance in speed than did any other habitats.

Both troops in both seasons entered quadrats less frequently the more scrub-grassland ("Bush") and scrub were present in the quadrat, and more frequently the more dry forest and riverine gallery forest were present. In the wet season both troops entered quadrats more frequently the more grassland on laterite was present in the quadrat.

The regression lines predicted that quadrats completely covered with a single habitat would be entered with a frequency which depended on the habitat (two-way anovar, $p < 0.001$) (Table 5.7). The regression lines predicted a negative frequency in scrub grassland (Bush) and in scrub, which is taken to mean that the baboons would be unlikely to enter a quadrat consisting entirely of one of these habitats.

The variance in the frequency with which the baboons entered any given quadrat accounted for by habitat was never more than 14.5%.

Table 5.7:

Frequency of Entry into Quadrats
Predicted Frequency of Entry into Quadrat
When Quadrat Contains 100% of Given Habitat

* = $p < 0.01$
** = $p < 0.001$

Troop	Season	Habitat						
		Bush	Scrub	Combr	Woods	Forest	Grass	Gallery
Fable	Wet	0[-.13]**	0[-.03]**	0.81**	0.39**	1.15**	0.68	9.01**
	Dry	0[-.19]**	0.02**	0.23	0.16	0.42**	0.54**	6.62**
Anecdote	Wet	0[-.37]**	0[-.14]**	0.46	0.64**	0.79**	0.75	10.07**
	Dry	0[-.20]**	0[-.14]**	0.35	0.35	0.51**	0.94**	9.88**

Numbers in square brackets are taken to imply zero.

Different habitats accounted for differing amounts of variance (Friedman's S; chi squared = 27.25; df = 6; $p < 0.005$). Combretum scrub accounted for particularly little of the variance in the frequency with which the baboons entered a quadrat, while scrub, and especially riverine gallery forest, accounted for more (Table 5.8).

Table 5.8:

Frequency of Entry into Quadrats
Percentage of Variance Explained by Given Habitat

Troop	Season	Habitat						
		Bush	Scrub	Combr	Woods	Forest	Grass	Gallery
Fable	Wet	1.0	3.9	0.6	0.4	3.7	0.1	10.4
	Dry	0.8	1.1	0.0	0.1	0.9	0.6	14.5
Anecdote	Wet	0.9	2.4	0.0	0.3	0.7	0.1	7.9
	Dry	0.5	2.3	0.0	0.0	0.4	1.0	13.0

5.6.6: Time Spent in Various Habitats

Neither troop shared out their time between habitats in proportion as those habitats occurred in the field area (Kendall's tau = 0.14 ns) (Table 5.9). The ratio of time spent to proportion of habitat available, a preference index, shows that riverine gallery forest, dry forest, and grass on laterite were used consistently more than expected by both troops in both seasons, while Combretum on laterite, scrub, and

scrub grassland (Bush) were used consistently less. Indeed the baboons spent nearly 35 times as much time as expected in riverine gallery forest and about 5 times less than expected in scrub (Table 5.10).

Table 5.9:

<u>Time Spent in Various Principal Habitats</u>								
Percentage of records of troop in quadrat with given principal habitat								
Troop	Season	Forest	Woods	Gallery	Combr	Grass	Scrub	Bush
Fable	Wet	39.0	22.1	11.3	13.1	7.0	5.6	1.9
	Dry	30.0	28.9	17.5	7.9	11.4	4.4	0.0
Anecdote	Wet	34.9	25.3	16.1	11.8	5.9	3.8	2.2
	Dry	25.4	31.2	10.7	8.8	17.6	4.9	1.5
Mean		32.5	26.7	13.5	10.6	10.5	4.7	1.5
% Rank		20.8 3	29.5 1	0.4 7	14.9 4	5.8 5	24.9 2	3.6 6

KEY: % in field area = percent of principal habitat in field area
Forest = Dry forest Woods = Open Woodland
Gallery = Riverine gallery forest Combr = Combretum scrub on laterite
Grass = Grass on laterite Bush = Scrub grassland

Table 5.10:

<u>Ratio of Time Spent to Habitat Available</u>								
Troop	Season	Forest	Woods	Gallery	Combr	Grass	Scrub	Bush
Fable	Wet	1.88	0.75	28.25	0.88	1.21	0.22	0.53
	Dry	1.44	0.98	43.75	0.53	1.97	0.18	0.00
Anecdote	Wet	1.68	0.86	40.25	0.79	1.02	0.15	0.61
	Dry	1.22	1.06	26.75	0.59	3.03	0.20	0.42
Mean		1.55	0.91	34.75	0.70	1.81	0.19	0.39
Rank		3	4	1	5	2	7	6

KEY: see Table 5.9

5.6.7: Topography

Topography was assessed by the method given in Chapter 2. A selection ratio for each topographic type was calculated for each troop as follows. The proportion of the entries into all quadrats of a given topography in the seasonal home range was divided by the proportion of

quadrats which contained that topography. When the selection ratio was less than one the troop entered quadrats containing that topographic type less frequently than expected on the basis of its frequency in the home range; when greater, more frequently.

Speed of movement was affected by topography (Friedman's $S = 941.5$; $\chi^2 = 31.38$; $df = 9$; $p < 0.005$), with the baboons moving fastest in quadrats characterised by marigots or in undifferentiated quadrats (at about 1.4 kph) and slowest in quadrats characterised by dry season water (about 0.75 kph) or by sleeping sites (about 0.6 kph)(Table 5.11).

Table 5.11:
Speeds of Movement of Two Troops in Quadrats Characterised by Various Topographic Features

Troop Season		Topographic Feature									
		Mgot	Undf	CaSt	Plat	Clif	Ridg	DrSt	Ravi	DrWa	SlSl
Fable	Wet	1.18	1.33	1.33	0.96	1.11	0.96	1.26	0.89	1.03	0.52
	Dry	1.68	1.51	1.21	1.45	1.03	1.07	1.33	1.07	0.73	0.44
Anecd	Wet	1.47	1.54	1.26	1.26	1.19	1.19	0.84	0.77	0.56	0.70
	Dry	1.20	1.00	1.16	1.21	1.10	1.10	0.68	0.82	0.63	0.47
Mean		1.38	1.35	1.24	1.22	1.11	1.08	1.03	0.89	0.74	0.59

Friedman's $S = 941.5$; $\chi^2 = 31.38$; $df = 9$; $p < 0.005$

Key: Mgot = Marigot Undf = Undifferentiated CaSt = Catchment Stream
 Plat = Plateau Clif = Cliff Ridg = Ridge
 DrSt = Drainage Stream Ravi = Ravine
 DrWa = Dry Season Water SlSl = Sleeping
 Site

For definitions of topographic types see Chapter 2.

The effects of topography on speed did not depend upon season or troop (Friedman's $S = 74$; $\chi^2 = 7.4$; $df = 3$; ns).

The effect of topography on speed of movement was probably mediated by the vegetation growing in the different topographic types. That this is so is suggested by the high percentages near the main diagonal of Table 5.12, in which both habitats and topographic types are arranged in descending order of the speed with which the troops moved through

them.

Table 5.12:
Percent of all Quadrats characterised by given Topographic Types
which was covered by a given Habitat

Major habitat in each topographic type is underlined

Topographic Type	Habitat						
	Bush	Scrub	Combr	Woods	Forest	Grass	Gallery
Marigot	0.0	2.5	<u>38.2</u>	19.6	23.0	16.5	0.2
Undifferentiated	9.9	<u>30.3</u>	12.6	27.3	16.9	3.0	0.0
Catchment Stream	12.8	<u>30.1</u>	3.9	<u>38.7</u>	12.4	2.2	0.0
Plateau	0.2	1.1	<u>48.1</u>	8.9	15.5	26.1	0.1
Cliff	3.4	10.4	16.6	<u>33.3</u>	28.0	8.2	0.2
Ridge	9.3	20.0	3.0	<u>44.1</u>	22.8	0.8	0.0
Drainage Stream	8.5	27.6	5.1	23.2	<u>32.2</u>	3.2	0.2
Ravine	0.0	0.4	19.4	11.2	<u>39.6</u>	20.8	8.6
Dry Season Water	4.0	13.8	15.4	10.2	<u>35.4</u>	15.0	6.2
Sleeping Site	0.5	1.2	18.1	4.9	28.2	13.9	<u>33.2</u>

The frequency with which each troop entered quadrats in both seasons depended on the topography of that quadrat (chi squared, p never > 0.025). Selection ratios varied between 0.27 and 3.61, with those for sleeping sites being significantly higher than those for any other topographic type except for ravines (Scheffe's multiple comparisons, p never > 0.025)(Table 5.13).

5.6.8: Shade and Visual Density

Shade and visual density was measured as described in Chapter 2. The shade and visual density in scrub and scrub grassland were assumed to be similar to those in Combretum scrub and grass on laterite respectively. The mean shade in each quadrat in each season was calculated by summing, for each habitat, the product of the percentage of that habitat in the quadrat and the mean proportion of the ground in dense shadow in that habitat. Mean visual density was assessed in a similar manner. Speed of movement and frequency of entry were regressed on the percentage of shade and degree of visual density in quadrats.

Table 5.13:
Frequency of Entry into Quadrats Characterised by
Various topographic Features

Topographic	Fable						Anecdote					
Feature	Wet			Dry			Wet			Dry		
	f	#	sr	f	#	sr	f	#	sr	f	#	sr
Plateau	137	70	1.05	45	35	0.76	118	48	0.94	88	195	0.27
Undiff.	313	219	0.77	67	49	0.81	110	48	0.87	48	26	1.11
Catch Str.	65	44	0.80	48	35	0.81	125	66	0.72	81	36	1.35
Marigot	17	12	0.76	3	3	0.59	56	24	0.89	38	16	1.43
Drain Str.	235	125	1.01	69	43	0.95	72	27	1.02	29	17	1.02
Ridges	67	41	0.88	26	20	0.77	147	65	0.86	141	49	1.73
Cliffs	221	107	1.11	113	73	0.92	225	75	1.14	122	51	1.43
Dry S. Wat.	54	16	1.82	38	12	1.88	23	10	0.87	36	10	2.16
Ravine	40	12	1.79	41	16	1.51	39	11	1.35	52	10	3.12
Sleep Site	81	15	2.90	57	14	2.41	95	10	3.61	71	13	3.27

KEY: f = Observed frequency with which troop was seen to enter quadrats of given topography
= Number of quadrats of given topography in seasonal home range
sr = Selection Ratio. Calculated from
(f/sum of f's) / (#/sum of #'s)

The mean proportion of the ground in any quadrat in dense shadow at noon was 20.0±15.9% (min 1.7%, max 70.2%) in the wet season, but only 9.3±9.9% (min 1.4%, max 53.9%) in the dry season.

In the wet season, Anecdote's troop entered quadrats more frequently the more shade they contained (p < 0.01), and in the dry season the frequency with which both troops entered quadrats was correlated with the amount of shade in the quadrat (p < 0.0001 in both cases, accounting for 20% of the variance in the frequency with which Fable's troop entered quadrats). For Fable's troop, shade had no apparent effect on the speed of movement across quadrats, while Anecdote's troop moved slower in both seasons (p < 0.05, with 2% of the variance accounted for in the wet; p < 0.0001, with 11% of the variance accounted for in the dry season).

Both troops tended to enter areas of poor visibility less frequently in the wet season (p < 0.0001 for Fable's troop, p < 0.01 for Anecdote's), but visual density had no apparent effect on speed in that season, contrary to expectation. In the dry season, however, both

troops entered areas more frequently ($p < 0.00001$) (about 13% of the variance in frequency accounted for) and moved through them more slowly ($p < 0.0001$) (about 10% of the variance in speed accounted for) if the visual density was higher.

DISCUSSION

5.7: Home Range Area

The two troops apparently differed greatly in predicted home range area. Anecdote's troop was almost always followed from one of two sleeping sites. Fable's troop was followed from 6 of 8 sites, many of which were only known to be used by that troop late in the study. Thus this troop continually invaded large areas new to the observer, while the other troop with its restricted number of known sleeping sites had less opportunity to "expand" its known home range. The apparent restriction of Anecdote's troop to two or three sleeping sites might have been due to the relative positions of the research station and the home range of the troop. It is possible that the known home range of the troop was only the westernmost limit of its true range, and that it ranged well to the north, south and east of Stella's Waterfall sleeping site.

The value of 18 or 19 sq km for the home range area of Anecdote's troop may well be an underestimate, but most of the home range of Fable's troop during the study year was probably known. The area covered in any single year of the life of a troop is probably smaller than the complete home range of the troop, firstly because it is unlikely that all the less commonly visited parts will be visited in any one year, and secondly the troop may shift its range during its existence.

5.8: Movements of Troops

Baboons at Mt. Assirik tended to travel further each day than did most recorded savanna baboon troops, but not as far as did troops of P. hamadryas. Long day ranges of P. hamadryas are presumably a consequence of unproductive habitat. At Mt. Assirik the long day ranges may have been a response to low productivity in the dry season and large troops in the wet season.

There was a trend for larger troops to travel further than did smaller troops (Fable's wet > Anecdote's wet > Fable's dry > Anecdote's dry) although this trend was not statistically significant. The data allow us to reject the hypothesis that the baboons travelled further in the dry season than they did in the wet. This lack of seasonal difference in day range length is not likely to be a result of small seasonal differences in productivity, as seems to be the case for Symphalangus syndactylus (Chivers et al. 1975) and Cercocebus albigena (Waser 1975), since seasonal differences in productivity at Mt. Assirik were marked. It seems possible that by foraging in smaller troops in the dry season the baboons were able to travel shorter distances than they would have had to had they remained in large wet season troops. The reduced size of the troops may have been compensating for the reduced productivity in the dry season.

The larger of the two troops moved slightly faster in the wet season than it did in the dry season. If the speed of movement was related linearly to the size of the troop, then interpolating between a dry season troop of about 90 members (Chapter 3) with a median speed of about 0.65 kph, and a troop of about 250 members and a median speed of about 0.80 kph (Fable's wet season troop), to a troop of about 135 members (Anecdote's wet season troop), we find that it should have a median speed of about 0.69 kph. This figure is close to the observed speed of 0.67 kph, and suggests that seasonal difference in the median speed of movement of the troops at Mt. Assirik may have been related to seasonal differences in troop sizes.

When the baboons had left the sleeping trees they often sat near the riverine gallery forest, sometimes in Combretum scrub on laterite. The median time of "entry" into these habitats therefore tended to be earlier

than those for any other habitat . The baboons tended to enter dry forest or open woods before 10:00 while the median time at which scrub and scrub-grassland were entered was after 10:00, and grass on laterite after noon. This suggests that the baboons were entering productive habitats (Chapter 8) earlier than less productive ones. The location and distribution of the various habitats relative to the sleeping sites was bound to influence the time at which the various habitats were entered, but it is not clear how this effect could be analysed. The baboons at Mt. Assirik moved fastest in the early and late parts of the day, and tended to be stationary, often feeding, in the middle of the day, earlier than the hottest time of day, which generally occurred at about 16:00hrs.

This pattern of speed with time of day suggests that the baboons might have been moving rapidly at the beginning of the day in order to find food and start feeding. Having satisfied their initial hunger they slowed down, and began to feed in a more leisurely way. Similarly, when returning to the sleeping sites they may have started back from good feeding sites rather late in the day, and crossed the intervening areas rapidly.

Most baboon troops, including the ones reported in this thesis, probably do not alter their day range lengths as daily maximum temperature changes. In some cases, for example at Ruaha, baboons travelled further each day in the hot dry season than they did in the cooler wet season (Lee pers comm), an effect, presumably, of seasonal differences in productivity rather than temperature. The data from Stoltz and Saayman (1970), which is by far the best-documented correlation between day range length and temperature, in fact show no relationship between day range length and temperature when each troop is taken separately (their Figure 4, page 112). It is only when data from both troops are pooled that a relationship emerges, although the relationship may be spurious, since the troop that tended to travel furthest (a mean of 10.5 against 6.4km) also tended to be watched on cooler days (means of 28.0°C and 29.9°C respectively). This difference (1.9°C) is 9.5% of the range of temperatures over which the data were collected, and is enough to account for the observed correlation.

The observation that day range length could be predicted with some precision from any time after 12:00, together with the fact that maximum temperatures were not reached until about 15:00 or 16:00 (Chapter 2) was consistent with the observation that daily maximum temperature was not a good predictor of day range length.

While successive day ranges varied greatly, the difference between the maximum temperatures of successive days, especially in the dry season, tended to be about one degree. To a human this difference was undetectable. Temperature, humidity and vapour pressure deficit failed to predict the speed of movement of the troops at Mt. Assirik, and there is little reason to suppose that any other climatic variable, such as sunshine (Chivers et al. 1975), radiant heat load (Russell and Harrop 1976) or the Temperature-Humidity Index (Gates 1972) might help account for changes in speeds of movement. If there was any relationship between climate and speed of movement it was apparently masked by the responses of the troops to the habitat and geography of the area through which they were moving.

The distribution of permanent water (Hamilton et al. 1976, Stoltz and Saayman 1970) or rainfall pools (Altmann and Altmann 1970, Sigg and Stolba in press) may be extremely important for baboons. At Mt. Assirik the effects on ranging of the location of dry season water and of sleeping sites were likely to be confounded, since they were normally found close together. I have not analysed here the effect of water, although there is some suggestion (Chapter 6) that the presence of superficial water may have influenced the ranging patterns of the baboons.

5.9: Habitat Variables

The speed with which the baboons moved through a quadrat was correlated with the proportion of any given habitat present in that quadrat, and may have been influenced in part by the number of food species to be found in that habitat (Chapter 8) and in part by the areas which the baboons used for social behaviour (Chapter 9). In particular, the presence of riverine gallery forest strongly influenced the speed with which the troops moved. In the wet season the baboons engaged in long

periods of social behaviour in and near to the riverine gallery forest before setting off on the day's ranging (Chapter 4). In the dry season they seldom showed these extended bouts of social behaviour, but returned to riverine gallery forest for water during the day on most days. The ravines were several degrees cooler than the surrounding woodland, and the troops often spent an hour or more sitting in the shade and grooming or playing.

The ravines containing riverine gallery forest ran through laterite plateaux. In the morning when the baboons left the trees and moved out of the gallery forest to socialise they were immediately in "grass on laterite plateau" habitat. The vegetation, elsewhere often wet from the night's rain, was here thin or absent, and the baboons could dry off and socialise within a few metres of the safety of the riverine gallery forest. This behaviour presumably accounted for the effect which grass on laterite plateau had on the speed of movement of the troops in the wet season.

Few food species grew in scrub and scrub grassland (Chapter 8), and the baboons moved rapidly through them. Open woodland, on the other hand, provided many food species, and Fable's troop moved more slowly through a quadrat the more open woodland it contained, but only in the dry season. I speculate that in the wet season the troop found enough food in other habitats for open woodland to become relatively less attractive than it was in the dry season. In the wet season dry forest provided much of the troop's food (Chapter 8), especially bamboo shoots. In the dry season, however, dry forest was somewhat less productive.

Baboons at Mt. Assirik probably altered their speeds in different habitats far more sensitively than this analysis has shown. The small variance accounted for by habitat suggests that there were other factors which influenced the speed of movement of the troops, the most important of which was probably the local concentration of food within the habitat.

The frequency with which the baboons entered quadrats depended on the proportion of the habitat types found in the quadrats. Forest and riverine gallery forest seemed to be attractive to them, the first possibly because of the quantity of food to be found there (Chapter 8) and

the second as a source of water and sleeping trees.

As predicted, shade apparently played an important part in deciding how frequently a quadrat was entered in the dry season, while in the wet season Fable's troop apparently ranged without regard to shade. These results suggest that the baboons may have responded to higher temperatures by seeking out the cooler areas. However, Fable's troop failed to adjust its speed with respect to shade, while Anecdote's troop was apparently sensitive to shade in both seasons. The reasons for this difference between troops is not clear.

While shade had rather equivocal effects on the frequency with which baboons entered quadrats in the wet season, the correlation between frequency of entry and visual density was strongly negative. This tends to support the hypothesis that the baboons avoided areas of poor visibility, and may lend support to the arguments given in Chapter 3 on predation and troop size. In the dry season, as predicted in the introduction, the baboons apparently preferentially entered areas of higher visual density. It was rare to see a troop far from trees in the dry season, and they seldom crossed a plateau after the grass had been burnt off. They also tended to move more slowly in areas where the visual density was higher, which may indicate that these areas were likely to be more productive than were areas of very good visibility.

Ranging patterns were strongly influenced by the distance to the nearest sleeping site. The probability of finding the baboons at any given distance from a sleeping site decreased linearly with distance. Similarly, the probability that they would enter a given quadrat decreased with the inverse square of their distance from the nearest sleeping site. This finding is apparently in direct contrast to that of Sigg and Stolba (in press) who showed that P. hamadryas did not exploit their environment in this way. However, the baboons they studied slept on cliffs one or more kilometres from the nearest waterholes, so that the baboons spent more time in quadrats the further they were from the sleeping cliffs. Further understanding of the manner in which baboons exploit the sort of environment found at Mt. Assirik, with sleeping sites and water normally together, may therefore benefit from research on refuging animals (eg

Andersson 1978, Bradbury and Vehrencamp 1976b, Covich 1976, Hamilton and Watt 1970).

Topographic types which were likely to contain few food items (Chapter 8) were moved through fastest, whereas topographic types which typically occurred in areas which they used for social behaviour were moved through slowest.

On some occasions the troops revisited areas on successive days, sometimes repeatedly for days at a stretch during the fruiting of a particular species. Some quadrats lay on well-defined routes, like those described for P. hamadryas by Sigg and Stolba (in press), and might be travelled through several times a week. Other quadrats were visited only once in the study. In general, however, it seemed that the troops tended to exploit the area systematically. Since the troops frequently (but not always) returned to the sleeping site that they had left that morning (Chapter 6), I believe that this systematic coverage of their home ranges was related to foraging, and was not, as suggested by Freeland (1976) a device to avoid reinfection with the pathogens of the troop.

CHAPTER 6: Sleeping Sites and Water

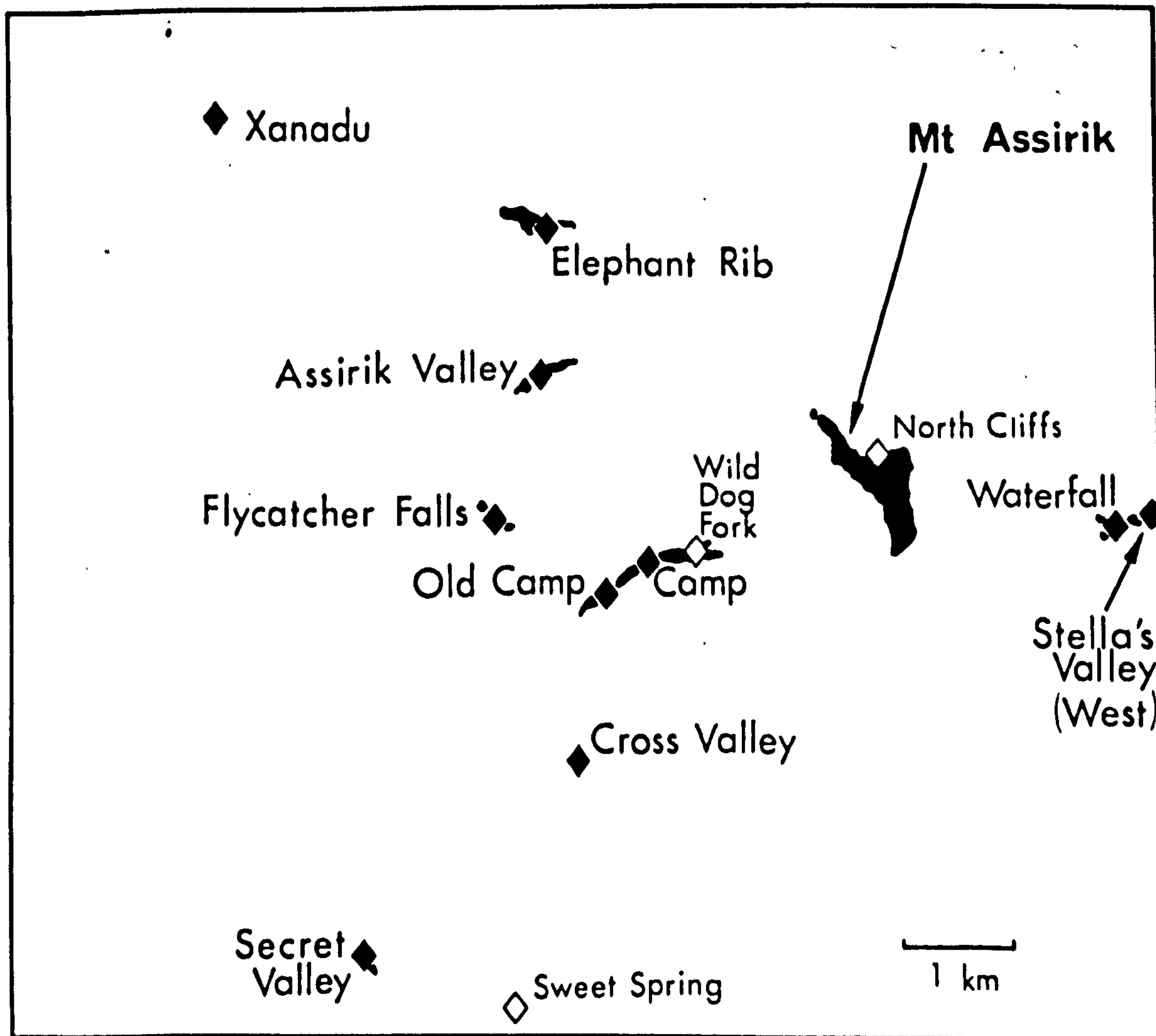
6.1: Sleeping Sites: Introduction

The presence or absence of sleeping sites may determine whether or not baboons are present in an area (Washburn and DeVore 1961). Rasmussen (1979) believes that the relative quality of the home ranges of neighbouring troops may be largely determined by the number of sleeping sites in their home ranges. Baboon troops normally use one to about ten or twelve (Rasmussen 1979) traditional sleeping sites (eg Bert et al. 1967b) even when many apparently suitable sites are available to them (Ransom 1971). In this they differ from Mandrillus sphinx (Jouventin 1975) and some of the macaques (eg Macaca sylvanus, Deag and Crook 1971). The greatest number of known sleeping sites used by a single baboon troop is 15 (Altmann and Altmann 1970). The number of sites used by a troop is probably a function of their availability. Müller (1980) found that troops sleeping upstream of a waterfall had one site each, while those sleeping in the gorge downstream had several. Of the sites that are used, some are usually preferred over others (Altmann and Altmann 1970, DeVore and Hall 1965), and in sleeping groves, some trees are preferred so that more than 70% of baboon nights may be accounted for by fewer than 20% of sleeping trees (Lumsden 1951). Although P. cynocephalus has only been reported to sleep in trees and P. hamadryas and T. gelada only on cliffs, the other three species of baboons are known to sleep in trees in some sites and on cliffs in others (P. anubis, Rowell 1964, Harding 1976; P. ursinus, Stoltz and Keith 1973; P. papio, Bert et al. 1967a, Emory pers comm).

Some primates may respond to the threat of predation by sleeping in small dispersed groups (eg Galago senegalensis, Bearder and Doyle 1974, Hylobates concolor, Chivers 1972, Erythrocebus patas, Hall 1965a, Hall et al. 1965), while baboons apparently rely on numbers, with groups often sharing sleeping sites with other groups (Bert et al. 1967b, Dunbar and Nathan 1972, Kummer 1968a, Kummer and Kurt 1963). The baboons in each group tend to sleep in subgroups within a single grove or on a single cliff face (Dunbar and Nathan 1972, Kummer 1968a, Kummer and Kurt 1963,

Map 6.1:

SLEEPING SITES IN VICINITY OF Mt ASSIRIK '77-'78



Key: ◆ Use common (but possibly seasonal)
◇ Use rare or unconfirmed

Muller 1980), thus giving some further protection from predation. They apparently sleep in the safest places available to them (DeVore and Hall 1965), either high in the highest trees (Bert et al. 1967b, Nagel 1973) or on sheer cliff faces (Kummer 1968a) even when trees are available (Booth 1956a, 1956b, Hamilton et al. 1976, Nagel 1973). No quantified data are available on what criteria baboons might use to choose one possible roost over another.

Baboons rarely move after dark. One such move occurred after a troop was displaced from a sleeping site by another troop (Saayman 1971c). A journey of 11 km from an occupied site to a second site has been observed in the closing hours of daylight (Kummer 1968a) and baboons have been seen to chase wild dogs from a sleeping grove at nightfall (Lee pers comm). One troop of baboons habitually left sleeping cliffs 50 minutes before sunrise (Davidge 1977). Baboons may therefore differ from troops of Macaca mulatta, which may move several hundred metres at night (Vessey 1973).

The location of sleeping sites has a major influence on the ranging of baboons (Chapter 5). For example, day range may differ depending on whether a troop returns to the site that it left that morning or moves to a new site (Hall 1962a).

6.2: Sleeping Sites: Results

The baboons at Mt. Assirik slept in trees, not on cliffs, although there were many cliffs in the field area. These cliffs may not have been suitable for sleeping sites, being made of laterite and having few ledges.

The trees they chose to sleep in normally grew in ravines and were in most cases close to permanent water (median distance 5m, range 0-35m). One troop used at least 8 well-separated sites (median distance between closest neighbouring sites 1.4 km) (Map 6.1) some of which contained several sleeping groves, separated by several hundred metres. The other troop had at least 6 in its home range, five of which were common to the first troop. One of these sites was only used once to my knowledge. This "site" was a single Ceiba pentandra growing below the cliffs with which the summit of Mt. Assirik was ringed, about 2 km from the nearest major

site. Its use as a sleeping site by about 10 baboons in the wet season suggests that there may have been other little-used sites which may have been of great importance to the baboons at Mt. Assirik, and of whose existence I am not aware. Of 52 trees censused in four sleeping sites (21, 14, 10 and 7 trees respectively), 44 were Ceiba pentandra. The remaining 7 trees came from three species (Cola cordifolia, Afzelia africana, and Erythrophloeum suaveolens).

In a survey of the trees growing in the ravines, the SAPP team collected data showing that 21 species of tree (excluding vines) reached 15m or taller, but only Ceiba pentandra, Khaya senegalensis, Cola cordifolia, Erythrophloeum suaveolens and two unknown species reached 25 m or taller. The median height of the trees slept in by the baboons was over 25m, principally because the baboons chose Ceiba pentandra preferentially over the other species in which they slept (Fisher exact, one-tailed, $p = 0.003$)(Table 6.1).

Table 6.1:

Dimensions (metres) of Trees used as Dormitories by Baboons

Species	n	S	Height of Tree		Height of first Branch		Diameter at 1m		Distance to Water		Distance to nearest Dormitory	
			Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
<u>Ceiba pentandra</u>	44	8	27.0±6.7		16.1±5.7		1.7±0.9		7.6±7.9		10.8±9.4	
<u>Cola cordifolia</u>	3	2	16.7±2.9		8.0±0.0		0.7±0.3		3.3±1.5		7.7±2.5	
<u>Erythrophloeum suaveolens</u>	4	5	20.5±8.4		4.6±3.9		0.9±0.4		3.5±1.3		9.8±4.5	
<u>Afzelia africana</u>	1	2	25.0	-	6.0	-	0.5	-	1.5	-	10.0	-

KEY: n = number found to be used as dormitories
s = number found in line transects of riverine gallery forest

Access routes into the sleeping trees were variable, with Ceiba pentandra having only one representative into which the baboons apparently climbed up the trunk of the tree itself (Table 6.2)

Table 6.2:

Access Routes into Sleeping Trees

Species	Number	Access Route other tree(s)	vines	self
<u>Ceiba</u> <u>pentandra</u>	63	54	8	1
<u>Cola</u> <u>cordifolia</u>	3	0	1	2
<u>Erythrophloeum</u> <u>suaveolens</u>	4	0	1	3
<u>Afzelia</u> <u>africana</u>	2	1	0	1

Fable's troop returned to the site that it left the previous morning on 4 of the full day ranges, while on 19 it moved to a different site ($\chi^2 = 9.75$; $df = 1$; $p < 0.005$). Anecdote's troop, however, was equally likely to return (12) as to move to a different site (14).

The troops were never known to move away from a site at night, but there was commonly much activity, with silent periods interspersed with bursts of loud vocalisations, including wahoos, roargrunts, weaning screams and geks (Ransom 1971), and with some squabbling, urination and defaecation. Copulation was observed during moonlit nights and copulation grunts were heard on other nights. Outbursts of calling were sometimes apparently spontaneous, but were readily triggered by the observer, by leopard calls, or by the sound of distant baboons. Occasionally vocalisations would accompany the wind preceding a storm. Silent periods seemed to be more frequent and of longer duration on dark nights and after midnight and before first light.

6.3: Sleeping Sites: Discussion

Ceiba pentandra is a buttressed tree with thorns covering its otherwise smooth bark. Its branches grow out nearly horizontally, often within only 5 m of the top of a 25 m tall tree. These trees were probably ideal protection for the baboons and it is hardly surprising that they were the trees that were most frequently used or that they were singled out by the baboons as sleeping trees. The upper surfaces of the branches of a dormitory C. pentandra were worn smooth, so that it was easy to distinguish between a traditional dormitory tree and one that was rarely or never used. Baboons moving through a tree or along a branch that was rarely used picked their way gingerly along the branches as they moved to or from their roosts, giving mute evidence of the usefulness of the thorns as a defence against predation.

6.4: Water: Introduction

The presence or absence of water, as much as the presence or absence of food or sleeping sites, limits the distribution of baboons (Hamilton et al. 1976, Nagel 1973, Washburn and DeVore 1961). Thus water is of major importance in the ecology of baboons, influencing both ranging (Altmann and Altmann 1970, Hamilton et al. 1976, Kummer 1968a, Sigg and Stolba in press, Stolba 1979) and social behaviour (Hamilton et al. 1976; Hall 1963b). Baboons are obligate drinkers (Hall 1966). The longest interval that any troop has been known to stay away from water is 5 days (Hamilton et al. 1976). When water is freely available, baboons, like Macaca mulatta (Lindburg 1971), probably drink every day, or, occasionally, every other day (Altmann and Altmann 1970 p140; Nagel 1973, Stoltz and Saayman 1970 p116). Most baboon populations that have been studied obtain their water in the dry season from rivers (Aldrich-Blake et al. 1971, Collins in prep, Lee pers comm, Nagel 1973, Stoltz and Keith 1973) or waterholes (Altmann and Altmann 1970, Hall 1966, Kummer 1968a, Stolba 1979, Washburn and DeVore 1961), though three populations are known to drink from fresh-water lakes (Hall 1963a, Hamilton et al. 1976, Ransom 1971). Some populations make use of water provided artificially for livestock (Harding 1976, Stoltz and Saayman

1970). At some sites, water stress may be severe in some months of the year (eg Hamilton et al. 1976 Kuiseb), while at others there is no season in which water shortage becomes critical (eg Hamilton et al. 1976 Okavango). When surface water is unavailable or foul, baboons may dig holes in the sand of riverbeds to obtain clear water (Crook and Aldrich-Blake 1968 p 214, Kummer 1968a p164), or enlarge and maintain similar holes made by other animals (Hamilton et al. 1976, Lee pers comm). One troop in the Kuiseb Canyon in the Namib desert has been seen to fight another troop for access to water (Hamilton et al. 1976), and it is likely that low-ranking baboons, like low-ranking Cercopithecus aethiops (Cheney et al. in press, Wrangham 1981), may die during times of water shortage (Hall 1963a).

Baboons apparently rarely travel far from water. Of 161 troops censused by Stoltz and Keith (1973), all but 19 had the estimated centre of their home ranges less than 5 km from a known source of permanent water. None of the 24 troops seen by Boese et al. (1975) were "more than an hour's walk" from water, and baboon damage to Euphorbia candelabrum in the Queen Elizabeth National Park in Uganda was high near water and absent 6km from water (Lock 1972). Artificial water sources provided for cattle have allowed baboons to spread into areas previously unused by them (Harding 1976). Home range size, shape, and usage may therefore depend on the presence or absence of surface water (Altmann and Altmann 1970, Hamilton et al. 1976, Sigg and Stolba in press). Troop size may be influenced by the location of the home range relative to permanent sources of water, with smaller troops (mean size 29) being found further from water than larger ones (mean size 41) ($t = 9.9$; $p < 0.001$) (data from Stoltz and Keith 1973).

The relationship between baboons and water in the GPN de NK is of particular interest, since as few as 57 days receive more than 1mm of rain in a year at a nearby meteorological station (McGrew et al. 1981), and "by the end of the rainy season the park is almost entirely under water, but...at the end of the dry season, it is like semi-desert" (Dupuy and Verschuren 1977). Most of the region around Mt. Assirik, with its greater relief, does not flood, but strong seasonality is still

apparent (Chapter 2).

6.4.1: Sleeping Sites, Home Range, and Water

The presence or absence of water near sleeping sites may be a powerful determinant of home range use. Kummer (1968a) found that two sleeping sites that were used in the dry season, being near to permanent water, were abandoned in the wet season, when surface water was widespread. Stoltz and Saayman (1970, p113) noted that the presence of water influenced the choice of sleeping sites for a troop of P. ursinus, and that this in turn influenced the day ranges of the troop. Unfortunately they give no data in support of this important statement.

6.4.2: Water and Group Cohesion

Baboons at Mt. Assirik live in large troops (Chapter 3) in large home ranges, and and travelled long distances in a day (Chapter 7) in poor visibility (Chapter 2). Furthermore, each troop had access to at least six sleeping sites each of which was separated from the next by more than a thousand metres. All of these features might have tended to cause the troops to fragment, and yet they displayed a remarkable cohesiveness, particularly in the wet season, when the visibility was at its worst.

Bands of P. hamadryas tended to fragment during the morning and coalesce temporarily in the early afternoon, usually near a good waterhole. This rendez-vous is prearranged by the troop with some certainty at the start of the day's ranging (Stolba 1979). A knowledge of the whereabouts of permanent water sources may have been important for the baboons at Mt. Assirik not only for survival, but also, if they were used for rendez-vous, for the dynamics of troop structure.

6.4.3: Parasites and Water

At Mt. Assirik many of the baboons were infested with Schistosoma mansonii (File et al. in prep). Schistosomiasis is transmitted to the intermediate host, any one of 17 species of pulmonate snails belonging to three genera, all of which live in marshy areas in slow-flowing

water, in the urine and faeces of infected animals (Barnes 1968). Infection occurs when contaminated water is drunk.

If, as Altmann and Altmann (1970) suggest, drinking were so strongly adapted to the avoidance of infection by schistosomes that "contact between lips and water" was minimised, baboons would be expected to avoid drinking from sources likely to be contaminated by schistosomes when there were sources available which were less likely to be contaminated.

6.5: Water: Methods

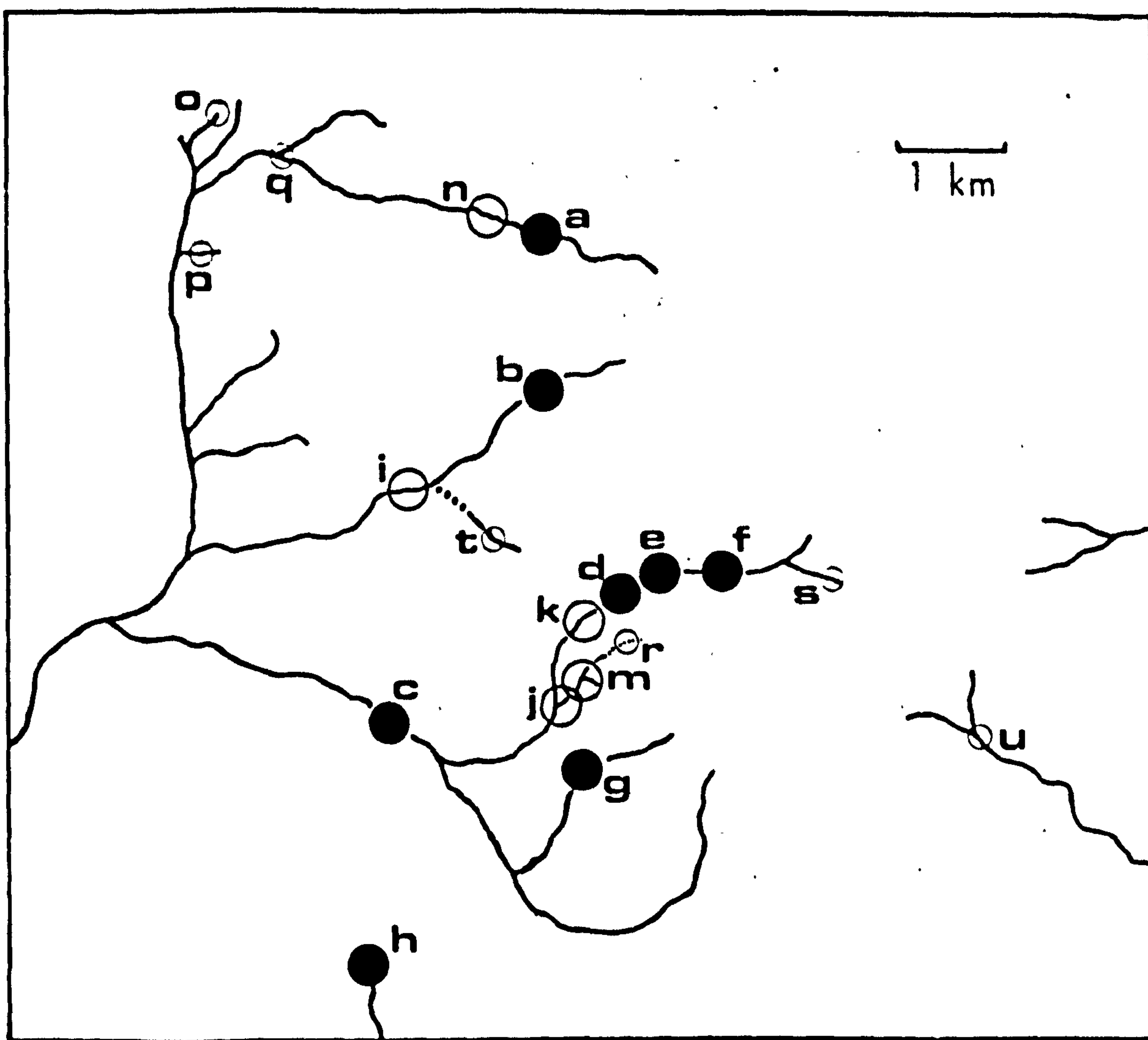
Water sources in the field area were monitored by noting the presence or absence of water, and, if present, whether or not it was flowing. The turbidity, depth, and extent of still water was recorded. Only one water source was monitored systematically (by McGrew, Harrison and myself). The state of other sources was recorded whenever they were seen, which was usually when I was led to them by the baboons. A map was prepared showing major riverbeds and permanent or semi-permanent water sources.

The water surface could not always be seen by the observer, and drinking was inferred by the attitude of the baboon or by the disappearance of the baboon into a depression in the ground in which there was water.

Sources at which baboons drank were defined as having a low risk of infestation by schistosomes if they were located (i) upstream of the first sleeping site on the stream (ii) more than 1km downstream of the last sleeping site or marshy area, whichever was closer, and (iii) in an area unassociated with sleeping sites (eg a rainwater pool on a laterite pan). Sites with a low risk of infestation are referred to as "uncontaminated" sites. Sources were defined as having a high risk of infestation, and referred to as "contaminated", if they were (i) located beneath or downstream of a sleeping site and less than 1km downstream of the last sleeping site or reedbed or (ii) a source unassociated with a sleeping site but surrounded by or draining from a reedbed.

Map 6.2:

Water sources in the field area in the dry seasons of the study.



Key: ● water throughout dry seasons of '76/7, '77/8
 ○ dry before start of rains
 ○ water at start of dry season

- a Elephant Rib
- b Assirik Valley
- c Poacher Bend
- d Lower Middle Lion Valley
- e Upper Middle Lion Valley
- f Head of the Waters
- g Cross Valley
- h Secret Valley
- i Snaking Rock
- j Tributary Fork
- k Sam's Kapok
- m Three Tribs
- n Lower Elephant Rib
- o Xanadu
- p Baboon Spring
- q Fork Falls
- r South Plateau Waterhole
- s Dead Kapok Rapids
- t Flycatcher Falls
- u Whaleback Wallow

6.6: Water: Results

The wet season lasted roughly from May to October. In the middle of the wet season, from about June to September, rain fell several times a week, typically in storms at night in which 50mm or more might fall in half an hour. In this season water was abundant, lying in puddles on the plateaux and running in rivulets to the small streams (Map 6.2), which flowed continuously, sometimes more than a metre deep.

Table 6.3:

Nature and Seasonality of Water Sources

Nature of Source	Season			
	Mid Wet	End Wet	Mid Dry	End Dry
	Aug	Nov	Feb	May
Rain water puddles	+			(+)
Running water on plateaux	+			
Stagnant water on plateaux		+		
Running water in deep ravines	+	+		
Stagnant water in deep ravines			+	+

In the dry season no rain fell, and by February water was restricted to 8 sites in the field area (Map 6.2 and Table 6.4). In March 1977 the only remaining water in the field area lay in stagnant pools at the bottom of sheltered ravines. The pools were all less than 5cm deep, filled with rotting vegetation, and in many cases, contaminated with faeces from the primates, mostly baboons, that slept in the trees overhanging the water.

6.6.1: Sleeping Sites, Home Range, and Water

In all but one known cases (n=239), baboons slept in trees within 35m of a streambed. The presence of water in the stream apparently affected the choice of sleeping site, since one sleeping site (Flycatcher Falls), near a seasonal stream, was rarely occupied unless the streambed contained water (chi squared = 6.46; df = 1; p < 0.02).

Table 6.4:

Number of Observations of Drinking at Various Water Sources

(See Map 1 for Locations)

Name of Source	Season		Visibility	Availability	
	Wet	Dry		Mid Dry	End Dry
Elephant Rib	1	0	Poor	+	+
Assirik Valley	4	5	Excellent	+	+
Poacher Bend	1	0	Good	+	+
Lower Middle Lion Valley	0	1	Poor	+	+
Upper Middle Lion Valley	1	3	Poor	+	+
Head of the Waters	9	7	Good	+	+
Cross Valley	5	9	Excellent	+	+
Secret Valley	0	0	Poor	+	+
Snaking Rock	4	3	Excellent	+	-
Tributary Fork	3	3	Poor	+	-
Sam's Kapok	0	1	Poor	+	-
Three Tribs	2	0	Good	+	-
Lower Elephant Rib	0	0	Excellent	+	-
Xanadu	1	0	Good	?	-
Baboon Spring	0	0	Good	?	-
Fork Falls	0	0	Poor	?	-
South Plateau Waterhole	0	0	Poor	-	-
Dead Kapok Rapids	0	1	Poor	-	-
Flycatcher Falls	0	0	Poor	-	-
Puddles, Rivulets, etc.	9	0	Variable	-	-

Range use may have changed when water was present at another sleeping site (Xanadu, Map 6.2). I was led to this site by the baboons for the first time on 14/7/78, in the middle of the wet season after 12 months of study. The troop subsequently visited this site on several occasions. There was no surface water at this site in the dry season, and there was no trace of its use as a sleeping site on 22/1/78, in the middle of the dry season. The areas in the north-western portion of the baboons' home range were only used when this sleeping site was known to have water.

Baboons were seen to drink on 73 occasions, 40 in the wet season and 33 in the dry. They drank from 14 sources, of which they were seen to drink from 6 only in the wet season and 3 only in the dry.

On 8 out of 12 occasions on which I followed fewer than about 20 baboons to one of the sites used in both seasons, baboons were either

already there or one or more groups of baboons arrived later. In 9 out of these 12 cases, all the baboons present at the site apparently moved off in a cohesive group. In two of the remaining cases the group fragmented into 2 (or possibly more) parts, while in the other case, I lost the baboons in the time taken to climb out of the ravine.

6.1.1: Drinking with Time of Day

Over the whole year, baboons were seen to drink more frequently between 12:00 and 14:00 and between 16:00 and 18:00 than they were between 14:00 and 16:00 (chi squared = 5.55; df = 1; $p < 0.05$ in both cases) (Table 6.5). No other significant differences were noted. The hottest time of day was usually between 14:00 and 16:00, which suggests that baboons at Mt. Assirik did not regulate their drinking with the heat of the day, but drank in the middle and at the end of the day's journey.

Table 6.5:

Frequency with which Baboons were seen to drink at various Times of Day

Time	Season		Year
	Wet	Dry	
06:00-07:59	6	6	12
08:00-09:59	7	2	9
10:00-11:59	3	4	7
12:00-13:59	8	6	14
14:00-15:59	1	3	4
16:00-17:59	10	4	14
18:00-19:59	5	8	13

6.1.2: Parasites and Water

The trees in which the baboons slept grew close to water (median distance 5m, range 0-35m), and their branches overhung the water in about 50-75% of cases. At the only site that was sampled there was a high probability that if the baboons had slept above the stream, faeces would be found in it in the morning. Reedy or marshy areas were

present intermittently along all of the larger streams, and while the invertebrate fauna of these reedbeds was not investigated, they may have formed suitable habitats for the intermediate hosts of Schistosoma mansonii. Conditions were therefore right for the transmission of schistosomes to any baboon drinking downstream of a sleeping site.

Sites which were less likely to be contaminated were also present. For example, Map 6.2 shows a water source named "Head of the Waters". This was a site at which water emerged from some underground source. Upstream of this spring water was not present above the ground for several months of the year. No sleeping sites existed upstream of this site; the nearest one was about 50m downstream. Water was present at this site throughout the dry seasons of 1976-77 and 1977-78.

Baboons were frequently seen to defaecate, often in the vicinity of a water source. They were never observed to defaecate directly into water except from trees. Marks on rocks bordering waterholes gave evidence that urine had on several occasions trickled into water. In general, baboons did not seem deliberately to avoid contaminating the water.

Although baboons apparently avoided drinking contaminated water (chi squared = 12.25; df = 1; p < 0.001) (Table 6.6), the uncontaminated sources were in general easier for the observer to see than were contaminated ones, so that the occasions on which baboons were seen to drink from contaminated sources are significant.

Table 6.6:

Frequency with which Baboons were seen to drink at Sources more or less likely to be Contaminated with Schistosomes

Probability of Contamination	Season		Total	n of major sites
	Wet	Dry		
Low	32*	23	55	7+
High	10	8	18	8

*includes 9 observations of baboons drinking from uncontaminated rainpools and rivulets in the Wet Season

Furthermore, the baboons tended to spend longer drinking from sources

which may have been contaminated than they did at puddles or rivulets (Table 6.7).

Table 6.7:

<u>Duration (sec) for which Baboons Drank from Different Sources</u>	
<u>From Puddle</u>	<u>From Stream</u>
2	12
5	23
6	27
6	27
6	27
8	30
8	31
9	32
10	38
13	
13	38
<hr/>	
Mann-Whitney U Test	
U = 1	
Two-tailed p < .002	
<hr/>	

6.2: Water: Discussion

At Mt. Assirik, the baboons experienced two different water regimes. In the wet season, water was abundant and readily obtained; baboons were seldom more than a few tens of metres from surface water. In the dry season, water became limited in its distribution with about 8 permanent water sources in 100 km² (compared with 14 in 40 km² for P. cynocephalus; Altmann and Altmann 1970, and 13 in 80 km² for P. hamadryas; Stolba 1979), and was everywhere contaminated with decomposing vegetable matter or animal waste. Although neither troop was restricted to as few permanent water sources as were the P. hamadryas groups studied by Kummer (1968a), which had only 2-4 sites, in a dry season more severe than that of 1977-78 several of the water sources which I have described as "permanent" might dry up, with the result that water shortage could become a serious problem for the baboons. Such an arid year may be fairly frequent, given that the

annual rainfall may differ between years by nearly 50% (McGrew et al. 1981).

Reduction in mean troop size in the dry season might allow the baboons to survive on water supplies too meagre to support large troops; replenishment of a pool from subsurface water might well be too slow for all the members of a large troop to satisfy their thirst in a reasonable time. If this were the case, then group size was in part limited by the same circumstances thought to limit group size of Shoshonean Indians in North America (Steward 1955).

6.2.1: Sleeping Sites, Home Range, and Water

There is evidence that sleeping sites were used when water was present nearby and disused when no water was present. Further evidence suggests that the use of a sleeping site permitted the baboons to range into an area which was not entered when the site was disused.

These data suggest that in the dry season, the home ranges of baboons at Mt. Assirik were in part governed by the presence or absence of water near potential sleeping sites.

This explanation was not applicable to an observed 18-fold increase in range size in a troop of P. cynocephalus, from a dry season home range centred on 5 permanent water holes to a wet season home range encompassing or touching on 9 permanent waterholes and 48 "major temporary rainpools" (Altmann and Altmann 1970). Although they postulated that home range was restricted by the availability of water, the "new" sleeping sites were within a few hundred metres of permanent water. It seems likely that the small initial known home range was due to small sample size, since they determined this range on the basis of one month's work. In general, then, the home ranges of baboon troops living in arid areas, and the home ranges of many troops in the dry season may be restricted in their area by the distribution of water. The home ranges of troops in less arid areas may be restricted not by water but by other aspects of their environment. For example, the troops at the Gombe Stream National Park in Tanzania had "unlimited" access to water and their home ranges were probably constrained by the

presence of neighbouring troops (Ransom 1971). It may therefore be difficult to interpret the results of correlations between home range size and any independent variable (eg Clutton-Brock and Harvey 1977, Milton and May 1976, Turner et al. 1970).

6.2.2: Water Sources and Group Cohesion

In the dry season, when visibility was relatively good, and mean foraging group size was smaller, group cohesion may not have been a problem, but in the wet season, baboons at Mt. Assirik may have used permanent water sources as focii for troop cohesion. When the troop was foraging in a given catchment area the separated foraging units reassembled at the associated permanent water source, even when there was surface water in many temporary sources. That these were not members of different troops, drawn together at the water (eg Washburn and DeVore 1961) was suggested by the high probability that on leaving the source, the whole group would move off together.

At Gombe Stream, where visibility was also generally poor, the movements of at least one troop were so regular and predictable that wandering troop members could always find the troop without difficulty (Ransom 1971). In a study of P. hamadryas Kummer (1968a p12) found that the dry season bands came together at midday at water, but did not stay together after they left the water. In the wet season such assembly was not seen. Aldrich-Blake et al. (1971) reported that a troop of P. anubis in an arid region split into parties and became widely scattered while foraging, to reassemble near the sleeping site in the evening. This reassembly at the end of the day's journey does not have the same significance as did that of the mid-journey assembly of the P. hamadryas troops studied by Sigg and Stolba (in press) or that of the baboons at Mt. Assirik.

6.2.3: Parasites and Water

There is clear evidence from Mt. Assirik that baboons drink at sources likely to be contaminated with schistosomes, and, possibly, other parasites. The baboons of Amboseli might have been subject to

different pressures from, and have evolved different strategies for dealing with, waterborne parasites from those experienced by baboons at Mt. Assirik. However, baboons at Mt. Assirik also drank in the cautious manner described by Altmann and Altmann (1970), which makes such an explanation untenable. In any case, when the baboon drinks, the parasite is ingested with the water. The "minimal contact" between lips and water is therefore irrelevant to the avoidance of infection. Humans have probably been exposed to schistosomiasis for as long as have baboons, and yet humans show no unlearned adaptive behaviour towards contaminated water despite high levels of infestation in many parts of the world. Baboons at Mt. Assirik did not seem to avoid defaecating or urinating into water.

The difference in duration of drinking at different sources may reflect the frequent opportunities the baboons had to drink from rivulets and puddles in the rainy season compared to the few they had to drink, from permanent water sources, in the dry. A similar correlation between how thirsty the animals were likely to be and the length of time for which they drank was found by Nagel (1973).

CHAPTER 7: Feeding

INTRODUCTION

7.1: Previous Work

There have been no previous studies published on the feeding ecology of P. papio. Reports on the feeding behaviour of other species of baboons include food lists (Hall 1962a, Harding 1976, Jouventin 1975), studies on selected food items (eg meat; Harding 1973, 1974, 1975, Harding and Strum 1976, Hausfater 1976, Strum 1975, 1976; tamarinds and sedges; Rhine and Westlund 1978; tree exudates; Hausfater and Bearce 1976), and thorough quantitative studies of diet (Iwamoto 1975, Post 1978,).

Such studies show that baboons are omnivorous, eating a wide variety of items, including fruit, seeds, grasses, leaves, roots and storage organs, bark, shoots, flowers, flower and leaf buds, gum twigs, mushrooms, and various classes of animals (eg Dunbar and Dunbar 1974c, Hamilton et al. 1978, Harding 1976, Moreno-Black and Maples 1977, Popp 1978, Post 1978, Strum 1976). Not only do they eat a wide variety of items, but their foods are often gathered from up to about 100 species of plants and animals at any one site (Aldrich-Blake et al. 1971, Altmann and Altmann 1970, Hall 1963a, 1966, Hausfater 1976, Post 1978, Rowell 1966a). The diets of P. hamadryas are not well known, but the available data suggest that P. hamadryas, too, fits into this generalist pattern (Kummer 1968a, Stolba 1979). The feeding ecology of P. papio is therefore of interest for three reasons. Firstly, the feeding behaviour of other baboons of the genus Papio is similar across the genus. Does P. papio belong to this array, or does it resemble other monkeys, for example T. gelada, in greater specialisation on a more restricted diet? Secondly, the baboons of Mt. Assirik live in a habitat different from that of baboons previously studied. These baboons may show adaptations to their environment which sets them apart from other baboons of the genus Papio. Thirdly, social organisation in monkeys is significantly influenced by feeding behaviour (Clutton-Brock 1974a, Hall 1963a, Hamilton et al. 1978, Iwamoto 1978). The differing social organisations of T. gelada, P. hamadryas, and the savanna baboons, P. anubis, P. cynocephalus, and P. ursinus are now well documented,

while that of P. papio is still uncertain (review in chapter 9). A comparison of the feeding ecology of P. papio with those of T. gelada, P. hamadryas, and the savanna baboons will indicate which, if any, of these other species it most resembles, and, by implication, which social organisation it is most likely to have.

7.2: Omnivory and Terrestriality

The proportion of animal matter in the diet of baboons tends to be low, normally accounting for less than 5% (see Hausfater 1976 and Strum 1976 pp 132-137 and 161-163 for reviews). If P. papio behaves similarly to other baboons of the genus Papio, then, we should expect them to be omnivorous, but to eat few animals.

Baboons are well adapted to terrestrial life (Etter 1973, Jolly 1970). T. gelada feeds almost exclusively at ground level (Crook and Aldrich-Blake 1968, Dunbar 1977a, Dunbar and Dunbar 1974c, Iwamoto 1975, Wrangham 1976). M.sphinx, which lives primarily in rainforest, is rarely seen high up in trees and feeds principally on the ground (Jouventin 1975). P. anubis, P. cynocephalus, P. ursinus, and P. hamadryas all feed largely at ground level but also exploit trees (Altmann and Altmann 1970, DeVore and Hall 1965, Hall 1962a, Kummer 1968a, 1968b) and at one site at least "do not seem any less competent as a forest animal than [do] other species" (Rowell 1966a). However, most other baboons whose diet has been studied lived in open country with few or scattered trees, or in areas with few species of trees (eg Hall 1963a, Hamilton et al. 1978 (Kuiseb), Popp 1978, Post 1978). The current literature on baboon diet is therefore biased towards populations of baboons which have a somewhat reduced opportunity to forage from trees. At Mt. Assirik they live in an environment with many species of tree (Baldwin 1979). Data from Senegal may therefore serve to redress this balance and to emphasize the dietary diversity of the genus Papio, since baboons at this site have the opportunity to eat items from many species of trees.

7.2.1: Seasonality of Diet

Since baboons feed on a wide variety of plant items their diet may be expected to change as different plant items become available. At some sites the plants of a given species leaf and fruit asynchronously (Chivers et al. 1975), and primates feeding on such species would not be expected to show seasonal variation in their diet. Most plant foods of chimpanzees (Pan troglodytes) at Mt. Assirik show seasonal cyclicity (Baldwin 1979, Hall in prep) related to rainfall. Chimpanzees (Pan troglodytes) and baboons (P. anubis) at Gombe Stream National Park, Tanzania, ate many of the same species of plants (Ransom 1971, Wrangham 1975). If the baboons at Mt. Assirik are similar to other baboons, and, indeed, to other primates (eg Colobus albigena, Waser 1975; Colobus guereza, Dunbar and Dunbar 1974d; Colobus badius, Struhsaker 1975; Cercopithecus aethiops, Struhsaker 1967b, Lee in prep, Harrison in prep), their diet should show seasonal changes related to rainfall.

7.2.2: Relative Importance of Items in Diet

Primates with varied diets do not eat all items in their diet with equal frequency, but typically depend strongly on a small proportion of the food types available to them. For example, Oates (1978) recorded Colobus guereza feeding on 43 plant species, but 50% of all feeding records concerned a single species, and 35% concerned a single food type from that species. Baboons are regarded as generalists (eg Rowell 1964 , 1966a), but most populations apparently specialise on relatively few of the foods available to them (Popp 1978, Post 1978). If P. papio resembles other baboons, relatively few food items will make up the bulk of their diet at Mt. Assirik.

The predominance of one class of food, such as fruit, in the diet of baboons at other study sites seems to depend partly upon habitat type. In general, the more wooded or forested the site, the more the baboons depend on fruit in their diet (data from Dunbar and Dunbar 1974, Hamilton et al. 1978, Popp 1978, Post 1978, Harding 1976). P. papio, in the well-wooded site at Mt. Assirik, should include the fruits of a large number of species in their diet, as do the chimpanzees there (Baldwin 1979).

7.3: Comparison of "Direct Observation" with "Feeding Remains"

Several studies on primates (eg Jouventin 1975, Baldwin 1979) have relied to a greater or lesser extent on feeding remains, that is, food items found discarded after the study animals had left a feeding site, for information about the diet of a species. Data from Mt. Assirik are used to test the hypothesis that there is no relationship between proportions of food types in the monthly diet estimated by feeding remains and estimated by direct, ad lib., observation. Feeding remains were not used for quantitative analysis except for this comparison.

7.4: Boulder-Rolling

Baboons at several sites have on occasion been seen to turn over stones (Altmann pers comm, Popp pers comm, Strum pers comm), ^{but} there are only three reports of this behaviour in the literature. Bolwig (1959) commented that "among wild baboons [P. ursinus] the turning of stones in search of insects is a common activity", while Hall (1962a) reported that P. ursinus baboons in South-West Africa were seen to roll rocks of up to 47x31x10cm in search of termites and two species of flightless cockroach. Fady (1972) observed that P. papio in the GPN de NK rolled boulders over in the course of their daily foraging.

Two questions arose from watching the baboons foraging under boulders. Firstly, were seasonal changes in the frequency with which the behaviour was seen correlated with the probability of finding any category of object beneath the boulder? This might indicate what it was that the baboons were searching for. Secondly, did they turn over boulders at random or choose boulders of a size most likely to conceal food objects?

7.4.1: Competition and Ecological Impact

The feeding ecology of baboons is of great importance to the management of the Grand Parc National du Niokolo-Koba. Dupuy and Verschuren (1977) suggested that the baboons are undergoing a demographic explosion and causing ecological damage to the park. Baboons are certainly the most numerous primate in the park, and are therefore probably responsible for more damage to trees and bushes than was any

other non-human primate. On the other hand they are almost certainly agents of dispersal for many of the plants whose fruits they eat. This is the first feeding study carried out on these baboons, and provides some evidence for the extent to which baboons influence their environment; specifically, in how far they compete with chimpanzees (Pan troglodytes), one of the rarest primates in the park, and whether or not they are likely to cause the ecological damage referred to by Dupuy and Verschuren (1977).

Chimpanzees (Pan troglodytes) and baboons (P. papio) at Mt. Assirik were both largely frugivorous, and both ate many of the same species of foods (Baldwin 1979, this study). They both ranged widely over the field area, the chimpanzees apparently having a home range which overlapped and encompassed the home ranges of many troops of baboons (Baldwin 1979; this study). Baboons were numerous, and if they competed directly for the same foods as chimpanzees, might have limited the numbers of chimpanzees.

Morse (1974) suggested that where two species whose diets overlap are sympatric, the species which is subordinate at feeding sites should have a broader diet than should the one which is dominant. Chimpanzees and baboons were seen to feed in the same tree on two occasions. On both occasions baboons were seen to move away from a feeding site in the tree when approached by chimpanzees. Chimpanzees seemed to be capable of displacing baboons at Mt. Assirik, and if this is true, may reasonably be considered to be dominant over baboons at Mt. Assirik, as they were at Gombe (Ransom 1971; Collins pers comm). Baboons might therefore be expected to have a broader diet than did chimpanzees.

METHODS

7.5: Collection of Data

Feeding behaviour was recorded by two methods. Firstly, "direct observations" included all sightings of baboons feeding on objects whether or not these objects were identified. Where possible, when a baboon was seen eating I recorded the time, the age and sex of the baboon, the species of plant or animal, and, where relevant, the part of the plant

on which it was feeding, and its behaviour relative to the food. In the attempt to make records of feeding independent of one another, several animals feeding at the same source were regarded as a single observation of feeding on that food although the age and sex of all animals eating that food were recorded. I could not depend on being in sight of baboons at regular intervals. I therefore scored as separate feeding records on the same food any observations of feeding separated by an interval of 1 minute or more during which I had not seen any baboon eating that food. Thus a single baboon, in view for an hour, eating three Adansonia digitata fruit in succession was scored as a single observation. The data consist of 2607 direct observations, of which 2024 concerned identified food items and 583 concerned feeding on objects whose identity was not established.

Direct observations were supplemented by 1015 observations of partially eaten or chewed and discarded plant foods. In the remainder of this chapter "feeding record" refers to the data collected from direct observation of baboons, and except where explicitly stated, neither includes nor refers to data collected from feeding remains. The feeding record is taken to be equivalent to the "apparent diet" of the baboons, although this may not represent the true composition of the diet of the baboons. Foraging effort refers to all observations of baboons eating or actively searching for food. In the latter category is included: rolling over boulders or rotten logs, both of which were regarded as efforts to find animal prey, making sweeping movements through leaf litter with the hands while carefully observing the ground, digging holes, and moving through trees, inspecting, tugging at, or apparently looking for, food.

Boulders were typically found in restricted areas, often but not always on laterite pans. These areas I call "boulder fields".

7.5.2: Analysis of the Data

In the analysis of feeding, the data from two troops (Anecdote's and Fable's) were combined.

The feeding records used in this analysis were collected over the final 12 months of the study.

Both the SAPP transect data and a subjective assessment were used to determine the habitats in which the various food species were most commonly found. This assessment was checked against an independent subjective assessment by Harrison (pers comm).

S. Hall and others recorded the leafing, flowering, and fruiting cycles of 20 species of trees, bushes and vines whose products were known to occur in the diets of the four anthropoidea in the field area. These data give an indication of the availability of the major foods in the area.

7.5.3: Dimensions of Boulders

The dimensions of 72 boulders that had been rolled over by baboons, and the nature of the substratum beneath them were recorded. The dimensions of 131 boulders, chosen at random from boulder fields through which baboons had recently been foraging, were also recorded. Dimensions were recorded by measuring the longest axis, then the longest axis orthogonal to the first, and then the longest axis orthogonal to the first two. The geometric mean of these three dimensions was taken as the geometric mean dimension (GMD) of the boulder.

I turned over 100 boulders in the wet season and 50 in the dry season, whose sizes included the range selected by the baboons. All potential items of food found beneath these boulders were recorded.

7.6: Damage to Plants

Faecal samples showed whether seeds ever survive physically undamaged their passage through the baboon gut. My notes on feeding methods always included any damage done to the plant. I assessed subjectively the importance of the baboons as agents of dispersal of seeds and as destructive agents of the plants.

7.7: Comparison of Diets of Baboons and Chimpanzees

Dietary data for chimpanzees at Mt. Assirik are based upon faecal samples (Baldwin 1979). Each faecal sample normally contained more than one food type, and could therefore be considered to reflect a fractional longitudinal sample of the diet of a single chimpanzee. The proportion of

major food types eaten by chimpanzees in each month could be estimated by considering the total number of samples containing that food type in that month, and the proportion of major classes calculated by summing the number of samples containing that food class. These data were compared month by month (using Kendall's tau) with the data from the same month of direct observation of baboons. No data for the diet of chimpanzees exist for October 1977. The fifteen food items ranking highest in the year's apparent diet of baboons and chimpanzees were compared. The frequency over the year with which foods ranked among the top three items for any month's feeding record for the two species were also compared.

RESULTS

7.8: Omnivory

Baboons at Mt. Assirik were omnivorous, although they were largely dependent on plant material. Of the 2607 direct observations of feeding or foraging, 77% were of baboons eating identifiable parts of plants and 1.2% eating animals (Table 7.1). Of all direct observations of feeding or foraging, 5.4% were of baboons rolling over boulders, apparently searching for invertebrate prey.

Known animal prey included termites, grasshoppers, and other insects, a lizard, and two hares. One other vertebrate, possibly a neonate gazelle (perhaps Tragelaphus scriptus or Cephalophus rufus) was seen to be eaten during the course of the study (McGrew et al. 1980) (Table 7.2).

The number of observations of feeding on animals was higher in the wet season than in the dry season (chi squared = 18.28; df = 1; $p < 0.001$). The proportion of all foraging effort which was apparently directed at discovering animals, together with the proportion of the feeding record concerning animals, was also higher in the wet season than in the dry (chi squared = 74.16; df = 1; $p < 0.001$). In June, 24% of all observations on feeding and foraging concerned baboons apparently searching for animals.

Table 7.1:

<u>Number of Observations in Feeding Record of Various Categories of Food</u>													
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Ident	165	115	205	254	109	159	202	150	168	135	154	124	1940
(%)	66.8	75.2	80.4	81.2	78.4	59.6	67.8	73.2	78.1	80.8	83.2	76.1	74.4
Part kn.	8	8	8	7	3	0	6	3	0	4	3	4	54
sp unk.	3.2	5.2	3.1	2.2	2.2	0.0	2.0	1.5	0.0	2.4	1.6	2.5	2.1
Animals	2	0	0	1	0	4	18	2	2	0	0	1	30
	0.8	0.0	0.0	0.3	0.0	1.5	6.0	1.0	0.9	0.0	0.0	0.6	1.2
Unknown	72	30	42	51	27	104	72	50	45	28	28	34	583
item	29.1	19.6	16.5	16.3	19.4	39.0	24.2	24.4	20.9	16.8	15.1	20.9	22.4
Total	247	153	255	313	139	267	298	205	215	167	185	163	2607
Observations													

Columns show monthly variation in sample size.
Rows show various categories of food which baboons were seen to eat.
Ident = identified food item
Part kn. sp unk. = identified part from unidentified species
Animals = all identified animal food
Unknown item = neither part nor species were identified
In each cell, top figure is sample size, lower figure represents percentage of observations in that month.

Table 7.2:

<u>Animals Known to be Included in Diet of Baboons at Mt. Assirik</u>		
Species	No. of direct Observations	
Termites	19	
Grasshoppers	2	
other INSECTA	6	
<u>Lepus crawshayi</u>	2	
<u>Agama agama</u>	1	
possibly <u>Tragelaphus scriptus</u>	1	
or <u>Cephalophus rufus</u>		

Figure 7.1:
Cumulative number of food items known to be included in the diet of baboons plotted against number of observations of feeding

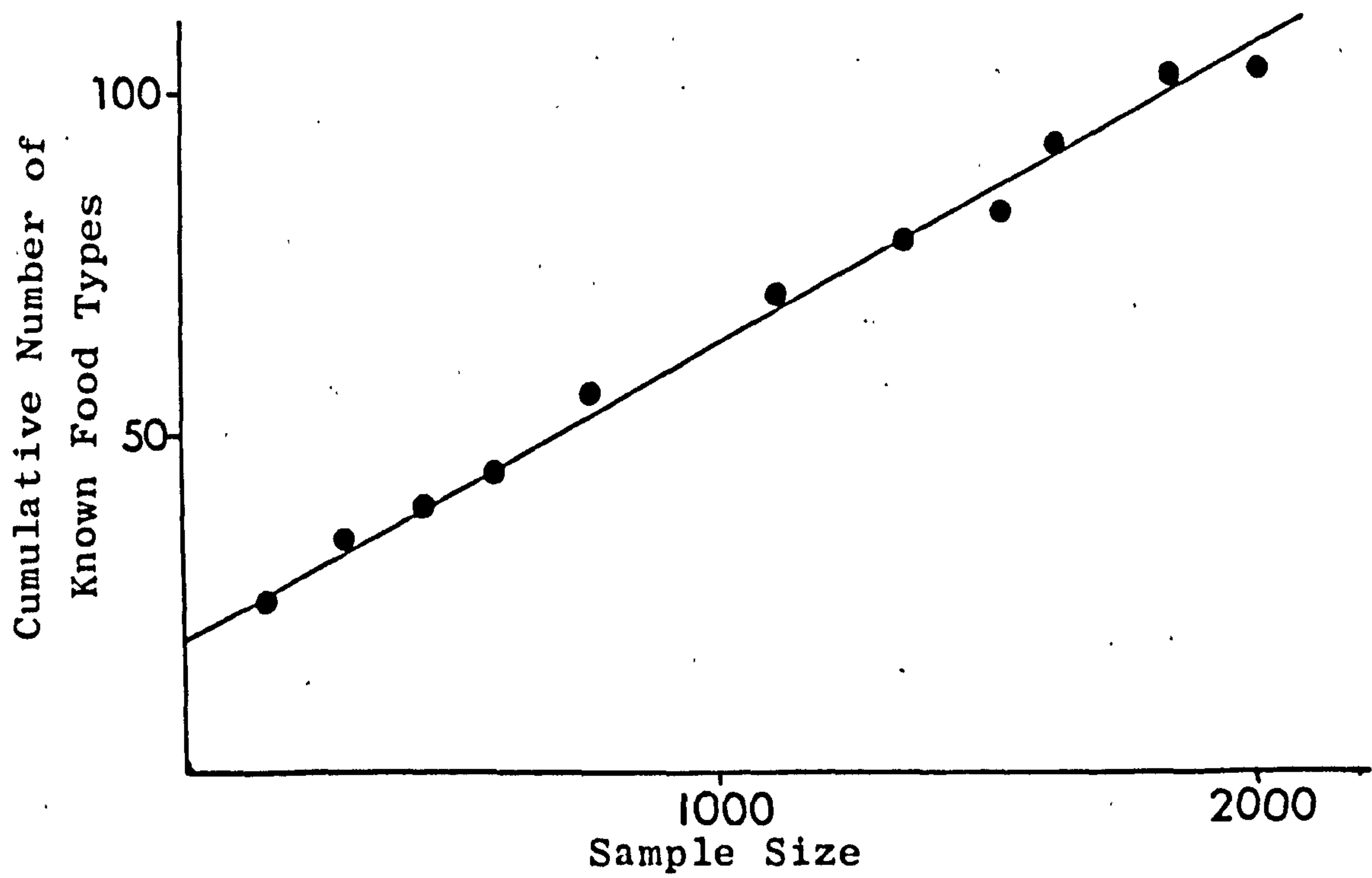


Figure 7.2:
 Percentage of this month's known food items which were also
 known to be eaten in previous month

Per Cent Overlap in Feeding Record

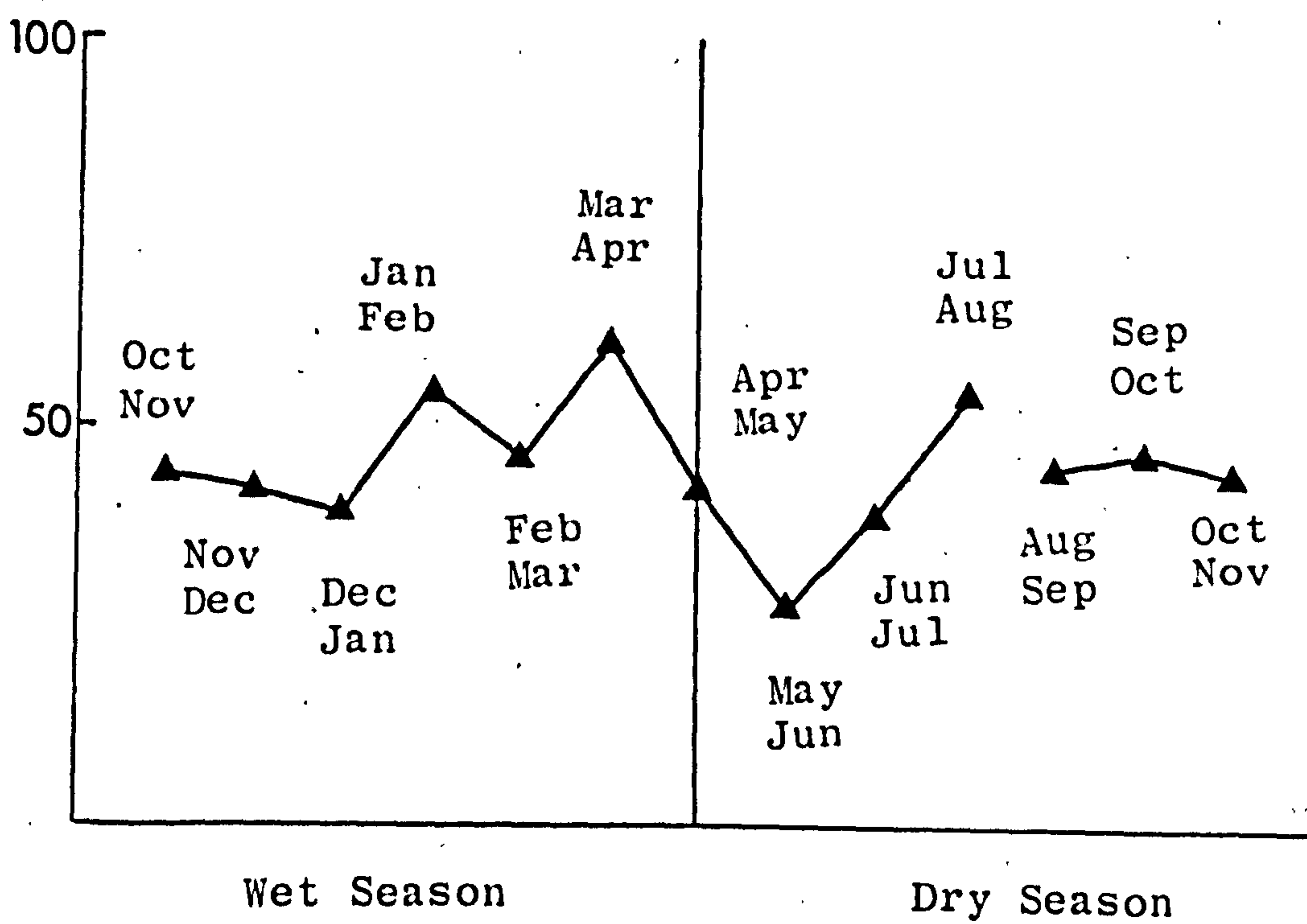
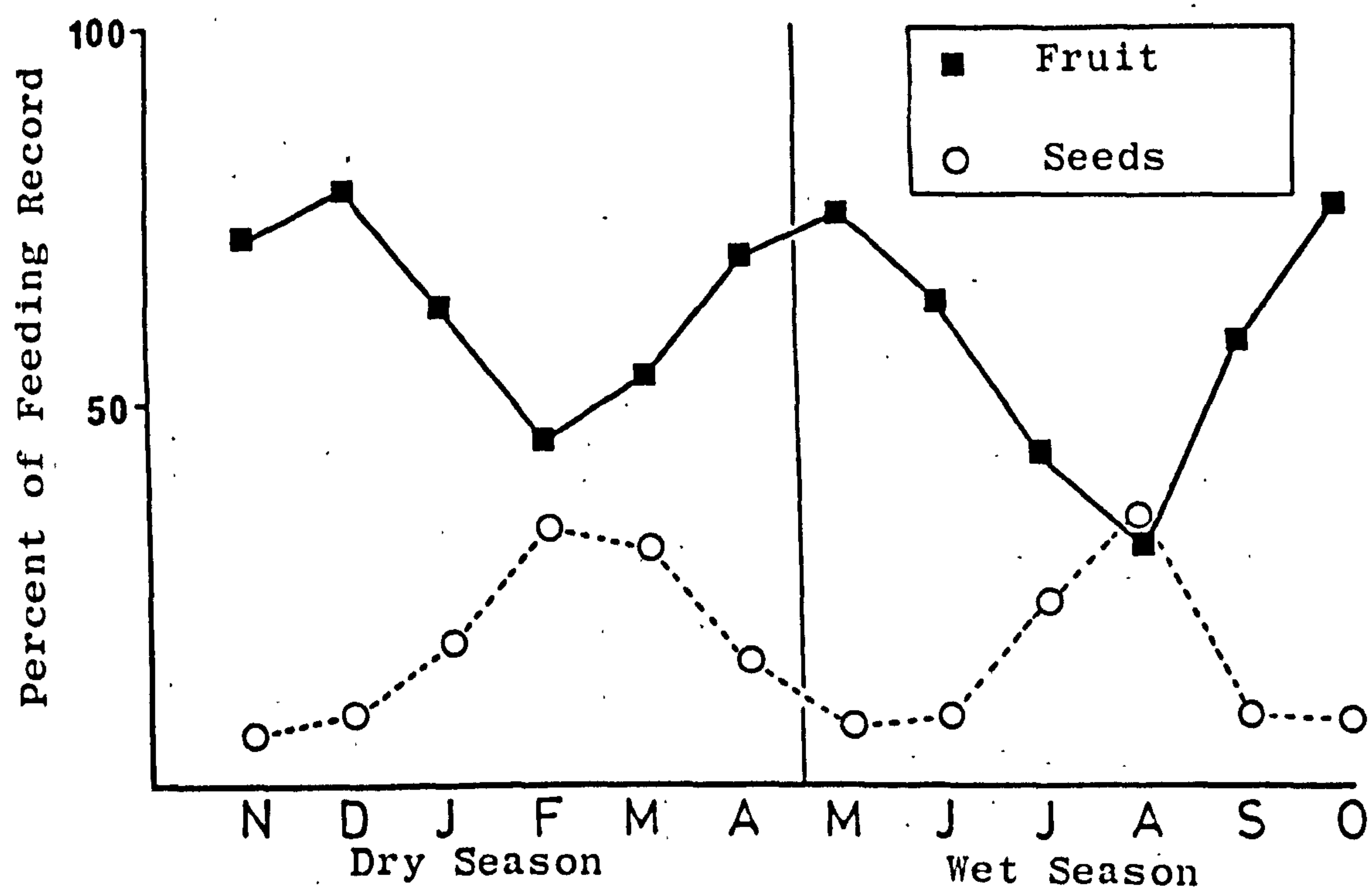


Figure 7.3:
Percent of observations of feeding on fruit and seeds



7.8.2: Breadth of Diet

Baboons ate at least 14 different classes of plant food from more than 58 species of plants (including at least 2, and probably many more, species of grass. In all, 95 different plant food items were recorded (Table 7.9) although most of them contributed little to the feeding record. The number of food items known to be included in the diet increased as sample size increased throughout the study (Fig 7.1). One new item was added to the list of known foods roughly once in every 25 observations.

In every month, baboons ate food types that they had eaten in the previous month, but also included food types that they had not eaten in the previous month. The mean overlap in the feeding record of any two consecutive months was $45\pm 8.8\%$; that is, roughly half of the items known to be eaten in each month belonged to food types that had not been seen to be eaten in the previous month (Fig 7.2).

Fifty per cent of the feeding record was made up by the nine items contributing most to the record (the fruits of Adansonia digitata, Saba senegalensis, and Lannea acida; shoots of Oxytenanthera abyssinica; seeds and fruits of Borassus aethiopum; fruits of Vitex madiensis and Spondias mombin, and seeds of Combretum spp.)

Seven of the nine items most frequently recorded were fruit, and two, seeds. Sixty-six per cent of the food species were exploited for their fruit, while 26% were exploited for their seeds. The emphasis on fruit and seeds was reflected in the feeding record. Baboons eating fruit made up 60% of the total feeding record (57.2% in the wet season, 63.4% in the dry), while 17% of the feeding record was made on baboons eating seeds (15.4% in the wet season, 18.9% in the dry) (Fig 7.3).

7.8.3: Seasonality of Diet

Fruit and seeds contributed almost equally to the feeding record in both wet and dry seasons (chi squared = 3.09; df = 1; ns for fruit; chi squared = 3.43; df = 1; ns for seeds), but the contribution of fruit and seeds together was higher in the dry season than in the wet (chi squared = 5.87; df = 1; $p < 0.02$). A strong seasonal difference, but

in the opposite direction, was also apparent in the degree to which the baboons were seen to eat bamboo and grass shoots and stems (13.2% in wet; 0.4% in dry; chi squared = 126.9; df = 1; p < 0.001).

These seasonal changes came about as a result of a dependence on different classes of foods from month to month. This is summarised in Fig 7.6. The proportions of many of the different food types included in the feeding record were apparently related to the rainfall in that month (Table 7.3).

Table 7.3:

Influence of Rainfall on Diet

Kendall's tau for correlation between
rainfall and proportion of food class in diet

Food Class	Kendall's <u>tau</u>	Direction of correln.	z	Significance
Shoot and Stem	0.96	+	4.3	< 0.001
Flush and Leaves	0.76	+	3.5	< 0.001
Gum	0.44	+	2.0	< 0.05
Bulb	1.10	+	2.2	< 0.001
Buds and Flowers	0.58	-	2.6	< 0.005
Roots	0.82	-	3.7	< 0.001
Other	0.48	-	2.2	< 0.02
Fruit	0.23	none	1.1	0.15
Seeds	0.10	none	0.5	0.33
Bark	0.33	none	1.5	0.07
(Fruit and Seeds	0.67	-	3.0	< 0.002)

The proportion of shoots and stems, flushing leaves, gum, bulbs, and animals was positively correlated with rainfall (Kendall's tau, p always < 0.05), while that of buds and flowers, roots, and fruits and seeds (taken together) was greater when rainfall was lower (Kendall's tau, p always < 0.005) (Table 7.3). While fruit and seeds together contributed a median of 80% to each month's feeding record (range 66% - 86%), the proportion of seeds was not independent of the proportion of fruit in the feeding record (Kendall's tau = -0.78; p < 0.001); the less fruit was eaten, the more seeds were eaten.

Since some fruits were overwhelmingly important in some months (eg Adansonia digitata fruit in December, Table 7.9), some of the variation in proportions of certain classes can be attributed largely to single food items. Thus the peak in seed eating in August was due to the large (10x7x3cm) seeds of Borassus aethiopum, which germinated in this month. The peak in seed eating in February was largely due to the seeds of Afzelia africana. The fruit of Adansonia digitata contributed greatly to the proportion of fruit eaten in the dry season (36.1% of all fruit eaten in the dry season, 1.3% of the wet), and this single species allowed the baboons to maintain their high intake of fruit in the dry season.

7.8.4: Distribution of Foods by Habitat

The plant food species eaten by baboons were not distributed evenly across the field area. Their distribution varied with habitat type (Table 7.4), although any one food species might be found in more than one habitat type, normally with different densities.

Thus Adansonia digitata could be found in both closed and open woodland, but was far more likely to be found in closed than in open woodland (Harrison in prep). Most (61%) of the known food species occurred in more than one habitat, and about 6% were found in 5 or more (Table 7.5). Habitats differed in the number of food species which might be found in them (chi squared = 61.83; df = 1; $p < 0.001$), with 71% of food species occurring in closed woodland and only 2% on grassy plateaux.

Riverine gallery forest and closed and open woodland between them contained 96% of all known plant food species, in contrast to scrub, scrub grassland, combretum and grass on plateaux, which between them contained 19.6%.

Table 7.4:

Proportion of Food Species Growing
in One, Two, or More Habitats

No of Habitats % of Species
in which sp.
was found

1	39.2
2	54.9
3	9.8
4	0
5	3.9
6	2.0

Table 7.5:

Distribution of Plant Food Species

The table shows the habitat in which various food species are most
commonly found Habitat Food Species Dry For

RGF	Woods	Scrub	Bush	Comb	Grass
<u>Acacia dudgeoni</u>				*	*
<u>Acacia sp</u>		*	*		
<u>Adansonia digitata</u>		*	*		
<u>Azelia africana</u>		*			
<u>Alphylus africanus</u>		*	*		
<u>Anona senegalensis</u>			*	*	
<u>Bombax costatum</u>		*			
<u>Borassus aethiopum</u>		*			
<u>Cassia sieberiana</u>			*		
<u>Ceiba pentandra</u>		*	*		
<u>Cissus populnea</u>		*	*	*	
<u>Cola cordifolia</u>		*	*		
<u>Cola sp. unknown</u>			*		
<u>Combretum tomentosum?</u>		*	*	*	*
<u>Cordia myxa</u>			*	*	
<u>Cordyla pinnata</u>		*			
<u>Diospyros mespiliformis</u>		*			
<u>Erythrophloeum suaveolens</u>		*	*		
<u>Ficus leucardi</u>		*			
<u>Ficus umbellata</u>			*		
<u>Gardenia erubescens</u>				*	
<u>Grewia lasiodiscus</u>		*	*		
<u>Hexalobus monopetalus</u>		*	*		
<u>Kaempferia aethiopica</u>			*	*	*
<u>Khaya senegalensis</u>		*			

Table 7.5: Distribution of Plant Food Species (cont)

Food Species	Habitat					
	Dry For	RGF	Woods	Scrub	Bush	Comb Grass
<hr/>						
<u>Landolphia heudelotti</u>	*	*				
<u>Lannea acida</u>	*		*			
<u>Lannea microcarpa</u>			*			*
<u>Malacantha alnifolia</u>	*	*				
<u>Manilkara multinervis</u>		*				
<hr/>						
<u>Nauclea latifolia</u>	*	*				
<u>Oncoba spinosa</u>	*	*				
<u>Oxytenanthera abyssinica</u>	*					
<u>Parkia biglobosa</u>	*		*			
<u>Pericopsis laxifolia</u>	*					
<hr/>						
<u>Piliostigma thoninngii</u>	*		*			
<u>Pseudospondias microcarpa</u>		*				
<u>Pterocarpus erinaceus</u>	*		*	*	*	*
<u>Raphia sudanica</u>		*				
<u>Saba senegalensis</u>	*	*				
<hr/>						
<u>Spondias mombin</u>	*	*				
<u>Sterculia setigera</u>	*					
<u>Strychnos spinosa</u>			*	*		
<u>Tamarindus indica</u>	*					
<u>Treculia africana</u>		*				
<hr/>						
<u>Trichilia prieuriana</u>		*				
<u>Urtica</u> sp. unknown	*					
<u>Vitex madiensis</u>			*			
<u>Zizyphus mucronata?</u>	*	*	*			
sp. of <u>Meliaceae</u> family				*		
<hr/>						
sp. of <u>Sapotaceae</u> family	*	*				
grass species	*		*	*	*	*
sp. unknown (1)			*			
sp. unknown (2)	*					
sp. unknown (3)	*					
<hr/>						
sp. unknown (4)	*		*			

KEY:

Dry For = Dry Forest, may be with bamboo understory

RGF = Riverine Gallery Forest

Woods = Open Woods

Scrub = Scrub

Combr = Combretum Scrub on Plateau

Grass = Grass on Plateau

Figure 7.4:
Monthly variation in percent of observations of feeding in
trees and bushes

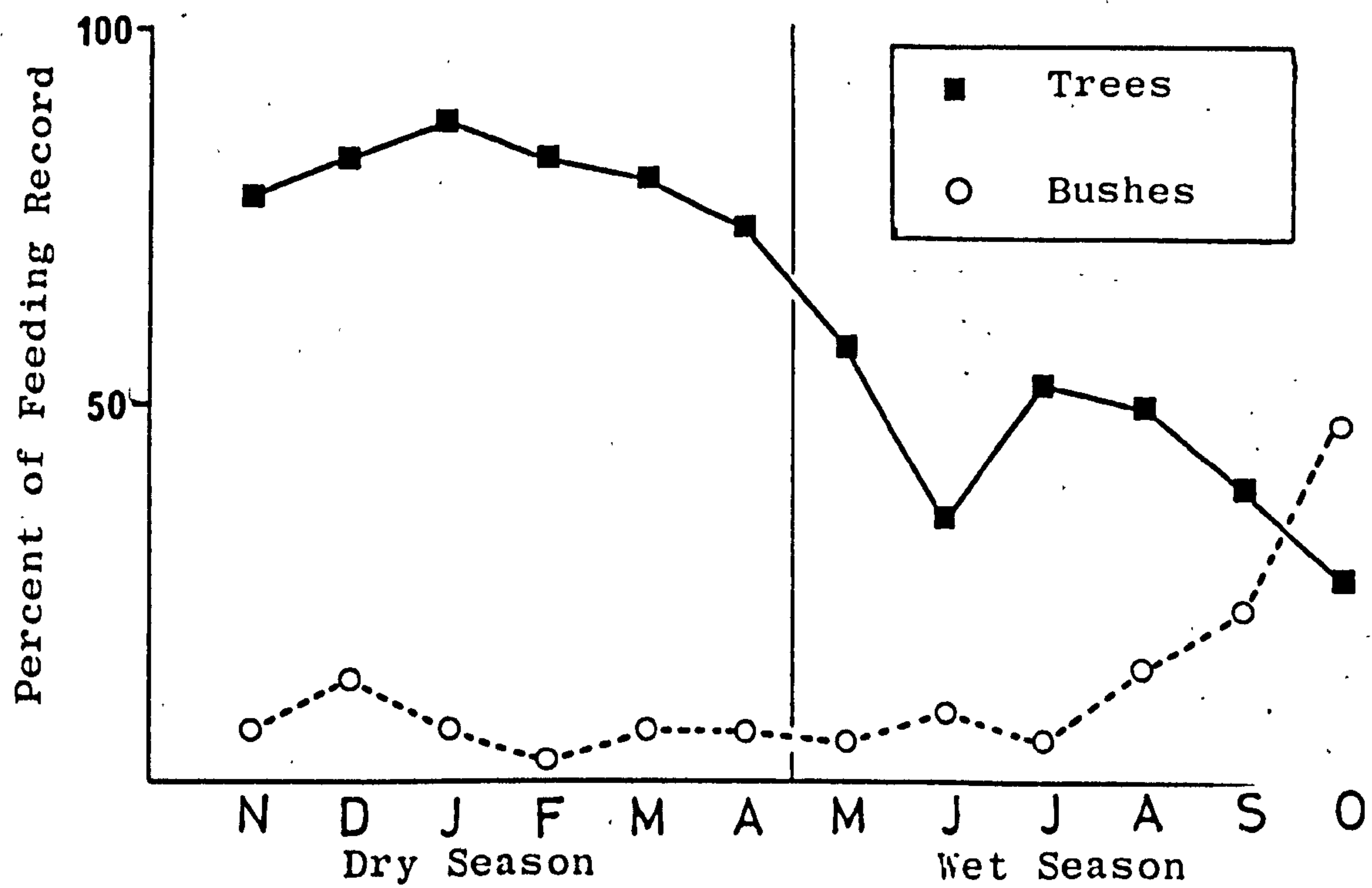
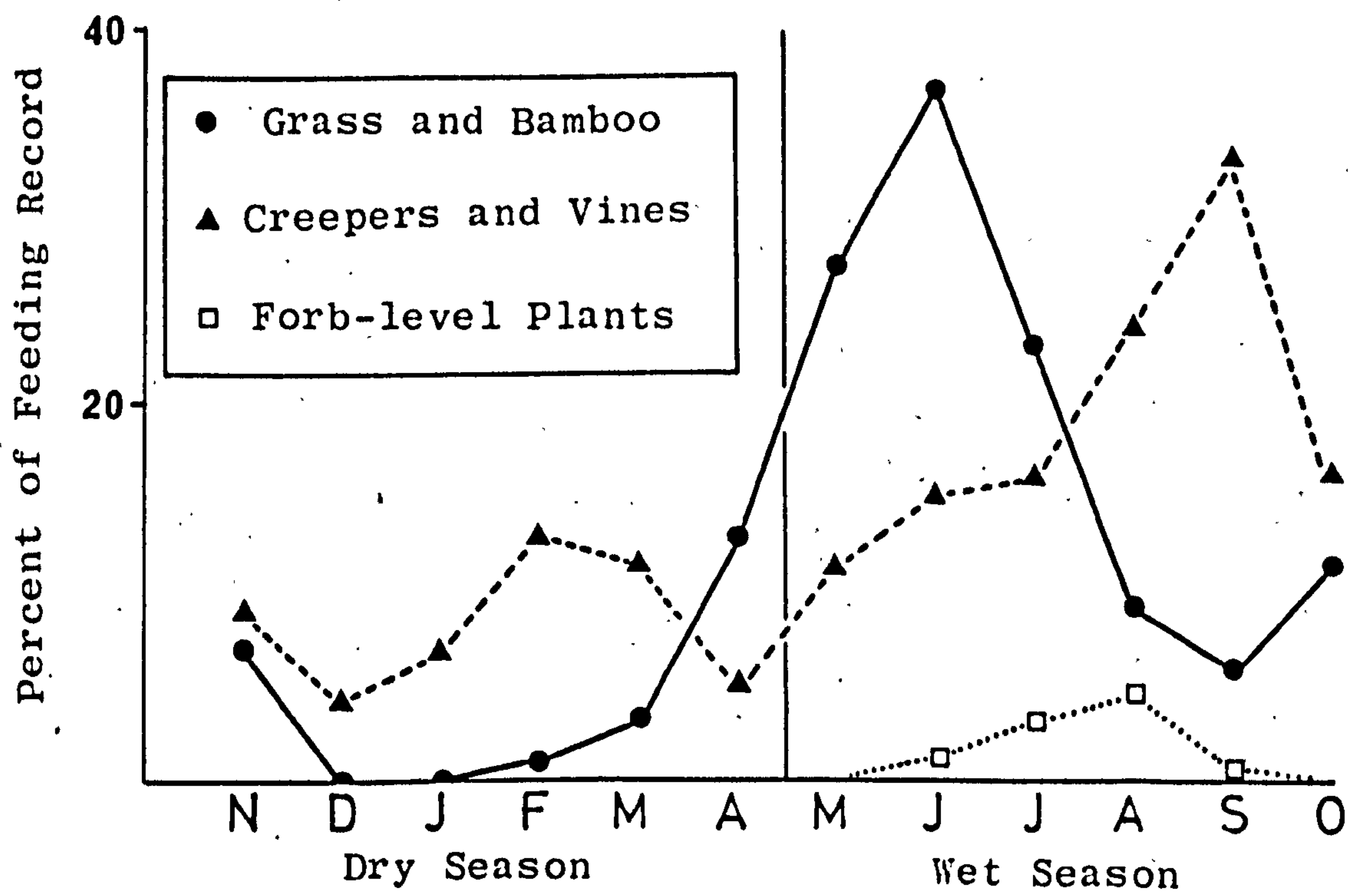


Figure 7.5:
Monthly variation in percent of observations of feeding in various types of plants



7.8.5: Arboreality

Of all known plant food species, 67% grew as trees (Table 7.6). This preponderance of trees was reflected in the feeding record, where 61.6% of all feeding observations were of baboons feeding in trees. Baboons were more likely to be seen feeding in trees in the dry season (80.5%) than in the wet (42.7%) (chi squared = 52.7; df = 1; p < 0.001) (Fig 7.4). The degree to which the baboons were seen to feed in bushes, grass, vines or forbs differed from month to month (Fig 7.4 and 7.5).

Table 7.6:

Growth Forms of Food Species

TREES

Acacia sp
Adansonia digitata
Afzelia africana
Allophylus africanus
Bombax costatum
Borassus aethiopum
Cassia siberiana
Ceiba pentandra
Cola cordifolia
Cola sp.
Cordyla pinnata
Diospyros mespiliformis
Erythrophloeum suaveolens
Ficus leucardii
Ficus umbellata
Khaya senegalensis
Lannea acida
Lannea microcarpa
Malacantha alnifolia
Manilkara multinervis
Oncoba spinosa
Parkia biglobosa
Pericopsis laxifolia
Piliostigma thonningii
Pseudospondias microcarpa
Pterocarpus erinaceous
Raphia sudanica
Spondias mombin
Sterculia setigera
Tamarindus indica
Treculia africana
Zizyphus mucronata?
Zizyphus spina-christi
Sapotaceae sp.

BUSHES

Acacia dudgeoni
Combretum
Cordia myxa
Gardenia erubescens
Grewia lasiodiscus
Hexalobus monopetalus
Meliaceae sp
Sorindeia juglandifolia
Strychnos spinosa
Trichilia prieuriana
Vitex madiensis

FORB LEVEL

Kaempferia aethiopica
Urtica sp.

GRASSES

Oxytenanthera abyssinica

VINES

Landolphia heudelotii
Nauclea latifolia
Saba senegalensis

The proportion of the feeding record in which baboons were using trees declined steadily from early in the dry season until the last month of the wet season. At the same time, the proportion of time spent feeding in bushes rose throughout the wet season and fell sharply with the start of the dry season. The high peak of feeding in bushes reached in October and its subsequent rapid decline in November was almost entirely due to the dependence of the baboons on the fruit of a single species, Vitex madiensis. In October, 34% of the feeding record concerned this food type, while in November, when there were very few ripe Vitex madiensis fruits remaining, the plant contributed only 0.6% to the feeding record.

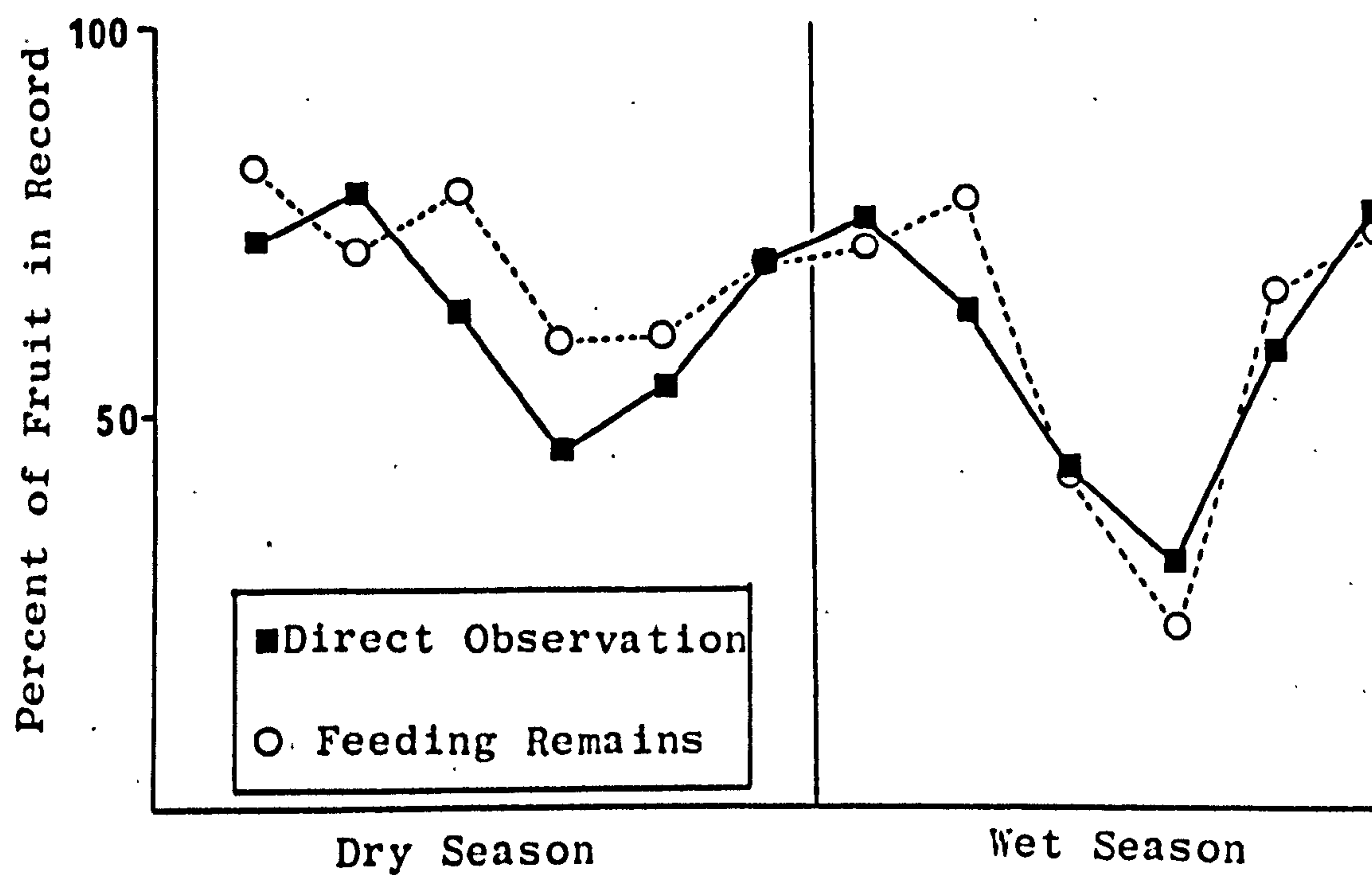
Feeding in vines occupied up to 37% of the feeding record early in the wet season, when Saba senegalensis was in fruit, while feeding in bamboo was most common late in the wet season, when shoots were abundant.

The proportion of the feeding record in which baboons were seen feeding in trees was negatively correlated with that month's rainfall (Kendall's tau = -0.63; $p < 0.01$), while those for bamboo and forbs were positively correlated (Kendall's tau = 0.71; $p < 0.002$ and Kendall's tau = 0.68; $p < 0.002$ respectively). The correlation between rainfall and bamboo is probably strongly influenced by the appearance and growth of bamboo shoots in the wet season, but the correlation with forbs is more obscure. The frequency with which baboons were seen feeding in bushes correlated poorly with rainfall in the same month, but well with the previous month's rain (Kendall's tau = 0.68; $p < 0.002$). On the other hand, the frequency with which they were seen to feed in vines was closely correlated with the next month's rain (Kendall's tau; $p < 0.001$). These results are discussed later.

7.8.6: Direct Observation and Feeding Remains

The rank order of the 20 food types of most frequent occurrence in the direct observation feeding record was not correlated with that for feeding remains. (Kendall's tau = 0.63; $n = 20$; $p = 0.5$). Direct observation and feeding remains do not give similar estimates of the relative importance of specific food items in the diet. However, the two

Figure 7.6:
Comparison of the monthly variation in the percentage of
fruit in the feeding records derived from direct observation
and from feeding remains



measures give similar estimates of the percentage of fruit present in the monthly diet (Kendall's $\tau = 0.62$; $n = 12$; $p < 0.001$) (Fig 7.6).

7.8.7: Comparison with other species

The baboons at Mt. Assirik were seen to eat a similar number of plant species as were baboons elsewhere (Table 7.7). Since Hall's list includes data from populations in South-West Africa and in Cape Province, South Africa, and is not based on the diets of baboons in a single area, it is not strictly comparable with other studies. Furthermore, several of the data in the table are drawn from repeated studies at the same site, and are therefore not independent.

Table 7.7:

Number of Species Known to be Eaten
by Papio, Theropithecus and Mandrillus at various field sites

Baboon species	# of plant spp.	rank	# of anim. spp.	Source of data
<u>P. ursinus</u>	94	1	14+	Hall 1963a
<u>P. anubis</u>	68	2		Popp 1978
<u>P. ursinus</u>	66	3		Hall 1960
<u>P. papio</u>	58	4	6+	This Study
<u>M. sphinx</u>	53	5		Jouventin 1975
<u>P. anubis</u>	42+	6		Dunbar and Dunbar 1974c
<u>P. cynocephalus</u>	25+	7	13+	Post 1978
<u>P. anubis</u>	25+	7		Harding 1976
<u>P. anubis</u>	24+	9		Rowell 1966a
<u>P. anubis</u>	21+	10	3+	Aldrich-Blake <u>et al.</u> 1971
<u>P. cynocephalus</u>	20+	11		Moreno-Black and Maples 1977
<u>P. cynocephalus</u>	17+	12		Altmann and Altmann 1970
<u>T. gelada</u>	15+	13		Dunbar and Dunbar 1974c

The true number of species eaten by baboons in this study site is undoubtedly higher (see Fig 7.1). Few of the species eaten by these baboons are known to be eaten by baboons elsewhere. Exceptions include Adansonia digitata, Annona senegalensis, Diospyros mespiliformis, Ficus umbellata, Lannea acida, Malacantha alnifolia, Nauclea latifolia, and Pseudospondias microcarpa.

P. papio was not greatly different from other baboons of the genus Papio in its heavy dependence on trees (Table 7.8), with two troops of P. ursinus and one of P. hamadryas depending more heavily on trees. This latter troop, as Kummer (1968a) points out, is more arboreal than many savanna baboon troops, despite being "desert" baboons.

Table 7.8:

Dependence of Baboons on Trees for Food

Baboon Species	% of Diet from Trees	Rank	Source of Data
<u>P. ursinus</u>	80.9	1	Hamilton et al. 1976
<u>P. ursinus</u>	76.1	2	Hamilton et al. 1976
<u>P. hamadryas</u>	69.5	3	Kummer 1968a
<u>P. papio</u>	61.6	4	This study
<u>P. anubis</u>	53.6	5	Dunbar and Dunbar 1974c
<u>P. anubis</u>	39.4	6	Popp 1978
<u>P. cynocephalus</u>	32.8	7	Post 1978
<u>P. ursinus</u>	10.0	8	Anderson 1980b
<u>P. anubis</u>	4.7	9	Dunbar and Dunbar 1974c
<u>T. gelada</u>	0.0	10	Dunbar and Dunbar 1975

Where there was a marked seasonal difference in the amount of food taken from trees, as there was at Mt. Assirik, baboons tended to depend more on trees in the dry season than in the wet (Wilcoxon signed-rank matched pairs; $p < 0.05$) (Table 7.8). Two of the troops which depended more on trees than did P. papio were living in arid areas (the Kuiseb Canyon, rainfall 18mm; Awash, estimated rainfall 665mm), and, for eight troops of baboons of the genus Papio for which there is data, the degree to which they depend upon trees in their annual diet is correlated with the length of the dry season (Kendall's tau = 0.62; $n = 8$; $p < 0.05$) (Data from Dunbar and Sharman in prep).

Table 7.9:

Feeding Record of Baboons at Mt. Assirik

Full names of species are given in Table 7.5
 Figures represent per cent of monthly feeding record.

Species	Part	Month											
		Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
<u>Aca dud</u>	Base					1.0	0.8	0.9					
<u>Aca sp</u>	Seed	1.3	0.8	3.6	1.7	1.5	0.4	0.9			1.3	0.6	
<u>Ada dig</u>	Bud								1.3		0.7		
	Flwr									1.5			
	Frt	51.3	57.3	38.8	12.2	2.0	0.4		1.9				3.0
<u>Afz afr</u>	Seed		1.6	6.1	10.4	2.4	1.2						
	Flsh						0.4						
	Bark									1.0			
<u>All afr</u>	Frt											0.6	
<u>Ano sen</u>	Bud								1.3				
	Frt									1.0	8.0	1.2	
<u>Bom cos</u>	Flwr		1.6	1.8									
	Seed			0.6									
<u>Bor aet</u>	Frt	1.3			3.5	3.9	13.9	20.2	5.7	1.0	4.7		
	Seed					1.0	1.6		2.5	16.8	27.3	5.4	2.2
<u>Cas sie</u>	Seed						0.4						
<u>Cei pen</u>	Bud	0.6	0.8										
	Flwr		1.6										
	Flsh				0.9	1.0							
<u>Cis pop</u>	Frt	1.3							2.5	1.0	0.7	3.6	1.5
	Leaf				1.7				1.9	0.5			
<u>Col cor</u>	Frt			0.6	0.9		1.6		4.4	16.3	1.3		
<u>Cola sp</u>	Seed					1.0							
<u>Comb sp</u>	Flwr			2.4			1.2						
	Seed	1.3	2.4	1.2	2.6	3.9	4.3	1.8	5.0			1.2	3.0
<u>Cor myx</u>	Frt		4.0										
<u>Cor pin</u>	Frt					3.4	2.4	2.8	1.3	0.5			
<u>Dio mes</u>	Frt		5.6	8.5	7.0	0.5	0.4						
<u>Ery sua</u>	Seed	3.9	3.2	1.8	0.9	1.0	1.2	0.9	1.3	3.5	3.3	2.4	
<u>Fic lec</u>	Frt		2.4	7.3	7.8	1.0	3.9	2.8		0.5			0.7
<u>Fic umb</u>	Frt			1.8	3.5	1.5	2.8	3.7	1.3	2.5	2.7		1.5

Table 7.9: Feeding Record of Baboons at Mt. Assirik

Species	Part	Month											
		Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
<u>Gar eru</u>	Frt			0.6	0.9						0.7		
<u>Gre las</u>	Frt	2.6	1.6							1.0	0.7	1.2	3.7
<u>Hex mon</u>	Frt										1.3	12.5	3.7
<u>Kae aet</u>	Bulb								1.3	2.0	2.0	1.2	
<u>Kha sen</u>	Flsh						1.2						
	Twig									1.0			
	Gum									1.5	0.7		
	Bark								1.3	3.0	0.7		
<u>Lan heu</u>	Frt								1.3	5.9	0.7		
<u>Lan aci</u>	Frt				6.1	30.7	17.3	13.8	1.3				
<u>Lan mic</u>	Frt					1.5	8.3	0.9	0.6				
<u>Mal aln</u>	Frt						1.2						
<u>Man mul</u>	Frt								1.3				
<u>Nau lat</u>	Frt	5.8									1.3	1.8	8.9
<u>Onc spi</u>	Flwr								1.3				
	Frt	1.9				3.4	5.1	5.5				3.6	3.7
<u>Oxy aby</u>	Flsh							1.8	3.1	1.5	2.7	1.8	
	Stem	1.3								2.0	1.3	1.8	3.7
	Base					1.0	0.4						
	Shoot						0.8	9.2	7.5	8.4	14.7	18.5	5.2
	Root			0.6		1.0	0.4						
	Litt			2.4	8.7	6.8	3.9						
<u>Par big</u>	Flwr					1.5	0.8	0.9					
<u>Par big</u>	Bud							0.9					
	Flwr					1.5	0.8	0.9					
	Seed					0.5	2.8	1.8	0.6				
	Bark							0.9					
	Unkn						0.4	0.9					
<u>Per lax</u>	Seed												2.2
<u>Pil tho</u>	Seed	0.6		5.5	3.5	10.7	2.0						
<u>Pse mic</u>	Frt												
<u>Pte eri</u>	Flwr			6.7	7.8								
	Seed				13.9	10.7	2.0						
	Leaf								0.9	1.9	1.0		
	Bud	0.6	4.0				0.8					2.7	0.6

Table 7.9: Feeding Record of Baboons at Mt. Assirik

Species	Part	Month											
		Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
<u>Rap sud</u>	Fr t									0.6			
<u>Sab sen</u>	Fr t					3.9	12.2	25.7	32.1	10.9	2.7		
	Seed									4.0	4.0		
	Flsh					0.5	1.6	0.9					
<u>Sor jug</u>	Fr t					0.5	1.2	0.9					
<u>Spo mom</u>	Fr t										1.3	25.6	8.9
<u>Ste set</u>	Fr t									1.0	0.7		
<u>Str spi</u>	Fr t	2.6	4.8	1.2		0.5						0.6	2.2
<u>Tam ind</u>	Seed												0.7
<u>Tre afr</u>	Fr t												
<u>Tri pri</u>	Fr t								3.1	2.0			
<u>Urt sp</u>	Base									1.0	0.7		
<u>Vit mad</u>	Fr t	0.6								0.5	3.3	4.8	34.1
	Seed							0.9		0.5			
	Bark							0.9					
<u>Ziz spi</u>	Fr t	1.3	3.2	2.4	2.6	0.5			0.6				1.5
<u>Ele gra</u>	Leaf									1.0			
	Stem								1.3		0.7		
<u>Sho gra</u>	Fr t	1.3	3.2	3.6	3.5	1.5						1.8	1.5
	Leaf	5.8	0.8						1.9	2.0	2.0	4.8	5.2
	Stem									1.0	2.0	2.4	0.7
	Unkn	0.6							3.8	2.0	1.3	2.4	
<u>Sap sp</u>	Bud			1.2									
	Fr t								5.0	1.0			
<u>Mel sp</u>	Fr t						0.4						
<u>Sp Un 1</u>	Fr t	3.2		1.2									1.5
<u>Sp Un 2</u>	Fr t										1.3		
<u>Sp Un 3</u>	Base										0.7		
<u>Sp Un 4</u>	Twig	0.6											
	Gum	1.9											
	Unkn	7.8	0.8										0.7
<u>Unk Ori</u>	Leaf			0.6				0.9		1.4	1.3		
	Bark									1.0	0.7		

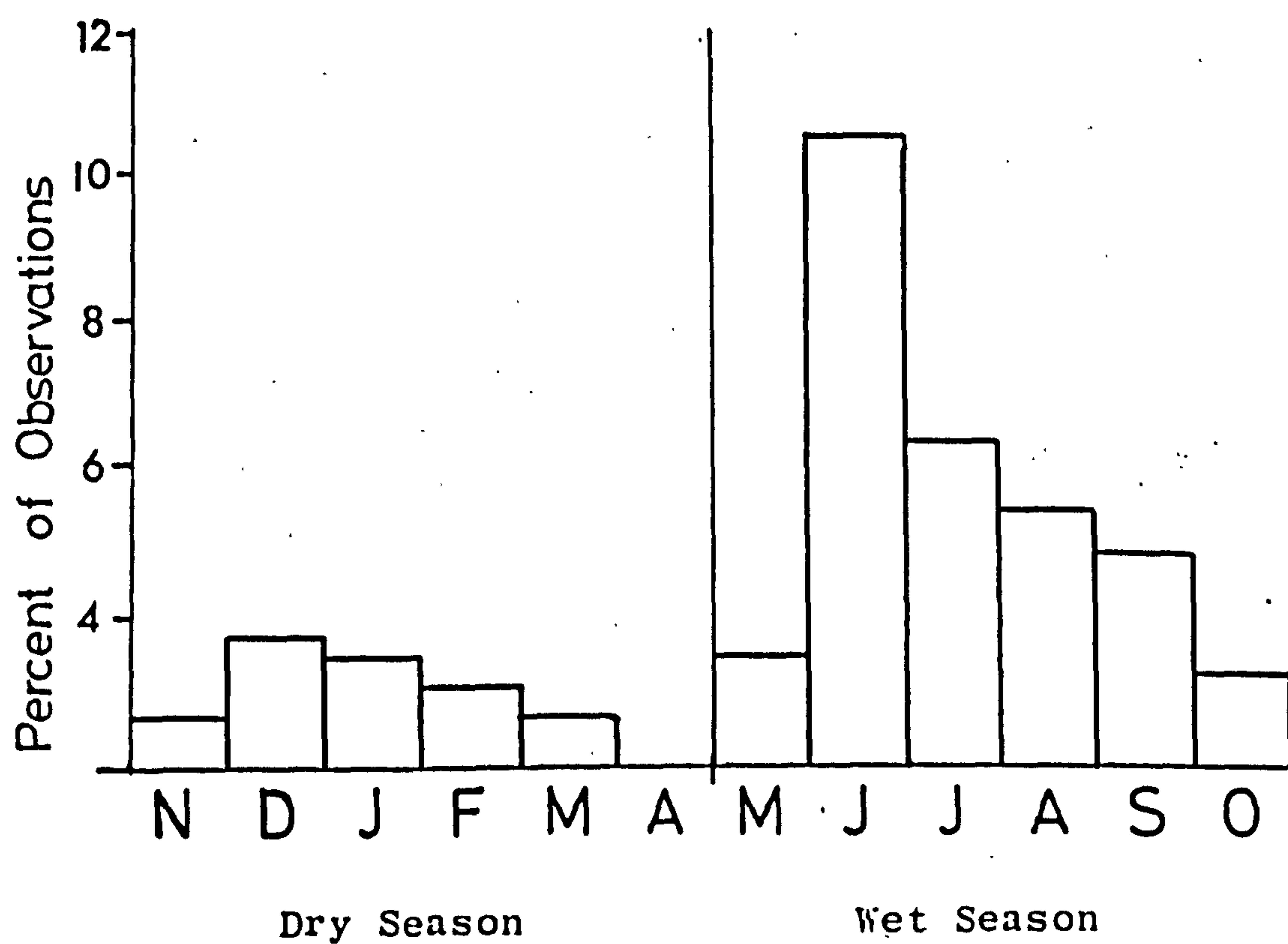
Table 7.9: Feeding Record of Baboons at Mt. Assirik

Species	Part	Month											
		Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
	Gum					0.9	0.8			0.5			
	Root	1.9	3.1	2.9	5.7	2.8	1.9	1.8					2.9
Ele	Fae Seed			1.2	0.8								
ANIMAL													
	Termites		0.8	1.1					2.5	4.0	1.3	0.6	
	Grasshoppers									0.9			
	Other Insect									2.7			
	Hare						0.4			0.4			
	Lizard											0.6	
Observations		157	129	175	123	213	262	112	163	226	155	170	139
Roll bouldrs		1.6	4.3	3.6	2.6	1.6		3.6	21.3	6.6	5.5	7.0	3.0
Roll logs				0.4					1.1		1.0		
Other ground		3.2	7.4	11.3	5.9	6.3	11.2	7.2	9.4	9.4	10.6	8.4	7.2
Off ground		7.6	4.9	10.1	8.5	6.7	2.9	5.0	4.5	1.0	2.5	4.7	4.2
Digging		2.7	4.3	3.2	2.6	2.0	2.2	2.9	1.9	3.5	2.5	0.9	2.4
Salt lick				0.4				0.7	0.7	0.3			
Observations		185	163	247	153	255	313	139	267	298	205	215	167

7.9: Boulder-Rolling: Results

Laterite boulders were abundant in many parts of the field area (Chapter 2). Laterite has no fracture plane, and when it weathers it forms irregularly shaped, often spheroidal, though occasionally plate-like boulders. The surfaces of the boulders are rough, and when resting on a hard surface the protruberances and indentations provide cavities in which animals can hide or plant detritus collect. Baboons could turn small boulders over with one hand. Larger boulders were turned by standing over the boulder, seizing the far edge with one hand, and levering the boulder up towards its chest. The baboon could then step around the upright boulder and push it over. To roll over the largest boulders the baboon straddled the boulder with its legs and

Figure 7.7:
Percent of monthly feeding record concerning boulder-rolling



pulled vigorously with its hands until the boulder started to lift. It continued to pull while stepping back to lever the boulder up and over. Boulders were occasionally abandoned after one or two strong tugs had failed to move them.

Boulder-rolling was seen on 157 occasions, and formed 21% of the feeding record in one month (June). Only one month (April) had no record of boulder-rolling (Fig 7.7). Baboons rolled over boulders more frequently in the wet season than in the dry season (chi squared = 69.6; df = 1; p < 0.001). In the wet season, a baboon that had turned over a boulder reached for one or more items previously covered by the boulder and placed something in its mouth on 32% of occasions (n=42). Comparable data for the dry season are not available. Twenty-two out of 72 boulders (31%) had been resting on crushed plant material, suggesting that the boulder had been rolled previously (Table 7.10).

Table 7.10:
Substratum on which Boulders had been Resting

Substratum	Wet Season	Dry Season
Embedded in ground	5	0
Boulders of similar size	0	0
Crushed plant material	16	6
Gravel	8	4
Laterite or large boulder	18	15

In any single boulder-field, consisting sometimes of several thousand boulders, several hundred might be turned by the baboons in a single passage through the field.

The distribution of the geometric mean dimension of boulders rolled by baboons and sampled from boulder-fields were dissimilar (chi squared = 58.3; df = 5; p < 0.001) (Table 7.11), largely because the baboons selected few of the smallest or largest boulders available to them.

Table 7.11:

Distribution of Sizes of Boulders

Geometric Mean Dimension	<= 10	11-15	16-20	21-25	26-30	>= 30
Rolled by baboons	10	13	24	17	5	3
Available in area	30	22	18	11	12	38

The nature of the objects which I found beneath boulders differed between the two seasons (Table 7.12). In the dry season 6% of the boulders concealed mobile animals, although 26% covered some form of animal life, including pupae and strong, densely-woven, silk-like webs of about 1cm in diameter, containing eggs or spiderlings, pasted flat over small cavities in the boulder. Of these 26%, 31% concealed more than one animal item (Table 7.12).

Table 7.12:

Possible Food Items Found Beneath Boulders

Numbers represent per cent of boulders (one - zero sampling)

Spiders	<u>Araneae</u>	20	2
Beetles	<u>Coleoptera</u>	18	2
Ants	<u>Formicidae</u>	14	
Termites	<u>Isoptera</u>	12	
Snail	<u>Gastropoda</u>	10	
Cricket	<u>Orthoptera</u>	8	2
Scorpion	<u>Scorpiones</u>	5	
Solifugid	<u>Solifugidae</u>	1	
Other invert.	<u>Chilopoda</u> , <u>Diplopoda</u> etc.	8	
Frog	<u>Salientia</u>	1	
Unidentified *		17	4
Plant detritus		not scored	96
Seed		not scored	42
Web		not scored	20
Chrysalis		not scored	8

* very small or very fast

In the wet season, 64% of the boulders concealed mobile animals (difference between wet and dry seasons statistically significant; chi squared = 25.1; df = 1; $p < 0.001$), and of these 64%, 56% had more than

Figure 7.8:
 Number of animals found beneath boulders of different sizes

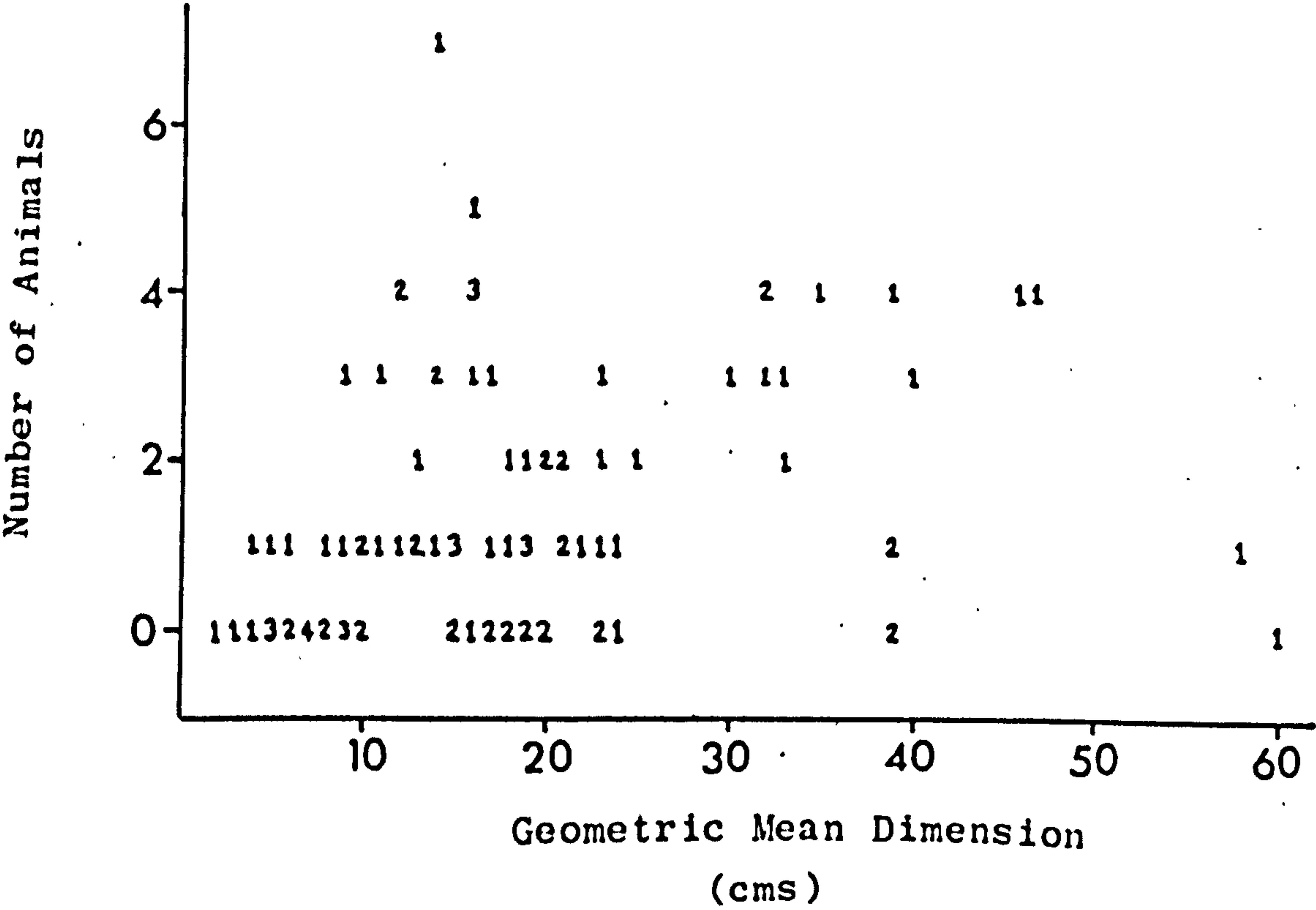


Figure 7.9:
Relationship between size of boulder and amount of plant debris found beneath it in the dry season

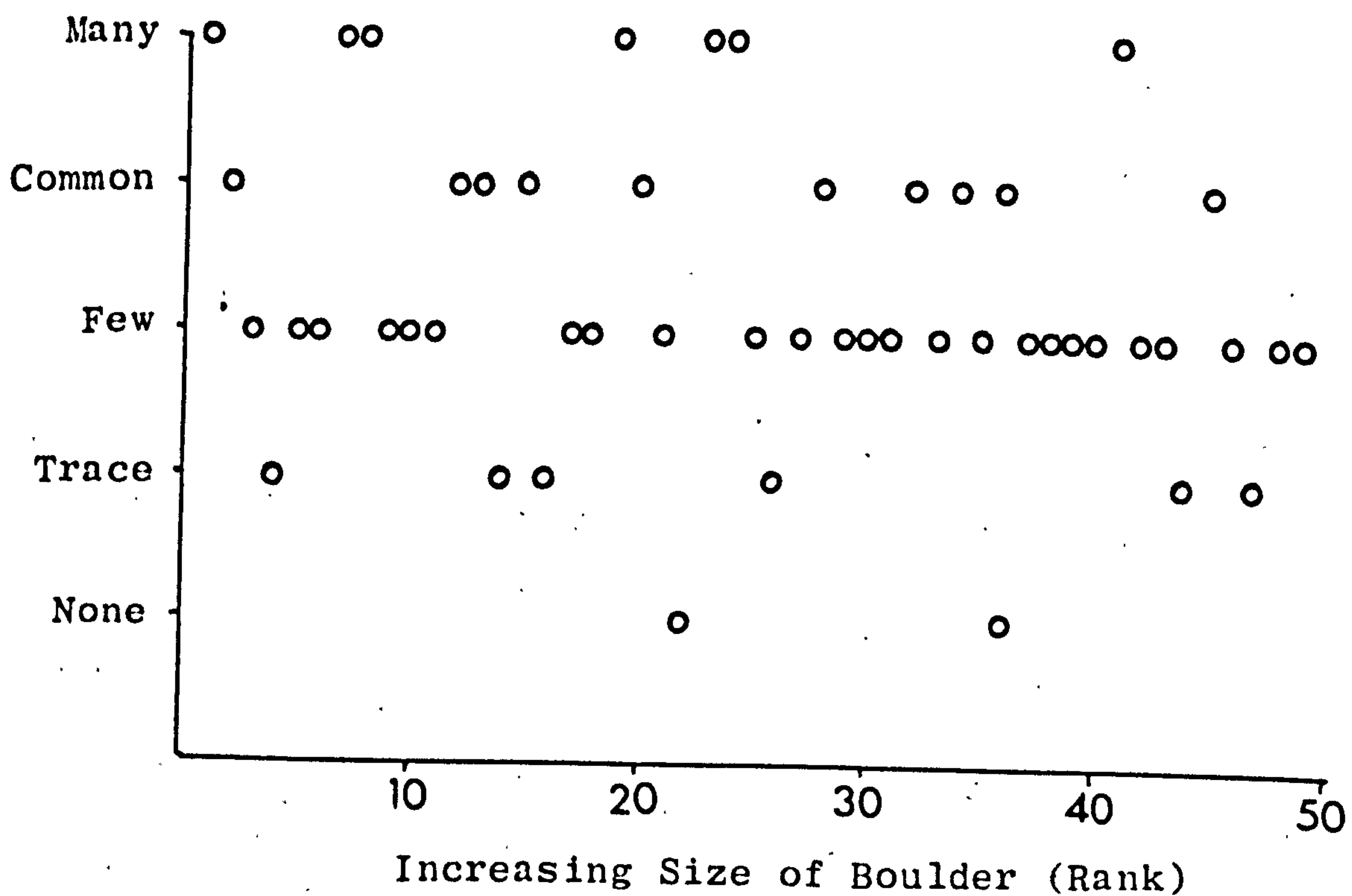


Figure 7.10:
Relationship between size of boulder and number of seeds found beneath it in the dry season

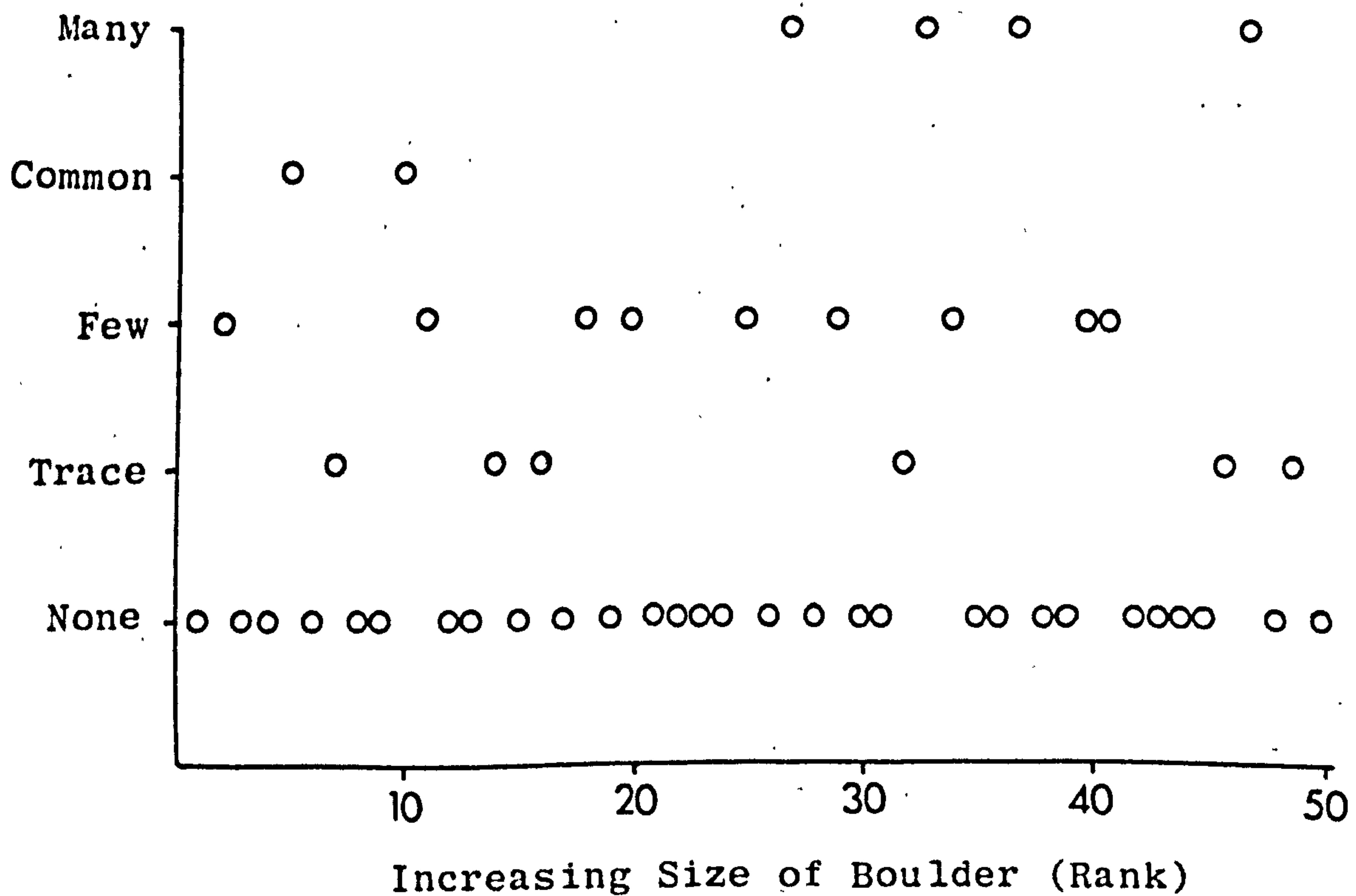
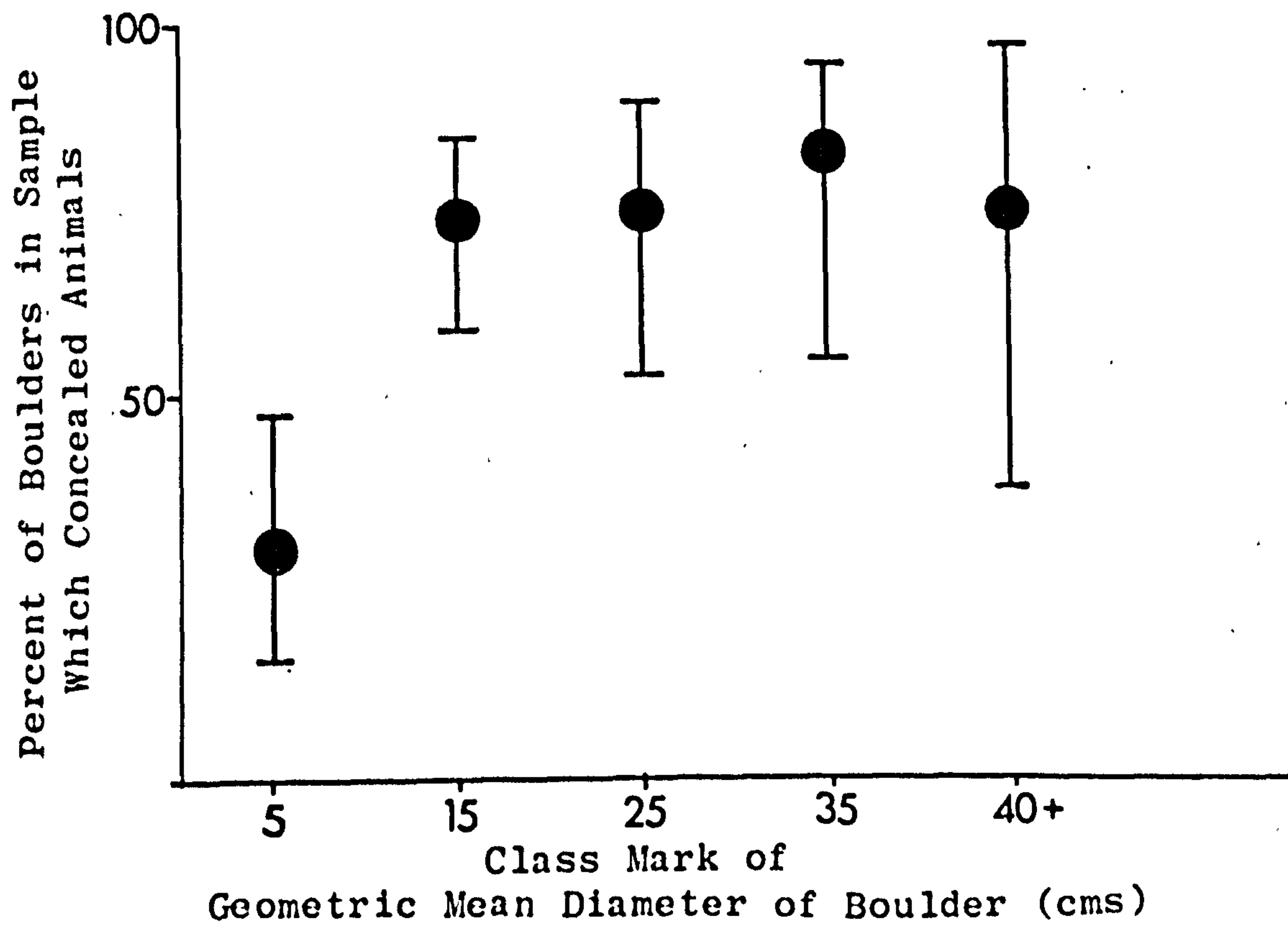


Figure 7.11:
 Relationship between size of boulder and chance of finding
 animal beneath it
 Vertical bars are 95% binomial confidence limits



one animal beneath them (Fig 7.8).

Plant detritus was found under nearly all boulders. Seeds, often from grasses, were found under 42% of the boulders in the dry season, and were scored as occurring frequently enough to be "common" under 12% of the boulders. Much of the rest of the plant detritus was probably useless as food; in the dry season, such remains included straw, dried leaves, small portions of dried bark, and so on. In the wet season, plant matter often consisted of mats of crushed, yellowing, and mildewed grass, or of white, etiolated stems.

7.9.1: Size of Boulder and Number of Objects

In the dry season there was no relationship between the size of boulder and the quantity of plant detritus or the number of seeds found beneath it (Figs 7.9 and 7.10).

In the wet season boulders smaller than 10cm GMD had fewer animals beneath them than did larger ones (chi squared = 6.54; $n = 1$; $p < 0.02$) (Fig 7.11).

7.10: Damage to Plants

Much of the conspicuous damage to plants involved breaking fruiting branches, but the baboons also destroyed buds, flowers, and seeds, and stripped bark from living trees. Baboons damaged 22 of the 57 known food species, and acted as possible agents of dispersal for 24. They both damaged and acted as possible agents of dispersal for 5 species.

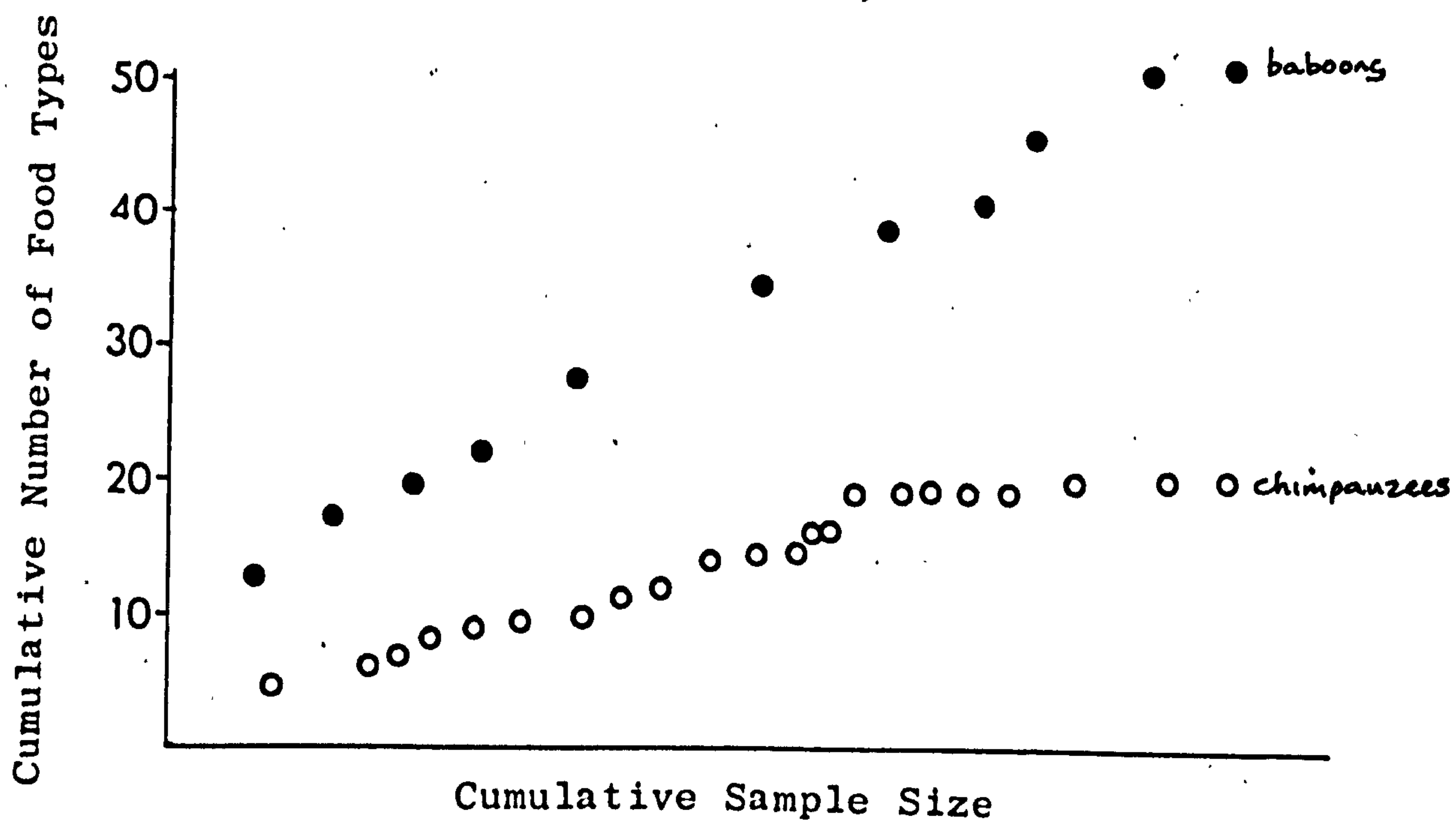
7.11: Comparison of Diets of Baboons and Chimpanzees

Of the 56 different vegetable foods eaten by chimpanzees at Mt. Assirik, three (fruits of Garcinia ovalifolia, Ipocina senegalensis, and Hanno undulata) are not known to be eaten by the baboons there. The proportion of fruit, seeds, flowers, shoots, bark, and flushing leaves in the apparent diets of baboons and chimpanzees are not correlated (Kendall's tau; p never < 0.05) (Table 7.13) across months; that is, the

Figure 7.12:

Comparison of cumulative number of food items known to be included in diet of baboons and chimpanzees with increasing sample size.

(Method of collecting samples different in the two species, so that no scale is given on the horizontal axis)



two species place different emphasis on different food classes in each month.

Table 7.13:

Proportions of Major Food Classes in Diet of Chimpanzee
Correlated with those in Diet of Baboon

Class of Food	Kendall's <u>tau</u>	n	significance
Fruit	-0.37	11	0.11 ns
Seeds	-0.07	11	0.75 ns
Flowers	-0.48	11	0.10 ns
Shoots	-0.35	11	0.18 ns
Bark	0.00	11	-
Flushing leaves	-0.28	11	0.26 ns

In each case, except that of bark, for which there is no correlation, the correlations tend to be negative.

Table 7.14 shows the frequency with which various species were recorded among the three most common species in the diet for any month. The rank order of the list for chimpanzees is not the same as that for baboons (Kendall's tau = 0.04; $p = 0.39$). (Any item that appeared in only one list was ranked 16th in the other list).

Chimpanzees were known to eat 35 plant food items (Baldwin 1979, Chapter 8, Table 4) at Mt. Assirik. The number of items known to be eaten is plotted against increasing sample size in Fig 7.12. The shape of the curve indicates that few new items will be recorded by further faecal sampling. By contrast, over 100 food items are known to be eaten by baboons at the same site (this chapter), and the curve shows little sign of reaching an asymptote. The diet of baboons is probably wider than that of chimpanzees at Mt. Assirik.

Table 7.14:

Frequency with which Food Species is one of the three
Items most commonly recorded in Monthly Feeding Record.

(max. freq. for Pan troglodytes = 11; for P. papio = 12)

	<u>Pan troglodytes</u>		<u>Papio papio</u>	
	Freq	Rank	Freq	Rank
Borassus aethiopum	-		5	1
Adansonia digitata	4	3	4	2=
Saba senegalensis	3	4	4	2=
Oxytenanthera abyssinica	1	9=	3	4=
Lannea acida	-		3	4=
Diospyros mespiliformis	1	9=	2	6=
Pterocarpus erinaceus	-		2	6=
Ficus spp.	6	1	1	8=
Cola cordifolia	2	5=	1	8=
Hexalobus monopetalus	2	5=	1	8=
Piliostigma thonningi	2	5=	1	8=
Afzelia africana	-		1	8=
Strychnos spinosa	-		1	8=
Sp. unknown	-		1	8=
Leaves	5	2	-	
Spondias mombin	2	5=	-	
Landolphia heudelottii	1	9=	-	
Grewia lasiodiscus	1	9=	-	
Tamarindus indica	1	9=	-	
Insects	1	9=	-	
Honey	1	9=	-	

DISCUSSION

7.12: Biases in the Feeding Record

In a study of this sort, bias is inevitable. Animals that were seen eating tended to be either conspicuous (adult males) or less timid than most (adolescents and juveniles). The attention of the observer was drawn to foods whose collection or processing was noisy (eg Erythrophloeum suaveolens and Borassus aethiopum seeds) or conspicuous (eg Adansonia digitata fruit and Afzelia africana seeds). These foods will tend to be overrepresented in the feeding record. Other foods, such as grass seeds or blades, can be collected and eaten inconspicuously by a moving baboon and are presumably underestimated in

the feeding record. Similar considerations apply to the feeding record based on feeding remains.

The degree to which a food item is over- or under-represented in the feeding record will not in general remain constant across months, since it will compete for the observer's attention with different rivals in each month. Observation conditions probably biased the results in favour of seeing baboons in trees, and foraging at ground level could often not be seen well enough to identify the food item.

This study, however, does not depend for its major conclusions on details of the diet. Instead, it gives a broad outline of the feeding ecology of P. papio, for which underlying biases will be less important.

7.13: Breadth and Nature of Diet

The baboons at Mt. Assirik ate flower and leaf buds, flowers, seeds, fruits, flushing leaves, shoots, stems, twigs, bark, gum, base of stems, bulbs, roots, and other, unknown, items from the plants on which they fed. They ate at least 58 species of plants, and also ate at least 6 species of animals from three orders. Despite their diverse diet, more than 50% of the feeding record was derived from the top 10 food items. Most (62%) of their food was apparently derived from trees. Their diet was not homogenous through the year but changed seasonally, probably in response to rainfall.

These observations thus expand the range of plant foods known to be eaten by baboons, as expected. They also support previous evidence that baboons of the genus Papio, while adapted to a terrestrial life, find a significant proportion of their food in trees. The implications of this for the adaptive radiation of baboons are discussed below.

7.13.1: Omnivory and Troop Size

Uneven distribution of food species across habitats together with a patchy distribution of the habitats themselves implies that there may be times when certain food sources can be monopolised by a few, presumably high-ranking, animals, (Hamilton et al. 1978) and when alternative sources of that food are not available within the current spread of the troop. This was seen to occur at Mt. Assirik, in particular with isolated stands of Ficus spp and Lannea spp. Subordinate animals would therefore be forced to search for alternative food sources. The wide diet of P. papio at Mt. Assirik may have meant that on few if any occasions was no food available for low-ranking animals near a major feeding site. Baboons in this field area were also capable of processing foods that other primates were not (eg Borassus aethiopum seeds) and were possibly able to overcome mechanical or chemical plant defenses of other potential foods (eg Acacia dudgeoni, Cola sp. unknown, Erythrophloeum suaveolens, Kaempferia aethiopica, Gardenia erubescens). This may have served to reduce competitive pressure on them from other primate species. All of these factors may have allowed P. papio to live at higher densities than did the other primates. In the dry season, when competition over food within the troop was presumably at its highest, the troops fragmented (Chapter 3), while high availability in the wet season allowed them to live in large troops.

7.13.2: Seasonality in Consumption of Animals

Baboons at other sites are facultative carnivores or insectivores; Strum (1975) showed that P. anubis baboons living in Kenya acquired and then abandoned a habit of hunting mammals, and Hamilton et al. (1978) documented a major increase in insect-eating by P. ursinus in Botswana during a plague of potential insect prey. Insect abundance is highly seasonal at Mt. Assirik (pers obs), with the peak occurring in the wet season. This presumably accounts for the change in the proportions of insects included in the feeding record between the wet and dry seasons.

That the four instances of eating vertebrates occurred in the wet season might be coincidental, or, since baboons normally discover vertebrate prey accidentally (Harding 1973, Hausfater 1976, Strum 1976), reflect the frequency with which baboons might stumble on prey in the wet season.

7.13.3: Seasonal and Annual Differences in Plant Foods Eaten

The influence of rainfall on the apparent diet probably stems from the predictable, strongly seasonal climate in the area. Predictability in times of peak rainfall is likely to entrain plant cycles, leading to temporary abundance of certain food items (eg Post 1968). This in turn may have permitted the baboons to concentrate on one, or a few, items at a time, which in turn had a major influence on the diet. Temporary overabundance of one type of food from a single species also had an effect on the timing of the peak of entire classes of food types. Thus the observation that the dependence by the baboons on bushes for food was correlated with the previous month's rainfall was better interpreted as a peak in dependence on a single species of bush, Vitex madiensis. A similar observation holds for the correlation of frequency of feeding on vines with the subsequent month's rainfall; again, a single species, Saba senegalensis, was largely responsible. Conversely, such strong dependence on single species may result in inter-annual variation if certain preferred species fail to leaf, flower, or fruit in any year. Thus in the year during which this feeding study was carried out, Hexalobus monopetalus and Pterocarpus erinaceus produced very poor crops of fruit and seeds respectively, compared with the previous and subsequent years (pers obs, Tutin, Baldwin, Harrison pers comm) Pseudospondias microcarpa entirely failed to fruit, while in the previous and subsequent years this fruit was apparently an overwhelmingly important food for the baboons, influencing their ranging patterns and perhaps social organisation during its fruiting season (Tutin, Harrison pers comm).

7.13.4: Relationship between Fruit and Seeds

The less fruit was eaten in any month, the more seeds were eaten. This relationship may indicate that the baboons depend upon having a small proportion of foods other than fruit or seeds in their diet, and that the rest of their diet may then be made up of either fruit or seeds.

7.13.5: Dependence on Trees

Dependence on trees in arid sites and in dry seasons may be related to a lack of grass and forb-level plants. At Mt. Assirik there is artificial loss of ground-level cover in the dry season since the whole park is burned every year at the beginning of the dry season as part of management policy (Dupuy and Verschuren 1977).

7.13.6: Direct Observation and Feeding Remains

While data collected by direct observation cannot be pooled item by item with data collected from feeding remains, they can be pooled if the data is considered in major classes such as "fruit". This smoothing effect of major classes presumably occurs because differential survival of individual food types as feeding remains, or differential observability of food types under direct observation, tend to cancel out when the diet is considered in coarser categories. This result, while not used in this thesis, may be useful in studies of "difficult" terrestrial primates such as Macaca nemestrina, Mandrillus sphinx, and Mandrillus leucophaeus.

7.14: Boulder-Rolling: Discussion

There was a marked seasonal change in the frequency with which boulders were rolled by baboons at Mt. Assirik. This was probably accounted for by the presence of animals, mostly insects, beneath the boulders in the wet season. Animals found beneath boulders may be the major source of animals in the diet of baboons at Mt. Assirik,

especially in the wet season. That boulder-rolling is so frequently observed at some times of year suggests that this form of foraging is highly profitable; perhaps animals are important sources of protein for the baboons, or perhaps such prey is particularly easy to find.

Very few boulders hid potentially dangerous animals such as scorpions, and the baboons were not noticeably cautious about gripping or rolling the boulders. Baboons were sometimes seen with swollen and obviously painful forearms, but the cause of these injuries was not known. A variety of possible causes can be imagined.

Baboons did not roll boulders at random, but selected boulders by size, tending to ignore small boulders, beneath which there were few animals, and large boulders, which required much effort to roll. On the basis of these data it is possible that the upper limit on the size of the boulders that the baboons rolled was set by the strength required to roll them and not by the expectation of returns. Experimental work by Fady (1972) suggests that this is not the case, since the baboons that he observed made very great efforts to turn over boulders that were too massive for them, in the expectation of rewards (peanuts) placed beneath them by the experimenter. Some baboons made small tunnels beneath the boulders to scoop out the food. Further experimental work could clarify in how far the upper limit was determined by strength and how much by expectation of reward. The baboons apparently sampled boulders which returned the highest probable benefit for the least cost.

7.15: Damage to Plants

The three plants most likely to be affected by baboons were probably A. digitata, B aethiopum, and P. erinaceous. However, A. dicitata probably gained a net benefit from the actions of the baboons, since many flowers survived to fruiting, and the seeds of ripe fruit were both spat out of the cheek pouches far from the parent tree and swallowed and deposited in faeces, often in places apparently suitable to the growth of new trees. It is possible that the baboons of Mt.

Assirik, like those of the Shai Hills, Ghana (Lieberman et al. 1979), have been responsible for the establishment of the characteristic groves of A. digitata, D. mespiliformis, M. alnifolia, and N. latifolia in the soil beneath the edges of the laterite plateaux and the spread of L. acida in the woodland.

Each P. erinaceous tree bears several thousand flowers, many of which survive to seed. The seeds are windborne, and if eaten by baboons they are destroyed. Their successful germination and maturation depends in part upon their avoiding the attentions of baboons, but many have survived, as evidenced by the success of this species in the field area.

B. aethiopum may suffer serious reproductive damage from baboons. Its germinating seeds are few and conspicuous, and baboons spent up to 2 hours beneath a single tree, eating the seeds. The survival of this plant may depend principally upon other agents of dispersal (such as elephants) depositing seeds long distances from their parent trees.

One plant whose reproduction is not threatened by baboons, but which baboons were frequently seen to damage, is Oxytenanthera abyssinica. By eating stems and shoots, baboons probably help to limit the vegetative growth of bamboo, but their impact on the population seemed insignificant. Much of the field area was covered with bamboo, and many bamboo shoots managed to survive to maturity.

The results presented here are insubstantial but indicate that further research into the relationship between P. papio and its environment should be carried out before baboons are culled on the grounds that they cause ecological damage.

Such research might also compare the damage done by baboons with the damage caused by burning the park each year. The annual fires not only destroy the undergrowth, but also consume trees. I have seen many P. erinaceous trees and several B. aethiopum palms destroyed by fire; such destruction of mature individuals, together with any damage of seedlings newly germinated, may easily have a far greater long-term

influence on the park than the baboons could cause. Burning may also increase the proportion of scrub and fire-resistant species at the expense of other species of plants. Man may therefore alter the diet of baboons by destroying or restricting the distribution of some food species while encouraging others in this national park.

7.16: Overlap in Diet between Baboons and Chimpanzees

Data from the study on chimpanzees at Mt. Assirik (Baldwin 1979) and data from this study are not strictly comparable, since the former was based largely on faecal sample analysis and this study on direct observation. The relationship between sampling by observing feeding and by examining scats is not clear (Lockie 1953). While some items may become too macerated for identification in scats, others may be distinguishable or discovered only by the examination of faecal samples (Moreno-Black 1978). It seems legitimate to draw some general conclusions, however.

Baboons and chimpanzees at Mt. Assirik eat many of the same foods, but to different extents, and, probably, at rather different times of year. We may conclude, rather tentatively, that baboons and chimpanzees did not in general compete for the same foods at the same times of year. On the basis of this analysis it seems unlikely that the baboons at Mt. Assirik are limiting the numbers of chimpanzees by direct feeding competition. Baboons probably had a wider diet than did chimpanzees at Mt. Assirik. They were also capable of eating some foods, such as the seeds of B. aethiopum, which the chimpanzees were apparently unable to open. This breadth of diet may have helped them to sustain a higher biomass than did the chimpanzees.

CHAPTER 8: The Influence of Food on Ranging and Troop Size

INTRODUCTION

8.1: Influence of Food Species on Ranging

The feeding behaviour of P. papio may help to provide an insight into the ranging behaviour of troops at Mt. Assirik, since the distribution of their food may alter ranging patterns. Thus both Rowell (1966a) and Hamilton et al. (1978) found that a fig tree or grove of fig trees, while fruiting, strongly influenced the ranging of troops of P. anubis and P. ursinus respectively. At Mt. Assirik, ranging by P. papio is responsive to gross habitat types (Chapter 5), but nothing is known about more detailed factors which may influence their ranging. In this chapter I test the hypothesis that no single species of food plant influenced the ranging pattern of baboons at Mt. Assirik.

8.1.2: Home Range Area, Troop Size, and the Proportion of Fruit in the Diet

In the region around Mt. Assirik, P. papio lived in exceptionally large troops (Chapter 3), at least one of which had an unusually large home range (Chapter 5).

Animals which depend largely on fruit tend to have larger home ranges than do animals which are more foliverous (Milton and May 1976, Schoener 1971), and tend to live in larger troops (Clutton-Brock and Harvey 1977). This suggests that baboon troops which include much fruit in their diet will have large home ranges. Data from the literature on baboons may be used to test this hypothesis. Data from Mt. Assirik were used to test the prediction that the baboons there depended particularly strongly upon fruit.

8.1.3: Home Range Area, Troop Size, and Clumping and Abundance of Food

Clutton-Brock and Harvey (1978) argue that clumped and dispersed food sources are best exploited by large groups of animals having large home ranges. This hypothesis would predict that P. papio's food was more clumped, or more dispersed, than that of other baboons with smaller home ranges.

Alternatively, the large troops of P. papio might be a response to abundant food. This proposition is suggested by at least two sets of data. Firstly, Iwamoto (1978) showed that a population of Macaca fuscata had been limited by their food supply. When the monkeys were supplied at a feeding station with large quantities of food for several years the population and troop size rose markedly, with a concomitant increase in population density. Further evidence comes from a study by Dittus (1977), who showed that during a severe drought, when food became scarce, the sizes of many troops of Macaca sinica diminished. Only one troop, living on a constant supply of refuse, increased in numbers.

Severe seasonality may impose restraints on a population similar to those imposed by aridity (Jolly 1972). Inadequate food can dramatically alter social structure (Hall 1963a, Hamilton et al. 1976), while a change in the distribution of food may influence foraging group size (Caraco and Wolf 1975, Clutton-Brock and Harvey 1978). We may therefore test whether the seasonally variable foraging group size seen at Mt. Assirik (Chapter 5) is a response either to seasonal differences in distribution of food or to seasonal changes in the abundance of food.

METHODS

8.2: Influence of a Single Food Species on Ranging

Adansonia digitata was chosen to examine the influence of one species on baboon ranging because (1) its fruit formed a major portion (14%) of the apparent diet of the baboons at this site; (2) its comparative rarity meant that the location of individuals of the species could be plotted; and (3) its conspicuousness meant that baboons in these trees could be seen from up to 2km away. A map was prepared showing the distribution of known A. digitata trees in one portion of the home range of one troop, and the distribution of trees on this map compared with the ranging of the troop on two days when A. digitata was fruiting.

8.2.2: Influence of Distribution of Food Species on Ranging

Each of the seven habitat types described in Chapter 2 is a characteristic community of plants. Some of these habitats were described by Baldwin (1979). Table 7.4 shows the distribution of food species across the habitat types, and from this table the degree of overlap between habitats was calculated. The rank order of the frequency with which baboons entered quadrats containing the various habitats (Chapter 5) was compared, using Kendall's tau, with the number of food species known to grow in those habitats.

The number of food species found in any habitat is only a rough measure of the potential amount of food available in that habitat. A better measure weights the species by their importance in the diet of the baboons. The measure is to be used as an independent estimate of food availability within habitats, in whose light we shall examine ranging behaviour. It is therefore invalid to use the frequencies with which baboons were seen to feed on the different species in different habitats, for the reasoning would then be circular. A measure free of such circularity is the "potential diet" available from each habitat. Potential diet was established by summing the contribution of each species weighted by the proportion which it contributed to the feeding record with the contribution of the other species in the same habitat. (A more sophisticated measure would also take into account the relative abundances of species within and across habitats.)

The rank order of the proportion of the diet potentially available in each habitat was compared, using Kendall's tau, with the rank order of the frequency with which baboons entered quadrats containing these habitats.

8.2.3: Influence of Clumping and Dispersion of Habitats on Ranging and Troop Size

Patch size and the dispersion of the patches of the various habitat types were measured by superimposing a grid on a map drawn from aerial photographs, and estimating the area covered by contiguous areas of the habitat to the nearest hectare. Median and modal patch size were calculated, and a mean patch size was estimated by dividing the area of

Figure 8.0:

calculation of mean distance between clumps of a habitat,
given mean clump size and number of clumps in known area.

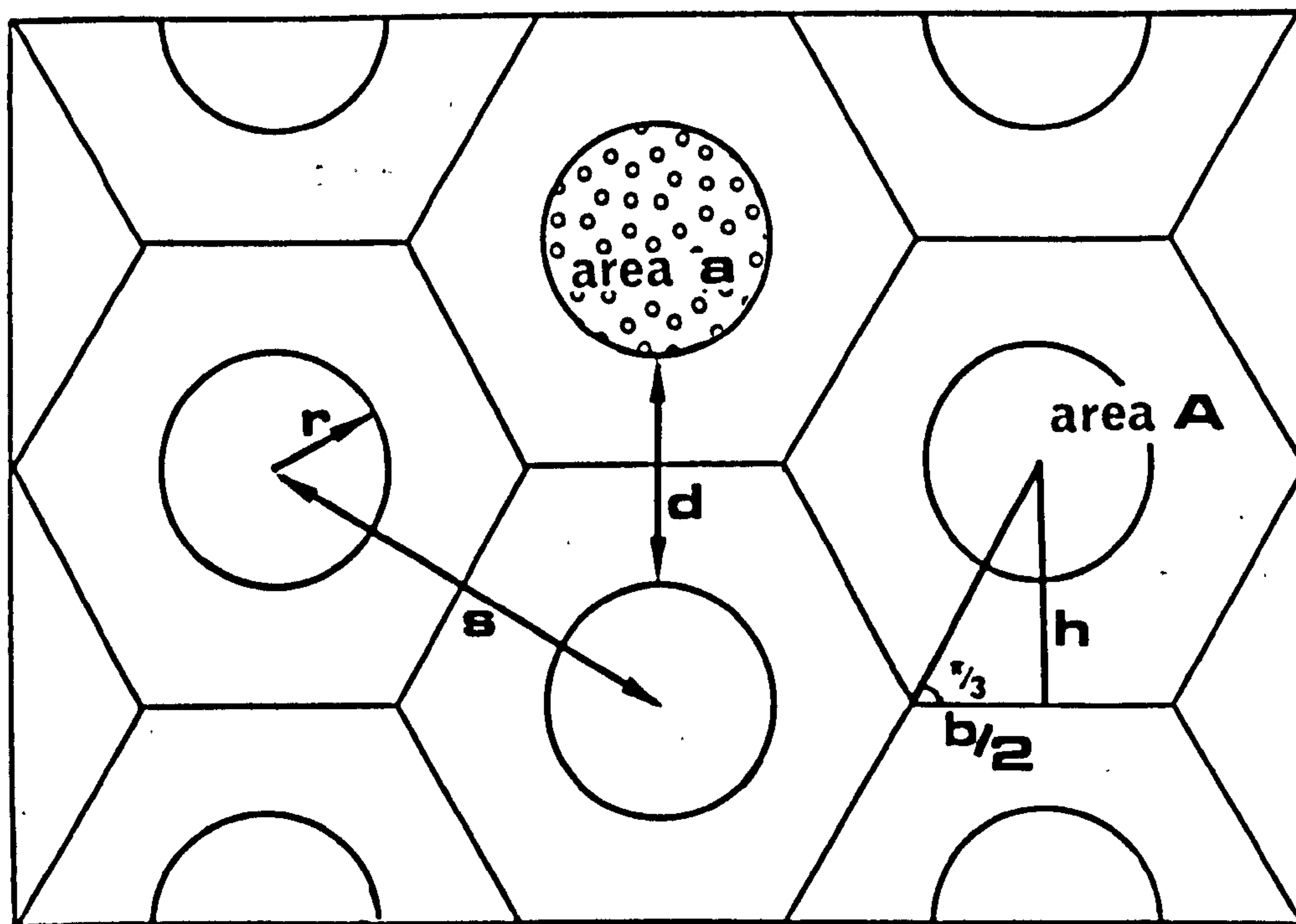
d = distance between nearest points of adjacent clumps

s = distance between centres of adjacent clumps

a = mean area of clump

r = mean radius of clump (calculated from area)

A = inverse of density of clumps



each habitat in the field area by the number of patches of that habitat. The mean distance between the nearest points of adjacent patches of a habitat were not measured directly, but were estimated as follows:

Assume regular, close packing of the patches (Fig 8.0).

Then the distance we require = d, where

$$d = 2 (h - r)$$

but

$$r = \text{square root} (a/\pi)$$

and

$$\begin{aligned} D &= 1/A \\ &= 4 / (2hb) \\ &= 1 / ((\text{sqrt } 3) \times h \text{ squared}) \end{aligned}$$

therefore

$$h = \text{sqrt} (1 / ((\text{sqrt } 3) \times D))$$

and

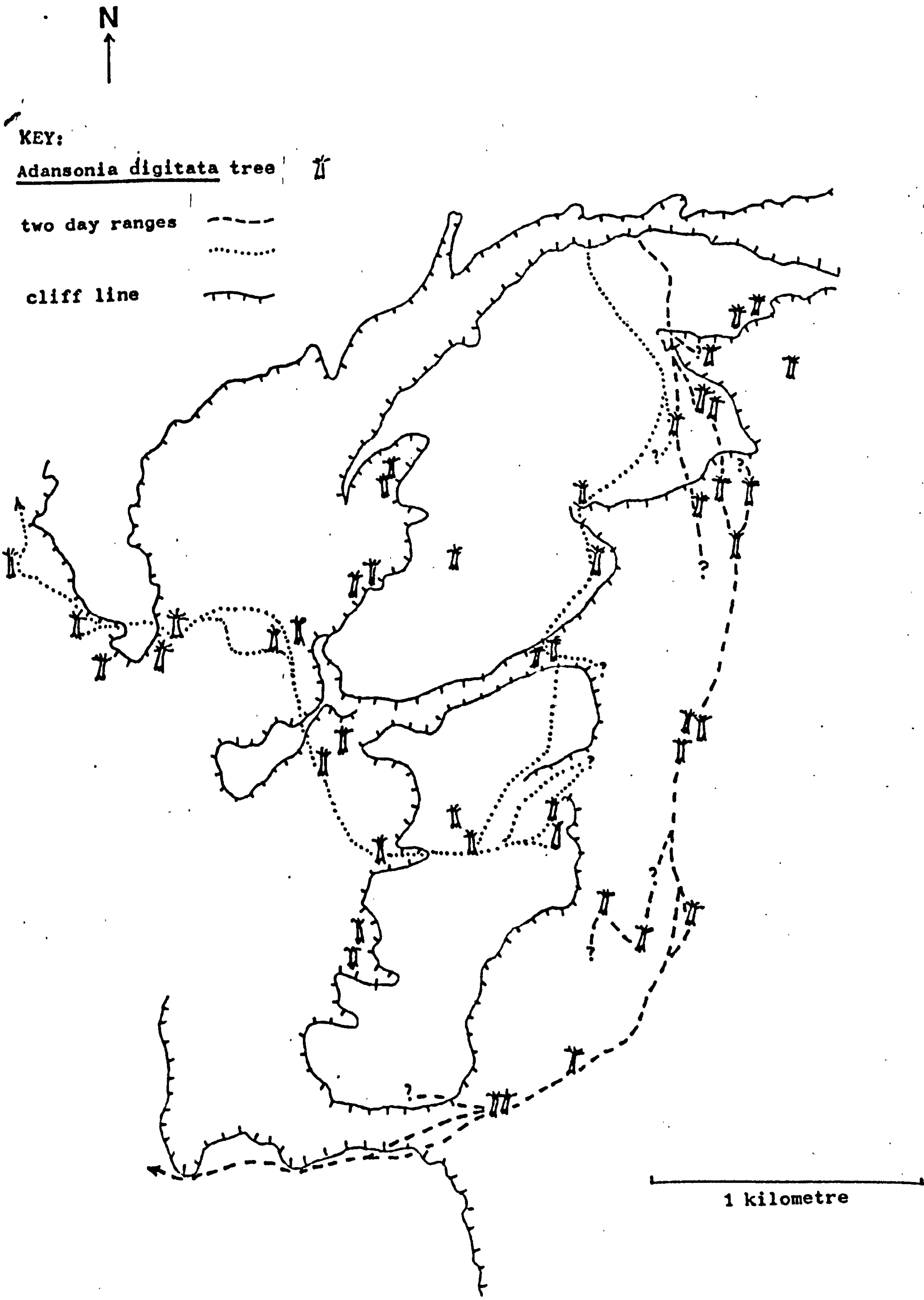
$$d = 2 \times ((\text{sqrt}(1 / ((\text{sqrt } 3) \times D)) - r))$$

Habitat maps prepared for publication in other studies on baboons apparently omit much detail (eg Aldrich-Blake et al. 1971, Dunbar and Dunbar 1974c, Harding 1976, Moreno-Black and Maples 1977, Nagel 1973, Rowell 1966a,) and cannot be used for comparison with this study. The map of the study site in the Awash valley in Ethiopia, where Aldrich-Blake et al. 1971 carried out their research, was prepared from an aerial photo to which Dunbar kindly gave me access. Mean clump size and inter-clump distances were calculated in the same way for this site as for the area around Mt. Assirik. The relationship between large-scale clumping of the habitat and the home range size and troop size could then be examined across two troops.

8.2.4: Home Range Area and Proportion of the Diet Consisting of Fruit

Data from the literature was also used to examine the correlation between the proportion of fruit in the diet and the home range area of troops of various species of baboons of the genus Papio. Home range area and proportion of fruit available might both be affected by rainfall in a way that obscured the relationship between them. A partial correlation

Map 8.1:
Part of two full-day ranges plotted relative to the distribution
of known Adansonia digitata trees.



between home range area and proportion of fruit in the diet, correcting for annual rainfall, was also carried out.

RESULTS

8.3: Influence of a Single Species on Ranging

The locations of all known A. digitata trees in the south-eastern portion of the home range of Fable's troop are plotted in Map 8.1. Parts of two full-day ranges are also plotted. Temporary fissions of the troop are indicated by forks in the path of the troop. Poor visibility meant that the exact path of the troop was not always known; in these cases the tracks end in question marks on the map. The baboons were seen to climb into and feed from 25 out of 45 A. digitata trees that they visited. They visited 29 out of 45 A. digitata trees in the area on one or both days.

In order to test the significance of this result, 24km of 200 metre-wide transects were drawn through the area and 29 trees counted in this survey. giving a density of 0.17 trees per sq km, or 1.2 trees per kilometre of transect. Roughly 9.5 km of day range is shown on Map 8.1, in which 21 trees were visited by the main group on each day range. They visited significantly more trees than expected (chi squared = 7.897; df = 1; $p < 0.01$).

8.3.2: Food Availability and Use of Home Range

The rank order of the frequencies with which the baboons tended to enter quadrats containing the various habitats was not the same as the rank order of numbers of food species contained within those habitats (Kendall's tau = 0.24; ns.), nor as the rank order of the proportion of the diet potentially available from each habitat (Kendall's tau = 0.14; ns.).

8.3.3: Clumping and Dispersal of Habitats

Seven habitats were distinguished in the aerial photograph (Chapter 2). These habitats were distributed in a mosaic over the field area (Plate 1.1). The largest contiguous area of any habitat in the field area

was one of 379ha of closed woodland , while the modal contiguous area for each habitat was less than one hectare (Table 8.1). Median patch sizes are also shown in this Table.

Table 8.1:

Central Tendency in Patch Size in Habitats at Mt. Assirik

Habitat	Median	Mode	Area (sq km) A	No. of patches n	A/n (ha)
Gallery Forest	6.00	-	0.4	7	5.7
Open Woods	3.18	<1	26.6	218	12.2
Closed Woods	2.15	<1	18.7	262	7.1
Scrub	1.41	<1	22.4	181	12.4
Grass on laterite	0.97	<1	5.2	275	1.9
<u>Combretum</u> scrub	0.88	<1	13.4	166	8.1
Scrub Grassland	0.32	<1	3.2	502	0.6

8.3.4: Clumping and Dispersion of Habitat, and Ranging and Group Size

The data from Mt. Assirik were compared with those from the area used by the troops studied by Aldrich-Blake et al. (1971). The largest single patch was a contiguous area of scrub-grassland extending over 1158ha in their field area (and over an unknown area beyond the boundary of the field area). Median clump sizes and mean distances between the nearest points of patches were comparable in both studies (median test $p = 0.5$ and $p = 0.46$ respectively). (Table 8.2).

We should therefore predict that troop sizes and home range areas are roughly comparable at the two sites. The home range areas were 44 kilometres square and 4.3 kilometres square, and the troop sizes 250 and 87 respectively (this study and Aldrich-Blake et al. 1971).

8.3.5: Effect of Food Abundance on Troop Size

Mean foraging group size was higher in the wet season, when food abundance was high, than it was in the dry season. It would be valuable to compare mean monthly foraging group size with rainfall for

Table 8.2:

Clumping and Dispersion of Habitats at Two Sites

Habitat	n of patches	mean of patches per sq km	mean area of patch (hectares)	distance between patches (m)
Mt. Assirik:				
Gallery Forest	7	0.08	5.7	5103
Open Woods	218	2.42	12.2	583
Closed Woods	262	2.91	7.1	590
Scrub	181	2.01	12.4	675
Grass on Laterite	275	3.06	1.9	713
<u>Combretum</u> Scrub	166	1.84	8.1	799
Scrub Grassland	502	5.58	0.6	556
Awash:				
Riverine Forest	1	0.06	101.0	-
Open Woods	0	0.0	-	-
Closed Woods	0	0.0	-	-
Scrub	134	7.55	2.9	360
Grass on laterite	0	0.0	-	-
<u>Combretum</u> Scrub	0	0.0	-	-
Scrub Grassland	82	4.62	14.1	283
Grass	43	2.42	2.8	787

that month, but mean monthly apparent party size could not be estimated accurately enough with the monthly sample sizes in this study.

8.3.6: Home Range Area and Proportion of Diet Made up by Fruit

Data from 5 troops of P. anubis, 2 of P. cynocephalus, and 1 of P. ursinus were used to test the relationship between home range area and the proportion of their diets found in fruiting trees (Table 8.3). There was a non-significant negative relationship between the size of the home range and the proportion of fruit in the diet (Kendall's tau = -0.25; $p = 0.38$), which became stronger when the correlation was

corrected for annual rainfall (partial correlation = 0.53; $p = 0.11$).

Table 8.3:

Home Range Area and Proportion of Fruit in the Diet
of 8 troops of baboons of the genus Papio

Species	Home Range	% Fruit	Source
<u>P. anubis</u>	0.90	40.8	Dunbar and Dunbar 1974c
<u>P. anubis</u>	1.12	82.7	Dunbar and Dunbar 1974c
<u>P. anubis</u>	1.12	48.6	Ransom 1971; Oliver unpub.
<u>P. ursinus</u>	6.7	77.0	Hamilton et al. 1978 (K)
<u>P. anubis</u>	19.7	9.5	Harding 1976
<u>P. cynocephalus</u>	40.2	27.1	Post 1978
<u>P. cynocephalus</u>	61.0*	15.5	Oliver unpubl. (Ruaha)
<u>P. anubis</u>	52.0	46.0	Popp 1978

Note 1: (K) = Kuiseb

2: *Oliver used 1 km. sq. quadrats to calculate this figure. Dunbar (in prep) has shown that large quadrats tend to give an over-estimate of the true area. He provides a correction, which, when applied to Oliver's estimate, gives 42 sq. km.

In both cases the correlation became worse when data for P. papio (fruit makes up 60.3% of diet; home range area = 44 sq km) were included (Kendall's tau = -0.14; $p = 0.6$; partial correlation = -0.31; $p = 0.23$).

Since the relationship between the proportion of fruit in the diet and home range area did not hold, the large home range area of P. papio cannot be attributed to the high proportion of fruit in its apparent diet.

DISCUSSION

8.4: Influence of Distribution of Food on Ranging

The location of food trees influences the day ranging of one troop of baboons at Mt. Assirik. Any explanation of ranging patterns must therefore be couched at least partly in terms of response to the distribution of food. With appropriate data, the rank order of

preference with which baboons entered quadrats containing the various habitats could be compared month by month with the proportion of the diet potentially available from each habitat. Frequency of entry into each quadrat was too low in this study for this analysis. However, data presented here shows that the use of the home range does not correspond closely with the number of food species found in different habitats, nor with the proportion of the diet potentially found in those habitats. Food availability is therefore probably not the only factor influencing ranging, which may also be affected by areas suitable for social behaviour, efficient routes between feeding sites, areas in which fragments of the troop are likely to detect or meet other fragments, and so on.

8.4.2: Clumping and Dispersal of Habitats

The size of an area which can be considered a "patch" depends upon the level of the analysis of the distribution of the food. The largest areas which could realistically be considered patches are probably the areas of habitat type, as dealt with here, though finer analysis would probably consider stands of food species, rather than areas of habitat, to be patches. Differences in the clumping and dispersal of habitat types identifiable from aerial photos do not appear to be responsible for differences in home range areas in two troops of baboons in widely separated locations in Africa. This analysis is confounded by the differences in the habitats themselves in these two sites. Future research on this topic at Mt. Assirik might cope with these problems by selecting small, intensively used areas for a detailed ecological survey, and noting accurately the behaviour of the baboons in those areas. If two troops with different home range areas could be found at the same field site, several dispersed quadrats in each range could be sampled at a slightly coarser level in the attempt to link home range area with food dispersal. Clumping and dispersal of food species may yet help to explain large home ranges where the clumping and dispersal of habitat types does not.

8.4.3: Fruit and Home Range Area

There was a non-significant trend for home ranges to be smaller when the proportion of fruit in the diet was higher, which is contrary to the predictions of Milton and May (1976) and Schoener (1971). Data from Mt. Assirik decreased the significance of the trend still further because these troops included much fruit in their apparent diet but had large home ranges. The proportion of fruit in the diet of baboons is therefore not a good explanation of variability in home range area of baboon troops.

It seems plausible that a combination of the proportion of fruit in the diet and the dispersal of the sources of fruit would be a strong predictor of home range area. To test such a prediction requires ecological analysis at a fineness of detail as yet unattempted in baboon behavioural ecology. Baboons, with their home range areas that are large by comparison with most other primates, are probably not the best group of animals on which to test such a relationship.

8.4.4: Ranging and Mental Maps

If day range corresponds closely with the distribution of food species currently forming the bulk of the diet, as seems probable, the baboons must possess a mental map of their home range area (Altmann and Altmann 1970). Circumstantial evidence for the existence of such a map arose repeatedly in the course of this study, for example; on one occasion the troop moved for over an hour in one direction through flat, featureless scrub, on a heavily overcast day, before arriving at a waterhole two kilometres from their starting place.

8.4.5: Use of Home Range

If food availability alone is considered, the baboons should discriminate between two habitats whenever the principal food which they are feeding on occurs at a higher density in one habitat than in the other. In particular, most tree food species found in open and closed woodlands were probably found in greater density in closed woodland since the trees in closed woodland tended to be closer together. If tree-based foods alone were considered, the baboons might have been expected to

discriminate in favour of closed woodland more strongly than is indicated by the analysis presented here, which depends only on presence or absence of the food species. This could well form the basis for future research at Mt. Assirik, since the baboons are now reasonably well habituated to human followers (Byrne pers comm). However, forb-level foods may have grown more densely in the open woodland (see Chapter 2, Visibility). These foods were probably under represented in the feeding record, and the baboons may have found a larger part of their diet in open woodland than is apparent here.

8.4.6: Testing Predictions of Optimal Foraging Theory

The manner in which P. papio responds to changes in its environment by altering its diet, and the degree to which it alters its foraging behaviour as expectations of benefit alter are both brought out by using data from Mt. Assirik to test two specific predictions of optimal foraging theory. These are:

(a) Abundance of Food and Quality of Diet

Firstly, Cody (1974), Ellis et al. (1976), Estabrook and Dunham (1976), Pyke et al. (1977) and Schoener (1971) all predict that as food abundance goes up so the quality of the food eaten goes up. (This prediction applies only to changes in food abundance that take place over a timescale much less than the generation time of the animal. Animal populations might respond to longer-term changes by an increase in numbers.) Data from the baboons at Mt. Assirik can be used to test this prediction.

(b) Abundance of Food and Diversity of Diet

Secondly, the above authors also predict that as food abundance goes up, so the diversity of the diet goes down. By contrast, Westoby (1974) predicts that the proportion of a food in the diet will not change with changing abundance once a threshold of abundance is reached. He suggests that availability only restricts consumption when it is low. Thus at times of low abundance the animal will include fewer items in its diet. Data from Mt. Assirik can be used to test between these conflicting predictions.

There is evidence from data collected on other primates to support the prediction that as food abundance increases so the quality of the food included in the diet also increases.

T. gelada eat rhizomes and roots in the dry season, but when in the wet season green grass is available, they eat almost nothing else, ignoring the roots which they would have to spend much time and energy in excavating (Wrangham 1976). Dunbar (1977a) showed that T. gelada eat different parts of the grass plant in response to changes in the nutritional quality of the various parts, seeking to include only high-quality parts in their diet. Further evidence comes from both P. anubis and P. cynocephalus troops, which in two sites depend upon roots and corms in the dry season but switch to flushing grass or to fruit when it becomes available (Altmann and Altmann 1970, Harding 1976). Finally, when energy-rich foods such as cereal grain are fed to wild Macaca fuscata troops, foods poorer in energy, such as leaves, are dropped from the diet (Iwamoto 1978).

There is also some evidence to support the prediction that as food abundance increases so dietary diversity decreases. For example, chimpanzees (Pan troglodytes) living in woodland savanna in west Tanzania, where food was scarce, ate a wider variety of food than did forest-dwelling Pan troglodytes in Uganda, where food was relatively abundant (Suzuki 1969, 1979).

METHODS

8.5: Quality of Food

The data from direct observation on feeding by baboons at Mt. Assirik were arranged into 16 broad categories (buds, flowers, seeds, fruit, flushing leaves, mature leaves, shoots, bark, stems, base of stems, bulbs, twigs, roots, gum, animals, and "other"). Those foods which were probably rich in proteins, fats or sugars, but probably low in secondary toxic compounds and relatively easy of access were regarded as high quality foods. Gum is difficult to categorise, since it is sometimes rich in

carbohydrates but sometimes contains high concentrations of tannins and other toxins depending on the species from which it is derived (Hausfater and Bearce 1976). Since it was only rarely eaten (12 out of 2607 records of feeding or foraging), I have tentatively classed it as a low-quality food. Bulbs, eaten in the wet season when the soil was soft, were classed as high-quality foods, while roots, which seemed to be difficult to dig up, I classed as low-quality foods. Thus animals, fruit, seeds, shoots, flowers, flower buds, flushing leaves, and bulbs were defined as "high-quality" foods, by contrast with the other categories which were defined as "low-quality".

8.5.2: Measures of Abundance

No direct measures of food abundance were available. Three indirect measures were therefore used. Firstly - Post (1978) showed that food abundance was correlated with rainfall in Amboseli National Park in Kenya. I have therefore used rainfall as a measure of monthly plant abundance at Mt. Assirik. Secondly, Schoener (1971) predicted that in times of food shortage, foraging would be extended into less profitable times of day. With baboons, and with some other primates, this apparently implies that foraging encroaches on social activities. Oliver and Lee (1978) showed that for a troop of P. cynocephalus baboons, an increase in the time spent moving in search of food in the dry season coincided with, and probably gave rise to, a reduction in social behaviour. Other studies on primates show a similar relationship between times of low food abundance and reduction in social activity (eg Hall 1963; Loy 1970, Post 1981). The proportion of time spent in social activity is used here as an index of food abundance; specifically, since the baboons showed less social behaviour in the dry season than in the wet, the abundance of food in the dry season is assumed to have been lower in the dry than in the wet season. A further measure of food abundance came from a study of the leafing, fruiting, and flowering cycles of twenty species of plants from which baboons fed. These data were collected by S. Hall and others, and are analysed here to provide an indication of seasonal changes in the availability of foods for the baboons.

8.5.3: Tests of Quality of Diet

The prediction that abundant food resources allowed the baboons to concentrate on high-quality foods was tested by comparing the proportion of high-quality foods in the monthly feeding record with that month's rainfall, using Kendall's tau. The frequency with which the baboons were seen to eat high-quality foods was compared across seasons (chi squared). The proportion of low-quality food in the diet was plotted across months and compared with rainfall.

8.5.4: Tests of Diversity of Diet

The number of observations of feeding in any month might influence the number of different food items included in that month's feeding record. The relationship between the sample size of feeding observations and the number of species in that month's feeding record was examined.

The prediction that the diversity of the diet fell as the abundance of food went up was tested by examining the relationship between measures of abundance and two measures of the diversity of the monthly feeding record. Firstly, the number of items that were included in each month's feeding record which had not been included in the previous month's feeding record was regressed on the difference in sample size between the two months. This had the effect of removing the influence of sample size in the comparison between wet and dry seasons. If baboons ate a more diverse diet in the dry season, the elevation of the regression line for the dry season would be higher than that for the regression line for the wet season. The transition between August and September could not be included in this analysis, since the feeding study began in September, and a comparison with August would have been with a month nearly a year in the future.

Secondly, Pielou's (1969) modification of Ginni's (1912) formula was used to examine the heterogeneity of each month's, each season's, and the year's diet. Pielou's index is:

$$\text{Diversity} = 1 - \text{SIGMA} ((n_1 \times (n_1 - 1)) / (N \times (N - 1)))$$

where $n(i)$ is the number of observations of the i th food type in that month's feeding record, and N is the total number of observations of

Figure 8.1:
Percent of low quality food plotted (graph) with rainfall
(histogram)

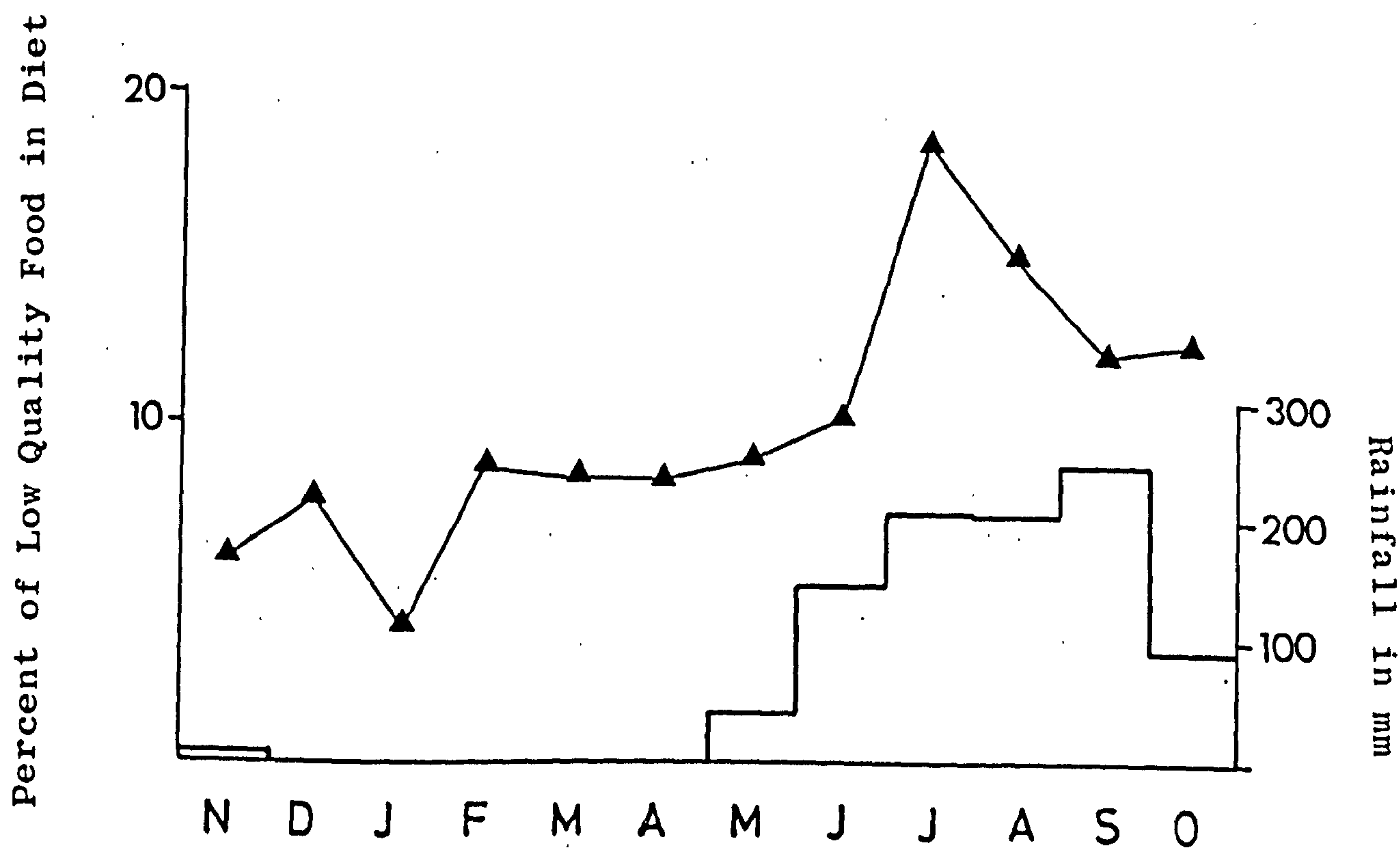
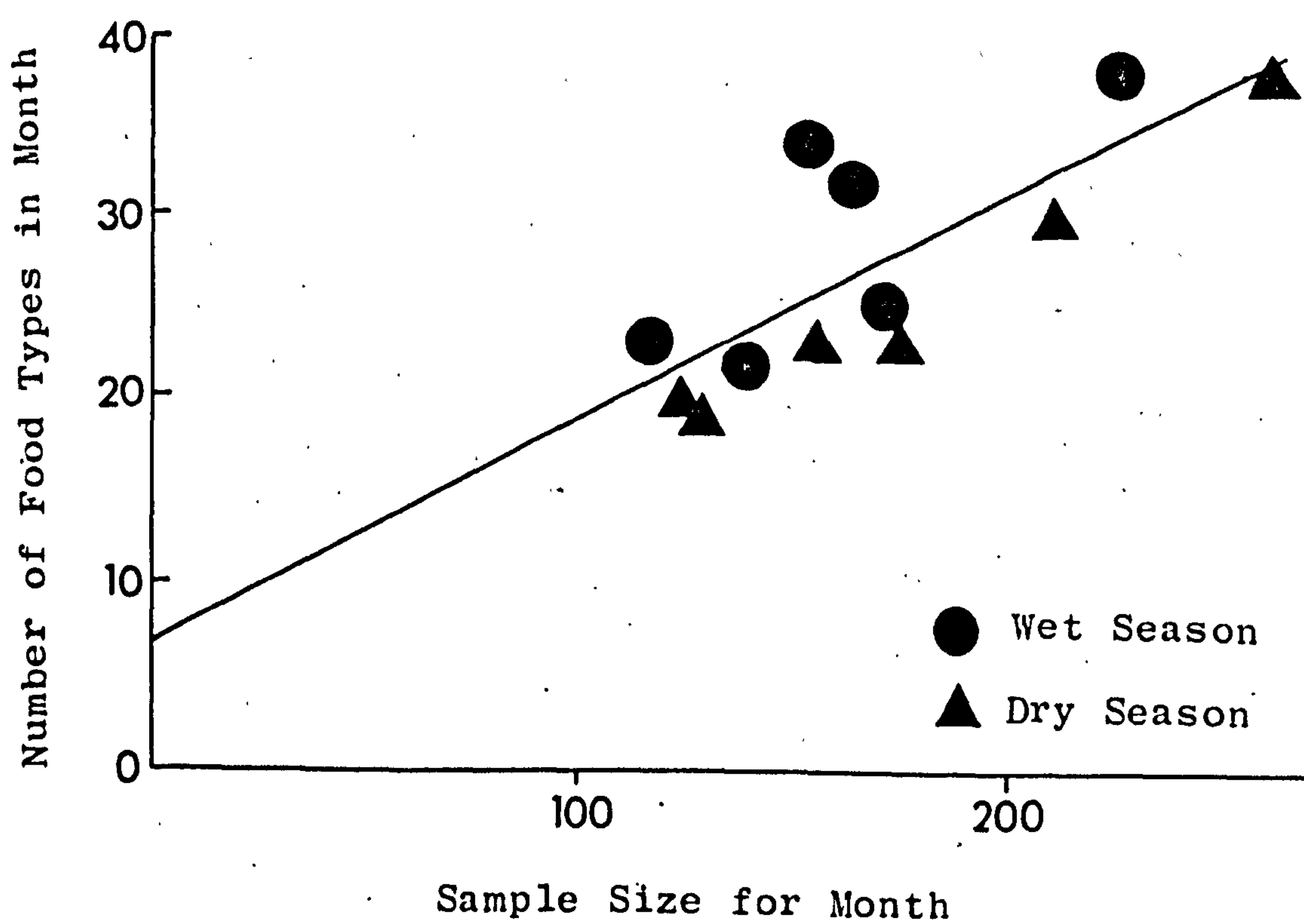


Figure 8.2:
Number of different food items in monthly feeding record
plotted against sample size for that month



feeding for that month. This index tends towards 1 as the food types (a) increase in number and (b) become similar in their relative importance. Thus if 10 observations are made which include 9 species, one of which is eaten twice, the feeding record has an index of 0.97, while if the 10 observations included only 2 species, one eaten 9 times, the index becomes 0.2. There is no known test for significance for this index, and Pielou's index, like most other indices of heterogeneity, is sensitive to the number of food types in the diet (Peet 1974). Any correlation between Pielou's index and rainfall might therefore be confounded by sample size. A partial correlation of Pielou's index against rainfall, controlling for sample size, was therefore computed.

RESULTS

8.6: Testing Predictions of Optimal Foraging Theory

The data collected by direct observation of feeding by baboons are given in Table 7.9.

The proportion of high-quality foods in the feeding record was negatively correlated with rainfall across months (Kendall's tau = 0.82; $p < 0.001$), and the proportion of low-quality foods was higher in the wet season than in the dry season (Table 8.4).

The variation in the proportion of low-quality foods in the feeding record and that of rainfall across months are shown in Fig 8.1.

The number of items in any given month's feeding record was correlated with sample size (Kendall's tau = 0.56; $p < 0.01$) (Fig 8.2). All four of the points lying above the least-squares regression line plotted through the data ($r(p) = 0.79$; $p < 0.01$) are data from the wet season. This trend is statistically significant (Fisher's Exact; $p = 0.030$); that is, within each month the feeding record contained a wider variety of items in the wet season than it did in the dry season when the effect of sample size was controlled for.

Figure 8.3:

Number of food items in each month's feeding record that were not in previous month's feeding record plotted against difference in sample size between successive months

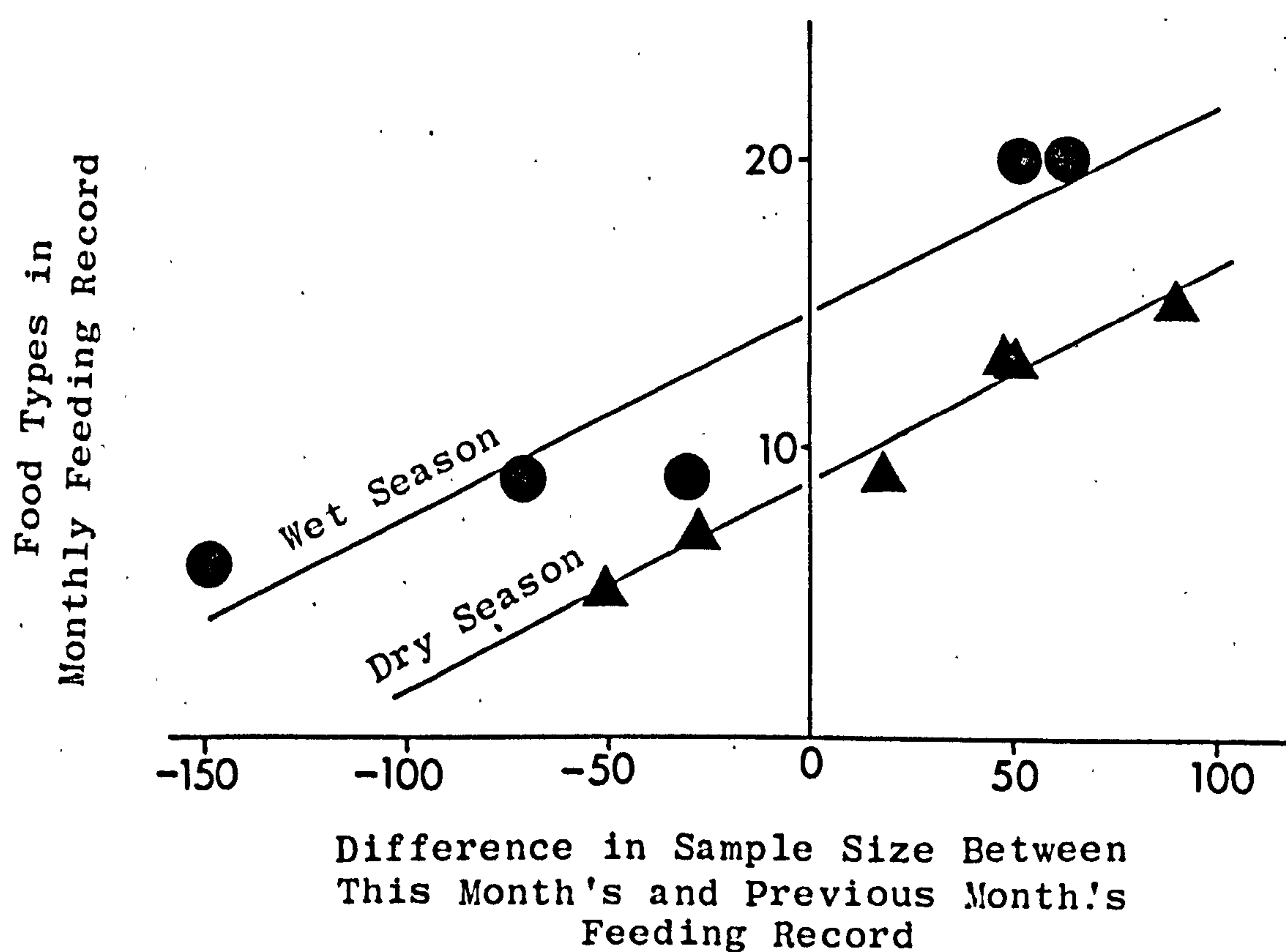


Table 8.4:

Contingency Table for Numbers of Observations of Feeding
on Low-Quality Foods in Wet and Dry Seasons

(Low-quality foods defined as leaves, bark, stem, base of stem,
twigs, roots, gum)

	Season	
	Wet	Dry
Observed	127	84
Expected	102.3	108.7

chi squared = 11.576; df = 1; p < 0.001

8.6.2: Change in Diet with Time

The signed difference in the number of entries in the feeding record between each pair of consecutive months ("difference in sample size") was calculated and is plotted on the horizontal axis of Fig 8.3. The number of food items included in each month's feeding record that were not included in the previous month's feeding record ("new food items") is plotted on the vertical axis. (The datum for the transition between August and September is not plotted for reasons explained in the Methods.)

There was a positive correlation ($r(p) = 0.78$; $p < 0.05$) between the number of new items in any month's diet and the difference in sample size between the months. The correlations within seasons were stronger ($r(p)$ (wet) = 0.94; $r(p)$ (dry) = 0.98). The slopes of the two regression lines were both significantly different from zero (dry season, $t = 10.9$; $p < 0.001$; wet season, $t = 4.89$; $p < 0.02$), but were not significantly different from each other. Thus the relationship between sample size and the number of new items in each month's feeding record was not dependent on the season.

The elevations of the seasonal regression lines were significantly different (for the dry season, intercept = 8.83 ± 0.98 (95% confidence

limits); for the wet season, intercept = 14.77 ± 3.89) (Fig 8.3). Thus irrespective of sample size five or six more food items were seen to be eaten in each month in the wet season than were seen in each month in the dry season.

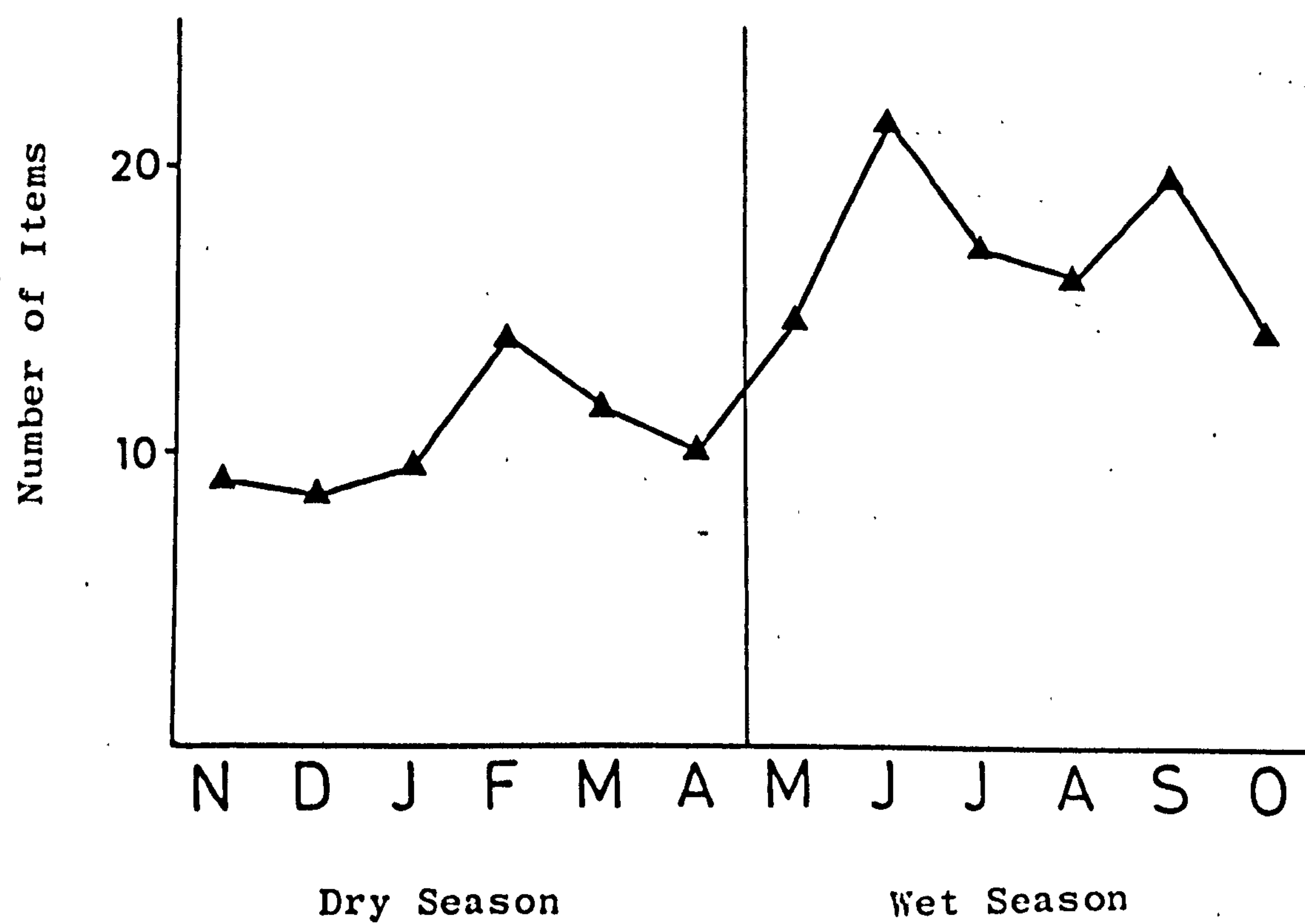
8.6.3: Heterogeneity of the Feeding Record

Pielou's index for the year's feeding record of baboons at Mt. Assirik is 0.96 (Table 8.5). The index for the wet (0.95) and dry (0.92) seasons are similar. Pielou's index is not correlated with rainfall when sample size is controlled for (partial correlation = 0.37; df = 9; p = 0.26), so that this index fails to show any relationship between diversity in the feeding record and food abundance.

Table 8.5:

<u>Pielou's Index of Heterogeneity for Plant Food Types by Month</u>						
<u>Dry Season</u>						
	Nov	Dec	Jan	Feb	Mar	Apr
Month	0.723	0.663	0.825	0.928	0.872	0.921
Season	0.924					
<u>Wet Season</u>						
	May	Jun	Jul	Aug	Sep	Oct
Month	0.866	0.879	0.919	0.891	0.876	0.859
Season	0.948					
Year	0.961					

Figure 8.7:
Monthly variation in number of different food items available
from 19 species whose fruiting and leafing cycles were
monitored



8.6.4: Seasonal Availability of Food

The baboons ate parts of 19 of the 20 species whose leafing, flowering, and fruiting cycles were monitored were eaten (Table 8.6).

Table 8.6:

Food Items Monitored Through Year

Species	Flush	Flowers	Fruit	Seeds	Shoots
<u>Adansonia digitata</u>			*	*	
<u>Azelia africana</u>	*			*	
<u>Bombax costatum</u>		*		*	
<u>Ceiba pentandra</u>	*	*			
<u>Cola cordifolia</u>			*		
<u>Diospyros mespiliformis</u>			*		
<u>Erythrophloeum suaveolens</u>				*	
<u>Ficus leucardii</u>			*		
<u>Ficus umbellata</u>			*		
<u>Grewia lasiodiscus</u>			*		
<u>Hexalobus monopetalus</u>			*		
<u>Khaya senegalensis</u>					
<u>Landolphia heudelottii</u>			*		
<u>Nauclea latifolia</u>					
<u>Oxytenanthera abyssinica</u>	*				*
<u>Parkia biglobosa</u>		*			
<u>Pterocarpus erinaceus</u>	*	*		*	
<u>Saba senegalensis</u>	*		*	*	
<u>Spondias mombin</u>			*		
<u>Strychnos spinosa</u>			*		
<u>Vitex madiensis</u>			*	*	
<u>sp. of Sapotaceae family</u>			*		

The number of edible items available from these 19 species is plotted month by month in Fig 8.7. More items were available in the wet season (median = 16.5) than in the dry season (median = 9.75) (medians test, $p = 0.004$). This small sample indicates that there may have been a wider variety of foods available to the baboons in the wet season than was available in the dry season.

8.6.5: Comparison with other species

Data from 14 troops of baboons can be used to examine the relationship between the proportion of high-quality food in the diet and annual rainfall (Table 8.7). Rainfall was estimated in some cases by

using published figures from nearby

Table 8.7:

Proportion of High-Quality Food (fruit, seeds, flowers, animals) in the Diet of 14 Populations of Baboons

Species	% high Quality	Rainfall (mm)	Source
<u>P. anubis</u>	14.4	595	Harding 1976
	46.9	1099	Popp 1978
	56.4	1105*	Dunbar and Dunbar 1974c
	65.2	1380*	Ransom 1971
	83.2	1105*	Dunbar and Dunbar 1974c
<u>P. cynocephalus</u>	25.3	1679	Oliver pers comm
	32.2	225	Post 1978
<u>P. ursinus</u>	74.6	18*	Hamilton et al. 1976
<u>P. hamadryas</u>	66.0	665*	Kummer 1968a
<u>P. papio</u>	84.3	941*	This study
<u>T. gelada</u>	21.4	1385	Dunbar and Dunbar 1975
	7.8	1476	Iwamoto pers comm
	7.5	1102	Dunbar and Dunbar 1974c*

* These figures are estimates from nearby meteorological stations meteorological stations (Dunbar and Sharman in prep). No relationship was found.

8.6.6: Quality, Diversity and Abundance

At times of high abundance, more items were included in the feeding record, for any given sample size, than when food abundance was low. Similarly, the rate at which new items were included in the feeding record was higher in the wet season months than it was in the dry season months. The diversity of each month's feeding record, measured by Pielou's modification of Ginni's index, was high, but was not correlated with rainfall. This may imply that the relative emphasis on different plant food items within each month is related not to total abundance of food, but to some other variable, such as relative abundance of single food items. For example, there was one food type (the fruit of Adansonia digitata) upon which the baboons depended heavily (Table 7.9) in the first half of the dry season. This need not imply that food, in

the form of A. digitata fruit, was abundant in the dry season, but might imply that this food type was overwhelmingly more available than any other food type at that time of year (Pulliam 1974).

When food abundance, as measured by rainfall, was high, the baboons ate more low-quality food. Data from Mt. Assirik therefore run counter to the prediction that as food abundance increases, so diversity of diet decreases, and seem to support the opposite prediction, due to Westoby (1974). However, Westoby's model assumes that food quality is more important than is food availability. This assumption is true when the amount of food that can be eaten is limited by digestion time rather than by time to find the food. This assumption is almost certainly not true for the baboons at Mt. Assirik, where, in the dry season, a large proportion of waking hours of the baboons were spent moving and searching for food (Chapter 4). Thus it seems unlikely that the decrease in the diversity of the feeding record in times of low abundance can be accounted for by Westoby's (1974) model. There are two further plausible explanations of decreased diversity of the feeding record in the dry season.

Firstly, the nature of the diet may have changed between the wet and dry seasons in such a way that the results were biased against recording an increase in the diversity of the diet in the dry season. Items that could be eaten with little or no discernible pause in the gait of a baboon were poorly represented in my sample of diet, and there is reason to believe that many of them were of importance (eg grasses, which in many populations account for a major proportion of the diet; insects; seeds on the ground; fungi; and so on). If more items of this nature were eaten in the dry season than in the wet, there would be a misleadingly low diversity in the feeding record for the dry season. Further research would be needed to examine this possibility.

Secondly, optimal foraging theory as it is currently understood assumes that while both abundance and value of foods may change, the diversity of foods available will not. In strongly seasonal environments, such as that at Mt. Assirik, this assumption is probably invalid; there is probably a wider variety of foods available to animals

in the growing season than there is in the non-growing season (eg Western 1973). If this is true at Mt. Assirik, the increased diversity in the feeding record for the wet season is a reflection of environmental changes with which optimal foraging theory has not concerned itself.

CHAPTER 9: Social Organisation

INTRODUCTION

9.1: Review of Earlier Work

The literature on the social organisation and mating system of the other baboons is extensive (eg Aldrich-Blake et al. 1971, Altmann and Altmann 1970, Anderson 1980b, Bolwig 1959, Crook 1966, DeVore and Hall 1965, DeVore and Washburn 1963, Dunbar 1973, 1978c, 1979b, Dunbar and Dunbar 1975, Hall 1962a, 1962b, Hall and DeVore 1965, Hausfater 1975b, Kummer 1968a, Kummer 1974a, Kummer and Kurt 1963, 1965, Mori and Kawai 1975, Müller 1980, Ohsawa and Kawai 1975, Ransom 1971, Rasmussen 1980, Rowell 1966a, 1967a, 1969, Saayman 1971a, 1971c, Seyfarth 1978, Sigg 1980, Sigg and Stolba in press, Stolba 1979, Wrangham 1976). By comparison, little has been published on the social organisation of P. papio in the wild.

Bert et al. (1967b) recorded the sequence in which troops of P. papio returned to their sleeping sites in the evening. They commented on the unstructured, anarchic appearance of the troops and speculated that this might be an adaptation to the poor visibility in south-east Senegal's dry forests. Their observations agree with those of Dupuy and Gaillard (1969), who described a homogeneous band without subgrouping.

In a report on a short study of P. papio in the GPN de NK, at a site about 100km from Mt. Assirik, Dunbar and Nathan (1972, p328) saw evidence for "some degree of substructuring within the P. papio troop." They went on to comment that "the bonds which attract the females [to the males] are relatively weak and allow the females considerable independence".

Boese (1973,1975) carried out a 9-week survey of P. papio in Senegal. He reported that his sightings (n=72) of foraging groups during this survey confirmed his observations made on a captive group in Brookfield Zoo, Chicago, that P. papio lived in social groups composed of a single adult male and one or more adult females, with associated young. These reproductive units were embedded in multi-male troops. This construction resembles that outlined by DeKeyser (1956) (quoted in Boese 1975). Boese (1973, p186) concluded that P. papio had a social organisation which was intermediate between those of P. hamadryas and the savanna baboons

(P. anubis, P. cynocephalus, P. ursinus).

Boese's conclusion has two important implications. P. papio and P. hamadryas are morphologically similar (as are P. anubis and P. ursinus), and P. papio seems to be morphologically intermediate between P. anubis and P. hamadryas (Hill 1970, p261). Were its social organisation also to occupy an intermediate position, we might conclude that P. papio represented an evolutionary link between P. hamadryas and the savanna baboons, such that either

- (1) P. papio was closely similar to the ancestral species from which the Papio species derived, or
- (2) in radiating from a form similar to the savanna baboons to the P. hamadryas form (or vice versa), the baboons passed through the P. papio form.

Alternatively, some remarkable near-parallel evolution has taken place, the reasons for which would also be of great theoretical interest.

The second major implication of Boese's suggestion goes beyond baboon taxonomy and evolution. If social organisation is adapted to ecological conditions, as we believe it is (see Clutton-Brock and Harvey 1976, 1977, Crook 1970b for reviews), then ecological explanation for the evolution of one-male groups must now account for its appearance within troops of P. papio. At least some of these baboons exist in habitats floristically richer and structurally more diverse than either those of baboons which live in one-male groups (P. hamadryas, Nagel 1971, 1973; T. gelada, Dunbar and Dunbar 1974c) or those of some baboons which live in multi-male troops (eg P. anubis at Gilgil, Harding 1976, Demment in prep, or P. cynocephalus at Amboseli, Altmann and Altmann 1970, Western and van Praet 1973). In the search for a unitary explanation for ecological pressures leading to the formation of one-male groups we would thus be presented with both a problem, and, possibly, a key to its solution, in the adaptation of P. papio.

However, some doubt exists whether Boese's account is correct. For example, Anthoney (1975) states that while Boese (1973) had shown that some adults interacted more often than expected with certain adults of the opposite sex, the data showed that adults did not form exclusive

relationships with other adults (Anthoney 1975 p654-660).

Any explanation proposed for the social organisation of the troops at Mt. Assirik must accommodate and perhaps account for the variability in troop size between wet and dry season (Chapter 3).

This thesis has so far shown that P. papio at Mt. Assirik behaved in many respects like other species of baboons elsewhere. The general assumption for this chapter is that the social organisation of these baboons can reasonably be compared with the known social organisations of baboon troops. These societies belong to:

- 1) The hamadryas, in which one-male groups whose memberships are stable (Kummer 1968a, Kummer and Kurt 1963, Sigg 1980), associate with other one-male groups in bands (Kummer 1968a) whose membership is closed and whose size does not vary seasonally. These bands may meet other bands peaceably at sleeping-cliffs (Kummer 1968a, Kummer and Kurt 1963, Müller 1980), where they form sleeping troops (Kummer 1968a, Kummer and Kurt 1963) whose membership is not stable (Kummer and Kurt 1963). The bands themselves are made up of two or more clans of related animals (Abegglen 1976, Stolba pers comm). The band often, but not always (Stolba 1979) moves to a foraging site as a unit (Kummer 1968a), but once there, fragments into small foraging parties each consisting of one or two one-male groups (Kummer 1968a, Stolba 1979). Such parties always contain at least one adult male (Kummer 1968a).
- 2) The gelada, in which one-male groups whose memberships are stable (Ohsawa and Kawai 1975), associate with other one-male groups to form bands all units of which have a common home range. Groups of one male units, making up either part or all of a band, or parts of several bands, come together to form herds (Crook 1966, Dunbar and Dunbar 1975), whose membership is somewhat variable (Ohsawa and Kawai 1975) and whose size changes seasonally (Crook 1966, Ohsawa and Kawai 1975). The herds graze cohesively, members of each one-male group mingling with members of others (Crook 1966, but see Mori and Kawai 1975).
- 3) The savanna baboons. The social unit of these baboons can be regarded as the troop (Hall and DeVore 1965), which usually forages cohesively, and whose size does not normally fluctuate seasonally (though see

Anderson 1980a, 1980b). Small foraging parties may separate from the main body of the troop (Aldrich-Blake et al. 1971, Rowell 1966a) occasionally overnight (Mu^{ll}ler 1980, Stoltz and Saayman 1970) or for a day or more (Anderson 1980b). Such parties are of unstable composition and do not necessarily contain an adult male (Aldrich-Blake et al. 1971, Hall 1963a, Stoltz and Saayman 1970).

- 4) Boese's (1973, 1975) model of the social organisation of P. papio suggests that these baboons live in multimale troops within which are one male groups. The multimale group would presumably correspond to the band of P. hamadryas, but it is not known whether P. hamadryas-like sleeping troops exist. The behaviour of the troop while foraging is said to resemble that of P. hamadryas.
- 5) P. hamadryas x P. anubis troops, whose social organisation was described by Sugawara (1979) and Mu^{ll}ler (1980). Stable one-male groups associate both with other one-male groups and with animals associating in a savanna-baboon-like troop. Separate foraging parties, some of constant, some of variable composition frequently detach themselves from the main group, often for a day or more (Nagel 1973, Sugawara 1979). It is not clear whether such parties always contain an adult male.

9.1.2: Approach

The direct, and preferable, approach to a study of the social organisation of a troop of primates depends upon having a large proportion of the individuals in a well-habituated troop recognisable to the observer. When this is not possible, much can be done with habituated troops whose members are not all recognisable (eg Hall 1962b, Hall and DeVore 1965, Rowell 1966a, Washburn and DeVore 1961), although the authors of such studies must be cautious in their interpretation (thus some of Washburn and DeVore's generalisations have been revised; see Aldrich-Blake et al. 1971, Altmann 1979, Anderson 1980b, Kummer and Kurt 1963). When the subject animals are timid, and individuals are not recognisable, various indirect approaches can be used (eg Aldrich-Blake et al. 1971).

The distinction that I have made between social organisation and mating systems in this and the following chapter is arbitrary, since almost all aspects of social organisation are influenced by the mating system. In this chapter I discuss the composition of foraging groups, association between age-sex classes in group movements, or progressions, and examine progression data for the possibility of all-male groups moving together. Intertroop interactions and transfer between troops are also discussed in the context of social organisation. In the next chapter I examine the composition of social groups, the identity of nearest neighbours, the inter-individual distances between adults in social periods, certain "indicator" behaviours between adult males and adult females, and those aspects of grooming which relate to mating systems. Finally I present a tentative model for the social organisation of the Guinea baboon at Mt. Assirik consistent with the data collected there. This model is interpreted in the light of the environment at the field site and predictions are made from the model which could form the basis of future research.

9.2: Foraging Groups: Introduction

When foraging, many troops of baboons of the genus Papio divide into smaller units (Aldrich-Blake et al. 1971, DeVore and Washburn 1963, Hall 1960, Kummer 1968a, Stoltz and Keith 1973, Stoltz and Saayman 1970, this study).

In P. hamadryas the composition of both foraging and social groups is probably similar, since the basis of both is the one-male group (Kummer 1968a). In savanna baboons the composition of foraging parties may be influenced by ecological pressures, such as feeding competition or predation, in a way that social groups are not. For example, Wrangham (1980) suggests that adult females in large coalitions may displace smaller coalitions from preferred food sources; we may predict that more foraging groups than expected contain several adult females or adult females and young. Furthermore, several authors suggest that adult males may protect other animals against predation by their presence (eg Hall and DeVore 1965, Rhine and Owens 1972). Animals of all age-sex classes may

therefore seek to forage near adult males, who would then be overdispersed through the foraging groups.

Some of the foraging groups of P. papio should therefore outwardly resemble P. hamadryas foraging parties, with groups containing adult females, young, and single adult males occurring rather more frequently than expected by chance. Such groupings have been noticed in savanna baboons troops (eg Aldrich-Blake et al. 1971, Anderson 1980b) and in P. papio (Boese 1973, Dunbar and Nathan 1972). Although there are no comparative data, the principal difference in foraging parties of P. hamadryas and those of the savanna baboons is probably that foraging groups containing adult females but no adult males are rare in P. hamadryas but common, although less common than expected at random, in the savanna baboons.

This section investigates the composition of foraging groups at Mt. Assirik and examines three propositions:

- 1) that adult males are likely to be found in a higher proportion of foraging groups than expected,
- 2) that groups containing adult males and adult females, possibly with young, are found more frequently than expected, and
- 3) that adult females are likely to be found in foraging groups containing other adult females more frequently than expected but in groups containing no other adult females less frequently than expected.

9.2.1: Foraging Groups: Methods

A foraging group was defined as a group of from two to five baboons, apparently spatially separated from any other baboons, most of whose members were either moving between food sources, or gathering or eating food (i.e. not resting or engaging in social activity). Poor visibility over much of the field area made a strict criterion of spatial separation impractical. Groups of more than 5 were excluded from this analysis because large groups might be made up of multiples of one-male groups (eg Kummer's "two-male teams") in which the appearance of more than one adult male would have biological significance which would be misinterpreted.

Smaller groups were less likely to include more than one one-male unit.

Whenever possible, when a foraging group was encountered its age-sex composition was recorded. All such records were classified by whether the group contained none, one, or more than one adult males and adult females. Results could therefore be tallied into a 3x3 matrix.

Expected frequencies for each cell of the matrix were calculated from the multinomial distribution using the known proportions of each age-sex class in the population.

9.2.2: Foraging Groups: Results

The troops usually set off from sleeping sites in a cohesive progression. Frequently they moved roughly in single file, with occasional bunching, before fanning out as they began to forage. When foraging in woodland the troop split up into small parties and spread out. Coordination of movement between parties may have been through quiet grunting or by cracking or splitting noises made in the course of processing food. The troops were known to split into subtroops which foraged independently, sometimes many kilometres apart, each subtroop itself often split into foraging parties (Sharman, Whiten and Hall in prep).

The area over which the coherent troop spread was normally very hard to determine, but was typically about 500m x 250m. When foraging in areas of good visibility, such as short-grass plateaux, the group usually became more cohesive and the parties indistinct. Dunbar and Nathan (1969) recorded that a troop of P. papio divided for a day or two.

There were 635 animals in the 215 foraging groups whose composition was recorded. Their age-sex composition is shown in Table 9.1. Adult males were slightly over-represented in foraging groups (Table 9.1).

Groups containing more than one adult male were slightly more common than expected, and foraging groups contained no adult females more often than expected (Table 9.2).

Both adult males and adult females were found in foraging groups containing at least two adult males more frequently than expected; (chi squared = 24.6; df = 1; $p < 0.001$ and chi squared = 9.7; df = 1;

Table 9.1:

Crude Age-Sex Distribution of Animals Sampled in
Foraging Groups - Expressed as Percentages

Figs in parentheses are 95% binomial confidence limits

Age-Sex Class	Foraging Group	Population
M	30.6 (28-34)	22.7 (20-26)
F	28.7 (26-32)	32.1 (29-35)
Y	40.8 (38-44)	45.2 (42-48)

Table 9.2:

Number of Foraging Groups Containing Various Numbers of Adult
Males and Adult Females

	Females		Males	
	obs	exp	obs	exp
none	85	66.8	77	97.3
one	84	87.7	87	86.9
more	46	60.5	51	30.8
	215		215	

$p < 0.01$ respectively) (Table 9.3).

Adult males were found more frequently than expected in foraging groups containing: other adult males, and either no adult females, or more than one adult female (chi squared = 18.51; $df = 1$; $p < 0.001$ and chi squared = 5.36; $df = 1$; $p < 0.05$ respectively)(Table 9.3). They were also found more often than expected, but not statistically significantly so, in foraging groups containing other adult males and a single adult female (chi squared = 3.21; $df = 1$; ns) (Table 9.3). As a result, adult males were found in foraging groups containing at least one other adult male more frequently than expected (chi squared = 24.59; $df = 1$; $p < 0.001$) contrary to prediction (Table 9.3).

Foraging groups containing at least one adult female, one adult male and one animal from another age-sex class were seen on 45

Table 9.3:
Number of Animals of Three Age-Sex Classes found in Foraging
Groups of 9 Compositions

		No Adult Females			One Adult Female			More Ad. Females		
		obs	exp	<u>chi</u>	obs	exp	<u>chi</u>	obs	exp	<u>chi</u>
No Adult Males		-	-	-	-	-	-	-	-	-
	Y	76	56.85	6.45	34	68.77	17.58	21	35.12	5.68
One Adult Male	M	26	28.83	0.28	46	34.86	3.56	15	23.22	2.91
	F	-	-	-	46	34.86	3.56	32	50.49	6.77
	Y	32	48.12	5.40	44	38.92	0.66	7	21.24	9.55
More Ad. Males	M	57	32.48	18.51	34	25.03	3.21	16	9.04	5.36
	F	-	-	-	16	11.63	1.64	19	9.18	10.50
	Y	29	16.04	10.41	15	10.67	1.76	1	2.01	0.51

Table 9.4:
Number of Animals of Three Age-Sex Classes found in Foraging
Groups of Various Compositions: Summary Table

This table represents the marginal totals of Table 9.3

Age-Sex Class		No Adult Females			One Adult Female			More Adult Females		
		obs	exp	<u>Chi</u>	obs	exp	<u>chi</u>	obs	exp	<u>chi</u>
M		83	61.31	7.67	80	59.89	6.75	31	32.26	0.05
F		-	-	-	84	87.68	0.15	98	134.95	10.12
Y		137	121.01	2.11	93	118.36	5.43	29	58.37	14.78
		No Adult Males			One Adult Male			More Adult Males		
M		-	-	-	87	86.91	0.00	107	66.55	24.59
F		69	116.47	19.35	78	85.35	0.36	35	20.81	9.68
Y		131	160.74	5.50	83	108.28	5.90	45	28.72	9.23

occasions, which was less frequent, though not significantly so, than expected (chi squared = 0.61; df = 1; ns). This does not support the predicted trend. While adult males were found in such groups with a

frequency similar to that expected by chance (chi squared = 0.32; df = 1; ns) adult females were unlikely to be found in them (chi squared = 0.32; df = 1; $p < 0.05$) principally because adult females were less likely than expected to be found in mixed groups in which another adult female was present (chi squared = 14.81; df = 1; $p < 0.001$).

9.2.3: Foraging Groups: Discussion

Kummer (1968a) reported that when foraging, groups of baboons sitting together in shade would normally be a complete one-male group. By contrast, between 15% and 30% of small foraging parties at Mt. Assirik contained adult females but no adult males, comparable with the 25% to 42% (95% confidence limits) of foraging parties seen by Aldrich-Blake et al. (1971) which contained adult females but no adult males. This observation makes it improbable that adult males attempted to maintain control over a harem of adult females while the troop was foraging. Indeed, it is hard to imagine how an adult male could do so under conditions of restricted visibility (Chapter 2). A mating system based on temporary consortship of oestrus females would still be feasible, as it was at Gombe Stream Reserve, where visibility was equally poor (eg Ransom 1971).

Adult females normally moved off shortly after I moved into sight, while immature animals especially and adult males occasionally might watch me for a while before starting to feed once more. This presumably accounts for the over-representation of adult males in the sample of foraging groups, and may have biased the results in favour of groups containing adult males and those containing no adult females.

In summary, foraging groups were apparently similar to those found in savanna baboons and rather unlike those found in P. hamadryas. Since the composition of social groups differed from that of foraging groups (Chapter 10), animals were probably free to associate differently in the two contexts. Foraging groups, unlike social groups, were unlikely to contain no adult males but, instead, were likely to contain more than one adult male. The observation that more foraging groups

than expected contained no adult female seemed to imply that adult females were likely to be found in each other's company, but this was not supported by more detailed examination of the data. There was some suggestion that females were more likely than expected to be found in foraging groups containing adult males, although this trend was not significant.

The observation that adult males tended to be found together suggests affiliation between adult males. Since adult females were found more frequently than expected in foraging groups containing at least two adult males, there are two possible hypotheses: (1) that adult males might form foraging coalitions or might forage together in mutual defense against predators, and that females also benefitted by foraging in these groups, or, (2) that adult males formed coalitions to restrict access of other adult males to associated adult females.

Since neither adult females nor adult males were found more frequently than expected in social groups containing more than one adult male, the second hypothesis seems unsupported. It is possible, however, that males in such sexual coalitions would tend to be found in adjacent but temporarily segregated social groups; until individuals are recognised these suggestions remain speculative.

9.3: Association between Age-Sex Classes: Introduction

In an environment like that at Mt. Assirik, where the troops typically fragmented into foraging parties, individuals might be expected to stay close to other particular individuals from whom they do not wish to be parted. Such attraction might result in certain age-sex classes being found next to each other in progressions.

9.3.1: Associations Between Age-Sex Classes: Methods

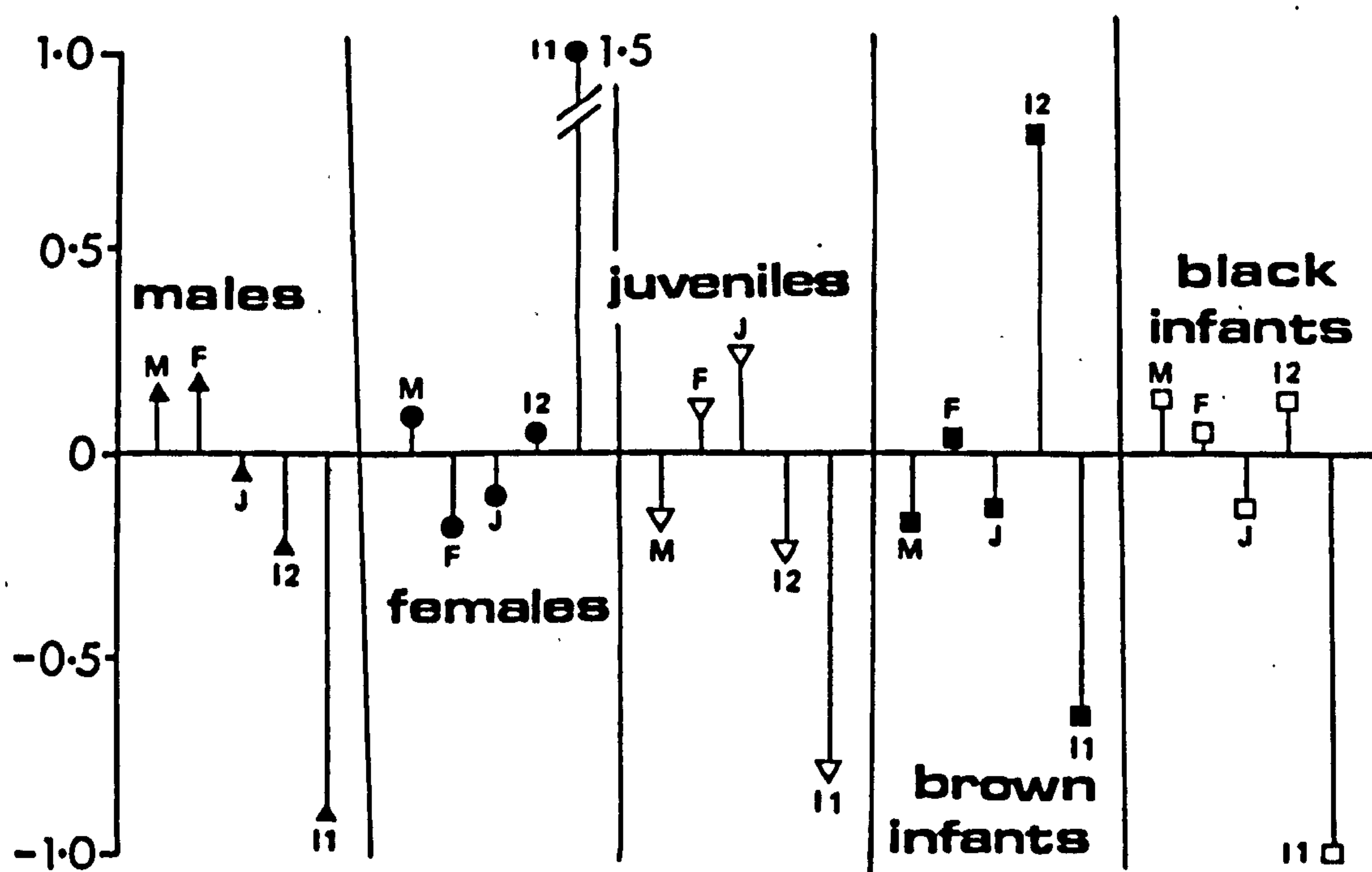
The methods by which censuses were taken is described in Chapter 3. The sequence in which animals passed a census point was preserved in the collection of the data. Most censuses fulfilled the criteria used by Altmann (1979) in his "Type III" progressions, in that every individual could be classified as an adult male, adult female, juvenile, or infant,

and its relative position in the progression was known. The 80 largest censuses were used in this analysis. This large sample was used because most progressions were several metres in width, with animals following several roughly parallel paths, so that the observer saw a stream of animals passing whose relative lateral positions was not always clear, especially given the foreshortening effect of binoculars. Furthermore, in recording a census of a progression a complicated and shifting pattern of animals was reduced to a single linear sequence. If A followed B in this resulting sequence A need not have followed, or even been near to, B in the progression. However, if age-sex class A were found to follow age-sex class B frequently enough, a real association between the age-sex classes might exist.

The age-sex class of and sequence within every pair of adjacent animals was tallied. The age-sex classes used in the analysis were: adult male (M), adult female of unknown reproductive status (F), female with swollen sexual skin (assumed to be in oestrus) (E), adult female carrying an infant dorsally (D), adult female carrying an infant ventrally (V), subadult male (S), older juvenile (O), younger juvenile (Y), and infant (I). Some age-sex classes were recorded too infrequently to be analysed separately and were pooled with other categories. Thus all classes of independent infant (black, transitional, and brown) were classed together as infants (I). Subadult females were pooled with the older juveniles, and pregnant females were pooled with adult females of unknown reproductive status. For this analysis the start and the end of progressions were treated as though they were a single age-sex class, "null", which could be followed or could follow. (Note that null could never follow null. One cell in the resulting matrix is therefore empty, and its statistically expected frequency (1.03) is not the same as its logically expected frequency (0). The error introduced by this was ignored, since it seemed unlikely to affect the results significantly; see Brown (1974), Enke (1977) and Fagen and Mankovich (1980).)

The frequencies in the resulting matrix were compared with the frequencies expected on the basis of the proportion of each age-sex

Figure 9.1:
Deviation from expected $((\text{Obs}-\text{Exp})/\text{Exp})$ in frequency with which given age-sex class was immediately followed in progressions by: M (adult males) F (adult females of any reproductive status) J (subadults and juveniles) I2 (brown infants) and I1 (black infants).



class in the eighty censuses. The tendency of the various age-sex classes to follow other age-sex classes was represented pictorially, using chi squared as a measure of association.

9.3.2: Associations between Age-Sex Classes: Results

The age-sex class of animals starting and ending progressions was not random. Adult males were over-represented at the start of progressions (chi squared = 36.08; df = 1; $p < 0.005$) being at the head of 58% of them, while subadult males brought up the rear in 10%, which was significantly more often than expected (chi squared = 8.84; df = 1; $p < 0.005$). Young juveniles were under-represented both in the first and in the last position in progressions (chi squared = 9.61; df = 1; $p < 0.005$ and chi squared = 5.19; df = 1; $p < 0.025$ respectively).

Five of the nine age-sex classes of baboons (adult male, adult female carrying an infant dorsally, older juvenile, younger juvenile, and infant) were likely to follow an animal of the same age-sex class significantly more often than they would by chance alone (chi squared, $p < 0.01$ for all classes but adult males, for which $p < 0.05$). Females carrying infants ventrally were also followed by adult females carrying infants dorsally more frequently than expected (chi squared = 7.457; df = 1; $p < 0.01$). Females of unknown reproductive status tended to follow adult males (chi squared = 4.64; df = 1; $p < 0.05$) and subadult males tended to follow older juveniles more frequently than expected from their frequency in the population (chi squared = 4.13; df = 1; $p < 0.05$). These relationships are summarised in Fig 9.1.

Of the 141 occasions on which oestrus females were seen in these censuses, 60% were either immediately following (30%) or being followed by (30%) an adult male. This association between the two classes was not statistically significantly greater than expected, but for reasons discussed below, there may have been an attraction between the two classes which the method used here was unable to detect.

Several of the age-sex classes were found to follow others less frequently than expected by chance. These results are summarised in

Figure 9.2:

Association between various age-sex classes in group progressions. Each line represents one unit of chi squared. Arrows point towards age-sex class that was followed.

For clarity, no lines are shown representing any given age-sex class following another member of that age-sex class.

Note that adult animals tend to follow other adults, and immature animals (with the exception of infants) tend to follow other immatures.

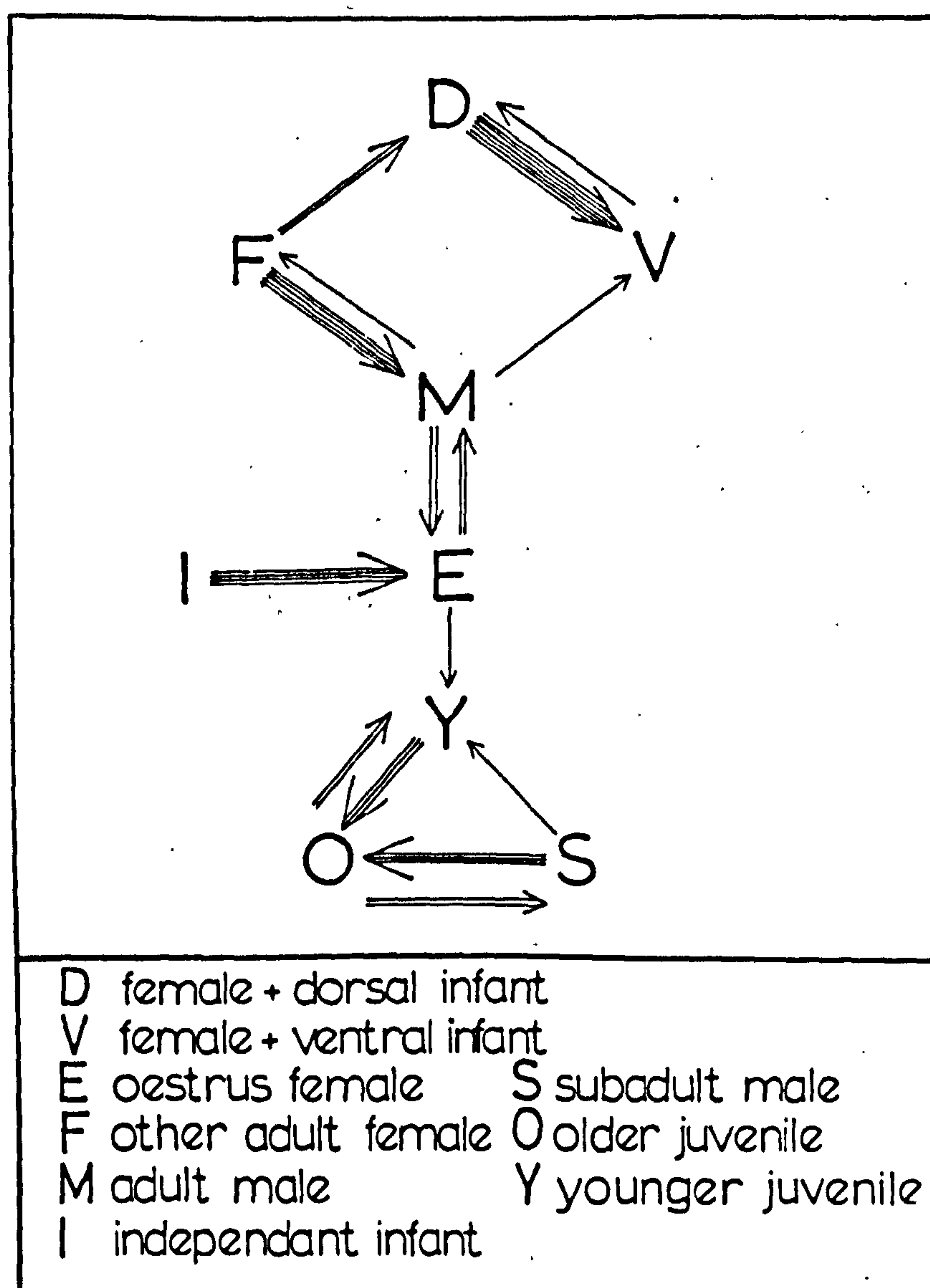


Fig 9.1.

The data suggest that adults tended to travel more with each other than with subadult and juvenile animals, who in turn associated amongst themselves (Fig 9.2).

9.3.3: Associations between Age-Sex Classes - Other Studies

These data were compared with those presented by Aldrich-Blake et al. (1971) for a troop of P. anubis. A qualitatively similar grouping was found, with subadult and juvenile individuals associating among themselves and adults associating with other adults, although age-sex classes were less likely to be seen with other members of the same age-sex class, with the strongest association being amongst young juveniles. The adult associations tended to be between males and females of various reproductive states, and not amongst the females. Oestrus females were followed by adult males on 50% of occasions (n=40) while they followed adult males on 30%.

The data were also compared with those given in Altmann (1979). The only qualitative difference was that in his study females followed other females less frequently than expected. However, Altmann defined infants riding on their mother as "following" their mothers. This affected 123 of the nominal 148 "following" infants. The number of females seen to be followed by other adult females therefore excludes an unknown number of females which by Altmann's definition would then be "following" the infant. In other respects the results are closely similar, with adult females following adult males more than expected, juveniles rarely following males, but often following another juvenile, and older infants travelling together.

Associations between age-sex classes in progressions at Mt. Assirik thus seems consistent with those of at least one troop of P. anubis and one of P. cynocephalus.

9.3.4: Association Between Age-Sex Classes: Discussion

The associations found in progressions did not distinguish clearly between social organisations, but suggested that adult females of various reproductive states were likely to maintain bonds amongst themselves and with adult males. Oestrus females were an exception to this generalisation, apparently associating little with other adult females and only weakly with adult males. This observation might suggest that adult males need not compete for oestrus females, which would be consistent with a harem society. In P. hamadryas groups, oestrus females are constrained to mate with only one male, so that males in P. hamadryas groups do not follow oestrus females more than the female follows the male (Mu"ller 1980, Nagel 1971). By contrast, in P. anubis groups, males compete for access to oestrus females, and males in P. anubis groups tend to follow oestrus females more frequently than the females follow the males (Mu"ller 1980, Nagel 1971). There are several objections to this interpretation of the data collected at Mt. Assirik.

- 1) Mu"ller (1980) was able to show that P. anubis males followed anoestrus females more than the females followed the males. This is apparently unusual for savanna baboons (eg Altmann 1979). Thus the strong tendency for males to follow oestrus females in Mu"ller's baboons might have been a local characteristic, although one study of P. cynocephalus has demonstrated a similar pronounced trend (Rasmussen 1980), and P. ursinus females are said to lead their male consorts (Saayman 1970).
- 2) Females here classed as "oestrus" were in fact any female with swollen sexual skin. This included females at all stages of this phase of the sexual cycle, some of whom would not have been attractive to mature males (Collins pers comm, Tayler and Saayman 1972). Female P. cynocephalus with partially swollen sex skin followed males far more frequently than they were followed by the males (Rasmussen 1980).
- 3) There is evidence that adult baboons formed consortships with some oestrus females. These pairs, in which the female was probably at

her most attractive to the male (Tayler and Saayman 1972), tended to be found on the periphery of the troop (pers obs). If this was generally the case then there was a bias against records of adult males in close association with sexually receptive females, since these pairs would have been less likely to be seen and recorded during censuses.

- 4) Finally, the method by which these censuses were recorded tended to compact progressions laterally (see Methods). Thus a male following 2m behind an oestrus female might be recorded as following a third animal which was several metres to one side of the pair.

The observation that 60% of all observed oestrus females were in close association with an adult male thus becomes biologically important.

9.3.5: Runs of Males: Introduction

Progression order appears not to distinguish clearly between the social organisation found in P. hamadryas and that found among the savanna baboons (Altmann 1973a, 1979, Altmann and Altmann 1970, Bert et al. 1967b, Boese 1973, DeVore 1965a, Hall and DeVore 1965, Harding 1977, Kummer 1968a, Popp 1978, Ransom 1971, Rhine 1975, Rhine and Owens 1972, Rowell 1969, Stoltz and Saayman 1970, Washburn and DeVore 1961).

Progression order does serve to distinguish baboons of the genus Papio from T. gelada, however. In T. gelada, the mating system, where one male takes over a group of related females, excludes some of the adult male population from the breeding group. These excluded males form all-male groups which, according to Crook and Aldrich-Blake (1968), are usually found at the head of the herd in progressions. If P. papio has a similar social system, with the existence of all-male groups, "runs" of adult males should occur in progressions more frequently than they would by chance.

9.3.6: Runs of Adult Males: Methods

Runs of adult males should occur particularly in the larger troops, where there would be more excluded adult males. The seven largest censuses, totalling 1853 age-sex records, were used in this analysis. The number of adult males seen adjacent to one another was recorded. In very large progressions we may ignore the error introduced by assuming replacement sampling, so that if males assort themselves at random relative to other adult males, then the probability of encountering an adult male in any position in the progression is $p=0.23$, the proportion of adult males in the population. If the chance of encountering an animal which is not an adult male in each position is $q = 1-p = 0.77$, then the probability of counting j adult males before reaching the first other animal is

$$p(j) = p^j q = 0.23^j \times 0.77 \quad (j=0,1,2,\dots)$$

which defines the geometric distribution (Pollard 1977). If adult males associate in all-male groups, the observed frequencies of large (eg 6 or more) groups of adult males will exceed the expected value calculated from the geometric distribution.

9.3.7: Runs of Adult Males: Results

Of the 299 adult males recorded in the 7 largest censuses, 198 (66%) were preceded and followed by an animal which was not another adult male (Table 9.5).

The frequency distribution of numbers of adult males found in sequence was not a statistically good fit to the geometric distribution (chi squared = 22.2; $df = 2$; $p < 0.001$). By inspection, this lack of fit was due to rather fewer males than expected being found alone and rather more than expected found in pairs and threes (Fig 9.3). Runs of adult males longer than 5 were not expected, but one run of 6 males was recorded. Thus although most males were seen with animals that were not adult males, more than expected were seen in the company of other adult males.

Table 9.5:

Frequency Distribution of Numbers of Adult Male Baboons
Found in Progressions

Number in run	Frequency obs	exp	chi sq
1	198	230.23	4.51
2	66	52.95	3.22
3	25	12.18	13.49
4	9	2.80	(13.73)
5	0	0.64	
6	1	0.15	
>6	0	0.03	
	299		22.22

9.3.8: Runs of Adult Males: Discussion

The data from Mt. Assirik suggested that adult males tend to be found in the vicinity of other adult males rather more frequently than they would by chance alone. The data do not suggest blocks of adult males travelling together, as would be expected in a population with large socially peripheral all-male groups, but seem consistent with a model in which a multimale group contained adult males which showed an attraction towards each other. This attraction between males may be general to the savanna baboons. Adult males of the "central hierarchy" were seen to associate closely by DeVore (1965), and a qualitatively similar pattern to that seen at Mt. Assirik was found in the data on P. cynocephalus presented by Altmann (1979). In the latter example adult males distributed at random would have been found in shorter runs than predicted by the geometric distribution, because the sample is small (484 individuals), the proportion of adult males is low (0.15) and no progression contained more than 8 adult males, so that replacement sampling could not be assumed.

9.4: Intertroop Encounters: Introduction

When two troops of baboons meet each other, the resulting interaction between the troops may be territorial (Hamilton et al. 1976), while others, though not necessarily territorial, involve overt fights, especially between adult males (Buskirk et al. 1974, Saayman 1971c). Many workers have observed encounters in which adult males herded adult females away from the other troop (eg Cheney and Seyfarth 1977, Saayman 1971a). DeVore and Hall (1965), Nagel (1973) and Harding (1976) had reason to believe that the troops that they were studying tended to avoid other troops. Other workers describe intertroop encounters which were seasonally peaceful (Paterson 1973), frequently peaceful (Ransom 1971), or invariably peaceful (Aldrich-Blake et al. 1971, Hall 1962b, 1963a, Kummer 1968a, Rasmussen pers comm), while a few report encounters in which troops mingled (Saayman 1971c, and, for herds of T. gelada, Crook 1966), or even exchanged members (Rowell 1966a).

Aggressive encounters between troops have been interpreted as competitive interactions over restricted and defensible resources (Hamilton et al. 1976, Saayman 1971a, 1971c), while highly peaceable interactions have been taken to imply that the troops involved have recently separated or are in the process of splitting (Aldrich-Blake et al. 1971, Rowell 1966a).

Males that are about to transfer out of their natal troops may start to establish relationships with members of other troops during intertroop interactions. If these interactions are peaceable, transfer may well be easier (Manzillillo in prep, Rasmussen pers comm).

9.4.1: Intertroop Encounters: Methods

It was extremely difficult to observe intertroop encounters, since (a) the majority of the troop was normally out of sight, and (b) I was normally moving at the back of the troop, and most encounters would presumably occur near the front or leading flanks of the troop, and (c) even when I could see two groups moving closer together I was rarely certain that they were two different troops and not subtroops of a

larger troop.

This was particularly true in the dry season, when the troops were generally smaller (Chapter 3), and I therefore included in this report an indication of the season in which the observations were made.

Peaceable interactions were judged to have happened when the number of animals in a progression exceeded the largest number (250) known to occur in any troop. Aggressive intertroop encounters are accompanied by characteristic behaviour, including vocalisation, in other species of baboons (pers obs) which would have been recorded at Mt. Assirik had it occurred.

9.4.2: Intertroop Encounters: Results

In the wet season troops were large and of apparently stable membership (Chapter 4). Encounters between these large troops were apparently peaceable, with at least some members of one troop moving into the other troop and peacefully associating with members of that troop. One such encounter occurred about 2 km from the nearest sleeping site, and the resulting large group moved together to the sleeping site (Chapter 3). At least 3 other similar encounters occurred near or at sleeping sites. Troops were observed to share sleeping sites on many occasions. After separation from the other troop, each troop seemed to keep its original membership.

In the dry season, the large troops fragmented (Chapter 4). These smaller troops apparently frequently rejoined each other and the resulting larger troops later fragmented. It is not known whether the membership of these fragments was constant. All such fissions and fusions of troops were peaceable, though usually prefaced and accompanied by increased loud barking (Byrne in press and pers obs).

The behaviours associated with aggressive intertroop encounters (described in Buskirk et al. 1974, Hamilton et al. 1975b, 1976, and Saayman 1971c) were not seen at Mt. Assirik in the context of intertroop encounters in either season.

9.4.3: Intertroop Encounters: Discussion

Peaceable interactions between troops at Mt. Assirik may owe their origin to the ecology of the area. The site contained a high proportion of productive habitat relative to most of the rest of the park, apparently capable of supporting a large biomass of baboons, but had few sleeping sites or sources of permanent water. The best data for home range area come from Fable's troop, which included 8 known sleeping sites, at least 7 of which it shared with one or more of at least 4 other troops (Chapter 5). By a rough calculation, if sleeping sites were used at random, each troop would share with at least one other on about one night in ten. Sleeping sites were widely dispersed (median distance to next nearest site = 1.5 km; Chapter 6), so that the cost of being displaced from a sleeping site was a journey whose median length was roughly 20% of the mean day range of the troops (Chapter 5). The cost of sharing most sleeping sites was probably low, since each site contained many trees (Chapter 6), and if communal roosting gives protection from predators (eg Bradbury and Vehrencamp 1976b) there might have been a net benefit in sharing the site. Under these circumstances peaceful interactions at sleeping sites would probably be to the advantage of both troops, and peaceable interactions elsewhere in their home range might help to reinforce the relationship. Whatever the reason for such peaceful intertroop interactions, they probably made it easier for individuals to transfer between troops.

9.5: Transfer Between Troops: Introduction

Irrespective of the environment, the ease with which adult males can transfer between troops of baboons varies greatly across baboon species, and is probably partly influenced by the mating structure of the species.

At least some one-male groups in T. gelada transfer readily between herds (Ohsawa and Kawai 1975), but there is no documented case of a P. hamadryas one-male group or solitary adult male moving between bands. Some evidence that entire one-male groups do not normally transfer between bands in P. hamadryas was provided by experiments (Kummer 1968a)

in which two one-male units were released near or among a strange sleeping troop. One unit was chased away by several of the resident male, while the females of the other unit were kidnapped by resident males and its adult male driven off, after severe fighting, by the entire sleeping troop (of 350 animals).

The difference between the ease with which T. gelada units can switch between herds and the difficulty experienced by P. hamadryas units may stem from the differences in their mating systems. Many T. gelada adult males are excluded from the breeding population and live in all-male groups on the periphery of the herds, occasionally succeeding in taking over a harem of a family of females from the previous harem male (Dunbar and Dunbar 1975). The transfer of an entire one-male group therefore represents no threat to, and may confer a benefit on, its recipient herd. By contrast, P. hamadryas males form harems by kidnapping single females, usually as juveniles or adolescents, but occasionally as adults from other one-male units, after fighting with the previous "owner" (Kummer 1968a, p49). The introduction to the band of a new adult male, especially one in late adolescence or early adulthood, must therefore present a threat to all of the resident males in the band, and is apparently resisted vigorously (Kummer 1968a, p112).

Among the savanna baboons the movement of males between troops is well documented (eg Packer 1975, 1977b, Rasmussen 1979) and nearly all male baboons probably transfer between troops at least once in their lifetime (Packer 1979, Manzilillo in prep, Hausfater 1973a). Transfer may be so easy in savanna baboons that adult males may sometimes move between troops temporarily, shifting back into their own troop later (Rowell 1966a, Tayler and Saayman 1972). In these baboons mating by any female is not restricted to any single male. Resident males who are highest in agonistic rank are often (eg Hausfater 1975b, Rasmussen 1980), but not always (eg Saayman 1971a, 1972a, Strum in prep), more likely to succeed in copulating with females at the period of their probable maximum fertility. Although newly transferred males may rapidly achieve high agonistic rank (Packer 1979, Manzilillo in prep),

they are likely to succeed in few potentially fertile copulations until they have been resident for about a year (Packer 1979, Strum in prep). Resistance to incoming males is therefore of little immediate reproductive benefit to the resident males, and may incur severe costs, such as debilitating injury. Packer (1979) has shown that the residents most likely to resist the new males are those of similar age, which are those which, presumably, have the most to lose by allowing the new males in.

9.5.1: Transfer Between Troops: Methods

At all times during the day, but especially during social periods, all visible baboons were scanned in detail for any characteristics which might serve to identify them at a later date. A register was made of all such individuals. The methods used for recognising, recording and indexing recognised individuals are given in Sharman (in prep). The presence of other known individuals was also recorded, and in this way a register of known individuals in each troop was compiled. Any movement of any recognised individual from one troop to another was recorded.

9.5.2: Transfer Between Troops: Results

On 8/8/78 two troops, containing between them about 450-500 individuals, coalesced and moved about 2km together (Chapter 3). An adult male with a characteristic and immediately recognisable tail was seen with this group. This individual had not been seen before, but was later seen on several occasions to groom and be groomed by adult females in Fable's group, while sitting near to a particular known adult male. He appeared unstressed and accepted by the troop.

9.5.3: Transfer Between Troops: Discussion

The observation of a previously unknown male with a characteristic tail might have come about by (a) a failure of the part of the observers to notice him on previous occasions, or (b) a fresh injury to his tail giving it its characteristic shape. However, by the time the first record of this male was made all other animals in both Fable's and

Anecdote's troops with such easily distinguished characteristics had been recorded. Furthermore, once he had been seen, he was seen repeatedly for the remaining three months of the study, and it is improbable that he had been missed for the first sixteen. The possibility of a fresh injury, however coincidental, cannot be ruled out, but he was never seen to pay any attention to his tail or to prevent it being groomed on several occasions. Other baboons with apparently recent injuries were seen to lick or to touch them and behave as if they were painful. In summary, the evidence suggests that this male had previously belonged to another troop and had transferred into Fable's troop when the two troops temporarily joined each other.

The evidence for male transfer between troops at Mt. Assirik is anecdotal, resting on one incident. However, this single example serves to reject the hypothesis that transfer between troops was as difficult for P. papio at Mt. Assirik as it was for P. hamadryas at Awash. By implication, then, if P. papio mates in one-male groups, the groups are more likely to be founded on groups of related females, as in T. gelada, than they are on kidnapped, coerced females as in P. hamadryas.

SUMMARY

The social organisation of P. papio is not yet clear, nor will it be until individuals are known. However, within populations of a single species of baboons, and indeed within one troop over time, one can find a range of different social organisations (Dunbar 1979^a, Altmann and Altmann 1979). This apparently depends partly on the demography of the troop. Members of groups as large as those observed in this study may form relationships in many complex ways (Hinde and Stevenson-Hinde 1976), so that it is perhaps not surprising that P. papio does not fit easily into any of the known social organisations of baboons. Despite this P. papio at Mt. Assirik resembled the savanna baboons in many aspects of their social organisation. They foraged in small groups, unlike T. gelada. About one in five of these foraging groups contained

adult females but no adult males, which is unlikely in P. hamadryas. Associations between age-sex classes were similar to those found in savanna baboons.

The males of P. hamadryas tend to be found in pairs in a moving clan (Kummer 1968a), but males in P. papio were found in runs of lengths that were close to that expected if the males were dispersed randomly through the progressions. In this also they apparently resemble savanna baboons. One transfer between troops was recorded, in which the animal was accepted easily. This is characteristic of some savanna baboon populations but not of P. hamadryas.

CHAPTER 10: Mating Systems

INTRODUCTION

10.1: Review of Earlier Work

The detailed mating strategy of any member of a troop probably depends upon its age, its rank, the number of other animals in the troop, whether or not it has kin in the troop, the age-sex structure of the troop, the presence and structure of neighbouring troops, and so on (Dunbar 1979a, Hausfater 1975b, Rasmussen 1980). Despite this variability, strong evidence exists that the fundamentals of baboon mating systems are species specific (Mu"ller 1980, Nagel 1971, Sugawara 1979). We may therefore find that the mating system of P. papio differs from that of other baboons.

Our current view of the mating system of P. papio rests largely on Boese's (1973, 1975) published work (reviewed briefly in Chapter 9). Since Boese's field work was not designed to examine mating structure, but to record the age-sex composition of foraging parties (Boese 1973), and since any account of social organisation based on observations of animals in captivity should be treated with caution (Kummer and Kurt 1963, Rowell 1967a), we should hesitate to ascribe to P. papio a mating system in which each breeding male has exclusive mating rights over one or more adult females.

In this chapter I assume that the mating system of the baboons at Mt. Assirik is similar to one or other of the five mating systems thought to exist in baboons. These are, in brief:

- 1) The mating system of P. hamadryas, described by Kummer and Kurt (1963) and by Kummer (1968a), in which particular adult females may only mate with particular adult males. Behaviour characteristic of such a mating system includes the herding of anoestrus females by adult males (Kummer 1968a, Kummer and Kurt 1963) and near-continual attention between particular adult females and particular adult males (Kummer 1968a, Kummer and Kurt 1963). Most of the time spatial proximity between members of the group is maintained by the females, but when an adult female strays from the adult male he will chase and sometimes bite or slap her (Kummer 1968a, Kummer and Kurt 1963). Oestrus

females will rarely interact with (Kummer 1968a) and never present openly for copulation to more than one adult male in succession (Kummer and Kurt 1963). There is some suggestion that the adult males recognise a dominance hierarchy (Abegglen 1976, Kummer 1968a), but males are never seen to compete for oestrus females: "at most, a male would follow the [sexual] swellings of a passing female with his eyes" (Kummer 1968a). Female members of different one-male groups sometimes interact and mingle (Abegglen 1976, Sigg 1980 p276, Stolba 1979).

- 2) The mating system found in T. gelada, with all-male groups on the periphery of mixed-sex herds (Crook 1966) which, unlike P. hamadryas, are made up of groups of related females (Dunbar 1979b). These females mate only with an adult male which is always associated with them (Dunbar 1979b). Group cohesion is largely maintained by the adult females, but the adult male spends most of his social time grooming the adult females (Dunbar 1978a), in which T. gelada differs again from P. hamadryas. The adult male attempts to prevent other adult males, particularly those belonging to the all-male groups, from interacting with adult females (Dunbar 1979b, Dunbar and Dunbar 1975). Adult females rarely interact with more than one adult male in succession, although a secondary male is sometimes associated with the group. The primary male usually interrupts any interaction of the secondary male with the females (Mori and Kawai 1975). In this P. hamadryas and T. gelada are similar.
- 3) The mating system of the savanna baboons. In these baboons, groups of related females, or matriline, interact amongst themselves and with females from other matriline within the troop (Cheney 1977, Ransom and Ransom 1971, Strum in prep). Consortships, or mating associations, are frequently seen between oestrus adult females and adult males (Collins in prep, Hall and DeVore 1965, Hausfater 1975a, Paterson 1973, Ransom 1971, Rasmussen 1980, Saayman 1971a). Individual adult females and adult males may form special associations which persist outside the female's oestrus periods (Altmann 1980, Packer 1977b, Ransom 1971, Rasmussen 1980, Seyfarth 1978). Herding of anoestrus females by adult

males is rarely seen except during intertroop encounters (Cheney and Seyfarth 1977) or during "gathering [of] troop members and chasing them in one direction" (Saayman 1971a). Oestrus adult females may frequently interact with or present for copulation to more than one adult male (Collins in prep, Seyfarth 1978) who will frequently ignore her invitation (Saayman 1970, Seyfarth 1978).

- 4) The model due to Boese (1973), in which one-male groups are embedded in multi-male troops. Adult males "consistently" herd and punish anoestrus adult and adolescent females (Boese 1975), in which P. papio would then resemble P. hamadryas but not T. gelada or the savanna baboons. Oestrus females never interact with or present for copulation to more than one adult male in succession (Boese 1973), again, like P. hamadryas or T. gelada. An adult male hierarchy exists (Boese 1973), so that unlike P. hamadryas, adult males interact over resources, although competition (presumably) never takes place between males for access to adult females (Boese 1973).
- 5) The mating system found in P. hamadryas x P. anubis troops by Sugawara (1979) and by Müller (1980). In these complicated societies some individuals behave like P. hamadryas and some like P. anubis. Thus behaviours characteristic of both mating systems are seen.

I have chosen to analyse five aspects of social life, each of which helps in some way to decide between these mating systems. Small groups of animals involved in social behaviour in a harem society will have different compositions from those of animals in a more liberal one. The age-sex class of the nearest neighbours of, for example, adult females, will depend upon whether it is they or adult males who are the focus of attention of other adult females. Inter-individual distances between adult animals depends on both the sex of the pair and on the species (Nagel 1971). Some behaviours of adults depend upon whether it is the male or the female that is responsible for the maintenance of proximity (Nagel 1971), and finally the nature of grooming relationships will depend on whether or not matrilineal kin groups exist (Dunbar and Dunbar 1975, Kummer 1968a, Müller 1980, Saayman 1971b).

10.2: Social Groups: Introduction

The composition of social groups of baboons is apparently sensitive to the mating structure in the troop. In a study of three troops of baboons of different species, Nagel (1971) found that in the P. hamadryas troop, where females were socially restricted by an adult male, 80% of social groups containing adult females also contained an adult male. By contrast, in the troop of P. anubis baboons, where adult females were free to interact with other individuals, only 49% of social groups containing adult females also contained an adult male ($t = 3.37$, $p = 0.001$).

10.2.1: Social Groups: Methods

Nagel (1971, p51) "recorded the size and composition of detached parties in each of the resting groups. The criterion of...detachment...was [that] the smallest distance between the [party] and another animal was greater than 4m and 4 times larger than the greatest distance between 2 neighbouring animals within the [party]". This criterion was also used at Mt. Assirik, although poor visibility meant that it was not always possible to see as great a distance as 4m around the detached party. In practice, the baboons at Mt. Assirik frequently sat and interacted in well-defined clumps of small radius, often with each of the animals in the clump in contact with one or more of its neighbours. Each clump was apparently behaviourally and spatially distinct from neighbouring animals. For this reason I have used the term "social group", implying that the group was at the time behaviourally isolated from neighbouring baboons, even though they might have been less than 4m from their neighbours.

Expected frequencies were calculated from the multinomial distribution, with the known frequencies of each age-sex class in the population and the observed numbers of groups of various sizes, irrespective of their composition.

10.2.2: Social Groups: Results

After the baboons left their sleeping trees, they collected in clear areas, either in the valleys amongst the rocks at the base of the laterite cliffs, or in areas of bare laterite or short grass on the plateau edges

bordering the valleys. The time spent here varied from a few minutes to several hours (Chapter 4). During this time many of the animals associated in groups of from 2 to 10 or more individuals. There was continual sporadic movement both within and between groups so that membership of a single group, especially if small, might stay constant for half-an-hour or more or might, especially with large groups, change several times in a few minutes.

There were 1372 animals, whose age-sex classes are shown in Table 10.1, in the 441 social groups included in the analysis. The frequency of groups containing none, one, or more females was indistinguishable from that expected by chance (chi squared = 1.13; df = 1; ns)(Table 10.2). Furthermore, the number of social groups (136) containing adult females but no adult males was not significantly different from the number expected (151.33) by chance alone (chi squared = 1.55; df = 1; ns).

Adult females tended not to be found in groups containing one adult male together with one or more other adult females (chi squared = 7.14; df = 1; p < 0.01) (Table 10.3) so that the number of adult females found in social groups containing other adult females was smaller than expected (chi squared = 4.33; df = 1; p < 0.01).

Table 10.1:

Crude Age-Sex Distribution of Animals Sampled in
Social Groups - Expressed as Percentages

Figures in parentheses are 95% binomial confidence limits

Age-Sex Class	Social Group	Population
M	24.2 (21-27)	22.7 (20-26)
F	31.2 (28-34)	32.1 (29-35)
Y	44.6 (42-48)	45.2 (42-48)

KEY: M = Adult and Young Adult Male
F = Adult Female
Y = Subadult and other Immature Animals

Social groups containing more than one adult male included neither adult males nor adult females more frequently than expected (chi squared, p > 0.05 in both cases)(Table 10.3). In particular, no social

Table 10.2:
Number of Social Groups Containing Various Numbers
of Adult Males and Adult Females

Expected frequencies calculated from multinomial distribution

	Females		Males	
	obs	exp	obs	exp
none	137	136.5	193	198.7
one	187	179.1	178	177.5
more	115	123.5	70	62.9
	441		441	

Table 10.3:
Number of Animals of Three Age-Sex Classes found in Social
Groups of 9 Compositions

Expected frequencies calculated from multinomial distribution

		No Females			One Female			More Females		
		obs	exp	chi	obs	exp	chi	obs	exp	chi
No Males	M	-	-	-	-	-	-	-	-	-
	F	-	-	-	65	84.11	4.34	149	153.66	0.14
	Y	153	116.09	11.74	111	140.40	6.16	70	71.69	0.04
One Male	M	45	58.87	3.27	97	71.19	9.36	36	47.43	2.75
	F	-	-	-	97	71.19	9.36	76	103.13	7.14
	Y	77	98.27	4.60	108	79.50	10.22	25	43.37	7.78
More than one Male	M	81	66.39	3.22	57	51.34	0.62	16	18.45	0.33
	F	-	-	-	27	23.75	0.44	16	18.75	0.40
	Y	32	24.59	2.23	30	21.79	3.09	6	4.10	0.88

groups of more than 3 animals were composed entirely of adult males.

10.2.3: Comparing social and foraging groups

The compositions of social groups and foraging groups were different (Tables 9.4 and 10.4). Among the more important results were the following:

Table 10.4:
Number of Animals of Three Age-Sex Classes found in Social Groups
of Various Compositions: Summary Table

This Table represents the marginal totals of Table 11.3

Age-Sex Class	No Adult Females			One Adult Female			More Adult Females		
	obs	exp	<u>chi</u>	obs	exp	<u>chi</u>	obs	exp	<u>chi</u>
M	126	125.26	0.00	154	122.53	8.08	52	65.88	2.92
F	-	-	-	189	179.05	0.55	241	275.54	4.33
Y	262	216.95	9.35	249	241.69	0.22	101	119.16	2.77

	No Adult Males			One Adult Male			More Adult Males		
M	-	-	-	178	177.49	0.00	154	136.18	2.33
F	214	237.77	2.38	173	174.32	0.01	43	42.5	0.01
Y	334	328.18	0.10	210	221.14	0.56	68	50.48	6.08

- 1) social groups were less likely than were foraging groups to contain more than one adult male (chi squared = 4.83; df = 1; p < 0.05).
- 2) while social groups containing no adult male were observed with a frequency close to chance (chi squared = 0.16; df = 1; ns) (Table 9.2) foraging groups containing no adult male were observed less frequently than expected (chi squared = 4.94; df = 1; p < 0.05) (Table 10.2).
- 3) By contrast, while social groups containing no adult female occurred with a frequency nearly equal to chance (Table 9.2), more foraging groups than expected contained no adult female (chi squared = 4.94; df = 1; p < 0.05) (Table 10.2).

10.2.4: Social Groups: Discussion

The tendency of P. papio at Mt. Assirik to socialise in small subgroups is apparently shared by other Papio troops (Washburn and DeVore 1961, Altmann 1979, Kummer 1968a). The manner in which animals moved through the socialising troop indicated a society in which individuals were free to interact without constraint, but in which there

was attraction between certain individuals.

About 31% of all social groups contained at least one adult female but no adult male. This observation indicates that adult females were not constrained to interact only within a one-male group, and hence suggests that P. papio at Mt. Assirik did not live in societies with exclusive mating.

Although the numbers of groups containing none, one, or more adult females were close to those expected by chance, adult females tended to associate with adult males only when there were no other adult females already in the group. Furthermore, groups containing more than one adult male and one or more adult females were found as frequently as expected by chance alone. Such behaviour is presumably not characteristic of a harem society.

10.3: Nearest Neighbours: Introduction

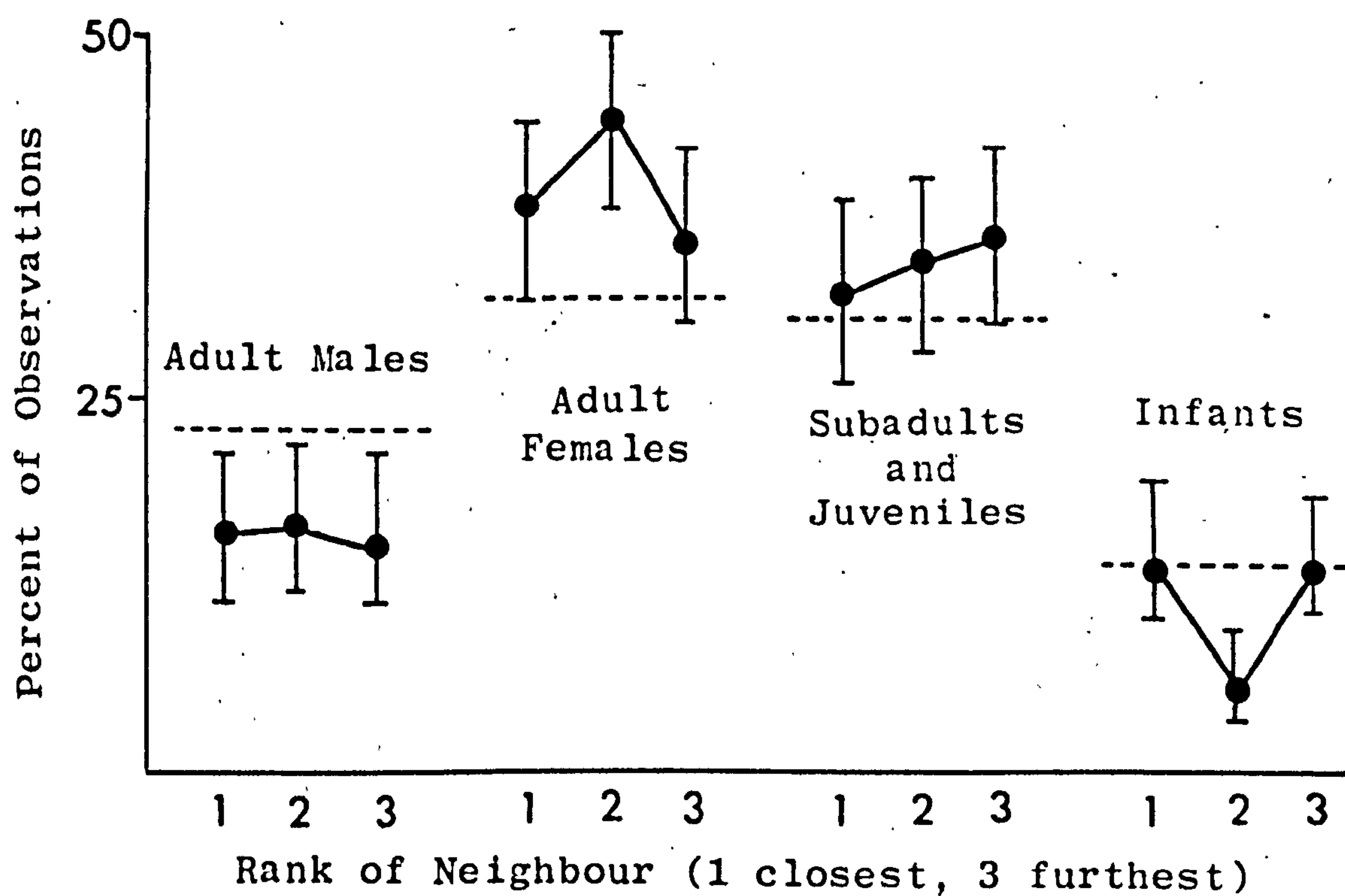
Some information on mating systems can be derived from the analysis of proximity between various age-sex classes during social periods. In particular, adult females with young infants form the foci of social behaviour in P. anubis (DeVore 1965b, Ransom and Rowell 1972,), P. cynocephalus (Altmann 1980), and P. ursinus (Seyfarth 1977), while adult males form the foci in P. hamadryas, especially for grooming relationships (Nagel 1971).

While adult males apparently foraged together and were less likely to be found together in social groups, they were unlike P. hamadryas in that social groups containing more than one adult male occurred more frequently than expected. In P. hamadryas, two male teams forage together but segregate into one-male groups in social times, and social groups containing more than one adult male are apparently rare.

10.3.1: Nearest Neighbours: Methods

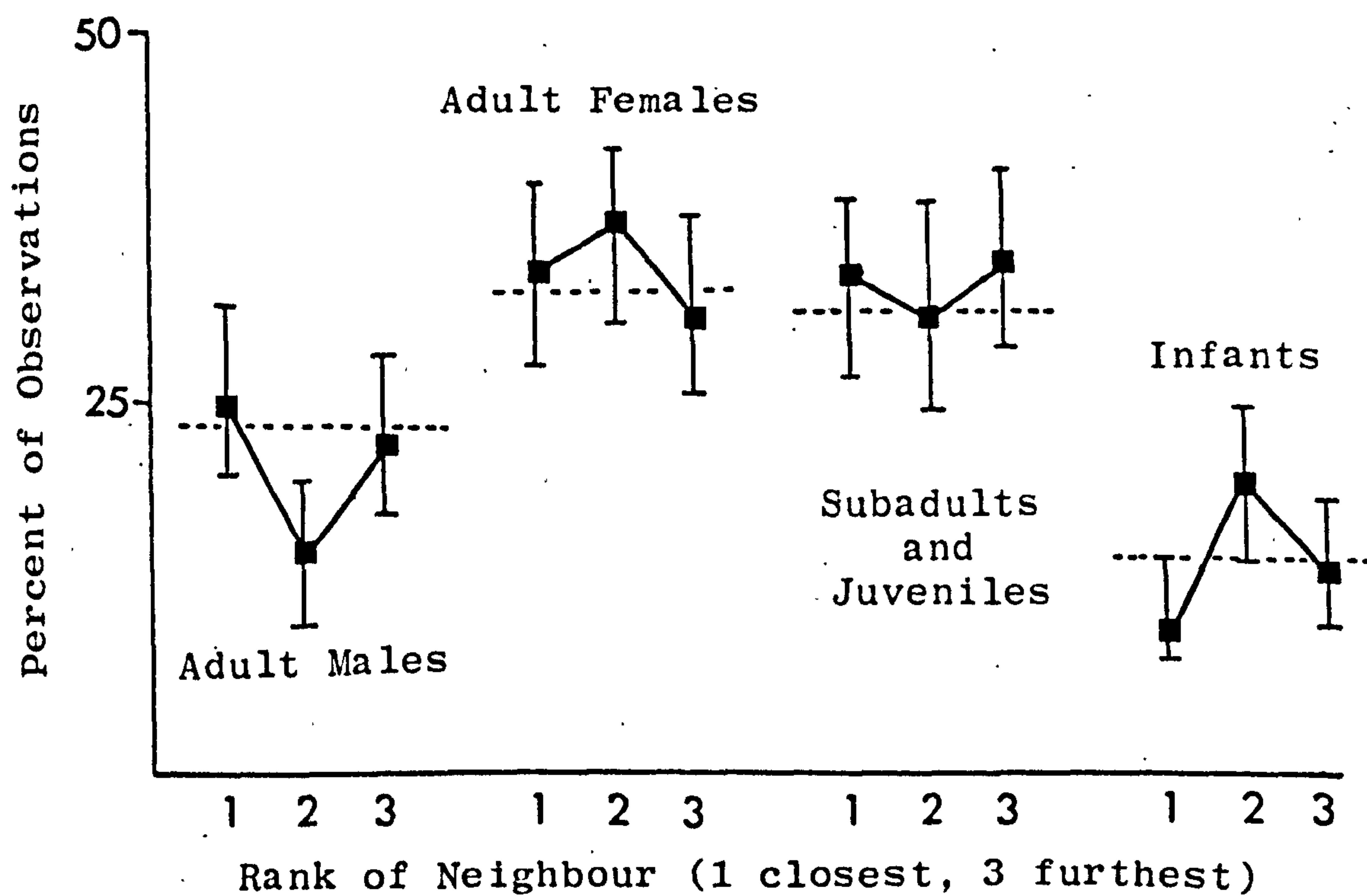
At intervals of 20 minutes during social periods when more than 10 animals were present adult animals were selected at random, with the restriction that these target individuals were chosen so that no vegetation was likely to hide any of the three animals nearest to them.

Figure 10.1:
Percentage of observations in which a given age-sex class
was nearest, second nearest, and third nearest neighbour
to an adult female during social periods



Dashed line represents proportion of that age-sex class
in the population

Figure 10.2:
 Percentage of observations in which a given age-sex class
 was nearest, second nearest, and third nearest neighbour
 to an adult male during social periods.



Dashed line represents proportion of that age-sex class
 in the population

The age and sex of the nearest three animals to this individual, together with their relative distances from the target, were recorded. Another target was chosen from the remaining animals and the process repeated.

The resulting data were tallied and compared with the frequencies expected from the proportion of the various age-sex classes in the population.

The frequencies with which the various age-sex classes were recorded among any of the three nearest neighbours were calculated and compared with data given by Kummer (1968a) and Dunbar (1973).

10.3.2: Nearest Neighbours: Results

For adult males, 306 records of the three nearest animals were made, while for adult females, 295 were made.

Infants were found as the closest animal to adult males on fewer occasions (9.5%) than expected (13.9%) (chi squared = 4.28; df = 1; $p < 0.05$) but in general the distribution among the age-sex classes of the closest animals to adult males did not deviate significantly from that expected by chance alone (chi squared = 6.6; df = 1; ns).

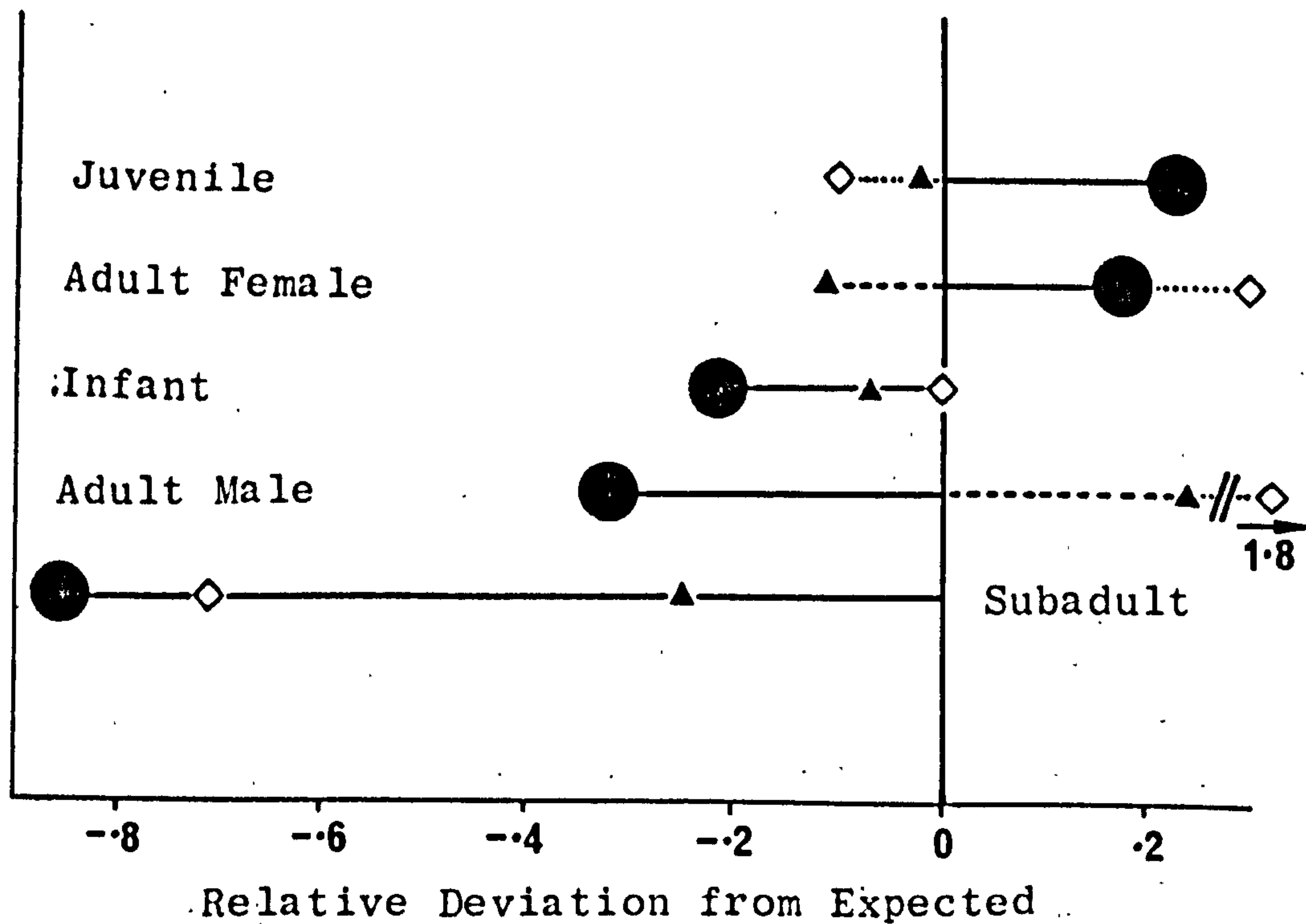
The probability that any given age-sex class was the closest to an adult female was not proportional to the occurrence of that class in the population (chi squared = 14.4; df = 1; $p < 0.01$) principally because adult and subadult males tended not to be the closest animal (chi squared = 5.99; df = 1; $p < 0.025$ and chi squared = 3.98; df = 1; $p < 0.05$ respectively). These results are summarised in Fig 10.1.

Subadult males were rather more likely than expected to be among the three nearest animals to an adult male (95% binomial confidence limits)(Fig 10.1), while infants were rather less. Adult females occurred among the three nearest neighbours with a probability similar to that expected by chance alone.

By contrast, adult males were among the three nearest neighbours of adult females less than expected, while other adult females occurred more frequently than expected (Fig 10.2).

Figure 10.3:
Relative deviation from expected frequency with which various
age-sex classes are nearest neighbour to adult female in
three species.

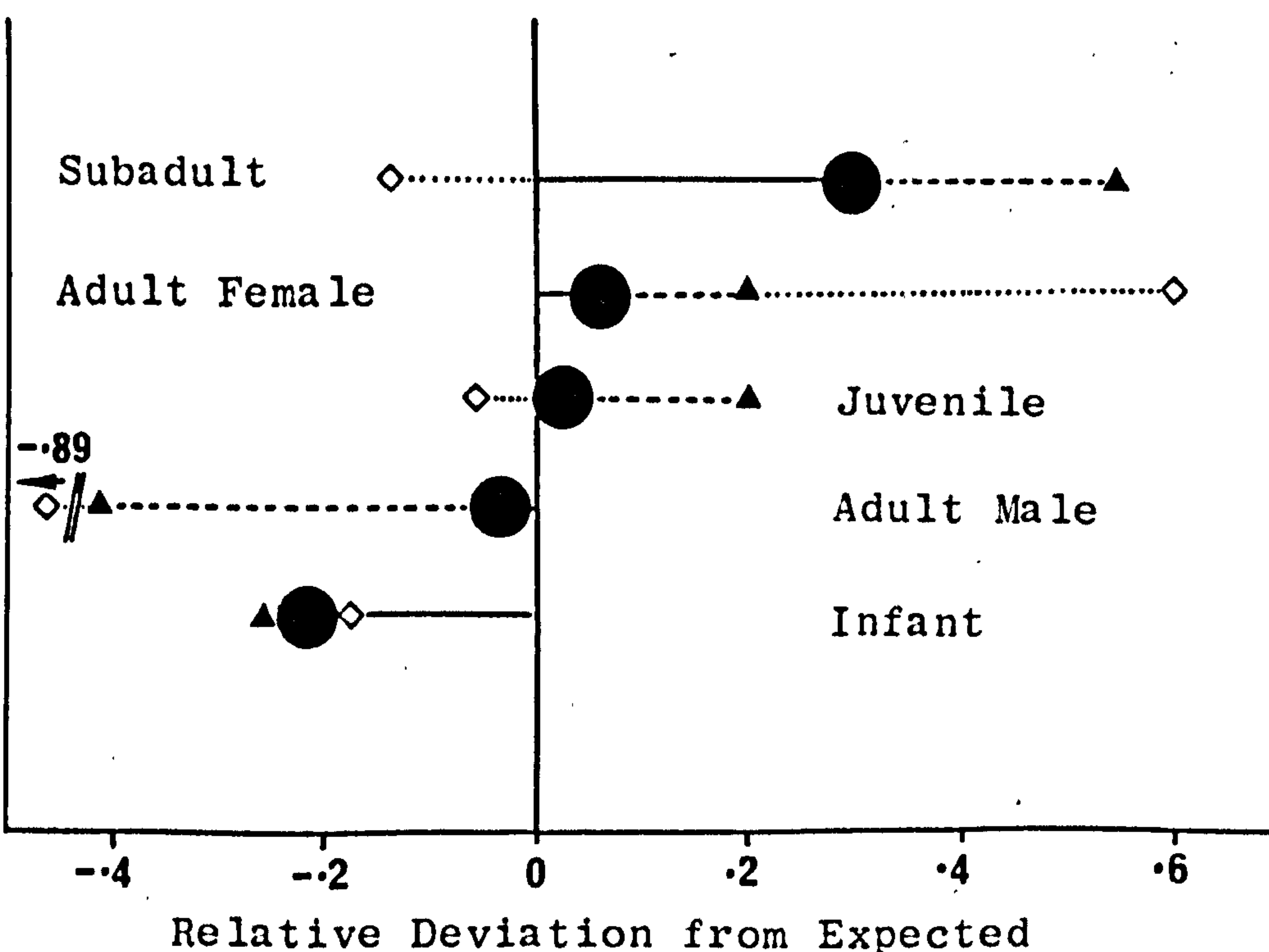
(Relative deviation calculated as: $(\text{Obs}-\text{Exp}) \div \text{Exp}$)



● *P. papio*
▲ *P. hamadryas*
◇ *T. gelada*

Figure 10.4:
Relative deviation from expected frequency with which
various age-sex classes are nearest neighbour to adult
male in three species.

(Relative deviation calculated as: $(\text{Obs}-\text{Exp}) \div \text{Exp}$)



10.3.3: Nearest Neighbours: Discussion

Adult females tended to be found as the nearest neighbours of other adult females and of juveniles. These data contrast markedly with those for T. gelada (Dunbar 1973) and less strongly with those for P. hamadryas (Kummer 1968a) (Fig 10.3). In both these species adult males were unlikely to have another adult male in the nearest three animals, and T. gelada females were found amongst the three nearest neighbours of adult males much more frequently than expected. Adult females of T. gelada were more likely than expected to have both an adult male and another adult female amongst the closest three animals.

Adult female P. papio tended to have both juveniles and adult females amongst their three nearest neighbours. This grouping suggests female social groups with associated young similar to the nurseries reported in troops of savanna baboons and is consistent with a social organisation based upon female kin groups. These data also suggest that P. papio females are in the company of adult males rather less frequently than expected by chance alone. This makes it improbable that the female social groups are socially bonded to adult males, as is the case in T. gelada.

The adult males of both T. gelada and P. hamadryas are rarely found in the company of other adult males, whereas P. papio males apparently associate with other adult males roughly in proportion as they occur in the population.

In summary, the nearest-neighbour data from Mt. Assirik suggest that the baboons there did not interact socially within the constraints of one-male groups similar to those of either T. gelada or P. hamadryas.

10.4: Inter-Individual Distances: Introduction

Inter-individual distance suggests relatedness between individuals in a troop (Schulman 1980). Furthermore the distances at which pairs of animals tend to space themselves form distributions which are species-specific and which reflect the social organisation of the species (Kummer 1974b). Nagel (1971) was able to show that P. anubis males tended to be found much further from adult females during social

Figure 10.5:
Distribution of distances between adult members of opposite sex

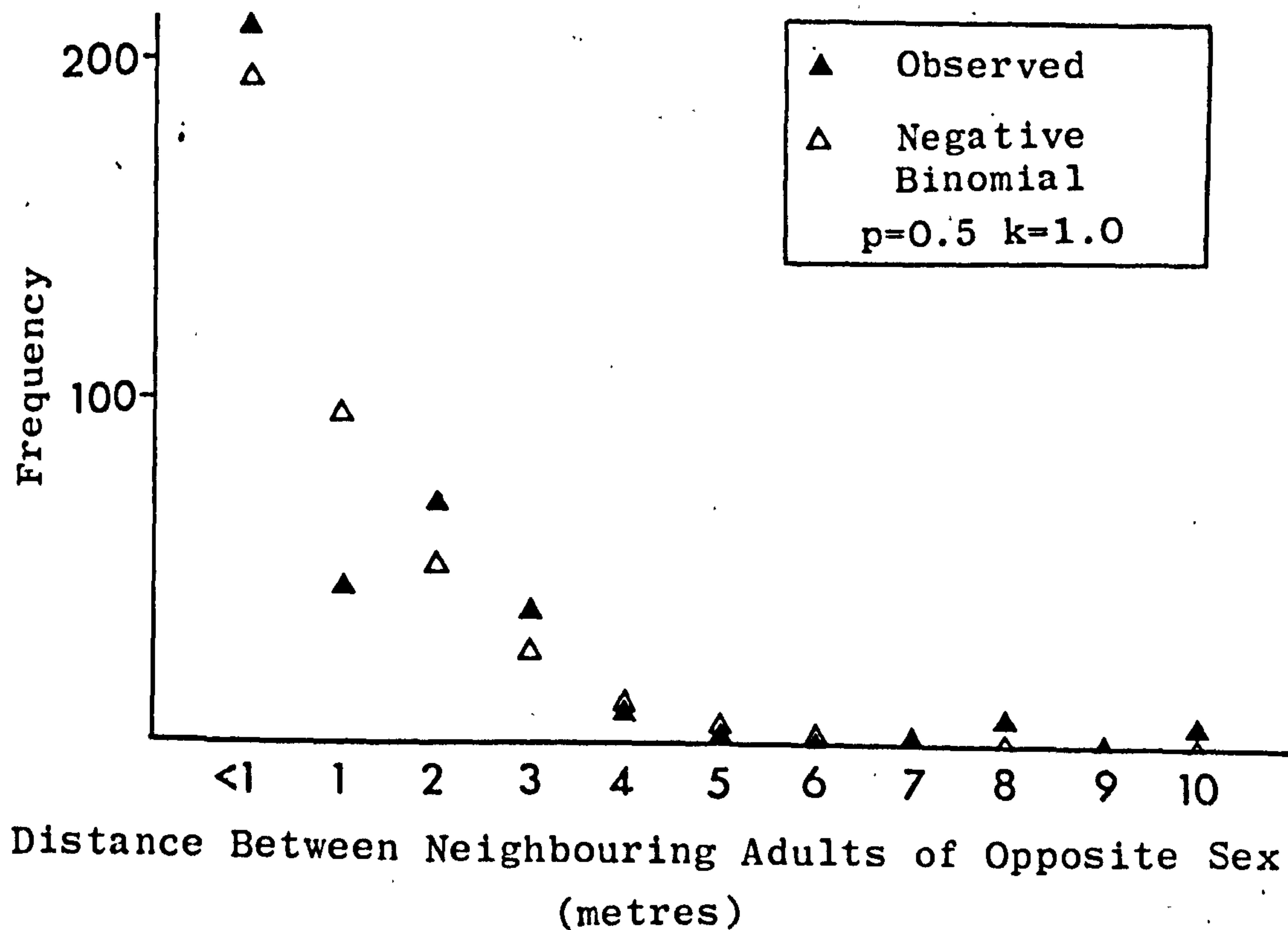


Figure 10.6:
Frequency distribution of distances between nearest adult females during social periods

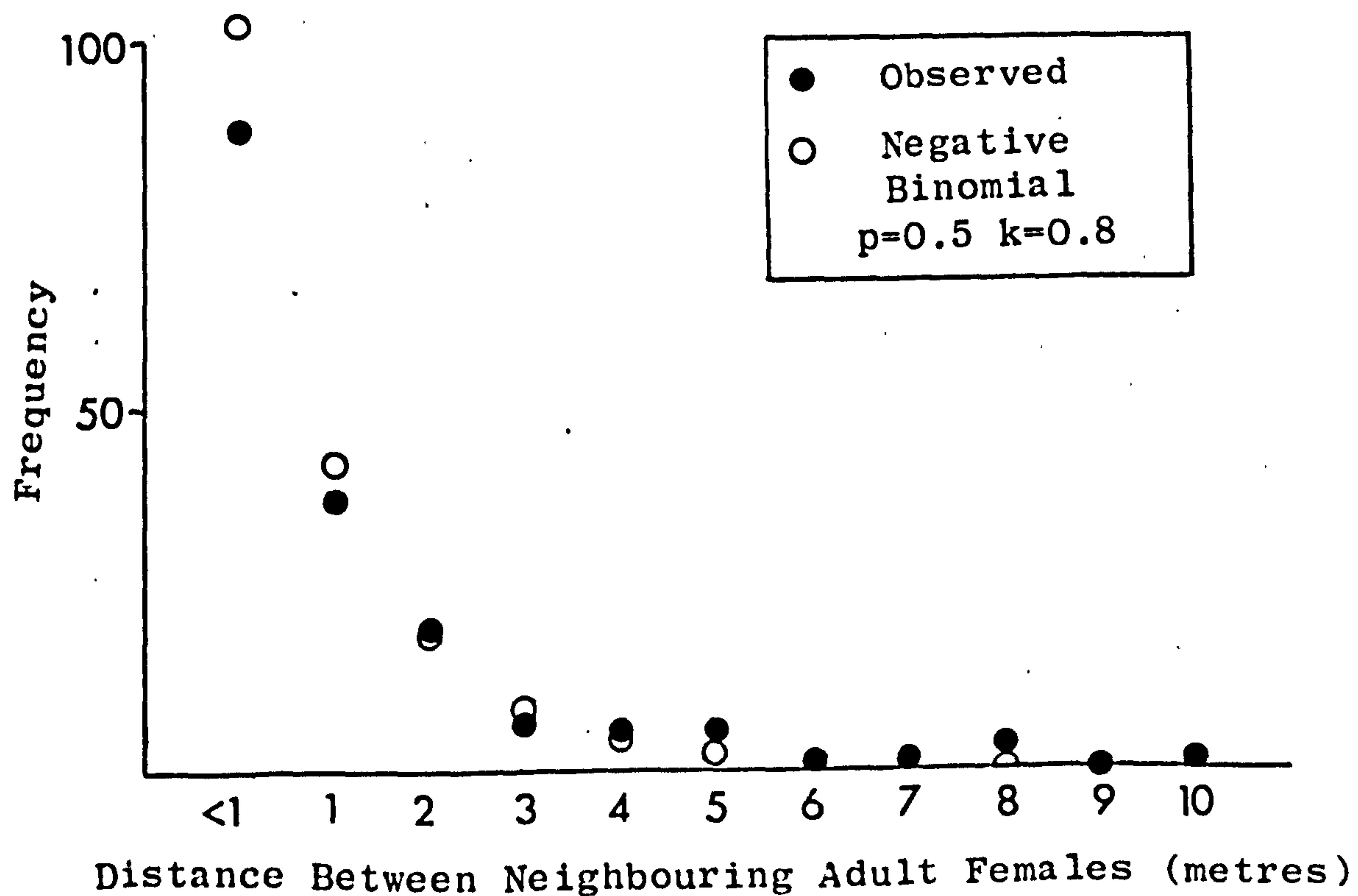
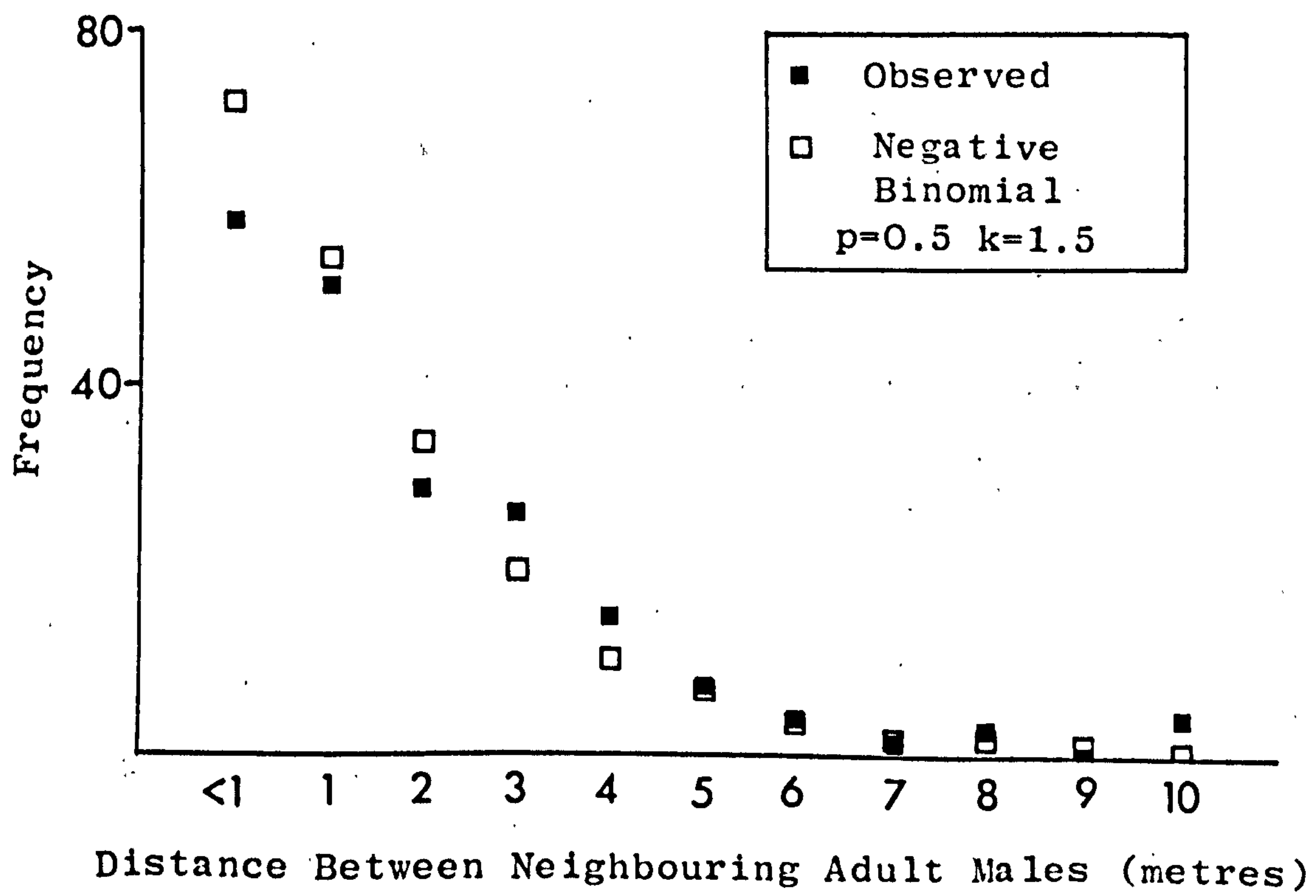


Figure 10.71:
Distribution of distances between adult males



behaviour than were P. hamadryas or P. hamadryas x P. anubis males. In all three troops he found that adult males were unlikely to be found close to other adult males, but that in the P. hamadryas troop the typical distance between adult males was much greater than it was in the other two troops. These findings, he suggested, reflected the mating systems of P. anubis and P. hamadryas; males were not restrictive towards adult females in P. anubis, but males were rather intolerant of each other in P. hamadryas.

10.4.1: Inter-Individual Distances: Methods

When at least 10 animals, 3 of which were adult males, were visible, I estimated the distance, to the nearest metre, from one of the adult males, chosen at random, to both the nearest visible adult male and the nearest visible adult female. Identical methods were used with adult females as the target individuals. Bamboo poles, marked with florescent orange tape at metre intervals, were placed on the ground in the areas where the baboons were observed. These markers helped to estimate distance and were ignored by the baboons. If the nearest adult male or female was more than 10m from the target animal no record was made. This restriction was introduced firstly because vegetation frequently prevented me from seeing animals more than ten metres apart, and secondly because during social periods inter-individual distances were generally small at Mt. Assirik (typically less than one metre; data in this chapter) and this arbitrary cut-off caused few data to be rejected.

10.4.2: Inter-Individual Distances: Results

In 95% of the observed cases (n=386), an adult animal was sitting within 5m of the nearest adult animal of the opposite sex. In 58% of cases they were less than 1m apart. Adult males had another adult male less than a metre away on 29% of all observed occasions (n=205), and less than 5m away on 91%. Similarly, adult females were within one metre of another adult female in 55% of cases, and within 5m in 96%.

Figure 10.8:
Distribution of distances between nearest adults of
opposite sex during social periods

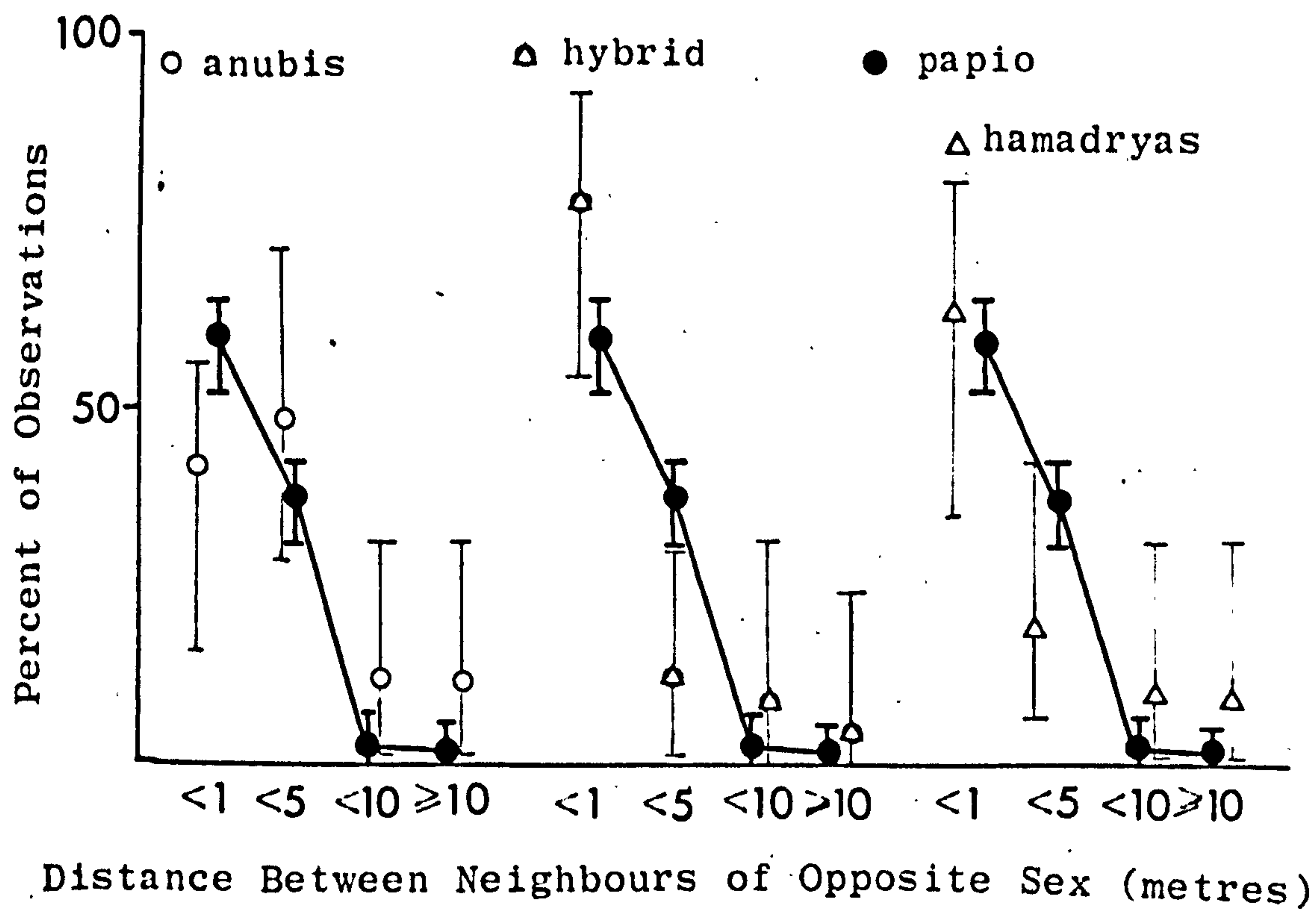
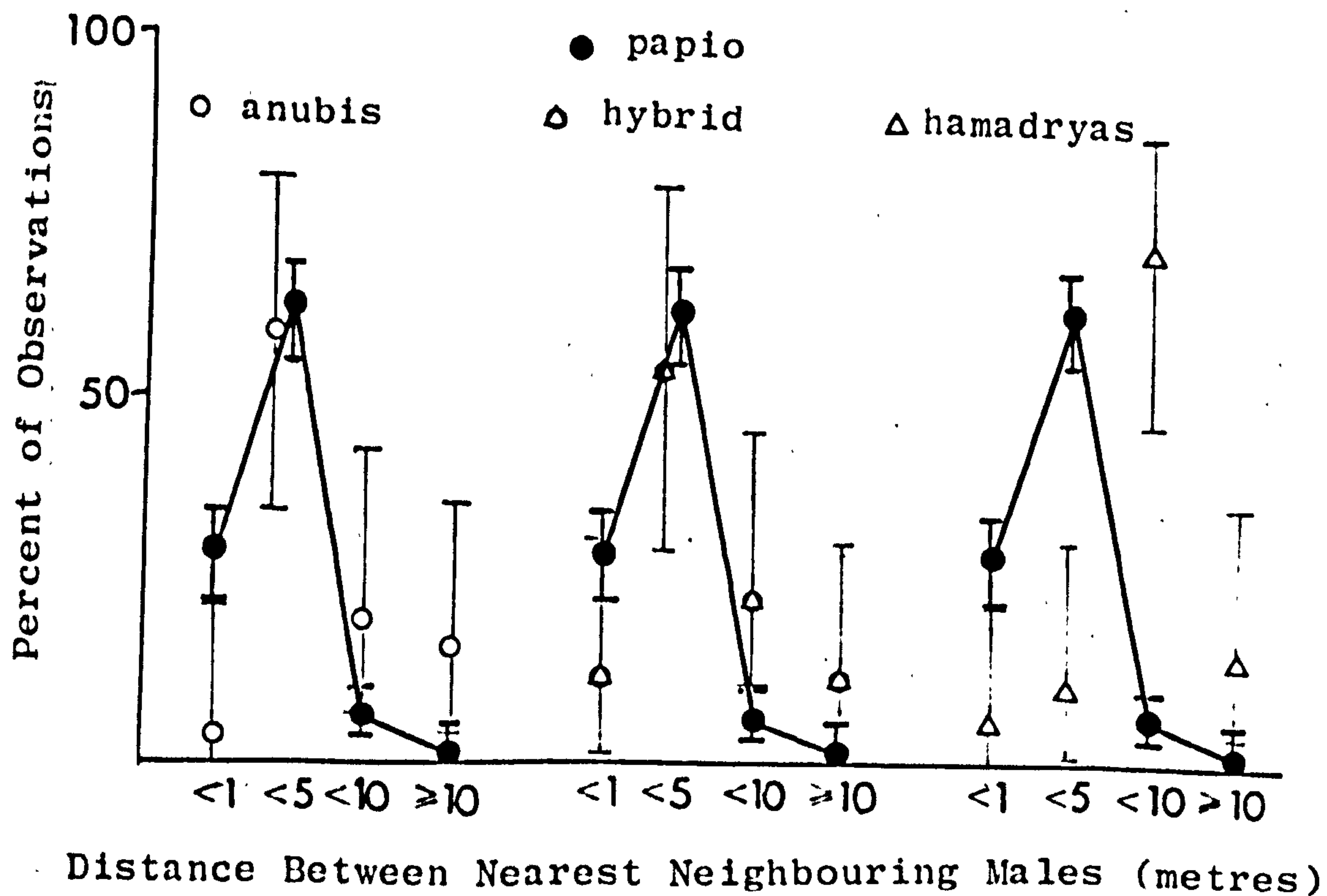


Figure 10.9:
Distribution of distances between adult males in three species



The distribution of distances given by Nagel (1971) between adult members of the opposite sex in P. anubis is significantly different from that found at Mt. Assirik (Kolmogorov-Smirnov two-sample test; chi squared = 8.52; df = 2; $p < 0.05$) (Fig 10.8). The distribution of distances between males in P. hamadryas, according to Nagel's (1971) data, is significantly different from that found at Mt. Assirik (Kolmogorov-Smirnov two-sample test; chi squared = 45.2; df = 2; $p < 0.001$) (Fig 10.9). The distributions of distances between adult males in P. papio might also have differed from those found by Nagel in the P. anubis troop and in the hybrid P. hamadryas x P. anubis troop (Kolmogorov-Smirnov two-sample test; chi squared = 6.50; df = 2; $p < 0.08$ and chi squared = 6.24; df = 2; $p < 0.09$ respectively) (Fig 10.5). (Pollard 1977, p152, warns against accepting the null hypothesis that two distributions are indistinguishable when the test statistic differs only slightly from the nominal critical value.)

In summary, the distribution of distances between adult males and adult females in P. papio resembles those found in P. hamadryas and in the P. hamadryas x P. anubis hybrids, but the adult males in P. papio tend to be found closer together than did males in any of the other troops, and especially those of P. hamadryas.

10.4.3: Inter-Individual Distances: Discussion

These baboons tended to sit closer together than did baboons of other species. It seems probable that this is a reflection of their social organisation, although it may have been a response to poor visibility or partly due to the large numbers of baboons in the troops, leading to crowding in the social areas. Inter-individual distances vary with activity (Schulman 1980), but since Nagel (1971) also took his data during social periods this should not be responsible for the differences between the two studies.

The data presented here for P. papio are clearly different from those presented by Nagel (1971) for P. hamadryas, especially because adult male P. papio were likely to be found within 5m of another adult male. These data are also different from those presented by Nagel on

P. anubis, since adult female P. papio were rather more likely to be found close to an adult male; in this respect they rather resembled the hybrid baboons that Nagel studied.

The observation that P. hamadryas males tended to avoid one another presumably reflects their segregation into one-male groups. The close association between adult males in P. papio makes their segregation into one-male groups improbable, and may indicate close genetic relationships between them (Schulman 1980).

10.5: Male and Female Interactions: Introduction

Nagel (1971) showed that differences in mating structures led to the interactions between adult male and adult female baboons differing on several counts depending on whether they belonged to P. hamadryas, P. anubis, or hybrid (P. hamadryas x P. anubis) troops. Nagel provides data for three 'indicator' behaviours, including:

- 1) whether or not the adult male glanced back when moving away from an adult female with whom he had been "associating", that is, with whom he had either been interacting, or sitting with in a detached party. P. hamadryas males tend to look back to check that the female is following, whereas P. anubis males do not.
- 2) whether or not the female followed the adult male shortly after he moved away, specifically, before he had gone 10m. Adult females in P. hamadryas troops nearly always follow, while P. anubis females do not.
- 3) whether or not the adult female glanced back when starting to move away from an adult male with whom she had been associating. In P. hamadryas groups, the female rarely walks off without checking back, while in P. anubis such behaviour is not usually seen.

10.5.1: Male and Female Interactions: Methods

At Mt. Assirik these data were recorded whenever it was possible to observe the movements of both individuals over about 10m from the position of their initial association. If the male moved out of sight and the female paid no attention, or if either began to interact with

another animal, or if both walked off in different directions, I assumed that social contact had been broken between the two.

10.5.2: Male and Female Interactions: Results

Females moved off first on 54 out of 86 occasions, and were thus more likely to terminate an interaction in this sample (chi squared = 5.63; df = 1; $p < 0.05$). In their 32 leavings, adult males were never observed to look back. Females followed on 6 occasions (19%). When females left first, they checked back on 6 occasions (13%) (Table 10.5).

Table 10.5:

Behaviour of Adults on Ending an Association

Behaviour	YES	NO	n
Male checks back	0	32	32
Female checks back	6	48	54
Female follows	6	26	32
Obedience	12	75	86

In Nagel's (1971) terminology, females gave 75 "disobedience" responses out of 86 opportunities (1:6). In this they resembled closely the 1:8 ratio observed by Nagel in P. anubis and were divergent from the 2:1 and 11:1 ratios of P. papio x P. anubis and P. hamadryas.

10.5.3: Male and Female Interactions: Discussion

Interactions between adult males and adult females in P. papio at Mt. Assirik, as measured by Nagel's indices, showed that these baboons lacked the coordination apparently typical of P. hamadryas, and that in this respect their behaviour corresponded closely with P. anubis at Awash. These results suggest that at Mt. Assirik P. papio showed no herding behaviour, and that these baboons were unlikely to live in harem groups maintained by the behaviour of the adult males; in short, they

were unlikely to possess a mating system like that of P. hamadryas.

10.6: Grooming: Introduction

Of all social activity, grooming took up most time (Chapter 4). Grooming is thought to have important social consequences in many primates, in particular, in the establishment and maintenance of social bonds (Sade 1965, Seyfarth 1977). The mating system is therefore likely to influence the patterns of grooming relationships within the troop. For example, Nagel (1971) showed that adult males groomed adult males in P. hamadryas but not in P. anubis or in the hybrid troops. He also showed that in the P. anubis group adult females were seen to groom adult females with infants significantly more often than expected from their frequency in the population. He related the second of these observations to the social organisation of the three groups. Females are not restrained by adult males from interacting with other individuals in P. anubis troops and are attracted to females with infants, who then form centres of social activity; this has been observed in many troops of savanna baboons (see Washburn and DeVore 1961, Collins in prep). In P. hamadryas, on the other hand, females frequently groom adult males, but are not free to interact with the females of other one-male units (Kummer 1968a, Kummer and Kurt 1963). The distribution of grooming between adult P. hamadryas males is also related to the social structure of this species, for while "the unit leaders do not approach each other at grooming distance, but ordinarily keep at least 1.5m apart...to keep their units from mingling", Kummer (1968a p47) notes that "adult males having no females often groom each other". He goes on to mention that adult males within one-male groups (the "leader" and "follower") may also, rarely, groom each other: "Thus the adult follower...engaged in grooming only with his leader" (Kummer 1968a, p55). Grooming between adult male P. anubis, P. cynocephalus and P. ursinus has not been reported.

If P. papio lives in one-male groups similar to those of T. gelada we predict:

- a) adult males groom one another

- b) adult females groom one another more frequently than expected on the basis of their abundance in the population, and
- c) adult females with infants are groomed more frequently than expected by other adult females.

If P. papio lives in one-male groups similar to those of P. hamadryas we predict:

- a) that adult males are seen to groom one another
- b) that adult females groom one another rather less than expected from their frequency in the population, and, in particular,
- c) that adult females with infants are not groomed by adult females more frequently than expected.

If P. papio resembles the savanna baboons, then

- a) adult males do not groom one another
- b) adult females groom one another more frequently than expected, and
- c) adult females with infants are groomed more frequently than expected by other adult females.

10.6.1: Grooming: Methods

The age and sex of the active partner (groomer) and of the recipient in all grooming pairs were recorded during each scan sample and the results tallied (Chapter 4). When the age and sex of one or other of the partners could not be determined the pair was excluded from the analysis.

I tested the following null hypotheses:

- 1) The age-sex classes were recorded as members of grooming pairs in proportion with their abundance in the population.
- 2) Given that each age-sex class occurred with a certain frequency as a member of a grooming pair, each class was equally likely to groom or be groomed.
- 3) Given the tendency of each age-sex class to groom or be groomed, each age-sex class chose its partners at random.

Several studies, notably that by Nagel (1971), calculate the expected frequency with which age-sex classes groom or are groomed from the proportion of those classes in the population. This could be

stated as the null hypothesis:

- 4) that the animals from each age-sex class were equally likely to groom any animal that they encountered.

The first null hypothesis was tested by tallying for each animal in each age-sex class the age-sex class of the animal which it was grooming. The resulting distribution was compared (chi squared goodness-of-fit) with that of the frequencies with which the age-sex classes occurred in the population.

The second null hypothesis was tested by dividing the participants into active groomers and recipients and comparing the resulting distributions (chi squared goodness-of-fit).

The third null hypothesis was tested by setting up an $n \times n$ matrix of the observed frequencies of grooming pairs with the two distributions (of groomers and recipients) giving the marginal totals. The expected values were calculated as $R \times C / T$ where R = sum of animals in a given age-sex class receiving grooming, C = sum of animals in given age-sex class actively grooming and T = total grooming episodes. For this analysis several age-sex classes were pooled in order to ensure that about 85% of the cells in the resulting matrix had expected values of 5 or more. Pregnant (P) and oestrus (E) females were pooled with adult females of unknown reproductive status (F). Females with infants were classed separately (Fi) as recipients of grooming, but were pooled with other females (F) as active groomers. Subadults (S or Z) older juveniles (O) and younger juveniles (Y) were all pooled (J). Independent infants of all ages (Br, Tr, or Bl) were classified as infants (I). Mature adult males (M) and young adult males ((M)) were pooled (M). This resulted in a 4×5 matrix.

The fourth null hypothesis was tested as follows. The age-sex classes were first pooled as before, then the 4×5 matrix was collapsed still further into the 3×3 matrix M F Y \times M F Y for comparison with the data in Nagel (1971). The expected frequency with which, for example, adult males were seen to groom adult females was computed by multiplying the proportion of adult males in the population (of scan samples) by the corresponding proportion of adult females, and

multiplying this product by the total number of grooming episodes seen.

10.6.2: Grooming: Results

In the scan samples 650 grooming pairs were recorded in which the age, and where appropriate, the sex of both participants could be determined. The various age-sex classes did not participate in grooming in proportion as they occurred in the population (chi squared goodness-of-fit; chi squared = 140; df = 13; $p < 0.001$) (Table 10.6).

Table 10.6:
Observed and expected frequencies of various age-sex classes
participating in grooming

Age-Sex Class	Prop- ortion	Observed grooming	Expected	<u>chi</u> squared
M	.254	340	330.0	0.30
F	.295	522	382.0	50.46
E	.014	21	17.7	0.62
P	.004	10	4.8	-
F1	.025	52	32.6	11.50
S	.031	21	39.7	8.77
Z	.002	4	2.6	-
O	.141	158	183.0	3.33
Y	.127	97	165.0	28.09
Br	.051	24	66.2	26.88
Tr	.005	3	6.2	1.68
Bl	.061	19	21.2	0.23
(J	.029	20	37.1	7.85)
(I	.009	9	11.1	0.38)
		1300	1299.25	140.09

The age-sex classes did not participate equally as groomer and recipient (chi squared = 102; df = 13; $p < 0.001$) (Table 10.7).

Given these tendencies to groom and be groomed the baboons did not distribute their grooming randomly among the available age-sex classes (chi squared = 47.7; df = 12; $p < 0.001$) (Table 10.8).

Adult males and juveniles did not distribute their grooming time in proportion to the available grooming partners, while both adult females and juveniles received grooming disproportionately from the various age-sex classes (Table 10.8).

Table 10.7:
Frequency of Observations of Grooming and Receiving Grooming by
Various Age-Sex Classes

Age-Sex	Groomer	Recipient	<u>chi</u> squared
M	117	223	33.05
F	318	204	24.90
E	6	15	3.86
P	2	8	3.60
F1	23	29	0.69
S	4	17	8.05
Z	2	2	0.00
O	95	63	6.48
Y	53	44	0.84
Br	10	14	0.67
Tr	0	3	-
Bl	1	18	15.21
(J	15	5	5.00)
(I	4	5	0.11)
	650	650	102.46

Table 10.8:
Contingency Table for Grooming Partners.
Expected values are given from marginal totals

		G R O O M E R S			
RECIPIENTS		M	F	J	I
M	obs	42	133	40	8
	exp	40.1	119.7	58.0	5.1
F	obs	56	101	67	3
	exp	40.9	121.9	59.0	5.2
F1	obs	4	21	4	0
	exp	5.2	15.6	7.5	0.7
J	obs	11	66	52	2
	exp	23.6	70.3	34.1	3.0
I	obs	4	28	6	2
	exp	7.2	21.5	10.4	0.9

Of particular interest to this study, adult males groomed adult males in proportion as they occurred as available grooming partners (Table 10.8). Adult males also groomed adult females more than expected (chi squared = 5.61; df = 1; $p < 0.05$) (Table 10.8). Adult females groomed females with infants more than expected but not significantly so (chi squared = 1.89; df = 1; ns).

Grooming partners are not distributed evenly among the age-sex classes as they occur in the population (chi squared = 258; df = 1; $p < 0.001$) (Table 10.9). Adult females groom adult females both with and without infants far more frequently than expected (chi squared = 43.7; df = 1; $p < 0.001$ and chi squared = 55.8; df = 1; $p < 0.001$ respectively)(Table 10.9).

Table 10.9:

Contingency table for grooming partners.

Expected values are given from proportion in population

		G R O O M E R S				
RECIPIENTS			M	F	J	I
M	obs		42	133	40	8
	exp		41.9	55.8	54.2	13.4
F	obs		56	101	67	3
	exp		51.7	68.8	66.7	16.5
F1	obs		4	21	4	0
	exp		4.1	5.5	5.3	1.3
J	obs		11	66	52	2
	exp		54.2	72.1	69.9	17.3
I	obs		4	28	6	2
	exp		13.4	17.8	17.3	4.3

10.6.3: Grooming: Discussion

Grooming relations in P. papio at Mt. Assirik suggested that adult males showed considerable affiliation to each other, strongly reminiscent of that exhibited by P. hamadryas or T. gelada males

excluded from the mating population. However, on one or two occasions I observed adult males grooming an adult female and an adult male consecutively, which suggests that at least some of the males who groomed one another were not excluded from the breeding population. At the same time, the adult females showed a freedom of interaction with other adult females equivalent to that found in T. gelada, P. anubis, P. cynocephalus, and P. ursinus. These data are not consistent with a social organisation based upon coercion of adult females, by adult males, to live in harem groups, as in P. hamadryas. Nor are they consistent with the low frequency of affiliative behaviour normally seen between adult males in savanna baboon societies. They are consistent with a society in which kin groups of females are "adopted" by an adult male, and, perhaps, in which some adult males are excluded from the breeding population, as in T. gelada. They are also consistent with a society in which adult females are free to interact with each other and with adult males, and in which adult males show strong affiliation for particular other adult males.

10.7: Summary

Exclusivity of mating rights by one male baboon over females in its social group is not entirely species-specific. There are many observations of adult males savanna baboons who consort a favourite female every time she comes into oestrus (Collins pers comm, Lee pers comm) and may also associate with her for much of the rest of the time (Strum pers comm, and see page 10.2 for other references).

In P. hamadryas and T. gelada this exclusivity persists for the entire time that the male has tenure over his group, and the male must defend his females from other males even when they are not sexually receptive. In order to establish that P. papio has a mating system based on one-male groups (cf Boese 1973, 1975) it would be necessary to follow known adult males and females through many oestrus cycles.

However, it is unlikely that P. papio at Mt. Assirik lived in a society with a mating system like that of P. hamadryas. In P. hamadryas adult males would have been found in all, or nearly all, social groups.

About a third of the social groups observed in this study contained adult females but no adult males. Social groups composed entirely of males such as those found in T. gelada were never seen. The age-sex classes of animals found as nearest neighbours of adult animals was unlike those found in P. hamadryas or T. gelada societies, but like those found in the savanna baboons. P. papio adults of both sexes tended to sit close to other adults, in huddles similar to T. gelada clusters when socialising. In this they apparently differ from both P. hamadryas and the savanna baboons. This may indicate a society with close genetic relationships between the individuals in the groups (Schulman 1980). Adult females did not behave as though they were responsible for maintaining proximity to adult males, being as "disobedient" as P. anubis females were towards males.

One of the most interesting results to have emerged from this study is the observation that adult males frequently groomed one another. This suggests that affiliative behaviour among the males was important in this society.

CHAPTER 11: Ecology, Social Organisation and Mating System of *P. papio*

Much of the variation in the social organisation of baboons has been related either directly, or indirectly through its effects on demography, to ecology. The diet of *P. papio* probably has a profound effect on its social organisation for at least three reasons. Firstly, although we cannot ascribe the ability of *P. papio* to survive in large groups in the wet season to a diet consisting solely of grass, as we can for *T. gelada*, it is possible that these large troops were able to form because food was seasonally superabundant at a time when risk of predation by ambush predators was probably highest. Secondly, strong seasonal change in productivity between the wet and the dry seasons apparently meant that the large wet season groups could not forage together in the dry season, so that there was a seasonal fragmentation of the social group. This seasonal fragmentation is known in only one other population of *Papio* baboons. Thirdly, since the food of these animals normally occurred in fruit trees, few animals were normally able to feed from the same food source at the same time. This led to the formation of small foraging groups within the moving troop, which in turn may have encouraged the animals to form cliques within the troops.

Diet has also apparently influenced the ranging of these baboons. Long day ranges suggest that the troop would have had some difficulty in finding enough food in smaller ranges, and the small or non-existent seasonal difference in the length of day ranges gives further evidence that fragmentation of the troops compensated for seasonal variation in productivity. The present study was able to show that habitat, even when coarsely classified, accounted for some of the changes in both speed of movement and the frequency with which various parts of the range were used by the baboons. That such a crude method was capable of predicting so much of the behaviour of these baboons is in itself remarkable, and suggests that the manner in which they used their ranges was determined largely by local differences in canopy cover, visibility, and productivity. About a third of the field area was made up of habitats which the baboons rarely visited and which they moved across rapidly when they did enter them. Since the habitats were distributed as a mosaic throughout

the home ranges of the baboons the existence of such little-used areas has led to apparent lacunae within their home ranges. Although the surface area ranged over by one troop was large, the productive part of that area was probably about a third smaller.

The position of permanent water was largely determined by the geology of the area. In turn, the permanent water sources supported gallery forest, and, in particular, one species of tree, Ceiba pentandra, which was used by the baboons as refuge at night. Individuals of this species of tree in the field area were often tall, with branches only in the topmost reaches of the tree. These branches grew almost horizontally from the trunk, forking near their ends. This shape provided roosting sites near the trunk and at few other points until near the ends of the branches, thus encouraging the formation of small rather isolated sleeping parties scattered throughout the branches of the tree. Social subdivision of the troop, often into units composed of mothers and offspring, was apparent here. These sleeping sites had a major influence on the ranging patterns of the troop, as did the location of permanent sources of water, and suggested that usage of various areas of the park by baboons could be predicted by the distribution of permanent water.

The limited number of sleeping sites in an area which was seasonally highly productive may have helped promote the formation of large troops and to encourage wide overlap of neighbouring home ranges.

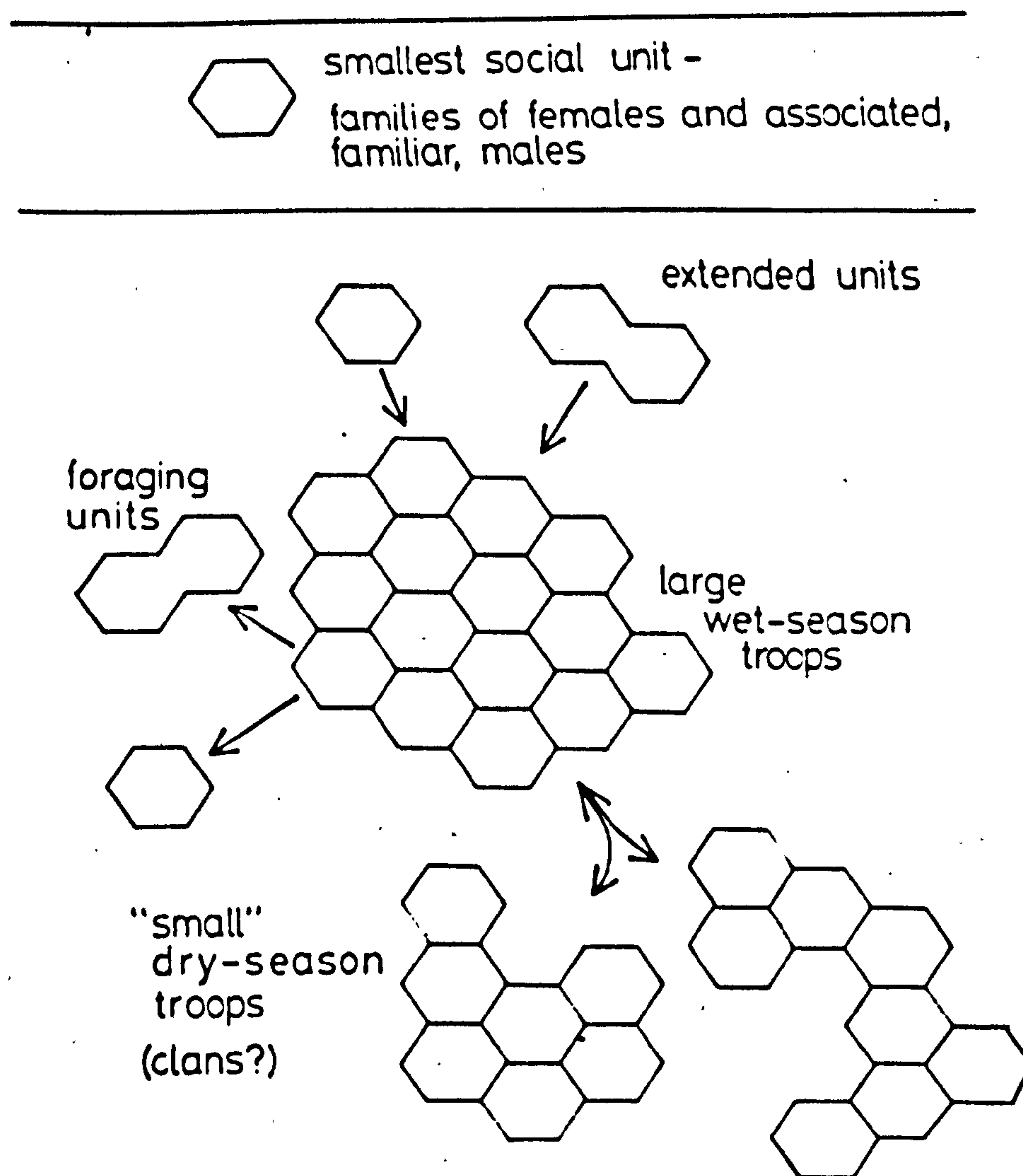
One effect of large troops may have been to force the baboons to spend much time feeding and moving in both seasons. High productivity in the wet season, which allowed large troops to form, apparently permitted the baboons to spend much of the time not spent foraging in social behaviour, although most of the individuals observed during peak times of social behaviour were engaged in solitary activity. This may suggest that extended social contact was not necessary, and that most social interaction took place within small subgroups rather than between all members of the troops. With such large groups, in which there were as many adult animals of either sex as there are individuals in most baboon troops, there would probably be opportunity for much substructuring within the troop. In such a society it is conceivable that males might not

always transfer out of their natal group, but remain within it to breed. This might lead to the formation of clans within the troop, analagous to those found in P. hamadryas, but with males transferring out of their natal clan to breed. The resolution of such intriguing possibilities must await further study.

The social organisation and mating system of P. papio at Mt. Assirik was apparently similar to that seen in the savanna baboons, with large, socially complex troops in which the adults competed for mates. The composition of both social groups and foraging parties were consistent with those seen in the savanna baboons, and is unlikely to be found in baboons with harem societies. Adult males were not found in large all-male groups, as might have been expected in a society like that of T. gelada. The probability that an animal of either sex had a nearest neighbour of a given age-sex class was not the same as that in either of the baboon species with one-male groups. Finally, the behaviour associated with the coercion of adult females by adult males seen in P. hamadryas, or the intense grooming of adult females by adult males seen in T. gelada, was not observed at Mt. Assirik. There were, however, some differences between P. papio and the savanna baboons, particularly among the adult males. There was considerable evidence that adult males were tolerant of each other and formed affiliations and probably coalitions. Grooming between adult males suggested that these animals may have had particularly strong relationships with one another. Agonistic interactions between adult males often involved much soliciting of support in threatening others and sometimes led to mutual threatening between groups of three or four male baboons. Such social and perhaps genetic ties among adult males would be unique in those baboon societies with competitive mating, and is worth further study.

A possible structure for the troops at Mt. Assirik consistent with the data presented here is one in which social units of matrilineal kin groups were more or less closely associated with one or more adult males and with other such kin groups to form a network throughout the troop. Ecological units, or foraging parties, might have corresponded fairly closely to these social units, although adult males may have foraged on

Figure 11.1:
Possible social structure of the troops of P. papio at Mt. Assirik.
(This figure is not referred to in the text)



their own, with other adult males or with immature animals more than with the social unit with which they were generally associated. In the dry season these large groups fragmented, probably with most or all of any one social unit staying together in the same fragment, with other closely associated social units, to form a subset of the wet season troop rather analogous to the clans of P. hamadryas. When these fragments met and socialised some movement of both individuals and social units between fragments may have occurred.

Although the blood groups of P. papio and P. ursinus are in some respects different from those of P. cynocephalus and P. anubis (Wiener et al. 1970), differences in blood groups in baboon species are in any case no greater than those among human races (Weiner and Moor-Jankowski 1969). Genetically the Guinea baboon is no more distinct from P. anubis than is P. cynocephalus or P. ursinus (Jolly and Brett 1973). Troops containing individuals of appearance intermediate between P. papio and P. anubis exist in Mali (Pollock pers comm). The behavioural ecology of P. papio further suggests that they should be included with the savanna baboons, possibly under the single species P. cynocephalus, subspecies papio.

Baboons of the genus Papio and possibly Mandrillus show facility in trees and seem to include as much fruit in their diet as possible. The original habitat of baboons may have been forest fringe or woodland, and terrestriality may have been an adaptation which enabled them to move easily between scattered fruit trees. More omnivorous individuals would find food on the ground between such trees. Thus the wider potential niche made available by increasing competence on the ground may have given increasing advantage to individuals with adaptations allowing them to exploit the new foods. Finally, this may have led to adaptive radiation into lush alpine meadows on the one hand, where decreasing competence in trees was no disadvantage, and into savanna and desert on the other. Simultaneously, the newly terrestrial animal probably reinvaded the deep forest, where it began to exploit foods found not in the canopy, but on or near the forest floor. These were the ancestral mandrills. Both mandrills and drills lack a tail, which tends to support the belief that these are not animals exploiting the niche from which all other baboons

radiated, but that theirs is a secondary adaptation. Thus Theropithecus and Mandrillus differentiated in opposite directions from a Papio-like form (Jolly 1970).

If this interpretation of the ancestral habitat of baboons is correct, then P. papio may be exploiting a habitat at Mt. Assirik similar to that in which the ancestral baboons evolved, especially given the correspondence in plant genera and patterns of habitat found at Mt. Assirik and in the Plio-Pleistocene of much of Africa (McGrew et al. 1981).

REFERENCES

- Abegglen J.J. (1976) On Socialization in the Hamadryas Baboon, PhD Thesis, Zurich.
- Adam J.G. (1971) Le milieu biologique. Flora et vegetation. In: Dupuy A.R. (ed.), Le Niokolo-Koba. Premier Grande Parc National de la Republique du Senegal., pp 43-62. G.I.A., Dakar.
- Adams L. & S.D. Davis (1967) The internal anatomy of home range. J. Mammal., 48:529-36.
- Aldrich-Blake F.P.G. (1970) Problems of social structure in forest monkeys. In: Crook J.H. (ed.), Social Behaviour in Birds and Mammals, pp 79-101. Academic Press, New York.
- Aldrich-Blake F.P.G., T.K. Bunn, R.I.M. Dunbar & P.M. Headley (1971) Observations on baboons, Papio anubis, in an arid region in Ethiopia. Folia primatol., 15:1-35.
- Altmann J. (1980) Baboon Mothers and Infants, Harvard University Press, Cambridge Mass.
- Altmann J., S.A. Altmann, G. Hausfater & S.A. McCuskey (1977) Life history of yellow baboons: Physical development, reproductive parameters, and infant mortality. Primates, 18(2):315-330.
- Altmann S.A. (1973a) Progression orders in baboons. Am. Zool., 13(4): 1265.
- Altmann S.A. (1973b) The pregnancy sign in savanna baboons. J. Zoo Anim. Med., 4(2):8-12.
- Altmann S.A. (1974) Baboons, space, time and energy. Am. Zool., 14:221-248.
- Altmann S.A. (1979) Baboon progressions: order or chaos? A study of one-dimensional group geometry. Anim. Behav., 27:46-80.
- Altmann S.A. & J. Altmann (1970) Baboon Ecology: African Field Research, University of Chicago Press, Chicago.
- Altmann S.A. & J. Altmann (1979) Demographic constraints on behaviour and social organisation. In: Bernstein I.S. & E.O. Smith (eds.), Primate Ecology and Human Origins, pp 47-64. Garland STMP, New York And London.
- Anderson C. (1980a) Sub-trooping in Chacma Baboons, Paper Delivered at The Seventh International Congress of Primatology, (Florence).
- Anderson C. (1980b) Chacma Baboon (Papio ursinus) Social Groups and Their Interrelationships in the Suikerbosrand Reserve, South Africa, PhD Thesis, University Of California, Riverside, California.
- Andersson M. (1978) Optimal foraging area: size and allocation of search effort. Theor. Popul. Biol., 13(3):397-409.
- Anthony T.R. (1975) Evolution of Social Structure in Baboons (Papio spp.): Detailed Analysis of Social Structure in a Captive Group of Guinea Baboons (P. papio) and a Comparative Review and Analysis of Social Structure in all Species of the Genus, PhD Thesis, University Of Chicago.

- Baker M.C., C.S. Belcher, L.C. Deutsch, G.L. Sherman & D.B. Thompson (1981) Foraging success in junco flocks and the effects of social hierarchy. Anim. Behav., 29:137-142.
- Baker R.R. (1978) The Evolutionary Ecology of Migration, Hodder And Stoughton, London.
- Baldwin J.D. & J. Baldwin (1972) The ecology and behaviour of squirrel monkeys (Saimiri oerstedii) in a natural forest in western Panama. Folia primatol., 18:161-184.
- Baldwin P.J. (1979) The Natural History of the Chimpanzee (Pan troglodytes verus) at Mt. Assirik, Senegal, PhD Thesis, University Of Stirling.
- Barnes R.D. (1968) Invertebrate Zoology, W.B. Saunders and Co., Philadelphia And London.
- Bearder S.K. & G.A. Doyle (1974) Field and laboratory studies of social organisation in bushbabies (Galago senegalensis). J. Hum. Evol., 3:37-50.
- Bernstein I.S. (1972) Principles of primate group organisation. In: Chiarelli A.B. (ed.), Perspectives in Primate Biology, pp 283-298. Plenum, New York.
- Bert J., H. Ayats, A. Martino & H. Collomb (1967a) Le sommeil nocturne chez le babouin Papio papio. Observations en milieu naturel et donnees electrophysiologiques. Folia primatol., 6:28-43.
- Bert J., H. Ayats, A. Martino & H. Collomb (1967b) Note sur l'organisation de la vigilance sociale chez le babouin Papio papio dans l'est Senegalais. Folia primatol., 6:44-47.
- Bert J. & V. Pegram (1969) L'electroencephalogramme du sommeil chez les cercopithecinae: Erythrocebus patas et Cercopithecus aethiops sabaeus. Folia primatol., 11:151-159.
- Boese G. (1973) Behavior and Social Organisation of the Guinea Baboon (Papio papio), PhD Thesis, Johns Hopkins University, Baltimore, Md.
- Boese G.K. (1975) Social behavior and ecological considerations of West African baboons (Papio papio). In: Tuttle R.H. (ed.), Socioecology and Psychology of Primates, pp 205-230. Mouton, The Hague.
- Boese G.K., E. Balzamo & M. Balzamo (1975) Population survey of Guinea baboons (Papio papio) in Niokolo-Koba National Park, Senegal, West Africa. Bull. Ecol. Soc. Am., 56: 31.
- Bolwig N. (1959) A study of the behaviour of the chacma baboon, Papio ursinus. Behaviour, 14:136-163.
- Booth A.H. (1956a) The distribution of primates in the Gold Coast. J. West. Afr. Sci. Assoc., 2:122-133.
- Booth A.H. (1956b) The cercopithecidae of the Gold and Ivory Coasts: geographic and systematic observations. Ann. Mag. Nat. Hist., 9(12):476-480.

- Bradbury J.W. & S.L. Vehrencamp (1976a) Social organisation and foraging in emballonurid bats. I: Field studies. Behav. Ecol. Sociobiol., 1:337-381.
- Bradbury J.W. & S.L. Vehrencamp (1976b) Social organisation and foraging in emballonurid bats. II: A model for the determination of group size. Behav. Ecol. Sociobiol., 1:383-404.
- Brain C.K. (1970) New finds at the Swartkrans Australopithecine site. Nature, 225:1112-1119.
- Bridges E.M. (1970) World Soils, Cambridge University Press, Cambridge.
- Brock V.E. & R.H. Riffenburgh (1960) Fish schooling: a possible factor in reducing predation. J. Cons. Perm. Int. Exp. Mar., 25:307-317.
- Brown J.L. (1975) The Evolution of Behavior, W.W. Norton and Co. Inc., New York.
- Brown J.L. & G.H. Orians (1970) Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst., 1:239-262.
- Buettner-Janusch J. (1966) A problem in evolutionary systematics - nomenclature and classification of baboons, genus Papio. Folia primatol., 4:288-308.
- Burt W.H. (1943) Territoriality and home range concepts as applied to mammals. J. Mammal., 24:346-352.
- Buskirk W.H., R.E. Buskirk & W.J. Hamilton (1974) Troop-mobilizing behaviour of adult male chacma baboons. Folia primatol., 22:9-18.
- Bygott J.D., B.C.R. Bertram & J.P. Hanby (1979) Male lions in large coalitions gain reproductive advantages. Nature, 282(5741):839-841.
- Byrne R.W. (in press) Uses of long-range calls during ranging by Guinea baboons. In: Chiarelli A.B. & R.S. Corruccini (eds.), Primate Behaviour and Sociobiology. Proceedings of the VIIIth Congress of the International Primate Society, Karger, Basel.
- Caraco T. & L.L. Wolf (1975) Ecological determinants of group sizes of foraging lions. Am. Nat., 109:343-352.
- Carpenter C.R. & A. Nishimura (1969) The Takasakiyama colony of Japanese macaques (Macaca fuscata). In: Carpenter C.R. (ed.), Proceedings of the Second International Congress of Primatology, Atlanta, Georgia. Vol I: Behaviour, pp 16-30. Karger, Basel.
- Casimir M.J. & E. Butenandt (1973) Migration and core area shifting in relation to some ecological factors in a mountain gorilla group (Gorilla gorilla beringei) in the Mt. Kahuzi Region (Republique du Zaïre). Z. Tierpsychol., 33:514-522.
- Chalmers N.R. (1968a) Group composition, ecology and daily activities of free-living mangabeys in Uganda. Folia primatol., 8:247-262.
- Chalmers N.R. (1968b) The social behaviour of free-living mangabeys in Uganda. Folia primatol., 8:263-281.

- Cheney D.L. (1977) The acquisition of rank and the development of reciprocal alliances among free-ranging immature baboons. Behav. Ecol. Sociobiol., 2:303-318.
- Cheney D.L., P.C. Lee & R.M. Seyfarth (in press) Behavioural correlates of non-random mortality among free-ranging female vervet monkeys. Behav. Ecol. Sociobiol.,
- Cheney D.L. & R.M. Seyfarth (1977) Behaviour of adult and immature baboons during intergroup encounters. Nature, 269:404-406.
- Chepko-Sade B.D. & T.J. Olivier (1979) Coefficients of genetic relationship and the probability of intergenealogical fission in Macaca mulatta. Behav. Ecol. Sociobiol., 5:263-278.
- Chepko-Sade B.D. & D.S. Sade (1979) Patterns of group splitting within matrilineal kinship groups. Behav. Ecol. Sociobiol., 5:67-86.
- Cheverud J.M., J. Buettner-Janusch & D. Sade (1978) Social group fission and the origin of intergroup genetic differentiation among the rhesus monkeys of Cayo Santiago. Am. J. Phys. Anthropol., 49:449-456.
- Chivers D.J. (1972) The siamang and the gibbon in the Malay peninsula. Gibbon And Siamang, 1:103-135.
- Chivers D.J., J.J. Raemakers & F.P.G. Aldrich-Blake (1975) Long-term observations of siamang behaviour. Folia primatol., 23:1-49.
- Cilliers W. (1963) Lions apparently do eat baboons. Afr. Wildl., 17:17-18.
- Clark P.J. & F.C. Evans (1954) Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology, 35:445-453.
- Clemans K.G. (1959) Confidence limits in the case of the geometric distribution. Biometrika, 46:260-264.
- Clutton-Brock T.H. (1972) Feeding and Ranging Behaviour of the Red Colobus Monkey, PhD Thesis, Cambridge.
- Clutton-Brock T.H. (1973) Feeding levels and feeding sites of red colobus (Colobus badius tephrosceles) in the Gombe National Park. Folia primatol., 19:368-379.
- Clutton-Brock T.H. (1974a) Primate social organisation and ecology. Nature, 250:539-542.
- Clutton-Brock T.H. (1974b) Activity patterns of red colobus (Colobus badius tephrosceles). Folia primatol., 21:161-187.
- Clutton-Brock T.H. (1975) Feeding behaviour of red colobus and black-and-white colobus in East Africa. Folia primatol., 23:165-207.
- Clutton-Brock T.H. & P.H. Harvey (1976) Evolutionary rules and primate societies. In: Bateson P.P.G. & R.A. Hinde (eds.), Growing Points in Ethology, pp 195-237. Cambridge University Press, Cambridge.
- Clutton-Brock T.H. & P.H. Harvey (1977) Primate ecology and social organisation. J. Zool. Lond., 183:1-39.

- Clutton-Brock T.H. & P.H. Harvey (1978) Mammals, resources, and reproductive strategies. Nature, 273:191-195.
- Clutton-Brock T.H. & P.H. Harvey (1979) Home range size, population density and phylogeny in primates. In: Bernstein I.S. & E.O. Smith (eds.), Primate Ecology and Human Origins, pp 201-214. Garland STMP, New York And London.
- Cody M.L. (1971) Finch flocks in the Mohave Desert. Theor. Popul. Biol., 2:142-158.
- Cody M.L. (1974) Optimisation in ecology. Science, 183:1156-1164.
- Cohen J.E. (1969) Natural troops and a stochastic population model. Am. Nat., 103:455-477.
- Cohen J.E. (1971) Social grouping and troop size in yellow baboons. In: Kummer H. (ed.), Proceedings of the Third International Congress of Primatology, Zurich: Volume III: Behaviour, pp 58-64. Karger, Basel.
- Cohen J.E. (1972) Casual Groups of Monkeys and Men, Harvard University Press, Cambridge, Mass.
- Collins D.A. (in prep.) Social behaviour and patterns of mating among adult yellow baboons (*Papio C. cynocephalus* L. 1766). PhD Thesis. University of Edinburgh.
- Cook D. & F.P. Martin (1974) A model for sampling with "visibility bias". J. Am. Stat. Assoc., 69:345-349.
- Covich A.P. (1976) Analyzing shapes of foraging areas: some ecological and economic theories. Ann. Rev. Ecol. Syst., 7:235-257.
- Crook J.H. (1966) Gelada baboon herd structure and movement: a comparative report. Symp. Zool. Soc. London, 18:237-258.
- Crook J.H. (1970a) Socio-ecology of primates. In: Crook J.H. (ed.), Social Behaviour of Birds and Mammals, pp 103-166. Academic Press, New York And London.
- Crook J.H. (1970b) Social organization and the environment. Aspects of contemporary social ethology. Anim. Behav., 18:197-207.
- Crook J.H. & P. Aldrich-Blake (1968) Ecological and behavioural contrasts between sympatric ground-dwelling primates in Ethiopia. Folia primatol., 8:192-227.
- Cushing D.H. & F.R. Harden-Jones (1968) Why do fish school?. Nature, 218:918-920.
- Damas D. (1972) The copper Eskimo. In: Bicchieri M.G. (ed.), Hunters and Gatherers Today, pp 3-50. Holt, Rinehart, Winston, New York.
- Datta S. (1981) The Dynamics of Dominance Among Rhesus Females, PhD Thesis, Cambridge.
- Davidge C. (1977) Activity patterns of chacma baboons (*Papio ursinus*) at Cape Point. Zoologica Afr., 13(1):143-155.

- Deag J.M. (1973) Intergroup encounters in the wild barbary macaque Macaca sylvanus L.. In: Michael R.P. & J.H. Crook (eds.), Comparative Ecology and Behaviour of Primates, pp 316-373. Academic Press, London.
- Deag J.M. & J.H. Crook (1971) Social behaviour and "Agonistic Buffering" in the wild barbary macaque Macaca sylvana L.. Folia primatol., 15:183-200.
- Delson E. (1975a) Evolutionary history of the cercopithecidae. Approaches to primate paleobiology. Contrib. Primatol., 5:167-217.
- Delson E. (1975b) Paleoecology and zoogeography of the Old World monkeys. In: Tuttle R.H. (ed.), Primate Functional Morphology and Evolution, pp 37-64. Mouton, The Hague.
- Delson E. (1976) Request for the determination of the generic name of the baboon and the mandrill (Mammalia: primates, cercopithecidae). Bull. Zool. Nomencl., 33(1):46-60.
- Delson E. (1977) Catarrhine phylogeny and classification: principles, methods, and comments. J. Hum. Evol., 6:433-459.
- Delson E. & P. Andrews (1975) Evolution and interrelationships of the catarrhine primates. In: Lockett W.P. & F.S. Szalay (eds.), Phylogeny of the Primates, pp 405-446. Plenum, New York.
- Demment M. (in prep.) Feeding Energetics in the Olive Baboon (Papio anubis), PhD Thesis, University of Wisconsin.
- Denham W.W. (1971) Energy relations and some basic properties of primate social organisation. Am. Anthropol., 73:77-95.
- DeVore I. (1965a) Changes in the population structure of Nairobi Park Baboons 1959-1963. In: Vagtborg H. (ed.), The Baboon in Medical Research, pp 17-28. University of Texas Press, Austin, Texas.
- DeVore I. (1965b) Male dominance and mating behaviour in baboons. In: Beech F.A. (ed.), Sex and Behaviour, pp 266-279. Wiley, New York.
- DeVore I. & K.R.L. Hall (1965) Baboon ecology. In: DeVore I. (ed.), Primate Behaviour. Field Studies of Monkeys and Apes, pp 20-52. Holt, Rinehart And Winston, New York.
- DeVore I. & S.L. Washburn (1963) Baboon ecology and human evolution. In: Howell F.C. & F. Bourliere (eds.), African Ecology and Human Evolution, pp 335-367. Aldine, Chicago.
- Dittus W.P.J. (1975) Population dynamics of the toque monkey, Macaca sinica. In: Tuttle R.H. (ed.), Socioecology and Psychology of Primates, pp 125-151. Mouton, The Hague.
- Dittus W.P.J. (1977) The social regulation of population density and age-sex distribution in the toque monkey. Behaviour, 53:281-322.
- Douglas-Hamilton I. & O. Douglas-Hamilton (1975) Among the Elephants, Collins And Harville Press, London.

- Dunbar R.I.M. (1973) Social Dynamics of the Gelada Baboon, Theropithecus gelada, PhD Thesis, Bristol.
- Dunbar R.I.M. (1976b) Australopithecine diet based on a baboon analogy. J. Hum. Evol., 5:161-167.
- Dunbar R.I.M. (1977a) Feeding ecology of gelada baboons: a preliminary report. In: Clutton-Brock T.H. (ed.), Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes, pp 251-273. Academic Press, London.
- Dunbar R.I.M. (1978a) Life with the geladas: a battle of the sexes. New Sci., 79(1110):28-30.
- Dunbar R.I.M. (1978c) Sexual behaviour and social relationships among gelada baboons. Anim. Behav., 26:167-178.
- Dunbar R.I.M. (1979a) Population demography, social organisation, and mating strategies. In: Bernstein I.S. & E.O. Smith (eds.), Primate Ecology and Human Origins, pp 65-88. Garland STMP, New York And London.
- Dunbar R.I.M. (1979b) Structure of gelada baboon reproductive units. I Stability of social relationships. Behaviour, 69(1/2):72-87.
- Dunbar R.I.M. (1979c) The myth of the model baboon. Primat. Eye, 11:11-13.
- Dunbar R.I.M. (1980a) Demographic and life-history variables of a population of gelada baboons (Theropithecus gelada). J. Anim. Ecol., 49:485-506.
- Dunbar R.I.M. (1981b) Reply to Shipman. Curr. Anthropol., 22:264-265.
- Dunbar R.I.M. & E.P. Dunbar (1974c) Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. Folia primatol., 21:36-60.
- Dunbar R.I.M. & E.P. Dunbar (1974d) Ecology and population dynamics of Colubus guereza in Ethiopia. Folia primatol., 21:188-208.
- Dunbar R.I.M. & E.P. Dunbar (1975) Social dynamics of gelada baboons. In: Kuhn H., W.P. Luckett, C.R. Noback, A.H. Schultz, D. Starck & F.S. Szalay (eds.), Contributions to Primatology Volume VI, pp 1-157. Karger, Basel.
- Dunbar R.I.M. & E.P. Dunbar (1976) Contrasts in social structure among black-and-white colobus monkey groups. Anim. Behav., 24:84-92.
- Dunbar R.I.M. & M.F. Nathan (1969) The Oxford University expedition to Senegal 1969. Oxford Univ. Exped. Club, 18(4):87-100.
- Dunbar R.I.M. & M.F. Nathan (1972) Social organisation of the Guinea baboon, Papio papio. Folia primatol., 17:321-334.
- Dunbar R.I.M. & M.J. Sharman (in prep.) Ecocorrelates of baboon populations.
- Duncan P. & N. Vigue (1979) The effect of group size in horses on the rate of attacks by blood-sucking flies. Anim. Behav., 27:623-625.

- Dupuy A.R. (1971) Le milieu biologique. Mammifères: le Cynocephale (Papio papio). In: Dupuy A.R. (ed.), Le Niokolo-Koba. Premier Grand Parc National de la République du Sénégal, pp 177-179. G.I.A., Dakar.
- Dupuy A.R. & D.R. Gaillard (1969) Capture d'un cynocephale présentant une anomalie de coloration. Mammalia, 33:732-733.
- Dupuy A.R. & J. Verschuren (1977) Wildlife and parks in Senegal. Oryx, 14(1):36-46.
- Ellis J.E., J.A. Wiens, C.F. Rodell & J.C. Anway (1976) A conceptual model of diet selection as an ecosystem process. J. Theor. Biol., 60:93-108.
- Emlen J.T. (1967) A rapid method for measuring arboreal canopy cover. Ecology, 48:158-160.
- Emlen S.T. & L.W. Oring (1977) Ecology, sexual selection, and the evolution of mating systems. Science, 197:215-223.
- Enke H. (1977) On the analysis of incomplete two-dimensional contingency tables. Biometry J., 19(7):561-573.
- Estabrook G.F. & A.E. Dunham (1976) Optimal diet as a function of absolute abundance, relative abundance, and relative value of available prey. Am. Nat., 110:401-413.
- Estes R.D. (1976) The significance of breeding synchrony in the wildebeest. East Afr. Wildl. J., 14:135-152.
- Etter H.F. (1973) Terrestrial adaptations in the hands of cercopithecinae. Folia primatol., 20:331-350.
- Fady J.C. (1972) Absence de coopération de type instrumental en milieu naturel chez Papio papio. Behaviour, 43(1/4):157-164.
- Fagen R.M. & N.J. Mankovich (1980) Two-act transitions, partitioned contingency tables, and the 'significant cells' problem. Anim. Behav., 28:1017-1023.
- File S., W.C. McGrew, C.E.G. Tutin & P.J. Baldwin (in prep.) Parasites in wild primates in Senegal.
- Freedman L. (1963) Growth of muzzle length relative to calvaria length in Papio. Growth, 26:117-128.
- Freeland W.J. (1976) Pathogens and the evolution of primate sociality. Biotropica, 8(1):12-24.
- Furuya Y. (1968) On the fission of troops of Japanese monkeys. Primates, 9:323-350.
- Gates D.M. (1972) Man and his Environment: Climate, Harper And Row, New York and London.
- Gautier-Hion A. (1970) L'organisation d'une bande de talapains (Miopithecus talapoin) dans le nord-est du Gabon. Folia primatol., 12:116-141.

- Gautier-Hion A. (1971) L'écologie du talapoin du Gabon. La Terre et la Vie, 25:427-490.
- Gilman J. & C. Gilbert (1956) The endocrine basis for body weight changes and the metabolism of water in the adult female baboon (Papio ursinus). Am. J. Anat., 98:321-271.
- Gilmer D.S., S.E. Miller & L.M. Cowardin (1973) Analysis of radiotracking data using digitized habitat maps. J. Wildl. Manage., 37(3):404-409.
- Glânder K.E. (1975) Habitat description and resource utilization: a preliminary report on mantled howling monkey ecology. In: Tuttle R.H. (ed.), Socioecology and Psychology of Primates, pp 37-57. Mouton, The Hague.
- Goosen C. (1980) Grooming in Old World Monkeys, PhD Thesis, University Of Leiden.
- Grubb P. (1973) Distribution, divergence and speciation of the drill and mandrill. Folia primatol., 20:161-177.
- Haddow A.J. (1952) Field and laboratory studies on an African monkey, Cercopithecus ascanius schmidtii Matschie. Proc. Zool. Soc. London, 122:297-394.
- Hall K.R.L. (1960) Social vigilance behaviour of the chacma baboon, Papio ursinus. Behaviour, 16:261-294.
- Hall K.R.L. (1962a) Numerical data, maintenance activities and locomotion of the wild chacma baboon Papio ursinus. Proc. Zool. Soc. London, 139:181-220.
- Hall K.R.L. (1962b) Sexual, derived social, and agonistic behaviour patterns in the wild chacma baboon, Papio ursinus. Proc. Zool. Soc. London, 139:284-327.
- Hall K.R.L. (1963a) Variations in the ecology of the chacma baboon Papio ursinus. Symp. Zool. Soc. London, 10:1-28.
- Hall K.R.L. (1963b) Some problems in the analysis and comparison of monkey and ape behaviour. In: Washburn S.L. (ed.), Classification and Human Evolution, pp 273-300. Viking Fund Publications in Anthropology, Location.
- Hall K.R.L. (1965a) Behaviour and ecology of the wild patas monkey, Erythrocebus patas, in Uganda. J. Zool. Lond., 148:15-87.
- Hall K.R.L. (1965b) Experimentation and quantification in the study of baboon behaviour in its natural habitat. In: Vagtborg H. (ed.), The Baboon in Medical Research, pp 29-42. University of Texas Press, San Antonio.
- Hall K.R.L. (1965c) Social organization of old world monkeys and apes. Symp. Zool. Soc. London, 14:265-289.
- Hall K.R.L. (1966) Distribution and adaptations of baboons. Symp. Zool. Soc. London, 17:49-73.

- Hall K.R.L., R.C. Boelkins & M.J. Goswell (1965) Behaviour of patas monkeys, Erythrocebus patas, in captivity, with notes on the natural habitat. Folia primatol., 3:22-49.
- Hall K.R.L. & I. DeVore (1965) Baboon social behaviour. In: DeVore I. (ed.), Primate Behaviour: Field Studies of Monkeys and Apes, pp 53-110. Holt Rinehart and Winston, New York.
- Hamilton W.D. (1971) Geometry for the selfish herd. J. Theor. Biol., 31:295-311.
- Hamilton W.J., R.E. Buskirk & W.H. Buskirk (1975b) Chacma baboon tactics during intertroop encounters. J. Mammal., 56(4):857-870.
- Hamilton W.J., R.E. Buskirk & W.H. Buskirk (1976) Defense of space and resources by chacma (Papio ursinus) baboon troops in an African desert and swamp. Ecology, 57:1264-1272.
- Hamilton W.J., R.E. Buskirk & W.H. Buskirk (1978) Omnivory and utilization of food resources by chacma baboons Papio ursinus. Am. Nat., 112:911-924.
- Hamilton W.J. & K.E.F. Watt (1970) Refuging. Ann. Rev. Ecol. Syst., 1:263-286.
- Harding R.S.O. (1973) Predation by a troop of olive baboons (Papio anubis). Am. J. Phys. Anthropol., 38:587-591.
- Harding R.S.O. (1974) The predatory baboon. Expedition, 16(2):30-39.
- Harding R.S.O. (1975) Meat-eating and hunting in baboons. In: Tuttle R.H. (ed.), Socioecology and Psychology of Primates, pp 246-257. Mouton, The Hague.
- Harding R.S.O. (1976) Ranging patterns of a troop of baboons (Papio anubis) in Kenya. Folia primatol., 25:143-185.
- Harding R.S.O. (1977) Patterns of movement in open-country baboons. Am. J. Phys. Anthropol., 47(2):349-353.
- Harding R.S.O. & S.C. Strum (1976) The predatory baboons of Kekopey. Nat.Hist., 85:46-53.
- Harrison M.J.S. (in prep.) The Ecology and Ethology of Green Monkeys, Cercopithecus sabaeus, in Senegal, West Africa, PhD Thesis, University of Stirling.
- Harvey W.J. & R.W. Barbour (1965) Home range of Microcebus ochrogaster as determined by a modified minimum area method. J. Mammal., 46:398-402.
- Harvey P.H. & T. Clutton-Brock (1981) Primate home range size and metabolic needs. Behav. Ecol. Sociobiol., 8(2):151-156.
- Hausfater G. (1973a) Aggressive dominance and reproductive success in yellow baboons (Papio cynocephalus). Am. Zool., 13(4): 1261.
- Hausfater G. (1973b) Knuckle-walking by a baboon (Papio cynocephalus). Am. J. Phys. Anthropol., 43(2):303-305.

- Hausfater G. (1975a) Estrus females: their effects on the social organization of the baboon troop. Symposium in the Fifth International Congress of Primatology, pp 117-128. Karger, Basel.
- Hausfater G. (1975b) Dominance and Reproduction in Baboons (Papio cynocephalus). A Quantitative Analysis, Contributions to Primatology, Volume Seven. Karger, Basel.
- Hausfater G. (1976) Predatory behaviour of yellow baboons. Behaviour, 56:44-68.
- Hausfater G. & W.H. Bearce (1976) Acacia tree exudates: their composition and use as a food source by baboons. East Afr. Wildl. J., 14:241-243.
- Hausfater G. & D.F. Watson (1976) Social and reproductive correlates of parasite ova emission by baboons. Nature, 262:688-689.
- Hayne D.W. (1949) Calculation of size of home range. J. Mammal., 30:1-18.
- Hebrard L. & P. Michel (1971) Apercu Geologique. In: Dupuy A.R. (ed.), Le Niokolo-Koba. Premier Grande Parc National de la Republique du Senegal, pp 20-41. G.i.a., Dakar.
- Hendrix A.G. & D.C. Kraemer (1969) Observation of the menstrual cycle, optimal mating time, and preimplantation embryos of the baboon, Papio anubis and Papio cynocephalus. J. Reproduct. Fertil. supplement, 6:119-128.
- Henty C.J. (in prep.) Behaviour and ecology of the patas monkey (Erythrocebus patas) at Mont Assirik, Senegal.
- Hill W.C.O. (1970) Primates: Comparative Anatomy and Taxonomy, Vol 8, Cynopithecinae, Edinburgh University Press, Edinburgh.
- Hinde R.A. (1975) Interactions, relationships, and social structure. Man, 11:1-17.
- Hinde R.A. & J. Stevenson-Hinde (1976) Towards understanding relationships: dynamic stability. In: Bateson P.P.G. & R.A. Hinde (eds.), Growing Points in Ethology, pp 451-480. Cambridge University Press, Cambridge.
- Hladik C.M. (1975) Ecology, diet and social patterning in old and new world primates. In: Tuttle R.H. (ed.), Socioecology and Psychology of Primates, pp 3-35. Mouton, The Hague.
- Holdridge L.R. (1962) The determination of atmospheric water movements. Ecology, 43(1):1-9.
- Homewood K.M. (1976) Ecology and Behaviour of the Tana Mangabey Cercocebus galeritus galeritus, PhD Thesis, University College, London.
- Hunter R.F. (1964) Home range behaviour in sheep. In: Crisp D.J. (ed.), Grazing in Terrestrial and Marine Environments, pp 155-171. Blackwell, Oxford.

- Iwamoto T. (1975) Food resource and the feeding activity: Studies of the gelada society III. In: Kondo S., M. Kawai & A. Ehara (eds.), Contemporary Primatology, pp 475-480. Karger, Basel.
- Iwamoto T. (1978) Food availability as a limiting factor on population density of the Japanese monkey and gelada baboon. In: Chivers D. & J. Herbert (eds.), Recent Advances in Primatology. I. Behaviour, pp 287-303. Academic Press, New York And London.
- Iwamoto T. & R.I.M. Dunbar (in prep.) Interhabitat variation in the behavioural ecology of gelada baboons.
- Jarman P.J. (1974) The social organisation of antelope in relation to their ecology. Behaviour, 48:213-267.
- Jennrich R.I. & F.B. Turner (1969) Measurement of noncircular home range. J. Theor. Biol., 22:227-237.
- Jewell P.A. (1966) The concept of home range in mammals. Symp. Zool. Soc. London, 18:85-109.
- Johns W.E. (1936) Biggles in Africa, Oxford University Press, London.
- Jolly A. (1972) The Evolution of Primate Behaviour, Macmillan, London.
- Jolly C.J. (1970) The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man, 5:5-26.
- Jolly C.J. & F.L. Brett (1973) Genetic markers and baboon biology. J. Med. Primatol., 2:85-99.
- Jones C. & J. Sabater Pi (1968) Comparative ecology of Cercocebus albigena (Gray) and Cercocebus torquatus (Kerr) in Rio Muni, West Africa. Folia primatol., 9:99-113.
- Jorde L.B. & J.N. Spuhler (1974) A statistical analysis of selected aspects of primate demography, ecology, and social behaviour. J. Anthropol. Res., 30:199-224.
- Jorgensen C.D. (1968) Home range as a measure of probable interactions among populations of small mammals. J. Mammal., 49:104-112.
- Jouventin P. (1975) Observations sur le socio-ecologie du mandrill. La Terre et la Vie, 29:493-532.
- King G.E. (1975) Socioterritorial units among carnivores and early hominids. J. Anthropol. Res., 31:69-87.
- Koeppel J.W., N.A. Slade & R.S. Hoffmann (1975) A bivariate home-range model with possible application to ethological data analysis. J. Mammal., 56:81-90.
- Koeppel J.W., N.A. Slade, K.S. Harris & R.S. Hoffmann (1977) A three-dimensional home range model. J. Mammal., 58:213-220.
- Kruuk H. & M. Turner (1967) Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. Mammalia, 31(1):1-27.

- Kummer H. (1968a) Social Organisation of Hamadryas Baboons, University of Chicago Press, Chicago.
- Kummer H. (1968b) Two variations in the social organisation of baboons. In: Jay P.C. (ed.), Primates: Studies in Adaptation and Variability, pp 293-312. Holt Rinehart Winston, New York.
- Kummer H. (1974a) Rules of dyad and group formation among captive gelada baboons (Theropithecus gelada). Symposia of the Fifth Congress of the International Primatological Society 129-160. Japan Science Press, Tokyo.
- Kummer H. (1974b) Distribution of interindividual distances in patas monkeys and gelada baboons. Species and sex differences. Folia primatol., 21:153-160.
- Kummer H. & F. Kurt (1963) Social units of a free-living population of hamadryas baboons. Folia primatol., 1:4-19.
- Kummer H. & F. Kurt (1965) A comparison of social behaviour in captive and wild hamadryas baboons. In: Vagtbourg H. (ed.), The Baboon in Medical Research, pp 65-80. University of Texas Press, Austin.
- Kuntz R.E. & J.A. Moore (1973) Commensals and parasites of African baboons (Papio cynocephalus L. 1766) captured in Rift Valley Province of central Kenya. J. Med. Primatol., 2:236-241.
- Lamprecht J. (1978) The relationship between food competition and foraging group sizes in some larger carnivores. A hypothesis. Z. Tierpsychol., 46:337-343.
- Lawick-Goodall J.V., H.V. Lawick & C. Packer (1973) Tool use in free-living baboons in the Gombe National Park, Tanzania. Nature, 241:212-213.
- Lazarus J. (1972) Natural selection and the functions of flocking in birds: a reply to Murdon. Ibis, 114:556-558.
- Lee P.C. (in prep.) Ecological and Social Influences on Development in Vervet Monkeys (Cercopithecus aethiops), PhD Thesis, Cambridge.
- Lee P.C. & J.I. Oliver (1979) Competition, dominance and the acquisition of rank in juvenile yellow baboons (Papio cynocephalus). Anim. Behav., 27:576-585.
- Lee R.B. (1972) The !Kung bushmen of Botswana. In: Bicchieri M.G. (ed.), Hunters and Gatherers Today, pp 326-368. Holt Rinehart Winston, New York.
- Lieberman D., J.B. Hall, M.D. Swaine & M. Lieberman (1979) Seed dispersal by baboons in the Shai Hills, Ghana. Ecology, 60:65-75.
- Lindburg D.G. (1971) The rhesus monkey in northern India: an ecological and behavioural study. Primat. Behav., 2:1-106.
- Lock J.M. (1972) Baboons feeding on Euphorbium candelabrum. East Afr. Wildl. J., 10:73-76.

- Lockie J. (1959) The estimation of the food of red foxes. J. Wildl. Manage., 23:224-227.
- Loy J. (1970) Behavioural responses of free-ranging rhesus monkeys to food shortage. Am. J. Phys. Anthropol., 33:263-272.
- Lumsden W.H.R. (1951) The night-resting habits of monkeys in a small area on the edge of the Semliki Forest, Uganda. A study in relation to the epidemiology of sylvian yellow fever. J. Anim. Ecol., 20:11-30.
- MacArthur R.H. & J.W. MacArthur (1961) On bird species diversity. Ecology, 42:594-598.
- MacDonald D.W., F.G. Ball & N.G. Hough (1980) The evaluation of home range size and configuration using radio tracking data. In: Amlander C.J. & D.W. MacDonald (eds.), A Handbook on Biotelemetry and Radio Tracking, pp 405-424. Permagon Press, Oxford and New York.
- Manzillillo D. (in prep.) Reproductive Strategies of Male Olive Baboons (Papio Anubis), PhD Thesis, University Of California, San Diego.
- Maples W.R. (1969) Adaptive behaviour of baboons. Am. J. Phys. Anthropol., 31:107-110.
- Marias E. (1969) The Soul of the Ape, Atheneum, New York.
- Massey A. (1977) Agonistic aids and kinship in a group of pigtail macaques. Behav. Ecol. Sociobiol., 2(1):31-40.
- Mauss M. (1906) Essai sur les variations saisonnieres des societies Eskimos. Etude de morphologie sociale. L'Annee Sociol., 9:39-132.
- Maxim P.E. & J. Buettner-Janusch (1963) A field study of the Kenya baboon. Am. J. Phys. Anthropol., 21:165-180.
- Mayr E. (1963) Animal Species and Evolution, Harvard University Press, Cambridge Mass.
- Mazurkewicz M. (1969) Elliptical modification of the home range pattern. Bull. Acad. Polish Sci., 17(7):427-431.
- McConnell E.E., P.A. Basson, V. de Voss, B.J. Myers & R.E. Kuntz (1974) A survey of diseases among 100 free-ranging baboons (Papio ursinus) from the Kruger National Park. Onderstepoort J. Vet. Res., 41(3):97-168.
- McGrew W.C., P.J. Baldwin & C.E.G. Tutin (1981) Chimpanzees in a hot, dry, and open habitat Mt. Assirik, Senegal, West Africa. J. Hum. Evol., 10:227-244.
- McGrew W.C., C.E.G. Tutin, P.J. Baldwin, M.J. Sharman & A. Whiten (1980) Primates preying on vertebrates: new records from West Africa. Carnivore, 1:41-45.
- McNab B.K. (1963) Bioenergetics and the determination of home range size. Am. Nat., 47:133-140.

- Meggitt M.J. (1962) Desert People: a Study of the Walbiri Aborigines of Central Australia, Angus And Robertson, Sydney And London.
- Metzgar L.H. (1972) The measurement of home range shape. J. Wildl. Manage., 36(2):643-645.
- Metzgar L.H. & A.L. Sheldon (1974) An index of home range size. J. Wildl. Manage., 38:546-551.
- Milton K. & M.L. May (1976) Body weight, diet, and home range area in primates. Nature, 259:459-462.
- Moen A.N. (1973) Wildlife Ecology, Freeman, San Fransisco.
- Mohr C.O. & W.A. Stumpf (1966) Comparison of methods for calculating areas of animal activity. J. Wildl. Manage., 30:293-304.
- Moreno-Black G. (1978) The use of scat samples in primate diet analysis. Primates, 19(1):215-221.
- Moreno-Black G. & W.R. Maples (1977) Differential habitat utilization of four Cercopithecidae in a Kenyan forest. Folia primatol., 27:85-107.
- Mori A. & M. Kawai (1975) Social relations and behaviour of gelada baboons. Studies of the gelada society II. In: Kondo S., M. Kawai & A. Ehara (eds.), Contemporary Primatology, pp 470-474. Karger, Basel.
- Morse D.H. (1974) Niche breadth as a function of social dominance. Am. Nat., 108:818-830.
- Mu"ller H. (1980) Variations of Social Behaviour in a Baboon Hybrid Zone (Papio anubis x Papio hamadryas) in Ethiopia, PhD Thesis, Zurich.
- Nagel U. (1971) Social organisation in a baboon hybrid zone. In: Kummer H. (ed.), Proceedings of the Third International Congress of Primatology, Zurich, pp 48-57. Karger, Basel.
- Nagel U. (1973) A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. Folia primatol., 19:104-165.
- Napier P.H. & N. Napier (1967) Handbook of the Living Primates, Academic Press, New York.
- Nash L.T. (1976) Troop fission in free-ranging baboons in the Gombe Stream National Park, Tanzania. Am. J. Phys. Anthropol., 44:63-77.
- Oates J.F. (1978) Water-plant and soil consumption by guereza monkeys (Colobus guereza): a relationship with minerals and toxins in the diet?. Biotropica, 10(4):241-253.
- Odum E.P. & E.J. Kuenzeler (1955) Measurement of territory and home range size in birds. Auk, 72:128-137.
- Ohsawa H. & M. Kawai (1975) Social structure of gelada baboons: studies of the gelada society. In: Kondo S., M. Kawai & A. Ehara (eds.), Contemporary Primatology, pp 464-469. Karger, Basel.

- Oliver J.I. & P.C. Lee (1978) Comparative aspects of the behaviour of juveniles in two species of baboon in Tanzania. In: Chivers D.J. & J. Herbert (eds.), Recent Advances in Primatology. Volume one: Behaviour, pp 151-153. Academic Press, London And New York.
- Olson F.C.W. (1964) The survival value of fish schooling. J. Cons. Perm. Int. Exp. Mar., 29:115-116.
- Owens N.W. (1972) The Development of Behaviour in Free-living Baboons (Papio anubis), PhD Thesis, Cambridge.
- Packer C. (1975) Male transfer in olive baboons. Nature, 255(5505):219-220.
- Packer C. (1977b) Inter-troop Transfer and Inbreeding Avoidance in Papio anubis in Tanzania, PhD Thesis, Sussex.
- Packer C. (1979) Inter-troop transfer and inbreeding avoidance in Papio anubis. Anim. Behav., 27:1-36.
- Paterson J.D. (1973) Ecologically differentiated patterns of aggressive and sexual behaviour in two troops of Uganda baboons, Papio anubis. Am. J. Phys. Anthropol., 38(2):641-647.
- Patterson B. (1954) The geologic history of non-hominid primates in the Old World. Hum. Biol., 26(3):191-209.
- Peet R.K. (1974) The measurement of species diversity. Ann. Rev. Ecol. Syst., 5:285-307.
- Pielou E.C. (1969) An Introduction to Mathematical Ecology, Wiley Interscience, New York.
- Pollard J.H. (1977) A Handbook of Numerical and Statistical Techniques. With Examples Mainly From the Life Sciences, Cambridge University Press, Cambridge.
- Popp J.L. (1978) Male Baboons and Evolutionary Principles, PhD Thesis, Harvard University, Cambridge, Mass.
- Post D. (1976) Feeding and ranging behaviour of the yellow baboon. Am. J. Phys. Anthropol., 44(1): 199.
- Post D.G. (1978) Feeding and Ranging Behavior of the Yellow Baboon (Papio cynocephalus), PhD Thesis, Yale University.
- Post D.G. (1981) Activity patterns of yellow baboons (Papio cynocephalus) in the Amboseli National Park, Kenya. Anim. Behav., 29:357-374.
- Post D.G., G. Hausfater & S.A. McCuskey (1980) Feeding behaviour of yellow baboons (Papio cynocephalus): relationships to age, gender and dominance rank. Folia primatol., 34:170-195.
- Powell G.V.N. (1974) Experimental analysis of the social value of flocking by starlings in relation to predation and foraging. Anim. Behav., 22:501-505.
- Pulliam H.R. (1973) On the advantages of flocking. J. Theor. Biol., 38:419-422.

- Pulliam H.R. (1974) On the theory of optimal diets. Am. Nat., 108:59-74.
- Pulliam H.R. (1976) The principle of optimal behaviour and the theory of communities. In: Bateson P.P.G. & P.H. Klopfer (eds.), Perspectives in Ethology, pp 311-332. Plenum Press, New York and London.
- Pyke G.H., H.R. Pulliam & E.L. Charnov (1977) Optimum foraging: a selective view of theory and tests. Q. Rev. Biol., 52(2):137-154.
- Ransom T.W. (1971) Ecology and Behaviour of Baboons (Papio anubis) at the Gombe National Park, PhD Thesis, University Of California, Berkeley.
- Ransom T.W. & B.S. Ransom (1971) Adult male-infant relations among baboons (Papio anubis). Folia primatol., 16:179-195.
- Ransom T.W. & T.E. Rowell (1972) Early social development of feral baboons. In: Poirer F.E. (ed.), Primate Socialization, pp 105-144. Random House, New York.
- Rasmussen D.R. (1979) Correlates of patterns of range use of a troop of yellow baboons (Papio cynocephalus) I. Sleeping sites, impregnable females, births, and male emigrations and immigrations. Anim. Behav., 27:1098-1112.
- Rasmussen K.L. (1979) Some developmental markers in yellow baboon infants of Mikumi National Park, Tanzania. Primates, 20(4):591-594.
- Rasmussen K.L. (1980) Consort Behaviour and Mate Selection in Yellow Baboons (Papio cynocephalus), PhD Thesis, Cambridge.
- Rhine R.J. (1975) The order of movement of yellow baboons (Papio cynocephalus). Folia primatol., 23:72-104.
- Rhine R.J. & N.W. Owens (1972) The order of movement of adult male and black infant baboons (Papio anubis) entering and leaving a potentially dangerous clearing. Folia primatol., 18:276-283.
- Rhine R.J. & B.J. Westlund (1978) The nature of a primary feeding habit in different age-sex classes of yellow baboons (Papio cynocephalus). Folia primatol., 30:64-79.
- Rosenzweig M.L. (1968) Net primary production of terrestrial communities: prediction from climatological data. Am. Nat., 102:67-74.
- Rowell T.E. (1964) The habit of baboons in Uganda. Proc. East. Afr. Acad., 2:121-127.
- Rowell T.E. (1966a) Forest-living baboons in Uganda. J. Zool. Lond., 147:344-364.
- Rowell T.E. (1967a) A quantitative comparison of the behaviour of a wild and a caged baboon group. Anim. Behav., 15:499-589.
- Rowell T.E. (1967b) Variability in the social organisation of primates. In: Morris D. (ed.), Primate Ethology, pp 219-235. Weidenfeld And Nicholson, London.

- Rowell T.E. (1969) Long-term changes in a population of Ugandan baboons. Folia primatol., 11:241-254.
- Rowell T.E. (1972) Toward a natural history of the talapoin monkey in Cameroon. Ann. Fac. Sci. Du Cameroon, 10:121-134.
- Rowell T.E. (1979) How would we know if social organisation were not adaptive?. In: Bernstein I.S. & E.O. Smith (eds.), Primate Ecology and Human Origins: Ecological Influences on Social Organisation, pp 1-22. Garland STMP, New York And London.
- Rubenstein D.I. (1978) On predation, competition, and the advantages of group living. In: Bateson P.P.G. & P. Klopfer (eds.), Perspectives in Ethology, pp 205-231. Plenum Press, New York and London.
- Russell E.M. & C.J.F. Harrop (1976) The behaviour of red kangaroos (Megaleia rufa) on hot summer days. Z. Tierpsychol., 40:396-426.
- Saayman G.S. (1970) The menstrual cycle and sexual behaviour in a troop of free-ranging chacma baboons (Papio ursinus). Folia primatol., 12:81-110.
- Saayman G.S. (1971a) Behaviour of the adult males in a troop of free-ranging chacma baboons (Papio ursinus). Folia primatol., 15:36-57.
- Saayman G.S. (1971b) Grooming behaviour in a troop of free-ranging chacma baboons (Papio ursinus). Folia primatol., 16:161-178.
- Saayman G.S. (1971c) Behaviour of chacma baboons. Afr. Wildl., 25:25-29.
- Saayman G.S. (1972a) Aggressive behaviour in free-ranging chacma baboons (Papio ursinus). J. Behav. Sci., 1(3):77-83.
- Sade D.S. (1965) Some aspects of parent-offspring and sibling relationships in a group of rhesus monkeys, with a discussion of grooming. Am. J. Phys. Anthropol., 23(1):1-18.
- Sadlier R.M.F.S. (1969) The Ecology of Reproduction in Wild and Domestic Mammals, Methuen, London.
- Sanderson G.C. (1966) The study of animal movements - a review. J. Wildl. Manage., 30(1):215-235.
- Sargeant A.B. (1972) Red fox spatial characteristics in relation to waterfowl predation. J. Wildl. Manage., 36(2):225-236.
- Schaller G.B. (1972) The Serengeti Lion. A Study of Predator-prey Relations, University of Chicago Press, Chicago.
- Schoener T.W. (1968) Sizes of feeding territories among birds. Ecology, 49(1):123-141.
- Schoener T.W. (1971) Theory of feeding strategies. Ann. Rev. Ecol. Syst., 2:369-404.
- Schulman S.R. (1980) Intragroup Spacing and Multiple Social Networks in Macaca mulatta, PhD Thesis, Yale.

- Seyfarth R.M. (1977) A model of social grooming among adult female monkeys. J. Theor. Biol., 65:671-698.
- Seyfarth R.M. (1978) Social relationships among adult male and female baboons. I: Behaviour during sexual consortship. Behaviour, 64(3/4):204-226.
- Seyfarth R.M. (1980) The distribution of grooming and related behaviours among adult female vervet monkeys. Anim. Behav., 28:798-813.
- Sharman M.J. (in prep.) Individual recognition of unhabituated baboons.
- Sharman M.J., A.W. Whiten & S.J. Hall (in prep.) Ranging behaviour of the Guinea baboon.
- Siegel S. (1956) Nonparametric Statistics for the Behavioural Sciences. International Student Edition, McGraw Hill Kogakusha Ltd, Tokyo.
- Sigg H. (1980) Differentiation of female positions in hamadryas one-male-units. Z. Tierpsychol., 53:265-302.
- Sigg H. & A. Stolba (in press) Home range and daily march in a hamadryas baboon troop. Folia primatol.,
- Silberbauer G.B. (1972) The G/wi bushmen. In: Bicchieri M.G. (ed.), Hunters and Gatherers Today, pp 271-326. Holt Rinehart Winston, New York.
- Sinha D.P. (1972) The Birhos. In: Bicchieri M.G. (ed.), Hunters and Gatherers Today, pp 371-403. Holt Rinehart Winston, New York.
- Siniff D.B. & C.R. Jessen (1969) A simulation model of animal movement patterns. Adv. Ecol. Res., 6:185-219.
- Slatkin M. (1975) A report on the feeding behaviour of two East African baboon species. In: Kondo S., M. Kawai & A. Ehara (eds.), Contemporary Primatology, pp 418-422. Karger, Basel.
- Smuts B. (in prep.) Social Relationships of Adult Female Baboons, PhD Thesis, Stanford University.
- Snedecor G.W. & W.G. Cochran (1967) Statistical Methods. Sixth Edition, Iowa State University Press, Ames Iowa.
- Sokal R.R. & F.J. Rohlf (1969) Biometry. The Principles and Practice of Statistics in Biological Research, Freeman, San Fransisco.
- Steward J.H. (1955) Theory of Culture Change, University of Illinois Press, Urbana.
- Stickel L.F. (1954) A comparison of certain methods of measuring ranges of small mammals. J. Mammal., 35:1-15.
- Stolba A. (1979) Entscheidungsfindung in Verba"nden von Papio hamadryas, PhD Thesis, Zurich.
- Stoltz L.P. & M.E. Keith (1973) A population survey of chacma baboons in the Northern Transvaal. J. Hum. Evol., 2:195-212.

- Stoltz L.P. & G.S. Saayman (1970) Ecology and behaviour of baboons in the Northern Transvaal. Ann. Transvaal Mus., 26:99-143.
- Struhsaker T.T. (1967a) Social structure among vervet monkeys (Cercopithecus aethiops). Behaviour, 29:6-121.
- Struhsaker T.T. (1967b) Ecology of vervet monkeys (Cercopithecus aethiops) in the Masai-Amboseli Game Reserve, Kenya. Ecology, 48:891-904.
- Struhsaker T.T. (1969) Correlates of ecology and social organisation among African cercopithecines. Folia primatol., 11:80-118.
- Struhsaker T.T. (1975) The Red Colobus Monkey, University of Chicago Press, Chicago.
- Struhsaker T.T. & J.S. Gartlan (1970) Observations on the behaviour and ecology of the patas monkey (Erythrocebus patas) in the Wasa Game Reserve, Cameroon. J. Zool. Lond., 161:49-63.
- Struhsaker T.T. & L. Leland (1979) Sociology of five sympatric monkey species in the Kibale Forest, Uganda. Adv. Study Behav., 9:159-227.
- Strum S.C. (1975) Primate predation: interim report on the development of a tradition in a troop of olive baboons. Science, 187:755-757.
- Strum S.C. (1976) Predatory Behaviour of Olive Baboons (Papio anubis) at Gilgil, Kenya, PhD Thesis, University Of California, Berkeley.
- Strum S.C. (in prep.) Correlates of social dominance in adult male olive baboons.
- Sugawara K. (1979) Sociological study of a wild group of hybrid baboons between Papio anubis and P. hamadryas in the Awash Valley, Ethiopia. Primates, 20(1):21-56.
- Suzuki A. (1969) An ecological study of chimpanzees in a savanna woodland. Primates, 10:103-148.
- Suzuki A. (1979) The variation and adaptation of social groups of chimpanzees and black-and-white colobus monkeys. In: Bernstein I.S. & E.O. Smith (eds.), Primate Ecology and Human Origins, pp 153-173. Garland STMP, New York and London.
- Tappen N. (1960) Problems of distribution and adaptation of the African monkey. Curr. Anthropol., 1:91-120.
- Tayler C.K. & G.S. Saayman (1972) The social organisation and behaviour of dolphins (Tursiops aduncus) and baboons (Papio ursinus): some comparisons and assessments. Ann. Cape Prov. Mus. (Nat. Hist.), 9(2):11-49.
- Taylor L.R. & R.A.J. Taylor (1977) Aggregation, migration and population mechanics. Nature, 265:415-421.
- Taylor R.J. (1976) Value of clumping to prey and evolutionary response of ambush predators. Am. Nat., 110:13-29.

- Thompson B.W. (1965) The Climate of Africa, Oxford University Press, London.
- Thompson W.A., I. Vertinsky & J.R. Krebs (1974) The survival value of flocking in birds - a simulation model. J. Anim. Ecol., 43:785-820.
- Triesman M. (1975a) Predation and the evolution of gregariousness. I: Models for concealment and evasion. Anim. Behav., 23:779-800.
- Trevor-Deutsch B. & D.F. Hackett (1980) An evaluation of several grid trapping methods by comparison with radio telemetry in a home range study of the eastern chipmunk (Tamias striatus L.). In: Amlander C.J. & D.W. MacDonald (eds.), A Handbook on Biotelemetry and Radio Tracking, pp 375-386. Permagon Press, Oxford And New York.
- Turner F.B., R.L. Jennrich & J.D. Weintraub (1970) Home ranges and body sizes of lizards. Ecology, 50:1076-1081.
- Van Roosmalen M.G.M. (1980) Habitat Preferences, Diet, Feeding Strategy and Social Organisation of the Black Spider Monkey (Ateles paniscus paniscus) in Surinam, PhD Thesis, Research Institute For Nature Management, Kasteel, Brocknisen, Leersun.
- Van Winkle W. (1975) Comparison of several probabilistic home-range models. J. Wildl. Manage., 39(1):118-123.
- Varley M. & D. Symmes (1966) The hierarchy of dominance in a group of macaques. Behaviour, 27:54-75.
- Vessey S. (1973) Night observations of free-ranging rhesus monkeys. Am. J. Phys. Anthropol., 38:613-620.
- Vine I. (1971) Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. J. Theor. Biol., 30:405-422.
- Voigt D.R. & R.R. Tinline (1980) Strategies for analyzing radio tracking data. In: Amlander C.J. & D.W. MacDonald (eds.), A Handbook on Biotelemetry and Radio Tracking, pp 387-404. Permagon Press, Oxford And New York.
- de Waal F. (1977) The organisation of agonistic relations within two captive groups of Java monkeys (Macaca fascicularis). Z. Tierpsychol., 44:225-282.
- Warner W.L. (1937) A Black Civilization: a Social Study of Australian Tribe, Harper, New York.
- Waser P.M. (1975) Monthly variations in feeding and activity patterns of the mangabey, Cercocebus albigena (Lydekker). East Afr. Wildl. J., 13:249-263.
- Waser P.M. (1976) Cercocebus albigena: site attachment, avoidance, and intergroup spacing. Am. Nat., 110:911-935.
- Waser P.M. (1977) Individual recognition, intragroup cohesion, and intergroup spacing: evidence from sound playback to forest monkeys. Behaviour, 60:28-74.

- Washburn S.L. & I. DeVore (1961) The social life of baboons. Sci. Am., 204(6):62-71.
- Watanabe K. (1979) Alliance formation in a free-ranging troop of Japanese macaques. Primates, 20(4):459-474.
- Western D. (1973) The Structure and Dynamics of the Amboseli Ecosystem, PhD Thesis, University Of Nairobi.
- Western D. & C. van Praet (1973) Cyclical changes in the habitat and climate of an African ecosystem. Nature, 241:104-106.
- Westoby M. (1974) An analysis of diet selection by large generalist herbivores. Am. Nat., 108:290-304.
- Weyman D. & V. Weyman (1977) Landscape Processes. An Introduction to Geomorphology, Allen and Unwin, London.
- Wiener A.S. & J. Moor-Jankowski (1969) The A-B-O blood groups of baboons. Am. J. Phys. Anthropol., 30(1):117-122.
- Wiener A.S., W.W. Socha, J. Moor-Jankowski & E.B. Gordon (1970) The Ap-Bp blood groups of baboons. Am. J. Phys. Anthropol., 31:170-175.
- Williams B.J. (1974) A model of band society. Am. Antiq., 29:1-138.
- Winick C. (1972) Dictionary of Anthropology, Littlefield, Adams & Co., New Jersey.
- Woodburn J. (1975) Stability and flexibility in Hadza residential groupings. In: Lee R.B. & I. DeVore (eds.), Man the Hunter, pp 103-110. Aldine, Chicago.
- Wrangham R.W. (1975) The Behavioural Ecology of Chimpanzees in Gombe National Park, Tanzania, PhD Thesis, University of Cambridge.
- Wrangham R.W. (1976) Aspects of Feeding and Social Behaviour in Gelada Baboons, A Report to The Science Research Council, London.
- Wrangham R.W. (1979) An the evolution of ape social systems. Soc. Sci. Inform., 18:335-368.
- Wrangham R.W. (1980) An ecological model of female-bonded primate groups. Behaviour, 75:262-299.
- Wrangham R.W. (1981) Drinking competition among vervet monkeys. Anim. Behav. (in press)
- Wrangham R.W. & P.G. Waterman (in press) Feeding behaviour of vervet monkeys on Acacia tortilis and Acacia xanthophloea: with special reference to reproductive strategies and condensed tannin production. J. Anim. Ecol.