A Study of Territoriality in *Cercopithecus diana*.
Do Females Take an Active Part in Territorial Defence?

Dissertation submitted to the University of London
for the degree of
Doctor of Philosophy

by

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January 1991

ABSTRACT

In the past, studies of territoriality in primates have concentrated on the role of males in territorial defence. But sociobiological theory of female strategies, and in particular Wrangham's model of female-bonded primate groups, suggest that in many species females should be investing considerable amounts of energy in defence of their food resources against other groups of females. The aims of this thesis are to:

1. investigate the roles of male and female *Cercopithecus diana* in territorial defence, and
2. determine whether female behaviour is consistent with food resource defence and male behaviour with reproductive resource defence as predicted by Wrangham's model.

Annual activity budgets, feeding, ranging and territorial calling behaviour of two groups of *C. diana* are presented, alongside information on plant production cycles and the spatial distribution of potential food resources.

Diana monkeys were observed living in groups of about 20 animals, comprising 1-2 adult males, 6-10 adult females, and subadults, juveniles and infants. Infants were born during the dry season.

Diana monkeys feed on fruits, flowers, leaves and arthropods. Diet varies across the seasons following plant production cycles. Ranging patterns are determined, at least in part, by the spatial distribution of particular flowers and fruits that are important components of the diet.

Females initiate territorial calling bouts significantly more often than does the group male. Intergroup encounters occurred very infrequently, but when they did it was the females, subadults and juveniles that were observed fighting with other groups while the males gave loud calls and jumping displays to one another.

The thesis looks at whether females are defending food resources against other females. Territorial calling is investigated with respect to location within territory, and spatial distribution of important food resources. Male calling behaviour and defence of reproductive females is also considered.

The implications of Diana monkeys calling behaviour are discussed in relation to theories of primate territoriality and defence with particular reference to Wrangham's model of female-bonded groups.

ACKNOWLEDGEMENTS

Among the many people who have contributed to this thesis my thanks are due first and foremost to my supervisor Dr. Katherine Homewood. Kathy's unfailing patience, encouragement and support throughout this project has been all that I could have wished, and for this I am truly grateful.

I would like to thank Professor John Oates of Hunter College New York, and Dr. Abu Sesay of Njala University College, Sierra Leone, for their permission to work on Tiwai, and invaluable help with wading through the bureaucracy necessary to obtain visas and permits. Also, thank you to John for introducing me to my study animals and helping me find my Tiwai feet.

There are many people I should like to thank for their friendship and support in Sierra Leone. Nigel and Rachel Wakeham, and their daughters Bisi and Femi, Dilys Morgan, Jimmy and Harry Whitworth, Glyn Davies and Sylvia Howe, Kevin Gager, Patrick Macaulay, Desmond Chavase, Anne McNicholas, Adrian Luty and David Lamont all deserve my heartfelt thanks for their overwhelmingly generous hospitality, friendship, and technical know-how!

I would like to thank the Paramount Chiefs of Koya and Barri Chiefdoms, and the people of Mapuma and Kambama who greeted yet another field worker with open arms. Particular thanks are due to the men who worked with me on Tiwai, Brima Nyala, Lamin Koroma, Bockarie Kamara, Mohamed Kallon, Kono II Koroma, Pa Laminah and Momo Magona. A very special thank you to Momodu Koroma who, with the help of his wife Soa, looked after me throughout my time on Tiwai.

The research was funded by a postgraduate studentship from the L.S.B. Leakey Trust. Fieldwork was supported by the Central Research Fund of the University of London, The Boise Fund of Oxford, the Emslie Horniman Trust, and the Make Monkeys Matter Appeal. Additional support was provided by a Thomas Witherden Batt Scholarship from University College London.

I have benefitted enormously from the editing skills of a number of people who have ploughed their way through draft versions of chapters, including Dr. Georgina Dasilva, Dr. Glyn Davies, Dr. Caroline Ross, and Guy Cowlishaw. I would like to thank them for their help, and claim full responsibility for all those occasions when I have ignored their good advice.

Thanks are due to Dr. Leslie Aiello for her calmness and great kindness during a minor computer crises in the very late stages of this thesis. And thanks also to Professor

Barrie Jay, without whom printing would have been a nightmare.

Many, many thanks are due to Dawn Hartley for her invaluable friendship and encouragement in and out of Sierra Leone, my parents for their understanding and considerable support over the years, and Liz, who has been unfortunate enough to have had to live with me over the last couple of months.

Finally, I should mention the Diana monkeys, who captivated me with their delightful calls and engaging behaviour, and without whom I would have no thesis.

TABLE OF CONTENTS

CHAPTER FIVE: RANGING BEHAVIOUR 142

CHAPTER SIX: TERRITORIAL CALLING 187

LIST OF TABLES

LIST OF FIGURES

CHAPTER ONE

INTRODUCTION

1.1 INTRODUCTION

In the past, studies of territoriality in primates have concentrated on the role of males in territorial defence. This reflects the emphasis on male territorial behaviour found throughout the extensive literature on territorial behaviour in birds, and on species that defend leks during the breeding season.

Emlen and Oring (1977), in their paper on the evolution of mating systems, proposed that in polygynous species males obtained mates either by:

1. resource defence polygyny,
2. female defence polygyny, or
3. male dominance polygyny.

In resource defence polygyny, males are assumed to defend resources essential to females (e.g. fiddler crab - Christy, 1983). Alternatively, if males adopt the female defence polygyny strategy, they should defend groups of gregarious females against potential rival males (e.g. red deer - Clutton-Brock et al, 1979). If males opt for the third strategy, male dominance polygyny, they will be seen occupying, and defending leks, or display grounds, to attract females (e.g. black grouse - Kruijt & Hogan, 1967). Thus within the literature, the emphasis has been primarily on males and their defence of resources, whether food or access to mates.

More recently, Wrangham's theoretical model suggests that patterns of social organization in female-bonded primate groups have arisen as a result of a compromise between male and female interests. Females need to defend food resources, and thus should be territorial, whereas males are defending their access to reproductive females (Wrangham 1980).

1.2 AN ECOLOGICAL MODEL OF FEMALE-BONDED PRIMATE GROUPS

Wrangham's model of female-bonded primate groups suggests that females defend their access to food resources, while males should defend their access to reproductive females (Wrangham, 1980). In female-bonded species, female patterns of dispersion are determined by the quality, quantity and distribution of food resources in any particular environment. Male patterns of distribution thus are determined by female spacing patterns. Consequently, patterns of social organization are expected to represent a compromise between male and female strategies.

Wrangham postulated that access to food resources was the major limiting factor determining female reproductive success, whereas access to reproductive females is thought to be the major limiting factor determining reproductive success in males (Trivers, 1972). Thus, the selective pressure favouring female sociality was the need to maximise the amount of food available to individuals.

The present thesis tests Wrangham's model. The thesis paradigm is constructed on the following assumptions and predictions of Wrangham's model.

Assumptions

Firstly, in female-bonded species it is the adult females that form the social and spatial core of the group. Secondly, although groups are likely to experience intra-group feeding competition, during periods when preferred foods are scarce, or unavailable, they change their dietary strategy, rather than reducing their foraging group size. Thirdly, it is assumed that inter-group competition is more costly to group members than intra-group competition.

Predictions[1]

1. Preferred foods are found in discrete, rare patches that are economically defensible by groups.
2. Competition over preferred food patches is more successful in larger groups that can displace smaller groups. Under such circumstances it is more advantageous to form coalitions with reliable allies, therefore stable kin groups are favoured over non-kin groups (Wrangham, 1982).
3. As a consequence of the high costs of inter-group competition, groups should be territorial, or be able to displace competing groups at food patches.
4. Where groups are territorial, females should take an active part in territorial defence, and thus defend the food resources contained within the group territory.

There have been many reports of females taking an active role in inter-group encounters in a range of species including _Propithecus verreauxi_ - Richard (1977), _Presbytis entellus_ - Ripley (1967), _Cercopithecus aethiops_ - Cheney, 1981, and _Hylobates pileatus_ - Brockelman & Srikosamatara (1984). However, there is little or no quantitative information available with respect to female territorial strategies, or the dichotomy between male and female strategies. Therefore, it seems important that this aspect of primate behaviour be investigated with respect to

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[1] Adapted from Wrangham (1987).

females.

Before presenting an outline of the thesis, I will consider briefly several alternative theories of primate sociality. This is necessary because it is my intention to discuss the results of the thesis in the light of the ultimate causes of primate sociality, as well as considering proximal factors determining group-living and group structure.

1.3 WHY DO PRIMATES LIVE IN GROUPS?

Over the years there has been much debate as to why most primate species are observed living in social groups. Four main reasons have been suggested to explain why primates live in groups, as outlined in Dunbar (1988):

1. to defend resources against competing conspecifics,
2. for protection against predators,
3. to improve foraging efficiency, and
4. for improved care-giving opportunities.

As summarised above, the resource defence hypothesis postulates that the distribution of resources within the environment is the determinant of the pattern of female dispersion, and thus the distribution of males through out the population (Crook & Gartlan, 1966; Emlen & Oring, 1977; Wrangham, 1980; Andelman, 1986).

The second hypothesis is that group living in primates has evolved in response to the risk of predation (Alexander, 1974; van Schaik, 1983; van Schaik & van Hooff, 1983; Terborgh, 1983; Terborgh & Janson, 1986; Dunbar, 1988).

The third suggestion, based on work on large carnivores and flocking species of birds mainly, proposes that foraging efficiency can be improved by group living.

1. Larger groups are able to catch and kill larger prey, as reported for lions (Schaller, 1972).
2. Animals in groups may harvest renewable resources more efficiently e.g. return rates of flocks of Brent geese are timed to maximise cropping of sea plantain shoots (Priris et al, 1980, in Krebs & Davies, 1981).
3. Group size may influence the rate at which food patches are detected (Pitcher et al, 1982), and
4. Communal nesting and sleeping sites may function as "sources of information" about food resources (Ward & Zahavi, 1973; deGroot, 1980).

The final hypothesis states that primates form groups to obtain help in rearing their young. Help in rearing offspring could take a number of forms such as helping in carrying infants (as seen in Siamangs and callitrichids) territorial defence, protection from harassment by other individuals, or adoption of orphans (Dunbar, 1988).

While the foraging efficiency and care-giving hypotheses do not appear particularly relevant in determining why primates specifically, are group-living (Dunbar, 1988), I have included them here because they may help explain proximal causes of the diversity of patterns of social grouping seen both within and across species, and/or the different patterns of social relationships seen within different types of groups.

1.4 AIMS AND STRUCTURE OF THE THESIS

The aim of this thesis is to use the framework set up by Wrangham's model to investigate whether:

1. female Diana monkeys are territorial,
2. if so, are they defending food resources as predicted by the model?
3. Are males defending territories alongside the females, or are they in fact defending access to reproductive females as predicted?

Thesis Outline

Chapter 2: General Methodology - presents data collection techniques, and methods of data analysis used in the thesis.

Chapter 3: Activity Patterns - daily and seasonal activity patterns are presented.

Chapter 4: Feeding Behaviour - an outline of spatial and temporal distribution of food resources is given, and annual diet and seasonal variation in dietary patterns are described.

Chapter 5: Ranging Behaviour - home range area and overlap with neighbouring groups, seasonal variation in range use, and determinants of ranging behaviour are considered in this chapter.

Chapter 6: Territorial Calling Behaviour - daily and seasonal territorial calling patterns are presented, and male and female roles in territorial calling bouts are analyzed. Vocal responses to outgroup calling are also considered.

Chapter 7: Testing an Ecological Model of Female-Bonded Primate Groups - in this chapter female territorial behaviour and defence of food resources are considered, along with male-male competition for access to reproductive females.

Chapter 8: Concluding Discussion

CHAPTER TWO

GENERAL METHODOLOGY

2.1 RATIONALE

1. (a) The hypothesis being tested is that female *Cercopithecus diana* use their chatter-scream vocalisations to incite their harem male into giving his territorial loud calls. If this is correct, then it is predicted that harem males will give significantly more loud calls following chatter-screams from their group females than spontaneously, or following loud calls from other males. In this context, "response" was taken to mean that animals gave chatter-screams or loud calls within 5 minutes of hearing the "stimulus" call.

(b) If female chatter-screams do incite males into giving loud calls, what stimulates females into giving their chatter-screams? Could it be loud calls from "neighbouring" or "stranger" males? If they are stimulated by outside males then it is expected that they will respond, giving significantly more chatter-screams on hearing outside males compared with those given spontaneously or following their harem male's loud calls.

2) An alternative hypothesis is that males give their loud calls in response to loud calls from other males, i.e.

potential rivals. If this is the correct hypothesis then males should give significantly more loud calls, following other loud calls, than they will spontaneously or following female chatter-screams.

3) A third possibility is that males give their loud calls spontaneously, and not in response to vocal stimuli from other intra- or extra-group animals. If this is the case, then the results should reflect this by demonstrating that there is no relationship between the occurrence of male loud calls and female chatter-screams, or loud calls from different males.

4) Assuming that females are participating in territorial defence, what are the benefits of such an investment? According to Wrangham's model (Wrangham, 1980), there is a dichotomy between the sexes. Males defend their access to reproductive females, but females defend their access to food resources. Possibly females can accrue other benefits by such behaviour, e.g. by helping the harem male defend the territory against possible takeovers by rivals they reduce the risk of infanticide by the incoming male. Although it has not been reported in Diana monkeys, there is an increasing amount of evidence in the literature suggesting that infanticide does occur in a number of *Cercopithecus* species, and that it is not as unusual as was previously thought (*C. ascanius* - Struhsaker, 1977; *C. mitis* - Butynski, 1982).

(a) Data was collected to test the hypothesis that females are investing in territorial behaviour to defend their food resources. If this hypothesis is correct then it is predicted that female territorial calling rates will reflect food quality and availability within the group's territory.

(b) A further possibility is that animals may devote more time/energy into defending particular food sources within their territories. If so, then this might be reflected in calling location, i.e. females call more frequently, or for longer periods, in the vicinity of favoured/important food items. If so, then calling location should vary both spatially and temporally, following the spatial distribution and phenology of food plants.

(c) Alternatively, females may be investing in such behaviours to minimise the chances of a new male moving into the group. This can be associated with considerable energetic costs on the part of the females, such as infanticide, and increased aggression within the group etc. If prevention of infanticide is an important factor then this may be reflected by a significant increase in female calling rates during periods when infants are vulnerable to infanticide (Diana monkeys are seasonal breeders, Stevenson, 1987; Whitesides, pers. comm.).

However, it has been suggested (Hrdy, 1977) that in cases where the breeding male remains overlong within the group (i.e. his daughters reach sexual maturity during his tenure) then females might actively encourage a group takeover, or at least solicit matings from non-group males. Furthermore, in one study of Colobus badius (Marsh, 1979) patterns of female intergroup transfer could not be explained solely as infanticide avoidance strategies. Females appeared to be able to assess an incoming male's ability to defend his troop against rivals, and thus moved between neighbouring groups accordingly.

Although it was not possible in this study to investigate the above systematically, where possible, opportunistic data on male takeover and length of tenure, and fertility and infant survival were collected, to try and help clarify the situation.

2.2 STUDY SITE

The site chosen for this study was Tiwai Island Wildlife Sanctuary, on the River Moa, in southern Sierra Leone. The island lies between 80-110m above sea level, and is the largest river island in the country, covering approximately 12km^2 (Whitesides, 1989).

A number of other studies of primate ecology have been carried out at this site; namely studies of colobine feeding and ranging behaviour (Procolobus badius, Davies, pers.

comm.: Colobus polykomos, Dasilva, 1989: Procolobus verus, Oates, pers. comm.) and a basic ecological study of Cercopithecus diana (Whitesides, in prep.).

The climate on Tiwai is tropical, with maximum temperatures of 29°C during the wet season and 40°C in the dry season. Rainfall and daily temperature were recorded systematically from the Tiwai Weather Station at the West Camp (See Fig 2.1). Maximum and minimum temperatures were recorded daily between 07.30 - 08.00. Rainfall was measured daily, in millimetres, and relative humidity recorded twice a day between 07.30 - 08.00, and at 14.00.

The Tiwai weather records for Oct'87 to Mar'89 inclusive, are presented in Fig. 2.2. Unfortunately the rain gauge sprang a leak sometime during late July/early August and went undetected until the end of August. Therefore when considering the rainfall data this should be taken into account. Because of the reasons outlined above, the rainfall data were considered too inaccurate when considering annual rainfall (Apr 88 - Mar 89: cumulative rainfall = 2288mm). The mean annual rainfall for 1983-1985 inclusive, was 2857mm (range 2417-3109mm) as outlined in Dasilva, 1989. Most of the rain falls in the May-Oct wet season: very little falls from mid-November to mid-March.

Tiwai lies within the Upper Guinean rain forest zone, close

Fig. 2.1: Tiwai - Showing Location of East and West Study Site Areas

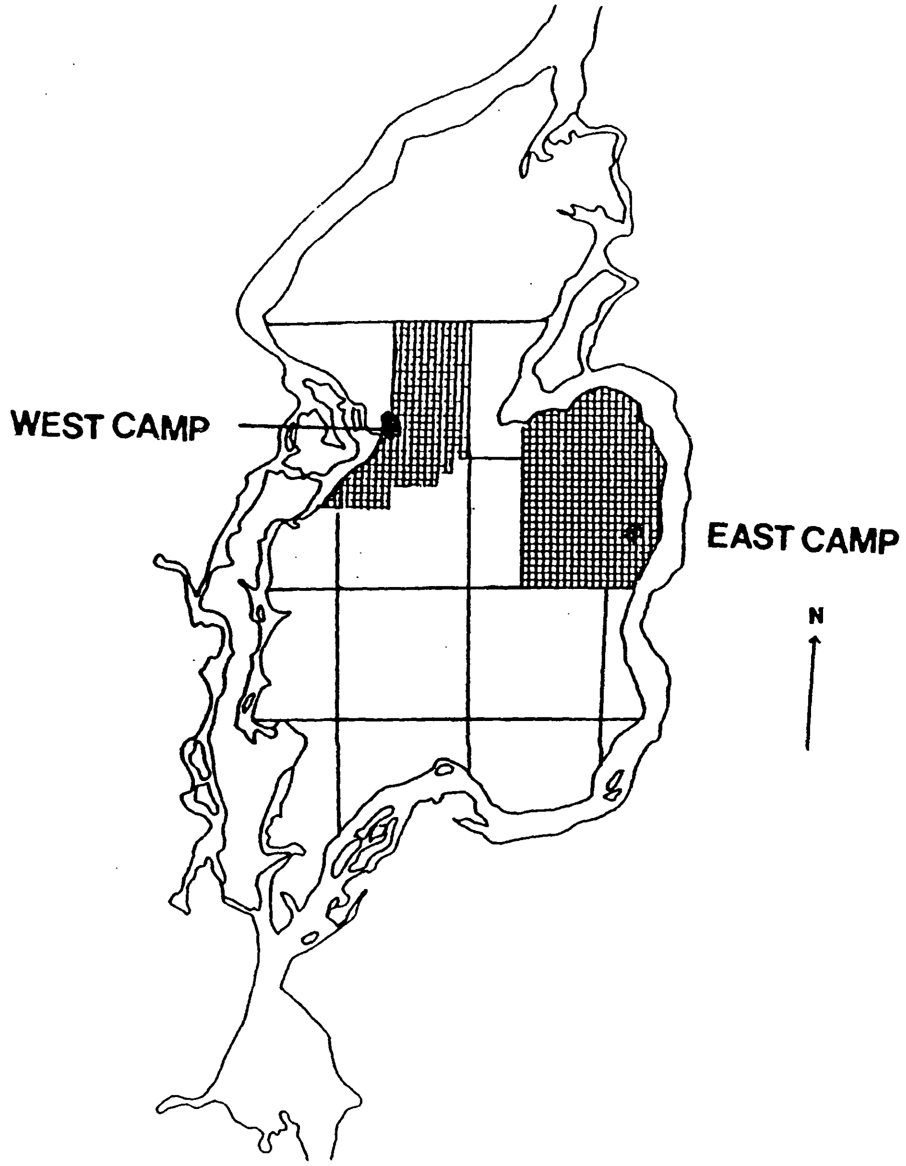
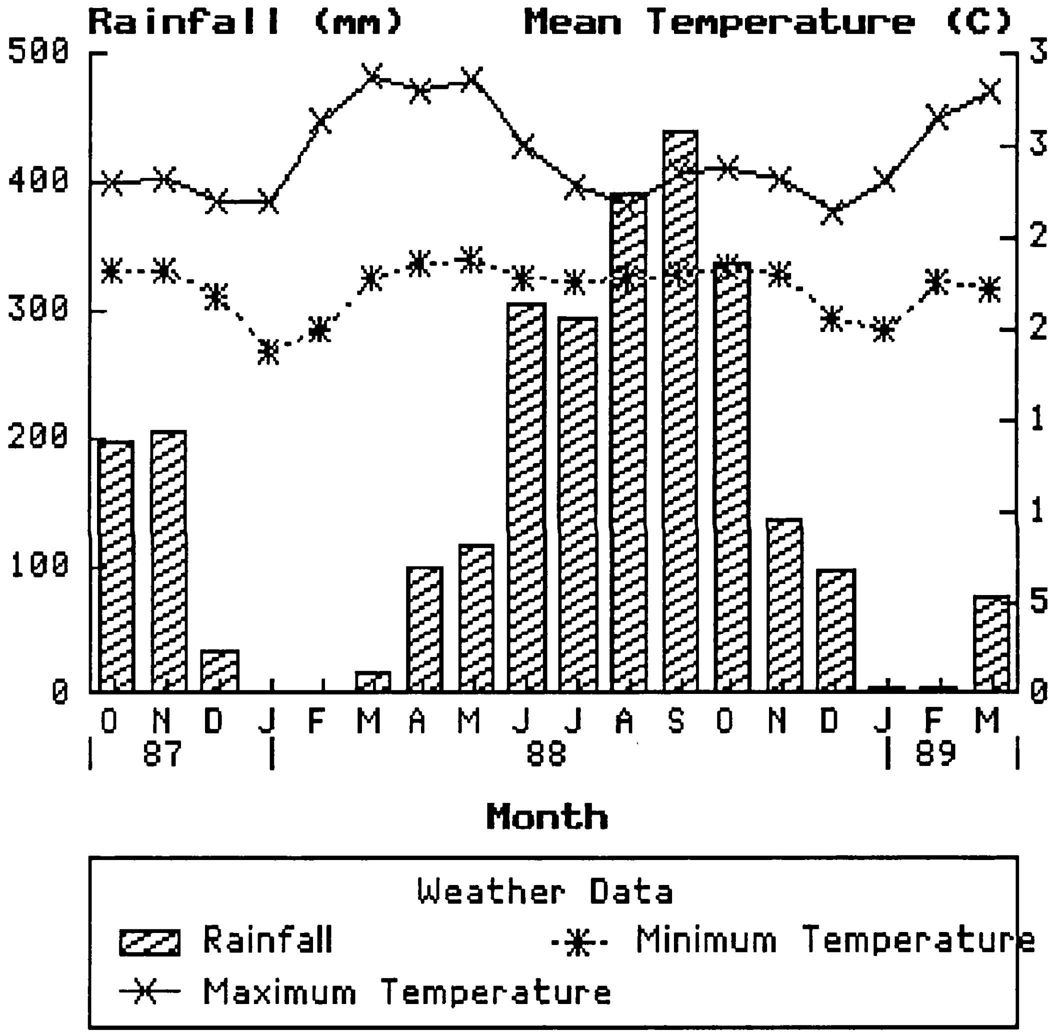


Fig. 2.2: Tiwai Weather Data From October 1987 - March 1989 Inclusive



to the western edge of the Gola West Forest Reserve (Davies, 1987). About half of the island supports old secondary forest, estimated to be 40-60 years old. The remainder is covered by a mosaic of swamp and riverine forest, young secondary forest, and several farms worked by local people.

There are two study sites on the island - the East site and the West site. Within these two areas a grid system of trails has been cut, with cells of 50m sides. The main camp lies on the Western side of the island close to the West study site. There is also a second, smaller camp, within the East site to facilitate working there. Throughout both study sites previous researchers have mapped, tagged and identified all trees over 15cm dbh (diameter at breast height). From their data the frequency and distribution of different species of tree has been determined for the two sites. Their results suggest that the East study site shows a greater number of species associated with moist conditions e.g. Pentaclethra macrophylla and Uapaca guineensis, compared with the West study site, where species characteristic of drier sites are more commonly found, e.g. Piptadeniastrum africanum and Antiaris africana, (Dasilva, 1989).

2.3 STUDY GROUPS

Two groups of Diana monkeys were studied: W in the West study area, and E living in the East study site. Both groups had previously been studied by Whitesides (pers. comm.) so were already habituated. During the pilot study (January - February 1987) a potential third study group, W_2, living adjacent to W was identified and followed, with a view to including it in the main field study. W_2 was subsequently followed intermittently for the first four months but further follows were dropped because there was not enough time available to habituate the group and continue working with W and E.

As outlined in Aldrich-Blake (1970a), there are many problems associated with studying forest primates, not least the problem of poor visibility. Poor visibility can result in misleading assessments of group size, composition, behavioural interactions and social relationships within the group.

Home ranges of both study groups included extensive areas of very dense vegetation. Coupled with the tendency for Diana monkey groups to spend much of their time spread over a wide area, and to travel in an "amoeboid-like fashion" (Whitesides, 1989), this made it difficult to obtain accurate group counts.

It was not possible to carry out systematic assessments of group size and composition. Instead, group counts were made opportunistically as troops crossed gaps in the vegetation, or moved into the exposed crowns of the tallest trees. Additional information was obtained from notes taken during scan samples.

Traditionally forest-dwelling Cercopithecus species were thought to live in uni-male harem groups (Struhsaker, 1969). However, as many more field studies are carried out on various species of forest-living guenons, it has become clear that Cercopithecus show great variation in their group structure, both between and within species. Aldrich-Blake (1970b) and Schlichte (1978) studied C. mitis living in uni-male groups whereas Rudran (1978a) and Tsingalia & Rowell (1984) reported groups with two or more adult males associated with them.

Several features do seem to be characteristic of guenon group and population structure, namely that the adult females are the permanent group members while males leave their natal group as sub-adults. When they leave the group sub-adult males have a number of options: they can live as solitary animals, or live in all-male or heterosexual associations (Cords, 1984, 1987).

The group structures presented below represent the minimum outline of group composition for the two study groups between January '88 and Mar '89.

Table 2.1: Composition of Groups W and E

Group	[1]AM	AF	SA	J	UNID.	I ('88/89)	Total
W	1	6	4	5	2	2/3	(20-21)
E	1/2*	10	3	3	4	0/3	(21-25)

* There were two adult males seen, and heard calling, in group E during follows carried out in March, November, and December '88, and January and February '89.

KEY
AM - Adult male
AF - Adult female
SA - Subadult
J -Juvenile
UNID - Unidentified
I - Infant

In previous studies carried out by Whitesides (pers. comm.) and Galat & Galat-Luong (1985), Diana monkeys have been observed living in uni-male harem groups, with 5-7 adult females, (See Table 2.2). From Table 2.1. it can be seen that there was a second calling male seen in association with group E for a total of five months. Curtin (in Cords, 1987) reported the presence of a second sexually mature male in their study group for several months. Thus, Diana monkeys would also appear to have a more flexible group structure than previously thought.

Solitary males were observed on numerous occasions within the ranges of the two study groups. They were seen to avoid encounters with groups, retreating rapidly from food sources or resting sites on hearing the approach of the resident group.

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[1] Age/sex classes as defined in Appendix I.

The numbers of infants born into the two study groups during 1988 and 1989 are given in Table 2.1. New babies appeared in late December, January and early February throughout the two breeding seasons covered by this study. Captive Diana monkeys show strong seasonality in the birth of their young, the bulk of them being born during the winter months of December through to March, (Stevenson, 1987). This captive data confirms that Diana monkeys are seasonal breeders and that infants are born at a particular time of year.

Table 2.2: A Comparison of Group Size and Structure in *Cercopithecus diana*.

Study		**AM**	**AF**	**SA**	**J/I**	**UNID**	**TOTAL**
Whitesides	**W**	1	7	0-1	3- 7		19-21
(1989)	**E**	1	7	0	5-14		21-27
Present	**W**	1	6	4	7-10	2	20-21
Study	**E**	1-2	10	3	3- 6	4	21-25
Galat & Galat-		1	5	0	5		11
Luong (1985)		1	6	0	10		17
Curtin (unpub.)							14-40
in Cords (1987)							(N=3)

KEY
AM - Adult Male
AF - Adult Female
SA - Subadult
J - Juvenile
I - Infant
UNID - Unidentified

Whitesides used a different system for classifying age/sex classes to that used in the present study. Therefore, the data presented in Table 2.2. has been lumped accordingly to make it comparable between studies.

The table above suggests that both study groups, W and E, have remained consistent in their size, though not their structure, from year to year. However, it is possible that this is an artefact of observation conditions allowing only partial group counts. Group sizes from the Tai Forest, Ivory Coast, appear smaller than those found on Tiwai, but resemble the other groups outlined above in their composition.

Unfortunately there is very little information available from Bia Forest, Ghana (Curtin, in Cords 1987): the three groups observed there showed a large range in group size, 14-40 individuals. To conclude, there does not seem to be a fixed group size for Diana monkeys. The data suggests that group size may be a compromise between various costs and benefits of group living, such as predation pressures, population density, intra- and inter-specific competition, and habitat quality.

2.4 SAMPLING METHODS

Taking into account the various problems associated with studying arboreal, forest-living primates, it is necessary to choose appropriate sampling techniques to collect an adequate amount of data while minimising biases resulting from observation conditions.

Every month both groups were followed for up to five consecutive days (dawn to dusk). During these five-day follows multiple sampling techniques were used to make maximal use of the time available, as suggested by Altmann, 1974. A total of 1200 hours was spent in visual and/or auditory contact with the study animals as shown below in Tables 2.3. and 2.4. An important consideration with respect to the methodology used in this study is that, where possible, it should be compatible with that previously used by Whitesides.

Scan Sampling

Scan sampling was carried out at regular intervals throughout the day, to collect information on day range length, home range size and patterns of use, and daily activity patterns. Previous studies, such as those carried out by Whitesides (1989) and Waser (1974) have used sample intervals of 20 and 30 minutes respectively. The advantage of using longer intervals is that with shorter intervals one cannot necessarily assume that the data points are independent.

Initially it was felt that not enough data would be accumulated without using a shorter interval so a sample interval of 10 minutes was used for the first two months of data collection, as in Mitani's study, (Mitani, 1985a).

Table 2.3: Total Observation Time for Group W

Month	No. of days	No. hrs in visual/ auditory contact/day	Mean. No. hrs in vis./aud.contact/day
Jan'88	5.0	59 hrs, 20 min	11 hrs, 52 min
Feb	5.0	59 hrs, 40 min	11 hrs, 56 min
Apr	6.0	68 hrs, 20 min	11 hrs, 23 min
May	5.0	57 hrs, 20 min	11 hrs, 28 min
Jun	5.0	54 hrs, 40 min	10 hrs, 56 min
Jul	5.0	38 hrs, 40 min	7 hrs, 44 min
Aug	5.0	53 hrs, 00 min	10 hrs, 36 min
Sep	4.0	30 hrs, 00 min	7 hrs, 30 min
Oct	5.0	59 hrs, 40 min	11 hrs, 56 min
Nov	4.5	49 hrs, 40 min	11 hrs, 02 min
Dec	4.0	47 hrs, 20 min	11 hrs, 50 min
Jan'89	4.0	46 hrs, 40 min	11 hrs, 40 min
Mar	3.5	36 hrs, 20 min	10 hrs, 23 min
Total	**61.0**	**660 hrs, 40 min**	**10 hrs, 50 min**

Table 2.4: Total Observation Time for Group E

Month	No. of days	No. hrs in visual/ auditory contact/day	Mean. No. hrs in vis./aud.contact/day
Jan'88	3.0	32 hrs, 40 min	10 hrs, 53 min
Feb	3.0	36 hrs, 00 min	12 hrs, 00 min
Mar	7.0	69 hrs, 00 min	9 hrs, 51 min
Apr	5.0	51 hrs, 20 min	10 hrs, 16 min
May	4.0	40 hrs, 20 min	10 hrs, 05 min
Jun	5.0	52 hrs, 40 min	10 hrs, 32 min
Jul	3.0	35 hrs, 40 min	8 hrs, 33 min
Aug	4.0	38 hrs, 00 min	9 hrs, 30 min
Oct	4.0	36 hrs, 40 min	9 hrs, 10 min
Nov	4.0	46 hrs, 00 min	11 hrs, 30 min
Dec	3.5	39 hrs, 00 min	11 hrs, 09 min
Jan	3.0	29 hrs, 40 min	9 hrs, 53 min
Total	**52.5**	**544 hrs, 40 min**	**10 hrs, 22 min**

Since only monthly averages are needed to investigate any variation in ranging and feeding behaviours, the lack of independence of individual data points would not have been a problem. All scan sample data collected after February 1988 were collected at 20 minute sampling intervals, starting on the hour, because it was found to be too difficult to sample groups using any smaller interval because of group dispersion throughout much of the sample period. Thus where data collected earlier than this has been included, only alternate sample periods have been used.

Diana monkeys live in groups of 20-25 individuals, and spend much of their time spread over a wide area. The purpose of scan sampling is to produce a picture of group activities, distribution etc. at a particular instant in time. In practice it is not possible to produce an instantaneous record for every individual. Therefore, it is important to have a cut-off point for each scan after which no more data is collected till the following scan. Because the groups were so dispersed, enough time was needed for the observer to walk round the cells throughout which the test group was spread. Thus each scan was continued for five minutes. Homewood (1976) showed that when comparing the results of activity estimates from instantaneous and 5-second delay sampling strategies, the results were biased towards movement and other behaviours incorporating movement. Thus, once an animal was clearly in view its instantaneous behaviour was recorded after a pause of five seconds. This delay between sighting the animal and recording its activity was used to reduce any bias inherent in scan sampling, where more conspicuous behaviours may be overrepresented in the sample (Chalmers, 1968; Clutton-Brock, 1977a). During each scan the monkeys were recorded in the order in which they were seen: the categories of behaviours used are outlined in Chapter Three. This procedure follows that used by Whitesides (1989). Scan sample data were collected on check sheets designed after Hinde (1973).

Ad libitum sampling

Ad libitum sampling was also used during follows, to supplement the data on the incidence and context of particular vocalisations, i.e. male loud calls and female chatter-screams. All instances of loud calls and chatter-screams were recorded, including calls from non-group animals. In addition, loud calls and alarm calls of other species e.g. Colobus polykomos and the focal animal's response to them was noted. Information was collected on check sheets as previously. During inter-group encounters a dictaphone was also used to facilitate recording event sequences very quickly.

One problem commonly cited for ad libitum sampling is that it can be biased towards conspicuous individuals and/or behaviours (Altmann, 1974; Martin & Bateson, 1986) and so should only be used when certain criteria are fulfilled, namely:

1. all animals must be equally visible, and
2. all animals must have the same chance of being observed when engaged in rare behaviours (Lee, 1983).

Both of these criteria are met in this study. All chatter-screams and loud calls are equally audible to the observer, fulfilling 1., and the relevant behaviours are detected aurally rather than visually, which satisfies the second requirement.

Focal Animal Sampling

One of the aims of this study was to investigate the context in which loud calls and chatter-screams were given, and the responses they elicit in both group members and extra-group animals. Although much of this information was collected using ad libitum sampling, it was originally hoped that this would be supplemented by focal animal work. Focal animal sampling, using continuous recording, was attempted during the first four months of the study to determine the behaviour of subjects before, during and after calling bouts. In captivity, individual Diana monkeys are easily identified, but in the wild this is not so. However, it was possible to determine age/sex class for animals, so focal animals were chosen on the basis of their age/sex class - either adult male or adult female.

Focal animal sampling was very difficult under the prevailing observation conditions. Dense vegetation, combined with group spread and patterns of movement, group size, and the limitations of only being able to identify individuals down to age/sex class resulted in the observer being in contact with any one individual for an average of 4 minutes, 24 seconds only. Consequently, it was felt that under these circumstances focal animal sampling was an inappropriate method (Dunbar, 1976) and therefore should be discontinued.

2.5 PHENOLOGY

To determine whether females are defending their food resources, data were needed to investigate the periodicity of plant part production with respect to important food species. For each group, 1 day/month was originally set aside to collect the necessary phenology data.

In previous primate studies carried out on Tiwai, two different methods have been used to collect phenology data. Whitesides's methodology evolved from that used by Oates and Struhsaker (Oates, 1974). He used a scale of 0-5 increasing in units of 0.5, like Davies and Dasilva, but his method differed from that used later by having no fixed value for maximum abundance. Davies and Dasilva used methods based on those outlined by Raemaekers (1980), and similar to those presented in NRC (1981), where abundance was estimated on a linear scale of 0-5, graduated in units of 0.5. The maximum abundance of any part that could be expected for a particular species was 5. Although both methods are subject to a number of errors, with respect to estimates of abundance levels, the latter system makes for a more easily standardised methodology, allowing greater consistency between observers, and between studies.

Whitesides established a phenology walk within the home range of the western group, W. He tagged 11 species of large trees (girth > 40 cm) and 1 species of liana. 5-10 individuals of each tree species were monitored at regular intervals along with 5 lianas. The criteria used to determine the individual plants within the sample was that each tree be clearly visible from the trail grid, and within the study group's home range. These 89-107 tagged trees and 5 lianas were used as a phenology sample in the present study.

In total, 6 phenophases were monitored: 2 vegetative phases - mature leaves, and young leaves and leaf buds - and 4 reproductive phases - flower buds, flowers, immature fruits and ripe fruits. (See Appendix II for definitions of the various phases). The abundance of each plant part was estimated on a linear scale of 0-5, increasing in units of 0.5, following the system used by Davies and Dasilva (A.G. Davies, pers. comm.). It was assumed that the whole crown area was capable of bearing foliage. The maximum abundance of all vegetative parts was then taken as 5, so that the estimated abundance for each phenophase was a percentage of the whole crown. In this way, there was a constant maximum abundance for each vegetative phase, promoting consistency between observers.

Ideally, a similar system should be enforced for the reproductive phases. Thus the combined maximum abundance estimates for flower buds, flowers, unripe and ripe fruits would be 5. (One problem with this would be if one wanted to compare the amounts of flowers and fruits available. By using a constant maximum for all reproductive phases this could lead to problems when comparing two species that have very different flowering and fruiting patterns, e.g. where species 1 has a combination of flowers and fruits present simultaneously, but species 2 produces flowers then fruits separately, without much overlap between the phases, (A.G. Davies, pers. comm.). At present there appears to be no easy solution to this problem of how to obtain consistent abundance estimates of reproductive parts between observers, or for one observer over a period of time.

Phenology data were collected at monthly intervals. Although monthly samples may not have been frequent enough to give a very accurate picture of the periodicity of certain phases (e.g. young leaves - A.G. Davies, pers. comm.) this is not a problem for this particular study. The data were being collected to try to determine whether there was any association between calling behaviour and food availability: therefore it was more important to have an accurate record of abundance of food parts at times when data on calling behaviour was also being recorded. To do this a second check sheet was carried at all times during follows to collect additional data on location and types of food sources being used, size of food plants and abundance of parts (measured on the 0-5 scale in the same way as the regular phenology data), and the number of animals observed feeding. This was collected at regular intervals of 20 min, concurrently with scan sampling, enabling a direct comparison between calling rates and locations, and food resources being exploited at that particular time.

Although the phenology data recorded during this study is not directly comparable with that collected by Whitesides, it will be possible to make some comparisons of maximum and minimum availability of plant parts, to obtain a general picture of seasonal variation in food resources. Possibly, this is the only valid way of comparing data sets between studies, irrespective of the data collection methods used. Although the methods used by Dasilva and Davies incorporate a standard numerical scale of abundance estimates, there are still likely to be substantial errors involved, particularly when assessing the availability of plant reproductive phases. Even if the observer is very familiar with each sample species, and the maximum abundance of each phenophase, these are likely to vary from year to year.

However, in the context of this project the important information is how food resources are perceived to fluctuate throughout the year, and whether calling behaviour patterns are in any way associated with those fluctuations, so data from previous studies are not of paramount importance.

2.6 DATA ANALYSIS

Because of the nature of the data collected during this study it is unrealistic to assume an underlying normal distribution. Therefore, the tests used in the analyses are nonparametric. They are described in Siegel & Castellan (1988). All results are accepted as being significant at the 0.05 level.

A step-wise multiple regression analysis was used in Chapter Five to investigate parameters determining ranging behaviour of the two study groups. This was carried out using SPSS/PC+ Version 3.1.

All graphics were produced using Harvard Graphics Version 1.0.

SUMMARY

1) This study attempts to test the hypothesis that females are investing in territorial behaviour to defend their food resources by means of territorial calling strategies.
2) Field work was carried out at Tiwai Island Wildlife Sanctuary, a forested riverine island in southern Sierra Leone.
3) Two groups of *Cercopithecus diana* were studied. Observation conditions create major problems in assessing group size and composition, but these varied between groups and throughout the study. Comparing the results of this study with that of others, it would appear that *C. diana* show considerable flexibility in their group size and structure, as do many other guenon species. Like other guenons, the females are the permanent group members while males leave their natal groups as young adults/sub-adults.
4) Several different sampling techniques were employed to collect information on day range length, home range size and patterns of use, daily activity patterns, contact calling and other social activities, and territorial calling and intergroup interactions.

CHAPTER THREE

ACTIVITY BUDGET

3.1 INTRODUCTION

Time and energy are central to activity patterns seen in primates. The interaction between these fundamental variables determines the types and amounts of behaviour seen (Coelho, 1986). Ecological and social constraints also play a part in determining activity patterns throughout the primate world. This can be illustrated by considering factors that are potentially influential in determining the amount of time an animal spends feeding. These include its body size, thermoregulatory constraints (both as a result of body size and habitat conditions), metabolic requirements, reproductive state, and food quality, availability, and handling or processing time (Altmann, 1970; Clutton-Brock & Harvey, 1977; Belovsky & Slade, 1986; Dunbar, 1988).

In this chapter I intend to consider the activity budget of Diana monkeys, and how they vary their activity patterns over the year. From the literature, thermoregulatory constraints and food type and distribution appear to be important determinants of primate activity patterns. Both ambient temperature and the acquisition of food are considered in the light of the animals' behaviour, and where relevant, important factors are discussed.

3.2 METHODS

Five day follows were completed on the study groups every month between January 1988 and March 1989. Scan sampling techniques, as outlined in the previous chapter, were used to gather general information on the Diana monkeys' behaviour. The following information was recorded for each animal scanned:

1. **age/sex class:** i.e. adult male, adult female, subadult, large juvenile, small juvenile, infant.
2. **weather conditions during the scan:** i.e. sunny, cloudy, raining, or dark.
3. **location:** a number corresponding to a position drawn onto a map of the study site.
4. **behaviour/activity:**

   Travel: animal engaged in any movement other than that involved in foraging, playing or aggressive encounters such as being chased by another group member.

   Feeding: this was differentiated into foraging and feeding. Foraging was recorded if the subject was observed pulling off fruits, leaves, bark etc: sorting through leaves, flowers etc: or searching for arthropods found within the canopy, or lower levels of the forest. An animal was scored as feeding only if it was actually observed ingesting and chewing food: however, it was not always possible to determine whether animals were swallowing food or storing it in their cheek pouches.

Resting: monkeys were recorded as resting when they were seen sitting, or lying, and were not engaging in social or feeding activities. Sleeping animals were also included in this category.

Vigilance: was recorded if animals were seen to look up and/or scan their surroundings, except in the context of feeding. On occasions some adults were seen to move to the top level of the canopy and look out over the forest - this behaviour was particularly characteristic of the adult males.

Play: animals were considered to be playing if they were observed in any of the following: tickling, wrestling, mock biting or mock chasing. Although occasionally seen amongst adult animals, these behaviours were most common amongst the juveniles and infants, though adult females were to be seen tickling and wrestling with their young infants.

Aggression: any aggressive encounter including at least one of the following: aggressive chasing, threat faces (lips flicked back quickly uncovering the canines), threat stance - standing on all fours, leaning forwards and staring at their opponent - this was usually accompanied by threat faces.

Grooming: divided into self and social grooming. Self grooming was defined as an animal scratching itself or engaging in any other self cleaning activity. Social grooming was recorded where any individual was being groomed by, or was grooming another individual.

Calling: all animals calling as they were scanned fell into this category. The type of call given was recorded, and if accompanying other types of behaviour, this was noted.

Miscellaneous: all other activities fell into this category e.g. urinating, defecating and various aspects of infant care.

For the purposes of this analysis, behaviour categories were lumped together as shown below. Travel, resting and vigilance remained as defined above. Foraging and feeding were lumped together as feeding. Calling, play, and social grooming were amalgamated into social, and miscellaneous included self grooming and aggressive interactions.

3.3 ANNUAL ACTIVITY BUDGET

Activity budgets were calculated by summing all activity scores for every month, and then calculating the mean percentage time spent in any behaviour for each follow.

The overall activity budgets for the two study groups are presented in Table 3.1.

Table 3.1: Activity Budgets for Groups W and E.

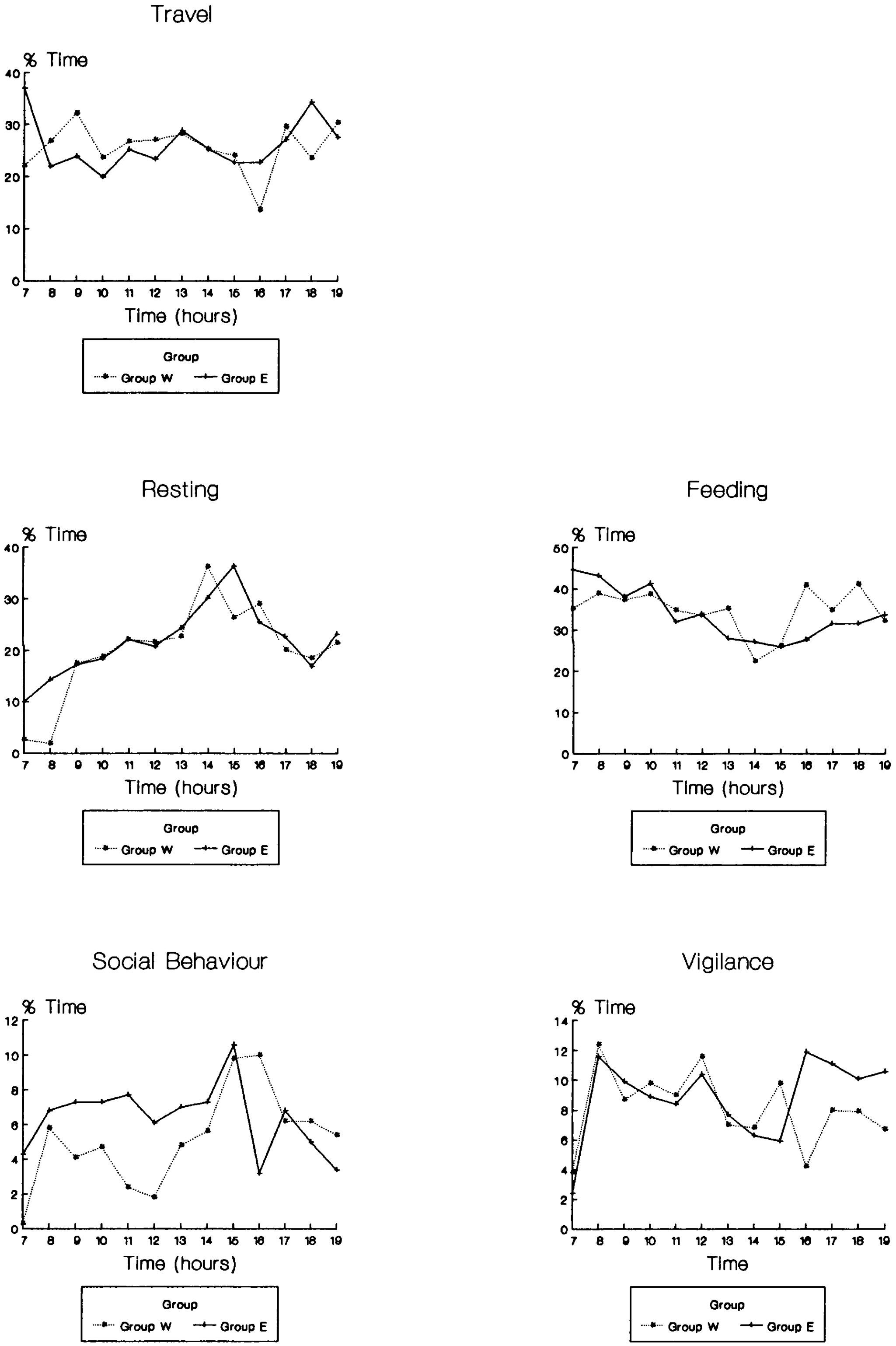
Group	% time spent Travel	Feed	Rest	Vigilance	Social	Misc.	N
W	24.0	34.4	21.7	8.9	6.7	4.3	4015
E	25.3	36.3	21.2	8.1	5.4	4.0	2967

Both groups have very similar time budgets with most of their time being split between feeding, travelling and resting. Statistically there were no significant differences between the activity scores for the two groups (Mann-Whitney, $n_1 = 6$, $n_2 = 6$, $p = 0.938$), suggesting that in Diana monkeys animals devote approximately 25% of their time to travelling, 35% of it to feeding, 20% to resting, 10% to vigilance, and 5% to social activities. Activity budgets for several other species of guenon, including Cercopithecus aethiops, C. ascanius, and C. mitis will be compared with the time budgets for C. diana in the discussion that concludes this chapter.

3.4 DIURNAL ACTIVITY RHYTHMS

The activity scores were summed for each hour between 06.00 -19.00 hours, then converted to percentage scores. The monthly average for each hour was then calculated to

Fig. 3.1: Daily Activity Pattern for the Two Study Groups.



give the percentage activity scores for each hour of daylight. It can be seen from Fig. 3.1 that both groups showed similar overall patterns of diurnal activity rhythms, though there are certain differences:

Travel: Members of Group W showed a quick burst of movement as the animals left their sleeping sites around 07.00 hours. They then underwent a period of steady travelling and foraging, peaking slightly at 13.00. Travelling was reduced during the hottest part of the day, 14.00 - 16.00; during this period the group remained relatively inactive. Individual animals occasionally left the resting site to forage or play earlier, but the bulk of the group set off again between 16.00 - 17.00. Travel again peaked at 18.00, as the animals moved to their sleeping sites. The monkeys did not often travel as a cohesive group, so group members started arriving at the sleeping site from 18.00 until just before dark.

Group E shows a similar pattern, though the bulk of their group appears to have left the sleeping site slightly later in the morning than did Group W (08.00 - 09.00 compared with 07.00). Group E also showed a very definite drop in travel at 16.00, corresponding to peaks in resting and feeding.

Feeding: Animals from Group W indulged in an early feeding bout prior to leaving their night trees. The graph suggests that they fed fairly steadily as they travelled throughout the morning: from observation this appeared to be so. Like travel, feeding rates were low from 14.00 - 15.00 (corresponding to a peak in resting). Some animals continued to feed throughout this hot period: they were gradually joined by others as the afternoon progressed. The group continued to feed as it travelled towards the sleeping site, and only ceased feeding as it became dark.

Again, Group E showed a similar pattern of feeding to that of Group W. But they showed a big drop in feeding by 14.00 (corresponding to a peak in resting) and another peak in the late afternoon, prior to settling down for the night. Feeding and resting behaviour were found to be negatively associated with each other ($r_s = -0.89$, $N = 12$, $p < 0.001$).

Resting: Resting increased throughout the morning, reaching a high in mid afternoon. Levels dropped off during the late afternoon as the group foraged, and travelled to its sleeping site. As dusk arrived, and the animals began to settle for the night, the number of animals classed as resting increased again.

Vigilance: There were similar fluctuations in the amount of vigilance behaviour observed in both groups across the day. Slight peaks in the amount of scanning by group members was observed in the morning, corresponding with their leaving their night trees. Again, as they left their resting sites in the late afternoon, a small increase in scanning was recorded.

Social: Low levels of social activity were recorded for the two groups throughout the day. Social activities peaked during the afternoon rest period when adult females gathered together to groom one another, and the young animals played together.

Daily Rhythms and Consumption of Different Food Types

Information on feeding was taken during scan sampling as outlined earlier. Details of the species and part being fed on, along with number of animals using that particular food resource, were recorded. The plant parts were classified as follows: Leaf Buds and Young Leaves: Mature Leaves: Flower Buds: Flowers: Immature Fruits - divided into pulpy fruits, and dry seeds: Mature Fruits - divided into pulpy fruits, and dry seeds: Arthropods: Unidentified[1].

For the purposes of this analysis the different categories were lumped into foliage, flowers, fruits, arthropods and unidentified.

Patterns of consumption of different plant parts and other

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[1] These categories are defined in Appendix II.

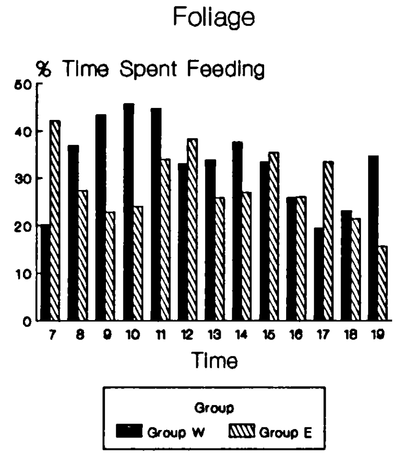
food types show similar diurnal variation for various species of guenon, including C. diana, from several different study sites (Gautier-Hion 1988). There is typically a high proportion of fruits and seeds eaten during the early morning, and again in the late afternoon. Prey (arthropods) are most often caught between 09.00 - 15.00.

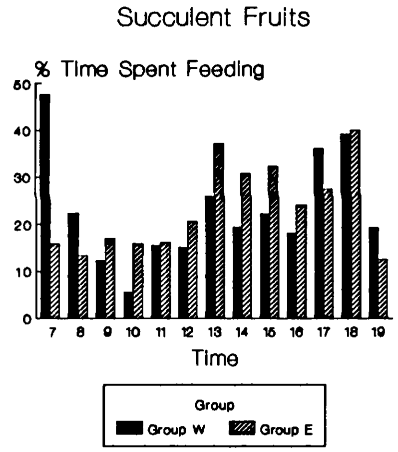
Fig. 3.2. illustrates that the two study groups, W and E, show certain differences to the overall pattern outlined above.

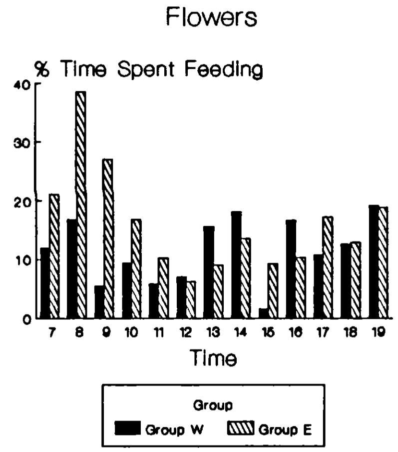
Data from Group W shows that the bulk of succulent fruit consumption occurred in the early morning and late afternoon as expected. Comparatively few seeds were eaten, though the distribution of consumption follows the same pattern. Group W differs from Gautier-Hion's results with respect to prey. Arthropod feeding occurred mainly between 08.00 - 17.00, with a drop during the early afternoon. This extended period for prey catching is possibly a result of different light and /or climatic conditions on Tiwai compared with other sites. Failing that, arthropods may be a more important dietary component for Diana monkeys than for other guenons.

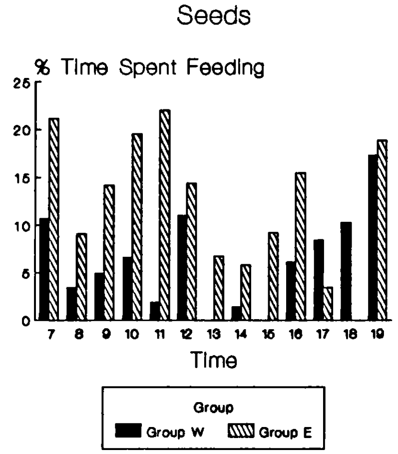
Group E does not show the same early morning peak in fruit consumption (Fig. 3.2). But from the graph it can be seen that this group ate more flower material in the early morning and late afternoon. Like fruits, flowers are high

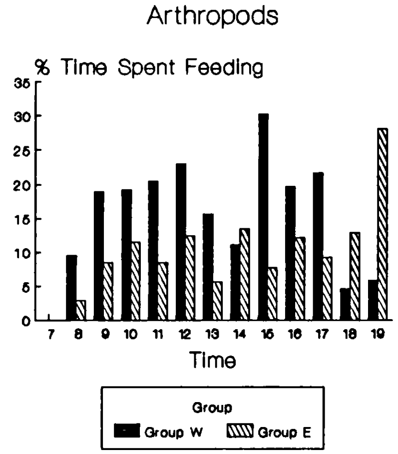
Fig. 3.2: Daily Pattern in Consumption of Different Food Types for the Two Study Groups











in various nutrients; particularly sugars and carbohydrates: possibly Group E used flowers instead of fruits. Overall they had a higher proportion of flowers in their diet than did Group W (likely to be as a result of differences in home range vegetation - See Chapter Four, Section 4.3). Also, animals in Group E were not seen to forage for arthropods as often as members of Group W were. Maybe this group relies on flowers to provide them with the nutrients often acquired from fruits and prey material in other groups.

3.5 MONTHLY VARIATION IN ACTIVITY BUDGETS

When the annual time budgets of the two study groups are broken down to show monthly activity patterns it can be seen that in both groups the percentage time spent in various activities changes across the months (Fig.3.3). This was confirmed using a Kruskal Wallis One Way ANOVA: the results are summarised in Table 3.2 below.

Table 3.2: Kruskal Wallis One Way ANOVA - Monthly Activity Budgets

Activity	K		Level of significance	
	Group W	Group E	Group W	Group E
Travelling	30.54	26.80	0.01	0.01
Feeding	15.91	26.90	NS	0.05
Resting	22.18	26.60	0.05	0.01
Vigilance	33.30	16.10	0.001	NS
Social	43.21	6.24	0.001	NS
Misc.	12.50	12.42	NS	NS

The results show that in Group W the percentage time spent in resting, vigilance, and social behaviours varied significantly throughout the year, but the time devoted to feeding did not. In Group E there were significant results for travelling, feeding and resting, but not for vigilance or social behaviour. One explanation of the difference between the two groups with respect to social and vigilance behaviours could be the lack of infants in Group E during 1988. The different result in feeding between the groups is not so easily explained. Possibly it is related to different food resources being available to the two groups: maybe the home range of Group E is more susceptible to seasonal effects than that of W (See Chapter Four).

Time spent travelling changes across the year for both groups, as shown in Fig.3.3. Both groups devoted most time to travelling during April. It seems surprising that these animals should have spent so much of their time travelling during the hottest part of the year. However, the fruits of Landolphia hirsuta, a common, and widely dispersed liana, dominated the diet of both groups during this month which may explain their behaviour. Group E also devoted a relatively high percentage of their time to travelling during January - why remains unclear (though see Chapter Seven, Section 7.3).

The monkeys generally devoted less of their rainy season time budget to travelling. Movement is likely to have been impeded by very heavy and prolonged bouts of rain during this period. However, Group W showed a peak in travel during August, coinciding with the peak of the breeding season (the implications of this are considered in Chapter Seven, Section 7.4). Time spent travelling was also relatively low during October (Group W), November (Group E) and March (Group W). In all three months the groups concerned, were observed feeding from single, large, fruiting trees, and would remain in that one patch for several hours, often returning day after day until the patch appeared severely depleted. During March, travel may have been restricted as a result of there being three young infants in the group at this time. March was the first month they were observed off their respective mothers for any length of time. Although they were not yet being allowed to travel off their mothers, their added weight may have hampered the females somewhat.

Fig. 3.3: Variation in Activity Patterns Across the Year for the Two Study Groups

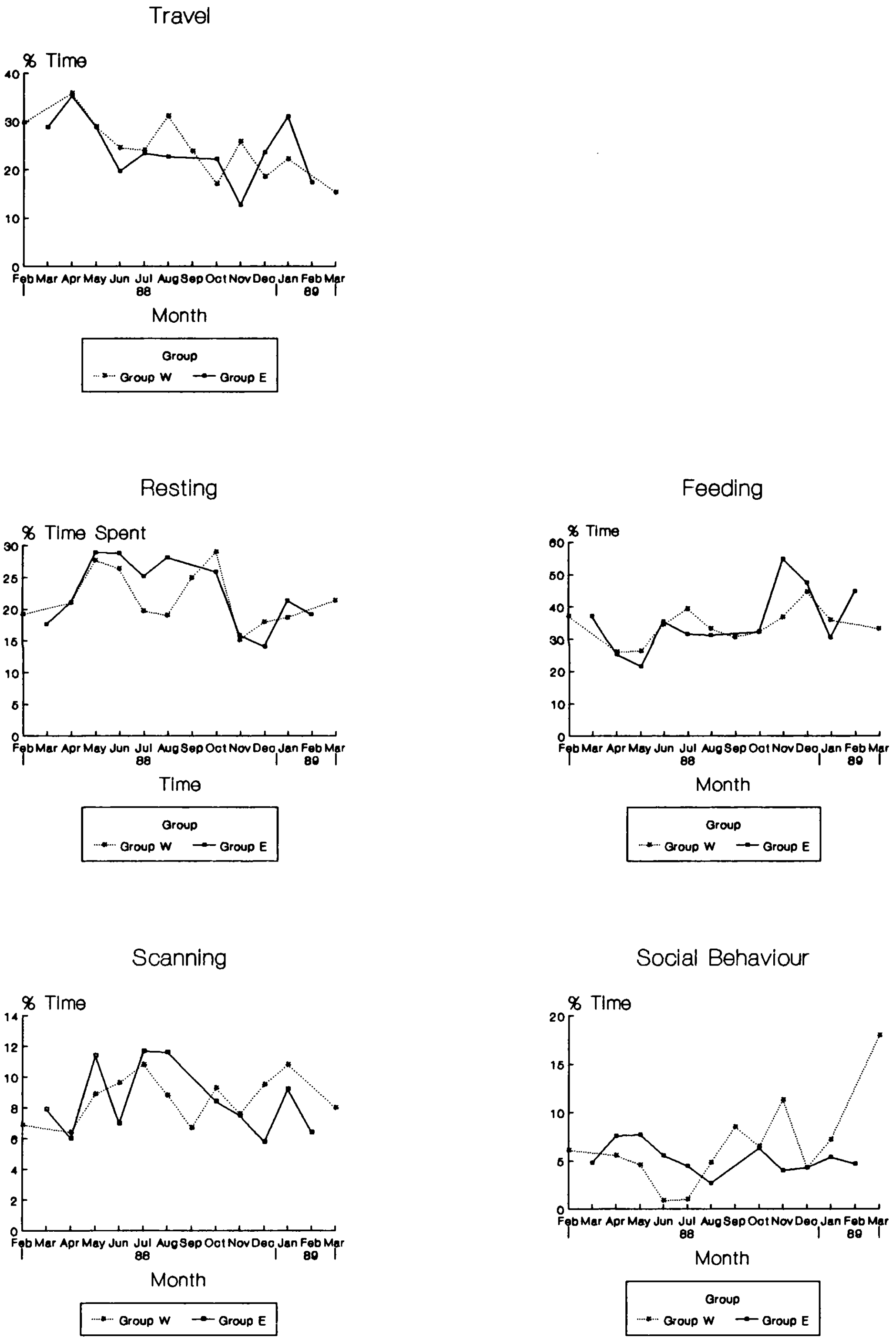


Fig. 3.4: Mean Day Range and Mean Percentage Time Spent Travelling for Group W

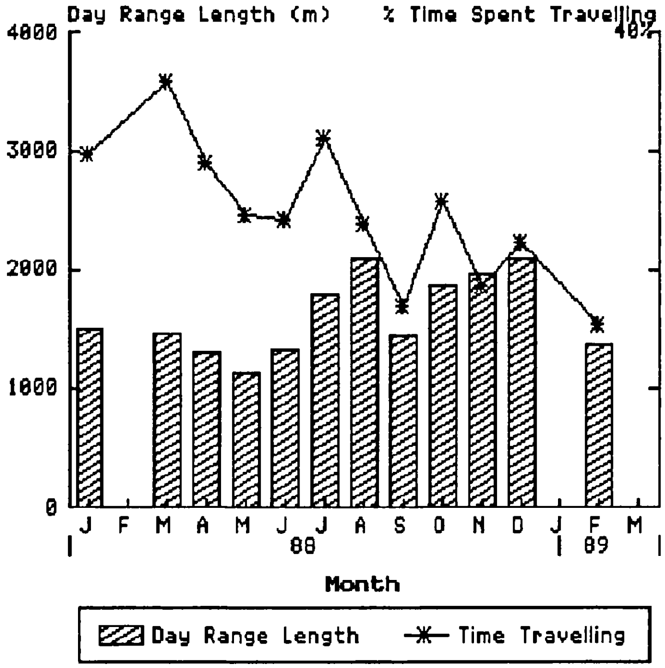
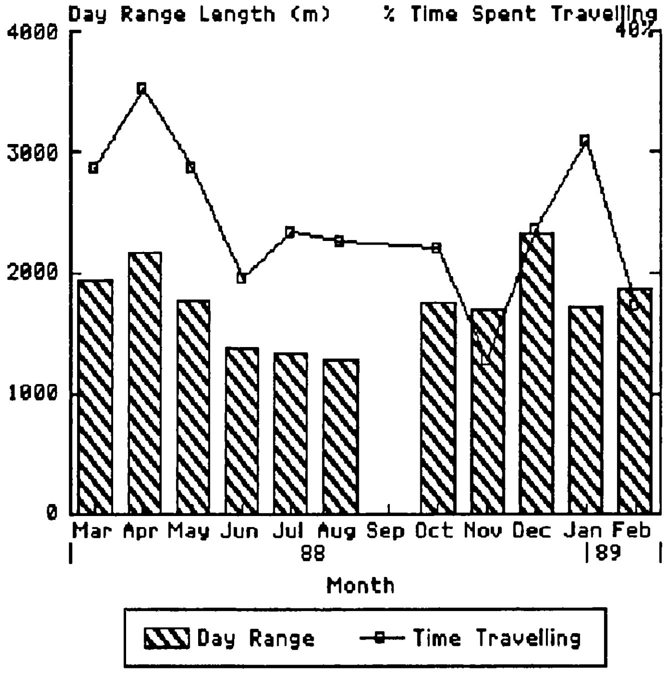


Fig. 3.5: Mean Day Range and Mean Percentage Time Spent Travelling for Group E



Figs. 3.4 & 3.5 demonstrate that in both groups monthly plots of average day range follow a similar pattern to monthly averages for percentage time spent travelling. Generally, Diana monkeys travel most during the early part of the dry season, and least during the transition period (dry-wet) and early wet season. However, there is no significant association between these two variables. Neither was there any correlation between average percentage time spent travelling and average number of quadrats used. But, where time spent travelling and day range length do not correspond, perhaps this is an indication of the type of travelling being carried out. Where there is a large day range recorded and a relatively small part of the time budget allotted to travelling, the animals may have moved quickly between well-spaced, clumped food resources such as flowers or fruits. And on occasions where groups spent a considerable portion of their time travelling, yet did not appear to range very far, they may be relying on readily available, equally-dispersed foods such as leaves, so that they effectively "browse" their way through the forest. Alternatively, they may be foraging on insects and again progressing through the forest slowly but steadily, flushing out insects as they travel (See Chapter Five, Section 5.6 where the implications of these results are considered further).

Feeding: Returning to Fig. 3.3, it can be seen that overall, the two groups showed similar patterns in time spent feeding across the year. It is likely that any discrepancy between them reflects phenological differences between the two sites. Peaks in time spent feeding occurred during the early wet season (June/July) and the early dry season (November/December). The first peak coincided with peaks in feeding on mature leaf petioles and arthropods. Both are likely to have entailed considerable handling costs. Diana monkeys appeared very selective when choosing mature leaves: often only the petiole was eaten while the leaf blade was discarded. When searching for, and capturing, arthropod prey, monkeys were observed searching the underside of leaves, pulling up pieces of bark[2], and occasionally leaping into the air to catch flying insects. In November and December the two groups concentrated on small fruits and seeds, again entailing considerable processing time for each item.

Percentage time devoted to feeding was lowest in the transition period from dry to wet season (April/May) and much of the wet season. During April both groups obtained approximately half their monthly diet from ripe _Landolphia hirsuta_ fruits. Although _Landolphia_ fruits require some time spent in removing the flesh, they are large, and brightly-coloured, therefore conspicuous, and easily located. Although there was no significant correlation found between travelling and feeding, all peaks of feeding

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[2] Only the adult male was observed ripping off strips of bark, presumably to pick up insect larvae in the dead wood below.

occurred in months with low travel. However, the reverse is not true.

Resting: The two groups showed similar patterns of monthly variation in resting levels (Fig.3.3). Levels of resting were lowest during the coolest times of the year, ie harmattan (December) and early dry season (January - February), reaching a peak in May when it was very hot. A slight decrease in levels was seen as the wet season progressed, reaching the lowest point in August, the height of the rains. There was a second high point in October, followed by a sudden drop as the rains finished and harmattan began. Significant negative correlations were found between feeding and resting for both groups (Group W; $z = -3.44$, $p < 0.001$: Group E; $z = -2.53$, $p < 0.005$). It has been shown in a number of cases (Dunbar, 1988; Dasilva, 1989) time allotted to resting is flexible, and varies according to the amount of time animals are devoting to travelling and feeding. The results from this study appear to conform to this pattern.

Vigilance: The proportion of time spent scanning appeared fairly constant throughout the year, with slight increases in July and August, and January. Three infants were born into each of the study groups during January '89. Possibly the appearance of new infants accounts for these slight increases at these times. The other peak coincided with the breeding season[3], when the two adult males may have been especially vigilant to detect potential rivals.

Social: The two groups showed different distributions of social behaviour across the year. There are two distinct peaks of social activity shown by members of Group W - November, and particularly March 1989. March was the month where the new infants were first seen off their mothers' ventra. Other group members showed great interest in the youngsters and would approach and groom the adult females to gain access to their infants. However there was no such peak seen in social behaviour between members of Group E, though there were also three new infants present in that group around that time. During March '89 Group W was observed to be undergoing fission: social behaviour seemed to escalate at this time, probably to ensure or reinforce social ties between the remaining animals (considered further in Chapter Seven, Section 7.3). Low levels of social behaviour observed during the wet season may have been, at least in part, as a result of very poor observation conditions.

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[3] C. diana - gestation period from captive studies is approximately 5-6 months.

Seasonal Effects on Activity Budgets

When the activity data are lumped seasonally, the patterns seen are similar to those seen in monthly plots[4].

Lumping the data "seasonally" rather than "monthly", appears to have a "smoothing" effect on the data. Possibly Diana monkeys are more subject to monthly, rather than seasonal effects, unlike Colobus polykomos (Dasilva, 1989). Their food species may show large monthly fluctuations rather than seasonal fluctuations in plant part production. Alternatively, by lumping data the number of data points is reduced and this could explain the smoothing effect seen above.

It is apparent that activity patterns change across the year, and that they appear to be influenced by both ecological and social factors.

3.7 ACTIVITY PATTERN AND CLIMATE

In an attempt to determine whether partitioning of monthly activity patterns is in response to climatic factors, correlations between activity and monthly mean maximum temperature, and cumulative rainfall were calculated. As mentioned previously in Chapter Two there were problems with

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[4] See Appendix III for season categories.

collection of rainfall data, and the estimates for August, and possibly September, are thought to be too low. However, activity data was also tested against the percentage of scans taken when it was raining. This was done for two reasons:

1. To compensate for the inaccurate rainfall data, and
2. To check whether rain does physically impede, or restrict the behaviour of the Diana monkeys.

From the results the monkeys appeared to reduce their activity during periods of extreme wet or heat, i.e. there were significant correlations found between maximum temperature and feeding ($r_s = -0.641$, $p < 0.05$, $N = 12$) and maximum temperature and resting scores ($r_s = +0.608$, $p < 0.05$, $N = 12$). Resting was also found to be positively associated with the percentage of scans taken when it was raining ($r_s = 0.604$, $p < 0.05$, $N = 11$). Interestingly, travel scores did not show any association with climatic variables, suggesting that it is more dependent on other factors such as spatial and temporal distribution of food resources, and social or demographic factors.

3.6 ACTIVITY PATTERNS AND FOOD

It was suggested earlier (3.3 Monthly Variation in Activity Budgets) that the Diana monkeys might be relying on a readily available, evenly distributed food source such as leaves during certain months where they devoted a considerable portion of their time budget to travelling. The positive association found between travelling time and amount of leaves being fed on would appear to support this idea for Group W ($r_s = +0.945$, $p < 0.001$, $N = 12$). At this stage though, it is not possible to decide whether groups have to increase their time devoted to travelling in order to find sufficient leaves for their nutritional requirements, or whether they are having to spend so much time on travelling for very different reasons and as a result have to utilize whatever they can while on the move. This will be discussed further in the next chapter, along with the question of why they are utilizing considerable amounts of foliage - is it because there is nothing else available to them at certain times of year, or are they choosing to eat leaves?

Group W appeared to devote less time to feeding (foraging and feeding combined) as the percentage of fruit and seeds in the diet increased ($r_s = -0.536$, $p < 0.05$, $N = 12$), whereas resting was found to be positively correlated with the amount of foliage being consumed ($r_s = +0.654$, $p < 0.05$, $N = 11$). From the above it would appear that when feeding on fruits and seeds Diana monkeys reduce the proportion of their day devoted to feeding. Possibly this is because these are high energy foods, thus they can meet their daily requirements more quickly. However, resting also appears to receive less time during these months, therefore they must be using that "extra" time in another way. Vigilance and social behaviour occupy small portions of the activity budget, and do not tend to vary enormously across the year. Thus, it seems likely that during these months, time spent travelling may be increased, possibly as a result of the monkeys having to travel between widely dispersed food patches.

3.8 DISCUSSION

It is difficult to make any finite comparison of activity budgets between studies because of the different types of methodology, and categories of behaviour used in different studies. However, it can be useful to compare overall activity budgets as in Table 3.3 below.

Table 3.3: Guenon Activity Budgets

		% Time Spent			
Species	Move	Feed	Rest	Scan	Social
C. diana[5]	24.6	35.4	21.4	8.5	6.0
C. cephus[6]	28.6	41.5	24.0		6.0
C. ascanius[7]	17.4	34.1	10.1	20.5	7.4
C. mitis[7]	16.5	38.1	29.0		12.0
C. mitis[8]	22.6	35.8	29.4	12.0	
C. aethiops[9]	32.0	31.0	44.0		

One thing that seems common to all of the species included above is that they devote relatively little of their time budget to social activities. Although there appears to be some variation between time spent moving, feeding and resting, allowing for differences in data collection, definitions and observation conditions, the spread is not very great in any category. Where there are larger differences, e.g. *C. cephus* - 41% observation time devoted to feeding, or *C. aethiops* - 44% observation time spent resting, these seem likely to reflect habitat differences, rather than species-specific patterns.

There seems to be good evidence that temperature influences the distribution of the activities of Diana monkeys both

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[5] Mean values from present study.

[6] Quris et al (1981).

[7] Struhsaker & Leland (1979).

[8] Lawes (1990).

[9] Clutton-Brock & Harvey (1977).

across the day and throughout the seasons. They show peaks in maintenance activities (travelling and feeding) early on and late in the day, avoiding being very active during the hottest part of the day. Similar patterns of activity have been reported for Cercopithecus sabaeus (Harrison, 1985) and also several species of grassland herbivore (Belorsky & Slade, 1986). But, several species of Aotus have been observed showing a similar bimodal distribution of activity throughout the night (Wright, 1978; Garcia & Braza, 1987). Thus it has been suggested that such activity patterns may reflect times of food digestion rather than as a response to ambient temperature. However, since timing of active and resting periods appears to vary slightly with season: with animals leaving their sleeping sites and stopping for their afternoon rest earlier during the hottest months, April and May, it would appear that temperature constraints are important. Also, they appear least active during the wettest, and hottest, times of the year, and most active during the cool, dry harmattan.

The availability and distribution of food resources also appeared to influence their activity patterns. The two study groups share the same overall daily pattern, feeding on high energy foods during the early morning feeding sessions, and again during the late afternoon, prior to settling down for the night. The proportion of resting, travelling and feeding changed across the months, apparently influenced by the proportion of fruits and leaves in the diet.

Although levels of scanning behaviour and social behaviour did not change greatly over the year, slight increases in vigilance behaviours coincided with the appearance of new infants in the group, and the peak of the breeding season. Peaks in social behaviour were seen at a time when one of the study groups was undergoing fission; the remaining group members appeared to invest more time in grooming, playing and contact calling, possibly to reinforce social bonds between themselves.

SUMMARY

1. These results support the idea that Diana monkeys, like many other primates, try to reduce activity and consequently increase time spent being inactive, as much as possible during periods of high temperatures.
2. Distribution of food, and food quality also appear to influence activity patterns.
3. Rather than take time away from vigilance or social behaviour in order to increase the portion of time devoted to feeding or travelling, time is deducted from the resting portion of the time budget.

CHAPTER FOUR

FEEDING BEHAVIOUR

4.1 INTRODUCTION

Links between the social organization of primate groups and their feeding behaviour have been postulated for a variety of species (Clutton-Brock & Harvey, 1977). Examples include the orangutan - thought to lead a semi-solitary existence as a consequence of its very large body size and the widely dispersed nature of its major food source (Rodman, 1973), and the langurs, Presbytis senex and P. entellus, thought to live in very different social groups as a result of environmental conditions (Hladik, 1977).

Recently, there has been an upsurge of interest in the effects of feeding competition (both within and between groups) as an evolutionary pressure on the structure of primate social relationships (Janson & van Schaik, 1988). A number of studies have concentrated on factors pertaining to resource distribution and their effects on female inclusive fitness. Van Schaik & van Noordwijk (1985) showed that in long-tailed macaques (Macaca fascicularis) the birth season coincided with peaks in fruit production, and that the birth rate was significantly higher in superabundant fruit years (mast years) compared with years of normal fruit production levels. Whitten (1983a) presents evidence that in female vervets (Cercopithecus aethiops) rank determined access to food resources, and this appeared to be advantageous with respect to reproductive timing and birth rate, though it did not have any effect on infant survival. Whitten also demonstrated that patch quality has a significant effect on food intake and foraging efficiency, and that females make use of their rank in order to gain access to high quality patches of flowers (Whitten, 1988).

This chapter is not intended to be a comprehensive study of the feeding ecology of Diana monkeys. Instead, its purpose is to outline how they made use of the resources available to them during the study period. This is in preparation for considering the question of whether females are defending food resources against other groups, as might be expected from sociobiological theories of female strategies.

4.2 FOOD RESOURCES AVAILABLE

When considering the availability of food resources it is important to take into account both the spatial and temporal distribution of food plants. While spatial distribution determines access to resources, patterns of plant periodicity govern periodic availability (Bahuchet, 1987; Frankie et al, 1974a). Therefore both the spatial and temporal distribution of available food resources will be outlined for the two study groups prior to describing the monkeys diet and foraging strategies across the year.

4.3 SPATIAL DISTRIBUTION OF FOOD RESOURCES

Old secondary forest on Tiwai is estimated to be between 40-60 years old. It comprises a broken canopy at about 25-30m, with taller emergents of up to 40m in height, and an understorey of trees and shrubs. A more detailed description of the forest structure can be found in Dasilva 1989.

All large trees (> 40cm dbh and/or > 20m height) within the two study sites have been identified and tagged by previous researchers at the field station. Over the years in excess of 3000 trees have been identified, more than 99% of them to species level. For the purposes of this study only those trees lying within the home ranges of the two study groups have been included in the analysis.

Tables 4.1 and 4.2 below show that the two home ranges vary somewhat in their species composition and abundance.

Table 4.1: 20 Most Common Species of Large Tree Found in the Home Range of Group W

Rank	Species	Frequency
1	Piptadeniastrum africanum	226
2	Funtumia africana	225
3	Cynometra leonensis	147
4	Pycnanthus angolensis	73
5	Xylopia aethiopica	53
6	Pentaclethra macrophylla	46
7	Uapaca guineensis	41
8	Amphimas pterocarpoides	37
9=	Albizia zygia	26
9=	Combtretodendron macrocarpum	26
11	Holarrhena floribunda	24
12	Parinari excelsa	20
13=	Xylia evansii	19
13=	Antiaris africana	19
15	Daniellia ogea	18
16	Samanea dinklagei	17
17=	Chlorophora regia	12
17=	Millettia rhodantha	12
19	Homalium letestui	10
20=	Alstonia boonei	9
20=	Ricinodendron heudelotii	9

Piptadeniastrum africanum, Funtumia africana and Cynometra leonensis are the dominant tree species found in the western group's range. F. africana is also a very common tree within group E's range, but Pentaclethra macrophylla and Uapaca guineensis predominate as can be seen in Table 4.2. This reflects differences in vegetation between the two study sites as outlined in Dasilva 1989. Full species lists for the two home range areas are given in Appendix IV.

Table 4.2: 20 Most Common Species of Large Tree Found in the Home Range of Group E

Rank	Species	Frequency
1	Pentaclethra macrophylla	258
2	Funtumia africana	249
3	Uapaca guineensis	246
4	Piptadeniastrum africanum	92
5	Parinari excelsa	59
6	Dialium dinklagei	47
7	Pycnanthus angolensis	37
8	Plagiosiphon emarginatus	35
9	Hannoa klaineana	27
10	Cynometra leonensis	26
11	Samanea dinklagei	25
12=	Holarrhena floribunda	21
12=	Cathormion altissimum	21
14=	Albizia zygia	16
14=	Parkia bicolor	16
16	Dialium guineense	15
17	Erythrophleum ivorense	14
18=	Albizia ferruginea	13
18=	Calpocalyx brevibracteatus	13
20	Antiaris africana	12

Species Richness and Diversity Within the Study Group Home Ranges

There are a number of different ways to compare the species composition of different areas; e.g. by using species richness or diversity indices.

Species richness is the total number of species present and is indicative of the relative wealth of species in a community, and thus is partly dependent on sample size (Peet, 1974). Several diversity, or heterogeneity, indices have been designed to measure diversity as a function of both the number of species and their abundance. Probably the most frequently used in primate studies is the Shannon-Weiner index H'. This has a minimum value of 1 for a monoculture and a maximum value of lnS for a community of S species (Usher, 1986). It is calculated from

$$H' = \sum p_i \log p_i$$

where p_i is the proportion of species i in the sample (Krebs,1978).

Alternatively, Simpson's index of diversity can be used:

$$D = \sum 1 - (p_i)^2$$

Where D = index of diversity and p_i is as above. $1/D \approx d$ is often used to give a minimum value for a monoculture and higher values for more diverse habitats.

These four measures were used to compare the diversity of potential food species available to the two study groups within their respective home ranges. The results are summarised in Table 4.3 below, alongside overall values for each of the study sites.

Table 4.3: Species Richness and Diversity Indices

	West Site		East Site	
	[1]Study site	W range	Study site	E range
Area	32.500km^2		30.000km^2	
S	74.000	60.000	101.000	83.000
H'	2.928	2.920	3.064	2.901
D	0.109	0.099	0.099	0.104
(1/D)	9.168	10.101	10.128	9.615

From the results it can be seen that the home ranges are fairly representative of the two study sites. A commonly cited problem of using diversity indices and measures of species richness to compare habitats is that these measures are all dependent on sample size, i.e. the larger the sample the more diverse it appears. A further point against diversity indices is that none of them takes into account spatial distribution of species, i.e. whether they are clumped or distributed randomly, which is important when considering patterns of primate feeding and ranging (Hubbell, 1979; Gautier-Hion et al, 1981). Therefore it is questionable as to how useful such values are when comparing habitats. Perhaps the most useful value for comparison of the two home ranges is the number of species present per unit area. Although species area curves ignore abundance levels they do at least give some indication of variation in species composition between two sites (Fig. 4.1).

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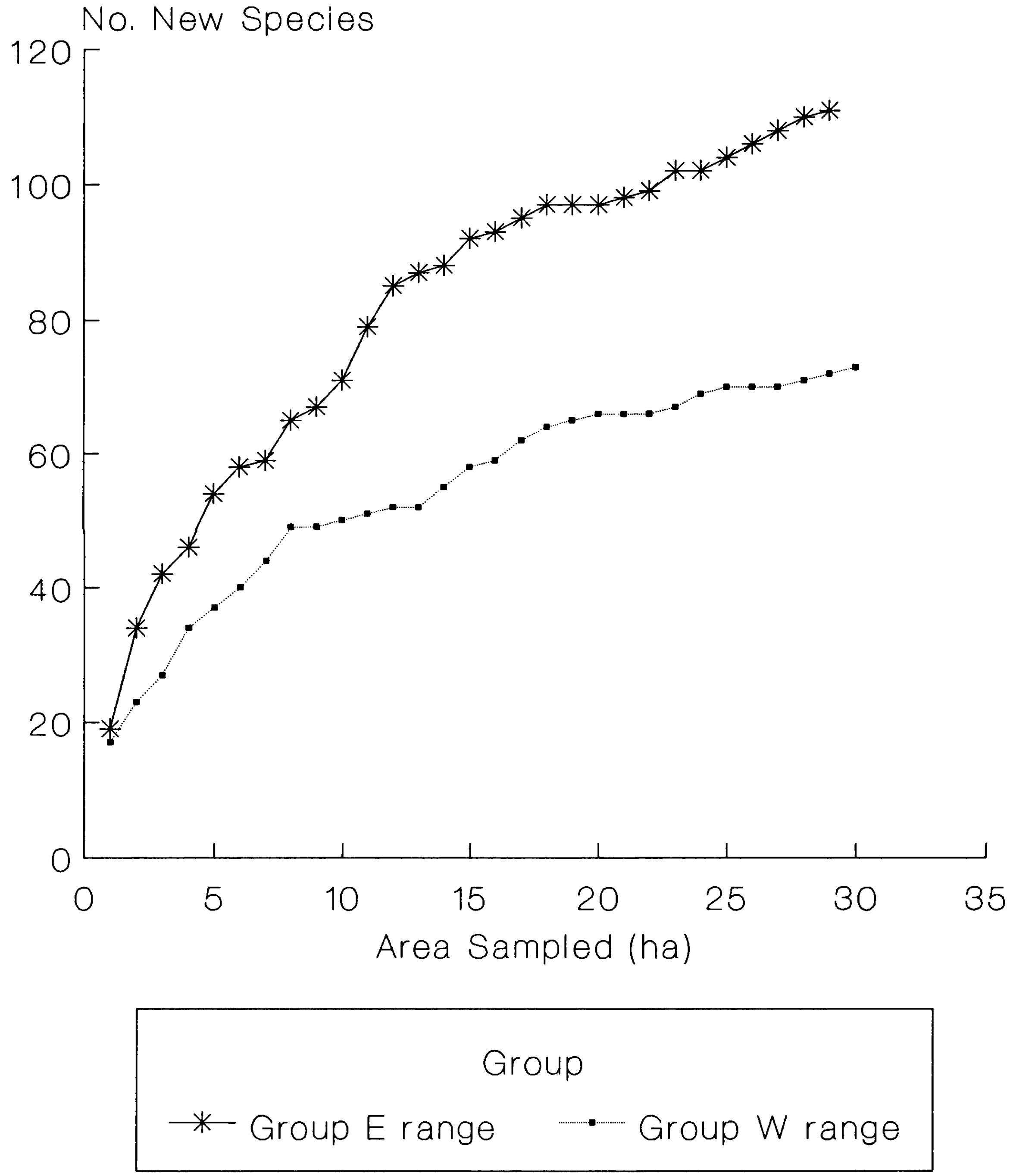
[1] All study site values taken from Dasilva 1989.

Fig. 4.1: Species Area Curves for the Study Groups' Home Ranges



To summarise: it would appear that group E occupies a home range that encompasses a greater diversity of potential food resources than does group W. But,

1. Animals are unlikely to be able to make use of all species available to them. Plants have evolved many strategies to minimise predation costs. Many primates are constrained by high tannin and phenol levels (Wrangham & Waterman, 1981) affecting digestibility (Oates et al, 1980) and will avoid foods of poor nutritional value where possible (Chivers & Raemaekers, 1986).
2. Spatial distribution per se does not determine food availability - temporal plant production patterns are also likely to be of great importance.

4.4 TEMPORAL DISTRIBUTION OF FOOD RESOURCES - PHENOLOGY

Sierra Leone falls within the Guinea-Congolian rain forest zone (White, 1983). Although it is subject to high annual rainfall there is a very pronounced dry season which is likely to affect forest productivity.

Previous phenology studies carried out at Tiwai have demonstrated that the Tiwai forest shows marked seasonality, and that there are periods when plant parts, other than mature leaves, are in short supply or unavailable (Dasilva, 1989; Whitesides, Oates, Dasilva & Davies, unpublished data). Therefore, in order to try to answer the question of whether female Diana monkeys are defending food resources, phenology data were collected to investigate cycles of food availability.

Methods

Information on plant part production was collected every month, as outlined earlier (Chapter Two, Section 2.5). Abundance scores for each species were summed and the mean abundance plotted against time. Plots of percentage of active trees against time were also made, in an attempt to investigate whether species were synchronous or asynchronous in their phenology cycles. Active trees are those that are exhibiting a particular phenophase.

Table 4.4: Species Composition of Phenology Sample at West Study Site

Species	Number in Sample	Number of Months Sampled
Antiaris africana	10	15
Combretodendron macrocarpum	10	15
Cynometra leonensis	10	15
Daniellia ogea	9	15
Diospyros	3	15
Funtumia africana	[2]9/10	15
Landolphia hirsuta	10	15
Nauclea diderrichii	5	15
Parinari excelsa	10	15
Piptadeniastrum africanum	10	15
Pycnanthus angolensis	10	15
Uapaca guinieensis	9/10	15
Xylopia aethiopica	8	15

Results

The relative abundance of vegetative and reproductive plant parts produced by trees and lianas during this study are presented in Fig. 4.2. Because of the structure of the sample[3] this is not necessarily a good representation of the forest's production cycles. The data were weighted to take into account the relative abundance and biomass within the forest of each of the species sampled. Overall forest production was calculated by summing these values for each

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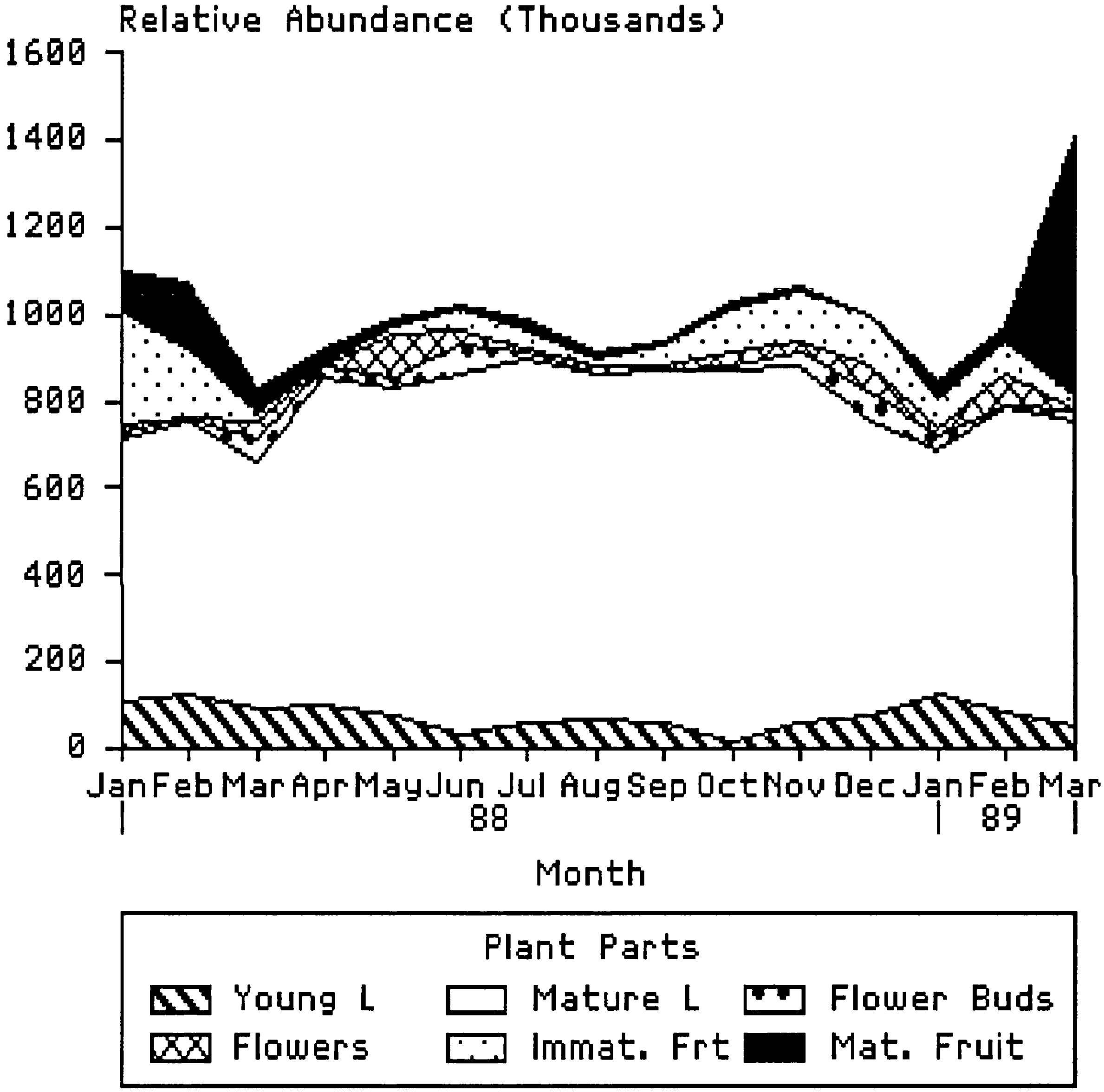
[2] During certain months poor visibility prevented several phenology trees being sampled.

[3] The species used in the phenology sample were chosen on the basis of their relative abundance within the forest and/or importance as species fed on by Diana monkeys.

Fig. 4.2: Tiwai Phenology - Relative Abundance



species, as in the equation below:

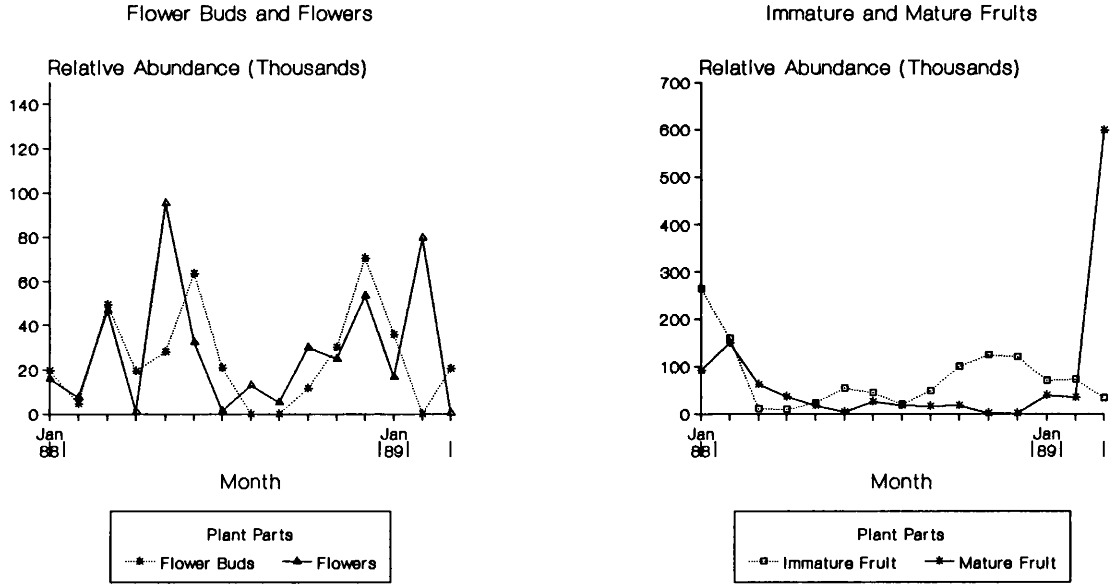
$$W_A = \quad A_i \text{ x } B_i$$

where W_A = weighted abundance units, A_i = mean abundance units for species i, and B_i = basal area ha^{-1} for species i (after Dasilva, 1989).

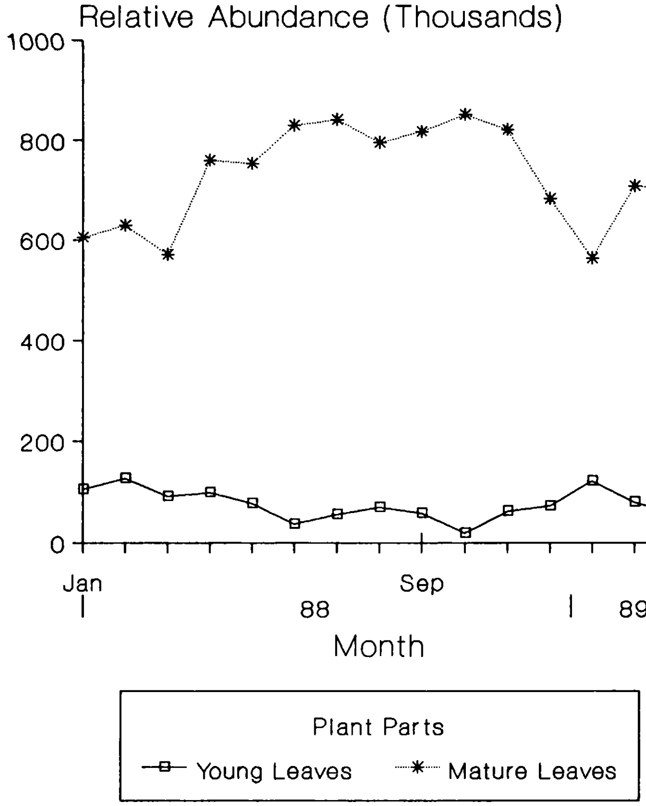
The plots of young and mature leaf production do not show very distinct peaks and troughs (Fig. 4.3). But the overall trend appears to be that more young leaves were produced during the dry season and that these were retained as mature leaves throughout the rains. Van Schaik (1986) reports a similar pattern for a Sumatran forest, though there were two dry seasons and therefore two periods of leaf flush. This was then followed by a low point in the abundance of mature leaves, corresponding to a peak in leaf fall during the early dry season, as can be seen from Fig. 4.3.

Richards (1981) concludes that in many rainforests flowering occurs mainly in the dry season, and that the onset of flowering is linked to climatic factors. Peaks in flower bud production were found to occur during the early dry season, with a corresponding peak in relative abundance of flowers in the following month. From Fig. 4.3 it appears that there were some flowers available throughout most of the year but only during the dry season were large quantities of flowers recorded.

Fig. 4.3: Tiwai Phenology Data - Plant Part Production


Flower Buds and Flowers

Immature and Mature Fruits


Young and Mature Leaves

Terborgh (1983) observed that fruiting peaks occurred during the early part of the rains. But he suggested that those species dependent on animal dispersal would do better to fruit asynchronously, so staggering the fruit crop and increasing their chances of dispersal. With respect to fruiting patterns within the forest on Tiwai, it would appear that there was some fruit available throughout most months with the exception of April[4] (late dry season). In reality, because the phenology sample represents

1. important Diana monkey foods (Whitesides) and
2. important common species,

it is possible that fruit availability within the forest is actually more restricted with respect to Diana monkeys than appears (this will be dealt with later). The main peak in abundance of immature fruit occurred at the very beginning of the dry season, and immature fruits continued to be available for much of the season. Interestingly, there was no corresponding peak in mature fruit abundance. This could be explained in part at least by predation of the immature fruits by insects, which are thought to be important predators of fruits. Also, many trees have a tendency to drop their fruit as it ripens, as a means of dispersal.

Fig. 4.4. presents information on the percentage of

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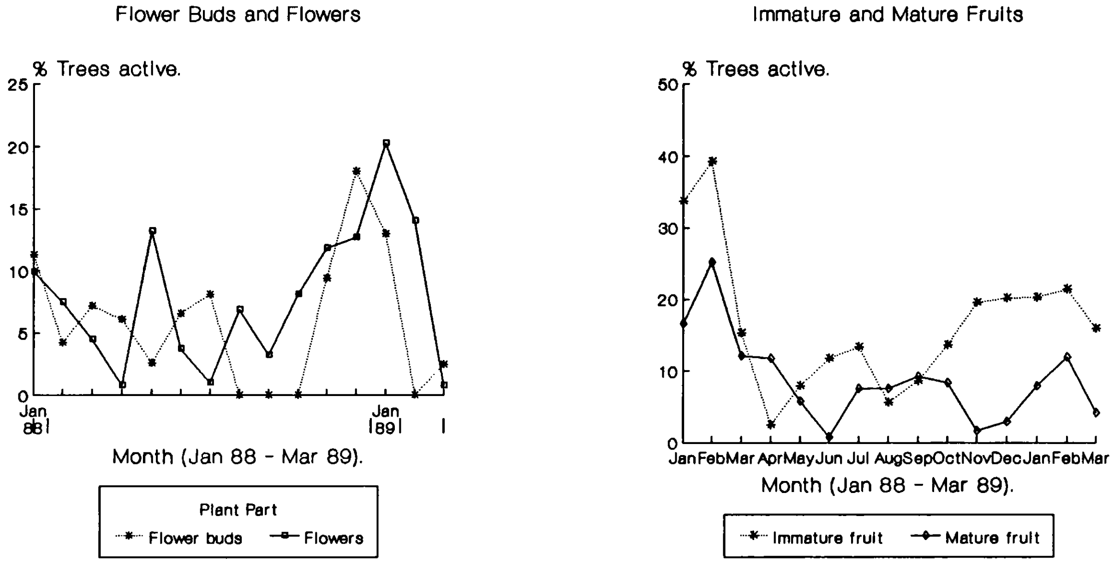
[4] Both study groups fed extensively on mature fruits of Landolphia throughout April, but none of the plants in the phenology sample was seen bearing much fruit at this time. The phenology data was collected after that month's follow had been completed in the West Study Site - perhaps the mature fruit resources had already been depleted by the time the survey was carried out.

trees/lianas in the sample bearing vegetative and reproductive parts. Overall, Fig. 4.4. suggests a general pattern of production cycles similar to that outlined previously. Although Heideman (1989) reports that the proportion of plants flowering or fruiting was not a good indicator of abundance, Raemaekers et al (1980) point out that the number or density of trees producing food parts at any one time is likely to be important in determining animals' ranging patterns. Certainly, by plotting the percentage of trees that are active it is possible to illustrate that there is no complete synchrony of plant part production within the forest. And if individual plots are drawn for different species it is found that whilst some species show almost complete synchrony (e.g. Combretodendron macrocarpum) others are asynchronous in their production cycles (e.g. Uapaca guineensis).

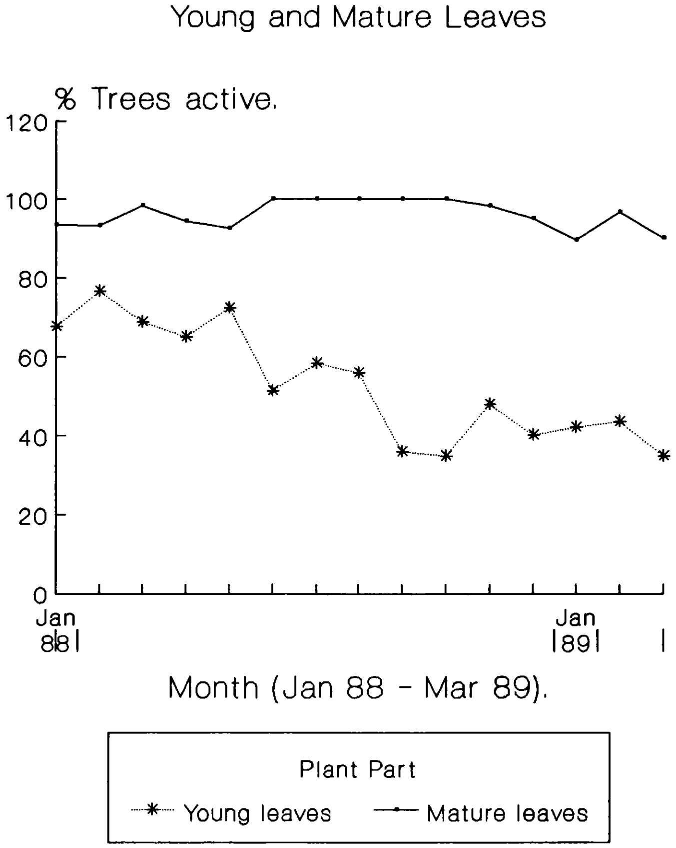
Following on from this it is interesting to note that while the numbers of trees bearing mature leaves followed a consistent pattern throughout the sampling period, this was not so for immature leaf production. Instead, the numbers of trees with young leaves declined across the seasons, and did not peak a second time in the early dry season as might have been predicted from Fig. 4.2. This result could be explained in several ways. Either there are species within the sample that do not operate on an annual cycle or much of the sample is asynchronous in leaf flushing.

To conclude, while the percentage of active trees may not be a

Fig. 4.4: Tiwai Phenology - Percentage of Active Trees in the Sample


Flower Buds and Flowers

Immature and Mature Fruits


Young and Mature Leaves

good measure of the relative abundance of plant part production, the results suggest that it is an important consideration when looking at spatial food distribution. Spatial distribution of food patches will have a bearing on the time which an animal devotes to feeding and associated behaviours. Depending on the costs and benefits of patch size, inter-patch travel time and various other factors, animals need to divide their time between various activities throughout the day.

Plots of the vegetative and reproductive cycles for individual species reveal several basic patterns of production:

1. Some species show continual young leaf production and mature leaf loss i.e. they appear to be evergreen rather than deciduous e.g. *Funtumia africana* (Fig. 4.5), *Nauclea diderrichii*, *Parinari excelsa*, and *Uapaca guineensis*. Fruiting appears synchronous but super-annual in some species such as *Parinari excelsa*, and asynchronous in others e.g. *Uapaca guineensis* (Savill and Fox, 1967).

2. Deciduous trees have a leaf flush coinciding with a dramatic loss of mature leaves, associated with different parts of the dry season according to species. *Pycnanthus angolensis* and *Antiaris africana* flush during the early part of the dry season; *Piptadeniastrum africanum* and *Daniellia ogea* (Fig. 4.6.), *Xylopia aethiopica* and *Landolphia hirsuta* experience leaf flushing between January and March, while *Combretodendron macrocarpum* flushes

Fig. 4.5: <u>Funtumia</u> <u>africana</u> - An Example of an Evergreen Tree

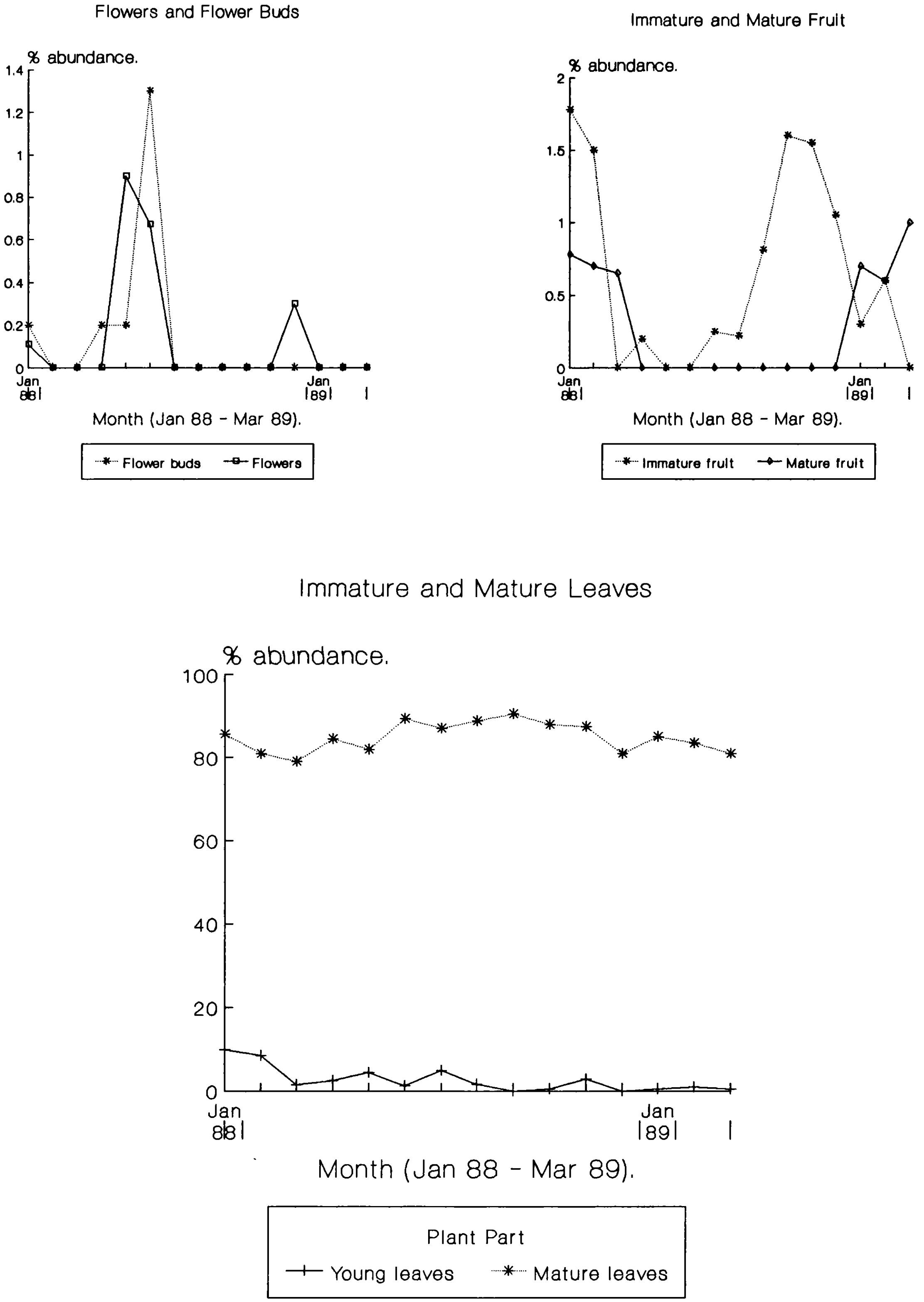
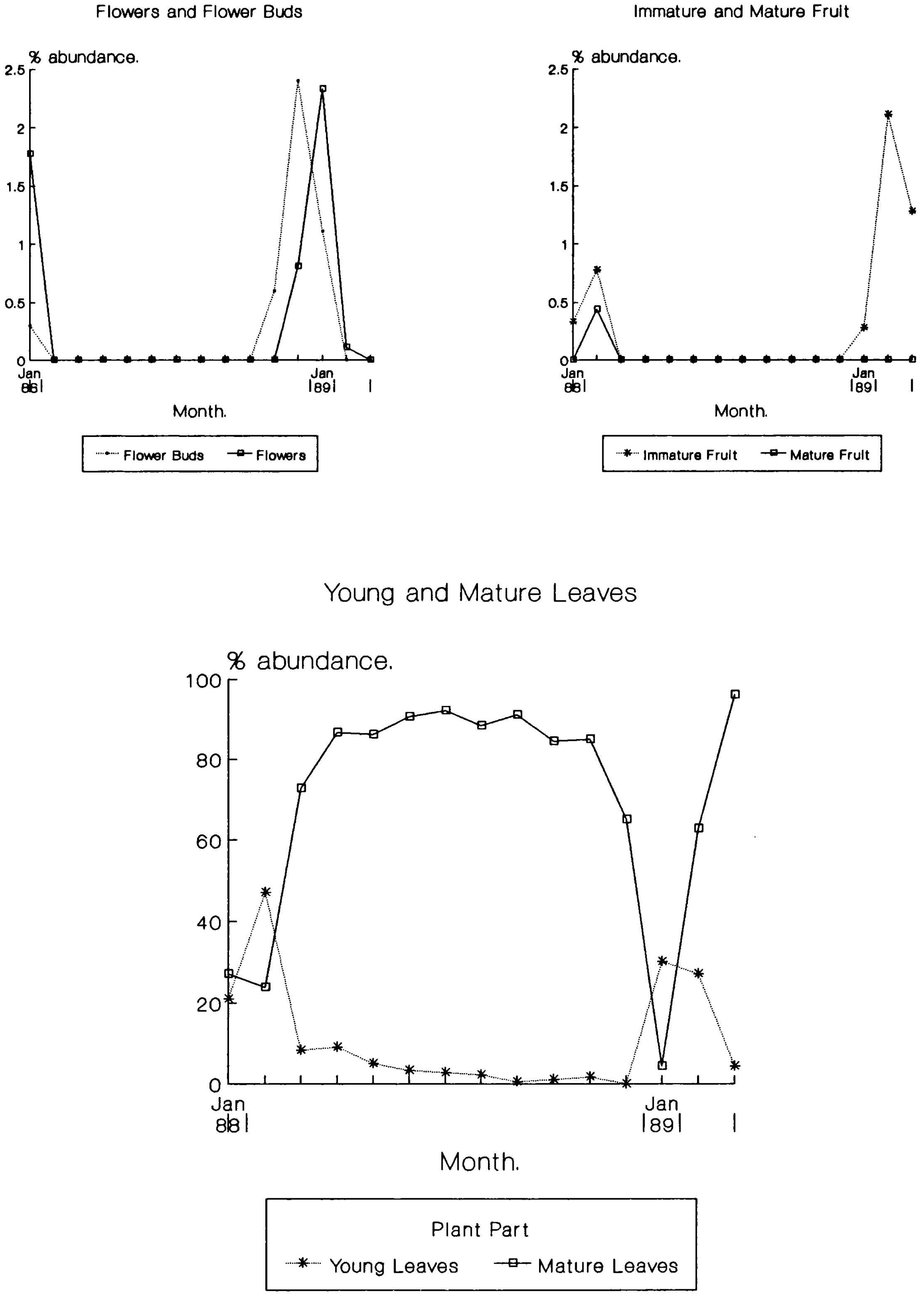


Fig. 4.6: *Daniellia ogea* - An Example of a Deciduous Tree



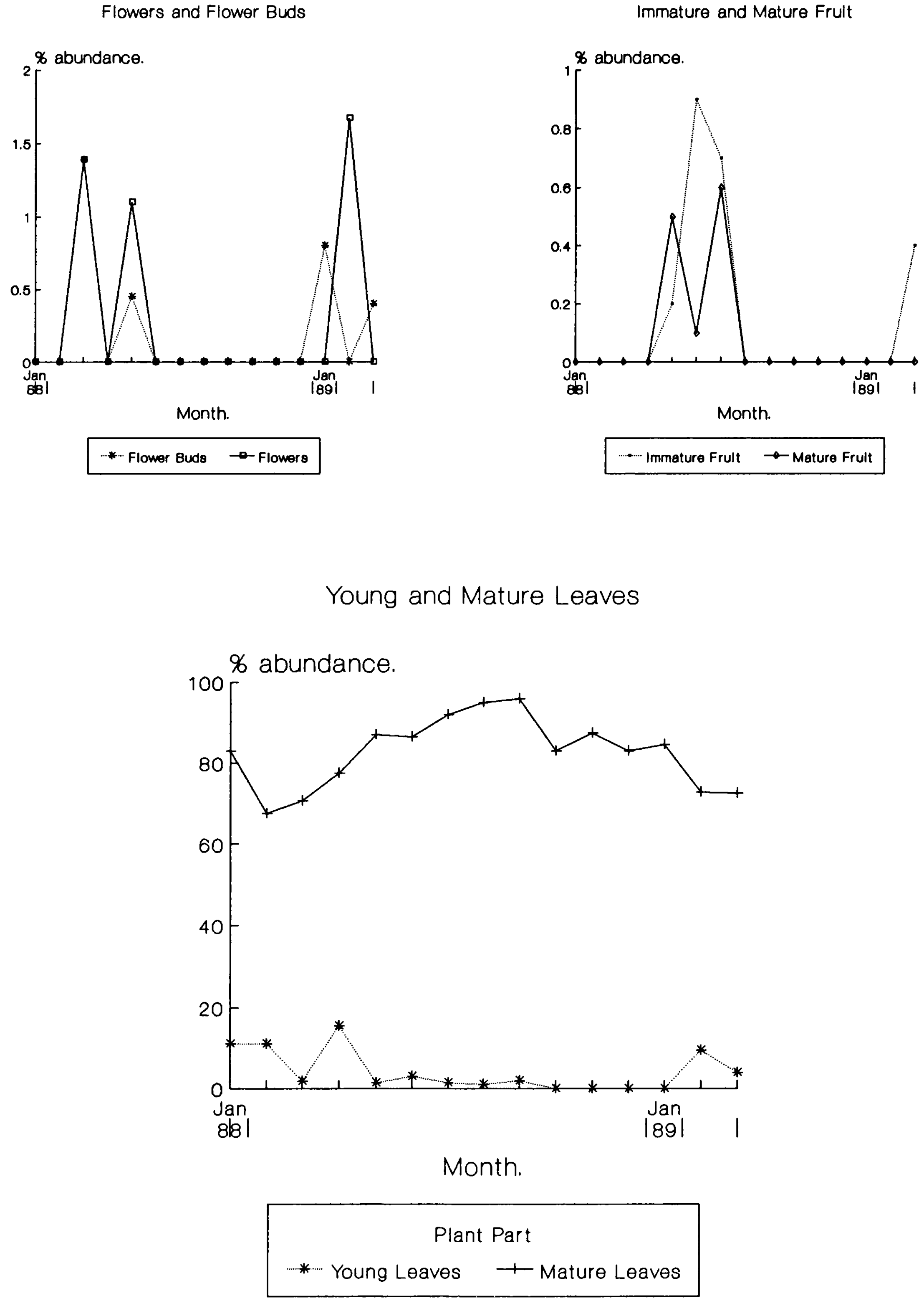


Fig. 4.7: ***Cynometra leonensis***

at the end of the dry season, April-May time.

One species, Cynometra leonensis (Fig. 4.7), seemed to behave as an evergreen tree throughout the study period, although it is not classified as such by Savill and Fox (1967).

Previous phenology data collected from the West Study Site phenology sample found similar patterns in plant cycles (Whitesides, Oates, Dasilva and Davies, unpublished data). Peak young leaf production occurred during the dry season and to a lesser extent during August. Dasilva reports two peaks of young leaf production for the East Study Site sample (Dasilva, 1989). The first was from March - May, coinciding with the onset of the first rains, and the second was during October and November as the rains were finishing. Leigh and Smythe (1978), Hladik (1978) and Medway (1972) all report leaf flushing occurring at the onset of the rains at their respective study sites, contrary to what was observed during the present study. Flowers showed production peaks during the early dry season. Immature fruits have previously been seen to be most readily available from May onwards (Whitesides et al, unpublished data). However, the results from the present study do not agree. Immature fruits showed greatest abundance from October/November time onwards until March the following year. This difference may be a result of climatic variation between the study periods, since temperature and rainfall are thought to have an effect on plant growth and reproduction (Frankie et al, 1974b). Similarly, mature fruits peaked during the dry season, though they were also available, but not in any great quantity, throughout much of the wet season.

4.5 FEEDING BEHAVIOUR

Methods

Feeding data were collected during scan sampling and for each sample the species, and part being eaten were identified where possible.

As shown in Chapter Three (Section 3.3), Diana monkeys spend approximately 35% of their time feeding (W - 34.4%; E - 36.3%), where feeding includes all activities classed as foraging or feeding.

A total of 1571 feeding scans were collected for W and 1103 for E, over a period of 12 months and 11 months respectively. In 5-10% of all feeding scans it was not possible to identify the species, and/or part, being exploited. But considering the overall sample size it is likely that the results are a reasonable estimate of dietary patterns during this study.

Kurland and Gaulin (1987) used regression analysis to determine the extent to which time sampling and weight estimates of diets are comparable. From their results they concluded that while both methods gave related estimates for vegetative material, when considering reproductive parts and arthropods, percentage time spent feeding underestimated the relative importance of fruits by up to 30%, and overestimated the importance of animal material by approximately 600%. In this study percentage time spent feeding on different plant and animal components was used to estimate dietary composition. But for the purposes of this study it is important to have an indication of food value i.e. where animals are willing to invest considerable amounts of time and energy in handling/processing foods the returns must be particularly valuable to them in some respect.

Annual Diet

Over the course of a year the two study groups made use of a variety of different species and items. Group W was observed feeding on a total of 67 species-items from 31 identified species (excludes species-items from up to 10 unidentified tree and liana species). Group E was seen to use 58 species-items from 28 identified species (up to 17 unidentified species of tree and liana). Lists of these species-items are given in Tables 4.5 & 4.6.

Although both groups made use of a large range of species-items, over 70% of their annual diet came from 20 items. This suggests that like many other supposedly frugivorous primates they concentrate on only a few items at a time, depending on what is available (Cercocebus albigena - Waser, 1974; Cercopithecus ascanius - Struhsaker, 1980). This is looked at more closely later in this chapter.

Insects were very important food resources for both groups but W relied on young leaves more than did E. The two groups also differed somewhat in the species they used, as well as the relative importance of different species-items over the year. An important consideration is whether these differences result from differences in the food resources available to each group, or whether they were actively choosing different foods. Abundance of trees in the home range was found to correlate significantly with relative dietary importance for both groups (W: $r_s = +0.543$, $N = 25$, $p<0.01$; E: $r_s = +0.733$, $N = 28$, $p<0.001$, two-tailed) supporting the idea that differences in annual diets between the two groups was a consequence of differences in forest make-up between the two sites.

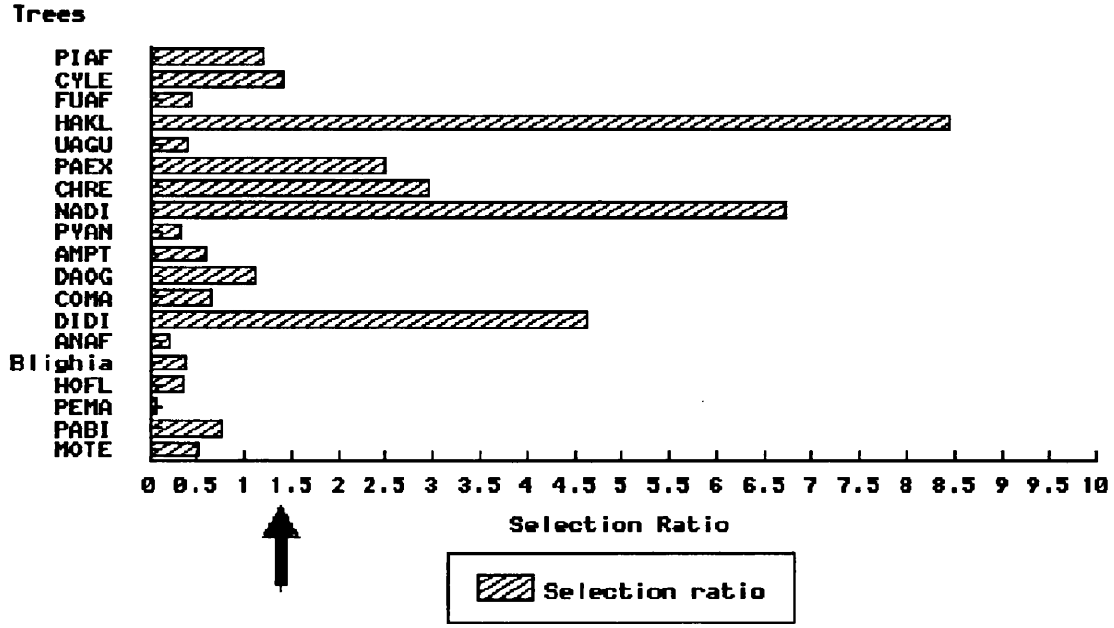
Selection ratios were calculated using

$$SR = \frac{\text{\% total feeding records made on a species}}{\text{\% trees of species in vegetation sample}}$$

(Sourd & Gautier-Hion, 1986). This assumes that the ratio of percentage time spent feeding on a species/percentage abundance of that species gives an estimate of the extent to which animals selected different tree species to feed in (Clutton-Brock, 1975). The results are summarised in Fig. 4.8. Sourd and Gautier-Hion (1986) used selection ratios

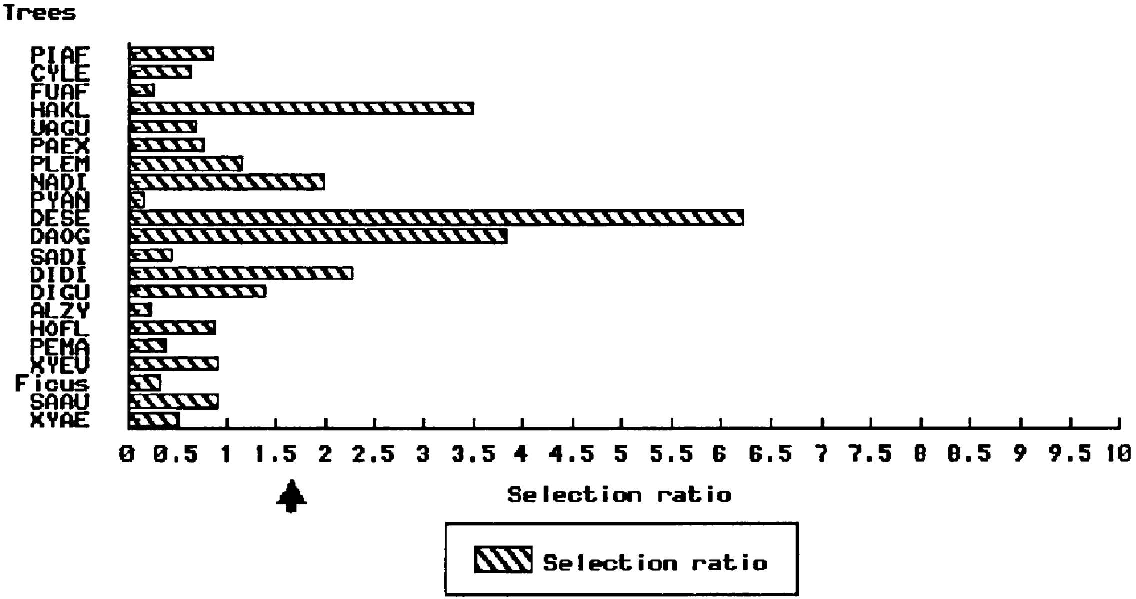
Fig. 4.8: Selection Ratios

Group W



Preferred species are those with SR > 1.5

Group E



Preferred species are those with SR > 1.5.

Table 4.5: Annual Diet for Group W group

SPECIES	PART	F	%	% Cum.	RANK
Invertebrates		186	11.8	11.8	1
Piptadeniastrum africanum	YL	144	9.2	21.0	2
Cynometra leonensis	YL	118	7.1	28.1	3
Landolphia hirsuta	MLP	110	7.0	35.1	4
Landolphia hirsuta	MFR	102	6.5	41.6	5
Hannoa klaineana	IFR	83	5.3	46.9	6
Funtumia africana	IFR	62	3.9	50.8	7
Piptadeniastrum africanum	ML	52	3.3	54.1	8
Funtumia africana	FL	50	3.2	57.3	9
Cynometra leonensis	ML	46	2.9	60.2	10
Chlorophora regia	FL	44	2.8	63.0	11
Nauclea diderrichii	MFR*	35	2.2	65.2	12
Amphimas pterocarpoides	IFR*	28	1.8	67.0	13
Piptadeniastrum africanum	MFR*	25	1.6	68.6	14
Millettia leonensis	FL	23	1.5	70.1	15
Parinari excelsa	MFR	22	1.4	71.5	16
Daniellia ogea	FL	19	1.2	72.7	17
Millettia leonensis	ML	16	1.0	73.7	18=
Piptadeniastrum africanum	BK	16	1.0	74.7	18=
Dialium dinklagei	MFR*	15	1.0	75.7	20
Millettia leonensis	YL	14	0.9	76.6	22=
Pycnanthus angolensis	MFR	14	0.9	77.5	22=
Landolphia hirsuta	YL	14	0.9	78.4	22=
Uapaca guineensis	IFR	11	0.7	79.1	24=
Parinari excelsa	YL	11	0.7	79.8	24=
Combretodendron macrocarpum	YL	10	0.6	80.4	26
Parinari excelsa	ML	9	0.6	81.0	27
Holarrhena floribunda	IFR	8	0.5	81.5	28=
Harungana madagascariensis	MFR	8	0.5	82.0	28=
Musanga cecropioides	MFR	7	0.4	82.4	30=
Uapaca guineensis	YL	7	0.4	82.8	30=
Combretodendron macrocarpum	IFR*	6	0.4	83.2	30=
Pycnanthus angolensis	IFR	6	0.4	83.6	30=
Cynometra leonensis	IFR*	5	0.3	83.9	34=
Musanga cecropioides	IFR	5	0.3	84.2	34=
Parkia bicolor	MFR	3	0.2	84.4	39=
Hannoa klaineana	MFR	3	0.2	84.6	39=
Daniellia ogea	YL	3	0.2	84.8	39=
Funtumia africana	YL	3	0.2	85.0	39=
Pycnanthus angolensis	ML	3	0.2	85.2	39=
Combretodendron macrocarpum	FL	3	0.2	85.4	39=
Xylopia aethiopica	IFR*	3	0.2	85.6	39=
Cynometra leonensis	FL	2	0.1	85.7	48=
Cynometra leonensis	BK	2	0.1	85.8	48=
Uapaca guineensis	FL	2	0.1	85.9	48=
Parinari excelsa	BK	2	0.1	86.0	48=
Blighia Sp	MFR	2	0.1	86.1	48=
Combretodendron macrocarpum	BK	2	0.1	86.2	48=
Dialium dinklagei	ML	2	0.1	86.3	48=
Holarrhena floribunda	MFR	2	0.1	86.4	48=
Pentaclethra macrophylla	ML	2	0.1	86.5	48=

Ficus mucosa	MFR	2	0.1	86.6	48=
Chlorophora regia	YL	2	0.1	86.7	48=
Pentaclethra macrophylla	FL	1	>0.1		62=
Ricinodendron heudelotii	IFR	1	>0.1		62=
Cleistopholis patens	ML	1	>0.1		62=
Monodora sp.	ML	1	>0.1		62=
Amphimas pterocarpoides	ML	1	>0.1		62=
Caloncoba echinata	MFR	1	>0.1		62=
Detarium senegalense	IFR	1	>0.1		62=
Xylia evansii	BK	1	>0.1		62=
Funtumia africana	ML	1	>0.1		62=
Funtumia africana	BK	1	>0.1		62=
Antiaris africana	YL	1	>0.1		62=
Pycnanthus angolensis	BK	1	>0.1		62=
Landolphia hirsuta	IFR	1	>0.1		62=
Combretodendron macrocarpum	ML	1	>0.1		62=
Unident.	YL	17	1.1		
	ML	15	1.0		
	FL	0	0.0		
	IFR	7	0.4		
	MFR	11	0.7		
	BR	1	>0.1		

KEY
* - Seeds
YL - Young Leaves
ML - Mature Leaves
MLP - Mature Leaf Petioles
FL - Flowers and Flower Buds
IFR - Immature Fruit
MFT - Mature Fruit

Table 4.6: Group E Annual Diet.

SPECIES	PART	F	%	CUM. %	RANK
Landolphia hirsuta	MLP	117	10.6	10.6	1
Invertebrates		88	7.9	18.5	2
Dialium dinklagei	MFR*	86	7.8	26.3	3
Pentaclethra macrophylla	FL	57	5.3	31.6	4
Detarium senegalense	FL	52	4.7	36.3	5
Hannoa klaineana	IFR	50	4.5	40.8	6
Landolphia hirsuta	MFR	46	4.2	45.0	7
Funtumia africana	FL	41	3.7	48.7	8
Unident. Strangler	IFR	37	3.4	52.1	9
Uapaca guineense	MFR	28	2.5	54.6	10
Uapaca guineense	IFR	27	2.4	57.0	11
Daniellia ogea	FL	24	2.2	59.2	13=
Plagiosiphon emarginatus	MFR*	24	2.2	61.4	13=
Piptadeniastrum africanum	YL	24	2.2	63.6	13=
Hannoa klaineana	MFR	23	2.1	65.7	15
Parinari excelsa	YL	21	1.9	67.6	16
Millettia leonensis	FL	13	1.2	68.8	18=
Holarrhena floribunda	IFR	13	1.2	70.0	18=
Landolphia hirsuta	YL	13	1.2	71.2	18=
Funtumia africana	IFR	11	1.0	72.2	20
Piptadeniastrum africanum	ML	10	0.9	73.1	21
Uapaca guineense	ML	9	0.8	73.9	22=
Uapaca guineense	FL	9	0.8	74.7	22=
Dialium guineense	MFR*	8	0.7	75.4	25=
Nauclea diderrichii	MFR*	8	0.7	76.1	25=
Millettia leonensis	ML	8	0.7	76.8	25=
Plagiosiphon emarginatus	ML	7	0.6	77.4	28=
Samanea dinklagei	FL	7	0.6	78.0	28=
Landolphia hirsuta	IFR	7	0.6	78.6	28=
Uapaca guineense	YL	7	0.6	79.2	28=
Dialium guineense	FL	6	0.5	79.7	31
Cynometra leonensis	ML	5	0.4	80.1	33=
Parinari excelsa	ML	5	0.4	80.5	33=
Musanga cecropioides	IFR	5	0.4	80.9	33=
Ficus	MFR	3	0.3	81.2	37=
Xylia evansii	ML	3	0.3	81.5	37=
Uapaca guineense	BK	3	0.3	81.8	37=
Sapium aubrevillei	IFR	3	0.3	82.1	37=
Pycnanthus angolensis	FL	3	0.3	82.4	37=
Hannoa klaineana	ML	2	0.2	82.6	43=
Hannoa klaineana	FL	2	0.2	82.8	43=
Samanea dinklagei	ML	2	0.2	83.0	43=
Xylopia aethiopica	MFR*	2	0.2	83.2	43=
Detarium senegalense	IFR	2	0.2	83.4	43=
Millettia leonensis	YL	2	0.2	83.6	43=
Afrosersalisia afzelii	IFR	2	0.2	83.8	43=
Piptadeniastrum africanum	BK	2	0.2	84.0	43=
Cynometra leonensis	YL	1	0.1	84.1	54=
Nauclea diderrichii	ML	1	0.1	84.2	54=
Nauclea diderrichii	BK	1	0.1	84.3	54=
Dialium	YL	1	0.1	84.4	54=

Holarrhena floribunda	ML	1	0.1	84.5	54=
Xylia evansii	MFR*	1	0.1	84.6	54=
Afrosersalisia afzelii	ML	1	0.1	84.7	54=
Ceiba pentandra	BK	1	0.1	84.8	54=
Funtumia africana	YL	1	0.1	84.9	54=
Pentaclethra macrophylla	BK	1	0.1	85.0	54=
Dialium guineense	YL	1	0.1	85.1	54=
Pycnanthus angolensis	IFR	1	0.1	85.2	54=
Caloncoba echinata	IFR	1	0.1	85.3	54=
Unident.	YL	4	0.4		
	ML	30	2.7		
	FL	10	0.9		
	IFR	5	0.4		
	MFR	9	0.8		
	BK	4	0.4		

in their analysis of fruit selection by Cercopithecus cephus. Using their criteria for categorising selection ratios, preferred species are those with ratios > 1.5. The results demonstrate that those trees most strongly selected are those used for flowers or fruits, rather than foliage.

An important point with respect to selection ratios is that they do not take into account seasonal variation in availability, size of tree etc. (Dasilva, 1989). But on this occasion the purpose of calculating selection ratios was to illustrate the point that irrespective of the strong seasonal variation in plant flowering and fruiting patterns and tree size, the study groups were highly selective in the tree species they were using, which is likely to be, at least partly, reflected in their ranging patterns.

Plant parts used

In the past many researchers have classified primate species as folivores, frugivores, insectivores etc. depending on whether leaves, fruits, or animal material predominated in their diet (Napier & Napier, 1967). More recently, this has been queried. Animals do not necessarily concentrate on the same types of foods throughout the year, as demonstrated by Chapman & Chapman (1990); and as more studies are completed it is becoming increasingly clear that many primate species are eclectic in their diets, and can adapt to a multitude of different conditions (Harding, 1981). More and more, primates appear less specialized, therefore perhaps more adaptable, than has traditionally been supposed.

The percentage contribution of plant and animal material to the annual diet of the two study groups is summarised in Figs. 4.9. and 4.10.

Foliage Selection: Figs. 4.9 & 4.10 show that group W had a greater proportion of leaf material in its diet over the year than did E. This is accounted for by the fact that members of group W ate more young leaves than did members of the second group: 56.6% of all foliage eaten by animals in W were immature leaves or leaf buds compared with 26.6% in E. Interestingly, both groups used lianas as a source of young leaves more than they did trees (W: 86.7% of young leaves from lianas; E: 74.7% of young leaves from lianas). Although the data available is limited, it appears that immature leaves of lianas contain higher protein and lower fibre levels than their tree counterparts (Dasilva, 1989). Similarly, group E also obtained 70.4% of their mature leaves from lianas rather than trees, whereas in group W it was approximately 50:50. Although there is no quantitative data available to verify this, from personal observation it appeared that the East Study Site may have had a larger liana load than in the West, and _Landolphia_ _hirsuta_ was particularly common - a species that both groups used

Fig. 4.9: Annual Diet of Group W

N = 1571

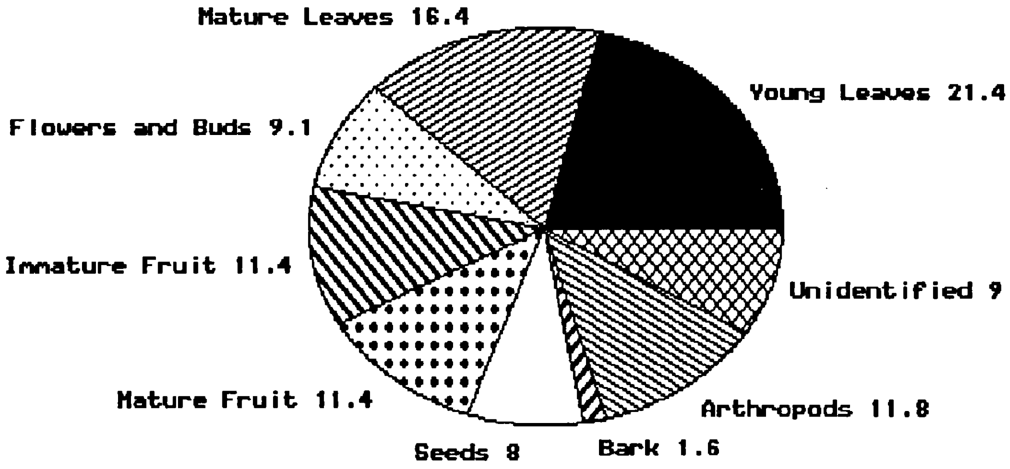
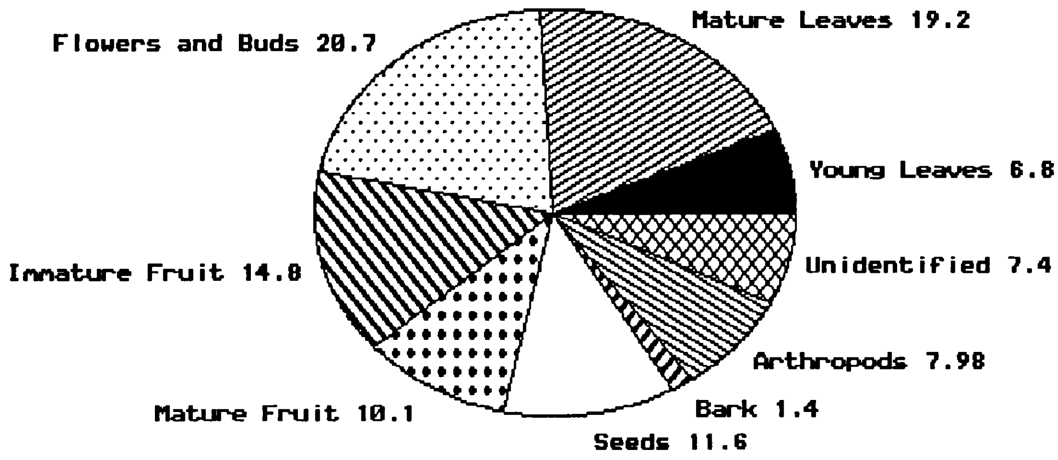


Fig 4.10: Annual Diet of Group E

N = 1103



extensively throughout most of the year. About 50% of the mature foliage used by the Eastern group came from this liana - they ate the mature leaf petiole only, discarding the leaf blade. W also made extensive use of Landolphia mature leaf petioles - possibly the petiole is more readily digested than the blade or has a higher nutritive value. Landolphia hirsuta mature leaf petioles appear to have a very low protein content (mean value = 6.38%) and a relatively low mean energy value (15.65 Kj/g^{-1} dry weight). Possibly they are low in plant secondary compounds, and this is why they are sought out during periods when there is little else other than arthropods and mature leaves which are likely to be relatively high in phenols and tannins. Waterman et al (1980) suggested that primates may select different parts of leaves on the basis of variation in protein or sugar concentrations within the leaf, which may apply with respect to Landolphia.

Flowers: As can be seen from the two pie charts, animals in group E spent more than twice as much of their time feeding on flowers and flower buds than did group W. Pentaclethra macrophylla and Detarium senegalense made up over 50% of all flower feeding records in group E, but only 0.7% in group W. Both groups ate similar amounts of Funtumia africana and Daniellia ogea flowers, and although E were seen feeding on a total of 10 flowering species and W only 8, W made extensive use of Chlorophora regia flowers - a species that was not available to E. It would appear that the difference between the two groups is likely to arise from vegetation differences between the two sides of the island. There were a total of 258 Pentaclethra macrophylla and 11 Detarium senegalense trees within group E's home range, compared to 46 of the former and 4 of the latter species available to group W. None of the Detarium senegalense was observed flowering during this study, and group W only ever encountered one Pentaclethra macrophylla in flower while being followed. Possibly in other years there might be more flowers available to group W, when flowers could prove to be a more important component of their diet, as with group E during the present study.

Fruit selection: A number of studies have not differentiated between immature and mature fruits, and seeds. In this study I divided all feeding records into these categories. It also seemed necessary to consider which part of a fruit was being eaten, the pulp, the seed, seedcoat, latex etc. Both study groups ate ripe Landolphia hirsuta fruits, discarding the outer inedible husk and eating the pulp surrounding the seeds. Funtumia africana and Holarrhena floribunda pods were collected when still unripe. Diana monkeys chewed the green pod and lapped up the sticky white latex oozing from the pulped pod. The remains were then discarded without either the pod or feathery seeds being ingested. In the case of Pycnanthus angolensis fruits I was never able to confirm which part was being ingested. The fruits comprise a hard, dark brown seed surrounded by a bright red aril, encased in a tough, thick, outer case (Savill & Fox, 1967). The Diana monkeys were seen to manipulate both immature and mature fruits - Whitesides reports that they eat only the aril (pers. comm.). Gautier-Hion (1989) reported finding P. angolensis arils and seeds in guenon stomachs. Different types or parts of fruits i.e. dry seeds versus pulpy fleshy parts are likely to be of different calorific and nutritive value to the animals feeding on them. Ripe fleshy fruits are likely to have relatively high levels of water and sugars while P. angolensis arils are reported to be high in fatty acids (Sourd & Gautier, 1986). Seeds have higher protein and fat content than fruit pulp - therefore it is probable that monkeys may select a variety of different types of fruit in order to obtain proteins, water, sugars, fats and minerals to meet their metabolic requirements.

From the literature most Cercopithecines select ripe fruit in preference to unripe fruits. Colobines are unable to cope with ripe sugary fruits so eat immature fruits before much of the carbohydrate content has been broken down into sugars. On Tiwai the Diana monkeys were observed to eat about 50% of their fruit when it was still unripe. There is a high Colobine biomass on the island (Oates et al, 1990). Possibly they are competing with the guenons for certain fruits e.g. Hannoa klaineana, thus compelling the Diana monkeys to eat them earlier than they might otherwise choose to.

The two groups varied somewhat in the species they used, and in the proportions of fruits and seeds which they ate. Species that were common to both groups include Hannoa klaineana, Landolphia hirsuta, Funtumia africana and Nauclea diderrichii. Group E had 47 Dialium dinklagei trees within their home range compared with 3 in W's home range. Although both groups fed on the mature seeds they formed 7.8% of E's annual diet but only 0.7% of W's. Again this is likely to be a reflection of difference in availability rather than active choice on the part of the animals concerned.

Arthropod Feeding: Both groups spent time foraging for arthropods. Over 80% of the time spent by members of group W feeding on arthropods was observed to take place in three species of trees, Piptadeniastrum africanum, Cynometra leonensis and Parinari excelsa, unlike group E, where arthropod feeding was observed in a greater variety of trees and lianas. Unfortunately there is no data available on infestation rates of different tree species, so we can only speculate as to whether the monkeys actively choose particular species for arthropod feeding. Piptadeniastrum africanum and Cynometra leonensis are among the three most common species found within the Western home range: they may not therefore have been specifically selected but simply encountered more frequently than other species. Not surprisingly, research carried out on arthropod feeding in forest passerines has demonstrated that various constraints are imposed on the birds' foraging strategies as a result of the structure and types of vegetation, as well as prey abundance (Robinson & Holmes, 1982). These factors possibly apply to insect-feeding in arboreal primates such as Diana monkeys. I hope to consider this further when looking at seasonal variation in feeding and ranging patterns. WHERE ?

Vertebrate prey: Captive Diana monkeys are known to catch and eat a variety of different vertebrates including birds, mice and frogs, given the opportunity. Two adult females and a juvenile were observed catching and killing birds on three separate occasions at Regents Park Zoo, London. On every occasion the adult male stole the prey and ate it (Hill, 1985). On Tiwai on one occasion two large juveniles from group W were seen nest raiding in a colony of forest weaver birds. It was not possible to determine whether the monkeys were feeding on eggs or nestlings.

4.6 SEASONAL USE OF FOOD RESOURCES

The mean percentage time spent feeding on leaves, flowers, fruits and arthropods was calculated on a monthly basis for the two study groups. The results are presented in Figs. 4.11 and 4.12 respectively.

Young leaves were primarily a late dry season food for both W and E. As outlined previously, there was no strong leaf

Fig. 4.11: Monthly Variation in Diet in Group W

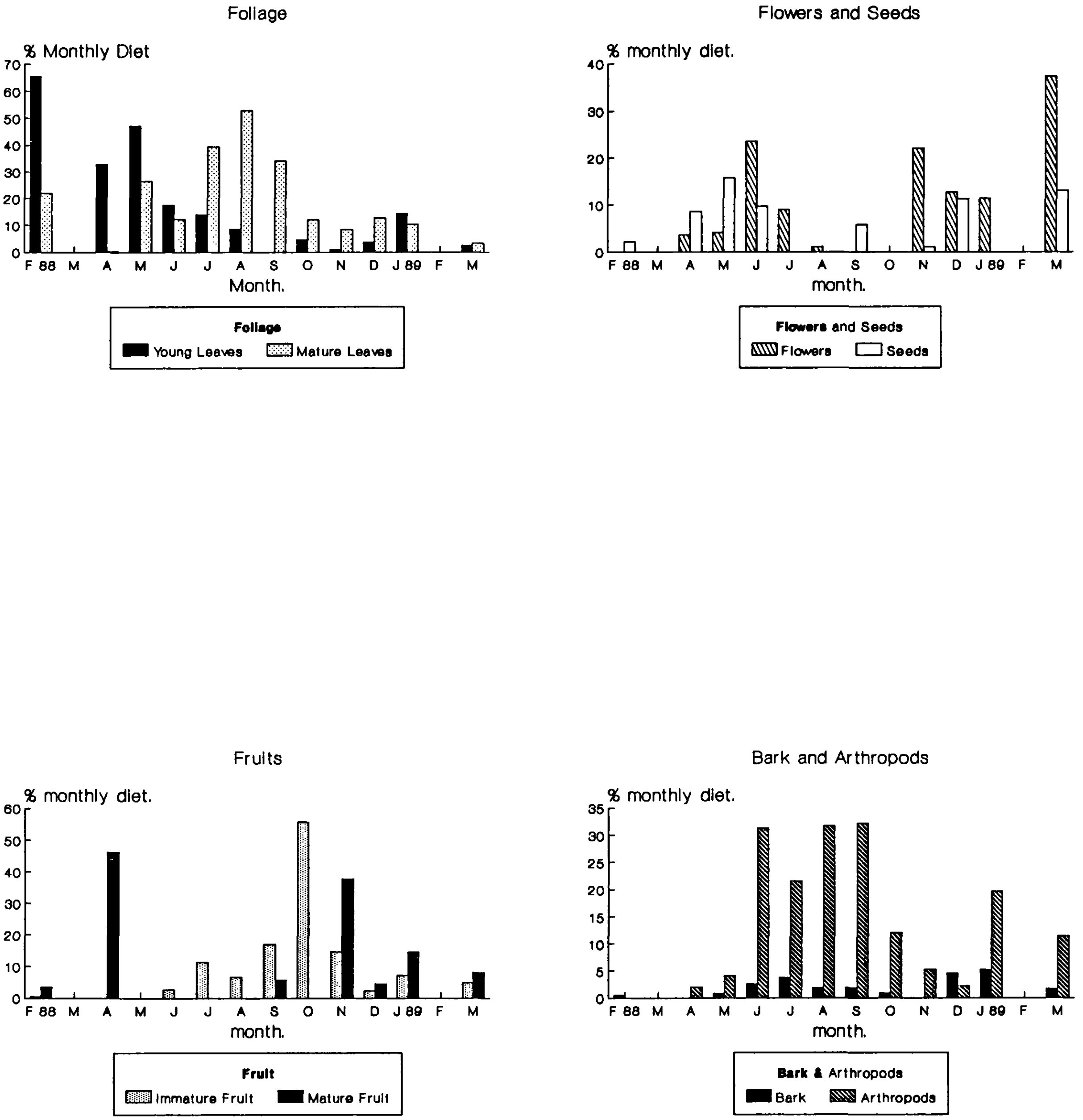
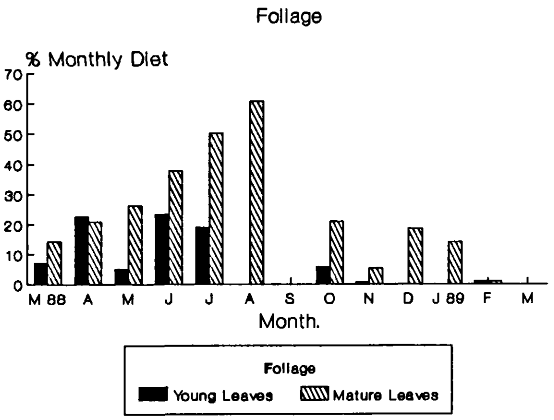
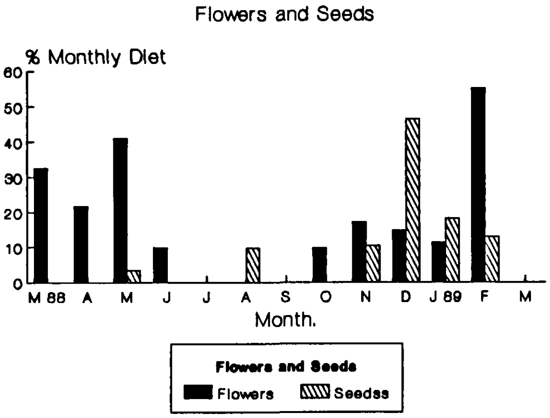
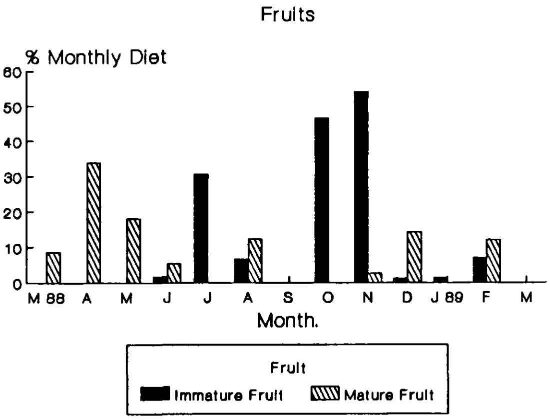
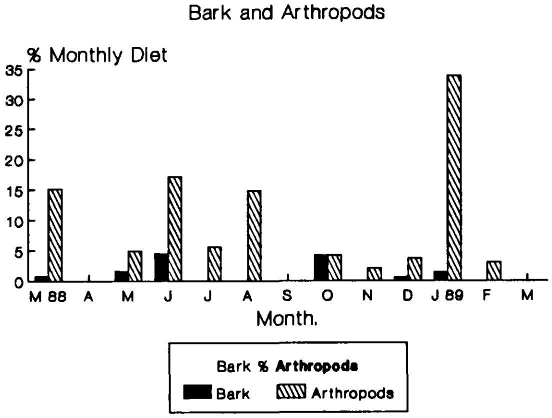


Fig. 4.12: Monthly Variation in Diet in Group E









flush during this study as has been reported for other sites, but there was a tendency towards a leaf flush after the rains, thus the Diana monkeys' use of young leaves seemed to follow tree production patterns on the island. This is substantiated by a significant positive correlation between the relative abundance of young leaves and their use across the year ($r_s = +0.531$, $p < 0.05$).

Mature leaves were a very important dietary component during the wet season, between July and September (June and August for E). The Eastern group seemed to show feeding patterns similar to W but often lagging by about one month. As with immature leaves, mature leaf production showed little periodicity, but trees retained their mature leaves throughout the wet season. Both groups relied very heavily on Landolphia mature leaf petioles, and to a lesser extent on mature leaves of the liana Millettia leonensis during this period.

Flowers and flower buds were used somewhat differently by the two groups. As explained earlier, the two groups used different species as a result of differences in their respective home ranges Section 4.3. This difference between the groups is well illustrated in Figs. 4.11 and 4.12. W showed three peaks in flower consumption: June, November and March, corresponding to three different species: Funtumia africana, Millettia leonensis, and Chlorophora regia. The percentage time spent feeding on flowers by

Group W correlated with forest production pattern ($T = =0.538$, $N = 12$, $p < 0.05$). On the other hand, group E ate most flowers during the dry season, extending into the transition period from dry to wet season: *Detarium senegalense* flowers were eaten in February, and *Pentaclethra macrophylla* flowers throughout March, April, and May, with some flowers from *Funtumia africana* being eaten in May as well.

Immature fruits were consumed mainly during the late rains and transition period from wet to dry season. Both groups also had a small peak in July, when they exploited latex from immature *Holarrhena floribunda* pods. In October and November, W fed on immature *Hannoa klaineana* fruits and unripe *Funtumia africana* pods, while E relied on *Uapaca guineensis* and *Funtumia africana*: during November W continued to feed on *Funtumia* pods while E exploited immature fruits from several large *Hannoa* trees, and an unidentified strangler. Again, not surprisingly, immature fruit consumption levels were associated with forest production patterns ($T = + 0.439$, $N = 12$, $p < 0.05$).

Relatively few species of primate, other than Colobines, regularly feed on unripe fruits. As mentioned earlier, Diana monkeys may be in competition with *Colobus polykomos* and *Procolobus badius* groups for certain fruits, e.g. *Hannoa klaineana*. However, an interesting alternative explanation might be that they were exploiting *Hannoa* fruit pulp and the immature seed contained within. Kinzey and Norconk (1990) report that seeds of immature fruits contain lower levels of condensed tannins, and that their overall nutritional value is higher than that of seeds from the mature fruits. However, the Diana monkeys would have to penetrate the hard seed coat in order to exploit the nutritious seed within it. I have no knowledge of whether they are able to do this or not.

Mature fruits were used most extensively by both groups during April. This was when the Landolphia fruits were ripe. W also fed on mature Parinari excelsa fruits, while E continued eating Landolphia into May, by which time there were none available to W. Whether this is as a result of the Western home range containing fewer Landolphia lianas, their not having so productive a fruit crop, or greater competition from other guenon species for these particular fruits is unclear. However, W also consumed sizeable amounts of mature fruits (approximately 15% of monthly diet) during November - these were from Musanga cecropioides and Harungana madagascariensis, two species common to disturbed areas such as regenerating farmbush where they are often found in association with one another (Savill & Fox, 1967). W was seen to use such areas extensively during November, sleeping, and feeding in the early morning and evening in the old farmbush just outside the main camp. During this period, other species of primate, including mangabeys (Cercocebus atys), spot-nose (Cercopithecus petaurista) and

Campbell's monkeys (C. campbellii) were often to be seen feeding alongside the Diana monkeys.[5]

There was no significant correlation found between the percentage of mature fruit in the diet and the relative abundance of mature fruits estimated from the phenology data. A possible explanation for this lies in the discrepancy between the species included in the phenology sample and those that are important food sources for the Diana monkeys. This illustrates a problem common to research workers first deciding on the species to include in any phenology sample. Where one is interested in production patterns, and relative abundance of food resources, it is necessary either to set up an enormous phenology sample, incorporating most, if not all available species, and adequate numbers of each: or to have already detailed knowledge of the study animals' dietary habits so as to be able to design the sample accordingly. The former would be enormously time consuming and labour intensive, and the latter not possible before completion of at least an initial twelve months study of the animals in question. Given fruiting patterns in West African tropical rain forests, where many species do not show a simple annual cycle, even this could lead to inappropriate sample design.

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[5] During this period several of the island's resident chimpanzees became frequent visitors to the Musanga cecropioides trees surrounding the camp area, and one old adult male actually ventured into camp several days running to feed in a large Musanga next to the main camp bafa.

Seed-eating peaked during the months of May and December in W, and December only in E. Again, this illustrates differences between the home ranges. W fed on Nauclea diderrichii in May, and Amphimas pterocarpoides and to a lesser extent Dialium dinklagei during December. Seed-eating in E was almost exclusively from Dialium dinklagei and Plagiosiphon emarginatus.

Arthropods formed the largest single component of W's wet season diet (June - September). Although they did not form such a large portion of E's diet over this period, they were still relatively important. This coincides with a period where mature leaves were fed on extensively - there was relatively little else available to the monkeys at this time of year - no flowers or seeds, and very few young leaves or fruits.

Arthropods were also important foods in January, particularly for group E. Arthropod abundance has been shown to vary seasonally (Wolda, 1978). Possibly there were peaks in arthropod abundance coinciding with leaf flushing as has been reported by Janzen & Schoener (1968).

Gautier-Hion (1980) observed that female guenons showed a dietary shift towards food-items containing relatively high protein levels, i.e. young leaves and arthropods, during the months when they were pregnant or lactating. In the present study infants appeared in the study groups mainly during

December and January - when young leaf and arthropod consumption were relatively high. However, this observation does not categorically verify that female Diana monkeys were shifting the emphasis of their diet as a consequence of their changing nutritional requirements while pregnant or lactating.

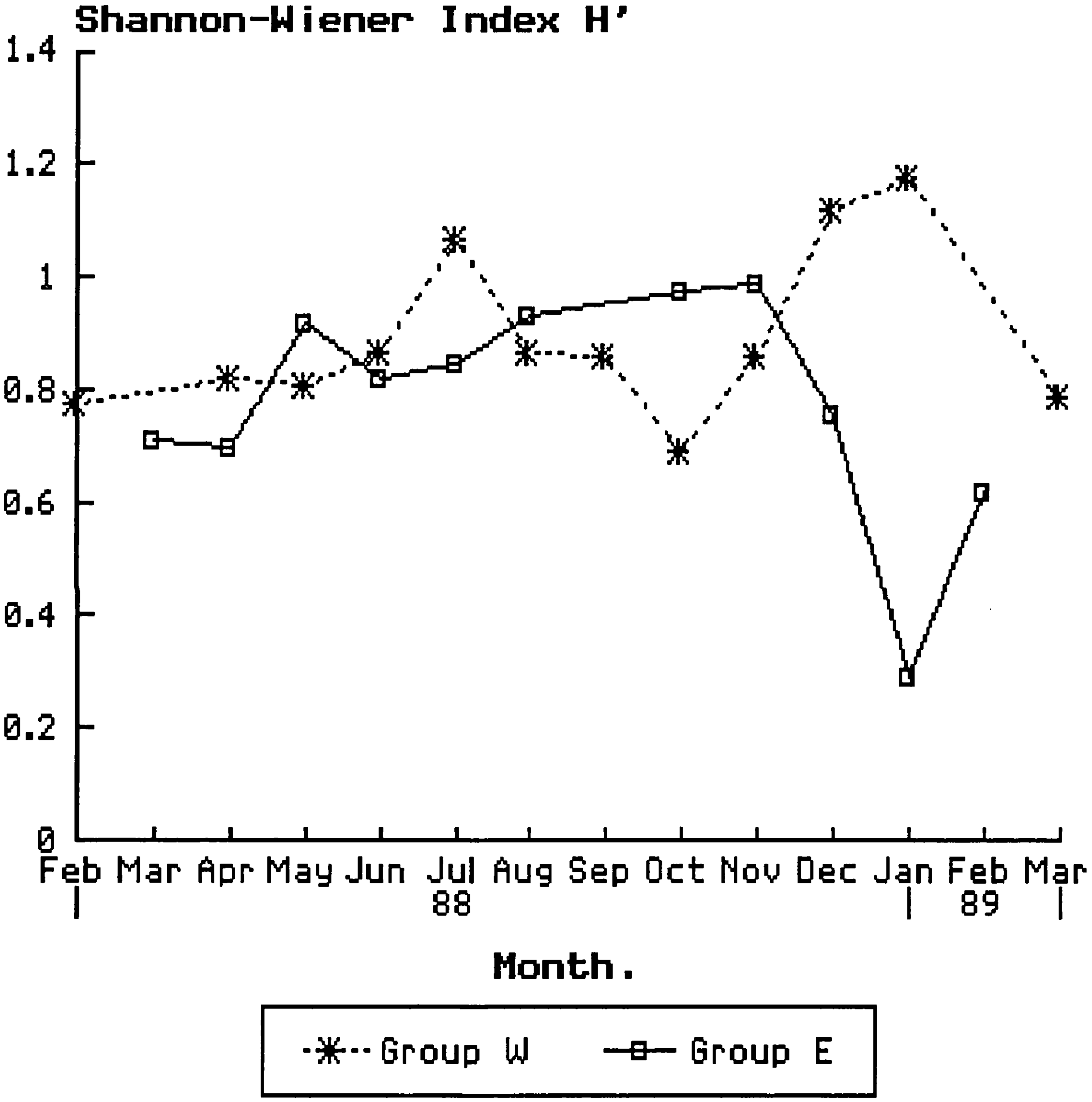
Overall, the study groups showed very similar patterns in seasonal use of food types. Most, if not all, differences could be explained by differences in resources available to the respective groups.

4.7 DIETARY DIVERSITY ACROSS THE YEAR

Diversity indices (Shannon-Wiener index) were calculated to investigate how the animals' diet varied from month to month. H' was calculated using all identified species-items used in any one month, rather than just species used. Because they use several plant parts from many of the species they exploit, species-items are likely to give a better indication of dietary diversity than species alone.

From the plot of H' across the months (Fig. 4.13) it is apparent that the two groups do not follow the same variation in dietetic diversity synchronously across the year. W showed peaks in dietary diversity during the height of the rains (July) and the early dry season (December -

Fig. 4.13: Dietary Diversity Indices for the Two Study Groups



January), and a small trough in October, while E had a slight peak in diversity during October - November (Transition from Wet - Dry) and a very definite drop in dietary diversity during January. Neither are the results consistent in predicting the types of foods being utilized. From the literature, one might predict that in periods when animals were relying extensively on foliage they would utilize small amounts of many different species, in an attempt to reduce/minimise the costs of feeding on low-quality, bulky and potentially toxic materials (Freeland & Janzen, 1974; Levin, 1976), thus they would show high H' values. Although W had a high percentage of mature foliage in its diet during July, it was feeding predominantly on seeds and insects during the second peak in dietary diversity[6]. Again, from the literature, low diversity in diet is commonly associated with periods of intensive fruit-feeding, where animals concentrate on only a few species in any one month (_Cercopithecus_ _ascanius_ - Struhsaker, 1980; _Alouatta_ _palliata_ - Estrada, 1984), though Clutton-Brock (1977b) suggests that species commonly regarded as folivores, and especially those found to specialize in feeding on mature leaves, tend to select a less diverse diet than do frugivores. Again the results of this study do not conform with patterns reported from other studies.

A comparison of the diversity indices of their diets over the year (W = 1.685; E = 1.438) and the mean monthly values

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[6] All arthropods were lumped into one species-item, irrespective of the substrate from which they had been collected.

of W = 0.89 (0.69 - 1.12) and E = 0.78 (0.29 - 0.99) confirm that while over the year Diana monkeys exploit a variety of food resources, they tend to concentrate on only a few food-items in any one month. Similar results were obtained for _C_. _mitis_ and _C_. _ascanius_ in Kibale (Struhsaker, 1978a).

Overlap of diet between months

Dietary overlap was calculated as the sum of shared percentage time spent feeding on each specific food item, as in Harrison (1984). All instances of invertebrate feeding were excluded for this particular analysis. The results are presented in Tables 4.7 & 4.8 respectively.

Table 4. 7: Dietary overlap in Group W

		F	M	A	M	J	J	A	S	O	ND	J
F	-	3.2	**25.4**	**51.7**	**21.8**	18.4	17.7	12.8	9.3	6.2	13.4	17.1
M[7]		-	9.3	13.0	0.8	7.8	2.7	1.9	5.1	2.0	6.2	4.1
A			-	**20.4**	17.4	9.9	7.1	0.4	1.3	0.4	5.5	10.3
M				-	**22.0**	18.3	**25.8**	16.9	9.1	5.2	9.7	**21.4**
J					-	**24.4**	16.8	10.9	9.1	4.4	11.6	11.3
J						-	**30.8**	**20.8**	17.2	7.8	18.7	16.1
A							-	**22.0**	13.6	11.0	14.3	14.2
S								-	17.7	13.7	12.3	7.5
O									-	17.6	12.6	8.4
N										-	11.8	2.0
D											-	14.5
J												-

All months where % overlap > 20%, the values are blocked.

Table 4. 8: Dietary overlap in Group E

	M	A	M	J	J	A	S	O	N	D	J	F
M	-	**36.6**	8.9	5.6	12.4	5.6	-	5.6	4.1	5.6	5.6	0
A		-	12.8	5.3	14.9	8.8	-	6.8	5.4	3.5	4.4	4.4
M			-	8.1	15.9	**24.5**	-	16.7	10.8	11.7	9.8	9.0
J				-	**28.7**	**29.7**	-	14.3	10.7	11.7	7.0	1.8
J					-	**29.9**	-	12.5	4.1	9.2	7.0	0
A						-	-	18.3	11.7	2.5	8.6	9.2
S							-	-	-	-	-	-
O								-	15.5	9.8	8.4	1.0
N									-	12.4	11.2	2.5
D										-	**28.1**	5.0
J											-	8.0
F												-

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[7] March 1989

A Mann-Whitney U test was used to determine whether there was a significant difference in the percentage dietary overlap between neighbouring and non-neighbouring groups. Group E showed a significant difference between the two conditions ($n_1 = 10$, $n_2 = 45$, $z = 3.513$, $p < 0.001$) whereas this was not the case for Group W. Possibly this reflects a difference in their dietary strategies: Group E fed on more flowers and fruits than did Group W, both of which are very seasonal in their occurrence.

In general, the percentage dietary overlap between consecutive months is greater than that between non-neighbouring months as shown below:

Table 4.9: Mean percentage dietary overlap between neighbouring and non-neighbouring months

	W	E
Mean % overlap between neighbouring months	20.1 (11.8 - 30.8)	20.0 (8.0 - 36.6)
Mean % overlap between non-neighbouring months	11.8 (0.4 - 51.7)	8.5 (0.0 - 29.7)

The extent to which diet changes from month to month is a good indicator of the seasonality of the habitat, thus the results reflect that Tiwai is a strongly seasonal habitat, and that the Diana monkeys living there are having to contend with a diet that changes considerably from month to month.

4.8 "STAPLE" AND "STANDBY" RESOURCES VERSUS "PREFERRED" FOOD SPECIES'

Tables 4.10 and 4.11 are a summary of the distribution of species-items eaten across the year by the two groups. One thing that stands out when first looking at these tables is that the monkeys appeared to show three distinct strategies

Table 4.10: Annual Diet for Group W

SPECIES	F	A	M	J	J	A	S	O	N	D	J	M
INVERT.		*	*	***	**	***	***	**	*	*	**	**
PIAF YL	***	**	***	*	*			+		*	*	
CYLE YL	***	**	*	**	*	*			*			
LAHI MLP	*		**	**	**	***	*	*	*	*	**	
LAHI MFR		***										*
HAKL IFR								***				
FUAF IFR				*	*	*	*	**	**	*		*
PIAF ML	*		*	*	*	*	*	+	*	*		
FUAF FL		*		**	*	*				*	*	+
CYLE ML	**	+			*	*	*	*		*		*
CHRE FL												***
NADI SE			**									**
AMPT SE										**		
PIAF SE	*	*										
MILE FL									**	*		
PAEX MFR		*										*
DAOG FL										*	*	
MILE ML					**	*			*	+		
PIAF BK				+	*	*				*	*	+
DIDI SE										**		
MILE YL					*			*	*	*	*	*
PYAN MFR	*										*	
LAHI YL		+	*	+	*	*	*				*	
UAGU IFR					*						*	*
PAEX YL	+				*	*						
COMA YL		*										
PAEX ML		*			*		**					
HOFL IFR					*	*	*					
HAMA MFR									*			
MUCE MFR									*			
UAGU YL	*				*							
COMA SE				*								
PYAN IFR											*	
CYLE SE				*								
MUCE IFR							*	+				
PABI MFR							*					
HAKL MFR									*			
DAOG YL	+	+										
FUAF YL			*									
PYAN ML					*	*		+				
COMA FL			*									
XYAE SE									*	*		
CYLE FL			*									
CYLE BK			+					+				
UAGU FL											*	
PAEX BK						*	*					
BLWE MFR	*											
DIDI ML			*									
HOFL MFR										*		
PEMA ML						*			*			
FIMU MFR									*	+		

Table 4.11: Group E Annual Diet.

SPECIES	M	A	M	J	J	A	S	O	N	D	J	F
LAHI MLP	*	*	**	***	***	***	-	*	*	*	*	
INVERT	**		*	**	*	**	-	*	*	*	***	*
DIDI SE							-		*	***	**	*
PEMA FL	***						-					
DESE FL							-					****
HAKL IFR							-		***			
LAHI MFR	*	***					-					
FUAF FL			***	*			-		*	*		
UNI. ST IFR							-		**			
UAGU MFR		*	**			*	-		+			*
UAGU IFR							-	**	*	+		
DAOG FL							-		*	**	*	
PLEM SE							-		*	*	*	*
PIAF YL	*	**	*		*		-		+			
HAKL MFR							-			**		
PAEX YL				**	*		-					
MILE FL							-	*	*			
HOFL IFR					***	*	-					
LAHI YL			*	*			-	*				
FUAF IFR					*		-	**	+			
PIAF ML						*	-			*		
UAGU ML	*	*			*		-					
UAGU FL							-				*	*
DIGU SE							-					*
NADI SE						*	-		*			
MILE ML				*			-					
PLEM ML		*			*		-					
SADI FL			*				-					
LAHI IFR							-					*
UAGU YL		*		+	*		-					
DIGU FL							-		*			
CYLE ML			*			*	-	*				
PAEX ML		+		+		*	-	*				*
MUCE IFR							-	*				
Ficus MFR			*				-		+			
XYEV ML					*		-					
UAGU BK			*	+			-	*				
SAAU IFR							-		*			
PYAN FL							-		*			
HAKL ML	+	+					-					
HAKL FL							-	*				
SADI ML						*	-					
XYAE SE			*				-					
DESE IFR				+			-	*				
MILE YL				*			-					
AFAF IFR							-	*				
PIAF BK				+			-				*	
CYLE YL							-	*				
NADI ML						*	-					
AFAF ML						*	-					
CEPE BK							-	*				
DIGU YL							-					*

Key: **** > 50% of monthly diet

*** 50% < 25% of monthly diet

** 25% < 10% of monthly diet

* 10% < 1% of monthly diet

+ > 1% of monthly d

Abbreviations of Food Species:

INVERT	Invertebrates
PIAF	*Piptadeniastrum africanum*
CYLE	*Cynometra leonensis*
LAHI	*Landolphia hirsuta*
HAKL	*Hannoa klaineana*
FUAF	*Funtumia africana*
CHRE	*Chlorophora regia*
NADI	*Nauclea diderrichii*
AMPT	*Amphimas pterocarpoides*
MILE	*Millettia leonensis*
PAEX	*Parinari excelsa*
DAOG	*Daniellia ogea*
DIDI	*Dialium dinklagei*
PYAN	*Pycnanthus angolensis*
UAGU	*Uapaca guineensis*
COMA	*Combretodendron macrocarpum*
HOFL	*Holarrhena floribunda*
HAMA	*Haraungana madagascariensis*
MUCE	*Musanga cecropioides*
PABI	*Parkia bicolor*
XYAE	*Xylopia aethiopica*
BLWE	*Blighia welwitschii*
FIMU	*Ficus mucoso*
PEMA	*Pentaclethra macrophylla*
DESE	*Detarium senegalense*
UNI. ST.	Unidentified Strangler
PLEM	*Plagiosiphon emarginatus*
DIGU	*Dialium guineense*
SADI	*Samanea dinklagei*
Ficus	*Ficus* species
XYEV	*Xylia evansii*
SAAU	*Sapium aubrevillei*
AFAF	*Afrosersalisia afzelia*

of food use. Firstly, there were those items that they concentrated on heavily throughout a particular month. All of these food-items were either flowers, or fruits and seeds of particular trees and lianas. These included fruits of <u>Landolphia</u>, <u>Hannoa</u>, and <u>Uapaca</u>, flowers from <u>Chlorophora</u>, <u>Pentaclethra</u> and <u>Detarium</u>, and seeds from a number of trees, including <u>Amphimas</u> and <u>Dialium</u>. These will be referred to as 'preferred' foods, since animals seemed to actively select them.

As has been stressed previously, the differences between the groups can be accounted for by considering the distribution of plant species between the two home ranges. Also, it is clear when comparing the two tables that group E had available and made use of, abundant flower, and fruit resources throughout more of the year than did W.

Secondly, there were those foods that the Diana monkeys used in varying quantities for much of the year. These included arthropods, young and mature leaves from a number of tree and liana species, and flowers and immature fruits of <u>Funtumia</u>. Arthropods and mature leaves were important resources during the wet season as were <u>Funtumia</u> fruits. Young leaves were used for much of the year, but were most important during the dry season.

Some immature leaves were eaten throughout the whole year. <u>Landolphia</u> was used from the middle of the dry season until the late wet season, after which young leaves from Millettia were eaten until the young Landolphia leaves became available again. This pattern of using leaves suggests that these are 'staple' food resources. Young leaves were used throughout the year: they are known to be much better sources of protein than fruits or mature leaves. Mature leaves and insects were available during much of the year, but were turned to particularly during periods of shortage when there was little else around ("standby" food resources).

E made far less use of these "staple" and "standby" resources than did W. As suggested earlier, they had more "preferred" foods in their home range, and thus apparently did not need to use leaves and insects so much, except during the wet season. Nor did they make the same use of young leaves during the year: at times of peak flower abundance they seemed able to meet their protein requirements from flowers instead of using young leaves as a supplement.

Thirdly, many of the food-items observed being eaten by the study animals were eaten very rarely, e.g. mature fruits of Ficus mucosa and fruits from other Ficus species. These were species that were encountered infrequently as the monkeys travelled around their ranges. They appeared to be eaten opportunistically, but were not actively sought after, so it is unlikely that they would have had any influence over the groups' day range routes.

It seems likely that foraging strategies would have had some influence over patterns of ranging behaviour. Thus it is postulated that the spatial distribution of those preferred foods such as Hannoa and Dialium, might be reflected in the animals, seasonal ranging patterns as reported in Chapman (1988a) where it was reported that a single fruit tree could influence range use patterns of three species of neotropical primate. The distribution of the liana Landolphia is not known for the two home ranges. However, it is not thought to have been uncommon in either range. But the spatial locations of Hannoa, Chlorophora etc. were all known and ranging patterns will be considered with respect to location of selected food species in the next chapter. One further point that should be introduced here is that if females are defending their food resources against neighbouring groups, then the location of such sought-after, patchily distributed resources should be investigated with respect to territorial calling behaviour: it makes sense, in terms of energy investment, to defend important discrete food patches, rather than those that are more widely distributed and less highly sought after. This will be dealt with more fully in Chapter Seven, Section 7.3).

"Staple" and "standby" resources tended to be from species that were relatively common and evenly dispersed within the study animals' respective home ranges and the food-items used had long or asynchronous production cycles such as shown by Funtumia flowers and Landolphia young leaves. Although these staple foods formed the basis of the monkeys' diet, it is thought unlikely that the Diana monkeys would have invested much time or energy defending them against neighbouring troops, since they were common within the forest. Neither is ranging behaviour likely to reflect their distribution, since animals were likely to encounter them frequently in most parts of their range. However, at times of year when the monkeys concentrated on such evenly distributed food resources this may have left time for additional patrolling of boundaries.

4.9 OPTIMAL FORAGING

Much research has been carried out to derive models of optimal foraging strategies for animals. Most of the original work was done using birds and insects to test model predictions e.g. Chipping sparrows (Pulliam, 1980) and Bumblebees (Pyke, 1979a). More recently several primate studies have been carried out within the optimal foraging paradigm to investigate foraging strategies (Chapman, 1988b; Harrison, 1984) and their potential effects on primate group size and structure (Chapman & Lefebvre, 1990; Isabirye-Basuta, 1988; Janson & van Schaik, 1988; Whitten, 1988).

Optimal foraging theory is based on the idea that selection favours those individuals that balance costs and benefits of feeding in such a way as to maximise their net energy gain. Assumptions underlying the theory are outlined in Pyke (1984). The model makes several predictions, namely that:

1. animals should prefer more profitable foods,
2. as abundance of preferred foods increases, animals should become increasingly more selective in their food choice, and
3. they should disregard unprofitable foods, irrespective of their abundance, as outlined in Garton (1979).

Optimal foraging theory may at least go some way towards explaining the variability in diet shown by many primates - they are likely to be employing specific foraging strategies to balance costs and benefits of foraging with respect to several currencies, including energy intake and nutritive balance.

Recent evidence from long-term studies has shown that primates exhibit enormous flexibility and variety in their dietary habits across the year (Oates, 1977 - Colobus guereza; Waser, 1977a - Cercocebus albigena). Chapman (1987) demonstrated that Ateles geoffroyi, Cebus capucinus and Alouatta palliata all showed little dietary overlap between months, thus illustrating the very variable nature of their diets. Harrison (1984) obtained similar results from a study of Cercopithecus sabaeus in Senegal. And most recently, Chapman and Chapman (1990) have investigated dietary variability using data from 46 long-term field studies. They conclude that primates often switch between dietary categories rather than consistently combining the same kinds of foods, as many past ecological classifications might suggest.

During this study data were not collected specifically to test whether Diana monkeys are optimal foragers or not. But it seems valuable to discuss the results in the light of predictions that arise from the model.
Firstly, animals should prefer more profitable foods. Diana monkeys selected fruit, and flowers when they were available; both of which are high in water and sugars.

Secondly, as these food items became more abundant, the proportion of mature leaves in the diet declined accordingly, as predicted by the model.

Considering the model's third prediction, that unprofitable foods should be ignored irrespective of their availability, the monkeys were never observed to sample many abundant items e.g. mature leaves of Funtumia africana, one of the most common trees in the forest. Also, on comparing annual dietary diversity values with vegetation diversity indices for the two home ranges, it is obvious that the Diana monkeys ignored many of the potential food species and items available to them.

A further point is that the monkeys maintained their intake of a mixture of young leaves and arthropods (known to be sources of protein) throughout the year, increasing their arthropod intake during the wet season when young leaves were unavailable. Seeds were taken during the dry season when pulpy fruit was scarce. Thus Diana monkeys appear to be trying to adjust their feeding behaviour across the year in such a way as to meet their energy and nutritive requirements as best they can, as predicted by optimal foraging theory.

4.10 A COMPARISON WITH OTHER STUDIES OF GUENONS

It is not the intention in this section to give a comprehensive overview or summary of guenon diets and feeding strategies since that has already been done in Gautier-Hion (1988). Instead I intend to

1. compare the results of this study with (i) those of Whitesides (Oates & Whitesides, 1990) carried out on the same study groups as the present study between 1982-1984, and (ii) a study carried out at Tai National Park, Ivory Coast where data on Diana monkey diets were collected (Galat & Galat-Luoung, 1985).
2. Discuss the implication of the feeding behaviour observed in this study with respect to other guenon species.

Data were collected on the ecology and behaviour of a number of primate species at Tai Forest, Ivory Coast between 1977 and 1983, *C. diana* being one of the species included in the sample. The results of their dietary habits is presented below alongside those from this study. Because of differences in the way food items have been categorised in the two studies, I have grouped the data according to the categories laid down by Galat & Galat-Luoung (1985).

Table 4.12: Comparing diets of *C. diana* at Tai Forest, Ivory Coast and Tiwai, Sierra Leone.

Site	Percentage of diet					
	Fol.	Flower	Fruit	Arth.	Misc.	N
Tai	7.7	5.0	76.3	4.0	6.4	299
Tiwai W	37.8	9.1	30.8	11.8	10.6	1571
E	26.0	20.7	36.5	7.9	8.8	1103
(Present study)						
Tiwai W	11.0	16.7	40.4	30.8	1.1	2482
E	14.1	15.5	45.1	24.5	0.8	1080
(Whitesides)						

The two studies carried out at Tiwai give rather different figures for percentage time spent feeding on different dietary items. The most obvious differences are those in the amount of time spent feeding on foliage, arthropods and fruits. A possible explanation is that phenological patterns within the forest varied considerably between the two study periods, therefore there were different types and amounts of food available to the two groups during the two studies.

An obvious problem with the Tai data is that it is a very small sample compared with the present study. Also, there is no indication whether the distribution of sample points are biased towards particular times of year which might account for the very different amounts of fruit being eaten between the two sites. However, the difference may stem, at least in part from differences in forest structure and species composition. Tai consists of primary, undisturbed forest unlike Tiwai where the Diana monkeys make use of a number of different disturbed habitats.

Overall, guenons appear to be primarily fruit-eaters, but depending on their body size, supplement their diet either with animal material such as insects, or leaves, or a combination of both. Larger species such as C. mitis increase their intake of foliar material during periods when fruit is scarce (Cords, 1986) whereas C. pogonias, a smaller-bodied guenon, has been observed to resort to increased insect-feeding at such times (Gautier-Hion, 1980). The results of this study suggest that the Diana monkeys used a combination of both leaves and arthropods during periods of low fruit abundance, though there were times when they resorted to very large quantities of foliage. This may be a reflection of their body size of 5.4 kg (guenon range: 3.0 - 7.5kg) - many studies have noted that the degree of folivory increases with increasing body size (Hladik, 1978b - guenons; Chivers & Raemaekers, 1986 - gibbons; Emmons et al, 1983).

In respect of dietary diversity, Diana monkeys fall into the same pattern as other guenons for which there is such data available, where a few species make up their staple diet resulting in low diversity indices for annual diets. But the species-items concentrated on change from month to month.

Evidence from this study suggests that while many foods are eaten as a result of their being abundant, others were actively selected more frequently than would have been predicted by their abundance alone. Similar trends have been recorded in studies of other species including *C. mitis* (Rudran, 1978a; Rudran, 1978b; Schlichte, 1978), *C. cephus* (Sourd & Gautier-Hion, 1986), and *C. aethiops* (Harrison, 1984).

Several studies have been carried out to investigate physical and nutritional factors influencing food choice among primates. For monkeys that feed extensively on fruits colour appears to play a role in their choice of food resources. Gautier-Hion et al (1985) showed that red, yellow and orange coloured fruits and succulent fruits were selected significantly more often than dull, dry dehiscent ones. On further analysis, it was found that these brightly coloured fruits had higher levels of water and sugar in them, thus colour might act as an indicator of nutritional value to foraging monkeys. Other studies have suggested that primates select foods on the basis of their nutritional value (Waterman, 1984) or at least, make choices to minimise intake of tannins, phenols and other toxic secondary plant compounds (Wrangham & Waterman, 1981). Beeson (1989) suggests that C. mitis in Malawi used only small quantities of particular fruits (with high fibre and tannin levels) in accordance with the hypothesis that monkeys will select against potential digestion inhibitors as outlined by Oates et al (1980).

As a group, guenons are very seldom recorded as feeding on immature fruits. Neither do they appear to be seed predators (Gautier-Hion, 1984). This would tend to support the hypothesis that Diana monkeys on Tiwai are exploiting immature fruits so extensively as a result of feeding competition with Colobines on the island.

A general assumption that is commonly made is that fruit is an abundant food resource with respect to forest guenons. As regards guenons on Tiwai, this is not an appropriate assumption. Frankie et al (1974b) discussed the differences in fruit production patterns between wet and dry forests, pointing out that the availability of mature fruit is lower in dry than in wet forests. Tiwai lies within a region of West African rain forest that experiences a distinct dry period within the year. This, combined with the vegetational structure of the island's forest, results in fruit being a very seasonal food resource, and thus would account for the very high degree of folivory of the monkeys on Tiwai compared with other guenon studies.

The relative scarcity of "preferred" foods available to the two study groups may result in both within- and between-group competition. From Wrangham's model of female-bonded primate groups (Wrangham, 1980) it is predicted that group-living primates will reduce within-group feeding competition by switching to more widely distributed resources such as leaves during periods when patchily distributed resources become scarce or unavailable. Diana monkeys would appear to be doing just that. According to Wrangham's model, between-group competition is expected to result in territoriality, or group dominance hierarchies. Thus, if Diana monkeys are territorial it is predicted that they would defend their access to these "preferred" food resources against other groups.

SUMMARY

1. The two study group home ranges were found to differ in species composition and relative abundance of particular tree species. Group E had a greater number of different species available to them in their home range area than did Group W.
2. From phenology records it was seen that the relative abundance of young leaves, flowers, fruits and seeds varies quite considerably throughout the year.

3. Diana monkeys appear to have an eclectic diet, feeding on foliage, flowers, fruits and seeds, and arthropods in varying amounts across the year, reflecting plant production cycles.
4. Both study groups were observed to select fruits and flowers when they were available. During periods of scarcity they changed their feeding behaviour, feeding on less patchily distributed food resources i.e. foliage, particularly mature leaves, and arthropods.

CHAPTER FIVE

RANGING BEHAVIOUR

5.1 INTRODUCTION

McNab (1963) proposed that home range area is dependent on body size, thus the area over which an animal foraged or hunted should be linearly proportional to its metabolic rate. More recently, Lindsfedt et al (1986) have demonstrated that home range size scales to body mass for carnivores, as for herbivores, supporting the hypothesis that animals select home range areas to fulfil their metabolic needs, and particularly to ensure their survival over periods of extreme environmental conditions. Other factors, including habitat productivity, and patterns of social organisation and behaviour are also likely to influence home range area for an animal or group. Similar results have been found in cross-species studies of primate home ranges (Mace et al, 1981), when considering gross categories such as folivorous versus frugivorous species. But in their comprehensive review Martin et al (1985) concluded that while ranging areas increased in excess of what might be predicted from the metabolic hypothesis, as yet this pattern has not been adequately explained.

Assuming that home range area is determined by an animal's metabolic requirements, it is not surprising that relationships exist between home range size, dietary habits, and metabolic needs (Harvey & Clutton-Brock, 1981). Thus it seems likely that food resources may influence primate ranging behaviour. A number of studies have shown that food resources can have a very strong influence on primate ranging patterns. In a study of Indri indri, ranging patterns reflected the distribution and availability of fruit and young leaves throughout the group's range (Pollock, 1977). Similar conclusions have been drawn from studies of Colobus badius (Marsh, 1981), Presbytis entellus (Curtin, 1982) and Hylobates lar (Raemaekers, 1980), to name but a few.

Distribution of food resources is not the only environmental factor found to influence primate ranging behaviour. Climatic factors can have a profound effect on animals' movement patterns: during periods of high rainfall, and high temperatures, primates tend to reduce their travel distances (e.g. Hylobates lar - Raemaekers, 1980; Colobus badius tephrosceles - Isbell, 1983; Cercocebus galeritus - Homewood, 1976).

Other limiting resources found to influence ranging patterns include the distribution of water holes (Harrison, 1983a), and sleeping sites. Primates occupying savanna regions are likely to need tall sleeping trees to protect them from nocturnal predators. Ranging behaviour in Yellow baboons (Rasmussen, 1979) and vervet monkeys (Harrison, 1983a) reflects these animals' need to secure safe sleeping sites. Studies of forest primates have also found that in some species, sleeping trees are important correlates of ranging behaviour (e.g. Kloss gibbon - Whitten, 1982a; banded langur - Bennett, 1983). Furthermore, habitat structure (Gautier-Hion et al, 1981), parasite avoidance (Freeland, 1980) and group size (Strier, 1987) have all been cited as determinants of ranging patterns, as have the presence of neighbouring groups (Struhsaker, 1974; Waser, 1974) and the need to patrol territorial boundaries (Dasilva, 1989).

In this chapter, ranging behaviour of Diana monkeys is described and environmental and social aspects likely to influence ranging behaviour are discussed.

5.2 METHODS

In the present study the term "home range" is defined as being any area entered by the study group at least once during the period they were being observed. It does not include any quadrats entered by the study groups while chasing neighbouring groups and/solitary animals.

Home range area was determined from data collected during all-day follows every month. Scan samples were taken at 20 minute intervals, and location and group dispersion recorded on a map at the same time. From these maps of the study groups' daily travel patterns it was possible to give estimates for:

home range area,
day range length, and
group spread.

5.3 HOME RANGE SIZE AND OVERLAP

Several studies have suggested that the magnitude of home range size estimates are influenced by the methods used to calculate them. Waser and Floody (1974) showed that the "arbitrary line around the most peripheral sightings" method gave a considerable overestimate of area used compared with the number of grid quadrats occupied. In her study of Colobus polykomos in Bia National Park, Ghana, Olson demonstrated that the observation time and grid size used was important with respect to home range area estimates (Olson, 1986). From the results, Olson concluded that 5-day follows and grid cells of 0.25ha (50m x 50m) gave reasonably accurate measures of home range area for this species and habitat. Although smaller quadrats are likely to give a more accurate assessment of home range size they are often impractical with respect to habitat structure, terrain, visibility and comparability with other field studies.

In the present study, home range area was estimated by summing the area of all quadrats entered by the groups until such a time when no new quadrats were entered. Although it is recognised that this method is likely to overestimate the area used, as a result of including areas of less than $50m^2$ that were never visited, it has the advantage of being easy to calculate, and is comparable with methods used in other studies.

Groups W and E were observed to enter a total of 158 and 146 quadrats respectively. Cumulative plots of quadrat use are presented in Figs. 5.1 & 5.2. Both graphs reach an asymptote after 11-12 months of data collection giving values of 39.5ha and 36.5ha, as home ranges for groups W and E.

In March 1988 few data were collected for W, giving a very low cumulative figure for that month. However, if the data from March 1989 are inserted in the "March" slot, the plot reaches an asymptote several months earlier, and gives a similarly shaped curve to that obtained for E. Consequently, it was decided to use the latter curve.

Both groups showed some degree of overlap in home range with those of neighbouring groups: of the 158 quadrats used by group W, 16.5% of them overlapped with neighbouring ranges, and E shared 28.8% of their 146 quadrats. However, within each group's range there was a region where other groups were never seen or heard. Home ranges and overlap zones are shown in Figs.5.3 and 5.4.

Fig. 5.1: Cumulative Use of Home Range Quadrats by Group W

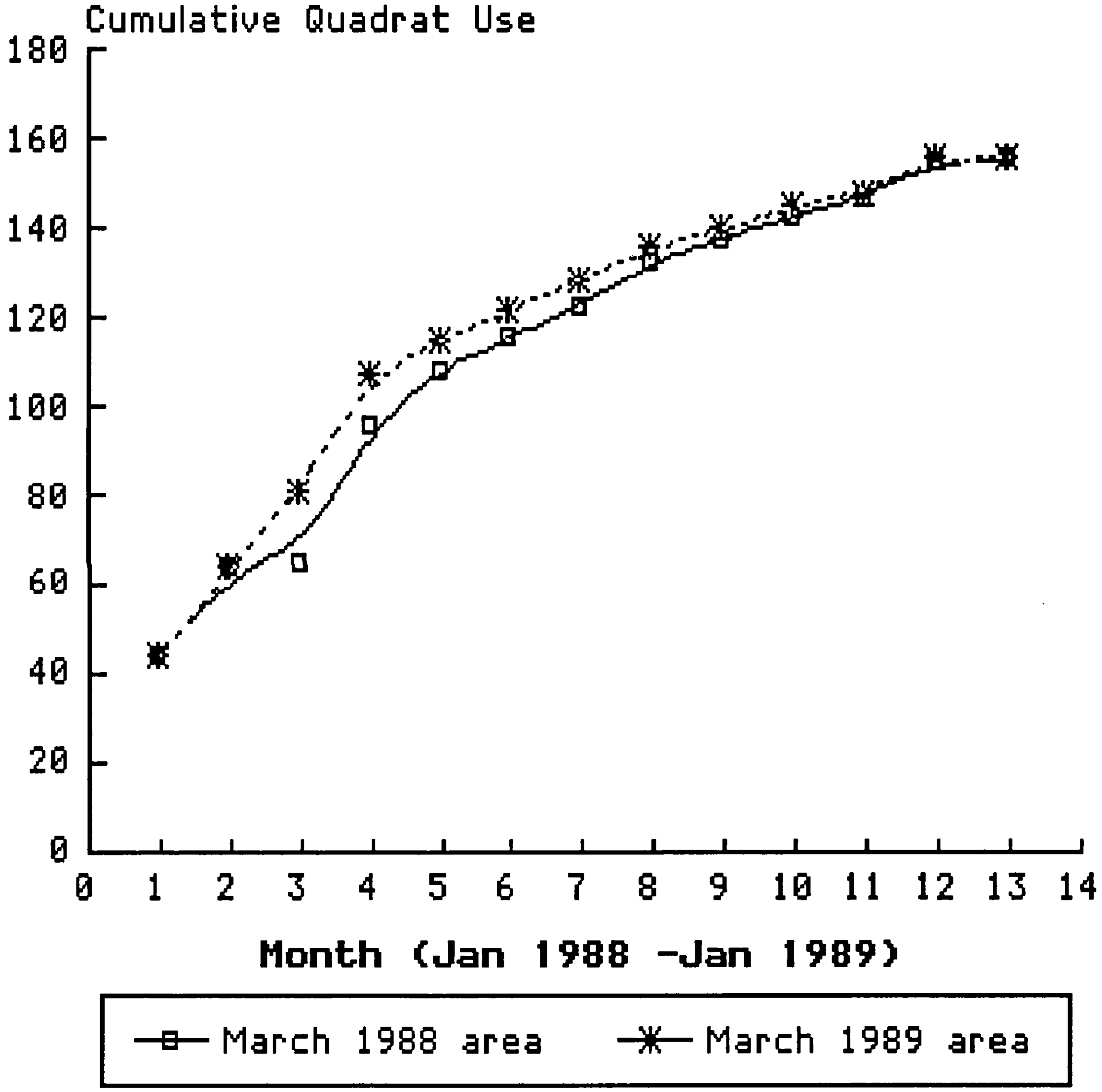
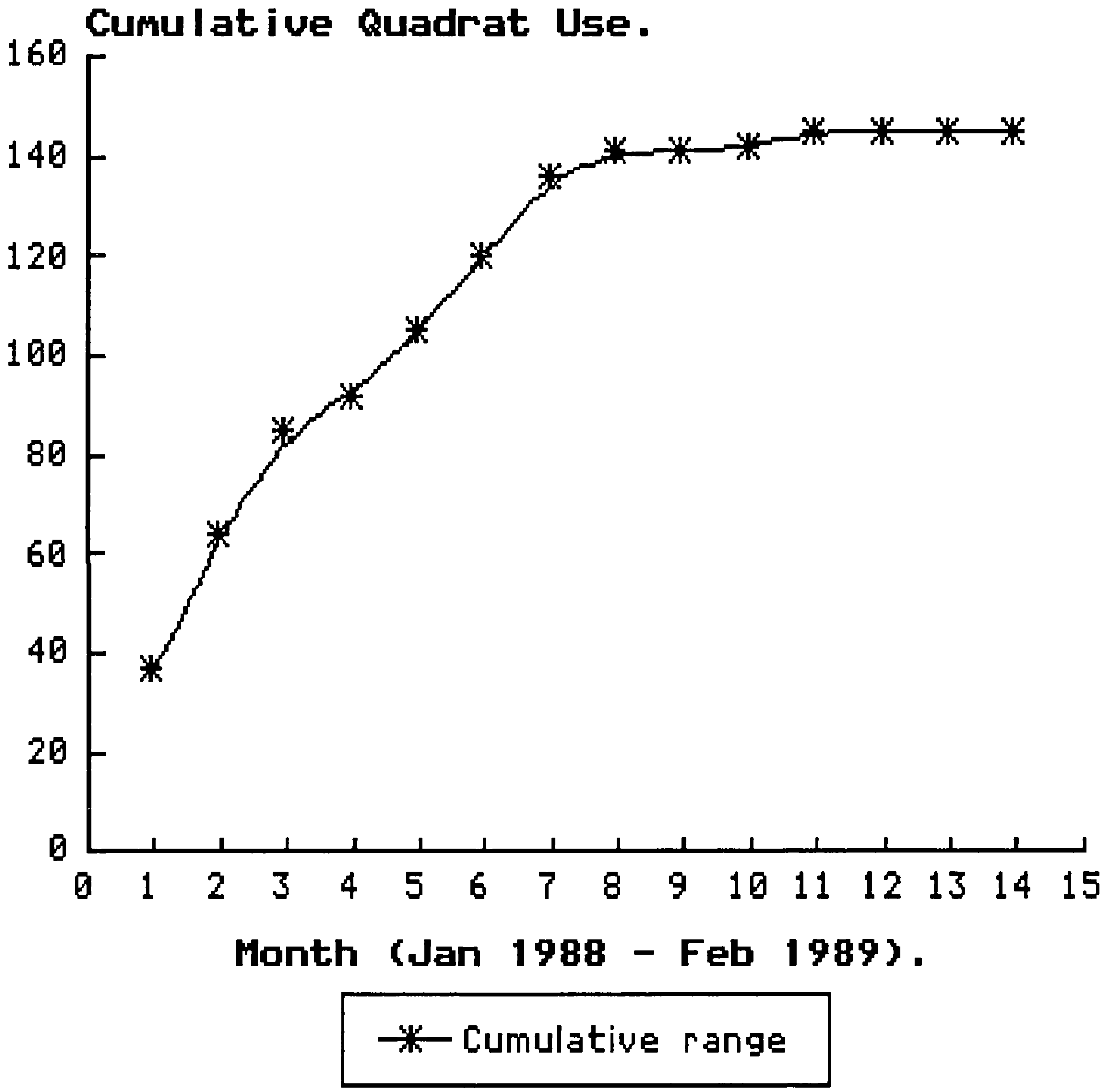


Fig. 5.2: Cumulative Use of Home Range Quadrats by Group E



In his study on Tiwai, Whitesides reported home range sizes of 41 ha for W and 29 ha for E. While the members of group W appear to have maintained the size of the area they occupy over the period covering the 2 studies (1983 -1989), group E appear to have expanded their range by 7.5 ha, as shown below.

Table 5.1: Home Range Estimates for Diana monkeys

	Whitesides (1989)	Present Study	Galat & Galat-Luong (1985)
W	41.0ha	39.5	93.0
E	29.0	36.5	

5.4 VARIATION IN DAY RANGE LENGTH

A number of different methods can be used to give a rough estimate of day range length. One way is to measure the movement of the study group's "centre of mass" between successive scans. An alternative method is to record the movement of a single individual being observed continuously or at very frequent intervals - this is impractical for an arboreal species because of problems of poor visibility. Both methods, and their underlying assumptions are discussed in Waser (1974) and Waser & Floody (1974).

It is important to remember that day range is only an estimate of the groups's lateral movements and does not take

Fig. 5.3: Group W Home Range - shaded areas indicate areas of overlap with neighbouring groups.

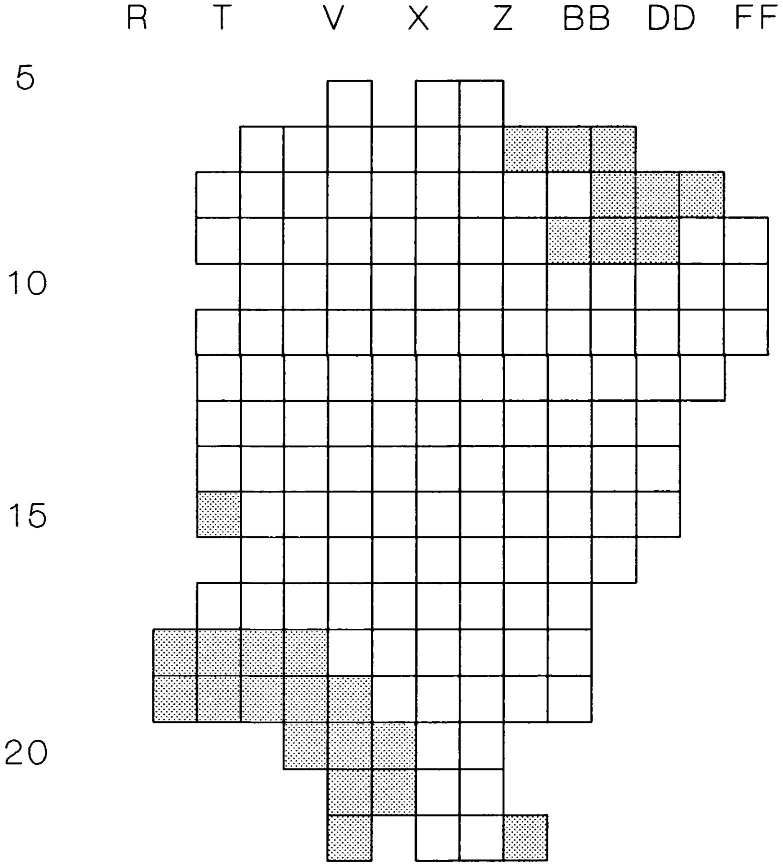
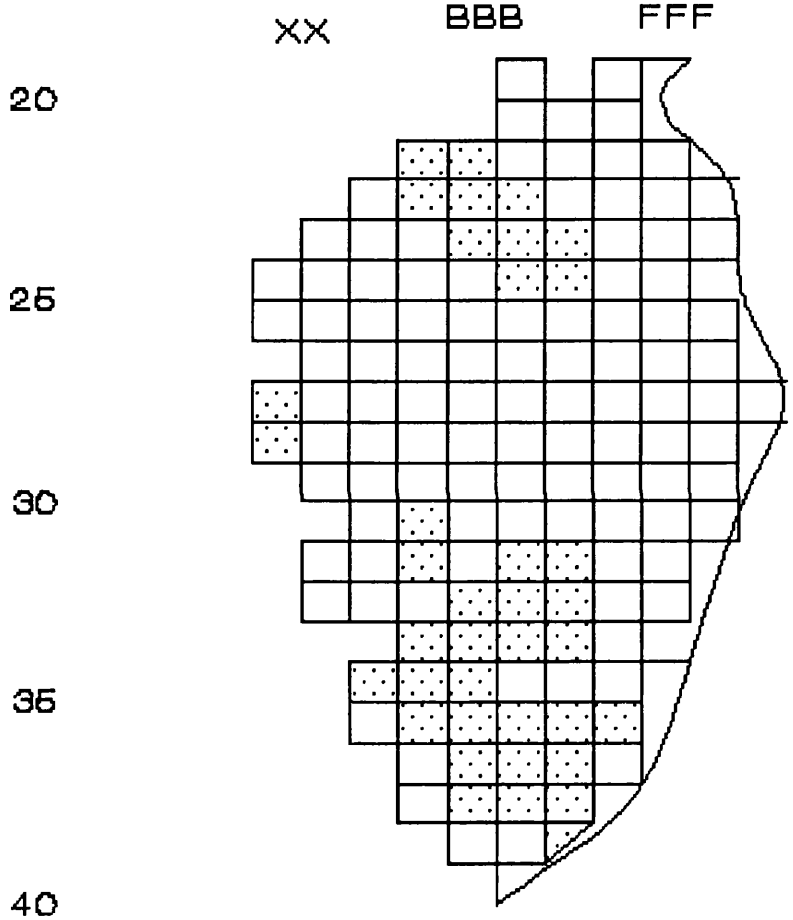


Fig. 5.4: **Group E Home Range - shaded quadrats indicate areas of overlap with neighbouring groups.**



into account their vertical movements within the forest. Although Diana monkeys do spend a large portion of their time in the tops of tall trees, they have also been observed at all levels in the forest, including the forest floor. Unlike red colobus, Diana monkeys do not travel in single file; instead they move through the forest in a large fluid mass, spread up to 200m across, making it very difficult to estimate the group centre.

For the purposes of this study daily distance travelled was calculated from location maps drawn up during follows. Similar methods to those used by Whitesides (1989) were employed. Group locations were sampled at 20 minute intervals, and distance travelled estimated by calculating the distance between the geometric centres of the grid cells occupied by the study group during consecutive sampling periods.

The results are presented below in Table 5.2. There is no significant difference in mean day range length between the two study sites (Mann Whitney, $z = -0.979$, $p > 0.164$).

Table 5.2: Mean Day Range Length.

	Present Study **mean & range**	N	**Whitesides (1989)** **mean & SE**
W	1575mday^{-1} (920 - 2730mday^{-1})	51	1018.9 +28.12mday^{-1}
E	1761mday^{-1} (730 - 3125mday^{-1})	48	1513.2 +63.72mday^{-1}

SE = standard error

On comparison with day range lengths from other studies 1575m and 1761m are similar to day range lengths quoted for other guenon species (Cercopithecus nictitans, home range = 67.0ha; day range = 1500m: C. pogonias, home range = 78.0ha; day range = 1750m, Struhsaker, 1969).

Day range is a measure of the linear distance travelled, but it is not necessarily indicative of the area visited. Number of quadrats visited in a day, when considered alongside day range length, gives a better indication of daily travel patterns, i.e. whether animals are travelling to many different parts of their range or doubling back on themselves, returning to regions visited earlier in the day. For this reason, "number of quadrats used per day" was also considered as a ranging parameter worth investigating, but because number of quadrats used was found to correlate strongly with day range length for both groups (W: r_s = +0.804, $P < 0.001$, $N = 52$; E: r_s = +0.764, $p < 0.001$, $N = 43$) it will be included in the analysis only where spatial ranging patterns are of interest.

5.5 MONTHLY VARIATION IN RANGE USE

Despite considerable day to day variation in day range length, monthly mean day range varies significantly across the year for both groups. This was tested using a Kruskal-Wallis one way analysis of variance (W, KW = 22.238, $p < 0.05$, df = 11; E, KW = 19.735, $p < 0.05$, df = 10). Quadrat use, time spent travelling and mean daily travel speed also varied significantly across the months, as illustrated in Figs 5.5, 5.6, 5.7, and 5.8, suggesting that Diana monkeys exhibit different ranging strategies at different times of year. However, the fact that there is no consistent pattern of monthly variation in day range between the two study groups ($r_s = +0.333$, $p > 0.05$, N = 9) may be indicative that the two groups were subject to different environmental and or social pressures during this study.

5.6 DETERMINANTS OF RANGING BEHAVIOUR

Ranging behaviour in Diana monkeys can be considered as having two different types of influence. One is the temporal or seasonal aspect of ranging which is linked to climatic factors, particularly rainfall and maximum temperature, their influence over phenological cycles of

Fig. 5.5: Mean Day Range Length and Number of Quadrats Visited Across the Year - Group W

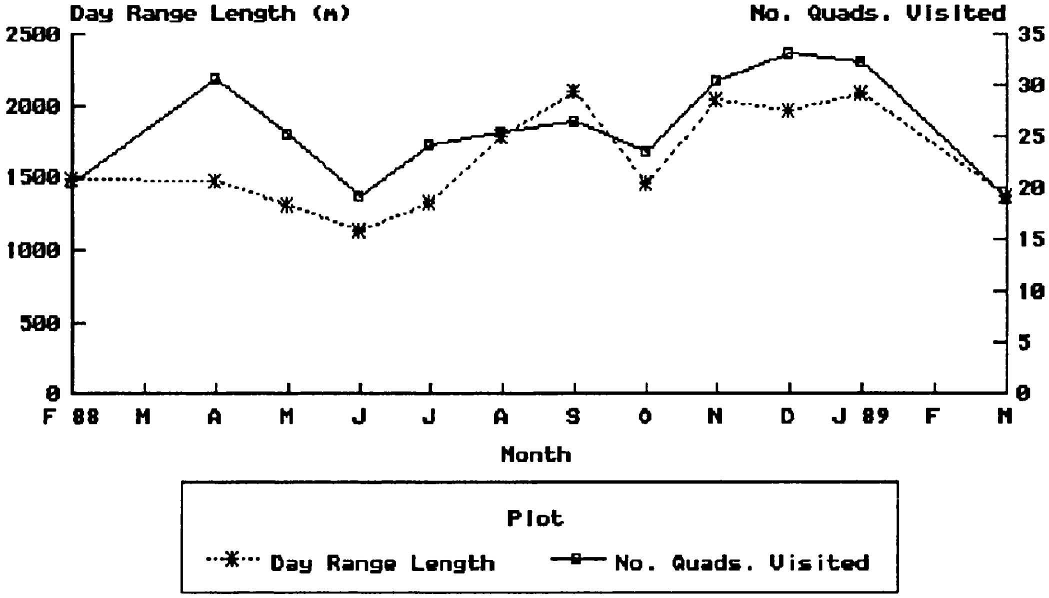


Fig. 5.6: Mean Day Range and Number of Quadrats Visited Across the Year - Group E

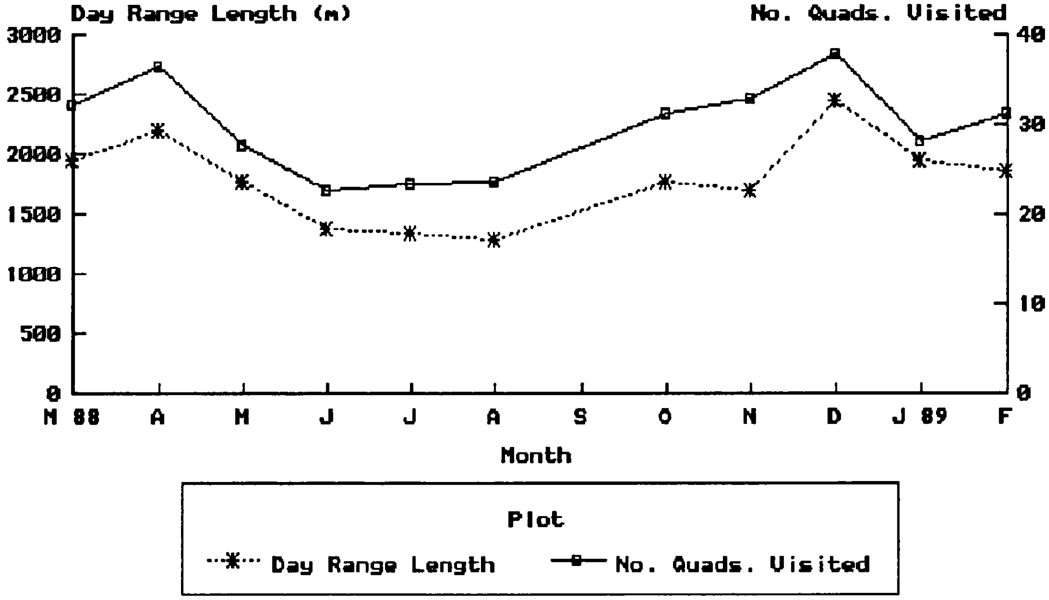


Fig. 5.7: Mean Percentage Time Spent Travelling and Mean Speed of Travel - Group W

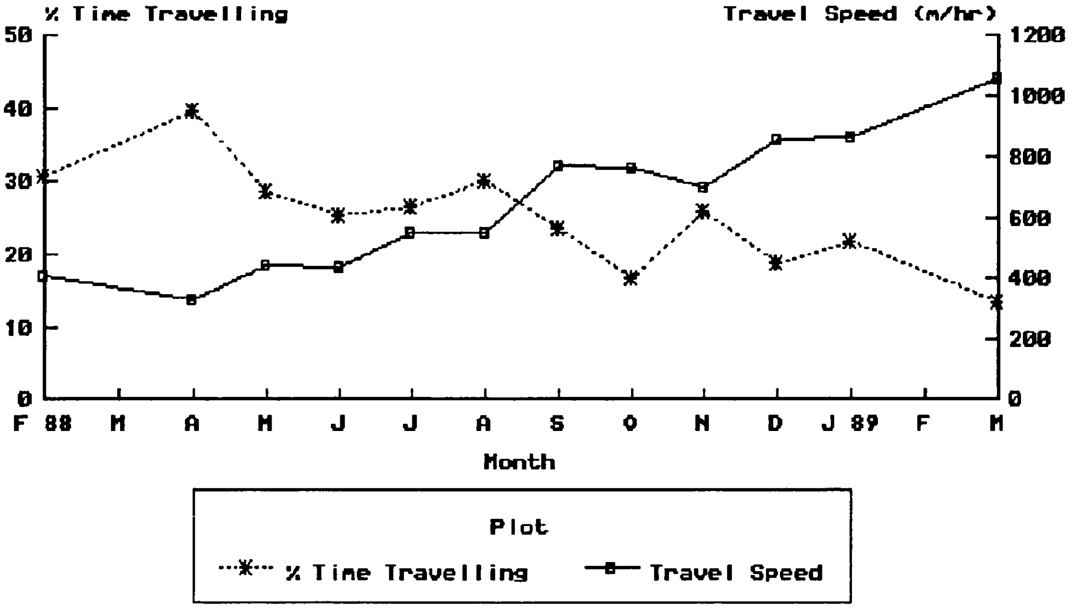
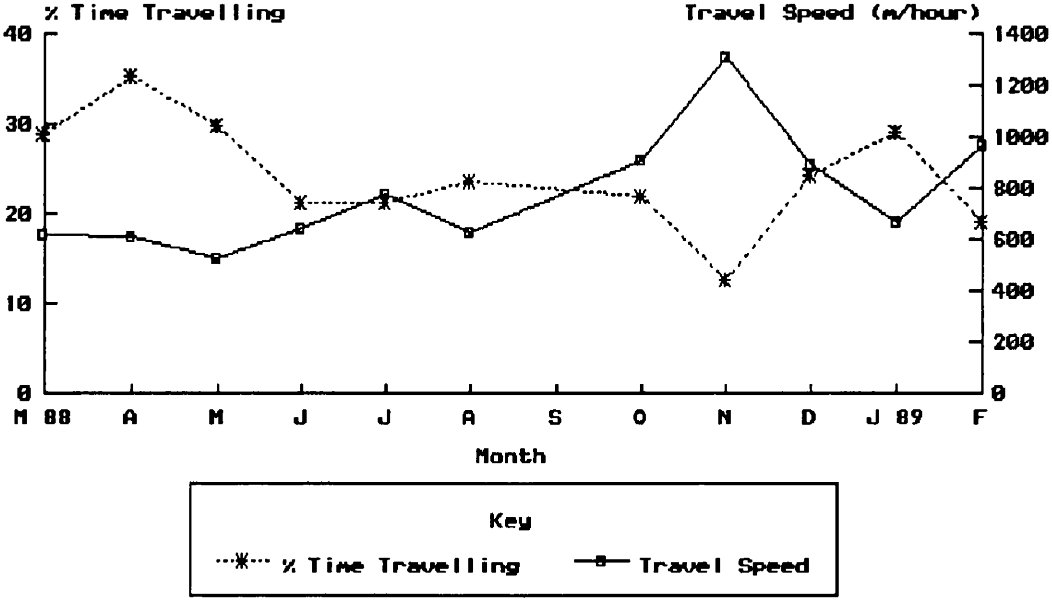


Fig. 5.8: Mean Percentage Time Spent Travelling and Mean Speed of Travel - Group E



food species, and possibly such things as the timing of mating and hence breeding seasons, which may determine relationships between neighbouring groups. Second is the spatial aspect: the geographical distribution of particular resources such as food, water and sleeping sites, may determine, at least in part, how the monkeys use their home range area. Obviously these two aspects are closely interwoven, and operate in conjunction with one another. But for the purposes of this chapter, "time" and "space"will initially be treated separately in an attempt to isolate any general factors that exert a strong influence on ranging behaviour across the seasons, and how these then influence the study animals' patterns of range use.

Climate

Other studies of primate ranging behaviour have reported that day range length is shorter in the wet season than in the dry (Colobus polykomos - Dasilva, 1989), and during the hot season (Cercocebus galeritus - Homewood, 1976). Interestingly, on comparing mean day range lengths between the 3 wettest (June - August)[1] and 3 driest months (January - March) it was found that animals in group E had significantly shorter day ranges during the wet period compared with the dry season (Mann-Whitney: z = 2.2887,

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[1] Based on Tiwai weather data collected during the study and presented in Chapter Two, Section 2.2.

$p < 0.002$, $m = n = 12$). However, when considering hot (March - May) versus cool months (November - January) members of group W travelled significantly further during the cooler part of the year than during the hot season (Mann-Whitney: $z = 3.575$, $p < 0.001$, $M = 12$, $N = 13$), whereas there was no significant difference in the distances travelled by members of E.

Rather than interpreting these results as the two groups responding differently to climatic conditions, or that they are spurious results and climatic conditions have no influence on ranging behaviour of Diana monkeys, I would suggest that they support the idea that while climatic effects are important to the animals, possibly they influence their behaviour more through their effects on forest productivity cycles. However, from observation it was obvious that on days when it rained heavily, Diana monkeys spent most of their day huddled in dense liana tangles, and did not travel any great distance. During very heavy rain storms it seems likely that it could be dangerous for monkeys to continue travelling: visibility was restricted, and the branches wet and slippery, making travelling during such extreme weather conditions hazardous.

To conclude, while heavy rain and extreme heat affect Diana monkey ranging behaviour, it would appear that there are other factors that probably play a more direct role in determining their ranging strategies.

Food Resources

In the previous chapter it was shown that while Diana monkeys have a considerable amount of foliage in their diets, they do feed on preferred or selected foods, namely certain species of fruits, seeds and flowers, whenever available. The major species used for foliage and arthropod feeding include Cynometra leonensis, Piptadeniastrum africanum and Landolphia hirsuta, all common species within the Tiwai forest. In contrast, many of the species used for fruit-, flower-, and seed-eating are very much less common, and are far less evenly distributed within the study groups' home ranges. This, combined with lack of synchrony in fruiting patterns of several of these species presents the monkeys with the problem of temporally and spatially patchy food resources. Consequently, one might predict that, as with other species such as Hylobates lar (Raemaekers, in Clutton-Brock, 1977c) and Cercopithecus sabaeus (Harrison, 1983a), Diana monkeys should exhibit greater day ranges in those periods when they are exploiting patchily distributed fruits and flowers.

Although there were no significant correlations between day range length and percentage fruits and seeds in the diet, group E did show a significant positive correlation between percentage flowers and day range ($r_s = +0.725$, $p < 0.01$, $N = 11$, one-tailed) as predicted. Interestingly, there was also a significant correlation between the mean number of quadrats visited per month and percentage of fruit in the diet ($r_s = + 0.761$, $P < 0.005$, $N = 11$, one-tailed), suggesting that when Diana monkeys were using patchily dispersed resources they travelled directly between food patches, and did not double-back on themselves, as they were often seen to do when "browsing" on leaves or searching for insects amongst the canopy foliage.

Day range and number of quadrats visited were compared between the top three fruit-eating months and the top three foliage/arthropod feeding months to determine whether animals travelled further during months when fruits and flowers made up most of that month's diet.[2] Neither measure of area visited was significantly greater for months when fruit or flowers predominated. However, when a similar analysis was carried out to investigate whether mean daily travel speed differed according to diet it was found that group E travelled faster when feeding on preferred fruits etc, than they did when concentrating on leaves and arthropods ($z = 2.711$, $p < 0.01$, $m = 10$, $n = 11$).

There are several plausible explanations for this:

1. Travel speed may reflect a difference in ranging strategy, i.e. when feeding on discrete, dispersed food patches Diana monkeys may move directly and quickly

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[2] Group W: top 3 fruit/flower months were October, December and March; top 3 foliage/arthropods months were February, May and August. Group E: top 3 fruit/flower months were November, December and February; top 3 foliage/arthropod months were March, April, and July.

between them. Conversely, when foraging for leaves and insects, monkeys might move more slowly, and with less direction, browsing as they travel.

2. Alternatively, travel speed may reflect energetic constraints (see Pyke, 1981). When exploiting high energy foods such as fruits and flowers Diana monkeys may be able to maintain higher travel speeds than at times when their energy intake is lower, as might be the case when eating a lot of leaves.

One way to test whether the second alternative is likely or not is to compare mean travel speeds between the two study groups. If energetic constraints are important here then one would expect that group W would exhibit lower travel speeds than E, considering their different dietary patterns as discussed in Chapter Four[3]. Using a Mann-Whitney U test there was no significant difference between the two groups. While this does not necessarily exclude the possibility that energetic constraints are important in determining travel speeds, in this context, it would suggest that foraging patterns may be the main constraint on travel speeds. Overall, it would seem that food resources do exert some influence on ranging behaviour in Diana monkeys. The results differ somewhat between the two groups, but this can be explained as a consequence of differences in food resources available to the study groups.

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[3] Group W - 39.9% of diet from flowers, fruits and seeds.
Group E - 57.2% of diet from flowers, fruits and seeds.

Neighbouring Groups

Within the literature there are several reports of daily ranging behaviour being influenced by the proximity of neighbouring groups and/or the numbers of intergroup encounters. Peres (1989) reports that golden-lion tamarins spent more time moving and less time feeding, and resting during intergroup encounters than in non-encounter contexts. Within the home range of a group of Diana monkeys there appears to be an area used exclusively by the resident group. Possibly these monkeys patrol their range boundaries to maintain the integrity of this exclusive zone. If so, then ranging behaviour is likely to reflect changes in patrolling in response to the threat of encroachment by neighbouring animals.

Adult male Diana monkeys, like males of other guenon species, give distinctive loud calls, that can travel distances in excess of 1000m through the forest. These male loud calls are traditionally thought to have a spacing function, as with other species. Intergroup encounters were very rarely seen, therefore numbers of outgroup male loud calls were used instead to assess how activities of neighbours might influence ranging behaviour in groups W and E.

There were no significant correlations found between mean day range and mean number of outgroup calls heard, but in both groups non-significant but predicted trends were seen, i.e. day range tended to increase in months when outgroup calling rates were highest. Possibly correlations are weak because these data are not appropriate for measuring effects of neighbours on group ranging - in some species, location of neighbouring calls determines whether or not the recipient will respond (Mitani, 1985d; Whitehead, 1989). As location was disregarded in this analysis this may explain the inconclusive results. However, there is a significant difference in area visited between the months when outgroup calling rates were highest (August, December, and March for group W; March, April and May for group E) compared with those when it was lowest (February, June and September for group W; June, July and August for group E), supporting the hypothesis that neighbouring groups do influence Diana monkey ranging behaviour (W: $z = 1.976$, $p < 0.05$, $m = 11$, $n = 12$; E: $z = 3.387$, $p < 0.0005$, $m = 12$, $n = 12$).

Therefore, it would appear that climate, distribution of food resources, and presence or activities of neighbouring groups all play an influential role in ranging behaviour in Diana monkeys. But the above analyses do not give any clear indication of how important the various factors may be in relation to one another i.e. do one or two variables influence ranging patterns more strongly than any others? In an attempt to distinguish further what factors determine ranging behaviour in Diana monkeys on Tiwai a step-wise multiple regression analysis was carried out using SPSS PC+

(version 3.0).

Regression Analysis

Two ranging parameters, day range and number of quadrats visited, were tested separately against monthly rainfall and mean maximum temperature, percentage fruit/seeds and percentage flowers consumed, and mean number of outgroup loud calls heard. When day range was the dependent variable the results did not prove very informative. But area visited, i.e. number of quadrats entered, proved more interesting.

Group W's results are shown in Table 5.3. The first variable selected was maximum temperature, accounting for 44.5% of the variance: the other variable to be pulled out was rainfall, accounting for a further 32.0% of the variance. No further variables were selected.

Group E's results are presented in Table 5.4. Here, percentage fruit/seeds eaten was selected as the first variable, accounting for 51.7% of variance; rainfall was the second variable, accounting for 23.1% of variance. Again, no other variables were selected as having a significant influence on monthly ranging patterns.

Rainfall was selected as an important variable for both groups. The differences between the two groups could result

Table 5.3 Results of a Step-wise Multiple Regression Analysis of Ranging Parameters - Group W

Dependent Variable: Number of Quadrats Visited

1. Maximum Temperature

R square	0.44516
Adjusted R square	0.38968
Standard Error	4.26063

2. Rainfall

R square	0.76491
Adjusted R square	0.71267
Standard Error	2.923338

Variables in the equation:

	B	SE B	Beta	T	Signif. T
Max. Temp.	-1.97960	.37303	-0.98064	-5.307	0.0005
Rainfall	-0.02265	6.47479E-03	-0.64652	-3.499	0.0067
Constant	88.79554	11.76982		7.544	0.0000

Table 5.4: Results of a Step-wise Multiple Regression Analysis of Ranging Parameters - Group E

Dependent variable: Number of Quadrats Visited

1. Percentage Fruit in Diet

R square	0.51656
Adjusted R square	0.46284
Standard Error	3.76324

2. Rainfall

R square	0.74821
Adjusted R square	0.68526
Standard Error	2.88063

Variables in the equation:

	B	SE B	Beta	T	Signif. T
% Fruit	.17496	.04833	.64894	3.620	.0068
Rainfall	-.01712	6.31220E-03	-.48633	-2.713	.0265
Constant	26.73676	2.15691		12.396	.0000

from differences in forest structure between the two study sites (see Chapter Four, Section 4.3). There was less fruit available to group W throughout the study - possibly fruit availability was so low that it has a negligible effect on their overall ranging patterns. The forest within group W's range was more disturbed, and thus the canopy more broken, than in group E's range - in the absence of fruits as an important determinant of ranging behaviour, possibly lack of complete canopy cover results in temperature becoming important in influencing movement patterns.

To conclude, while weather and distribution of food resources appear to influence ranging behaviour most strongly across the year, there is evidence that Diana monkeys need to monitor neighbouring groups and probably patrol their range boundaries and that these factors also influence patterns of range use.

5.7 PATTERNS OF RANGE USE

Many studies of ranging behaviour in mammals have demonstrated that animals do not use all areas of their home ranges equally (Martinsen, 1968; Rasmussen, 1979). Instead, they tend to use some areas in preference to others - those areas receiving concentrated use by residents have been termed "core areas" as in Samuel et al (1985).

Fig. 5.9: Group W - Home Range Core Area - Frequency of Visits per Quadrat

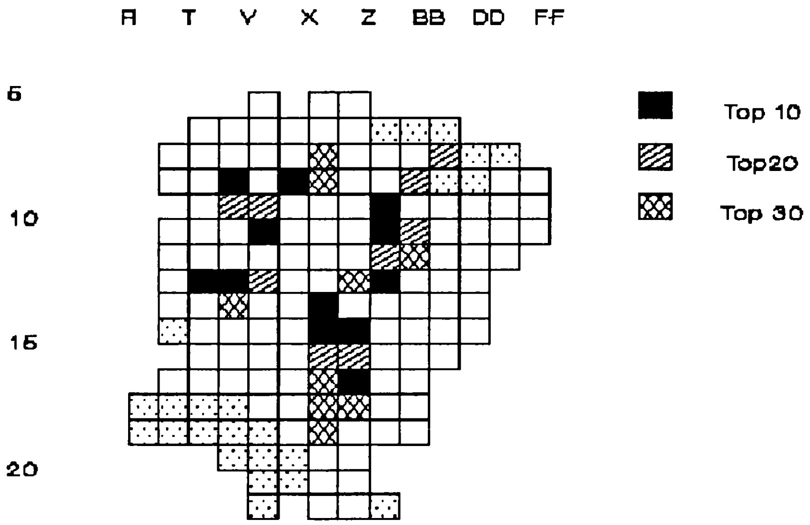


Fig 5.10: Group E - Home Range Core Area - Frequency of Entry of Quadrats

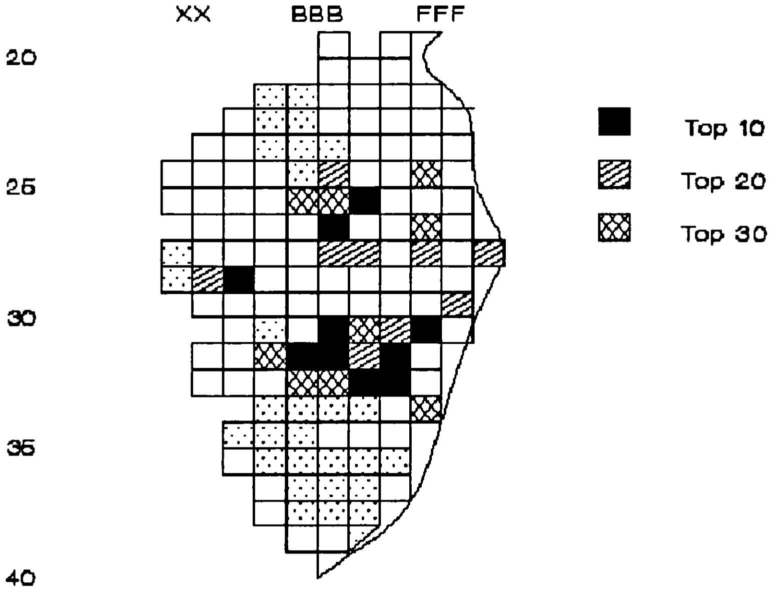


Fig. 5.11: Group W - Home Range Core Area - Number of Monthly Visits

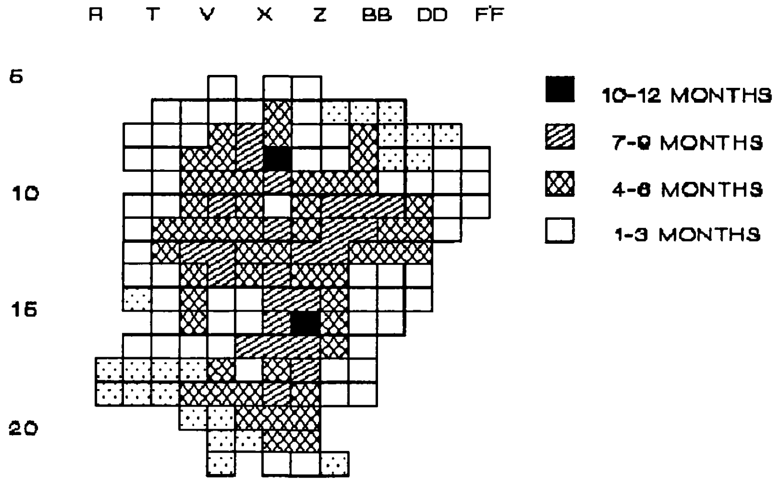


Fig. 5.12: Group E - Home Range Core Area - Number of Monthly Visits

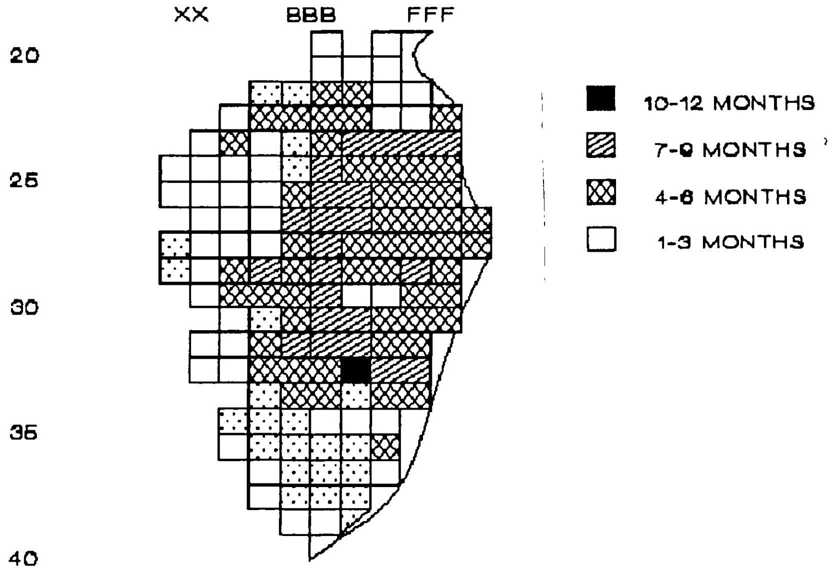


Fig. 5.13: Group W - Home Range Core Area - Number of Daily Visits per Quadrat.

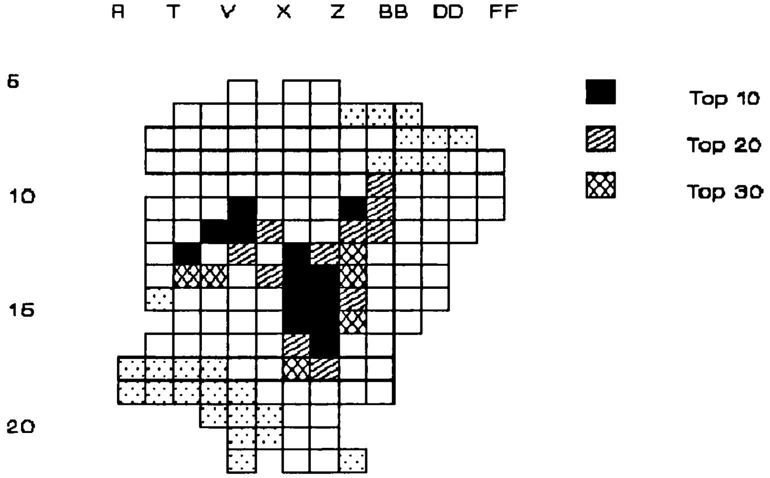
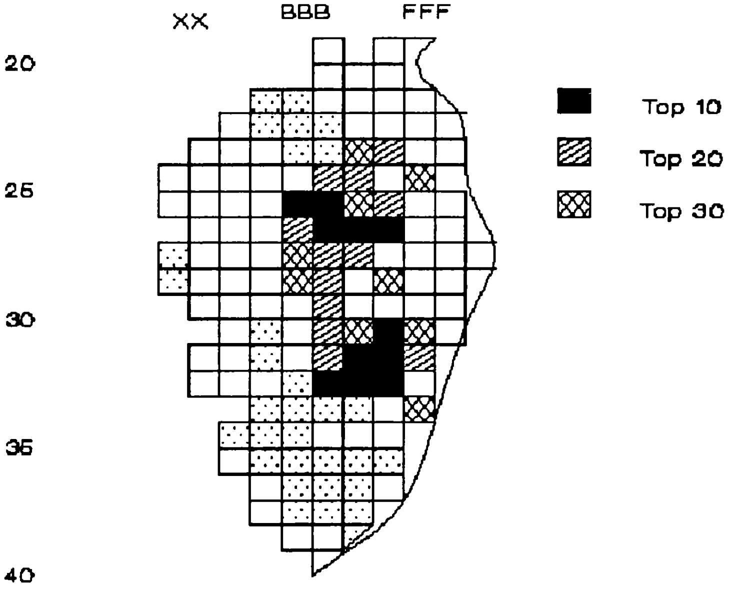


Fig. 5.14: Group E - Home Range Core Area - Number of Daily Visits per Quadrat



In an attempt to determine whether Diana monkeys have "core areas" within their ranges, range quadrats were ranked according to

1. how frequently the resident group entered them (Fig.5.9 - 5.10),
2. during how many months of the year they were used, (Fig.5.11 -5.12), and
3. how often they were entered on a daily basis (Fig. 5.13 - 5.14).

Of the three methods used, only the last, i.e. number of daily visits per quadrat, gave any indication that Diana monkeys might have a core area within their home range.

Interestingly, from the maps (Figs. 5.9 - 14) quadrats within, and close to, overlap zones, appear to have been used more frequently than others, and boundaries where no overlap region had been identified used far less than others. Whether this concentration of activity in and around overlap zones results from a need to monitor other groups and maintain a high profile in areas of contested ownership, or because they are regions of high quality resources, and thus worth contesting, is not known.

In the previous section it was demonstrated that food resources, most particularly fruit and seed resources, correlate with and probably influence ranging patterns, at least in group E. Therefore, it would seem possible that the spatial distribution of such resources might influence patterns of range use by these animals, along with the spatial distribution of other resources, such as water, sleeping sites, and calling sites.

Water resources

Diana monkeys were never observed to drink from the river or standing water in tree trunks, or pools. Occasionally, they were seen lapping water drips from the underside of small branches and twigs after rain storms, or in the early morning after a heavy dew. However, water is unlikely to have been a limiting resource: only in arid and semi-arid environments does water seem to influence primate ranging behaviour (Rasmussen, 1979; Harrison, 1983a), thus it will not be considered further in this analysis.

Sleeping sites

Distribution of sleeping sites has been reported as influencing ranging behaviour in a number of species, including _Cercocebus albigena_ (Freeland, 1980) and _Papio cynocephalus_ (Rasmussen, 1979). Unlike _Colobus polykomos_ (Dasilva 1989) and gibbons and siamangs that live in small or family groups, where all group members are able to sleep in a single large tree together, Diana groups are too large. They tend to sleep in small groups distributed up to 100m

Fig. 5.15: Group W - Sleeping Sites Used Throughout the Year

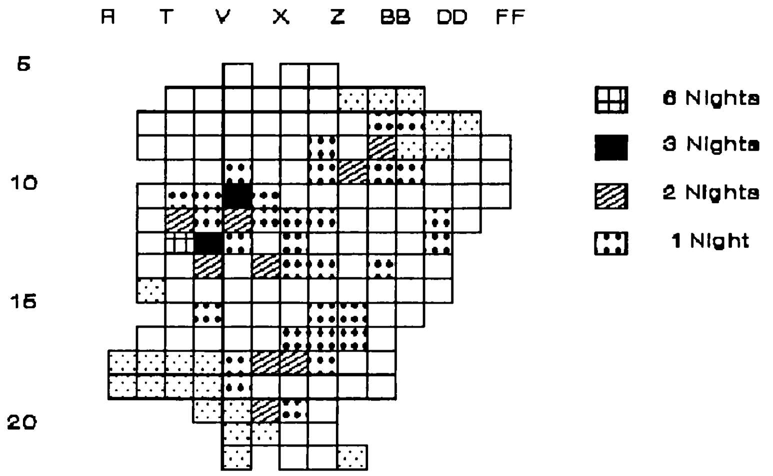
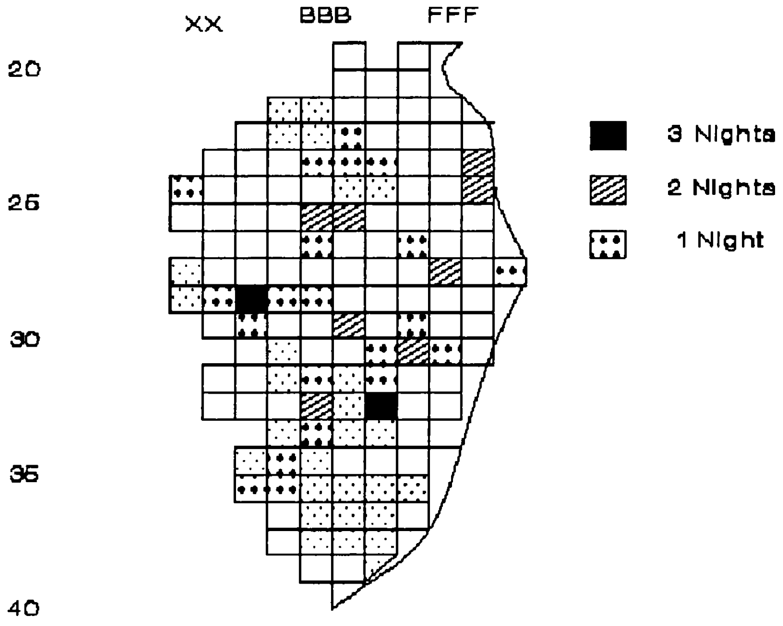


Fig. 5.16: Group E - Sleeping Sites Used Throughout the year



apart, and do not appear to have specific sleeping trees that they frequently return to.

Sleeping sites are illustrated for the two groups, in Figs 5.15 & 5.16. Sleeping sites were distributed throughout much of the respective ranges, though they tended to avoid boundaries, except in overlap regions. During the late afternoon animals tended to leave their afternoon resting sites in small groups led by adult females, and make their way through the forest at a leisurely pace towards the last feeding site of the day. Whether feeding was constrained by where they wanted to sleep, or vice versa, is questionable. But, it seems more likely that they slept wherever they finished their last feeding bout, providing there were adequate numbers of suitable large trees in the vicinity. On occasions where they were feeding in farmbush or in low, scrubby, secondary forest they would move quickly into the nearest large trees as the sun went down.

Generally though, and especially during periods when fruits and seeds were available to them, they would start the day feeding in large fruit trees, move away as the morning warmed up, and then return to the same spot in the late afternoon to feed prior to settling down for the night. As shown in Chapter Three (Section 3.7), Diana monkeys have a tendency to feed on high energy foods such as fruits and flowers during the early morning. Their ranging patterns ensured that they were close to such foods, suggesting that sleeping sites were more likely to have been determined by feeding patterns than the converse. Similar results were obtained by Chapman et al (1989) in their study of multiple central place foraging where spider monkeys were observed to sleep in the nearest suitable site to the particular food source they were exploiting.

Food resources

Numbers of food trees per quadrat was found to correlate with frequency of use ($z = 2.749$, p , 0.005, $N = 120$; E: $z = 4.887$, $p < 0.001$, $N = 111$); however, there was also a significant correlation between number of large trees per quadrat and frequency of use (W: $z = 2.531$, $p < 0.01$, $N = 120$; E: $z = 3.765$, $p < 0.001$, $N = 111$). Rather than interpret this as conclusive evidence that quadrat use is associated with food resources available, I would argue that it is more an indication of habitat preference. Diana monkeys prefer mature, undisturbed forest, and because they feed extensively on common species, particularly during periods of shortage, the results obtained are not surprising. Instead, less common, selected species of fruits, seeds and flowers might be more likely to influence range use, at least at times of year when they predominate within the diet.

Call sites

Calling sites were distributed throughout much of the two groups' respective range areas, but appeared to be concentrated around overlap zones and in other areas used very frequently as shown in Figs.5.17 and 5.18. As with sleeping sites, calling sites are not found particularly close to boundaries, except those shared with neighbouring groups, and seem to coincide with core areas. It is difficult to separate out whether they enter quadrats frequently in order to call from them, or whether they call from wherever they happen to be; though from observation they appear to do the latter.

In an attempt to determine whether distribution of food resources, location of sleeping and calling sites, and the need to monitor neighbouring groups and/or patrol range boundaries, are important determinants of ranging behaviour in Diana monkeys a step-wise multiple regression analysis was carried out.

Fig. 5.17: Group W - Call Sites Used Throughout the Year

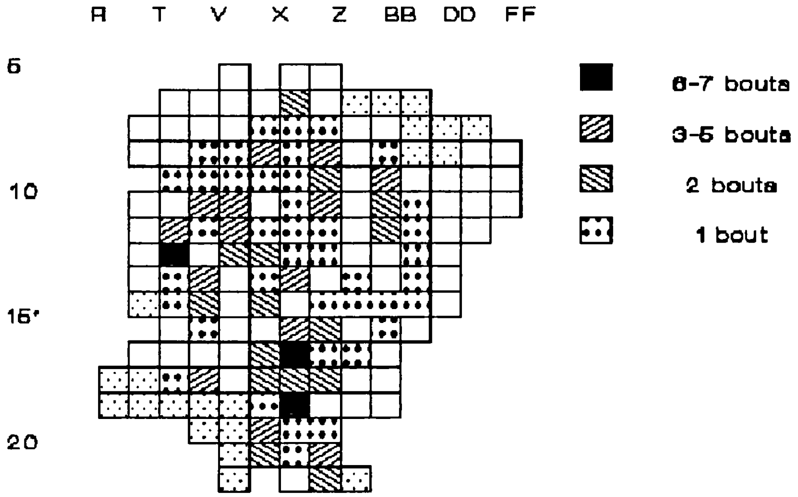
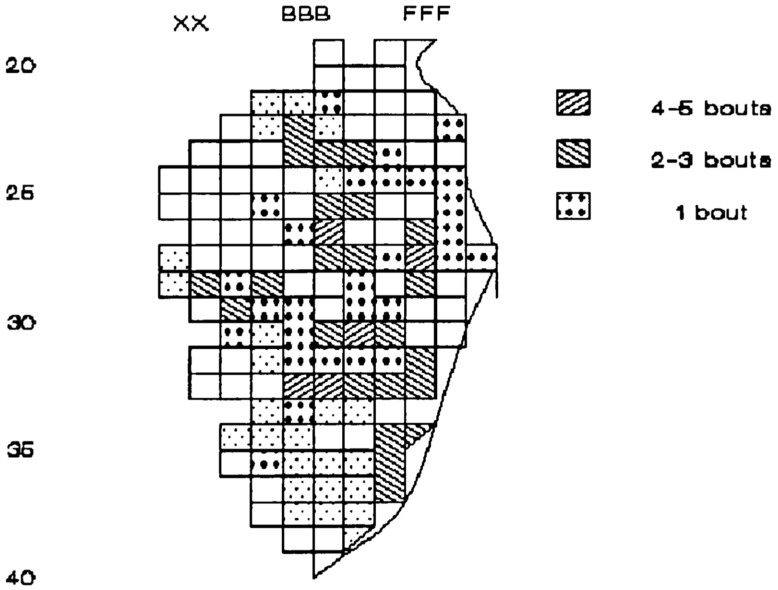


Fig. 5.18: Group E - Call Sites Used Throughout the Year



Regression Analysis

For each home range quadrat the following variables were determined:

1. frequency of entry,
2. number of times the resident group slept there,
3. number of times they called from that quadrat,
4. number of potential fruit- and seed-bearing trees present,
5. number of trees that provided them with flowers, and
6. distance from the boundary.

Frequency of quadrat entry was considered to be the dependent variable; the others, the independent variables. The data were analyzed by month for each group. The results are summarised in Table 5.5 and 5.6.

Table 5.5: Results of a Step-wise Multiple Regression Analysis of Ranging Parameters - Group W

Dependent variable: Frequency of use of quadrat

April 1988

1. Call Site

R square	0.14508
Adjusted R square	0.12371
Standard Error	3.10397

Variables in the equation:

	B	SE B	Beta	T	Sig. T
Call Site	2.68504	1.03058	.38089	2.605	0.0128
Constant	2.49606	0.52741		4.733	0.0000

May 1988

1. Sleeping Sites

R square	0.40871
Adjusted R square	0.39315
Standard Error	4.54766

2. Distance to Boundary

R square	0.48343
Adjusted R square	0.45550
Standard Error	4.30768

Variables in the equation:

	B	SE B	Beta	T	Sig T
Sleeping Site	10.92744	2.06157	.62694	5.301	0.0000
Dist. Boundary	-0.02154	9.31187E-03	-.27363	-2.313	0.0264
Constant	6.05761	1.41265		4.288	0.0001

June 1988

1. Call Site

R square	0.20030
Adjusted R square	0.18430
Standard Error	2.43189

Variables in the equation:

	B	SE B	Beta	T	Sig T
Call Site	2.51064	0.70946	.44755	3.539	0.0009
Constant	3.02619	0.38104		7.942	0.0000

Table 5.5: Results of Regression Analysis ctd.

July 1988

1. Call Site

R square	0.08865
Adjusted R square	0.06840
Standard Error	1.57898

Variables in the equation:

	B	SE B	Beta	T	Sig T
Call Site	1.17112	0.55974	0.29775	2.092	0.0421
Constant	2.20865	0.24494		9.017	0.0000

August 1988

No variables selected.

September 1988

1. Call Sites

R square	0.23152
Adjusted R square	0.19811
Standard Error	3.29346

Variables in the equation:

	B	SE B	Beta	T	Sig T
Call Sites	6.39130	2.42797	0.48117	2.632	0.0149
Constant	2.60870	0.68673		3.799	0.0009

October 1988

1. Call Site

R square	0.23219
Adjusted R square	0.21512
Standard Error	2.46226

2. Sleeping Sites

R square	0.39214
Adjusted R square	0.36451
Standard Error	2.46226

Variables in the equation:

	B	SE B	Beta	T	Sig T
Call Sites	3.56522	0.81178	0.51835	4.392	0.0001
Sleeping Sites	6.07971	1.78675	0.40160	3.403	0.0014
Constant	3.42029	0.40136		8.522	0.0000

Table 5.5: Results of Regression Analysis ctd

November 1988

No variables selected.

December 1988

No variables selected

January 1989

1. Distance to the Boundary

R square	0.12839
Adjusted R square	0.10984
Standard Error	2.44660

2. Flowers - location of

R square	0.29521
Adjusted R square	0.26456
Standard Error	2.22383

3. Sleeping Sites

R square	0.36822
Adjusted R square	0.32610
Standard Error	2.12876

Variables in the equation:

	B	SE B	Beta	T	Sig T
Dist. Boundary	0.01797	4.86018E-03	0.45835	3.697	0.0006
Flower Trees	0.28174	0.07519	0.46837	3.747	0.0005
Sleep. Sites	1.83475	0.80455	0.27527	2.280	0.0274
Constant	-.68028	0.91075		-.747	0.4590

March 1989

No variables selected.

Table 5.6: Results of a Step-wise Multiple Regression Analysis - Group E

March 1988

No variables selected.

April 1988

No variables selected.

May 1988

No variables selected.

June 1988

1. Distance from Boundary

R square	0.20938
Adjusted R square	0.19256
Standard Error	1.58804

2. Fruit Trees

R square	0.29378
Adjusted R square	0.26307
Standard Error	1.51712

3. Call Sites

R square	0.37855
Adjusted R square	0.33712
Standard Error	1.43888

Variables in the equation:

	B	SE B	Beta	T	Sig T
Dist. Boundary	-0.01187	2.77911E-03	-0.50630	-4.272	0.0001
Fruit Tree	0.09971	0.03829	0.30882	2.604	0.0124
Call Site	1.16865	0.47169	0.29180	2.478	0.0170
Constant	4.30438	0.60540		7.110	0.0000

July 1988

No variables selected.

August 1988

No variables selected.

October 1988

No variables selected.

November 1988

No variables selected.

December 1988

```
1. Sleeping Sites
R square               0.27065
Adjusted R square      0.25763
Standard Error         1.60788

2. Distance from Boundary
R square               0.33070
Adjusted R square      0.30636
Standard Error         1.55421

Variables in the equation:

                    B        SE B       Beta    T       Sig
                                                         T
Sleep. Sites  3.90690     0.74968 0.64315     5.211    0.0000
Dist. Bound. 4.420334E-03, 1.98994E-03, 0.27414, 2.221, 0.0305
```

February 1989

```
1. Distance from Boundary
R square               0.29881
Adjusted R square      0.28171
Standard Error         1.29982

2. Call Sites
R square               0.36980
Adjusted R square      0.33829
Standard Error         1.24758

Variables in the equation:

                    B        SE B       Beta    T       Sig
                                                         T
Dist. Bound. 7.770473E-03, 2.03555E-03, 0.48990, 3.817, 0.0005
Call Site    1.96072         0.92369   0.27241 2.123    0.0400
Constant     -0.37464     0.60328             -0.621   0.5381
```

The results for group W appear much more clear than those for group E. They confirm that a number of different factors influence patterns of range use, and these are likely to change according to the time of year. Calling sites and sleeping sites were the most frequently selected variables. However, as outlined earlier, Diana monkeys tend to call and sleep within their core areas i.e. the areas they occupied most frequently. Therefore, location of these calling and sleeping sites may not be the primary force behind patterns of range use. Instead, they may be as a consequence of ranging patterns determined by other factors.

Distribution of species of trees from which Diana monkeys ate the flowers, fruits and seeds, were selected for certain months, as was distance from the boundary. Food trees were never selected during the peak wet season - this was to be expected because animals were feeding mainly on leaves and insects during this period. Where distance from the boundary was selected, study groups were spending considerable amounts of their time away from the central areas of their respective ranges. This suggests that they may have been patrolling boundary regions to deter neighbouring groups from trespassing. Quadrats at the boundary were rarely, if ever fed in, although the monkeys were seen to feed in most of their range, further supporting the idea that they were patrolling boundary regions.

5.8 DISCUSSION

To conclude, climate seems to be a major factor determining ranging behaviour of primates on Tiwai. In Dasilva's study of <u>Colobus polykomos</u>, rainfall was found to have a strong influence on ranging as in this study (Dasilva, 1989). While rainfall and temperature are likely to influence plant phenological patterns, and thus may indirectly influence ranging patterns through distribution and availability of food resources, these two variables appear to have a direct effect on the animals ranging behaviour.

Distribution of particular, selected foods, namely fruits and flowers, are also important, though their impact changes with the seasons, as would be expected. Similar results have been obtained in other studies where primates were observed to shift their ranging areas, and particularly their core areas, with the seasons (De Moor & Steffens, 1972; Mitani, 1989). Terborgh (1983) and van Schaik et al (1985) reported that distribution of fruit, rather than arthropods and young leaves, governed patterns of range use in their respective study animals. Furthermore, Terborgh, comparing ranging behaviour in tamarins and two species of <u>Cebus</u> monkeys found that the tamarins had a diet that changed little across the seasons, unlike the <u>Cebus</u> monkeys. And the tamarins showed correspondingly little change in their ranging patterns across the seasons. Distribution of abundant foods i.e. leaves and arthropods did not determine where Diana monkeys ranged. However, depending on their diet, Diana monkeys appeared to change their travel patterns, travelling directly, and quickly, to dispersed food patches such as fruiting trees, or travelling more slowly and with less obvious direction when feeding on foliage or arthropods.

Ranging behaviour of the study groups was also affected by their neighbours. Groups visited more of the quadrats of their ranges in those months when outgroup calling rates were highest, tended to range away from the central regions of their ranges, and spent considerable amounts of their time in and around range overlap zones. Very few intergroup contests were observed during this study - either groups avoided one another, or contest and reassertion of ownership were achieved by some other means such as bouts of loud calls.

Theoretically, animals should be able to maximise their access to resources by defending ranges, or more accurately perhaps, territories, against competitors. But only where the benefits of defending limiting resources outweigh the costs will animals opt for a territorial strategy, as outlined in Davies & Houston (1984) and Dunbar (1988) in their reviews of the economics of territoriality.

SUMMARY

1. Regression analysis demonstrates that ranging behaviour in Diana monkeys was dependent on a number of factors.
2. Rainfall and temperature were found to be important determinants of ranging behaviour throughout the year.
3. Distribution of fruits, seeds and flowers appeared to determine patterns of range use at certain times of year.
4. Groups responded to neighbouring groups, visiting more of their home range at times when outgroup calling was high, and visiting boundary areas though they were never seen to feed there.

CHAPTER SIX

TERRITORIAL CALLING

6.1 INTRODUCTION

In the previous chapter it was shown that the two study groups occupy home ranges in the order of 30 - 40 ha, and that there is some degree of overlap between neighbouring groups' home ranges. Within both study group ranges there appeared to be a core area, a region where other groups were never seen or heard. The data are summarised in Table 6.1 below.

Table 6.1: Home Range Size, Overlap, and Exclusive Zones.

Group	Home Range Area (ha)	% Overlap	Exclusive Area (ha)
W	39.5	16.5	33.0
E	36.5	28.8	26.0

As was outlined by Bates in his review of territorial behaviour in primates, an important feature of primate home ranges is that they often include a zone used exclusively by the resident group. Although in many species these regions are rarely seen to be actively defended, the fact that adjacent troops are rarely, if ever, observed in such exclusive zones, suggests that there is some kind of spacing mechanism in operation (Bates, 1970). In his review of definitions and functions of dominance and territoriality, Kaufmann emphasized that priority of access to resources by the resident, rather than exclusive occupancy of an area per se, was the important issue. The importance of passive avoidance of conspecifics was also emphasized, and considered to be a legitimate component of territorial behaviour (Kaufmann, 1983).

In this chapter data will be presented to investigate whether Diana monkeys defend territories against conspecifics, and if so do the females play a part in the defence of the group territory.

6.2 INTER-GROUP ENCOUNTER RATE

Waser's theoretical model of random motion estimates the expected intergroup encounter rate for a primate population, taking into account group spread, day range length, population density, and the distance at which groups detect one another (Waser, 1974; but see van Schaik et al 1985). It is expressed as:

$$f = 4pv/ (2d + s)$$

where p = population density, v = day range/velocity, d = detection distance, and s = group spread. The expected encounter rates were calculated for both study groups at detection distances of 50m and 100m respectively, and compared with the observed encounter rates for the two groups as shown below.

Table 6.2: Expected versus Observed Encounter Rates.

Group	Detection distance (m)	Expected rate of encounter (day^{-1})	Observed rate of encounter (day^{-1})
W	50.0	0.90 - 1.30	0.180
	100.0	1.33 - 1.94	0.426
E	50.0	1.02 - 1.49	0.188
	100.0	1.51 - 2.20	0.354

During 18 months field observations a total of 3 inter-group encounters involving any kind of "fighting" or physical contact were observed: E fought on two occasions and W was observed fighting with a neighbouring group only once. Therefore, encounters were defined as all occasions when the study group was in visual and/or auditory contact with neighbouring groups.

From Table 6.2 it can be seen that the observed encounter rates for both groups at 50 m and 100m are considerably lower than predicted on the basis of Waser's random motion model. Thus it would seem likely that there is some kind of spacing mechanism in operation here.

Assuming that this is the case how does it operate? Are groups of Diana monkeys distributed as a result of mutual avoidance strategies as have been found for mangabeys (Waser, 1976), howler monkeys (Whitehead, 1987), Orangutans (Mitani, 1985b), cheetahs (Eaton, 1970) and wolves (Harrington & Mech, 1983), or are they actively defending exclusive territories as seen in many primate species, including Lemurs (Klopfer & Jolly, 1970), _Tarsius_ _bancarus_ (Neimitz, 1979), _Colobus_ _guereza_ (Marler, 1969), _Cercopithecus_ _mitis_ (Marler, 1973), and the agile gibbon (Gittins, 1980)?

An animal's home range has been defined as the area over which the animal normally travels whilst foraging (Burt, 1943). A territory is generally considered as a fixed area that is actively defended by physical eviction or by the resident advertising his presence to potential intruders (Noble, 1939, in Bates, 1970; Wilson, 1972). While most animals occupy home ranges, only those who actively maintain territories are said to be territorial (but see Kaufmann, 1983).

There is considerable evidence from field studies that animals should only defend territories when there is a particular resource in short supply and the benefits of defending it outweigh the costs of such an action (Brown, 1964; Kinzey & Robinson, 1983). This will be discussed further in the following chapter.

If an animal is territorial it needs to be able to defend its territory against intruders, whether by chasing off and/or fighting with intruders, or engaging in some kind of advertisement of its ownership. But even where animals use bluff to avoid physical conflict with another of that species, their signals need to be "honest", i.e. criteria used to assess some measure of phenotypic quality to defend the territory should reflect differences in ability to engage in fighting (Clutton-Brock & Albon, 1979; Zahavi, 1979; Zahavi, 1987). Whatever means they use to defend their territory, animals need to be able to move around their range to check boundaries, reinforce ownership signals, and repel potential intruders.

6.3 INDEX OF DEFENDABILITY

Mitani and Rodman (1979) argued that in order to maintain its territory, an individual must be capable of visiting its range boundaries sufficiently frequently to monitor potential intruders effectively. They devised an index of defendability (D) that gave a measure of the frequency with which an individual, or a group, could visit their range boundaries in a set time period.

$$D = d/\sqrt{4A/\pi}$$

where A is the home range area, and d is day range length. They showed that while a high index value (greater than 1) is a necessary condition for territorial primates, it is not a causal factor, thus while all species that have been shown to be territorial have D > 1, not all those with high index values do defend territories.

Defendability index values were calculated for the two study groups, both for home ranges and exclusive zones, as shown below:

Table 6.3: Mitani & Rodman (1979) Index of Defendability.

Group	Home Range	Exclusive Zone
W	2.29	2.75
E	2.50	3.26

According to Mitani and Rodman's theory, both groups are mobile enough to be able to defend their home ranges or territories against neighbouring groups. The evidence suggests that Diana monkeys are employing some kind of spacing mechanism to maintain spatial dispersion of groups, and that they are mobile enough to defend territories. Do they actively defend and advertise a part of their home range against other members of their species?

6.4 LONG DISTANCE CALLING

In habitats where visibility is poor, such as in a rainforest, it is expected that most animals will make use of vocal or chemical modes of communication. Diana monkeys live in such an environment, and although their brightly-coloured pelage may serve a signalling function (Morike, 1973; Kingdon, 1988) it is unlikely to be of importance for inter-group communication, except when two groups meet, which is a very rare occurrence. Instead, they appear to make use of loud calls, as do many other forest guenons (*Cercopithecus mitis* kandti - Aveling, 1984; *C. campbelli lowei* - Bourliere et al, 1970; *C. neglectus* - Gautier-Hion & Gautier, 1978).

A considerable amount of work has been carried out to investigate the relationship between the design of vocal signals, their adaptations for use in particular habitats, and their function (Morton, 1975; Marten et al, 1977; Wiley & Richards, 1978; Waser & Brown, 1986). Many male bird songs serve a dual purpose: they are used for mate attraction and as a means of spacing. In primates there is some evidence that while male loud calls act as spacing calls they do not necessarily attract mates very effectively (Orangutan - Mitani, 1985; Gibbons - Marler & Mitani, 1988). But, irrespective of whether they do or do not function to attract females, it is important that:

1. they carry a long distance, and
2. they are easily locatable (Snowden, 1986).

Marten et al (1977) demonstrated that low frequency sounds carried better in a forest environment than did high frequency noise. Primate loud calls tend to be low-pitched (frequency < 1kHz) and Brown has shown that the long-distance spacing calls of mangabeys and blue monkeys have an audible range of approximately twice the diameter of their mean home range (Brown, 1989). Further support for the argument that low frequency calls are more appropriate than high frequency ones for the transmission of information across a distance comes from the observation that high frequency sounds show much greater attenuation than do low frequency ones.

A number of field studies have found that primate loud calls show a bimodal distribution throughout the day, with peaks in loud calling during the early morning and late afternoon/evening (Horwich, 1976; Waser, 1977b; Deputte, 1982; Tenaza, 1989). Similar results were obtained during this study as can be seen from Figs. 6.1 & 6.2. Following on from these observations that primate long distance calls tended to be concentrated during a particular time of day, Waser & Waser (1977) carried out a series of experiments to investigate attenuation rates of loud calls of Cercocebus albigena, Cercopithecus mitis, C. ascanius and Colobus guereza throughout the day. They demonstrated that attenuation rates are lowest during the early morning, during the time period when these animals loud-call most frequently. They suggested that primates were calling at times when atmospheric conditions would have a minimal effect on the transmission of their low frequency loud calls. But more recently, environmental explanations for differences in call structure are no longer thought to be so

Fig. 6.1: Daily Pattern of Territorial Calling in Group W

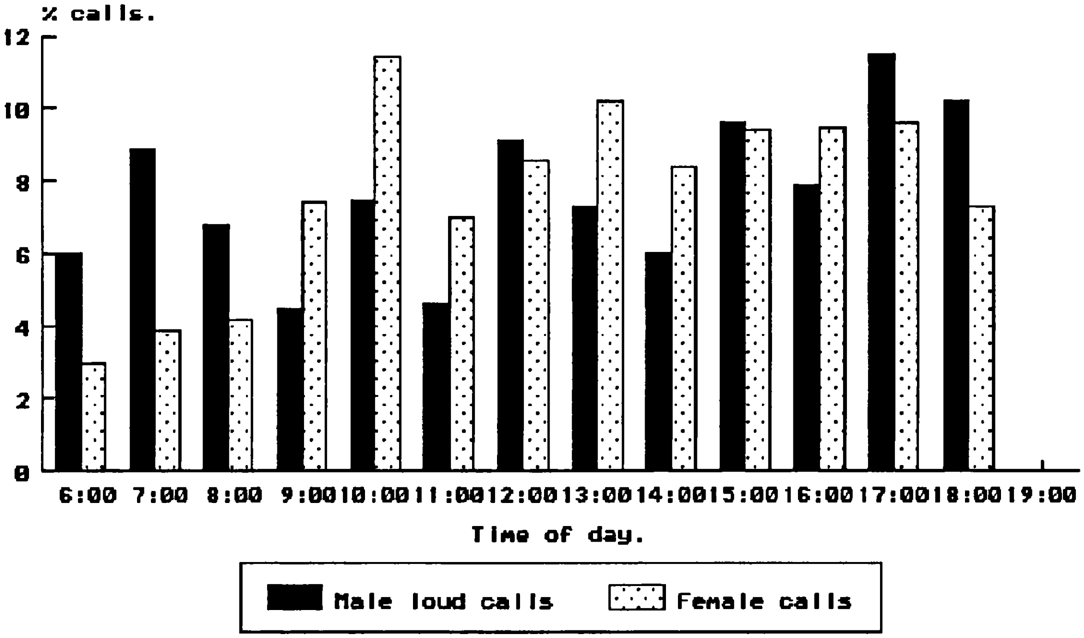
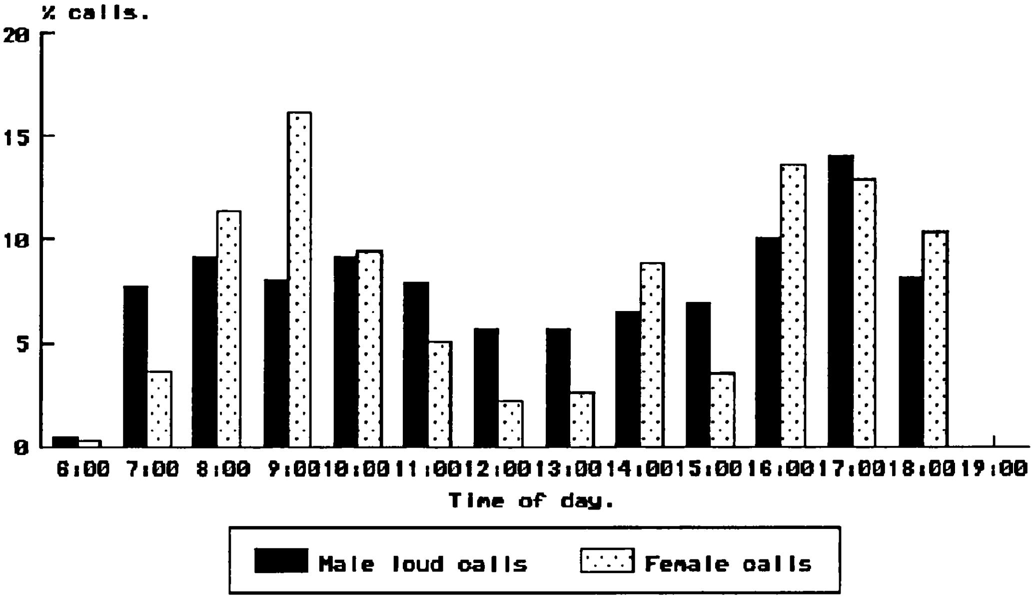


Fig. 6.2: Daily Pattern of Territorial Calling in Group E



plausible. Waser (1982) has looked at the loud call structure of a number of baboon and macaque species inhabiting a wide variety of habitats. He has shown that environmental factors do not appear to be the major factors shaping these animals' loud calls.

Loud calls need to be easily located, and for this they should be of relatively low frequency with several time-of-arrival cues incorporated into their structure. This can be achieved either by having a series of several short syllables with strong onset of sound, or by using a frequency modulated signal (Brown, 1982; Snowdon, 1986). The male Diana monkey loud call consists of a train of syllables following an initial bark noise: the initial bark may alert and/or orient distant recipients.

Gautier & Gautier (1974) categorise Old World monkey loud calls into two different classes: Type 1 and Type 2. Male Diana loud calls fall into the Type 1 category, i.e. they are highly stereotyped, only given by the male monkey, and appear to be used as a territorial call. But female Diana monkeys also have a sex-specific call termed a chatter-scream. Chatter-scream vocalizations are not unlike male loud calls in their gross patterning, i.e. an initial sharp sound preceding a train of sounds. However, it is much quieter and of shorter duration than the male call, and its source is not easily located, unlike that of the male loud call. Preliminary observations carried out at Tiwai, and playback experiments with captive groups completed prior to beginning this study, showed that adult females give their distinctive chatter-screams during territorial calling bouts and intergroup encounters. Female chatter-screams also follow the same diurnal pattern of production as do male loud calls (W, $r_s = +0.513$, $N = 14$, $p < 0.05$, one-tailed: E, $r_s = +0.821$, $N = 14$, $p < 0.0005$, one-tailed), i.e. two peaks of production, one in the morning and the other in the afternoon, as shown in Figs. 6.1 & 6.2.

6.5 SAMPLING METHODS

Both study groups were followed for up to 5 days each month. During these sample periods all instances of loud calls and chatter-screams were recorded, including calls from non-group animals, together with estimated distance and direction of call source. In addition, loud calls and alarm calls of other species e.g. Colobus polykomos, and the study group's response to them were noted.

6.6 MONTHLY TERRITORIAL CALLING PATTERNS

In Figs. 6.3 and 6.4 I have used average number of territorial calls (male loud calls and female chatter-screams) given/day instead of the average number of territorial calling bouts/day. Plots of calling bouts give

Fig. 6.3: Monthly Variation in Territorial Calling in Group W

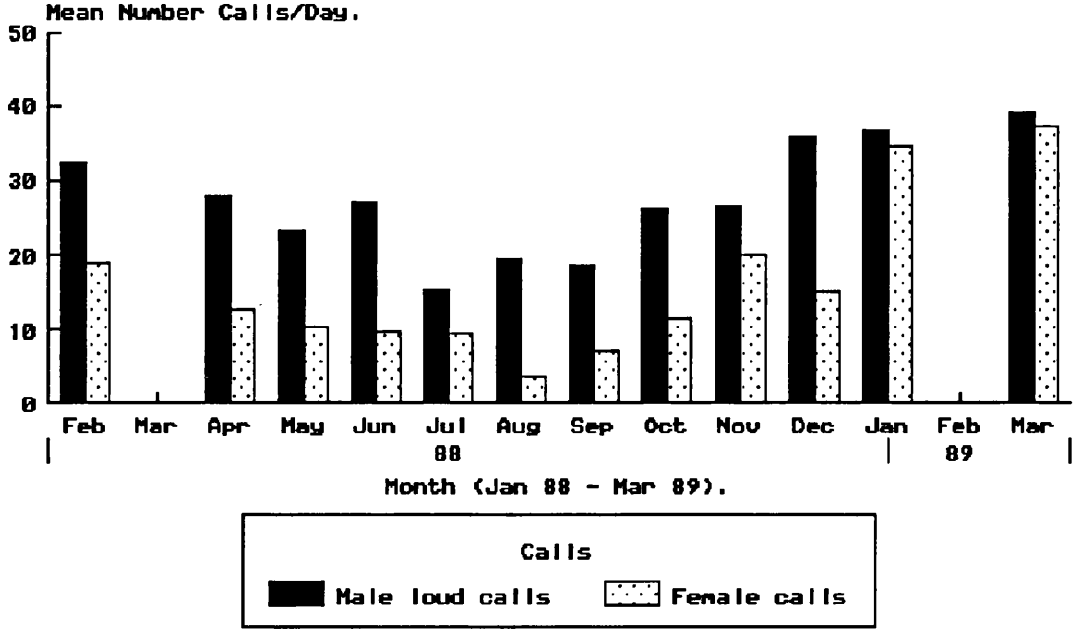
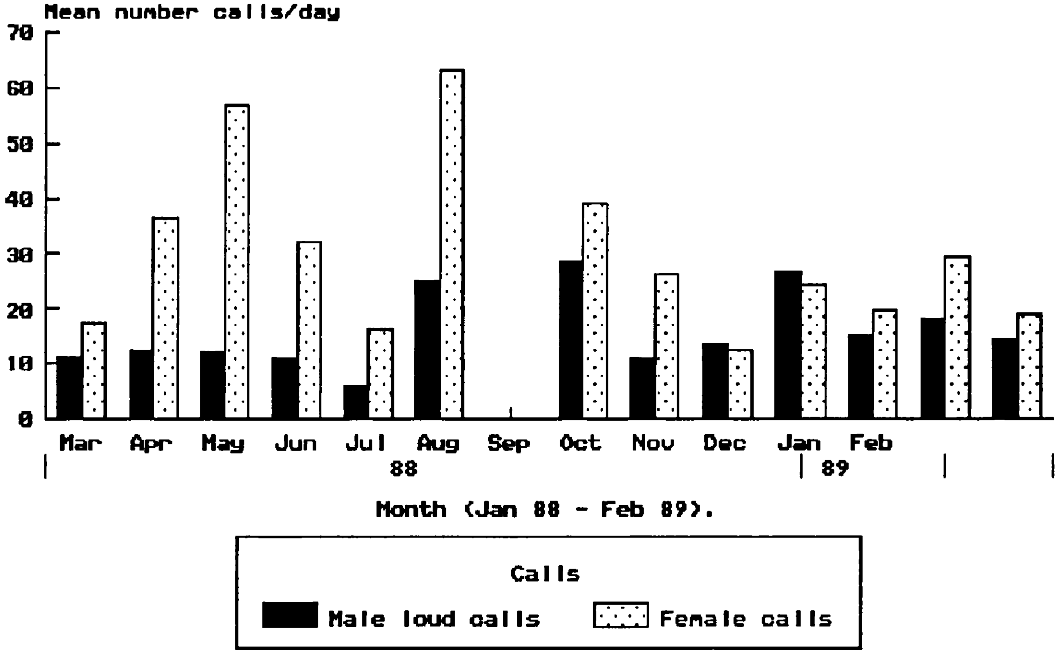


Fig. 6.4: Monthly Variation in Territorial Calling in Group E



the same overall calling pattern but the calling peaks occur in different months - this can be explained by the fact that in some months the animals call for longer periods but less frequently, whereas at other times calls are given in numerous short bouts. For the moment I shall continue to use number of calls rather than bouts since this is likely to be a more accurate indication of the amount of time being invested in territorial calling.

From Figs. 6.3 and 6.4 there are two points I would like to make:
Firstly, the two study groups show differences in their overall calling strategies - in the western group, the resident male called noticeably more frequently than did the females, even though there are up to six adult females calling compared with only one adult male (Mann-Whitney U: $n_1 = 11$, $n_2 = 11$, $U = 8$, $p < 0.001$, one-tailed). In the eastern group, there were more female chatter-screams given than male loud calls (Mann-Whitney U: $n_1 = 11$, $n_2 = 11$, $U = 7$, $p < 0.001$, one-tailed), but here there were a maximum of ten adult females and, depending on the time of year, two adult males calling in the group, which may, at least in part, account for the differences between the two groups.

Secondly, the timing of calling peaks differs between the two groups. In the western group, both the male and the females called more during the early part of the dry season, though this was not so for the females during January 1988.

They also showed a slight calling peak in August, at the height of the wet season. In the other group, calling peaks occurred in May and August, (just prior to the start of the rains and at the height of the rainy season), and then tailed off during the dry season.

Figs. 6.3 and 6.4 demonstrate that the two study groups showed very different patterns in their territorial calling behaviour. Possibly different ecological factors are driving the two groups in different ways. However, it is important to consider that the results may reflect differences in group structure rather than different territorial calling strategies per se.

In both groups there is a significant positive correlation between the numbers of loud calls and chatter-screams given, supporting the hypothesis that these calls are given in association with one another (W, $r_s = +0.658$, $N = 63$, $p < 0.001$; E, $r_s = +0.413$, $N = 49$, $p < 0.005$). Also, in respect of whether males or females are initiating calling bouts, both groups show similar trends, as shown in Table 6.4.

Table 6.4: Are Calling Bouts Initiated By Adult Males or Adult Females?

	W		E	
MONTH	**Male starts calling**	**Female starts calling**	**Male starts calling**	**Female starts calling**
Jan	1	4	2	5
Feb	2	6	1	5
Mar	-	-	4	13
Apr	1	7	2	11
May	3	3	0	9
Jun	9	4	1	9
Jul	0	6	0	3
Aug	3	7	4	15
Sep	2	4	-	-
Oct	2	6	1	6
Nov	1	8	1	6
Dec	2	4	1	6
Jan	3	3	2	9
Feb	-	-	2	4
Mar	1	7	-	-
Total	**30**	**69**	**21**	**101**

6.7 INITIATION OF CALLING BOUTS

Although calling patterns are very different between the two groups, in both cases females initiate calling bouts more often than do either of the resident males. Still, however, we have the problem of there being potentially more females than males calling in the two groups - thus there is always the possibility that the results are an artefact of the sex ratio of the group. Therefore a correction was made for this. By considering the number of females calling prior to the male in any territorial calling bout it was found that in group W a mean of 1.75 females called before the adult male and in group E, a mean of 2.4 females called prior to the male giving his loud call. Assuming that in Table 6.4 the number of bouts represents those initiated by a mean of 1.75 and 2.4 females respectively, then the proportion of bouts initiated by only one female can be calculated to give the following results.

Table 6.5: Are Calling Bouts Initiated By Adult Males or Adult Females?

	W		**E**	
MONTH	**Male starts**	**Female starts**	**Male starts**	**Female starts**
Jan	1.0	2.3	2.0	2.1
Feb	2.0	3.4	1.0	2.1
Mar	-	-	4.0	5.4
Apr	1.0	4.0	2.0	4.6
May	3.0	1.7	0.0	3.8
Jun	9.0	2.3	1.0	3.8
Jul	0.0	3.4	0.0	1.2
Aug	3.0	4.0	4.0	6.2
Sep	2.0	2.3	-	-
Oct	2.0	3.4	1.0	2.5
Nov	1.0	4.6	1.0	2.5
Dec	2.0	2.3	1.0	2.5
Jan	3.0	1.7	2.0	3.8
Feb	-	-	2.0	1.7
Mar	1.0	4.0	-	-
Total	**30.0**	**39.4**	**21.0**	**42.2**

The results show that in both study groups calling bouts were initiated more frequently by group females than by the group male, even when the ratio of males to females had been taken into consideration (Mann-Whitney test: W, $z = -2.35$, $p < 0.01$; E, $z = -2.87$, $p < 0.005$).

Thus it would appear that females are involved in territorial calling bouts, and that although calling rates are very different between the groups, the females are more likely to initiate calling than is the male.

6.8 FEMALE ROLE IN TERRITORIAL CALLING

According to the literature, vocalisations specific to females are nearly always affiliative, and often only noted from captive animals (Mitchell, 1979). Diana monkey chatter-screams do not conform to such patterns. Although they may serve primarily as intra-group calls with respect to stimulating the group's male rather than outgroup animals, it is not an affiliative call. It is rarely if ever heard in captivity, except in response to playbacks of stranger male loud calls. Territorial calls are unlikely to be of great importance to captive animals, unless there are several captive groups of that species in the same location. Captive male Diana monkeys do give loud calls but not frequently, and they are often in response to an alarming situation e.g. a helicopter flying overhead, a large truck passing close by or the appearance of a dog (pers. obs.). The fact that females do not give chatter-screams in captivity is further support for this being a territorial call, possibly given in response to hearing neighbouring groups.

Study Rationale

Given that the data support the idea that females take part in territorial calling bouts, how are male and female calling behaviours inter-related?

1. If females are using their chatter-scream vocalisations to stimulate their group male into giving his loud calls, then one would predict that male loud calls should be given more frequently following group female chatter-screams than either spontaneously, or following loud calls from other males.

2. Or, if males are stimulated to call by loud calls from out-group males then they should give more loud calls following these outgroup calls than they give spontaneously or following female chatter-screams.

3. A third possibility is that males may be calling spontaneously and not following intra- or extra-group calls; if so, then as many or more male calls should be given spontaneously than following other Diana monkeys.

Up to now I have used the actual numbers of calls given. From the results presented earlier, we know that females initiate calling more often than do the males, yet in the western group females give significantly fewer calls overall than does the male, suggesting that having initiated a calling bout they then stop calling, or only call infrequently to encourage the male to continue with his display. Also, within any calling bout where there are more than two animals calling, it is not possible to determine what, if anything, is stimulating each animal. Therefore, perhaps in this instance we should look at calling bouts, rather than calls per se.

The data were divided into 10 minute blocks and the number of blocks where male loud calls occurred were categorised accordingly. The results are presented in Tables 6.6 & 6.7 below.

Table 6.6: Male calling - Frequency of Response to Group W Chatter-Screams and Outgroup Loud Calls.

No. 10 min blocks	LCs given spontaneously	LCs given after CSs	LCs given after outgp LCs
LCs	70	89	19
No LCs	3792	32	94

Table 6.7: Male calling - Frequency of Response to Group E Chatter-Screams and Outgroup Loud Calls.

No. 10 min. blocks	LCs given spontaneously	LCs given after CSs	LCs given after outgp LCs
LCs	26	93	4
No LCs	3001	73	47

A Chi-square test was used to demonstrate that adult males do not give their loud calls randomly with respect to the three conditions (W: $X^2 = 1496.1$, df = 2, $p < 0.001$; E: $X^2 = 1315.2$, df = 2, $p < 0.001$). By partitioning the overall X^2 values it was possible to examine the data in further detail. The results are as follows:

Partition	**Group W**	**Group E**
1	1452.6 ($p<0.001$)	1312.8 ($p<0.001$)
2	43.5 ($p<0.001$)	2.3
X^2	1496.1	1315.2

These results support prediction 1 and exclude predictions 2 and 3, ie. male loud calls are given more frequently following group female chatter-screams than either spontaneously or following loud calls from other males.

Given that the data are consistent with the hypothesis that females do stimulate territorial calling in their group males, we may ask what stimulates the females into giving territorial calls in the first place? Are they responding to loud calls from neighbouring or stranger males, or to some other stimulus?

Are Females Responding to Outgroup Calls?

If they are responding to outgroup males then one would predict that they should give more calls following outgroup loud calls than spontaneously or in response to their own group male's calls.

The data were partitioned as above and the results are shown in Tables 6.8 & 6.9 below.

Again, a Chi-square test was used to demonstrate that female chatter-screams are not distributed randomly across the three condition (W: $X^2 = 156.4$, df = 2, $p < 0.001$; E: $X^2 = 392.9$, df = 2, $p < 0.001$). On partitioning the degrees of freedom the following results were obtained.

Partition	**Group W**	**Group E**
1	104.3 ($p<0.001$)	322.2 ($p<0.001$)
2	52.1 ($p<0.001$)	70.7 ($p<0.001$)
	156.4	392.9

Table 6.8: Female calling - Frequency of Response to Group W Loud Calls and Outgroup Loud Calls.

No. 10 Min Blocks	CSs given spontaneously	CSs given after gp LCs	CSs given after outgp LCs
CS	109	18	20
No CSs	3784	52	113

Table 6.9: Female calling - Frequency of Response to Group E Loud Calls and Outgroup Loud Calls.

No. 10 Min Blocks	CSs given spontaneously	CSs given after gp LCs	CSs given after outgp LCs
CS	73	14	13
No CS	3093	5	47

The results do not conform with the predicted pattern with respect to females' responses to their own males compared with giving chatter-screams spontaneously. However, females are responding to outgroup loud calls more frequently than one would predict by chance.

One further thing to consider is that although loud calls are audible over considerable distances (500-1000+m) they are not heard all that frequently compared with calls from the study groups. Consequently, it is worthwhile considering what percentage of outgroup loud calls were actually responded to by the study groups, and then whether responses were initiated more frequently by the male or by the females.

Table 6.10: Do Females Respond to Outgroup Loud Calls More Frequently than does the Male?

	W		E	
Month	**Male Response**	**Female Response**	**Male Response**	**Female Response**
Jan 1988	3	1	0	3
Feb	2	2	0	0
Mar	-	-	0	1
Apr	9	2	1	2
May	3	1	0	4
Jun	4	1	1	1
Jul	2	1	0	0
Aug	0	1	0	0
Sep	0	0	-	-
Oct	3	2	0	1
Nov	2	3	0	0
Dec	5	1	2	2
Jan 1989	2	3	0	0
Feb	-	-	1	0
Mar	0	1	-	-
Total	**35**	**19**	**5**	**15**

Interestingly, both groups "ignored" about 55% of all outgroup loud calls. But, as can be seen from the above table a slightly different picture emerges for the two groups. In the western group the male responded more often to outside loud calls than did the females, but in the eastern group, females initiated the responses to these outgroup calls considerably more often than did the male ($z = -2.38$, $N = 13$, $p < 0.01$). However, when the monthly scores are adjusted to account for the sex ratio within E (1 adult male: 10 adult females) this result is no longer valid.

From this it would seem that we need to look at factors associated with outgroup calling in more detail to consider the effects of such things as

1. Whether the location of the resident group within their range is important, and
2. Whether the location of the other group is important - in previous studies of howler monkeys (Whitehead, 1989), gibbons (Mitani, 1985b; Raemaekers & Raemaekers, 1985) and titi monkeys (Robinson, 1979) location of neighbouring groups has been shown to determine whether residents will respond and if so, in what way they do so. This could include factors such as whether the outgroup are intruding into the residents territory, their proximity to food sources etc.

6.9 RESPONSE TO OUTGROUP CALLING - RESIDENT GROUP'S LOCATION WITHIN THEIR HOME RANGE

As mentioned above, the two groups were found to respond to approximately 45% of all outgroup calling bouts, ignoring 55% of the bouts heard by the observer.

The distribution of Group W and Group E's responses to outgroup calls across their ranges are summarized below in Tables 6.11 and 6.12.

Table 6.11: Response to Outgroup Calls - Is it Dependent on Group W's Location Within Their Range?

	Core	Boundary/Overlap
Response	17	28
No Response	41	30

Table 6.12: Response to Outgroup Calls - Is it Dependent on Group E's Location Within Their Range?

	Core	Boundary/Overlap
Response	7	17
No Response	15	10

A statistical analysis of the results confirms that resident groups respond significantly more frequently to outgroup calls heard when at their range boundary than when in more central areas (Group W: $X^2 = 5.288$, $df = 1$, $p < 0.05$; Group E: $X^2 = 6.034$, $df = 1$, $p < 0.02$), as illustrated in Figs. 6.5 & 6.6.

While the above demonstrates that resident groups are more responsive to outgroup calls when at their territory boundaries, it tells us very little about how this spacing mechanism may operate. However, it does illustrate that while Diana monkeys do respond vocally to outgroup calls, they are selective, and make decisions about whether to respond, rather than using a "blanket-decision" strategy of responding to all stimuli, or conversely, responding to no

Fig. 6.5: Group W - Response to Outgroup Loud Calls - Is it Dependent on Resident Group's Location Within Their Range?

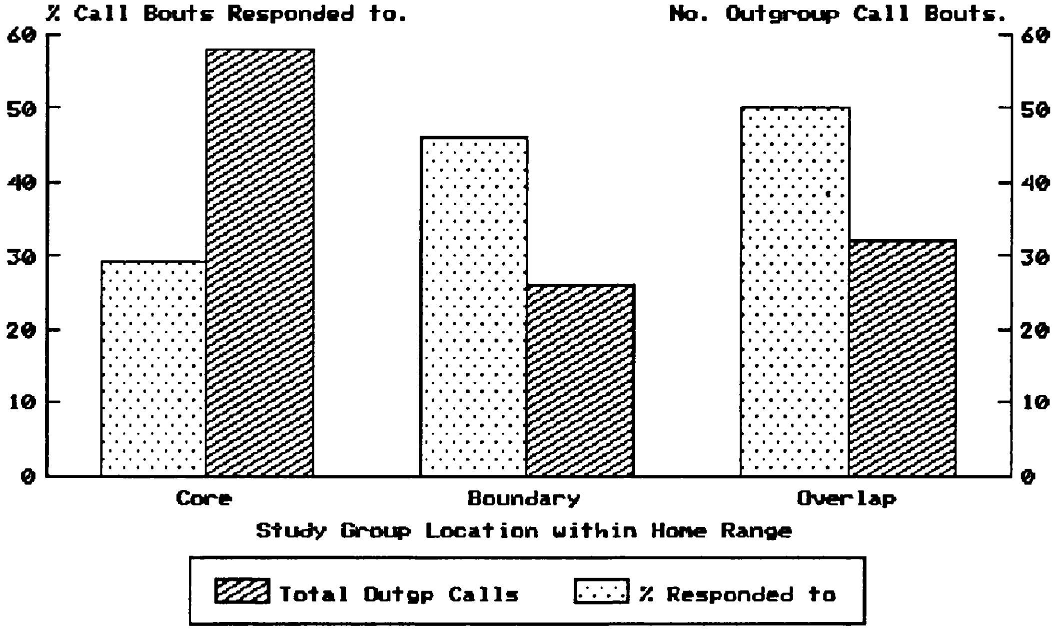
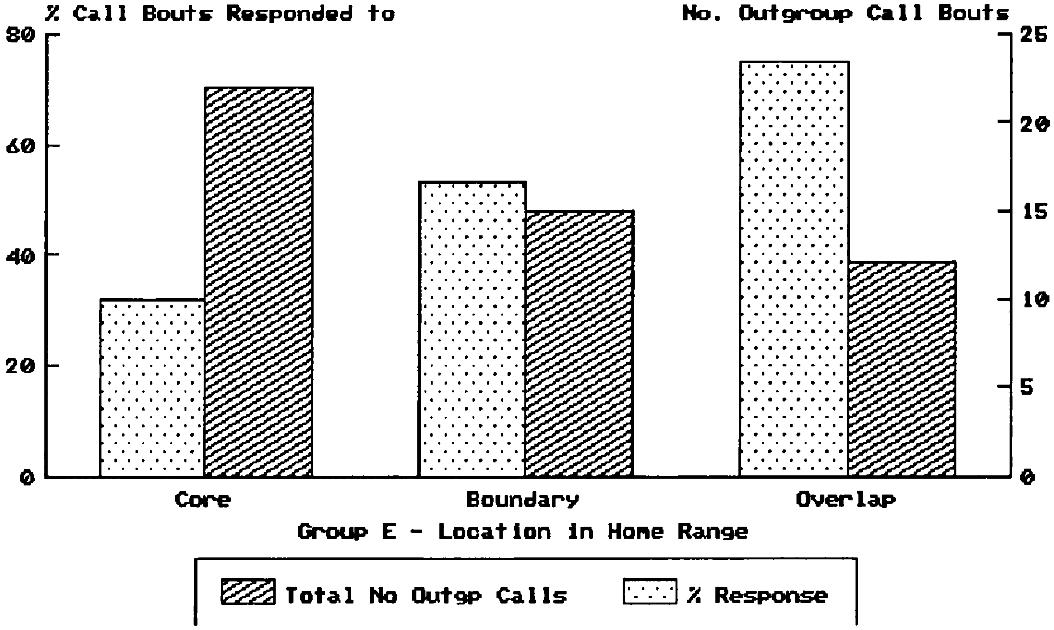


Fig. 6.6: Group E - Response to Loud Calls - Is it Dependent on Resident Group's Location Within Their Range?



outgroup calls. Previous studies have demonstrated the importance of distance (howler monkeys - Chivers, 1969; mangabeys - Waser, 1975) and location (titi monkeys - Robinson, 1979a; 1979b; gibbons - Mitani, 1985b; howler monkeys - Whitehead, 1989) in determining a resident group's response to calling and/or intrusion by another group.

6.10 RESPONSE TO OUTGROUP CALLING - OUTGROUP' LOCATION WITH RESPECT TO RESIDENT GROUP

Data on outgroup calling and resident groups responses were partitioned as shown in Table 6.13 below.

Table 6.13: Response to Outgroup Calling in Group W & E - Is it Dependent on Outgroup Location?

	Near/Middle		Distant/Very Distant	
	W	E	W	E
Response	23	7	22	16
No Response	4	3	66	21

From Figs. 6.7 and 6.8 it can be seen that both groups showed a tendency to respond to outgroup calls heard close to them (near and middle categories), irrespective of their own location within their range. Group W shows a significant difference in response rate depending on outgroup location ($X^2 = 28.944$, df = 1, $p < 0.001$) and there is a similar, but non-significant trend in Group E. From

Fig. 6.7a: Group W - Response to Outgroup Loud Calls From Different Locations

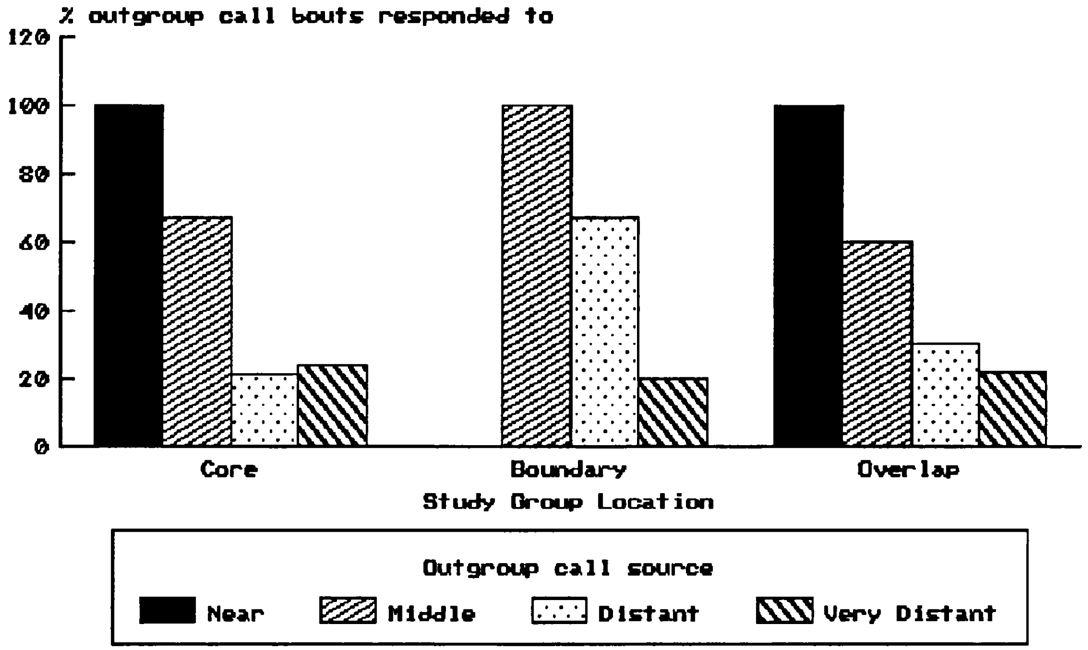


Fig. 6.7b: Group W - Total Outgroup Calls Heard From Different Locations

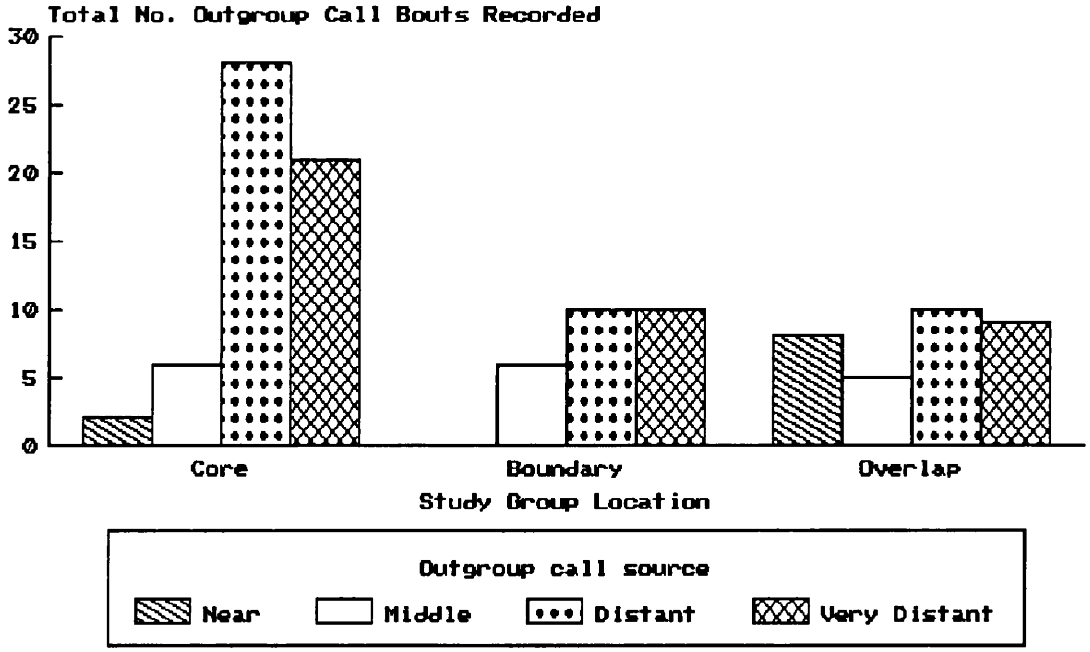


Fig. 6.8a: Group E - Response to Outgroup Loud Calls From Different Locations

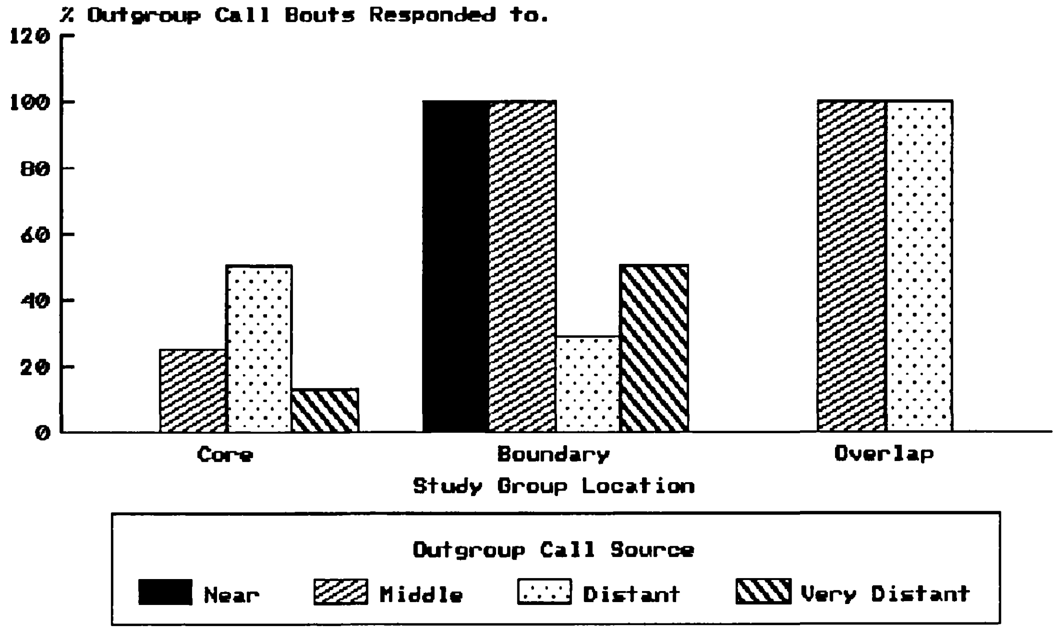
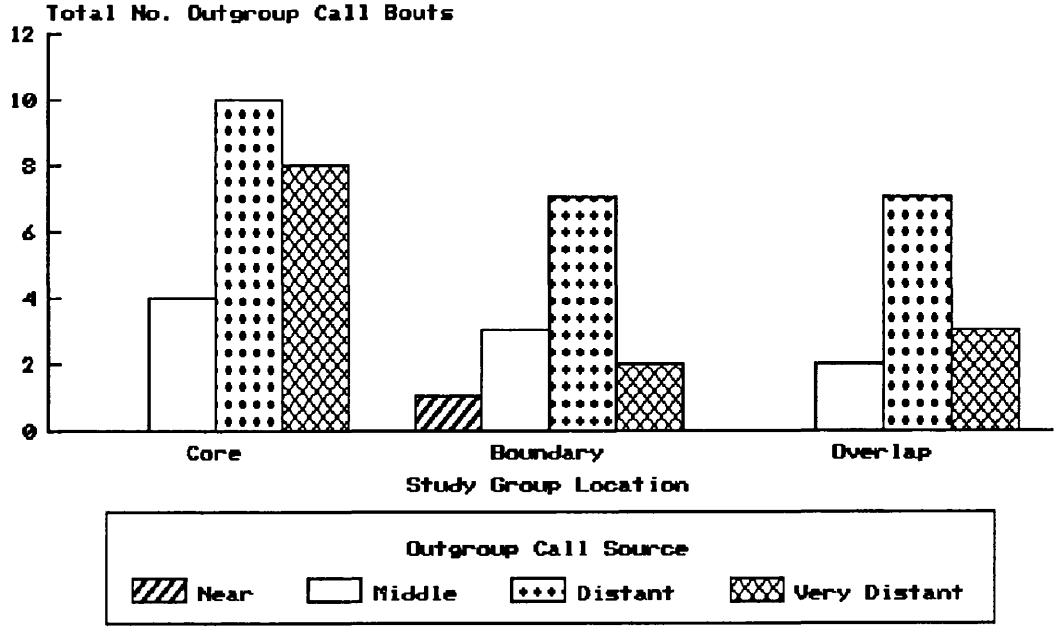


Fig. 6.8b: Group E - Total Outgroup Calls Heard From Different Locations



observation, Group E always responded to calls from Group N and Group S[1]. Group S was known to have arisen by fission from Group E prior to the beginning of the present study (Whitesides, pers. comm.). Also, on two occasions intergroup calling encounters with Groups N and S were observed to escalate into fights, which may help account for their responding to all calls heard from these two groups, irrespective of distance or location.

From the above results it would appear that resident groups respond more when at their territory boundaries, or in contested overlap zones, than when in areas of exclusive use. They are more likely to respond when outgroup calls originate close to them compared with those at a distance. Overall, distance of outgroup call source from the resident group seems to be the most important factor determining whether they will respond vocally or not.

6.11 DISCUSSION

From the results presented above it would appear that adult females play an important role in territorial calling, using their chatter-scream vocalizations to incite the group male to give his loud call. Cheyney (1981) and Cheyney and Seyfarth (1982) report that adult female vervet monkeys are

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[1] Group N and Group S occupied ranges that overlapped with that of Group E in the northern and southern parts of E's range as shown in Chapter 5, Fig. 5.4.

almost exclusively responsible for intergroup calls (but see Harrison, 1983b). Several other field workers have noted females giving particular grunt vocalizations prior to male loud calls in blue monkeys (Butynski, 1982; M. Lawes, pers.comm.). Female calling behaviour has also been recorded from primates other than guenons, e.g. titi monkeys (Robinson, 1981), Kloss and Moloch gibbons (Tenaza, 1976; Kappeler, 1984), and howler monkeys (Sekulic, 1982; Whitehead, 1989). This lends support to the hypothesis that in monogamous species, and some species living in larger social groups, female monkeys assist in maintaining intergroup spacing patterns.

Primate loud calls have a postulated function as intergroup spacing calls (Snowden et al, 1983). Such vocally mediated spacing mechanisms can operate in several different ways, inducing mutual avoidance of neighbouring groups in non-territorial species, or alternatively, in territorial species, loud calls may attract neighbouring groups, and thus are associated with intergroup aggression (Cheney, 1987).

The literature contains many examples of vocally mediated mutual avoidance spacing strategies, e.g. Siamangs (Chivers & Mackinnon, 1977), Callicebus torquatus (Kinzey & Robinson, 1983), Presbytis melalophos (Johns, 1985), Colobus badius (Struhsaker, 1975) and wolves (Harrington & Mech, 1979). However, perhaps the most fully documented example is that of <u>Cercocebus albigena</u>. Playback experiments were carried out to investigate how groups responded to outgroup male whoop-gobble vocalizations. The mangabeys responded in a group- and distance-specific fashion, but their responses were not site-specific. In other words, mangabey groups moved away from outgroup whoop-gobbles originating within 500m from them, and their response was the same throughout their home range area (Waser, 1974; 1976; 1977b).

Unlike <u>Presbytis entellus</u>, who have been reported to engage in intertroop encounters regularly (Ripley, 1969), Diana monkeys on Tiwai have a very low intergroup encounter rate. They appear to depend on a spacing mechanism involving mutual avoidance of neighbouring groups. However, unlike mangabeys, their responses to neighbouring groups are site-dependent, as in <u>Callicebus moloch</u> (Robinson, 1981), <u>Cercopithecus mitis</u> and <u>Colobus guereza</u> (Waser, 1977b). This behavioural strategy results in resident groups having exclusive access to a particular area, and thus they can be considered to be territorial.

In their review of intergroup calling and spacing in Cebids Robinson et al (1987) outlined mechanisms by which primates might maintain exclusive access to an area. These included:

1. site-dependent aggression and the regular advertisement of ownership and boundary locations,
2. defence of specific resources within an area, and

3. site attachment and the avoidance of neighbours home ranges.

It would appear from the present study that Diana monkeys rely on mutual avoidance of neighbouring groups, and when necessary, site-dependent aggression. On those rare occasions when intruding groups did not retreat, females and youngsters chased, bit and grappled with members of the intruding group. Throughout each of the three intergroup encounters observed the adult males continued to loud call and display to one another from the tops of tall trees either side of the boundary. On no occasion were the adult males seen to join the rest of their group in physically repelling the intruders. Similar observations have been reported for other territorial guenon species, where females take a very active role in aggressive intergroup interactions (*Cercopithecus ascanius* and *C. mitis* - Struhsaker & Leland, 1979; *C. mitis* - Rudran, 1978a).

A number of studies have demonstrated that territorial behaviour in some species may be influenced by intergroup competition for resources, and social and demographic factors (wolves - Harrington & Mech, 1979; vervet monkeys - Harrison, 1983b; Kavanagh, 1981; Cheney, 1987; Kloss gibbon - Tenaza, 1976; Whitten, 1982).

A current hypothesis favouring female sociality in primates suggests that by living in groups with female kin, females can maximize their individual access to food resources (Emlen & Oring, 1977; Wrangham, 1980). In his model of female-bonded primate groups, Wrangham suggested that females living in such groups should actively defend patchily distributed food resources against other groups of females. Certainly there seems to be strong evidence that female Diana monkeys are defending territories against other groups. The question of whether their territorial strategies act to defend food resources will be considered in the next chapter.

SUMMARY

1. Female Diana monkeys appear to use their chatter-screams as territorial vocalisations.
2. They initiate territorial calling bouts significantly more frequently than does the group male.
3. Territorial boundaries between groups of conspecifics are maintained by territorial calling bouts that induce mutual avoidance by neighbouring groups.
4. While there is some evidence that loud calls from other groups may act as a stimulus for female calling, it would appear that there are other factors involved, as yet not identified that are likely to be of considerable importance when considering male and female roles in territorial defence.

CHAPTER SEVEN

TESTING AN ECOLOGICAL MODEL OF FEMALE-BONDED PRIMATE GROUPS

7.1 INTRODUCTION

In the past, studies of territoriality in primates have concentrated on the role of the males in territorial defence. But from Wrangham's model of female-bonded primate groups (Wrangham, 1980) females should be investing considerable amounts of energy in defence of territories, while males should defend access to reproductive females. Thus, in female-bonded species, patterns of social organisation should reflect the dichotomy of interests between the sexes.

This model of female sociality makes a number of assumptions which are described and assessed below to ensure that this model may be applied to Diana monkeys. The predictions of the model will then be presented. The results of the study will be considered within the framework of this model, and discussed with respect to an alternative model of primate sociality, the predation risk hypothesis.

7.2 ASSUMPTIONS OF THE MODEL

1. In order to be considered a female-bonded species, the following criteria need to be met, namely that

(a) Females remain within their natal group, and

(b) it is predominantly males that undergo intergroup transfer, dispersing from their natal groups before, or around, the time of sexual maturity.

(c) There are consistent, differentiated relationships between female group members.

2. Food is an important limiting factor with respect to individual female reproductive success.

3(a) Females in groups will incur costs as a result of both intra-group and inter-group feeding competition, but

(b) any costs of intr-agroup competition are outweighed by the benefits of female cooperation in competing with other groups.

4. It is assumed that while access to food resources and safety is an important determinant of male survival, it is access to reproductive females that is the limiting factor when considering male reproductive success.

Assumption 1: Groups are Female-Bonded: Females remain in their natal group while males transfer between groups. There are consistent, differentiated relationships between female group members.

While there is no direct evidence that female Diana monkeys remain within their natal groups, field observations have demonstrated the occurrence of solitary males within the population at Tiwai (Oates et al, 1990; pers. obs.) which secondarily supports this. Also, within the literature there is evidence that other female guenons do remain and breed within their natal groups (Erythrocebus patas - Chism et al, 1984; forest guenons - Cords, 1987), while many field workers have reported seeing solitary males (e.g. Allenopithecus nigroviridis - Gautier, 1985; Cercopithecus aethiops - Henzi & Lucas, 1980; C. ascanius - Haddow, 1952; Ghiglieri, 1984; C. campbelli - Bourliere et al, 1970; C. mitis - Rudran, 1978a; Aveling, 1984), and in some cases, all male groups (e.g. E. patas - Hall, 1965; C. mitis - Rowell, 1988a). Furthermore, reports suggest that in some guenons females and their offspring form the stable core of the social group (C. cephus - Quris et al, 1981; E. patas - Chism & Rowell, 1988), as predicted by the model. Evidence from captive studies has verified this for several groups of Diana monkey, where females were found to form the social and spatial core of the group (Byrne et al, 1983; Hill, 1985). To conclude, it would appear that many, if not all, species of guenon studied to date are female-bonded and that consequently Diana monkeys might be expected to conform to this particular model of social structure and behaviour.

Assumption 2: Food is important with respect to female reproductive success.

There is some evidence available, from a number of studies, that access to food resources is an important variable when considering female reproductive success. Reproductive success is defined as the number of offspring surviving to maturity. Whitten reported that the availability of flowers of *Acacia elatior* was important in determining the timing of the onset of mating, and thus conception, in female vervets (Whitten, 1983b). This makes the assumption that the timing of mating and conception are related to reproductive success. Similar results were found by van Schaik & van Noordwijk in their study of female long-tailed macaques (van Schaik & van Noordwijk, 1985), where the timing of conception was dependent on the physical condition of a female, and her previous reproductive history. In years when fruit was superabundant (mast years) females achieved the required body condition very quickly, and even those females who would otherwise have not bred until the following year were able to conceive. Robinson, in his study of *Cebus olivaceus*, suggested that differences in female reproductive success were a result of variation in access to "monopolizable fruit trees" (Robinson, 1988).

Thus, it would appear that access to food is an important determinant of female reproductive success; its effects influencing female fecundity and infant survival (Whitten, 1982; Cheney & Seyfarth, 1987; Harcourt, 1987; Lee, 1987).

Assumption 3: Females in groups incur costs as a result of both intra-group and inter-group feeding competition, but any costs of intra-group competition are outweighed by the benefits of female cooperation in competing with other groups.

In recent years within-group competition has been documented for a number of primate species, particularly over access to water, food and social resources (Cheney et al, 1988; van Schaik & van Noordwijk, 1988; Whitten, 1982; Silk, 1987). Several studies have attempted to assess levels of intra-group feeding competition, and whether it is influenced by group size. In a study of Cebus apella aggression rates during feeding bouts were found to increase significantly as group size increased (Janson, 1988; but see Whitten, 1988). However, while feeding competition appears to exist within social groups, some animals appear to make use of strategies which minimise the costs it may impose on individuals. Evidence suggests that in species where dominance hierarchies operate between group members, high rank confers priority of access (Whitten, 1983a). Low-ranking animals may tend to avoid feeding competition, or at least minimise its effects, by feeding away from higher ranking animals (van Noordwijk & van Schaik, 1987). However, this strategy may entail other costs such as the risk of predation (Janson, 1985).

Intergroup competition for resources is assumed to exist on the justification that (i) there is little inter-group tolerance in many primate species, and (ii) primates have utilized a number of spacing strategies, which despite wide variation in proximate mechanisms always ultimately act to separate groups of conspecifics, spatially and/or temporally, from one another.

Vervet range size and quality is thought to be influenced by resource competition between groups (Cheney & Seyfarth, 1987; larger groups, containing more adult females have proved more effective in displacing smaller groups, and females in these groups would appear to incur lower costs during territorial encounters (Cheney & Seyfarth, 1987). Garber (1988) in his study of mixed species groups of _Saguinus_ _mystax_ and _S_. _fuscicolis_ in Peru, reported that stable polyspecific groups cooperatively defended territories throughout the year. There was, apparently, no adverse effect of increased group size on feeding efficiency. Instead, larger group size appeared advantageous in ensuring success in defence of major food trees. Unsuccessful resource defence resulted in an increase in time spent travelling between food sites at the expense of feeding time, hence indicating that unsuccessful inter-group competition was more costly on this occasion than intra-group feeding competition. Conversely, Janson (1985) reported that intra-group feeding competition incurred much greater costs on capuchin monkeys than did inter-group competition.

To summarise: intra-group competition appears to entail costs on primates living in groups, and some appear to have incorporated adaptive behavioural strategies to circumvent, or at least reduce, such costs incurred by group living. However, few studies appear to have addressed the problem of evaluating the relative costs and benefits of intra-group versus inter-group competition. Many studies infer that the benefits to individuals gained by cooperative behaviour amongst kin do outweigh any costs exacted on an individual's inclusive fitness as a result of intra-group competition. Possibly this is not always warranted because where within- and between-group competition have been considered the results are variable, suggesting that there may be different environmental or social factors in operation, depending on the example.

Assumption 4: Access to reproductive females is the limiting factor for male reproductive success.

Males can increase the number of offspring they produce by mating with more females. Females are generally unable to increase their fecundity by mating with more males. Instead they are expected to be discriminating, choosing mates that contribute most, either behaviourally or genetically, to female reproductive success. Thus, females are thought to function as a limiting resource for male reproductive success (Darwin, 1871; Trivers, 1972).

Having established that Diana monkeys are female-bonded, and that there is good evidence that food plays an important role in female reproductive success, is there any evidence that the costs of inter-group competition outweigh those of intra-group feeding competition? Unfortunately, there is no information available to test this directly - the fact that Diana monkeys appear to defend territories (Chapter Six), or that dominance hierarchies have been described for captive groups (Hill, 1985) is not conclusive evidence for this. As mentioned above Cheney & Seyfarth (1987) investigated this with respect to vervet monkeys, but there is no other information available for other guenon species. Because the principal purpose for using the paradigm of Wrangham's model is to investigate female territoriality and male-male competition, this third assumption will be taken to hold for the present discussion. However, it is an area where there is a further need for good empirical data if the intention is to discuss the ultimate causality of group-living in primates. The fourth assumption, that access to breeding females is the factor limiting male reproductive success, intuitively, holds for all animals that reproduce sexually.

7.3 TESTING THE MODEL

Predictions of Wrangham's model of female-bonded primates

1. During periods of food abundance, female-bonded groups are expected to concentrate on feeding from discrete, and defensible food patches.
2. Groups will continue to feed together even when food resources are scarce, but during periods of scarcity they should switch to uniformly distributed, lower quality foods to reduce feeding competition.
3. There should be inter-group competition for access to valuable food patches, and
4. in territorial species, females should play an active role in defending their group territory, and thus access to food resources.
5. According to this model, females recruit males into the group to fulfil their own interests. The primary reason for female sociality is to reduce feeding competition. Males may compete with females for food resources, thus females should prefer, where possible to live in one

male groups. But, as a result of their own reproductive strategies, it is predicted that males will pursue their own interests by (i) preventing incoming males from joining the group, and (ii) blocking female recruitment of new males. Males should thereby be defending their access to reproductive females.

Predictions 1 & 2: Female-bonded groups are expected to concentrate on feeding from discrete, and defensible food patches, but switch to more abundant and uniformly distributed resources during periods of scarcity.

From feeding and ranging data presented in Chapters Four and Five it has been shown that:

(i) Diana monkeys select patchily distributed fruits and flowers when available,

(ii) patterns of ranging are influenced by distribution of selected fruit resources, and

(iii) during periods of food scarcity, they switch to more uniformly distributed mature leaves and arthropods.

Predictions 3, 4 & 5: In territorial species females should defend group territories and the food resources contained therein, while males should compete for access to females.

Chapter Six provided evidence that the females of this species play a very important role in defence of the group territory: initiating calling bouts, stimulating the male to give his loud call vocalizations, and physically repelling intruding groups when necessary. Hence, it would appear that inter-group competition is important in shaping these animals' interactions with groups of conspecifics. But as yet, predictions 4 and 5, i.e. females defend access to food resources, while males are defending access to females, have not been fully tested. The remainder of this chapter will attempt to do just that.

7.4 ARE FEMALE DIANA MONKEYS DEFENDING ACCESS TO FOOD RESOURCES?

If females are defending selected food resources one might predict that female calling patterns should follow seasonal variation in the percentage of fruits and flowers eaten by the two groups.

In Group E there were no significant correlations between the frequency of female calling bouts and percentage of fruits and seeds, or flowers, in the diet. However, data from Group W did show a significant positive association between monthly calling behaviour and flowers consumed[1] (T = +0.462, N = 12, $p < 0.05$; one tailed) and interestingly, a significant negative correlation between calling rates and the amount of foliage being consumed across the year (T = -0.394, N = 12, $p < 0.05$).

With respect to the observed association between calling behaviour and consumption of flowers, there is a confounding variable that needs to be considered. During January 1989, social relationships between members of Group W seemed uncharacteristically volatile, with high rates of contact calls and "grunt" and "chitter" vocalizations. Grunts and chitters are commonly given during aggressive intra-group interactions. When the group was re-contacted in March 1989 it became apparent that it was undergoing fission.

The animals that were splitting off from Group W appeared to be inhabiting an area on the north eastern border of the study group's range. Throughout the March sample Group W fed extensively from a female <u>Chlorophora</u> <u>regia</u>[2] tree that was in flower. The location of this tree is shown in Fig.7.1.

On two occasions group W approached the tree, and members of the break-away group were seen fleeing from it.

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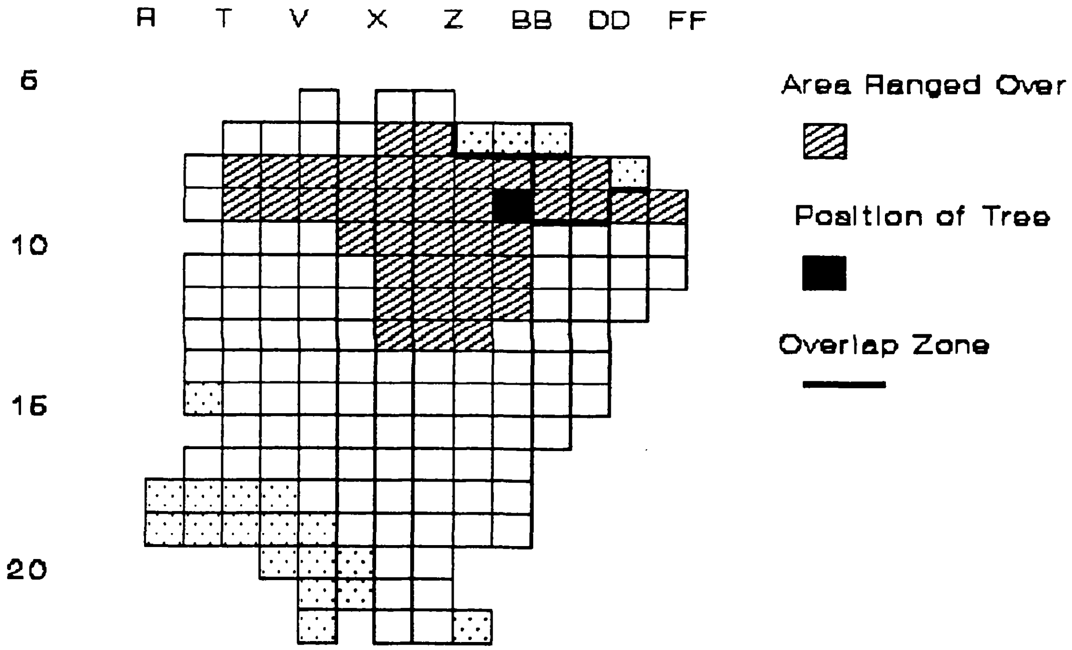
[1] assuming the amount of flowers consumed is proportional to the time spent feeding on flowers.

[2] 35.8% of their monthly diet was obtained from this particular tree.

Fig. 7.1: Group W - Location of <u>Chlorophora</u> <u>regia</u> Tree Fed From in March 1989



On the third occasion, as Group W were travelling towards quadrat AA-9 (the location of the flowering tree) contact whistles were heard from the direction of the tree. Group W raced through the trees; some females giving chatter-screams as they ran. The adult male gave several loud calls before I caught up with the group at the tree. By this time the resident male of the study group was giving loud calls and displaying from a neighbouring quadrat. Meanwhile, females, subadults and juveniles drove their opponents out of the tree and chased them over 50m northwards into the next quadrat. Females from both groups continued to chatter-scream while their respective group males called and gave stiff-legged bouncing displays from the tops of trees approximately 150m apart. At no time did the resident male leave his display site, and it is assumed that this is also the case for the intruder male because his loud calls appeared to originate from the same location throughout this episode.

On this occasion, the encounter appeared to be a contest to determine which group should have access to this particular food patch. But because of the circumstances in which it occurred, i.e. during group fission, it cannot be considered as conclusive evidence that female Diana monkeys are indeed defending access to food resources.

However, as we have already seen from Chapter Four, the availability of fruits and flowers is very variable over time and space. Thus it seems likely that the defence of specific, highly seasonal resources might be confined to those times of year when the benefits of defending such resources outweigh the associated costs of defence. Tables 7.1 and 7.2 provide a summary of the months during which one would predict that females should be defending food resources, i.e. those months in which fruits and flowers comprised a minimum of 20% of the monthly diet.

Table 7.1: Summary of Months When Group W is Expected to Defend Food Resources

Month	Plant Part	% Comp. Diet	Species & Location
Apr 88	Fruit	38.0	Landolphia hirsuta common liana, dispersed throughout forest.
Oct	Fruit	38.4	Hannoa klaineana - fed from 1 tree, >200m from nearest contested boundary.
Nov	Fruit &	13.7	Funtumia africana - 2nd most common species in West Study Site.
	Flowers	22.1	Millettia leonensis - common liana species.
Dec	Seeds	20.9	Amphimas pterocarpoides - fed in 1 tree >200m from boundary.
Mar 89	Flowers	35.8	Chlorophora regia - 1 from 1 tree, 50m from boundary

Table 7.2: Summary of Months When Group E is Expected to Defend Food Resources

Month	Plant Part	% Comp. Diet	Species & Location
Mar 88	Flowers	32.6	<u>Pentaclethra macrophylla</u> - most common large tree in East Study Site.
Apr	Fruit	30.4	<u>Landolphia hirsuta</u> - most common species of liana in East Study Site.
May	Fruit &	14.8	<u>Uapaca guineensis</u> - 3rd most common species.
	Flowers	29.5	<u>Funtumia africana</u> - 2nd most common species.
Oct	Fruit	12.5	<u>Funtumia africana</u> - as above.
		22.2	<u>Uapaca guineensis</u> - as above.
Nov	Fruit	25.9	<u>Hannoa klaineana</u> - 2 trees in overlap zone.
Dec	Seeds,	42.6	<u>Dialium dinklagei</u> - riverine strip & overlap zone.
	Fruits &	14.2	<u>Hannoa klaineana</u> - overlap zone.
	Flowers	12.3	<u>Daniellia ogea</u> - close to boundary.
Feb 89	Flowers	52.0	<u>Detarium senegalense</u> - 1 tree next to river.

It is predicted that females should defend food resources when fruits, flowers and seeds are important dietary components. However, there are several other factors that need to be considered before testing the above prediction. Firstly, Wrangham's model predicts that females will defend rare and patchily distributed resources, thus flowers and fruits from common widely distributed species such as _Funtumia africana_ and _Uapaca guineense_ are unlikely to be defended. Secondly, the location of food patches within the territory is also likely to be important - only those patches within overlap zones are likely to be predated by intruding groups and will hence need to be defended.

A partial correlation analysis was performed to determine whether there was a significant association between percentage time spent feeding in a quadrat and frequency of calling from that quadrat, when frequency of quadrat use was kept constant.

From consideration of their monthly diet alone, one would expect females in Group W to actively defend their range against potential competitors during April, October - December, and March. The results of the partial correlation analysis do not support this, with the exception of the results from March ($T_{xy.z} = +0.495$, $z = 3.677$, $N = 28$, $p < 0.001$). However, when relative abundance of individual species and location of food patches are taken into account, a rather different picture emerges. During April and

November, monkeys in the western study group were feeding on fruits of Landolphia hirsuta and Funtumia africana, both common species within the Tiwai forest[3]. As shown previously in Chapter Four, the Shannon-Wiener index of diversity for Group W's home range is no different to that of the West Study Site forest (2.92 cf 2.928). It would therefore seem justifiable to assume that neighbouring groups, living in similar forest, are also likely to have easy access to both these species within their own home ranges. During October, December and March, Group W concentrated on eating immature fruits of Hannoa klaineana, seeds from Amphimas pterocarpoides and Dialium dinklagei, and the female flowers of Chlorophora regia[4]. Why did they apparently not defend fruiting trees during the months of October and December? I would suggest that the location of the particular trees visited is the key to the answer.

In October only two Hannoa trees were fed from. Both trees were located at T-13-3[5], over 200m away from the nearest contested boundary. In December a total of one fruiting

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[3] Funtumia africana is ranked the 2nd most common species of large tree in the West Study Site. There is no data on abundance of Landolphia hirsuta, but it was ranked alongside Millettia leonensis as the most common species of liana in the East Study Site, and lianas were considered to make a significant contribution towards the forest productivity on Tiwai (Dasilva, 1989).

[4] Chlorophora regia is a dioecious species (Savill & Fox, 1967).

[5] T-13-3 denotes the quadrat with T-13 intersection at its south-west corner, in the third quarter in a clockwise direction from that intersection.

Amphimas tree and three Dialium trees were fed from - again, these trees were located in the core areas of the group's territory, well away from overlap zones or boundaries.

In March they fed from a tree very close to their range boundary, in an area vulnerable to intrusion by other groups, thus they are likely to have needed to defend it against competing conspecifics.

It would appear that by maintaining an area exclusive to the resident group, food patches located within that portion of their range are safe from predation by intruding conspecifics. It is only those preferred and consequently highly valued species, located in areas where they may be "poached", for which it is necessary to proclaim ownership. Probably, areas of overlap do contain highly sought-after trees, and this is why these areas are contested by neighbouring groups.

From analysis of patterns of range use throughout the year (Chapter Five, Section 5.7) it was noted that quadrats within, and close to, overlap zones appeared to be visited more frequently than either other, non-contested boundary zones or more central regions. I would suggest that this concentration of activity in and around overlap zones is, at least in part, a strategy to enable the resident group to monitor other groups and reinforce boundary locations. By investing time and energy to regularly re-confirm ownership, even outside periods when contested foods are available, Diana monkeys may ensure that when priority of access might be contested, then they will have precedence over intruders, and will consequently succeed in repelling an invading group. Perhaps the real question here is which is least costly; to defend territorial boundaries at all times, or continuously to re-establish and defend boundaries when necessary (cf Lima, 1984).

From Wrangham's model it is predicted that Group E females should be active in range defence during March - May, October - December, and February. Again, the results initially seem inconclusive, but on consideration of species abundance and location the picture becomes clearer. In March through to May, Group E made extensive use of *Pentaclethra macrophylla* and *Funtumia africana* flowers, and *Uapaca guineensis* and *Landolphia hirsuta* fruits. *Pentaclethra*, *Funtumia* and *Uapaca* are ranked 1, 2 and 3 respectively as the most common species of large tree in the East Study Site, thus they are assumed to be equally available to all groups living in that part of the forest. A similar explanation holds for the lack of a significant association between feeding and calling during October. In November and December there were significant correlations as predicted as shown in Table 7.3.

Table 7.3: Partial Correlation Coefficients for Group E

November	$T_{xy} = +0.516$	
N = 61	$T_{xz} = +0.273$	
	$T_{yz} = +0.794$	
	$T_{xy.z} = + 0.512$	$z = 5.827$ $p < 0.001$
December	$T_{xy} = +0.229$	
N = 71	$T_{xz} = +0.177$	
	$T_{yz} = +0.696$	
	$T_{xy.z} = +0.150$	$z = 1.847$ $p < 0.05$

N = Number of quadrats
x = frequency of feeding in quadrat
y = frequency of calling from quadrat
z = frequency of quadrat use

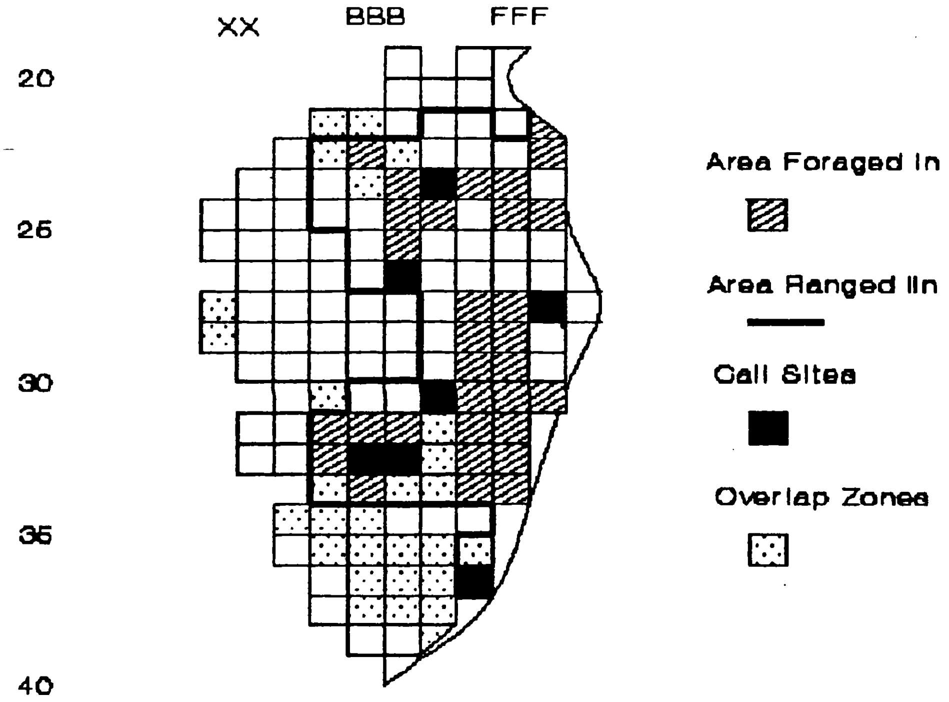
During these two months Group E utilized discrete food patches in and around overlap zones. In February, although Detarium senegalense flowers accounted for 52% of the group's monthly food intake, it all came from one tree, located at GGG-28-3 (see Fig. 7.2). This tree was well within the central portion of their range, close to the river, so there was no threat of predation by conspecifics.

In conclusion, the results from Group E conform to the pattern seen in Group W, with respect to defence of flowers and fruits.

In January 1989, Group E showed a significant negative correlation between feeding and calling behaviour, suggesting that feeding and calling occurred in different range quadrats ($T_{xy.z} = -0.161$, $z = 1.853$, $N = 62$, $p < 0.05$). They fed primarily on arthropods during this sample, and spent much of their feeding time in riverine and central quadrats, away from their range boundaries. Feeding, ranging and calling locations are represented in Fig 7.2 - a possible explanation is that their feeding sites were constrained by having to feed in areas of insect abundance. 33.8% of their monthly feeding time was devoted to catching and eating arthropods, two thirds of which were caught in _Piptadeniastrum_ _africanum_ trees, a species characteristic of mature secondary forest. From a comparison of the distribution of main habitat types within the East Side forest (Dasilva, 1989: Fig. 7.8), and ranging behaviour during January, Group E appeared to centre their foraging activities within the old forest. From Fig. 7.2 - calling sites were predominantly close to, or within, overlap zones, and away from areas that they were foraging in. Thus it would appear that they were indeed foraging and calling from separate locations, suggesting that calling location was not chosen on the basis of food availability, but some other factor. There was a small peak in the number of outgroup calls heard during the January follow (Fig. 7.7) and possibly Group E's behaviour was influenced by this.

The two study groups showed significant partial correlations between feeding and calling locations during August (Group W: $T_{xy.z} = +0.213$, $z = 2.318$, $N = 56$, $p < 0.05$; Group E: $T_{xy.z} = +0.407$, $z = 4.435$, $N = 56$, $p < 0.001$). Both groups were observed feeding almost exclusively on mature leaves andpetioles, and invertebrates during this period (height of the wet season).

Fig. 7.2: Group E - Calling Sites During January 1989



Both groups were observed to range extensively in quadrats close to their range boundaries. Whether they were "patrolling" boundaries or were travelling over such a wide area in search of food remains unclear. There was a significant correlation between distance to the boundary and calling locations (Group W: $T = +0.224$, $z = 2.438$, $p < 0.01$, $N = 56$), but when a partial correlation coefficient was calculated, keeping time spent feeding constant, it was not significant. While this does not support the idea that they were monitoring territory boundaries, it does not negate it. The need to "patrol" the boundaries may have been the reason why they visited those areas, and because there was food available there they were able to feed at the same time and in the same locations. There is some circumstantial evidence from calling behaviour that patrolling might be a valid proposition; results of a step-wise multiple regression analysis carried out on monthly ranging data suggested that female call sites were the most influential variable affecting patterns of range use by Group E during August (Chapter Five). However, further evidence is required before one could reject of the hypothesis that their ranging patterns were as a result of spatial distribution of food resources.

To conclude, female territorial calling behaviour appears to be influenced by a need to defend food resources against other groups of Diana monkeys. This was demonstrated particularly clearly in Group E, where fruit and flowers comprise a larger proportion of the annual diet than for Group W.

Female calling also appears to be associated with group fission (the highest female calling rates in Group W were heard during January and March 1989 when the group was undergoing fission). Cords & Rowell (1986), in their account of group fission in a group of Cercopithecus mitis, reported that the two daughter groups had become spatially and socially separate within a month. It may therefore be the case that group fission is completed quickly in guenons. However, Struhsaker & Leland (1988) reported a longer duration of 4-6 months for completion of group fission in a group of C. ascanius at Kibale (Struhsaker, 1988). This variation between studies may be explained by the fact that the timing and mechanics of guenon group fission is thought to be determined by females resident in the group (Cords & Rowell, 1986), and that it is associated with partitioning of access to food resources (Struhsaker & Leland, 1988).

In conclusion, while the available evidence suggests that the protection of access to valuable food patches is an important determinant of female territorial calling in Diana monkeys, other ecological, social or demographic factors may influence calling patterns in males and females at certain times of the year.

7.5 ARE MALES AND FEMALES FOLLOWING THE SAME STRATEGIES OF TERRITORIAL CALLING AND DEFENCE?

Outgroup calling rates recorded during the two August follows were comparatively low compared with other months: they were very low throughout the major part of the wet season in the East Study Site (Figs. 7.3 & 7.4). Yet, both study groups showed peaks in male and female calling during this period, as shown in Figs. 7.5 & 7.6. As can be seen from the graphs, the peak in female calling from members of Group E was particularly large, being the highest calling peak for both males and females throughout the study period.

It is interesting to consider why, when the two groups exhibit such different patterns of calling from one another for most of the year, they are apparently suddenly conforming to similar patterns. Could the same factor be dictating the pattern of their calling behaviour?

Both groups fed predominantly on arthropods and mature foliage (leaf blades and especially leaf petioles) during this time. But if female territorial defence behaviour is indeed conforming to the predictions of Wrangham's model for female primate groups, then it seems highly unlikely that they would invest considerable time, and possibly energy, in defending widely dispersed and abundant types of foods. Also, other studies have reported that primates do not defend insect resources (Terborgh, 1983; but see Peres

Fig. 7.3: Outgroup Loud Calls Heard by Group W

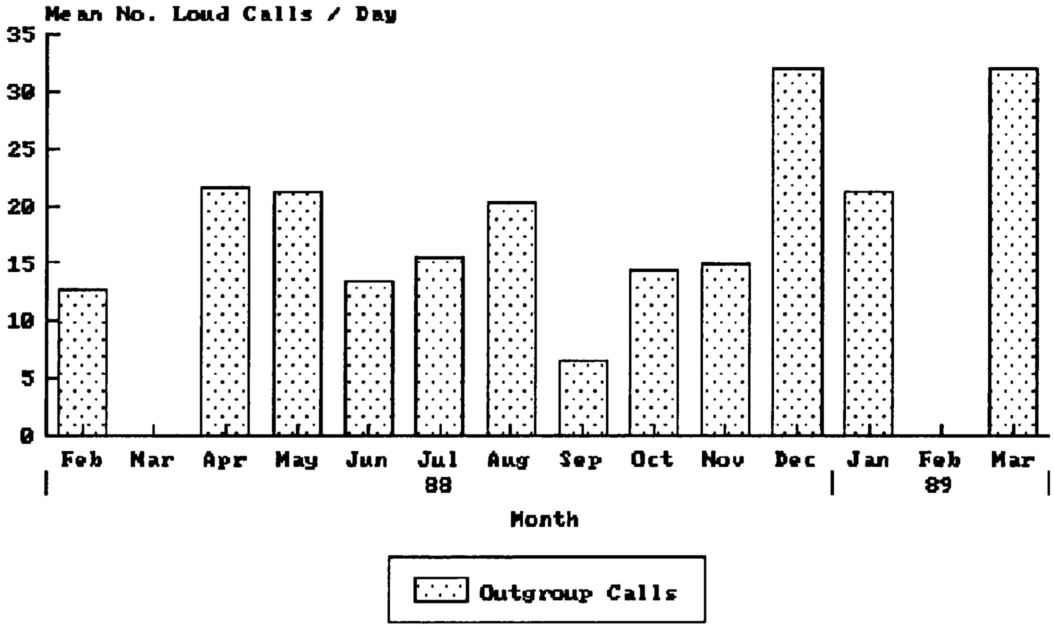


Fig. 7.4: Outgroup Loud Calls Heard by Group E

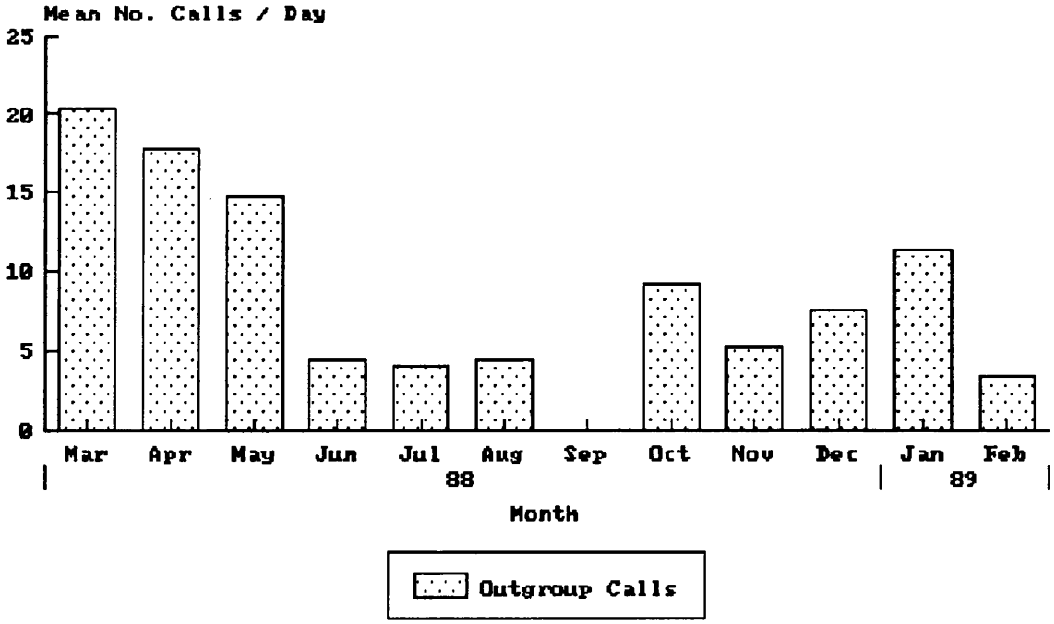
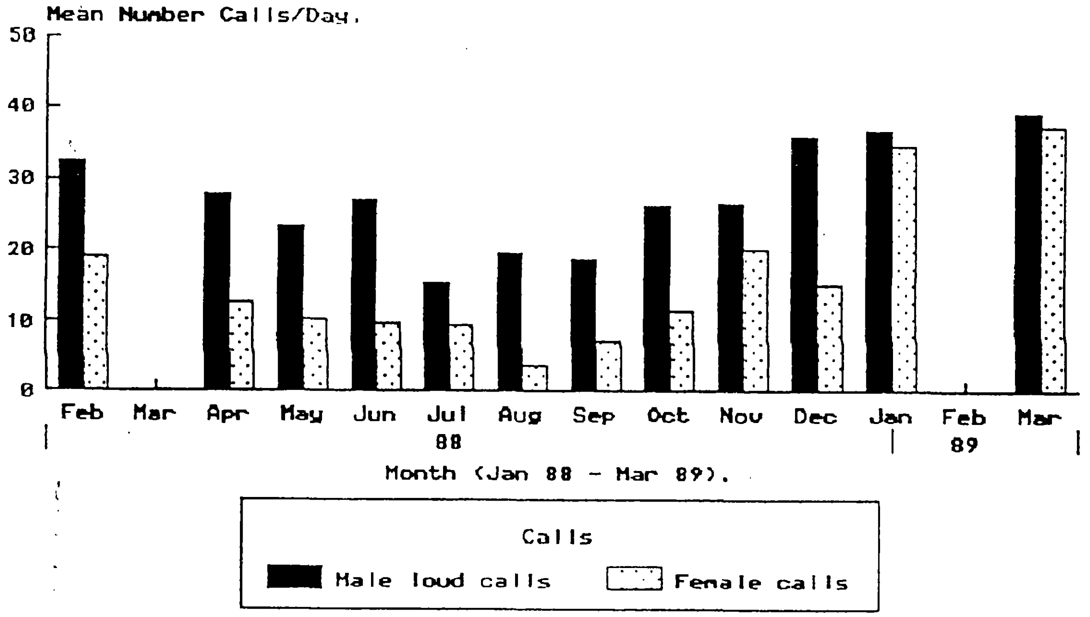
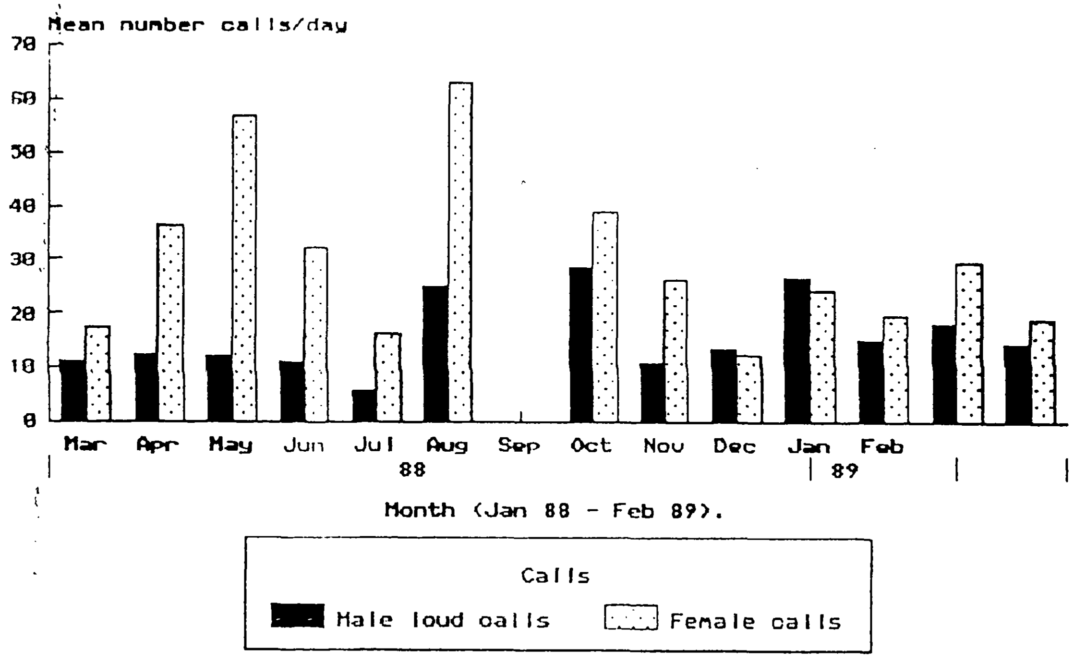


Fig. 7.5: **Monthly Variation in Territorial Calling in Group W**



Blank columns occur in months when no data was collected.

Fig. 7.6: **Monthly Variation in Territorial Calling in Group E**



Blank columns occur in months when no data was collected.

This is further supported by the observation that there was no correlation found between the mean monthly percentage of arthropods consumed and the proportion of boundary quadrats visited for either of the study groups.

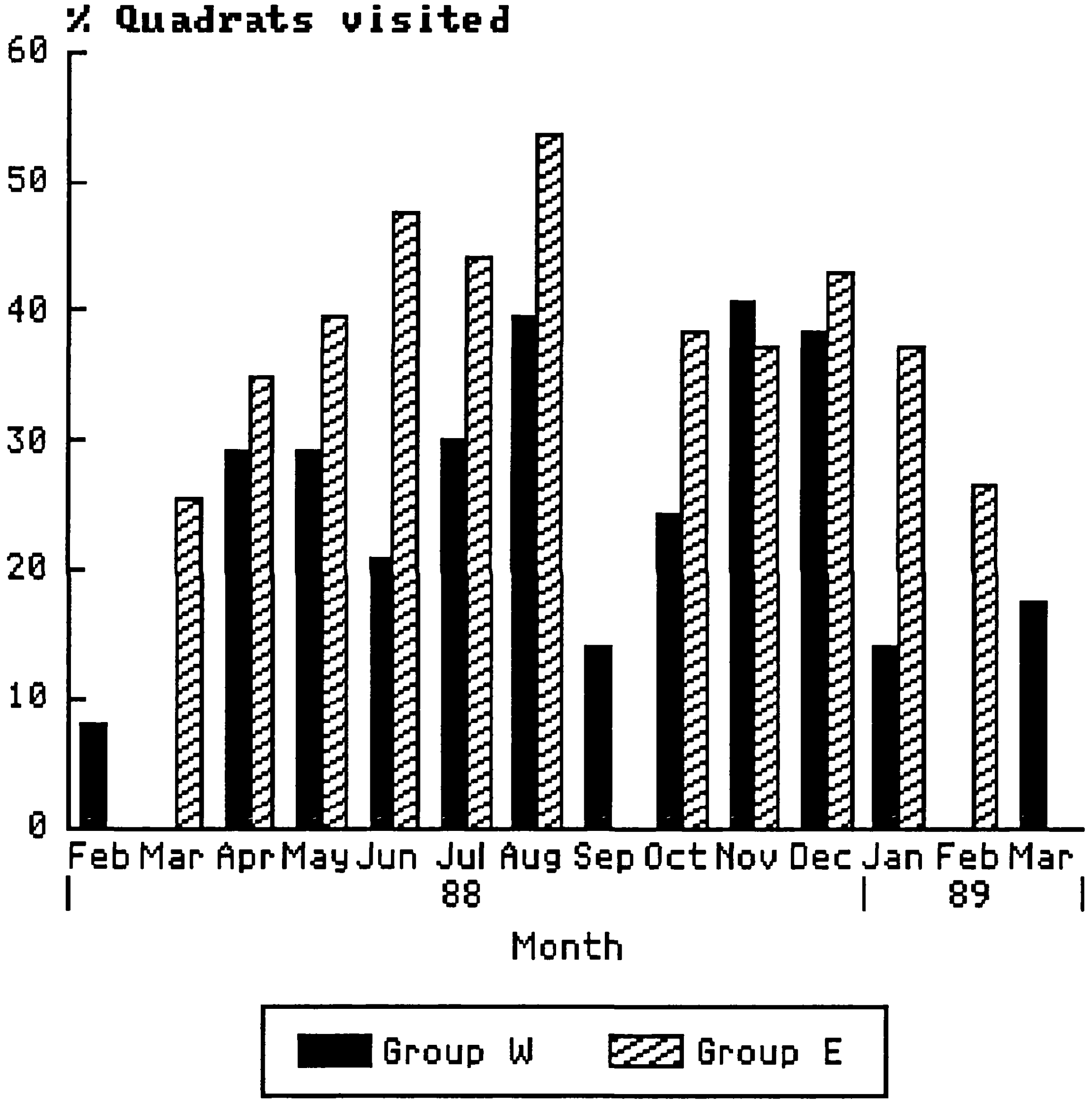
1989). Another interesting observation is that from range maps drawn up for both groups during their respective follows, the two groups appeared to visit a greater proportion of their boundary quadrats than in many other months. This is shown graphically in Fig. 7.7, where the percentage of boundary quadrats visited is plotted against month for both groups. While it is conceivable that the monkeys travelled to these areas in search of food, I would argue that they are likely to have been able to find adequate amounts of food throughout much of their respective ranges, and without having to travel such distances at a time of year when travelling was likely to be difficult because of frequent, heavy rain storms, and when food quality may have been relatively low so disadvantaging them energetically. Considering travel costs, and the time/energy constraints resulting from bulky leaves or time-consuming arthropod feeding, it seems somewhat unlikely that both groups should "choose" to range along their boundaries at the same time of year unless for a specific purpose.

As observed earlier, levels of territorial calling were raised during August. Were calling rates inflated because animals were ranging close to their boundaries and were consequently in areas where

1. they might hear more outgroup loud calls, and
2. they would be more predisposed to answer them (Chapter Six, Section 6.10)?

Considering the proportion of outgroup calling bouts each

Fig. 7.7: Proportion of Boundary Quadrats Visited Across the Year by the Two Groups



group responded to, it would appear that, if anything, the study groups tended to respond to very few bouts heard when compared with other months. Group W responded to 7.1% of audible outgroup bouts (annual mean = 44.3%) and Group E were not observed to respond vocally to any outgroup bouts during the August follow (annual mean = 41.2%). Therefore, I suggest that the inflated calling rates heard from the study animals were not in response to outgroup calling behaviour, but rather that they apparently arose spontaneously. Why?

The mean gestation period for forest dwelling guenons is 5.5 months (Butynski, 1988). All infants sighted in 1989 were estimated to have been born between the last week of December and the first week of February (3 in Group W and 3 in Group E). From extrapolation, August is likely to have been the height of the breeding season. While only one attempted copulation was recorded (Group W - occurred in early October 1988) mating behaviour must have been more frequent than was observed (3 infants born into each group verifies that). Notably, copulations are also rarely seen in captive animals yet in British zoos births occur in most years (Stevenson, 1987,1988,1989).

Why Should Groups Call More During the Breeding Season?

Wrangham (1980) proposed that patterns of social organization seen in female-bonded groups represented a compromise between male and female strategies. Food resources are thought to be a major limiting factor to female reproductive success, thus females should minimise intergroup competition for food resources by defending feeding sites. Reproductive females are the limiting resource for male monkeys, therefore Wrangham's model predicts that males should be defending their access to reproductive females.

Inter-group calling rates seen during August possibly reflect this compromise between male and female strategies. By increasing calling rates, males may be signalling to potential rivals their ability to defend their females against other males. Their loud calls could, theoretically, also attract females from other groups. While loud calls in birds may serve as mate attractants, there seems very little evidence that primate loud calls serve this function (Raemaekers & Raemaekers, 1984; Mitani, 1985b; 1988). Furthermore, there is little evidence of female transfer between guenon groups, except in the recruitment of vervet females to boost female numbers in a declining group. In this instance a group's success in intergroup encounters appeared to be a function of the number of resident females (Cheney & Seyfarth, 1987).

A number of different studies have considered male-male competition and assessment of rivals by means of calling behaviour (Tenaza, 1976; Clutton-Brock & Albon, 1979;

Butynski, 1982; Sekulic, 1982; Sekulic & Chivers, 1985; Whitten, A.J., 1984; Searcy & Andersson, 1986; Cowlishaw, in prep.). If males are competing with each other for breeding purposes, why should female calling also show an increase at this time of year, as shown particularly strongly by Group E?

In the previous chapter it was demonstrated that females are initiating territorial calling bouts and stimulating the group male to loud call. As more and more field data are collected on guenon species, it is becoming increasingly obvious that infanticide is not an unusual phenomenon during male takeovers and multi-male influxes (C. ascanius - Struhsaker, 1977; 1988; Cords, 1984; C. mitis - Butynski, 1982; possibly for C. cambelli - Galat & Galat-Luong, 1979). Females with young infants may have a vested interest in supporting and encouraging the resident male to maintain his position as harem male. Alternatively, some females might be interested in assessing the phenotypic condition of alternative mating partners. But whatever their "intention" it is predicted that females would be advised to encourage the resident male to call; either to keep other males out (Hypothesis 1) or to incite male-male competition in order to facilitate female mate choice (Hypothesis 2). Interestingly, these arguments infer that male calling behaviour could have the same proximate (advertisement of male quality) and ultimate (male repulsion) function. The question here is why females should stimulate it.

To distinguish between these two hypotheses, it would be necessary to determine whether female calling strategies followed one of the patterns outlined below.

Hypothesis 1: Prevention of Infanticide - females should encourage calling only when there are infants present, and hence presumably, not in the breeding season.

Hypothesis 2: Male Quality - females should encourage calling during the breeding season, or when there is least opportunity for infanticide to occur.

Unfortunately, there are no data available from the present study to test whether females are inciting male-male competition as a means of selecting new mating partners (Hypothesis 2), as reported for several mammals (elephants - Poole, 1989; elephant seals - Cox & LeBoeuf, 1977; red howler monkeys - Sekulic, 1983). In order to unravel this, detailed demographic information would be needed on identified females over a considerable time period, along with knowledge of mating partners over this same period. These data were not collectable, nor was it possible to identify individual female callers to determine whether females with infants vulnerable to infanticide called more than those with older, weaned youngsters. As mentioned earlier, visibility conditions within the forest, and group spread, etc, prevented the collection of such information.

However, it is possible to test whether males were engaging in bouts of counter-calling aside from the territorial calling initiated by group females; therefore, it should be possible to go some way towards testing hypothesis 1.

7.6 ARE MALE DIANA MONKEYS DEFENDING THEIR ACCESS TO REPRODUCTIVE FEMALES?

Until now I have considered only those calling bouts where the group male and group females were calling together. But on occasions males do initiate calling bouts, and call on their own, without other members of the group joining in. The resident male in Group W gave 24.4% of all loud calls within male-only calling bouts, where either (i) he called on his own, or (ii) in conjunction with an outgroup male. Similarly, the male from Group E gave 18.5% of his loud calls under the same conditions.

It has already been established that when males and females call together, it is the females that tend to initiate calling bouts (Chapter Six, Section 6.7), thus determining group calling frequency, and possibly the duration of calling bouts. This lends support to the hypothesis that the most plausible explanation of the purpose of these particular calling bouts is to further female reproductive strategies by means of territorial defence. An important question is whether these male-only calling bouts serve a separate function from group calling bouts. If indeed they are given in different contexts and follow different patterns from group calling bouts, this would be further evidence that males and females are pursuing different strategies.

Several studies of male calling behaviour in gibbons have suggested that male calls are used as an advertisement of male quality, or fitness. In Hylobates klossii male songs become increasingly elaborate as the bout progresses, culminating in a complex trill phase (Tenaza, 1976; Whitten, 1980). Several authors have postulated that males use these protracted and elaborate calling bouts to advertise their willingness (Gittins, 1978) or ability (Whitten, 1984) to defend a territory. In his recent review of gibbon song function Cowlishaw concludes that male singing behaviour, in male solo song bouts (and possibly duets), is best explained as an advertisement of male quality, and can be looked upon as a strategy to deter challenges by other males that might result in the loss of mate and offspring (Cowlishaw, in prep.)

From their study of male roaring in red deer, Clutton-Brock & Albon (1979) demonstrated that roaring ability reflected body condition, and thus strength and stamina, in rutting stags. From field observations, and a series of playback experiments, they concluded that stags used roaring bout frequency and length as a means of assessing their chances of beating an opponent in any encounter. Whether stags would then engage in physical fights with one another appeared to be determined by the outcome of roaring matches.

Loud calls of male Diana monkeys do not differ in form between mixed and male-only calling bouts. They are stereotyped, and repetitive, thus limiting the amount of information likely to be carried in them. It is these sorts of calls that Zahavi (1987) suggests would transmit information describing condition, rather than complex calls where it would be difficult to detect small individual differences. Therefore, if they are used by males to transmit information about an individual's phenotypic condition, there appear to be two parameters that might convey relevant information, namely frequency and duration of bout.

If males are using loud calls as a form of male-male competition it is expected that they will attempt to match bout frequency and duration with each other. Correlations were used to test whether there was a significant association between frequency, and mean duration, of resident male loud calls with those of outgroup calling males. Because male-male competition was the hypothesis being tested, only those calling bouts where the resident male called alone were considered. While outgroup calling bouts may have been initiated, and participated in by females, this is unlikely to be a problem as female chatter-

Fig. 7.8a: Male Counter-Calling - Group W - Bout Frequency

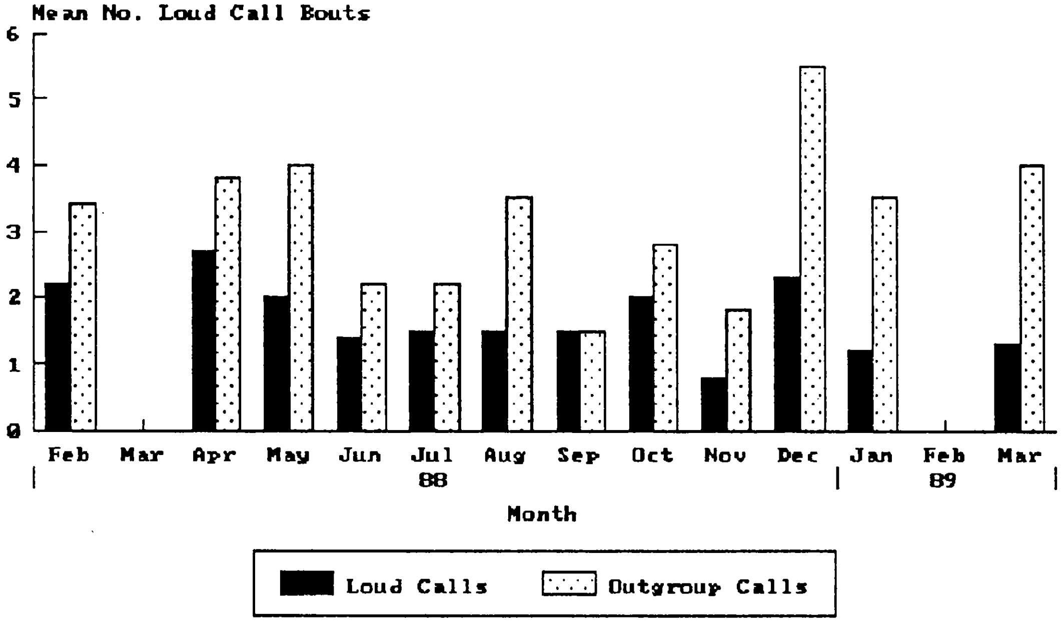
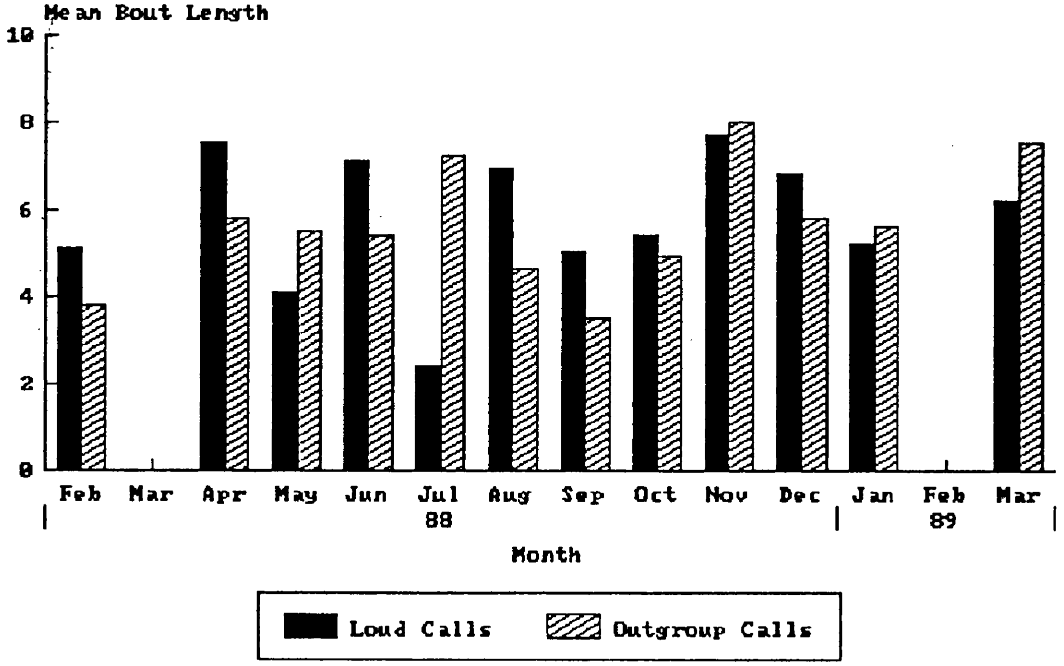


Fig. 7.8b: Male Counter-Calling - Group W - Bout Length



screams are markedly less audible over distance. Any outgroup calling bout where the neighbouring group was close enough that female calls could also be detected was excluded from the analysis, and it is assumed that in all other cases where groups were further away the study group male would have been unable to hear and therefore respond to any female contribution to the bout.

The results are presented graphically in Figs. 7.8 & 7.9 , where mean calling bout frequency and duration are plotted alongside outgroup calling behaviour. While frequency of calling bouts of the resident male in Group W were significantly correlated with bout frequency of neighbouring males ($T = +0.199$, $z + 2.166$, $N = 56$, $p < 0.05$), there was no significant association found for mean calling bout duration across the year. The resident male from Group E appeared to be matching his calling bouts to those of neighbouring males, with significant positive correlations with bout frequency ($T = +0.384$, $z = 3.719$, $N = 45$, $p < 0.001$) and mean bout duration ($T = +0.252$, $z = 2.44$, $N = 45$, $p < 0.01$).

While these results are consistent with the hypothesis that males are matching bout frequency and duration with one another, there is no indication of whether males are changing their calling behaviour according to the context in which it occurs, i.e. is this matching of calling parameters a feature of male-only calling bouts, or do they do this

Fig. 7.9a: Male Counter-Calling - Group E - Bout Frequency

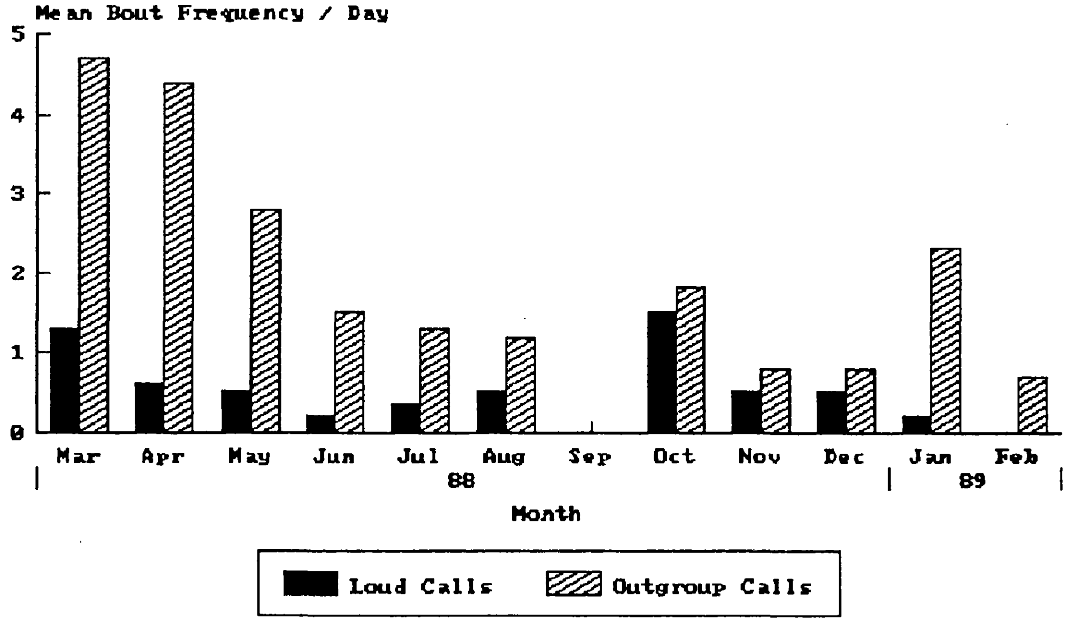
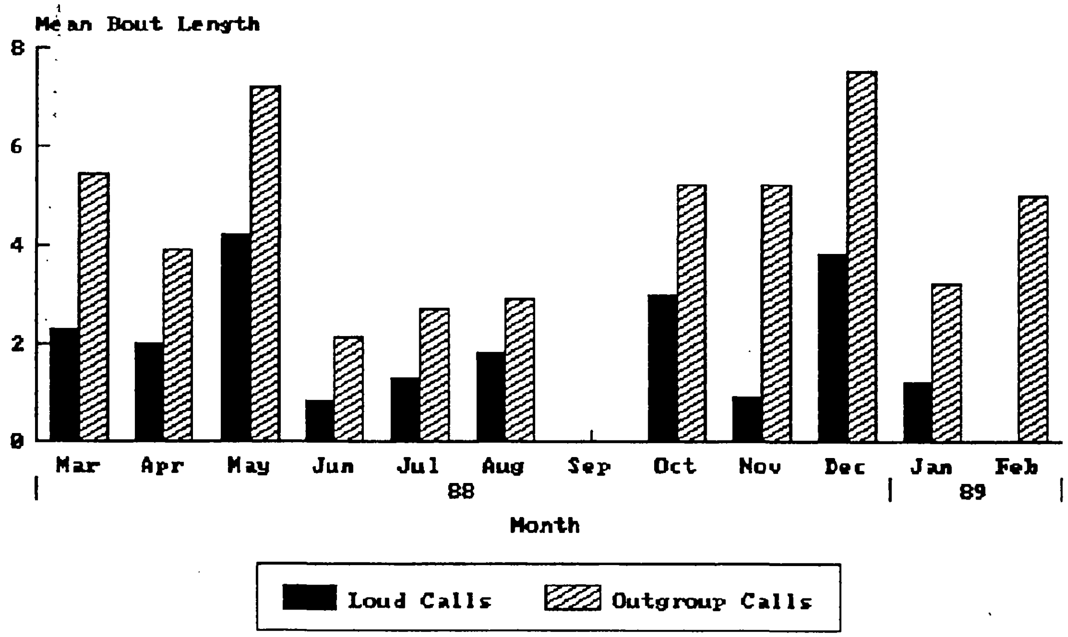


Fig. 7.9b: Male Counter-Calling - Group E - Bout Length



when calling alongside group females? To test this, a further series of correlations was carried out to determine whether males were matching mean frequency and duration of bouts against those of outgroup males, when calling with group females. Within Group W, there was no evidence to suggest that male calling behaviour within the two types of calling bout followed the same patterns, supporting the hypothesis that the two calling patterns result from different causal strategies. With Group E, male calling frequency correlated with outgroup calling frequency ($T = +0.219$, $z = 2.043$, $N = 42$, $p < 0.05$). However, male calling frequency correlates with female calling frequency (Chapter Six). When a partial correlation was calculated, keeping female calling fixed, male calling patterns showed no correlation with outgroup calling ($T_{xy.z.} = 0.110$, $z_{xy.z} = 1.026$, $p > 0.05$, $N = 46$). Thus the results confirm that males are behaving differently according to the context in which they are calling.

Interestingly, when male calling was kept fixed female calling rates did correlate significantly with outgroup Loud calling rates ($T_{zy.x} = +0.184$, $z_{zy.x} = 1.717$, $p < 0.05$). This would appear to confirm that when calling alongside females the male's calling behaviour is manipulated by the females in such a way as to serve their own purposes. However, when calling on his own, the male is following his own strategy, matching his calling behaviour to that of potential rivals.

7.7 GUENONS - FEMALE TERRITORIALITY AND MALE-MALE COMPETITION?

On reviewing the guenon literature, there is detailed information available on inter-group encounters in four species other than the present study. Although none of the published studies have specifically concentrated on female guenon roles in such encounters, researchers have reported their participation as summarized in Table 7.4.

In both the studies of West African green monkeys, unlike the Kenyan vervets, females were not observed to play an active role in intergroup encounters. Kavanagh gives very little information about the form that encounters took, and explains variation in territoriality between study groups as a consequence of differences in food supply and predation pressures (Kavanagh, 1981).

Table 7.4: Male and Female Participation in Inter-group Encounters

Species	**Study Site**	**Comments**	**Reference**
C. ascanius	Kibale	females defend territory	Struhsaker, (1977)
	Kakamega	females & juv.s defend territory, males not territorial.	Cords 1984
C. mitis		females & juv.s defend territory	Tsingalia & Rowell 1984
		males do not defend territory, but join in during breeding season.	Cords & Rowell 1986
E. patas		females & juv.s intergroup spacing. males drive off males.	Struhsaker & Gartlan 1970
		females - intergroup encounters - male joins in during breeding season.	Chism et al 1984
C. aethiops	Amboseli	female vocalizations in encounters - males & females join in. most aggression to males.	Cheney & Seyfarth, 1982; Cheney, 1981
		males and females active in encounters.	Whitten 1984
C. tantalus	Cameroon	territorial & non-territorial groups.	Kavanagh 1981
C. sabaeus	Senegal	seasonal variation in territoriality.	Harrison, 1983b

Reinterpretation of a Case Study

In Harrison's paper a very detailed picture of the form of encounters, and some information as to the contexts in which they were given, is presented (Harrison, 1983b). Harrison reported that males were predominantly responsible for group defence, and that most encounters involved ritualised male jumping displays that escalated into male-male aggression between groups. Although females and juveniles did sometimes vocalize during encounters, they were only observed to join in group defence on 3 out of 27 occasions. There were significantly more encounters in the wet season compared with the dry season, and Harrison explained this apparent seasonality in territorial defence as being a consequence of seasonal inter-group competition for valuable food resources in overlap zones.

West African green monkeys would thus appear to be behaving very differently from their East African counterparts. Fieldwork carried out at Amboseli, Kenya, has shown that both males and females take part in inter-group encounters (Cheney, 1981) and that females are predominantly responsible for intergroup vocalisations (Cheney & Seyfarth, 1982). Alongside this, there appears to be year round defence of group territories.

Harrison (1983b) compared his own results with those from Amboseli. He observed that over 50% of all inter-group encounters at Amboseli involved vocalizations only, and that relatively few encounters escalated into fights. He also noted that the three encounters at Mt. Assirik where females joined in took place in open woodland or bamboo. With the exception of infants, all group members took part during these encounters, biting, rushing and chasing the opposing group members on the ground. It was suggested that these encounters took a different form from usual because of the lack of trees -

> "males had no continuous canopy to carry out their leaping and crashing displays, interpreted as the ritualized expression of intergroup aggression"
> (Harrison, 1983b)

Because of the similarity in habitat structure with that found in Amboseli, i.e. lack of continuous canopy for males to display in, Harrison postulated that this might in part explain the difference in format of encounters between the two sites.

From comparison of differences in habitat quality and population densities between the two sites, Harrison suggested that year round territorial defence at Amboseli could be explained as a consequence of a combination of poorer habitat quality, necessitating defence of food resources, and a higher density of monkeys, resulting in smaller home ranges that could be effectively defended. Higher population densities and smaller home ranges would also explain the higher encounter rates observed at Amboseli (group size was similar for both sites), and might explain why animals resorted to presumably less costly calling bouts, rather than the potentially more costly displays and physical contests.

In the light of the results of the present study, and information presented in Table 7.3, I would like to present an alternative explanation to account for Harrison's results and suggest that green monkeys at Mt. Assirik and vervets at Amboseli are likely to be following similar strategies, and that their behaviour is, in fact, not different at the two sites.

Firstly, I would like to summarise the results of this study and then show that Harrison's results might fit the paradigm of this thesis as well. I would argue that female Diana monkeys are territorial (Chapter Six) and that their chatter-scream vocalisations incite group males to give loud calls which advertise and re-affirm boundary location (Chapter Six, Section 6.7). Secondly, male Diana monkeys are not territorial in terms of defending a specific area and thus the resources contained within it (Section 7.5). Instead, evidence suggests that they are defending their access to reproductive females, and that loud calls might be used to assess some aspect of male quality as a result of male-male competition. However, as a consequence of female groups remaining within their specific territories, male calling behaviour appears site specific and thus could mistakenly be interpreted as territorial. While females might make use of this, either passively or by active manipulation of the male, the motivational force behind male calling is apparently one of male-male competition for females, and not the defence of a specific area and/or the food resources contained therein. Observations from other studies of guenon behaviour would appear to corroborate this (see Table 7.3).

While I do not dispute that green monkeys are likely to be showing seasonal defence of food resources, and that differences in availability and distribution of those foods may account for the differences in territorial encounter rates between the two sites, I would suggest that Harrison's results do not necessarily reflect seasonality of territorial defence but rather seasonal variation in levels of male-male competition.

There were significantly more encounters during the wet season compared with the dry at Mt. Assirik (Harrison, 1983b). The birth season extends from January to April, with a birth peak in March (Harrison, 1982 in Butynski, 1988). Thus, assuming a gestation of 5.5 months the height of the breeding season would have been during September and October. This further confirms that the results reflect seasonality in male-male competition. There may well be seasonal defence of food resources occurring here but I would suggest that the results presented by Harrison reflect seasonal variation in male-male competition for access to reproductive females that escalates during the breeding season, which coincides with the wet season.

Harrison assigns similar motivational states to the different patterns of inter-group encounters seen at Mt. Assirik. I would suggest that only those encounters where either females (i) called, or (ii) joined in physical disputes, should be considered territorial; all others are likely to be examples of male-male competition.

From Harrison's paper, the 3 encounters where females were protagonists all occurred in open woodland or bamboo. The majority of overlap zones corresponded to these habitat types, and from maps of food tree distribution, there were trees of contested species in those areas (See Harrison, 1983; Figs. 1 & 2). Female participation on these occasions may have been to defend food resources against other groups, and nothing to do with lack of trees for male displays. Because the motivation behind these encounters was territorial, and not male-male competition, these encounters were more like those seen at Amboseli.

This particular paradigm of female territorial defence and male-male competition for mates, also provides a good explanation for differences seen between Mt. Assirik and Amboseli monkeys. If, as Harrison postulated, food stress is less severe at Mt. Assirik than Amboseli, it is predicted that intergroup feeding competition will be less;

territorial encounter rates should be lower, and concentrated in seasons when food is scarce for green monkeys compared with vervets. This appears to be the case, with female vervets possibly using vocalizations (cf *C. diana*) to repel approaching groups.

When vocal encounters are excluded from the Amboseli sample, encounter rates were found to be very similar across the two sites (Harrison, 1983b). Possibly this reflects similar levels of male-male competition within the two populations.

To conclude: variation in patterns of inter-group encounters across the year at Mt. Assirik, and variation between a population of green monkeys in West Africa and vervets in East Africa, can best be explained within the paradigm presented here.

7.8 DISCUSSION

It would appear that there is good evidence that Diana monkey groups are female-bonded, and that they fit the predictions of Wrangham's ecological model (Wrangham, 1980). Their dietary patterns follow those predicted by the model. When available, they select discrete, and therefore defendable, food resources such as fruits and flowers. During periods of scarcity they switch to more uniformly distributed and common resources such as leaves and arthropods. Thus, they appear to adapt to periods of potentially high intra-group feeding competition by switching their diet, rather than changing the size of their feeding group, as predicted, and observed, in non-female bonded species (e.g. howler monkeys - Sekulic, 1982; spider monkeys - Chapman & Lefebvre, 1990).

Diana monkeys are territorial and, as predicted by Wrangham, the females play an important role in defence of the group territory. Evidence suggests that females use their chatter-scream vocalisations to encourage the group male to loud call. An interesting question is why do the females manipulate the male in this way?

One possibility is that it is energetically costly to engage in the regular, long-distance calling bouts, that are needed to advertise and defend territorial boundaries. Possibly as a consequence of energetic constraints imposed by pregnancy and lactation, females are forced to adopt the particular strategy that they do. While there is no data available as to the energetic costs of calling for Diana monkeys, there is a considerable amount of evidence from a variety of mammals confirming that pregnancy and lactation are energetically expensive for females (Nicolson, 1987). Also, within the gibbon literature, it has been suggested that increased singing activity seen during periods of peak fruit availability may reflect the high levels of energy-rich foods being taken (Chivers, 1976). However, this could be interpreted rather differently, if it is assumed that calling behaviour is territorial and thus these animals are defending food resources.

Alternatively, females might be opting to get males to call to reduce the potential risk of predation to themselves and their offspring. While male loud calls appear to travel distances of upwards of 1km through the forest, female chatter-screams appear to be audible over several hundred metres only. Also, unlike the male, females are not easily located when they give chatter-screams.

Possibly by making use of the characteristics of male loud calls i.e. they can travel over a long distance and are easily located, females can reduce their risk of predation, particularly from arboreal raptors. Males tend to sit apart from the main body of the group, and seem to spend more of their time in the crowns of emergent trees. Possibly they sit higher up to provide a better vantage point for detecting predators, and potential rivals. Because of its loudness, and the ease with which the caller's location can be determined from loud calls, predators maybe are likely to be more attracted to the source location of loud calls than the rest of the group, so giving females and youngsters an opportunity to escape.

Females, can presumably afford risking losing the group male to a predator. There are solitary males within the population, and it is likely that should a resident male be killed, or seriously injured, a replacement male would readily join the group. Certainly, there are no reports of sightings of groups of Diana monkeys without an adult male present.

If females are following such a strategy where does that leave the male? Do the benefits of being resident in a group of females outweigh the predation risks? At present this discussion can only remain at a speculative level. However, it is worth considering (i) the information necessary to test such a hypothesis, and (ii) what evidence, if any, is already available to support or refute it.

Firstly, loud calls and chatter-screams could be analyzed using a sonogram. By determining frequency and wavelength characteristics of the two call types, it would be possible to demonstrate that they differ in their abilities to carry over distances, and provide source location cues.

Secondly, it would be necessary to assess the levels of predation of primates within Diana monkey habitats to investigate the age/sex class structure of prey animals. Izor (1985) suggested that animals at the periphery of a group are more vulnerable to predation. Group males are spatially peripheral - consequently this may confer a greater risk from predators. Struhsaker and Leakey (1990) investigated the impact of predation by crowned-hawk eagles on primates at Kibale. They reported that adult male Cercopithecus mitis and Colobus guereza experienced higher predation levels than expected from species and age/sex class density estimates. Apparently adult Colobus badius and Cercopithecus ascanius do not loud call as frequently as the other two species. The authors suggested that Cercopithecus mitis and Colobus guereza were possibly made more vulnerable to predation as a consequence of their giving frequent loud calls.

Male Diana monkeys might prove more vulnerable to raptors as a result of their peripheral position and frequent loud calling behaviour. However, males preyed upon in the above study may have been solitary animals and not resident in groups. Cheney and Wrangham (1987) in their review of predation on primates concluded that

> "the protective behaviour of males against less threatening predators such as cheetah may sometimes be due more to the males' relative lack of vulnerability than to a high motivation to defend the group"

On only one occasion was a predator seen to attempt to prey on a Diana monkey during the present study.

> During June two females from group W were heard alarm-calling from about 200m away from the main body of the group. The adult male responded immediately, running back to the females, giving loud calls as he ran. While the two females, and an infant of about 5 months old, sat huddled together continuing to alarm call, the adult male gave the characteristic stiff-legged jumping display towards the large bird. He pursued the predator for about 200m stopping to call and give threat displays

every few jumps while the bird retreated slowly.[6]

If females are using male loud calls as a means of reducing their own risk of predation either the reproductive advantages of being a group male are very considerable indeed, or the risk of predation is not that great, at least with respect to males. However, without further information there seems little point in additional speculation along these lines.

Why do male Diana monkeys invest time and energy in territorial calling bouts on behalf of the group females? Interestingly, the results of this study also suggest that males may use the same loud call vocalisation as an advertisement of some aspect of male quality. I would like to suggest that maybe this explains, in part, why males are apparently willing to invest in female territorial strategies.

Possibly calling for the females entails very little extra cost to a male because he would call anyway to deter rivals. This could be interpreted as an example of male territoriality. However, the results demonstrate that when males and females call together it is the females that initiate calling and determine the length of a calling bout (female calls were found to match outgroup calls when

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[6] A large Diana monkey was observed chasing a crowned-hawk eagle along a path in Tai National Park, Ivory Coast, (Newing, pers.comm.)

females and males called together). Only when group males call on their own, without their group females, does their calling behaviour match that of potential rivals.

The most plausible explanation would seem to be that female Diana monkeys are territorial, but that they require the services of male loud calls to advertise and defend their territorial boundaries, possibly as a result of energetic constraints or to reduce the risk of predation. Males use their loud calls to defend their access to reproductive females. While they may suffer extra energetic costs as a result of calling on behalf of group females, these costs may be outweighed by outgroup males interpreting territorial calls as an advertisement of phenotypic condition.

7.9 A BRIEF DISCUSSION OF THE ULTIMATE CAUSES OF PRIMATE SOCIALITY

Wrangham's model of female-bonded primate groups postulated that primate sociality arose in order to defend a year-round supply of food to ensure the survival of females and their offspring (Wrangham, 1980). An alternative hypothesis, known as the predation risk hypothesis, suggests that group-living evolved in response to the risk of predation (Andelmann, 1974; van Schaik, 1983).

Evidence in Support of the Predation Hypothesis:

1. If predation is an important factor promoting primate sociality, we might expect that animals in larger groups are less susceptible to predation than those in smaller groups. This is supported by van Schaik (1983) who found that in populations where there were no predators, juveniles had higher mortality rates in larger groups compared with small groups, presumably as a result of greater intra-group competition. But in populations where there was the risk of predation, juveniles in smaller groups suffered higher rates of mortality than those in larger groups. While van Schaik's results lend support to the predation hypothesis, he points out that they can not be considered conclusive because of the variability between studies.

2. It has been found that predator detection rates are higher in larger groups (van Schaik et al, 1983). However, Pulliam and Caraco (1984) argue that larger groups might be predicted to show more vigilance irrespective of their adaptive significance. Perhaps the most important consideration here is whether individuals can reduce their vigilance costs when within a group, and yet still be safer. There is good evidence that this is the case for flocking birds (Jennings & Evans, 1980). In primates, many observers have reported that males invest more time in vigilance behaviour than do females and their young (Cheney & Seyfarth, 1981), and that they appear to reduce their time

spent foraging and feeding in order to do this (van Schaik & van Noordwijk, 1989). If males are devoting more time to scanning for predators (though at least some of their scanning behaviour is likely to be in order to detect potential rivals), and in multi-male groups, all resident males follow this pattern, then possibly it is advantageous to live in multi-male groups in areas of high predation risk over and above the advantages of being in a larger group. While males may not actively defend their groups against predators, they may help provide a particularly efficient early warning system, enabling females and youngsters to escape.

3. Further circumstantial evidence that group living developed as a response to predation pressure comes from the observation that interspecific differences in group size appear to correlate with the risk of predation in different habitats. Terrestrial and savanna-dwelling species tend to live in larger groups than do arboreal, forest species (Crook & Gartlan, 1966; Clutton-Brock & Harvey, 1977).

4. It has been suggested by a number of different people that some species form polyspecific associations in response to predation pressure (Gautier & Gautier-Hion, 1983; Gautier-Hion et al, 1983). In their study of the association between olive colobus and Diana monkeys in Sierra Leone Oates and Whitesides (1990) suggest that the olive colobus formed associations with other species to

reduce the predation risk, being a small-bodied monkey that habitually forages in small, dispersed groups.

5. Finally, although the evolution of discrete predator-specific alarm calls in vervet monkeys (Seyfarth et al, 1980a; 1980b) can not be considered to be evidence supporting predation pressure promoting group living (alarm calling seems to benefit the caller more than potential recipients - Cheney & Seyfarth, 1981), it is indicative that predation pressure must have been of significance during the evolution of these monkeys.

As pointed out by Dunbar (1988) much of the evidence in support of the predation risk hypothesis comes from studies of terrestrial species of primates, where the risk of predation may be of more relevance than for arboreal, forest species such as Diana monkeys. The present study was not designed to investigate the ultimate causality of group-living in primates. Rather, it was set up to investigate male and female strategies within female-bonded species. Although the present study provides some anecdotal data suggesting that Diana monkeys are occasionally subject to attempted predation by raptors, there is little evidence that such attacks carry a high risk of mortality, either for Diana monkeys or other guenons. However, there is some evidence that adult male blue monkeys in Kibale are more vulnerable than other age/sex classes or guenon species at that site. It is possible that this lack of quantitative data on predation in guenons, and other arboreal primates, is as much a consequence of poor observation conditions as a reflection of reality.

More recently, several authors have favoured the idea that predation may be the ultimate cause of group living, so defining the lower limit on group size. Nevertheless, it is distribution of food resources and intragroup competition that sets the upper limit on group size, and apparently explains much of the social organization and behaviour patterns observed in living primates (Wrangham & Rubenstein, 1986; Wrangham, 1987; van Schaik, 1989).

To conclude: Wrangham's model provides a very useful framework for discussing territoriality, and male and female mating strategies, in the Diana monkey. What little evidence is available suggests that other guenons would also fit the theory. But while it is a very useful model for describing proximate causation and function of male and female strategies, and highlights the dichotomy between the sexes, it may not necessarily reflect the evolutionary selective pressures responsible for current patterns of female sociality.

SUMMARY

1. In this chapter the assumptions and predictions made by Wrangham's model of female-bonded primate groups are outlined, and discussed with respect to Diana monkeys.
2. Data is presented to show that female Diana monkeys do defend their access to patchily distributed resources as predicted by the model.
3. Males appear to use their loud calls in several different contexts. When calling with group females they appear to serve a territorial function, on behalf of the females. When males call on their own calling patterns appear to reflect male-male competition, possibly for access to reproductive females.
4. The data support the predictions of Wrangham's model, and it is suggested that male and female calling behaviour appear to reflect the dichotomy between male and female strategies.

CHAPTER EIGHT

GENERAL CONCLUSIONS

> **"The knowledge of subtle differences ... is a knowledge invaluable to mankind. What is more the knowledge of differences leads to an understanding of relationships" (Embler, 1951)**

As stated in the Introduction the purpose of this thesis was to use the paradigm of Wrangham's model of female-bonded primate groups to investigate the dichotomy between male and female strategies in a female-bonded species *Cercopithecus diana*. The specific aims were to

1. investigate whether female Diana monkeys are territorial, and if so, how do they defend their territories against conspecifics.
2. Determine whether guaranteeing access to specific food resources was the proximal function for their behaviour.
3. Test whether males are defending access to reproductive females rather than maintaining territories.

From results presented in Chapter Six females appear to use their chatter-scream vocalisations as territorial calls. Females in both study groups were found to initiate inter-group calling bouts significantly more frequently than did either of the group males, though calling rates varied both between the sexes, and between the groups. Female chatter-screams appear to incite males into giving their loud calls which appear to advertise territory boundaries and ownership. Territorial calling bouts seem to result in mutual avoidance by neighbouring groups at home range boundaries. However, on those few occasions when intruding groups did not retreat at the approach of the resident group it was the females, subadults and juveniles that drove the intruders back into their own ranges while both males called and displayed to the opposing group. Thus the available evidence suggests that female Diana monkeys are indeed involved in territorial defence of their group territories, using specific calls to enlist the help of the resident male in giving long distance calls.

From Chapter Three it would appear that distribution of food and food quality influence the activity patterns shown by the two groups. Evidence presented in Chapter Four demonstrated that while Diana monkeys appear to eat patchily distributed fruits, flowers and seeds when available, during periods of scarcity they switch to feeding on more ubiquitous food resources such as mature leaves and arthropods, as predicted by Wrangham's ecological model. Ranging data presented in Chapter Five suggests that ranging patterns were determined at least in part by climatic factors and the distribution of food resources. Thus it would appear that the acquisition and processing of food plays a very important role in structuring these animals day to day existence, and Chapter Seven does provide some evidence that females do indeed act to defend their food resources against conspecifics.

The third aim was to determine whether males were territorial or, as predicted by the model, defending their access to reproductive females rather than defending a territory per se. From Chapter Seven there was some indication that during the breeding season the two groups travelled far more extensively in boundary and overlap zones of their respective home ranges than at any other time of year. And males were found to use their loud call vocalisations in several different contexts. When calling in response to group females, male calls appeared to serve a territorial function on behalf of the females in the group. But when males called on their own or in conjunction with outgroup males, their calling appeared to serve a different function. During these calling bouts males were found to match frequency of bout and bout length with that of outgroup calling males, suggesting that males may use these calls as an advertisement of phenotypic condition in male-male competition. There is no conclusive evidence presented in this thesis to show that males are indeed competing for access to breeding females. However, male calling, independent of female calling, peaked during the breeding season which would seem to provide some support for the hypothesis that males are defending access to reproductive females.

Before ending this discussion I would like to introduce one further point that I have not as yet considered in this thesis but which is of particular importance when considering male strategies. As pointed out by Rowell (1988b) sociobiology has tended to make the assumption that social systems reflect mating systems. The guenons provide evidence to refute this. A number of studies have reported that forest guenons live in uni-male groups (Struhsaker, 1969; Rudran, 1978a; Hall, 1965), but with continuing long term studies of these monkeys it is becoming increasingly evident that while for much of the time groups are uni-male this is not necessarily an accurate representation of their mating system. Chism & Rowell (1986) reported that during the breeding season uni-male groups of Erythrocebus patas became multi-male and females showed promiscuous mating behaviour. Tsinglia & Rowell (1984), Cords et al (1986), and Henzi & Lawes (1988) have all reported similar occurrences for Cercopithecus mitis.

It has been suggested that in breeding seasons where more than two females are in oestrus the resident male is unable to monopolize them therefore providing an opportunity for incoming males to mate with group females. In this study a second adult male was seen travelling with Group E from November 1988 - February 1989. The second male behaved very much like the group male, sitting peripheral to the group. He did give loud calls in response to group females' chatter-screams but did not call as often as the resident male and was never heard to initiate a calling bout or call on his own. Three infants were born into this group during the birth season. It is tempting to consider this as evidence that the resident male was unable to defend three breeding females against a rival. However, the second male was not seen to copulate with group females and there is no evidence that he was the father of any of the ensuing offspring.

To conclude: When considered within the paradigm set up by Wrangham's model of female-bonded primate groups the results of this study are presented to demonstrate that males and females are pursuing different strategies. The resultant social system reflects the compromise between male and female strategies as well as differences in individual strategies as might be seen between the resident females. In order to comprehend how social and mating systems function and inter-relate it is important to have a detailed understanding of the different reproductive strategies of the animals concerned including those living in uni-male groups, solitary males and all male bands. Only when life-time reproductive strategies of males as well as females are understood will it be possible to determine the ways in which individual strategies influence group structure and mating systems.

APPENDIX I: Age/Sex Classes

AM	**Adult Male**	
AF	**Adult Female**	Only those animals with visible nipples were classed as adult females. Nulliparous adult females would have been missed using this criterion, but because this thesis is interested primarily in reproductive females it was felt to be an appropriate means of categorising animals.
SA	**Sub-Adult**	This category included all animals of near to adult size, and any animals of adult size whose sex was unknown. These animals are likely to have been either large sub-adult males or nulliparous adult females.
J	**Juvenile**	All animals estimated to be between the ages of 1 year and approximately 2.5-3 years were included in this category. Age estimations were made on the basis of shape and size of body.
I	**Infant**	All animals estimated to be between 0-12 months old were classed as infants. Age was estimated on the basis of body size, coat colour and beard, degree of dependency on mother, and suckling behaviour.

APPENDIX II: Description of Phenophases

The following are the definitions of plant parts as used by Davies and Dasilva, (Davies, pers. comm.). The same definitions were used in this study.

1 Vegetative Parts

- **Mature Leaves:** these were leaves that were fully developed and had a species-specific size, shape and appearance.
- **Young Leaves:** foliage was classified as young leaves if it fulfilled 2 or more of the following criteria:
  (i) different colour
  (ii) lower turgidity, and
  (iii) smaller size
  when compared with that classified as mature foliage. Leaf buds were included in this category.

2 Reproductive Parts

- **Flower Buds and Flowers**
- **Immature Fruits:** fruits that have not attained full size, or coloration yet.
- **Mature Fruits:** these are fruits that have attained full size, full coloration, and there is evidence that they are being dispersed from the tree.

APPENDIX III: Seasons on Tiwai

(Adapted from Dasilva, 1989; Table 3.1, pg 67)

TIWAI SEASON

NUMBER	NAME	DATE	BRIEF DESCRIPTION
1	Early Dry	Dec-Jan	Little or no rain, relatively cool nights, cool or hot days.
2	Late Dry	Feb-Mar	Mainly dry, warm nights and hot days. Relative humidity <60%
3	Dry-Wet (Transition)	April	Light showers become more frequent, relative humidity 60%.
4	Early Rains	May-Jun	Rainfall increases, showers more frequent and heavier, night temperatures quite high, but day temperatures drop as rainfall increases. Relative humidity >75%.
5	Main Rains	Jul-Aug	Prolonged & heavy rainfall, day temperatures rel. cool, night temperatures remain as before. Relative humidity 80-90%.
6	Late Rains	Sep-Oct	Heavy showers but of shorter duration. Day temperatures increase slightly. Relative humidity >80%.
7	Wet-Dry (Transition)	Nov	Rainfall decreases rapidly but very heavy showers can occur. Temperatures remain as before. Relative humidity >80%.

APPENDIX IV

SPECIES	Abr.	W freq.	E freq.
Afrosersalisia afzelia	AFAF	4	1
Afzelia bella (var. gacilior)	AFBE	4	0
Albizia		0	2
Albizia ferruginea	ALFE	7	13
Albizia zygia	ALZY	26	16
Allanblackia floribunda	ALFL	1	0
Alstonia boonei	ALBO	9	3
Amphimas pterocarpoides	AMPT	37	9
Anisophyllea meniaudi	ANME	3	0
Anopyxis klaineana	ANKL	7	0
Anthocloista nobilis	ANNO	1	0
Antiaris africana	ANAF	19	12
Aubrevillea platycarpa	AUPL	2	0
Berlinia confusa	BECO	0	1
Berlinia occidentalis	BEOC	0	2
Bombax buonopozense	BOBU	3	1
Blighia welwitschii	BLWE	8	1
Bridelia		2	0
Bridelia grandis	BRGR	4	3
Bussea occidentalis	BUOC	9	2
Cathormium altissimum	CAAL	0	21
Calpocalyx brevibracteatus	CABR	3	13
Canarium schweinfurthii	CASC	3	6
Copaifer salikounda	COSA	0	3
Canthium subcordatum	CASU	1	2
Ceiba pentandra	CEPE	0	1
Chlorophora regia	CHRE	12	0
Cleistopholis patens	CLPA	1	0
Combretodendron macrocarpum	COMA	26	4
Croton penduliflorus	CRPE	2	0
Cynometra leonensis	CYLE	147	26

Daniellia ogea	DAOG	18	8
Daniellia thirifera	DATH	1	0
Detarium senegalense	DESE	4	11
Dialium dinklagei	DIDI	3	47
Dialium guineense	DIGU	0	15
Discoglypremna caloneura	DICA	1	0
Distemonanthus benthamianus	DIBE	0	3
Entandrophragma cylindricum	ENCY	1	0
Erythrina mildbraedii	ERMI	0	1
Erythrophleum ivorense	ERIV	0	14
Erythroxylum mannii	ERMA	0	1
Ficus		3	5
Ficus mucosa	FIMU	8	0
Ficus Sp 1		0	2
Ficus Sp 2		0	2
Ficus Sp 3		0	1
Ficus Sp 4		0	1
Funtumia africana	FUAF	225	249
Garcinia kola	GAKO	1	0
Guarea cedrata	GUCE	0	1
Hannoa klaineana	HAKL	8	27
Holarrhena floribunda	HOFL	24	21
Homalium letestui	HOLE	10	0
Hymenocardia lyrata	HYLY	0	1
Irvingia grandifolia	IRGR	0	1
Klainedexa gabonensis	KLGA	0	4
Lovoa trichiliodes	LOTR	1	0
Macaranga barteri	MABA	0	1
Maesobotrya barteri	MABA	0	1

Mammea africana	MAAF	0	1
Millettia rhodantha	MIRH	12	7
Monodora tennifolia	MOTE	3	0
Nauclea diderrichii	NADI	4	8
Newtonia aubrevillei	NEAU	1	7
Ochthocosmus africanus	OCAF	0	1
Oldfieldia africana	OLAF	0	1
Pachypodanthium staudtii	PAST	0	1
	PAPO	0	2
Parinari excelsa	PAEX	20	59
Parinari glabra	PAGL	0	5
Parkia bicolor	PABI	3	16
Pentaclethra macrophylla	PEMA	46	258
Piptadeniastrum africanum	PIAF	226	92
Plagiosiphon emarginatus	PLEM	0	35
Pycnanthus angolensis	PYAN	73	37
Ricinodendron heudelotii	RIHE	9	1
Samanea dinklagei	SADI	17	25
Sapium aubrevillei	SAAU	0	4
Sapotaceae		0	1
Scottellia coriacea	SCCO	0	2
Sterculia tragacantha	STTR	2	0
Strombosia glaucescens	STGL	4	0
Terminalia ivorensis	TEIV	2	9
Treculia africana	TRAF	1	2
Uapaca 1		0	5
Uapaca guineensis	UAGU	41	246
Uapaca heudelotii	UAHE	0	2
Vitex micrantha	VIMI	0	2

Xylia evansii	XYEV	19	8
Xylopia aethiopica	XYAE	53	7
Xylopia quintasii	XYQU	1	1
Zanthoxylum		4	4
Zanthoxylum gilletii	ZAGI	6	2
Unident.		10	17
Unident. 34		0	3
Unident. 68		0	1
Unident. 69		0	3
Unident. 70		0	1
Unident. 71		0	2
Unident. *		0	4
Unident. **		0	4
Unident. ***		0	2
2574		0	4

N = 1196 (+10) = 1328 (+17)

W Species Richness = 60 (+ Unidentified species)

E Species Richness = 83 (+ Unidentified species)

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