The Behaviour and Ecology of the Buffy-Headed Marmoset, *Callithrix flaviceps* (O. Thomas, 1903)

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Abstract

This thesis presents the results of the first long-term field study of the buffy-headed marmoset, *Callithrix flaviceps*, a rare primate species with a small natural range in southeastern Brazil. The introductory discussion presents the species in the context of a review of the available literature on the taxonomy, evolution, behaviour and ecology of the primates of the family Callitrichidae. The study animals, study site and methodology are then described. A detailed description of seasonal fluctuations in the abundance and distribution of dietary resources at the site provides a frame of reference for the analysis of the study group's behaviour. General patterns in the group's use of time and space are outlined in the context of these variables and comparisons are made with other callitrichid species. A number of behavioural strategies are identified. A more detailed analysis of seasonal patterns in the group's foraging and feeding behaviour emphasizes the systematic nature of its exploitation of resources. The gum-feeding adaptation of the marmosets is seen as having far-reaching implications for many aspects of their behaviour and ecology. Behavioural specialisations for the capture of certain types of prey and the exploitation of secondary and disturbed forest habitats are also proposed. It is concluded that most features of the group's foraging behaviour support predictions drawn from optimality models, in the context of an overall "time-minimising" strategy in particular. As much of the behavioural repertoire of this species appears to be broadly similar to that of other callitrichids, these findings offer a number of important insights into their ecological adaptations.

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Plate 1

Adult female Callithrix flaviceps *"Cuba" in typical* Acacia paniculata *vegetation.*

Preface

Field work is all about solving problems. Like most scientific research, it is aimed at the solving of theoretical problems in order to expand our understanding of complex natural phenomena. Unlike most other research, primate field work presents a number of more practical problems which can have an even greater influence, not just on the eventual outcome of a project, but on the daily life of the field worker himself. This thesis is in my name, but it owes its successful completion to the many people who helped me solve these problems.

First and foremost, I would like to express my sincerest gratitude to my supervisor, Bob Martin. While he can be seen as the instigator of most of the problems I have encountered over the past four and a half years, he has also been instrumental in solving all of them, offering me constant inspiration, detailed supervision and practical help throughout this time, both at University College London and here in Zürich.

My first practical problem began in October 1983, in London, and was only solved a year later. I was able, at least, to learn a lot about marmosets in the meantime and I would like to thank everyone at the Wellcome Laboratories, Zoological Society of London who taught me what they knew about them, especially Dave Abbott and Lynne George. I received advice, encouragement and practical help from a number of people during this year, and would like to thank, in particular, Simon Bearder, John Cooper, Daphne Garwood, John Hatton, Miranda Stevenson and everyone at the Anthropology Department, University College London. I would also like to thank Ray and Marie-Claude Cook, and all at the British Council, Rio de Janeiro, who not only pointed me in the right direction once I arrived in Brazil, but made me feel very much at home.

Special thanks are due to Senhor Feliciano Miguel Abdalla, without whose goodwill, towards me, the monkeys and the remaining forest at "Fazenda Montes Claros", the field work could not have taken place:

Muito obrigado, Senhor Feliciano.

I would also like to say *muito obrigado* to everyone who nurtured me at the fazenda, especially Lada Alves and Jairo Gomes, and Joachim Fifi, who made me laugh at least once every day. *Muito obrigado* to the people of Ipanema as well, all of whom offered me both help and friendship, especially the families of Dona Leda das Neves and "Zezito" Ferreira.

The success of my project owes a great deal to many other Brazilians, and "quasi-Brazilians", both in Belo Horizonte and in other parts of the country. I am especially grateful to my project supervisor in Brazil, Célio Valle, whose enthusiasm and encouragement match those of Bob Martin. Almost everyone else at the Zoology Department, Universidade Federal de Minas Gerais, also helped me out in some way, but a special mention is due to Gustavo Bouchardet da Fonseca, Ilmar Bastos Santos, Maria Cristina Alves and Ney Carnevalli.

I am especially grateful to Anthony Rylands, now at U.F.M.G., both for sharing his considerable wisdom on the study of marmosets and for allowing me to make detailed comparisons of my own data with those contained in his doctoral thesis.

Many others also helped me, directly or indirectly, with my field-work. Daniel Louzada da Silva nursed me through the first two months (when I wasn't nursing him), while Dida Mendes accompanied me through the last two. In the meantime, Adelmar Coimbra-Filho, James and Lou Anne Dietz, Karen Strier, Milton Thiago de Mello, Priscila Moreira de Andrade and Sérgio Mendes all contributed, in their own ways, to the success of my project.

One other Brazilian, my wife, Cida, has made by far the most important contribution both to the success of my project and my daily life. Without her, the field work would not have been a success. Without her hard work and dedication, in fact, the writing of the pages that follow may never have been possible.

Having completed my field work, the next problem involved the analysis of the considerable quantities of data I had collected and the writing of this thesis. This was greatly facilitated by the hospitality of the Anthropological Institute of the University of Zürich-Irchel, and the practical help and advice of Marco Gagliardi and Zdenka Nechvátalová, in particular. I would also like to thank Gustl Anzenberger of the Psychology Institute at the same university for his help in reviewing this thesis before submission.

Practical help at a different level came from a number of institutions. I received a postgraduate studentship from the Medical Research Council of Great Britain during the first three years of my work. I obtained additional grants for materials from the Boise Fund of Oxford University, the Central Research Fund of London University and the Leakey Trust. In Brazil, authorisation for my research was given by the *Conselho Nacional de Desenvolvimento Científico e Tecnológico* of the brazilian government, and the project was supported by the *Fundação Brasileira pela Conservação da Natureza.* My work in Zürich was sponsored by the A.H. Schultz-Stiftung. I am indebted to all these organisations for their support.

Finally, I would like to dedicate this thesis to the three people without whose support it would truly not have been possible: my supervisor, Bob Martin, my wife, Cida Lopes Ferrari and my father, Franco Ferrari.

1

Introduction

The marmosets and tamarins are the smallest extant anthropoids, and constitute, together with Goeldi's monkey, the large neotropical primate family, the Callitrichidae, comprising at least 20 species. Their small size, cryptic colouration and preference for dense arboreal habitats make them difficult to observe in the wild. Long-term field studies of callitrichid species began a little more than ten years ago, and very little is known of the habits of most species in the wild. Of the seven probable species of *Callithrix* (the taxonomy of the genus will be discussed below), only one, *Callithrix humeralifer*, has been the subject of a field study lasting more than six months [Rylands, 1982]. Despite this paucity of information on their natural habits, however, marmosets, especially *Callithrix jacchus*, are popular laboratory primates and there is a great deal of information available on many aspects of their biology [*e.g.* Gengozian & Deinhardt, 1978; Rothe *et al.*, 1978]. This information, despite its obvious limitations, forms a useful reference for field studies.

This thesis is based on data collected during the first long-term field study of the buffy-headed marmoset, *Callithrix flaviceps* [Thomas, 1903], which was carried out at a private forest reserve on the Fazenda Montes Claros (FMC), a large privately-owned ranch in the municipality of Caratinga, Minas Gerais, Brazil. The species is known locally as *"mico"*, *"macaquinho de cheiro"* or *"sagüí taquara"*, the latter name referring to its preference for secondary forest in which a number of species of *"taquara"* or bamboo are commonly found. *C. flaviceps* has the smallest distribution of any *Callithrix* species and is the least well known (there were only three individuals known by the author to have been in captivity in 1986). Apart from a short study carried out at FMC [Alves, 1985] and more general observations on its distribution [Coimbra-Filho & Mittermeier, 1973a; Mittermeier *et al.*, 1980;

Coimbra-Filho *et al.*, 1981], nothing is known about the ecology, social organisation or behaviour of this species.

The primates of the Atlantic coast forest of Brazil are under increasing threat from habitat destruction [Mittermeier *et al.*, 1982], and *C. flaviceps*, with its originally small distribution, is one of the most seriously affected. While the species may occur frequently in small isolated remnants of the original forest cover [pers. obs.], it possibly exists in only one officially protected reserve, *Reserva Biológica de Nova Lombardia*, Espírito Santo [Mittermeier *et al.*, 1982], although Coimbra-Filho [1984] also reports its presence in the *Parque Nacional do Caparaó*. It is hoped that this study will not only document the habits of this species and provide useful insights into the behaviour and ecology of the callitrichids in general, but will also contribute to its survival in the wild.

Taxonomy and Evolution of the Callitrichidae

The family Callitrichidae includes the genera *Callithrix*, *Cebuella*, *Leontopithecus* and *Saguinus*. The monospecific genus *Callimico* has been variously placed in the Callitrichidae [*e.g.* Napier & Napier, 1967; Rosenberger, 1981], the Cebidae [originally by Thomas, 1913] and in its own family, Callimiconidae [Hershkovitz, 1977]. The most recent review of the Callitrichidae [Sussman & Kinzey, 1984] follows the former classification, with *Callimico* as the sole member of the sub-family Callimiconinae and the remaining four genera forming the sub-family Callitrichinae. While accepting this classification, however, Sussman & Kinzey exclude *Callimico* from the majority of their discussion of the Callitrichidae. This usage emphasizes the ambiguity of this genus, which shares some important features such as claw-like nails with the other four genera, but lacks others, such as twinning and the complete loss of the third molar. The classification of Sussman & Kinzey [1984] is followed in this thesis, thus the sub-family Callitrichinae contains the genera *Callithrix*, *Cebuella*, *Leontopithecus* and *Saguinus*, and the family Callitrichidae contains these four genera plus *Callimico*.

The marmosets and tamarins are the smallest extant platyrrhines. None exceeds 1kg in body weight and *Cebuella pygmaea*, at between 100 and 120 g [Sussman & Kinzey, 1984], is the smallest living anthropoid. All species of the Callitrichinae are also characterised by twinning, claw-like nails, tritubercular upper molars and the absence of a third molar, features which are rare or unique among higher primates. These characteristics, along with their highly insectivorous diet, can be seen as part of the evolutionary adaptation for a "small energy package" niche [Eisenberg, 1978]. These features also seem to enable the occupation of an apparently successful rôle as colonising animals, which they have done throughout the forested areas of central and southern America [Moynihan, 1970]. The geographical distribution of the marmosets and tamarins is only slightly less wide than that of the cebids, although, as Pook [1978] points out, they exhibit much less variation in most features ranging from body size to social structure, implying that their original radiation was far more rapid.

Hershkovitz [1970, 1972, 1977] sees the small body size of the callitrichids as a primitive retention, along with other characteristics including their claw-like nails and tritubercular upper molars. More recently, however, a number of studies have suggested that these features, along with the tendency for twin births, absence of the third molar and even monogamy, have arisen as part of a process of phyletic dwarfism [Leutenegger, 1973, 1980; Rosenberger, 1977, 1984; Maier, 1978; Peters, 1978; Ford, 1980]. While there is good reason to suggest that most of these traits are derived, there is no conclusive evidence that they result from a process of dwarfing. Sussman & Kinzey [1984] have argued, on the other hand, that the lack of any relative increase in brain size is contrary to a dwarfing hypothesis.

Garber [1980] points out that clawed digits are not found in the majority of extant primates with a body weight of 900 g or less, and that the evolution of claw-like tegulae is most likely a specialised adaptation to exudate feeding rather than a consequence of dwarfing. Similarly, while tritubercular molars are associated with insectivory [Rosenberger, 1977; Ford, 1980], there is no specific reason to see them as a result of dwarfing, although the loss of the third molar has been correlated with the shortening of the skull in a number of primate species [Rosenberger, 1977]. A Miocene fossil M^1 assigned to the species *Micodon kiotensis* [Setugoshi & Rosenberger, 1985] has been interpreted as an indication that an early reduction in body size preceded the reduction of cusps in the callitrichid lineage, although without further evidence, this is inconclusive. As a unique characteristic among primates, the twinning of the marmosets and tamarins seems to be a "highly derived condition" [Sussman & Kinzey, 1984, p.443], although whether this is an allometric correlate of reduced body size as suggested by Leutenegger [1973] is unclear, especially as an apparent process of dwarfism in the smaller *Galago* species has not resulted in a similar tendency [Nash, 1983].

Evidence, both from captive studies [Hearn, 1978; Lunn & McNeilly, 1982] and records of birth intervals in the wild (including those of the present study), indicates that post-partum ovulation may be a universal feature of the reproduction of the marmosets and tamarins. This, in addition to their small size, tendency to have twin births and exploitation of a niche which demands a high degree of adaptability, has led to the suggestion that these primates have undergone "*r*-selection" [Eisenberg, 1978]. There are a number of features which contradict this view, however. Captive studies have shown that reproduction is physiologically suppressed in all but a single female in family groups [Abbott, 1979]. Virtually all studies[1] in the wild have also reported that groups contain a single reproductive female, even when more than one adult female is present, and that groups containing a number of adult females are not only common, but may remain stable for long periods [Rylands, 1982; present study]. Furthermore, the development of a complex system of infant care which may involve all group members and even the voluntary transfer of food [Brown & Mack, 1978; Cleveland & Snowdon, 1984; Feistner & Chamove, 1985; Ferrari, in press] again contradicts the idea that callitrichines have been "*r*-selected". It thus seems possible that the development of the features which point to an "*r*-selected" strategy are outweighed by the demands on a small primate of rearing a relatively large litter, at least under the conditions encountered by most groups.

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[1] ***Ramirez [1984] reported two females with young in a*** Saguinus mystax ***group, although one female and her offspring died shortly after its birth [Sussman & Garber, 1987]. Terborgh & Goldizen [1985] also found circumstantial evidence of the presence of two breeding females in a*** Saguinus fuscicollis weddelli ***group. In neither case, however, was there any good evidence to indicate that both females had conceived in the same group.***

While all species share a unique and complex set of characteristics which has important implications for their evolutionary history and ecology, the four genera may be separated into two groups on the basis of the lower anterior dentition which in *Callithrix* and *Cebuella* is specialised for the gouging of bark to stimulate the flow of plant exudates [the "short-tusked" form, Coimbra-Filho & Mittermeier, 1978]. While not embodied in formal taxonomic classification, these two groups are generally distinguished in English by the common names "marmoset" (*Callithrix* and *Cebuella*) and "tamarin" (*Leontopithecus* and *Saguinus*), and these names are used in this thesis for ease of reference, where appropriate. The mandibular incisors of marmosets are relatively long and narrow, while the canines are incisiform. Together with their lack of lingual enamel, they form an efficient chisel-like structure [Rosenberger, 1978; Maier, 1984; see Sussman & Kinzey, 1984: figure 1, p. 420]. The specialisation of the anterior dentition in the marmosets has important implications for their ability to exploit certain marginal habitats. This feature may, in turn, have an important influence on a number of characteristics of marmoset behaviour, ecology and possibly even social organisation, particularly in comparison with the "long-tusked" tamarins which are only able to exploit plant exudates in an opportunistic fashion.

The geographical distribution of the genus *Callithrix* shows a clear separation of two main groups of species. The bare-ear and tassel-ear marmosets [*Callithrix argentata* group: Hershkovitz, 1977] are confined to the Amazonian forest south of the Amazonas and Madeira rivers, while the tufted-ear marmosets [*Callithrix jacchus* group: *ibid*] are found both in the Atlantic coast forest of eastern Brazil and in the adjoining *"cerrado"* (savanna). Hershkovitz [1977, pp. 568-569] is unsure of the presence of the *C. argentata* group in the east of Mato Grosso and the south of Pará, but the Araguaia river forms a considerable geographical barrier between the two groups in this region and it thus seems unlikely that, human intervention notwithstanding, there are any areas of sympatry between them.

The *C. argentata* group contains two species, *C. argentata* and *C. humeralifer*, each containing 3 sub-species, a classification which is agreed on by Hershkovitz [1977], Mittermeier & Coimbra-Filho [1981], and Sussman & Kinzey [1984]. The classification of the *C. jacchus* group, however, shows less consensus. Hershkovitz [1977] identifies a single species, *C. jacchus* containing five subspecies; *C.j. aurita*, *C.j. flaviceps*, *C.j. geoffroyi*, *C.j. jacchus* and *C.j. penicillata*. Mittermeier & Coimbra-Filho [1981], on the other hand, give species status to each of these subspecies. In addition, they identify two sub-species of *C. aurita* (*C.a. aurita* and *C.a. petronius*) and of *C. penicillata* (*C.p. kuhlii* and *C.p. penicillata*). While unsure of the validity of *C. a. petronius*, they propose possible full species status for *C.p. kuhlii*. Sussman & Kinzey [1984] follow the classification of latter authors, which does seem to be the best interpretation of the available evidence, although, as Mittermeier & Coimbra-Filho [1981: p. 35] point out, "reasonable arguments can be made" for both interpretations.

However, four of the five proposed species of the *C. jacchus* group have produced fertile hybrids in various combinations in captivity [Coimbra-Filho, 1970, 1971, 1973, 1978a, pers. comm.]. Hershkovitz [1968, 1975, 1977], in addition, presents detailed evidence of what is interpreted as geographical metachromism and intergradation within a single species of *C. jacchus*. Mittermeier & Coimbra-Filho [1981], on the other hand, argue that such evidence may be related both to intra-specific variation and the presence of sub-specific populations, and that there is no good evidence of intergradation in the wild. Much of Hershkovitz's argument does, in fact, rely heavily on the examination of museum specimens, many of which, especially of the rarer species, are poorly catalogued and few in number. In the case of *C. flaviceps*, for example, Hershkovitz was only able to examine three specimens, all from the same collection in Santa Teresa, Espírito Santo. Ruschi [1964, 1965], working in the same area of Espírito Santo, recorded the presence of *C. aurita* in Domingos Martins a year after reporting the presence of *C. flaviceps* in this area and there seems to have been a great deal of confusion in the cataloguing of the distribution of the marmoset species of Espírito Santo [see Hershkovitz, 1977]. Individuals of *C. flaviceps* at FMC exhibit an unexpected degree of variation in pelage, particularly of the head and ventral surface of the body (tones ranging from black to a pale buff), despite the relatively small size of the population, which has been isolated for at least 40 years. Detailed observation of the study group at FMC also indicate that there are seasonal changes in pelage, which may further compound difficulties in the interpretation of intergradation between species on the basis of museum specimens, especially when dealing with such small samples.

One of the major problems of interpreting the available evidence is the effect of human interference, both in terms of habitat destruction and the introduction of species into areas outside their original distribution, notably that of *C. jacchus* into Rio de Janeiro [Hershkovitz, 1977; pers. obs.]. Coimbra-Filho & Mittermeier [1973a] argue that habitat destruction in Espírito Santo has favoured *C. geoffroyi*, which has thus encroached into areas that were originally within the distribution of *C. flaviceps*. The Atlantic forest has been rapidly and systematically reduced to approximately 5% of its original area in this century [Mittermeier *et al.*, 1982] and exists today in relatively small and isolated patches, a fact which may have led to hybridisation in effectively captive populations, possibly the case in Rio Doce state park [C.M.C. Valle, pers. comm.].

A recent study of the dental characteristics of all members of the genus [Natori, 1986] also supports their classification into seven species, although the samples sizes for *C. aurita* and especially *C. flaviceps* are again small. The relationships between the species, based on dental structure, do, however, correlate with their probable phylogeny based on both morphological characteristics and their distribution, which also corresponds with the possible isolation of the *C. jacchus* group in forest refuges during different periods of their evolutionary history [Kinzey, 1982]. There is also good evidence to support the idea that the five species are ecologically distinct, such as the relative success of introduced species in some areas and the apparent importance of altitude in the separation of the distributions of *C. flaviceps* and *C. geoffroyi* in Espírito Santo [Coimbra-Filho & Mittermeier, 1973a]. These topics will be discussed further on.

While human intervention may have permanently erased the possibilities of verifying the systematics of the *C. jacchus* group, the available evidence does seem to favour its classification as five full species on the basis of apparent differences in morphology and ecology. This classification is followed in this thesis.

Chapter 1

Ecology of the Marmosets and their Distribution in Eastern Brazil

The callitrichids are small, highly insectivorous primates adapted to the exploitation of a wide variety of arboreal habitats. Most field studies have recorded a distinct preference for disturbed and secondary forest, and edge vegetation in particular or rather, in the case of *Saguinus geoffroyi* at least, a preference for the "vicinity of edge" [Moynihan, 1970]. This preference may correlate with the abundance of insects in these forest types [Janzen 1973a, 1973b; Cates & Orians, 1975; Opler, 1978]. In all forest types, callitrichids prefer lower levels in the canopy, in contrast with most cebid species [Sussman & Kinzey, 1984]. This may be related to the types of insect which make up the majority of their prey (see chapters 6 and 7). The major feature which distinguishes the marmosets from the tamarins, the ability of the former to gouge bark and stimulate the flow of plant exudates, appears to have far-reaching consequences for their adaptability, ecology and survival potential. This must be kept in mind, especially as the majority of any discussion of callitrichid ecology relies, through necessity, on the relatively abundant information available for the genus *Saguinus*.

Group Size and Ranging

Marmoset and tamarin groups are, in general, relatively small (table 1.1a/b). It is interesting to note that the tamarin species exhibit the widest range of group size, and that, while lone individuals have been commonly observed in studies of tamarins, they have only rarely been observed in studies of marmosets. In contrast with this, the mean group size for the marmoset species is consistently higher than that of the tamarins. These differences seem to reflect observed differences in group stability. Whereas tamarin groups in general appear to be relatively volatile [Sussman & Garber, 1987], especially in marginal habitats and during periods when resources are scarce [Dawson, 1978; Neyman, 1978; Soini, in press], marmoset groups appear, on the

Table 1.1a

Marmoset Group Size

Species	Group size: Range	Group size: Mean	Groups observed	Source
***Callithrix*:**				
C. argentata melanura	5-6	-	2	Freese *et al.* [1982]
C. aurita	6-8	-	1	Muskin [1984a]
C. flaviceps	5-15	9.8	5	Present study
C. jacchus	3-7	-	3	Maier *et al.* [1982]
C. jacchus	3-13	8.56	12	Hubrecht [1984]
C. jacchus	4-13	8.8	3	Stevenson & Rylands [in press]
C.h. intermedius	8-15	11.5	8	Rylands [1982]
C.p. kuhlii	4-9	6.56	8	Rylands [1982]
C.p. penicillata	3-8	-	1	Santos de Faria [1984a]
C.p. penicillata	4-5	-	2	Bouchardet da Fonseca & Lacher [1984]
***Cebuella*:**				
C. pygmaea	10-15	-	-	Hernández-Camacho & Cooper [1976]
C. pygmaea	3-6	-	6	Moynihan [1976]
C. pygmaea	7-9	-	-	Ramirez *et al.* [1978]
C. pygmaea	2-9	6.4	76	Soini [1982]

whole, to be far more stable [Rylands, 1982; present study]. While migrations between marmoset groups have been observed, they seem to be more systematically related to natural increases in group size through births.

The available information on callitrichid ranging suggests that tamarins utilise larger home ranges, in general, than marmosets (table 1.2), although the exclusion of the tiny *Cebuella* and the somewhat equivocal data for *Callithrix jacchus* (the habitats at both the sites from which data are available for this latter species have undergone extensive alteration) would probably give a more realistic comparison. It seems likely that most differences in home range size between species reflect local differences in habitat, population density and group size rather than any absolute differences in evolutionary adaptations.

Table 1.1b

Tamarin Group Size

	Group size:			
Species	Range	Mean	Groups observed	Source
***Leontopithecus*:**				
L.r. chrysomelas	5-8	6.67	3	Rylands [1982]
L. rosalia rosalia	2-8	-	-	Coimbra-Filho & Mittermeier [1973b]
***Saguinus*:**				
S. fuscicollis	1-7	4.1	21	Moynihan [1976]
S. fuscicollis	1-17	5.74	375	Sussman & Kinzey [1984]
S. fuscicollis	2-9	6.8	12	Sussman & Garber [1987]
S. fuscicollis	4-10	5.5	9	Ramirez [1984]
S.f. illigeri	1-10	-	-	Soini [in press]
S.f. weddelli	2-7	-	-	Yoneda [1984]
S.f. weddelli	2-9	5	16	Freese *et al.* [1982]
S.f. weddelli	-	5	-	Terborgh [1983]
S. geoffroyi	1-9	3.39	28	Moynihan [1970]
S. geoffroyi	1-19	6.93	71	Dawson [1978]
S. geoffroyi	1-8	5.3	21	Lindsay [1979]
S. geoffroyi	5-10	-	-	Garber [1980]
S. imperator	2-8	4	-	Terborgh [1983]
S. labiatus	1-13	5.7	7	Freese *et al.* [1982]
S. labiatus	3-8	6.6	27	Sussman & Kinzey [1984]
S. midas	2-6	3.4	8	Thorington [1968]
S. midas	6	-	1	Mittermeier & van Roosmalen [1981]
S. mystax	1-16	5.25	374	Sussman & Kinzey [1984]
S. mystax	3-11	6.08	12	Sussman & Garber [1987]
S. mystax	3-8	5.2	9	Garber *et al.* [1984]
S. mystax	3-7	5.2	9	Ramirez [1984]
S. nigricollis	4-8	6.3	10	Izawa [1978]
S. nigricollis	7	-	1	Freese *et al.* [1982]
S.n. graellsi	4-12	6.2	10	Moynihan [1976]
S. oedipus	3-13	-	6	Neyman [1978]

Rylands [1982], on the other hand, found that the home range of the *Leontopithecus rosalia chrysomelas* study group at Una, Bahia was not only more than three and a half times larger than that of the similarly-sized *C.p. kuhlii* group in the same area of the study site, but also overlapped with those of neighbouring conspecific groups far less. It is also interesting to note the considerable contrast between the home range estimate presented here for

Table 1.2

Home Range and Day Range Values for Marmoset and Tamarin Groups

		Daily Path Length (km):		
Species	Home Range (ha)	Mean	Range	Source
Callithrix:				
C. aurita	>17	-	-	Stevenson & Rylands [in press]
C. flaviceps	35.5	1.22	0.65-2.67	Present study
C.h. intermedius	28.25	1.2-1.77[1]	0.77-2.11	Rylands [1982]
C. jacchus	0.72-1.62	0.53-0.98[2]	-	Hubrecht [1985]
C. jacchus	0.5	-	0.1-0.2	Stevenson & Rylands [in press]
C. p. kuhlii	10	0.94-1.08[1]	0.83-1.2	Rylands [1982]
Cebuella				
C. pygmaea	0.8-1.3	-	-	Castro & Soini [1978]
C. pygmaea	2.8-3.0	-	-	Ramirez *et al.* [1978]
C. pygmaea	0.2-0.4	-	-	Soini [1982]
C. pygmaea	0.1	-	-	Terborgh [1983]
Leontopithecus:				
L.r. chrysomelas	36	1.6-1.95[1]	1.4-2.2	Rylands [1982]
Saguinus:				
S.f. illigeri	15.7-16.5	1.40	1.11-1.92[1]	Soini [in press]
S.f. weddelli	30	1.22	1.16-1.29[1]	Terborgh [1983]
S.f. weddelli	30-120	-	-	Terborgh & Stern [1987]
S. geoffroyi	26-43+	2.06	-	Dawson [1979]
S. imperator	30	1.42	1.09-1.63[1]	Terborgh [1983]
S. nigricollis	30-50	1.0[3]	-	Izawa [1978]
S. oedipus	7.8-10	-	1.5-1.9	Neyman [1978]

[1] Range of monthly means.
[2] Range of mean values for 3 groups.
[3] Approximation - no quantitative data given.

C. flaviceps and that of *C. jacchus* at Tapacura, Pernambuco [Hubrecht, 1985; Stevenson & Rylands, in press]. The relative abundance of exudate at the latter site (due to a neighbouring plantation of cashew, *Anacardium occidentale*, trees) has been interpreted as being the major determinant of the extremely high population density of *C. jacchus*. As we shall see in chapter 3, however, exudate was also relatively abundant within the range of the *C. flaviceps* study group at FMC.

Figures for day ranges for most marmoset and tamarin groups (table

1.2) also show that they travel relatively long distances during the course of the day. The picture is again somewhat clouded by the inclusion of the available data on *Callithrix jacchus* and *Cebuella pygmaea*, although the latter may travel relatively long distances during certain times of the year [Terborgh, 1983]. *Callithrix humeralifer*, on the other hand, may greatly reduce its daily ranging when foraging above army ant swarms [Rylands, 1986].

Territoriality

Territoriality, "in terms of the defense of a range" [Rylands, 1982: p. 141], seems to be a particularly flexible characteristic for *Callithrix* species. All exhibit behaviours which are seen as being associated with the definition and defence of territorial limits and, although rarely the total area of a group's home range, the access to some specific area is usually defended from neighbouring groups. Maier *et al.* [1982] found that a *C. jacchus* group actively and aggressively defended only its main exudate tree. Hubrecht [1985: p. 519] found that *C. jacchus* groups at Tapacura territorially defended "an area almost equivalent to the home range", although Stevenson found a 52% overlap in the home range of one group at the same site [Stevenson & Rylands, in press]. Rylands [1982] found a 22% overlap in the home range of the *C.h. intermedius* study group at Rio Aripuanã, Mato Grosso, whereas 50% of the much smaller home range of the *C.p. kuhlii* study group at Una was encroached by neighbouring groups during a three month study. Lacher *et al.* [1981] also found overlapping ranges in *C.p. penicillata* groups at Cabeça do Veado, Brasília, which also shared exudate trees.

The home range of the *C. flaviceps* study group at FMC also showed considerable overlap (see chapter 5), which increased towards the end of the study, following the emigration of four individuals. This group was surprisingly tolerant of its neighbours in overlap areas, although it did appear to recognise specific boundaries at which it frequently gave long calls before advancing. Apparently aggressive, or at least agitated, encounters between *C. flaviceps* groups were observed in other parts of the FMC forest.

The picture of territoriality in the tamarins is similarly confused.

Rylands [1982] recorded that only 7% of the home range of *L.r. chrysomelas* overlapped with those of neighbouring groups. Terborgh [1983] also found that *Saguinus imperator* and *S. f. weddelli* groups in Manu National Park, Peru, defended the whole of their joint home ranges as territories and were reluctant to cross boundaries, even in the absence of neighbouring groups. The home range of a *Saguinus fuscicollis illigeri* group at Río Pacaya, Peru, on the other hand, overlapped by as much as 26% with that of its neighbour [Soini, in press], while in Bolivia, Yoneda [1981] found overlap of as much as 79% for *S.f. weddelli*. Dawson [1979] found significant differences in the use of space and territoriality in *S. geoffroyi* groups occupying ecologically different areas of the same study site in Panama. The "lowland" group had access to stable and ample supplies of resources and defended its home range as a territory with very little overlap while the "upland" group increased its range and overlap in response to seasonal fluctuations in resources. It is also interesting to note that, while no studies of marmosets have reported groups congregating for foraging or other activities (ten studies, including the present one), six of the 17 studies of tamarins referred to by Sussman & Kinzey [1984, not counting studies where only one group was observed] report this type of behaviour.

Overall, if the definition of Sussman & Kinzey is accepted and territoriality is "the active defense of an area by actual or ritualized agonistic encounters, thereby maintaining virtually its exclusive use" [1984: p. 440], the marmosets and tamarins present an equivocal case, but the evidence does suggest that there is a tendency for such behaviour. This behaviour shows great variability both between and within species, and reflects their great adaptability, but it does seem that marmosets will defend important resources, where possible, even if that resource is a single tree, as in the case of *C. jacchus* at João Pessoa, Paraíba [Maier *et al.*, 1982]. Whether a single tree constitutes a territory or not is perhaps a separate question, but this does seem to be an extreme example of what can be seen as a general tendency.

The expression of instinctive territorial behaviour in marmoset and tamarin groups is clearly affected by the availability of resources, especially if the potential for their defence is seen in terms of costs and benefits [*cf.* Terborgh, 1983]. The fact that the home ranges of many marmoset groups show (sometimes considerable) overlap does not mean that they do not defend territories, as proposed by Sussman & Kinzey [1984], in apparent contradiction of their own definition. The adaptability of the marmosets and tamarins undoubtedly contributes to both the considerable variability shown in the expression of their territorial behaviour and the degree of confusion in its interpretation *e.g.* "in Bolivia adjacent groups of *S. fuscicollis* have a 79% territorial overlap" [Sussman & Kinzey, 1984: p. 441].

Diet

Animal Material

Foraging for prey seems to be the main daily activity of most callitrichids, although they probably spend less time overall in this type of activity than other insectivorous platyrrhines such as *Saimiri* and *Cebus* [Terborgh, 1983], reflecting strategies appropriate to differences in the types of insects most commonly preyed on, in particular. While callitrichids concentrate on large, mobile insects (especially grasshoppers), the cebids tend to feed on a larger proportion of smaller, less mobile (frequently immature) forms. Whereas marmosets and tamarins forage by stealth, spending long periods scanning for signs of camouflaged insects, the cebids forage by persistence, spending much of their time manipulating substrates. Thus, in addition to their preference for the dense vegetation of the understorey of disturbed and secondary forest, these small-bodied primates most commonly capture large, leaf-eating insects using very different techniques from the larger insectivorous cebids. These broad differences are an important basis for the understanding of their foraging behaviour, as marmosets clearly follow specific foraging strategies which have important implications for all other aspects of their ecology.

Large orthopterans, mainly grasshoppers, constitute the majority of identified prey items in all detailed ecological studies [*e.g.* Dawson, 1978; Izawa, 1978; Rylands, 1982; Soini, 1982, in press]. Orthopterans constituted between 65.7% and 77.3% of the volume of insect material in the stomach contents of *S. geoffroyi* at Rodman and Barro Colorado Island (BCI), Panama [Garber, 1984a]. 61% of the identified prey items of *S.f. weddelli* and 57% of that of *S. imperator* at Manu were orthopterans [Terborgh, 1983]. While a wide variety of prey was observed being captured by the *C.flaviceps* study group, an apparent preference for orthopterans was also recorded (chapter 6), although vertebrates were captured with unexpected frequency.

In addition to these apparent specialisations in prey and forest type, and foraging technique, the strategies followed by the marmosets and tamarins may also include the concentration of activity during certain periods of the day. Most studies have recorded that groups delay the start to their daily activity period and usually retire to a sleep-tree at least one hour before dusk. This pattern was also recorded for the *C.flaviceps* study group which, in fact, regularly retired to roost more than 2 hours before full darkness (during the dry season in particular), on at least one occasion retiring before 14:00. A number of ecological studies have found that groups generally forage for insects most during the mid-morning, tend to rest during the middle of the day and the early afternoon, and show a smaller peak of foraging in the late afternoon shortly before roosting. It must be remembered that these patterns are trends rather than absolute divisions of the daily activity period, as insect foraging is a constant activity throughout the day and activity patterns vary considerably, even on consecutive days (such variation may in itself be an integral part of marmoset foraging strategies, see chapter 7).

Dawson [1979] has proposed that the preference for larger insects is the main factor determining the concentration of activity in the early hours of the day in the case of *S. geoffroyi.* Large insects, with a low surface area to body ratio, tend to warm up relatively slowly in the morning, but also to cool down more slowly later in the day. Such insects would thus be more vulnerable to predation in the morning, before reaching optimal body temperature, and least vulnerable during the later part of the day. The activity patterns recorded for most marmosets and tamarins certainly contrasts with those of *Cebus* and *Saimiri,* both of which appear to forage intensively throughout the whole of the daylight period. *Saimiri* may even be active for up to one or two hours after dark [Baldwin & Baldwin, 1981]. While the metabolic characteristics of large-bodied insects may have some influence on the observed activity patterns, a full understanding of the foraging behaviour of the marmosets and tamarins requires the careful consideration of a number of other factors.

The late start of daily activity is possibly due primarily to the nocturnal torpor which appears to be a common feature of all species, rather than to an avoidance of foraging at this time. Dawson's observations of *S. geoffroyi* support Moynihan's hypothesis [1970] that these tamarins become torpid or semi-torpid at night. Studies of *Callithrix jacchus* [Morrison & Simões, 1962; Hetherington, 1978] and *Cebuella pygmaea* [Morrison & Middleton, 1967] recorded a marked depression of body temperature at night, and a smaller drop around midday, corresponding with the observed depression of activity at this time of day. This appears to indicate that they are able to physiologically reduce their metabolic expenditure during such periods. The author's own observations of captive *Callithrix jacchus* at night support these findings, as the animals show an extreme state of drowsiness, in considerable contrast with their diurnal alertness. It seems likely that animals in such a state of torpor would require a certain amount of time to become fully alert in the morning, especially if activity is triggered by the onset of daylight, and would be reluctant to leave the relative safety of the sleep-tree until completely awake. Hethington [1978: p.108] notes, in fact, that the increase in body temperature of *C. jacchus* "tended to be more gradual than the decrease".

Qualitatively, the *C. flaviceps* study group at FMC appeared to descend from their sleep-tree later after full light on colder mornings than on warmer ones. In addition, while the delay in the start of activity was usually around twenty minutes, it normally came to an end at least one hour before dark. The evidence suggests that the nocturnal torpor of the marmosets and tamarins can be seen as an important and integral part of a "time-minimizing" foraging strategy [Schoener, 1971], which may also include the preference for large insect prey [see Terborgh, 1983]. Time-minimising foragers theoretically aim at the acquisition of an adequate diet in as short a period of time each day as possible, thus maximising both their time at rest and avoidance of predation. This contrasts with an "energy-maximising" strategy, in which the foraging animal aims at the maximisation of energy gain during a set period of time. Any reduction of metabolic expenditure will obviously contribute to a time-minimising strategy by reducing dietary requirements and thus the amount of time necessary for the acquisition of an adequate supply of nutrients. It seems more useful, in this case, to see the late start of activity as part of such a strategy rather than as an active avoidance of foraging at this time of day, as implied by Dawson.

As most other studies (including the present one) have reported late afternoon peaks in insect foraging, it does seem that factors other than the size of prey may be more important determinants of these patterns. These may include the metabolic requirements of the monkeys themselves which, being relatively small-bodied, are unable to store significant quantities of nutrients in either body fat or the gut [Calder, 1984; Temerin *et al.*, 1984]. While it may be possible for these animals to hunt most efficiently during the morning, they are probably not able, physically, either to capture or to consume their daily requirement of animal material at this time. In this case, the most efficient strategy would be to rest through the hot midday period and then "stock up" with insects before retiring for the night. This pattern may also reflect changes in the motivational state of the monkeys themselves. Ultimately, however, the rewards of continued foraging may be outweighed by the energy-saving benefits of the night-time huddle and torpor, especially during periods when insects are scarce and temperatures are relatively low.

Certain characteristics of the typical marmoset prey, other than their large size, may be equally important determinants of their foraging patterns. Most of the orthopterans commonly consumed are not only relatively poor fliers, but also rely on elaborate systems of camouflage, rather than their agility, to escape predation (notably the stick insects, Phasmidae, and the nocturnal grasshoppers, Tettigonidae). Most of the animals making up the other major prey categories (*i.e.* caterpillars, coleopterans, lizards, snails and tree frogs, see chapter 6), share these characteristics of predator avoidance. It thus seems likely that they would not only be particularly vulnerable to the stealthy "scan-and-pounce" foraging technique of the marmosets and tamarins, but would be equally vulnerable throughout the day. The final line of defence of most of these animals when disturbed is to fall or glide away to a new position and remain motionless. In falling to the ground, further escape is usually impossible. As well as foraging at relatively low levels, both marmosets and tamarins will come to the ground to capture prey [Rylands, 1982; Soini, in press; present study], and it thus seems that their preference for low foraging levels in secondary forest may be influenced, in part, by these characteristics of their prey, an idea which will be discussed in detail in chapter 7.

Rather than determining the timing of their foraging activities, then, the characteristics of the typical prey animals of marmosets and tamarins may have other important influences on their foraging behaviour. It seems likely, for example, that most of these large poikilothermic animals will be found at relatively high levels in the canopy at the time of day, *i.e.* during the morning, when the absorption of the sun's heat is imperative [Janzen, 1973b]. Later on, however, when this heat is more intense, these animals will seek shelter at lower levels in the forest. In this case, marmoset groups would be expected to forage at relatively higher levels during the earlier part of the day. If, in addition, the capture of disturbed prey is an important aspect of their foraging activities, greater success would be expected during the later part of the day, in contrast to Dawson's hypothesis. In presenting detailed data on the foraging behaviour of the *C. flaviceps* study group, this thesis will explore these and other aspects of marmoset foraging strategies.

Plant Exudates

In addition to animal material, marmosets rely heavily on plant exudates as a food source. Exudates are of three main types: sap, gum and resin [see Bearder & Martin, 1980, for definitions]. Sap, being the fluid contents of the phloem and xylem, is found in all woody plants. Gum is a water-soluble exudate produced by many plants in response to physical damage. A number of plant families, including the Anacardiaceae, Leguminosae, Meliaceae and Vochysiaceae, all of which are frequently cited as sources of exudates for marmosets, produce gums. Resin is also produced by plants, notably conifers, in response to damage, but is insoluble in water and probably toxic in most cases. Gums are the principal exudate used by all exudate-eating primates [Bearder & Martin, 1980] including the marmosets. Stevenson & Rylands [in press] review their use by *Callithrix*.

Gums contain high proportions of carbohydrates (polysaccharides) as well as a number of minerals including calcium, magnesium and potassium, and may even contain, occasionally, important amounts of protein [Anderson *et al.*, 1972; Garber, 1984a]. They provide many primates species with an important source of carbohydrates [Nash, 1986], especially during periods of fruit scarcity, although the digestion of the complex polysaccharides may limit their inclusion in the diets of unspecialised animals [Booth *et al.*, 1963; Bearder & Martin, 1980]. Many "gummivorous" [*cf.* Nash, 1986] primates are also highly insectivorous, and it seems likely that gums provide a crucial source of calcium for many of these species.

Gums usually contain around 1% calcium by weight, but only small quantities of phosphorus. Insects, on the other hand, contain relatively large quantities of phosphorus and very much smaller quantities of calcium. Robinson [1980] has reported that the optimal calcium:phosphorus ratio for most mammals falls within the range 1:1 to 2:1. Severe imbalances of this ratio can have serious effects, such as the retardation of skeletal development and a decrease in reproductive output, among others. Primates with a large insect proportion in their diets may thus require a balancing source of calcium, particularly at certain times of the year, such as during the breeding season [see *e.g.* Garber, 1984a].

Apart from *Phaner furcifer*, which is able to elicit the flow of exudate from the intact surfaces of plants but is primarily dependent upon natural formations [Petter *et al.*, 1971], marmosets are the only primates able to gouge holes in plants to initiate exudate flow. This gives them access to sap as well as to gum. While it does not necessarily contain different nutrients, the water content of the sap may both prolong and increase the flow of gum, and make it more easily digested. *C.h. intermedius* may consume the sap of two species of Rutaceae [Rylands, 1982]. *C. penicillata* has been reported using the latex of *Hancornia speciosa* [Rizzini & Coimbra-Filho, 1981]. Rylands [1982] also observed both *C.h. intermedius* and *C.p. kuhlii* stripping and chewing the bark of plants during gum feeding, although it was not known if either ingested this material.

In addition to their claw-like nails, specialised dentition and regular use of gum sources [Soini, 1982; Stevenson & Rylands, in press], marmosets also appear to have a relatively large and well-developed caecum in comparison with tamarins [Coimbra-Filho *et al.*, 1980]. An enlarged caecum and hind gut are probably important for the efficient digestion of gums [Bearder & Martin, 1980]. Marmosets do appear to lack, on the other hand, any specialisation of the tongue in relation to exudate feeding [Hershkovitz, 1977]. However, as this characteristic of gummivorous prosimians such as

Galago and *Phaner furcifer* appears to be related to "reaching gum hidden in crevices and insect holes" [Bearder & Martin, 1980: p. 126], the specialisation of the dentition has probably by-passed any need for such an adaptation of tongue morphology. Marmosets thus seem to be more highly specialised for the exploitation of a gum-feeding niche than any prosimian.

Apart from claw-like nails, the tamarins appear to exhibit none of these specialisations, and their use of plant exudate as a source of food is generally both random and opportunistic. All species have, however, been reported to feed on exudate, and it may be an important source of nutrients during periods of scarcity. Soini [in press], for example, reports that the *S.f. illigeri* study group at Río Pacaya spent 58% of its plant-feeding time consuming gum during one dry season month. Garber [1984a], in addition, suggests that gum is a crucial source of calcium for *S. geoffroyi* during certain times of year.

The ability to utilise exudate in such a systematic fashion may enable marmosets to achieve high population densities at some locations, such as the hypothetical figure of 700 individuals per square km recorded for *C. jacchus* at Tapacura [Stevenson & Rylands, in press]. The long-term stability of such resources may also contribute significantly to the stability of marmoset groups in comparison with those of tamarins. They also appear to be able to exploit habitats which would not support tamarins. This would probably be the case for much of the available forest habitat at FMC, for example, in which edible fruit appears to be scarce or even absent for long periods (see chapter 3). *Brachyteles arachnoides*, inhabiting primary forest at this site, may depend on leaves for up to 78% of its diet during certain months [Strier, 1986]. The apparent absence of the frugivorous *Callicebus* at the reserve [Valle *et al.*, 1984] can be seen as a further indication of the unsuitability of this site for species which may be unable to systematically utilise alternative plant resources, either leaves or exudates. Whether this has always been the case in this region, or is an effect of habitat degradation, is not known.

It is also interesting to note that the anterior dentition of the *C. argentata* group, inhabiting the relatively less seasonal Amazonian forest, appears to be less specialised for gum feeding than that of the *C. jacchus* group [Maier *et al.*, 1982]. The lower canine of the marmosets of the *C. argentata* group is both less incisoriform and:

> "...in all other respects, intermediate between the incisiform canine of lower marmosets and the true caniniform tooth of *Saguinus* and other higher platyrrhines." [Hershkovitz, 1977: p. 576].

C.h. intermedius, the only member of this group which has been studied in detail [Rylands, 1982] seems to rely much less heavily on exudate as a food source than the *C. jacchus* group species for which data is available. This may, however, be a reflection of local habitat differences rather than an indication of absolute differences in ecological adaptations. The distribution of the *C. argentata* group does include areas of *cerrado*-like vegetation within the overall distribution of the Amazonian forest. *C.a. argentata* utilises this type of habitat in Santarém, Pará, where high densities of cashew trees (*A. occidentale*), an important characteristic of the site at Tapacura, are common [pers. obs.]. *Cebuella pygmaea*, on the other hand, another inhabitant of the Amazonian forest, seems to rely more heavily on exudate than perhaps any other marmoset [Ramirez *et al.*, 1978; Soini, 1982], although nectar seems to be an important resource during the dry season at Manu [Terborgh, 1983].

Here again, as for so many other features, local differences in habitat may be the primary determinants of observed differences in the behaviour and ecology of different marmoset species. The present study of *C. flaviceps* is no exception. The intensive study of a single group inhabiting an isolated remnant of disturbed forest can not be seen as the definitive documentation of the behavioural ecology of this species, but it is hoped that the data collected will provide an important reference for further study of both this rare species and other eastern Brazilian marmosets.

The effective "parasitism" [Lacher *et al.*, 1984] of exudate-producing plants by marmoset groups has a deleterious effect on the plant, and could eventually lead to a reduction in exudate flow and even death. There is a good deal of evidence from a number of studies, however, which indicates that marmoset groups exploit exudate-producing plants in a way which ensures a regular and continuing supply of exudates in the long term, suggesting specific behavioural adaptations in addition to morphological specialisations (this will be discussed in detail in chapter 6). This systematic use of exudate-producing plants appears, in turn, to have important implications for many other aspects of marmoset ecology.

Fruit, Flowers and Nectar

As well as the exudate of plants, marmosets feed on a variety of reproductive parts, especially fruit, although flowers, flower buds and nectar can be seasonally important sources of nutrients. While there are some reports of marmosets eating leaf buds and shoots [Soini, 1982; Stevenson & Rylands, in press], mature leaves do not appear to be a part of their diets. In general, the importance of reproductive plant parts in their diets is inversely related to that of exudate, hence tamarins rely on fruit the most, marmosets the least. Certain characteristics of fruit feeding such as the preferential use of the fruits of certain species, however, appear to be common to most species. Many of the plants exploited are often found in relatively high densities, especially in areas of disturbed forest.

Fruit and nectar may constitute up to 70% of tamarin diets [Sussman & Kinzey, 1984]. *S. geoffroyi* feeds primarily on fruits with a diameter of less than 1.5 cm in Panama [Dawson, 1978; Garber, 1980], while the "major resource" fruits of *S. imperator* and *S.f. weddelli* at Manu [Terborgh, 1983] are all 1 cm drupes. The fruit of *Cecropia obtusifolia* made up 69% of the stomach contents of *S. geoffroyi* during the period of maximum abundance and diversity of fruit at Rodman [Dawson, 1978]. A similar situation was observed in the case of *S.f. weddelli* at Manu in its use of *Guatteria* sp. during the early wet season at Manu. The tamarin group utilised the fruit of only 14 of the plant species bearing fruit (*Cebus* groups were using around 30 at this time of year) and *Guatteria* was consumed during 61% of observed fruit-feeding time. Such preferential use of plant resources contrasts markedly with the cebid species inhabiting the same forest at Manu and was seen throughout the year, as Terborgh reports:

> "The tendency for the tamarins to concentrate their feeding activity on one plant species at a time is remarkable. It is a habit they appear to follow at all times of year, regardless of how many alternative resources may be available within their territories...It is not that all these fruits are too large or otherwise unmanageable for the tamarins; they do in fact sample a good many of them. They just do not eat them in any quantity." [Terborgh, 1983, p. 88].

A similar pattern has been recorded for *S.f. illigeri* at Río Pacaya [Soini, in press]. In addition to their small size, many of these species bear mature fruit in "piecemeal" fashion [Opler *et al.*, 1980], giving the tamarins a regular supply through relatively long periods, but making them relatively unattractive resources for the larger and more gregarious cebids.

The fact that exudates substitute fruit to a greater or lesser extent in the diets of most marmosets dilutes any such tendency, although it is still seen to a certain extent in the available data. The most frugivorous marmoset studied so far is *C.h. intermedius*. Rylands [1982] reports that two or three species of plant provided 50% to 80% of the fruits consumed by the study group in all but one month. Two of these species, in particular, show many of the characteristics of the "major resource" species used by tamarins at Manu, including the slow ripening of the fruits. *Cecropia sciadophylla* provided between 13% and 49% of fruit-feeding records during a period of 4 months and *Inga thibaudiana* 46% to 50% of fruits during the preceding 3 months. Both these species were also the main source of fruit during the periods they appear in the records. Rylands also notes that these two species, along with three other important sources, were found exclusively in areas of secondary growth. The *C. flaviceps* study group exhibited a similar tendency to feed on the fruit of one or a few species (chapter 6), although fruit was only an important component of its diet during two months.

Nectar was an important resource during the dry season for both *Cebuella* and the two tamarin species at Manu, with two plant species (*Combretum fruticosum* and *Quararibea cordata*) again providing the majority of the material consumed [Terborgh, 1983; Terborgh & Stern, 1987]. While nectar provided as much as 13% of the plant material consumed by *S.f. illigeri* at Río Pacaya during the dry season months, the nectar of only *Combretum fruticosum*, was exploited [Soini, in press]. *C. flaviceps* was observed feeding on the nectar of *Mabea fistulifera* during the early dry season at FMC. It has been suggested that the use of nectar as a food by these primates may be important for the pollination of a number of plant species [Janson *et al.*, 1981]. While both *Cebuella* [Terborgh, 1983] and *Callithrix* [Stevenson & Rylands, in press] have been reported feeding on flowers, rather than nectar, such behaviour was never observed in *C. flaviceps*.

The use of fruit, flowers and nectar by both marmosets and tamarins appears, on the whole, to reflect some of the more systematic characteristics of the use of exudate trees by marmosets. One aspect of this is the relative exclusivity of use of these resources in many cases, another is the concentration of feeding on a few individuals or species, even when the available choice is much wider. These characteristics may be part of a broader foraging strategy common to all marmoset and tamarin species, whether primarily gummivorous or frugivorous.

Water

One further dietary requirement of marmosets is water. The acquisition of water by marmosets in the wild is rarely reported in the literature, possibly because of its rapidity or infrequency. In many habitats, water is probably readily available either on the surfaces of leaves or in holes and fissures in branches and trunks. The marmosets at FMC were seen acquiring water from these sources during much of the year, either licking it directly from leaves or pools, or using a "hand-in" technique, reaching in to relatively inaccessible sources in tree holes and then licking the water from the hair. This technique has also been reported for *S.f. illigeri* [Soini, in press].

The *C. flaviceps* study group utilised a number of "water holes" situated in the ground under tree roots which it also visited frequently. During the late dry season of 1986, water seemed to be particularly scarce, and the group eventually seemed obliged to use the river as their primary source. As group members were both usually reluctant to come to the ground to drink and had been observed taking water from a hole in a tree situated only 4 m from the river, it seems probable that it was not a preferred source. While the lack of available drinking water may have had some influence on its movements during the dry season, it seems likely to have had only a small effect as the group exhibited a marked preference for the more humid part of its range, along the riverbank in particular, during most of the year (see chapter 5).

Chapter 1

Activity Patterns

As discussed previously, most marmosets and tamarins are active for a relatively short period each day, during which insect foraging is usually a major activity, and relatively long distances are travelled. Despite this, it also seems that they rest during the day far more than other insectivorous neotropical primates and spend relatively more time socialising. The available data on the activity patterns of the five sympatric insectivorous primates at Manu show that the two *Saguinus* species spent considerably more time at rest each day than the three cebids (*Cebus albifrons*, *Cebus apella* and *Saimiri sciureus*), a difference that was consistent throughout the year [Terborgh, 1983: table 4.2, p.49, figure 4.3, p. 55]. While the time spent travelling each day was almost the same for all species (except in the case of *Saimiri*, which spent about 25% more time travelling each day), the cebid species devoted far more time to insect foraging than the tamarins, particularly *Cebus apella* and *Saimiri sciureus*, which both spent around 50% of their time looking for insects.

The daily activity of marmosets and tamarins usually includes a midday rest period which may involve a depression of metabolic activity [Morrison & Simões, 1962; Morrison & Middleton, 1967] and seems to be linked to their sensitivity to extremes in ambient temperature. Activity is frequently curtailed on rainy days [Dawson, 1978; Soini, in press; Stevenson & Rylands, in press; this study]. A heavily pregnant female or carried infants may also increase a group's propensity to rest [Terborgh, 1983].

On a broader scale, the distribution of daily activity may be affected by a number of variables. Terborgh's data are particularly interesting as they show that, while the two tamarin species spent much the same time travelling each day (which would be expected as they usually travelled together within their joint territories), *S.f. weddelli* rested almost twice as much as *S. imperator* (44% versus 25%) but spent less than half the time foraging for insects (16% versus 34%). While the latter species is slightly larger than the former, it seems likely that this contrast is influenced primarily by the different foraging techniques used by the two species, which may also have been accentuated by differential observational bias (see chapter 4).

C. jacchus has been reported to spend as much as 53% of its time at rest during the acutely hot dry season at Tapacura [Stevenson & Rylands, in press]. Both *C.p. kuhlii* and *C.h. humeralifer*, on the other hand, were found to spend only about 14% of their time at rest or socialising [Rylands, 1982]. Differences in the overall length of the daily activity period, along with those in the observational methods used, may have a significant influence on these contrasts. Soini [in press], for example, reports that *S.f. illigeri* spent 45% of its time foraging for insects each day, but only 6% travelling, even though path lengths were at least as large as those reported for most other species (table 1.2). The results of the present study, while demonstrating that the activity patterns of *C. flaviceps* are broadly similar to those of other species, also highlight the difficulties of drawing meaningful comparisons between studies, even those based on similar methodology (chapter 4).

Relations with Other Animals and Sleep-Trees

Relations with Other Primates

Callitrichid species may be sympatric with as many as twelve other primates (*e.g.* in Manu) or as few as none (as at Tapacura or João Pessoa). The most common associations seem to be with other callitrichids, as in the case of *S. fuscicollis* which has been reported forming mixed associations with *S. nigricollis* [Hernández-Camacho & Cooper, 1976], *S. mystax* [Castro & Soini, 1978], *S. labiatus* and *Callimico goeldii* [Pook & Pook, 1982] and *S. imperator* [Terborgh, 1983]. *Cebuella pygmaea* has also been reported to form mixed associations with *Saguinus* sp. [D. Pearson, pers. comm. to Ramirez *et al.*, 1978]. *Callithrix penicillata* sometimes associated with *L.r. chrysomelas* at Una [A.B. Rylands, 1982, pers. comm.], although the latter did not always tolerate the presence of the former.

S.f. weddelli has also been observed forming more or less stable associations with *Callicebus moloch*, *Pithecia monachus* and *Alouatta seniculus* [Pook & Pook, 1982]. *S. nigricollis* may also form associations with *P. monachus* [Izawa, 1978]. *Callithrix humeralifer* was sometimes seen travelling and foraging together with *Callicebus moloch* at Aripuanã [Rylands, 1982]. Solitary individuals or small groups of *Saimiri boliviensis* were seen associating with *Saguinus fuscicollis* over periods of "several days" at Río Pacaya [Soini, in press].

Cebus apella, on the other hand, has been observed to stimulate typical predator avoidance behaviour (alarm calls and rapid avoidance) in a number of species [Hladik & Hladik, 1969; Neyman, 1978; Pook & Pook, 1982; Soini, in press; J. Dietz, pers. comm.]. *Cebus apella* has been observed preying on squirrels [Freese & Oppenheimer, 1981], so it might be considered among the potential predators of the marmosets and tamarins, although *Callithrix aurita* has been observed foraging within 1 m of this species [Muskin, 1984a].

Similarly, while the *Callithrix flaviceps* study group was sometimes obviously startled by the sudden appearance of a *Cebus apella* group, it tended to ignore this larger cebid and would even forage in the same tree with no obvious signs of tension. *Callithrix flaviceps* was observed actively interacting with another primate species only once. On this occasion, a pair of marmosets was playing close to an adult female *Alouatta fusca*. They approached to investigate, and one of them touched the howler monkey, which then moved rapidly away. The dietary and habitat preferences of the callitrichids, as discussed above, may avoid, to a greater or lesser extent, possible competition for resources with most cebid species.

Relations with Other Animals

Callitrichids, being relatively small, are potential prey for a large number of other animals. Attacks on *S.f. weddelli* groups at Manu "occur about once per week per group" [Goldizen, 1987a: p. 107]. The effects, or potential effects, of predation may have had an important rôle in the evolution of many aspects of callitrichid biology, including their cryptic colouration and vocalisations, habitat preferences and other aspects of their behaviour. They are probably able to escape predation by most terrestrial animals through their extreme agility, although the predation of tamarins by an ocelot (*Felis pardalis*) and an anaconda (*Eunectes murinus*) has been reported [Goldizen, 1987a; Heymann, 1987]. Moynihan [1970] also reports the sighting of a tayra (*Eira barbara*) carrying a dead tamarin. Apart from the tiny *Cebuella*, callitrichids also mob potential predators, often with very loud vocalisations ["tsik-tsik" calls, Pook, 1978]. Rylands observed *Callithrix humeralifer* mobbing tayras and hawks in this fashion [Stevenson & Rylands, in press].

C. flaviceps was also observed mobbing a tayra in this fashion, until the latter finally came down to the ground and fled. In the case of a raccoon (*Procyon cancrivorus*), however, the group's mobbing behaviour proved ineffective. While the movements of almost any harmless animal (*e.g.* tapitis, *Sylvilagus brasiliensis*, and teid lizards) on the ground would sometimes provoke typical mobbing vocalisations, snakes always stimulated a different response. On perceiving a snake, the whole group would approach, sometimes coming to within 1 m, vocalising constantly. The typical vocalisation in this case was also of the "tsik-tsik" type, but very much quieter, interspersed with nervous chattering. Any sudden movement in the immediate environment, usually of other group members, provoked rapid avoidance and loud alarm calls. It is interesting to note that the youngest group members invariably came closest to the snake, and it is possible that such behaviour is important for the learning of predator recognition. Similar snake-mobbing behaviour has been reported for *S. mystax* [Bartecki & Heymann, in press].

Flying predators seem to present the greatest danger to callitrichids, and have been involved in the majority of observed attacks on groups in the wild [Dawson, 1978; Neyman, 1978; Izawa, 1978; Terborgh, 1983; Goldizen, 1987a]. All species exhibit highly specific patterns of behaviour related to the avoidance of predation by birds, including high-pitched alarm calls, rapid hiding and freezing. Members of a *S. nigricollis* group remained motionless for 37 minutes following an attack by a falcon which resulted in the death of one tamarin [Izawa, 1978]. Such avoidance behaviour may be initiated by almost any large flying object, even falling leaves in the case of *C. flaviceps*, although the degree of the response seemed to vary according to the potential danger. The *C. flaviceps* group would give "low-level" alarm calls in response to many types of bird, but the passing of hawks would invariably evoke an acute and decisive reaction. Unlike *C.h. intermedius*, however, the study group did not react to hawks perched in trees. On one occasion, group members were observed on the same branch as, and even approaching, a kestrel (*Falco sparverius*). Similar behaviour has been reported for *S. oedipus* [Neyman, 1978].

Callitrichids may also compete with animals for certain resources. *C.h. intermedius* was observed competing for *Cecropia* fruits with a potential predator, the tayra, at Aripuanã [Rylands, 1982]. Toucanets, *Selenidera maculirostris*, also displaced the marmosets when feeding on these fruits, and there were a number of displacements between *Pionus menstruus* parrots and *C.h. intermedius* when both were feeding on *Inga thibaudiana*. Stevenson found a number of bird species feeding in the same trees as *C. jacchus* at Tapacura, where local residents reported "combats" between marmosets and birds over fruit. Agonistic interactions between *S.f. illigeri* and birds (notably *Ramphastes cuvieri*, *Pteroglossus castanotis* and *Ortalis guttata*) competing for the same resources are apparently "common" at Río Pacaya [Soini, in press].

The competition for resources between *C. flaviceps* and birds appeared to be less direct, on the whole, and agonistic interactions were not recorded. Throughout October, for example, when adult cicadas were emerging from the ground in large numbers, a kite, *Ictinia plumbea*, closely followed the study group and was frequently observed capturing cicadas disturbed by the marmosets, who were less adept at capturing these insects than their typical prey (see chapter 6). Parrots, *Ara maracana*, and *"guaxos"*, *Cacicus haemorrhous*, were observed feeding on *M. fistulifera* nectar in close proximity to *C. flaviceps*, but no interactions were observed.

Sleep Trees

One important aspect of the predator avoidance of marmosets is their choice and use of sleeping sites. In most cases, sleeping sites are situated within a dense tangle of vines, although *Leontopithecus* may depend on holes in trees [Coimbra-Filho, 1978b]. Dawson [1979] notes that the sleep-trees chosen by *S. geoffroyi* lacked physical connection with the surrounding vegetation, which may make the approach of a predator more noticeable. The characteristic night-time huddle may also contribute to predator avoidance, creating a form which may not be easily recognisable and perhaps even mimics a larger animal.

C.h. intermedius utilised a variety of sleeping sites, most often in densely overgrown trees between 10 and 20 metres high, although they also used sites in dense undergrowth at around 5 m, a hole in a dead *Goupia glabra* tree at 21 m and the horizontal stem of a large liana at around 0.5 m above the ground [Rylands, 1982]. *C. p. kuhlii* chose similar sites, and also utilised large epiphytes. Both *C.h. intermedius* [Rylands, 1982] and *C. p. penicillata* may utilise sleeping sites which are also used for "siestas" during the day. The relative lack of variety in the sleeping sites used by *C. jacchus* at Tapacura, including one group which used the same site each night, may be due mainly to the lack of choice within their small home ranges [Hubrecht, 1985; Stevenson & Rylands, in press]. A similar situation was evident for *C. jacchus* at João Pessoa [Alonso, 1984]. The *C. flaviceps* study group utilised a large number of sites, again usually in dense tangles of climbers between 10 m and 20 m above the ground (chapter 5). Only once during the field study was a site used on consecutive nights. The systematic variation of sites and the behaviour associated with their use indicates that the avoidance of predation is a major influence on site choice. Similar patterns were observed in *C.h. intermedius* [Rylands, 1982].

The Distribution of *Callithrix* in Eastern Brazil

The five species of the*C. jacchus* group are found in the east of Brazil, predominantly in the Atlantic coast forest, but also in adjoining areas of the *cerrado* where they inhabit gallery forest and the more or less open woodland of the *cerradão*. Their distribution covers almost 20° of latitude, stretching across virtually the whole of the southern tropical zone, and includes a considerable variety of vegetation types and topography, including coastal lowlands and mountains over 2000 m in height (figure 1.1a/b). In spite of (or, perhaps, because of) the relatively long history of european colonisation of most of this area, the distribution of the genus is relatively poorly known. Hershkovitz [1977: figure IX.5, p. 490], for example, has no data on the species present in the state of Rio Grande do Norte and in large areas of

Maranhão, Ceará, Bahia and Minas Gerais. Interpretation of the available evidence is further hampered by the as yet unresolved controversy over the taxonomy of the species and the influence of the human population, both in terms of habitat destruction and the introduction of non-endemic species into the ranges of others [Coimbra-Filho & Mittermeier, 1973a; Hershkovitz, 1977; Mittermeier *et al.*, 1982]. This section will thus present a broad overview of the available evidence, with the emphasis on *C. flaviceps*, rather than a definitive account of the distribution of the *C. jacchus* group.

C. penicillata has the widest distribution of the five species, covering possibly as much as one million square km (figure 1.1a). Hershkovitz [1975: pp.141-150] presents evidence of the geographical intergradation between this species and both *C. geoffroyi* and *C. jacchus* in southern and northeastern Bahia respectively. Its distribution in the south of Bahia and north of Espírito Santo is confused. Hershkovitz [1975, 1977] refers to the presence of an intergrade between *C. geoffroyi* and *C. penicillata* in this area, while Mittermeier & Coimbra-Filho [1981] see this form as either a subspecies of *C. penicillata* (*C.p. kuhlii*) or a separate species, *Callithrix kuhlii*.

The geographical range of *C. jacchus* is approximately half as extensive as that of *C. penicillata* (figure 1.1a). As mentioned above, Hershkovitz [1975, 1977] has no information on the presence of this species in Rio Grande do Norte, but it seems unlikely that it is absent from this state. The remaining three species have much smaller ranges. *C. geoffroyi* is found throughout the lowlands of Espírito Santo, in eastern Minas Gerais and southern Bahia. *C. aurita* has the most southerly range of the group, covering Rio de Janeiro, southern Minas Gerais and the southern half of São Paulo. Muskin [1984b] presents evidence for the presence of this species at locations in São Paulo and Minas Gerais which are within the distribution of *C. penicillata* as defined by Hershkovitz [1975, 1977]. The presence of this species alongside *C. geoffroyi* in the state park of Rio Doce, however, may be due to its recent introduction [C.M.C. Valle, pers. comm.].

C. flaviceps has a much smaller range than any of the other species (see figure 1.1b), probably covering no more than 3000 to 5000 square km of Espírito Santo, Minas Gerais, and possibly also adjacent parts of Rio de Janeiro [Hershkovitz, 1975, 1977], most of which has already lost its original forest cover. The division of its range from those of other species appears to

Figure 1.1a (facing page)

Distribution of the Genus Callithrix *in Eastern Brazil*

Figure 1.1a shows the approximate distribution of the genus Callithrix *in eastern Brazil. The map is adapted from that of Hershkovitz [1977: figure IX.5, p. 490] in which the five species are treated as sub-species of* C. jacchus. *The crossed shading indicates areas for which there are no records, either of the existence of the genus itself or of the particular species present.*

Key:

▥	Callithrix aurita
▓	Callithrix flaviceps
▤	Callithrix geoffroyi
▨	Callithrix jacchus
▧	Callithrix penicillata
▩	*No data on the presence of the genus*

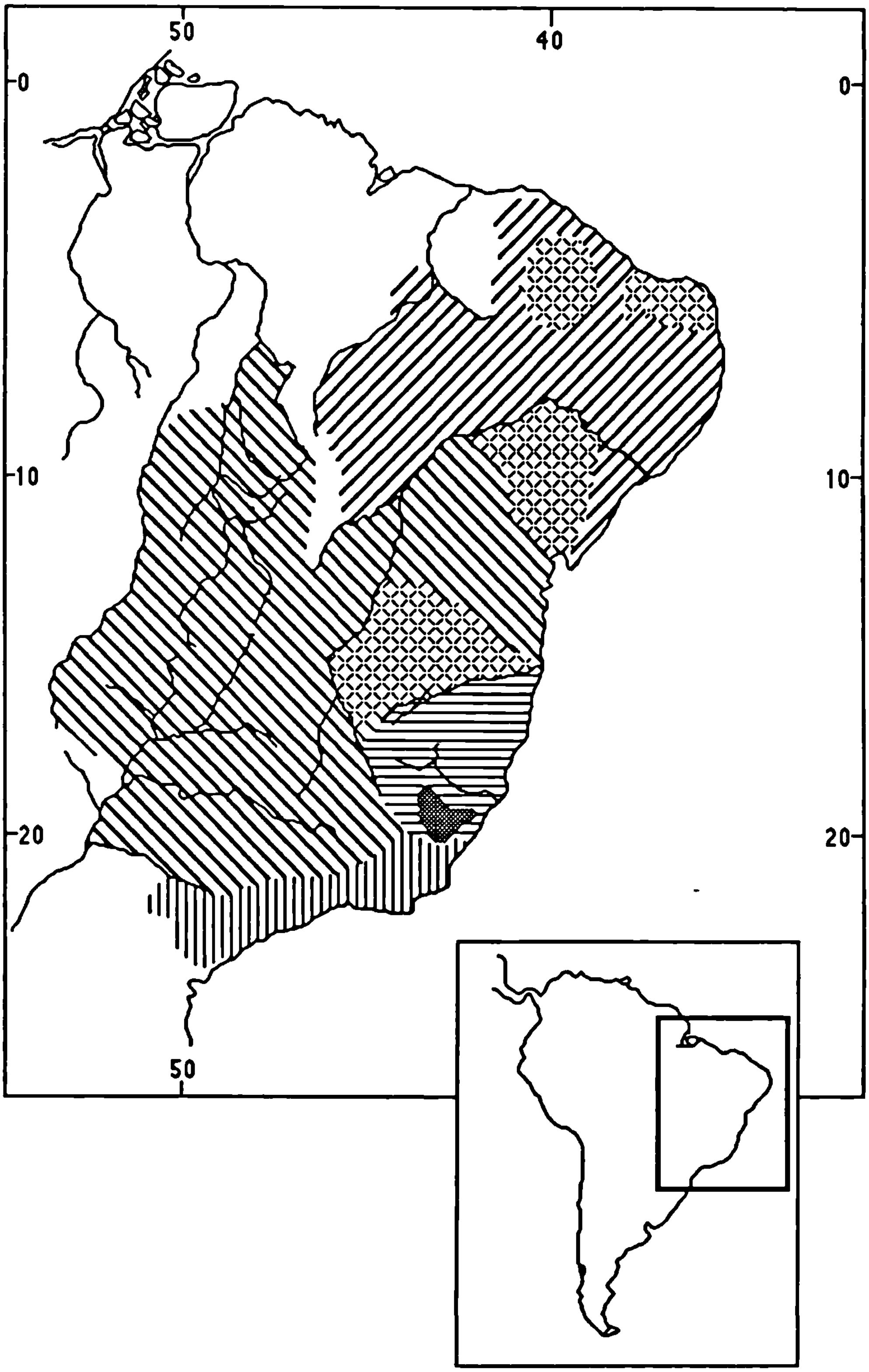

50
40
0
0
10
10
20
20
50

Figure 1.1b (facing page)

Recorded Localities for Callithrix flaviceps

This map shows the localities at which the presence of C. flaviceps *has been recorded. The nearest recorded localities for* C. aurita *and* C. geoffroyi *are also included for reference. As well as information collected during the present study, records are taken from Hershkovitz [1977], Mittermeier* et al. *[1982], Coimbra-Filho [1984] and Muskin [1984b].*

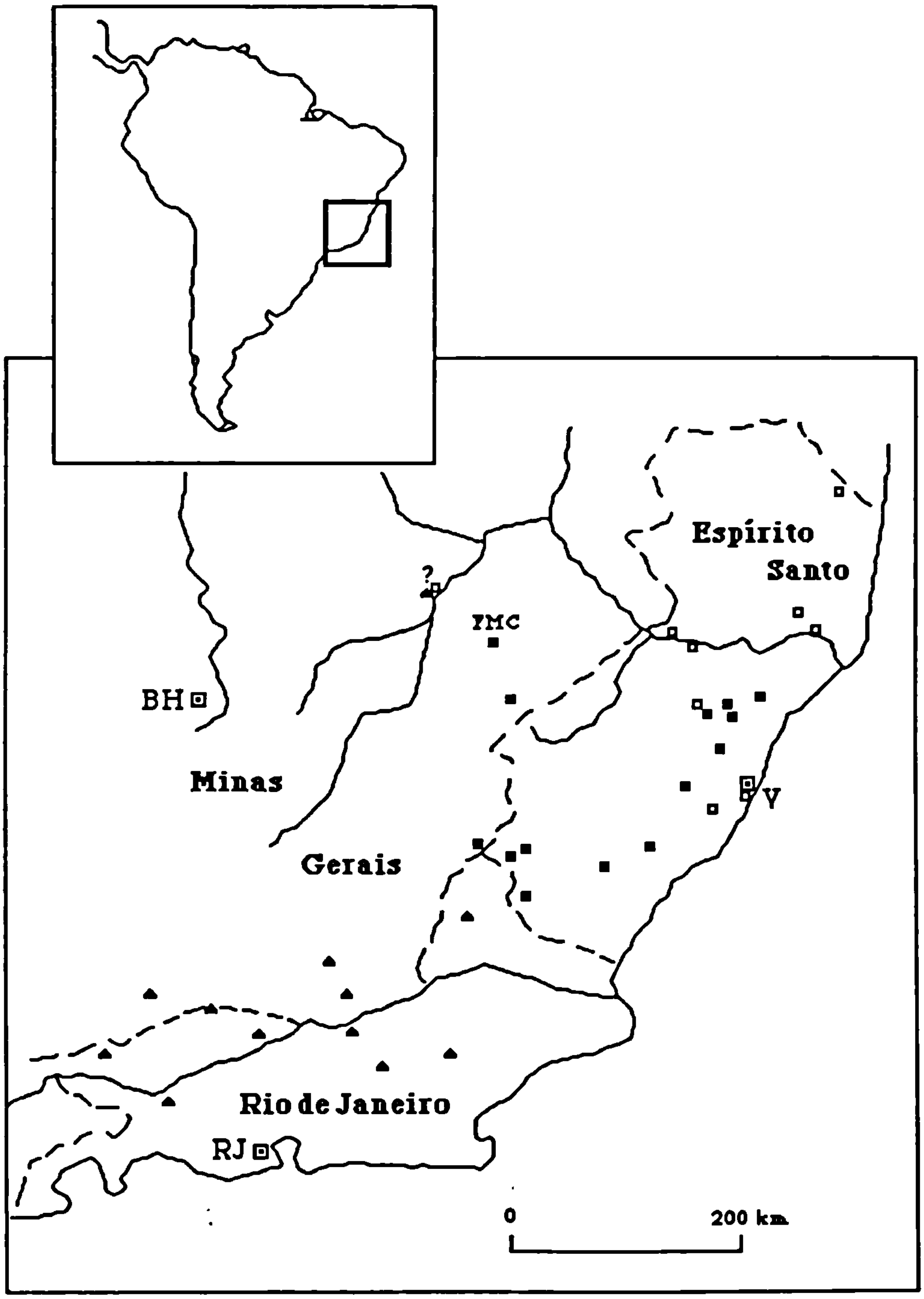
Localitites:

■ Callithrix flaviceps

□ Callithrix geoffroyi

▲ Callithrix aurita

⊡ *State capital (BH = Belo Horizonte, RJ = Rio de Janeiro, V = Vitória)*


?
YMC
Espirito
Santo
BH
Minas
Gerais
Y
Rio de Janeiro
RJ
0
200 km

be determined, at least in part, by altitude [Coimbra-Filho & Mittermeier, 1973a, Mittermeier *et al.*, 1982]. There is some confusion over this point [Hershkovitz, 1977: pp. 526-527], although it does appear that the altitudinal ranges of *C. flaviceps* and *C. geoffroyi* in Espírito Santo do overlap.

It is interesting to note that *C. flaviceps* appears to occur at lower altitudes in Minas Gerais than it does in Espírito Santo. The boundary between the two states in this area corresponds with the watershed of the Mantiqueira mountain range (see chapter 2), and a division between the relatively more humid coastal climate of Espírito Santo to the east (which is similar to that at Una, southern Bahia) and the drier, far more seasonal climate of Minas Gerais to the west. Rizzini [1979] noted characteristic differences between the types of vegetation found on the windward and leeward slopes of this coastal range. During the dry season, the forest at FMC is characterised by extensive loss of leaf cover, and an overall lack of edible fruits (see chapter 3). At the same time of year at Nova Lombardia (and at much higher altitudes, over 700 m, compared with between 318 and 682 m at FMC), there was apparently little leaf fall, and small fruits of the type eaten by marmosets (*e.g.* Melastomataceae, an important source for *C.p. kuhlii* at Una) were abundant [pers. obs.].

While far from conclusive, such evidence does appear to indicate the basis of certain differences between species, and it seems that this should be borne in mind when comparing the available information on marmoset ecology. The study sites of *C.p. kuhlii* at Una [Rylands, 1982] and *C. jacchus* at Tapacura [Hubrecht, 1984, 1985; Stevenson & Rylands, in press] and João Pessoa [Maier *et al.*, 1982; Alonso, 1984] are all on or near the coast and have relatively stable, humid climates, similar to that of Espírito Santo. Other studies of the eastern Brazilian species, on the other hand, have taken place much further inland, at far more seasonal sites, similar to that at FMC [Lacher *et al.*, 1981, 1984; Bouchardet da Fonseca & Lacher, 1984; Muskin, 1984a, 1984b; Santos de Faria, 1984a, 1984b].

Chapter 1

The Social Organisation and Behaviour of the Marmosets

The discussion of the social behaviour of the marmosets is facilitated by the comparative wealth of information available from captive studies, particularly of *C. jacchus*. As well as an ethogram for this species [Stevenson & Poole, 1976], there have been classifications of marmoset vocal repertoires [Epple, 1968; Pook, 1978] and a number of studies of various aspects of marmoset behaviour [see Stevenson and Rylands, in press, for a review of the work on *Callithrix*]. The laboratory environment is, of course, much simplified in comparison with natural habitats, emphasizing the need for caution in the use of captive data as a means of understanding the observed behaviour of groups in the wild.

One much-debated aspect of callitrichid biology is their social organisation. As most species will form successful breeding pairs in captivity, they have generally been seen as monogamous in the past [Kleiman, 1977], although there is a growing body of data which suggests that this classification does not reflect the true nature of their social structure nor, in particular, the flexibility of this organisation in response to different environmental conditions [Terborgh & Goldizen, 1985; Garber *et al.*, 1984; Sussman & Garber, 1987]. Much of this debate has again, however, centred on evidence from studies of tamarin species, and its application should thus, it is felt, be treated with some caution.

Social Organisation

While marmosets live in relatively small groups (table 1.1a), they are clearly often larger than would be expected if the group consisted solely of a breeding pair and its immature offspring (4 to 8 individuals), a characteristic of other monogamous neotropical primates such as *Aotus* [Wright, 1981] and *Callicebus* [Kinzey, 1981]. Breeding is normally restricted to a single female in both captive and wild groups, a characteristic which has a physiological basis in captive animals [Hearn, 1978; Abbott, 1979, 1984; Abbott *et al.*, 1981], although whether this is also the case in the wild is not yet known. Large family groups of *C. jacchus* [up to 19 individuals, Rothe, 1978] may remain stable for long periods in captivity, and the available data on wild *Callithrix* groups indicate that sexually mature, non-breeding individuals often remain in groups for periods of more than one year [Stevenson & Rylands, in press; present study].

While such individuals are usually the mature progeny of the breeding female, non-related animals are frequently present, especially in tamarin groups [Sussman & Garber, 1987]. Studies of captive *C. jacchus* and *S. oedipus* have shown that non-breeding adults will help with the rearing of unrelated offspring [Abbott, 1978; Cleveland & Snowdon, 1984], and it is possible that such co-operation ensures the toleration of non-related individuals in the group. Experience of infant care may also have benefits in terms of the reproductive success of young females [Epple, 1978; Kirkwood *et al.*, 1983; Tardif *et al.*, 1984], while the presence of helpers, especially males, may increase the reproductive success of the group [Málaga, 1985; Goldizen, 1987b; Sussman & Garber, 1987].

The breeding female appears to be the dominant animal in marmoset groups in the wild [Stevenson & Rylands, in press; present study], not only displacing others from food sources, but also (as in the case of the *C. flaviceps* group studied) taking food from them in the same way as infants [Ferrari, in press]. While this female may form a dominant pair with an adult male, in particular in captivity [Stevenson & Rylands, in press], this does not seem to be a universal characteristic of marmoset groups. The breeding female in Rylands' study group of *C.h. intermedius*, for example, appeared to associate with two rather than a single male (although with one male more than the other). In the case of the *C. flaviceps* group studied here, the reproductive female was also observed "consorting" with two different males. While other group members may be dominant over one another, there is no evidence to indicate the presence of a rigid linear dominance hierarchy in wild marmoset groups "in the strict primate sense" [Epple, quoted in Stevenson & Rylands, in press], although Rothe [1978] does report such a situation for captive *C. jacchus* groups.

Similarly, while mating may be restricted to a single pair in many captive groups, exceptions have been observed, even among closely-related animals in family groups [Rothe, 1975] and dominant females in artificial groups may copulate with a number of males [Abbott, 1978]. While Rylands [1982] reported a "copulation frenzy" in the *C.h. intermedius* study group, he was not certain of the frequency of intromission. "Copulations" in which intromission and, more importantly, ejaculation do not take place are obviously very different, in functional terms, from those in which it does. Unfortunately, the rapidity of such behaviour and the usually poor visibility in the field generally inhibits the perception of such distinctions, so it appears that only provisional conclusions on the breeding system of the callitrichids should be drawn at the present time. The reproductive condition of the breeding female is another important factor about which very little is known.

The current discussion and re-assessment of callitrichid breeding systems is based mainly on evidence from field studies of *Saguinus* species, along with observations of "polyandrous" matings in captive studies of this and the two marmoset genera. The tendency in most publications, however, is to see the available data on the behaviour of *Saguinus* species as representative of that of callitrichids as a whole [Sussman & Kinzey, 1984; Goldizen, 1987a; Sussman & Garber, 1987]. While some characteristics, such as a single breeding female and the frequent presence of more than a pair of adults, are also found in most marmoset groups, there do seem to be a number of differences which suggest that their organisation may not be the same as that of tamarin groups.

Most significantly, perhaps, is the apparent stability of marmoset groups. All long-term studies of *Saguinus* have shown that apparently random migrations between groups are extremely common [see Sussman & Garber, 1987], whereas the available evidence [Rylands, 1982; present study] indicates that they are relatively rare in marmoset populations [except perhaps for *Cebuella pygmaea*, Soini, 1982]. The merging of groups, observed in at least four tamarin species [*S. midas*, Thorington, 1968; *S. geoffroyi*, Dawson, 1979; *S. fuscicollis*, Castro & Soini, 1978 and *S. nigricollis*, Izawa, 1978] has never been recorded for marmosets. In addition, the fact that two reproductive females have been observed in groups of *S. mystax* [Ramirez, 1984] and *S.f. weddelli* [Terborgh & Goldizen, 1985], implies either that even pregnant females migrate between groups or that breeding exclusivity is not as rigidly upheld as in wild marmoset groups.

The stability of marmoset groups is probably most closely related to their specialised adaptations for exudate feeding, effectively ensuring a steady supply of nutrients which is not only available throughout the year, but is usually concentrated into a small, easily defendable area. There is some evidence to support this idea from Dawson's study of *S. geoffroyi* [1979]. The "lowland" group, with its relatively more stable food supply during the dry season months, exhibited far more stability in composition and ranging behaviour than the "upland" group. This stability also implies that most marmoset group members will usually be related, and that they can usually be seen, in functional terms, as extended family units. This contrasts with Sussman & Garber's view [1987: p.74] of callitrichid social structure being based on units "consisting of unrelated and perhaps related adults...with communal care of the young, provided principally by adult males".

In the present study, for example, the observed formation of a new breeding unit involved three adult females from the study group joining two adult males from a neighbouring group (see chapter 2). The females were very probably siblings, although the relationship of the males is not known. In functional terms, this may be a significantly different type of social group from that proposed as typical of callitrichids by Sussman & Garber [1987].

The situation is complex and suffers from a lack of evidence, but it may be useful to propose that important functional differences between the social organisation of the marmosets and the tamarins should be recognised. These differences are not clear-cut at present, and can be seen more as tendencies within a continuum, the marmosets tending towards stable units of related members, the tamarins tending towards unstable aggregations of unrelated individuals. The expression of these tendencies seems to depend on environmental factors. In general, however, while tamarins may form stable, single pair family units, marmoset groups have never been seen to exhibit the extremes of instability recorded in most studies of tamarins.

If monogamy is defined as a mating system in which an individual reproduces "with only one partner of the opposite sex" [Wickler & Seibt, 1983: p. 46], there is a good deal of evidence to suggest that callitrichids should not be seen as strictly monogamous. In the case of the marmosets and tamarins, a single female breeds in each group, may mate with more than one male and is assisted in the rearing of her offspring by a number of often unrelated adults of both sexes, a situation similar to that seen in a number of bird species [*e.g.* Stacey, 1979]. This communal breeding system is referred to as "cooperative polyandry" by Terborgh & Goldizen [1985].

However, while this may be an adequate description of the breeding system of tamarins, it may not strictly apply to the case of the marmosets without qualification. The relative stability of marmoset groups implies that they are, on the whole, family units, especially if the concept of the extended family unit is broadened to include siblings of the reproductive group members. In such a situation, toleration of the breeding behaviour of group members of the same sex takes on a new meaning when seen in terms of the theory of kin selection [Hamilton, 1964; Axelrod & Hamilton, 1981]. The formation of new groups by siblings of both sexes is a situation seen in lions [Bertram, 1976] and has numerous advantages for group members in terms of kin selection. Such a situation would, in turn, contribute to and ensure group stability. If marmoset groups are based on such a system, then a clear distinction should be made between this and that of the organisation of tamarin groups, although it does seem that there is insufficient evidence at present to draw definitive conclusions on this point.

Social Behaviour

Callitrichids are highly social animals, both under captive conditions and in the wild, where social activities may occupy a much larger proportion of their daily activity period than is the case for comparable sympatric primates such as *Saimiri* and *Cebus* [Terborgh, 1983]. Marmoset groups in the wild seem to be characterised by very low levels of aggression and are, in general, closely-knit during the course of their daily activities. Such well-developed sociality is probably very important for many aspects of marmoset ecology, from the more obvious features such as the avoidance of predation and the benefits of the night-time huddle, to the possible advantages of the coordination of foraging activities (see chapter 7). Many aspects of marmoset behaviour have been well documented elsewhere [*e.g.* Epple, 1975; Stevenson & Poole, 1976; Box, 1978; Stevenson & Rylands, in press] and will not be dealt with in fine detail in this thesis, although detailed descriptions of specific behaviours will be given when necessary.

Overall, the behavioural patterns and vocalisations of the *C. flaviceps* study group were very similar to those recorded for *C. jacchus* both in captivity and in the wild [Stevenson & Rylands, in press; pers. obs.]. Observed differences were usually small and seemed to represent variations of the patterns observed in other species rather than absolutely different types of behaviour (especially if the discussion is restricted to the *C. jacchus* group species). However, as only a few animals from a small, isolated population were observed, such variations may reflect local differences related to factors such as habitat type, and even learned traditions, rather than any specific differences in behaviour between species.

Play behaviour in the study group, for example, was similar to that seen in *C. jacchus* [Stevenson & Poole, 1976; Stevenson, 1978] both in its repertoire and ontogeny. An interesting difference is that, while the play of *C. jacchus* at Tapacura was "always arboreal" [Stevenson & Rylands, in press], all members of the *C. flaviceps* study group were observed playing on the ground, sometimes engaging in sessions of wrestling and chasing which lasted almost an hour. The *C. flaviceps* study group, as discussed above, also appeared to be more tolerant of its neighbours than seems to be the case for most marmoset groups studied in the wild, although obvious agitation and excitement was displayed during inter-group encounters. In other parts of the same forest, the more intense excitement of such encounters suggests the influence of local factors, such as differences in population density or, possibly, the degree of relatedness of the members of neighbouring groups.

Scent-marking behaviour in the *C. flaviceps* study group was similar to that seen in other species, including the gouging and circumgenital marking of trees which do not produce edible exudate. However, while suprapubic marking has not been observed in *C. jacchus*, the members of the *C. flaviceps* study group were observed engaging in a type of behaviour which seemed to be similar to the pattern of "drag" marking seen in the *C.h. intermedius* study group [Rylands, 1982]. It was not ascertained, however, whether this was a type of scent-marking behaviour. The fact that the *C. argentata* group species do engage in such marking behaviour seems to be related to differences in the area of the suprapubic glandular tissue [Stevenson & Rylands, in press] and, while there is no information available at present, comparative data on the morphology of *C. flaviceps* would be useful for the assessment of this observation.

One common pattern which was not recorded for the *C. flaviceps* study group was that of "genital present" [Stevenson & Poole, 1976]. It is again not possible at present to assert whether this represents a local difference specific to this group or population, or whether it does, in fact, indicate the existence of important differences in the behaviour patterns of *C. flaviceps* and other marmoset species.

The food-sharing behaviour of the *C. flaviceps* study group included the calling and "active" sharing of food with infants, a pattern which has never been previously recorded in studies of wild callitrichids [Ferrari, in press], although this has been observed in captive *L. rosalia* [Brown & Mack, 1978], *S. oedipus* [Cleveland & Snowdon, 1984; Feistner & Chamove, 1985] and *C. jacchus* [G. Anzenberger, pers. comm.]. It is possible that this type of transfer may also take place in *C.h. intermedius* [A.B. Rylands, pers. comm.], and that it may be more widespread, although the difficulty of its observation in the field may have been the main cause for its absence from the data so far.

Overall, the patterns of social behaviour exhibited by the *C. flaviceps* study group show only minor differences from those recorded for other marmoset species, and are probably most similar to those of *C. jacchus*. Some of these differences may, however, point to interspecific differences and may, in turn, be related to broad ecological differences. As for most other features of marmoset ecology, however, there are too few data to allow the systematic analysis of such hypotheses.

Summary

This thesis presents data from the first long term field study of the buffy-headed marmoset *Callithrix flaviceps* [Thomas, 1903], a relatively poorly-known and endangered primate species found in a relatively small area of the Atlantic coast forest of southeastern Brazil. This preliminary discussion has introduced a number of aspects of the biology of this species in the context of a review of the information available for other members of the Callitrichinae, and has outlined the major themes of this thesis. The main points of this discussion are:

1. There is little general consensus on most aspects of the evolutionary history and taxonomy of the Callitrichidae. Eastern Brazilian forms of the genus *Callithrix* have been classified both as sub-species of a single species, *C. jacchus* [Hershkovitz, 1977] and as five distinct species [Mittermeier & Coimbra-Filho, 1981; Sussman & Kinzey, 1984]. On the basis of morphological and ecological differentiation between the forms, the latter classification is followed, with provisions, in this thesis.

2. Marmosets and tamarins tend to form relatively small groups (1 to 19 individuals), most species inhabiting home ranges of between 0.1 and 40 ha, with the former, in general, utilising smaller ranges than the latter. Marmoset groups also appear to be, on average, larger and more stable than those of tamarins. The expression of territorial behaviour is highly variable. Day ranges are relatively large for primates of this size. While highly adaptable, the dense vegetation of secondary and disturbed forest habitats is preferred.

3. All callitrichids are omnivorous, feeding on fruit, seeds, flowers, nectar, plant exudates, and vertebrate and invertebrate prey. Preferences for certain types of resource, *e.g.* orthopterans and "piecemeal fruiting" plant species, have been recorded for most species. These preferences appear to be related to a number of aspects of their foraging behaviour. The ability of the marmosets to systematically exploit plant exudates has further important implications for their ecology, especially in comparison with the tamarins.

4. Daily activity patterns are characterised by a delayed start, early cessation and relatively high levels of day-time resting. Foraging also appears to be less intense than for comparable insectivorous primates. These patterns may be

related, in part, to specific metabolic adaptations.

5. The vulnerability of these small-bodied primates to predation appears to have had an important influence on many aspects of their behavioural evolution, including habitat preferences and the use of sleeping sites.

6. Recent findings on the behaviour of groups in the wild has led to a re-assessment of their social organisation. While a single reproductive female is generally the norm, both in captivity and the wild, there is a growing body of evidence which suggests that they are not monogamous family units. However, while social groups may be based on "cooperative polyandry", these units may be functionally different for marmosets and tamarins, being based primarily on stable aggregations of related individuals in the former and on relatively volatile groups of unrelated individuals in the latter.

2

Study Site, Study Group and Methods

The Study Site

The study of *Callithrix flaviceps* presented here was carried out at the *"Estação Biológica de Caratinga"*, situated in the privately-owned forest reserve on the Fazenda Montes Claros (FMC) in the municipality of Caratinga, state of Minas Gerais, Brazil. The reserve is situated at 19°50'S 41°50'W (approximately 300 km north of Rio de Janeiro and 350 km east of Belo Horizonte, state capital of Minas Gerais) in the *"Serra da Mantiqueira"*, a mountain range which extends across four Brazilian states and forms the central area of the original distribution of the Brazilian Atlantic coast forest (figure 2.1). This ecosystem has been defined as "broad-leafed evergreen rain-forest" [Andrade Lima, 1966], and was originally distributed along almost the whole of the Atlantic coast from Rio Grande do Norte in the north, to Rio Grande do Sul in the south. The exact distribution of this type of vegetation has been defined differently by a number of authors [see Romaniz, 1968; da Silva, 1980], reflecting marked differences in the humidity of the windward and leeward slopes of the main coastal range, although that of Mittermeier *et al.* [1982] is followed here. Thought to have originally covered an area of some one million square km, this forest has been reduced to only 5% of this in the present day, scattered in relatively small and isolated patches, of which less than half can probably be considered primary [Mittermeier *et al.*, 1982; Bouchardet da Fonseca, 1985]. The Atlantic coast forest contains numerous endemic mammals, including the muriqui, *Brachyteles arachnoides*, the largest neotropical primate and the largest animal endemic to Brazil [Kinzey, 1982].

Figure 2.1

Original Distribution of the Atlantic Coast Forest of Eastern Brazil

[Following Mittermeier et al., *1982]*

The reserve at FMC consists of approximately 880 ha of forest and scrub, more than half of which has been felled or burnt in the past. The remaining area forms a core of relatively well-preserved forest which has been degraded through selective logging, both in the past and in the present day, but has been classified as primary forest in recent studies [Hatton *et al.*, 1983; Moreira de Andrade & Lopes, 1986]. The reserve covers two main valleys, Matão and Jaó, and a series of hills rising up from 318 m on the west bank of the Manhuaçú river to 682 m at its highest point. The forest has been isolated for at least 40 years, since the present owner purchased the land, although it is possible that it was contiguous with surrounding forest prior to this, according to a local contact who was resident on the fazenda with the previous owner. The area surrounding the reserve is predominantly open pasture, interspersed with plantations of coffee, sugar cane and maize. The inhabitants of the fazenda utilise the forest for the collection of timber, firewood, palm hearts and various medicinal products, but do not collect fruit or hunt. It appears, however, that *Cebus apella* may be shot when stealing crops. Muriqui were hunted in the past, but this is now strictly prohibited by the owner [Strier, 1986]. It seems unlikely that the *Callithrix flaviceps* population has ever suffered from hunting. Some residents of the fazenda have never, in fact, seen these shy monkeys.

Apart from *Callithrix flaviceps*, three other primate species are found in the reserve: the muriqui or *"mono"*, as it is locally known (*B. arachnoides*), of which there are at least two groups, containing almost 50 individuals [Strier, 1986, pers. comm.], the brown howler monkey (*Alouatta fusca*) known as *"barbado"*, of which there may be more than 500 in the reserve [Mendes, 1985, pers. comm.] and the black capuchin monkey (*Cebus apella nigritus*) or *"macaco"*, for which there are no details of population size, although this species is often encountered both in the forest and in surrounding plantations, and even in the fazenda's cane mill. Titi monkeys, *Callicebus* sp., have never been observed in the reserve by biologists [Valle *et al.*, 1984] nor by the local residents.

A previous estimate of the population of *C. flaviceps* at FMC was of between 50 and 60 individuals [Alves, 1985]. The present study found, however, that there were probably more than twice this number of marmosets in the reserve. While no systematic censusing was carried out, the presence of at least eleven different groups was recorded, and the majority of these were clearly relatively large. At the end of the field study, for example, the four groups occupying the northern end of the Jaó valley contained a total of 34 individuals. The five groups counted reliably during the study contained between 5 and 15 individuals, with a mean group size, over the study period, of 9.8 individuals. Reports from local residents, while probably not reliable (groups of 20 to 30 individuals were said to be common), also indicate that this mean value is a realistic estimate of the size of groups in the reserve.

Without systematic censusing, estimates of the density of the marmoset population cannot be reliably made but, if the study group is seen as typical (a mean of 13 animals occupying a total area of 35.5 ha), there could be as many as 37 marmosets per square km, and up to 320 in the reserve as a whole. There are two problems with such an estimate. On the one hand, the study group's home range overlapped considerably with those of its neighbours, which, if typical of all other groups at the site, would effectively increase this estimate by as much as 100%. Much of the reserve, on the other hand, appears to provide less than optimal habitat, and it seems that marmosets were either absent from, or present at only very low densities in some areas. Thus, while the *C. flaviceps* population seemed to be more concentrated in some parts of the reserve, the overall density was probably no more than 40 individuals per square km.

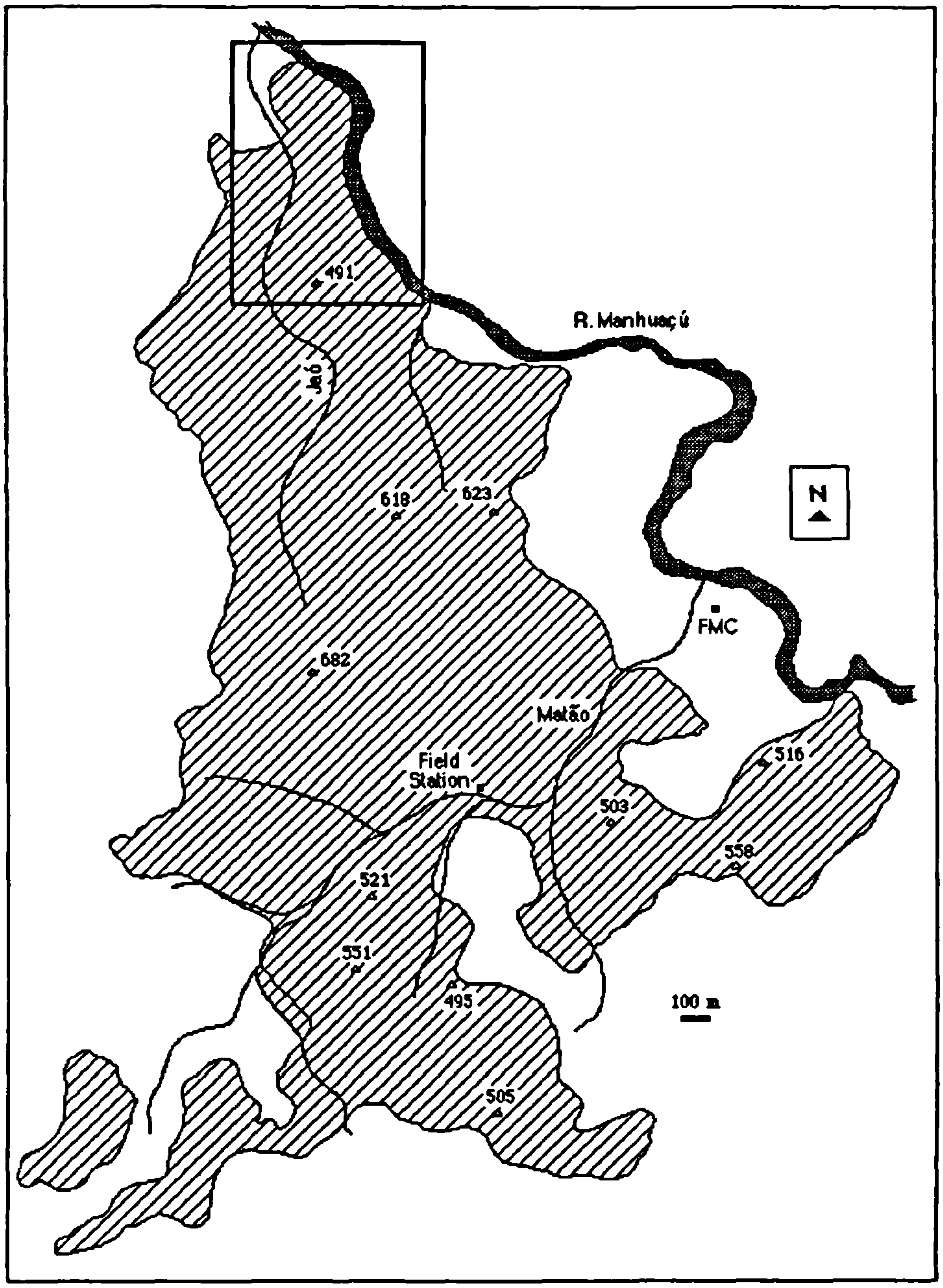
Rylands [1982] also found major differences in the density of the *C.h. intermedius* population in different habitats at Aripuanã. In undisturbed primary forest, densities were estimated at between 7.5 and 11.5 individuals per square km, while in areas characterised by extensive patches of disturbed forest, densities were estimated at between 31.25 and 54.4 individuals per square km. The density of the *C.p. kuhlii* population at Una was estimated at between 50 and 68.1 individuals per square km [Rylands, 1982]. *C. jacchus* appears to occur at even higher densities at Tapacura [Hubrecht, 1985; Stevenson & Rylands, in press], although the highly disturbed and patchy nature of the forest seems to have contributed to values as high as 700 individuals per square km. In general terms, then, *C. flaviceps* appears to occur in similar densities at FMC to those recorded for other *Callithrix* species which are, in turn, somewhat higher than those recorded for tamarins [see Sussman & Kinzey, 1984: table 6, p. 441].

A diverse vertebrate fauna exists at FMC, although a number of mammals which were almost certainly present in the past, such as the tapir (*Tapirus terrestris*), peccaries (*Tyassu* spp.) and the jaguar (*Panthera onca*), are no longer found in this region. A number of potential predators of marmosets are known to exist in the reserve, however. A variety of birds of prey, perhaps the biggest danger to these small primates (see chapter 1), have

Figure 2.2 (facing page)

The Forest Reserve at the Fazenda Montes Claros, Minas Gerais

This map, adapted from Hatton et al. *[1983] shows the approximate extent of the forest reserve at FMC (diagonal shading). The locations of the field station and the farmhouse (marked FMC) are also shown, along with the elevation in metres of the highest points in the different parts of the reserve. Please note that, while the shaded area does correspond with the limits of the reserve, some unforested areas of bracken and cultivated land are included. The location of the present study at the northern end of the Jaó valley is outlined.*


491
R. Manhuaçú
Jaó
618
623
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FMC
682
Matão
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516
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been recorded at this site (*e.g. Buteo albicaudatus, Falco* spp., *Herpetotheres cachinnans, Ictinea plumbea, Leptodon cayanensis, Leucopternis lacernulata, Miralgo chimachima* and *Polyborus plancus*). Mammalian predators include tayras (*Eira barbara*), raccoons (*Procyon cancrivorus*) and coatimundis (*Nasua nasua*). Snakes such as *Bothrops jararaca, Bothrops neuwiedi, Lachesis* sp. and *Micrurus* sp. are also present. Aerial raptors were the most conspicuous at the Jaó study site, being observed in relatively close proximity to the study group almost daily. Terrestrial predators, on the other hand, were observed only infrequently, although this may have been a direct consequence of the presence of the observer.

The Study Group

The Jaó study group of *Callithrix flaviceps*, JG1, occupies a home range at the northernmost extreme of the reserve, which is also its lowest point (figure 2.2). Preliminary observations carried out at the reserve in December, 1984, indicated that this group was one of the least disturbed by the presence of the observer. This may have been due, in part, to the location of its range and the proximity of local dwellings, although the neighbouring group, JG2, remained one of the most nervous encountered in the forest, despite frequent contact with the observer. JG1 had also been observed periodically during a previous study [Alves, 1985] and by a number of visiting biologists, which may also have contributed to its relative habituation. A number of other factors, such as its size and the relatively easy access of its home range, also contributed to the choice of this group as the principal one for study.

The first reliable group count was taken in mid March, 1985, when the group contained 11 members, including a set of twins, one male and one female, which were apparently born in February. The group may have contained more than 9 individuals prior to this, but counts were unreliable, so this cannot be confirmed. Evidence indicates that these twins were offspring of the reproductive female BM. Male twins were born during the night of July 27th, so the group contained 13 members at the start of the main study, in August 1985. The previous twins were a little more than five months old at this time, and would thus be classified as adolescents according to Ingram's terminology [1977]. All of the remaining nine individuals were judged, from their size and pelage, to have been adults (more than 15 months old). Five of

Table 2.1

Composition of the Study Group During the Main Study Period

	Age/sex Class[1]:				
Sample	Adult females	Adult males	Subadults (11-15 mo)	Adolescent (6-10 mo)	Infant/ juvenile (0-5 mo)
August 1985	5	4	-	2	2
September	5	4	-	2	2
October	5	4	-	2	2
November	5	4	-	2	2
December 1985	5	4	-	2	2
January 1986[2]	5	4	2	2	2
February	5	4	2	2	2
March	5	4	2	2	2
April	5	4	2	2	2
May	5	4	2	2	2
June	6/3[3]	4	2	2	-
July	3	4	2	2	-
August 1986	3	4	2	2	-

[1] Classes according to Ingram [1977].
[2] Month during which infants were born.
[3] 6 adult females were present in the first half of June, but only 3 in the second half.

these adults were female and four were male (table 2.1). The first change in group composition during the main study period came on the night of January 10th when a second set of twins was born, increasing the size of the group to 15 individuals.

The next change came at the end of May or the beginning of June, when the adult male Simão (Si, see table 2.2) left the study group to join the neighbouring group, JG2. As this emigration took place during the interval between observation periods, the circumstances were not recorded. JG2 contained seven individuals when it had been reliably counted in March, comprising one adult female, two adult males, one sub-adult, one adolescent and two juveniles whose size indicated that they were probably born in December 1985. At the beginning of observations in June, then, JG1 contained 14 individuals, while JG2 had increased in size to eight. On June 9th, the three adult females Sp, FS and Di left JG1 and joined the two original resident adult males from JG2 to form a new group of five individuals (JG4). Both JG2 and JG4 were subsequently observed within JG1's home range far more regularly than the original JG2, and the degree of range overlap increased (see chapter 5). JG1 continued with 11 members until the end of the

Table 2.2

Study Group Members

Individual (notation)	Notes[1]
Black Maggie (BM)	Reproductive female throughout main study (three births)
Spock (Sp)	Mature adult female, possibly twin of Si
Cuba (FS)	Mature adult female, possibly twin of Sm
Dida (Di)	Young adult female in 08/85, possibly twin of Ma
Máscara (Ma)	Young adult female in 08/85, possibly twin of Di
Gordão (Go)	Mature adult male, possibly oldest group member
Bob Tail (Bo)	Mature adult male, possibly reproductively active
Simão (Si)	Mature adult male, largest group member, possibly twin of Sp, possibly reproductively active
Smell (Sm)	Youngest adult male, possibly twin of FS
Jimmy (WJ)	Male, born 02/85, twin of BJ
Jocky (BJ)	Female, born 02/85, twin of WJ
Pablo (Pa)	Male, born 27 or 28/07/85, twin of PF, known sibling of Oz1 & Oz2
Paxo (PF)	Male, born 27 or 28/07/85, twin of Pa, known sibling of Oz1 & Oz2
(Oz1)	Possibly male, born 10 or 11/01/86, twin of Oz2, known sibling of Pa & PF
(Oz2)	Possibly female, born 10 or 11/01/86, twin of Oz1, known sibling of Pa & PF

[1] Speculations on relationships between adult group members are based on perceived morphological similarities.

main study, although a new set of twins was observed in the group at the end of October. These twins were apparently less than one month old, and it is thus interesting to note that the probable date of their conception coincides with the period preceding the emigration of Si.

Despite their small size, it was possible to distinguish all adult group members through differences in their pelage by the third month of the main study (table 2.2). One individual, Bo, was easily distinguishable from the others by the 7 cm of white hair at the tip of his tail, apparently the result of an injury. The reproductive female, BM, was also easily recognised, through the black pelage on the ventral surface of her body, her stout appearance and behavioural dominance over other group members. She was the group's reproductive female throughout the course of the study. It was also possible to distinguish the male twins born in July during the latter half of the main study.

By the time the main study was under way, the group was fully habituated and would regularly allow the observer to approach to within 1 m. Some individuals, the older and the younger group members in particular, were less calm in close proximity to the observer, but their behaviour rarely seemed to be affected. In fact, they would sometimes turn around to remove the observer from view (but not move away), whereupon they would become visibly less nervous.

Methods

Field work was carried out at the FMC reserve between December, 1984 and October, 1986. The period of the "main study", which constitutes the majority of the data presented here, was from August 1985 to August 1986, a thirteen-month period which covers the end of the 1985 dry season, the 1985/1986 wet season and the majority of the 1986 dry season (seasonality is discussed in chapter 3). Various aspects of the behaviour and ecology of JG1 were intensively studied during this period. Behavioural data consist of a main set of 125 full days of observation (sleep-tree to sleep-tree), 10 days in each month except September 1985 (9 days), December 1985 and August 1986 (8 days each). Complementary data were collected on plant phenology, and on the availability of exudates and arthropods. In addition, daily maximum and minimum temperatures, and rainfall were recorded throughout the period of field work. Less systematic observations of other marmoset groups in the reserve were also carried out, along with the collection of additional botanical data. The analysis of these data is aimed at the formulation of a detailed understanding of various aspects of the group's behaviour and ecology, in the context of seasonal changes in the environment and the evolutionary adaptations of the species in particular.

Preparation

Preparations for the study took place during the period from December 1984 to June 1985. The work was hampered at the start by the exceptional rainfall during the months of December and January which, among other things, blocked the road between the fazenda and the nearest town, and made marmosets more than usually difficult to locate, observe or follow. The

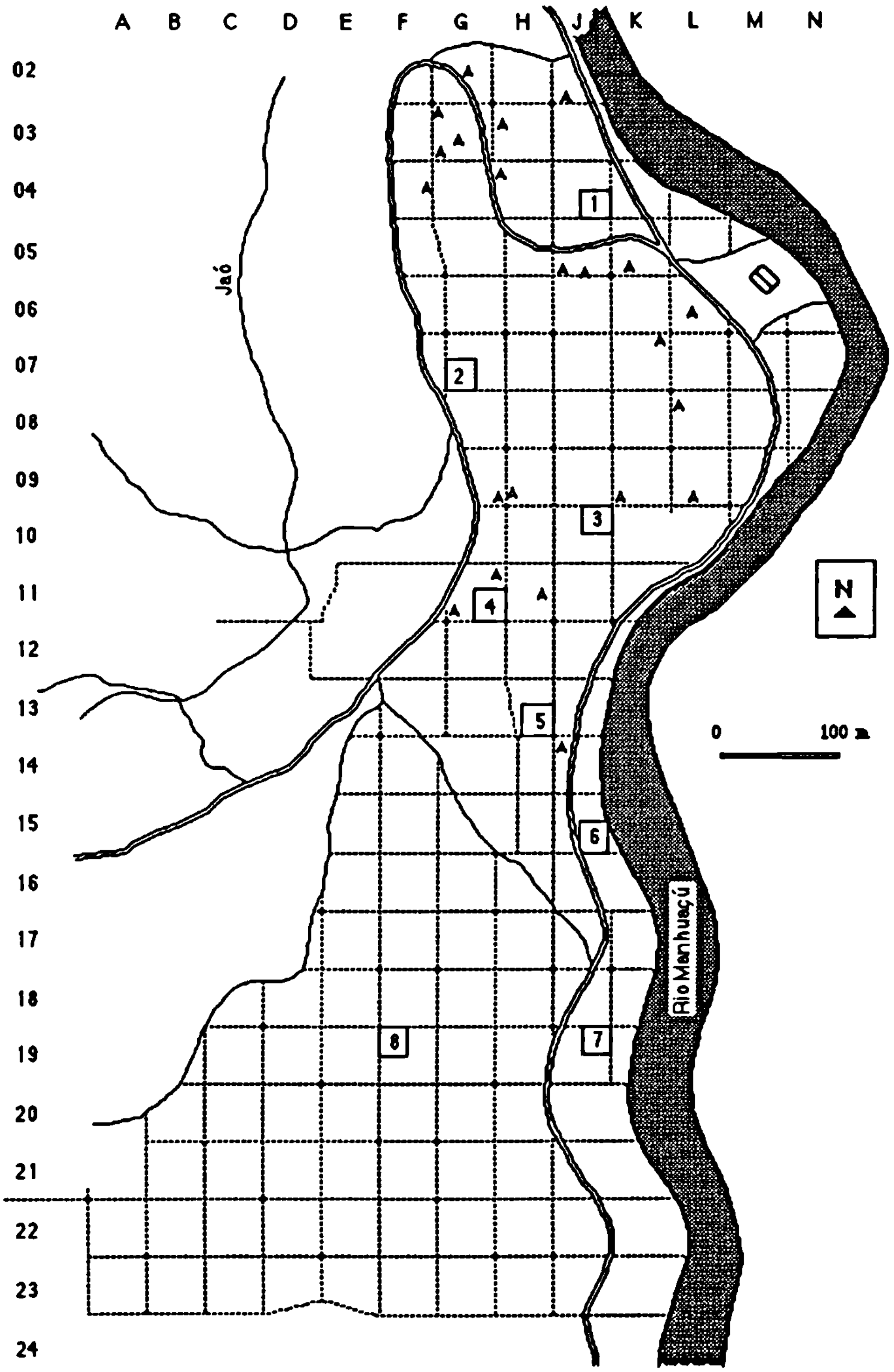
Figure 2.3 (facing page)

The Trail System at the Jaó Study Site

The Jaó study site is shown here in detail (for location, see fig. 2.2). The trail grid, phenology quadrats, locations of the angico *sample trees and other features mentioned in the text are shown. The letters (A to N) and the numbers (02 to 24) show the coordinates corresponding with the quadrats used for the analysis of the group's ranging—see fig. 5.1 and the ranging diagrams in chap.s 5, 6 and 7, and appendix IV.*

Key:

------	*Trail*
5	*Phenology quadrat*
▲	*Sample* angico *tree*


A B C D E F G H J K L M N
02 03 04 05 06 07 08 09 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
1
2
3
4
5
6
7
8
Jaó
Rio Manhuaçú
N
0 100 m

original plan for the study involved the capture and radio tracking of a number of groups to enable the study of population dynamics. Under the circumstances, however, it was decided that the study should concentrate on a single group at first and then expand to include others, if possible. It was also clear at this stage both that home ranges were much larger than had been expected and that a comprehensive trail system would be necessary to maintain contact with any group in the dense vegetation they typically occupy.

The first stage of preparation following the choice of JG1 as study group was the cutting of a trail system. Considering the small size of the animals and the density of the vegetation within their home range, a 50 m by 50 m grid was seen as the necessary minimum. A north/south, east/west orientation was decided upon for the grid, as this corresponded more or less with the orientation of the hillside. Trails were cut with the aid of a compass and measuring tape, and were coded and marked with coloured forester's tape (trails were judged to be generally accurate to within 5 m). The bulk of this grid was finished by March, 1985, although additions were made up until June, in accordance with observations of the group's movements (figure 2.3).

Once the cutting of the trail system was well advanced, an attempt was made to capture the group, following methods adapted from those used in studies of tamarins [Dawson, 1978; Neyman, 1978; J. Dietz, pers. comm.]. A number of problems were encountered, however, including human interference with pre-baited traps, the group's apparent dislike of strange fruits and its indifference to a live decoy marmoset. It is also possible that an exceptional abundance of food during this period (see chapter 3) may have reinforced the animals' natural suspicion of strange objects. By the time a successful bait (grasshoppers) had been found, the group was already well habituated to the observer's presence, and it was decided that their capture at that time may have hindered, rather than helped, the study.

For the study of plant phenology, eight quadrats of 25 m by 25 m (a total area of 0.5 ha), were randomly selected from areas chosen to represent observed differences of altitude and vegetation within the group's home range (figure 2.3). Within these quadrats, all trees with a height of 3 m or more were numbered and marked with coloured tape. The height, diameter at breast height and number of trunks of each marked tree were also recorded. This information was also collected for two separate samples of trees selected along transects located within the two main vegetation types found within the group's home range (for methods and results, see chapter 3). As preliminary observations of the study group had shown that they opportunistically utilise exudate caused by insect damage (particularly from the abundant *"angico prego"*, *Anadenanthera peregrina*, trees), an additional sample of 22 large *angicos* was similarly numbered and marked for the monitoring of exudate production (figure 2.3).

Plant Phenology

Fruit, flowers and nectar are important components of the diets of most marmoset species (chapter 1), so a measure of the availability of these resources within the home range of JG1 was obtained on a monthly basis, using the marked quadrats described above. In addition, a measure of mature and new leaf cover was also obtained. While not utilised by marmosets as food, the majority of the insects they prey on are folivorous, and it was thus thought that some measure of the availability of leaves within these quadrats would contribute to the understanding of the availability and distribution of these insects, and hence to the foraging behaviour of the study group.

It was originally hoped that the methods used by Strier [1986] as part of a study of *B. arachnoides* at the same reserve could be followed closely as this would have entailed a degree of consistency which would have been useful both in comparison between these studies and as a reference for future studies at the same site. However, major differences in forest structure and home range size led to adaptations in methodology, although the choice of height, rather than trunk diameter, was seen as an appropriate criterion for the choice of trees, given the nature of the forest and observations of its use by JG1.

The extreme density of the vegetation, particularly of lianas and other climbing plants, made the assessment of tree crowns not only both difficult and time-consuming, but also open to a number of observational biases. Preliminary observations of JG1 also indicated that fruit was either a minor component of or absent from its diet, at that time of year, at least (indications which later proved applicable to the majority of both the year and tree species). The methods finally decided on recorded the presence or absence of reproductive parts (flower buds, flowers and fruit) in the crowns of each of the 1329 marked trees, but did not record any estimate of the abundance of this material. When appropriate, notes on the numbers of fruit, or their maturity, were made. The presence of such material on climbing plants located within the crowns of marked trees and other details, such as the presence of exudate, were also recorded. The phenological status of each quadrat was recorded at the middle of each calendar month (in order to coincide with the mid-point of each "observation month"), *i.e.* more or less every 30 days, between May 1985 and August 1986.

Leaf cover was recorded less systematically, although at least half the quadrats were monitored on a bi-monthly basis. The quadrats were sampled in a way which allowed broad differences in vegetation and altitude to be assessed. The estimated proportion of the crown covered by mature and new leaves was recorded for each marked tree. Some details of changes in leaf colour were also recorded, when appropriate. Finally, an attempt was made to collect samples of the reproductive parts, or leaves when no such parts were produced, of all marked trees for their identification. Details of their identification are given in appendix I.

The Availability of Exudate

Many plant species produce exudates, often edible gums, in response to physical damage (see chapter 1). Such exudates, as we have seen, are an important resource for marmosets, which can stimulate their flow through the use of their specialised dentition. The availability of exudates for a marmoset group at any point in time is thus influenced by a number of factors, including the abundance of exudate-producing plants, insect activity and the gouging of the marmosets themselves. Preliminary observations of the study group indicated that their use of gums was frequently opportunistic, relying on damage caused to plants by insects or other phenomena (high winds, for example), rather than through their own activities. Throughout the course of the field study, in fact, the characteristic gouging of exudate-producing plants was seen only in the case of one species, *Acacia paniculata*, although this was the group's principal source of exudates during most months (chapter 6). Even in the case of this species, however, much of the group's feeding appeared to be opportunistic.

A. paniculata is a climbing plant which is particularly abundant throughout much of the group's range. Because of its habitus, quantification of the number of individuals in any area is virtually impossible. Study group members were observed feeding on gum produced by shoots, which may or may not have been individual plants, as little as 20 cm tall and 1-2 mm in diameter. Many larger stems, on the other hand, even those within one or two metres of similar ones which were heavily used, were left untouched by the group throughout the period of the study, implying that they may have been surplus to their needs during this time. As the group also ignored both the possibility of gouging individuals of other exudate-producing species and the exudate present on such individuals, it was concluded that exudate is probably available within its range in excess of its overall needs.

Nevertheless, as it was apparent from preliminary observations that *angico* trees provided a large proportion of the gum consumed by the group (this was confirmed in the main study), it was decided that some measure of the natural availability of this exudate would be a useful parameter for the analysis of its behaviour. Twenty-two *angicos* were monitored, eight of which were known to have been used as exudate sources by the group. The trees were observed in the middle of each "observation month" as for the phenology quadrats and the method of assessment of exudate availability was similar to that used by Bearder & Martin [1980]. All exudate deposits on the trunk of each tree below a height of 2 m were located and their length (or maximum dimension) measured. The nature, colour and consistency of the deposits were also recorded, as well as the leafing and fruiting phenology of the sample trees. The fact that this sample of *angicos* lies within JG1's home range and that the exudate of a number of these trees was used by the group presents the possibility of certain biases, although this was minimised by carrying out the measurement on a single day each month, during as short a period of time as possible. In addition, gum streaks were often found to remain undisturbed for periods of a number of months. This again emphasizes previous conclusions on the abundance (and possible super-abundance) of exudate within the group's home range.

Arthropod Abundance

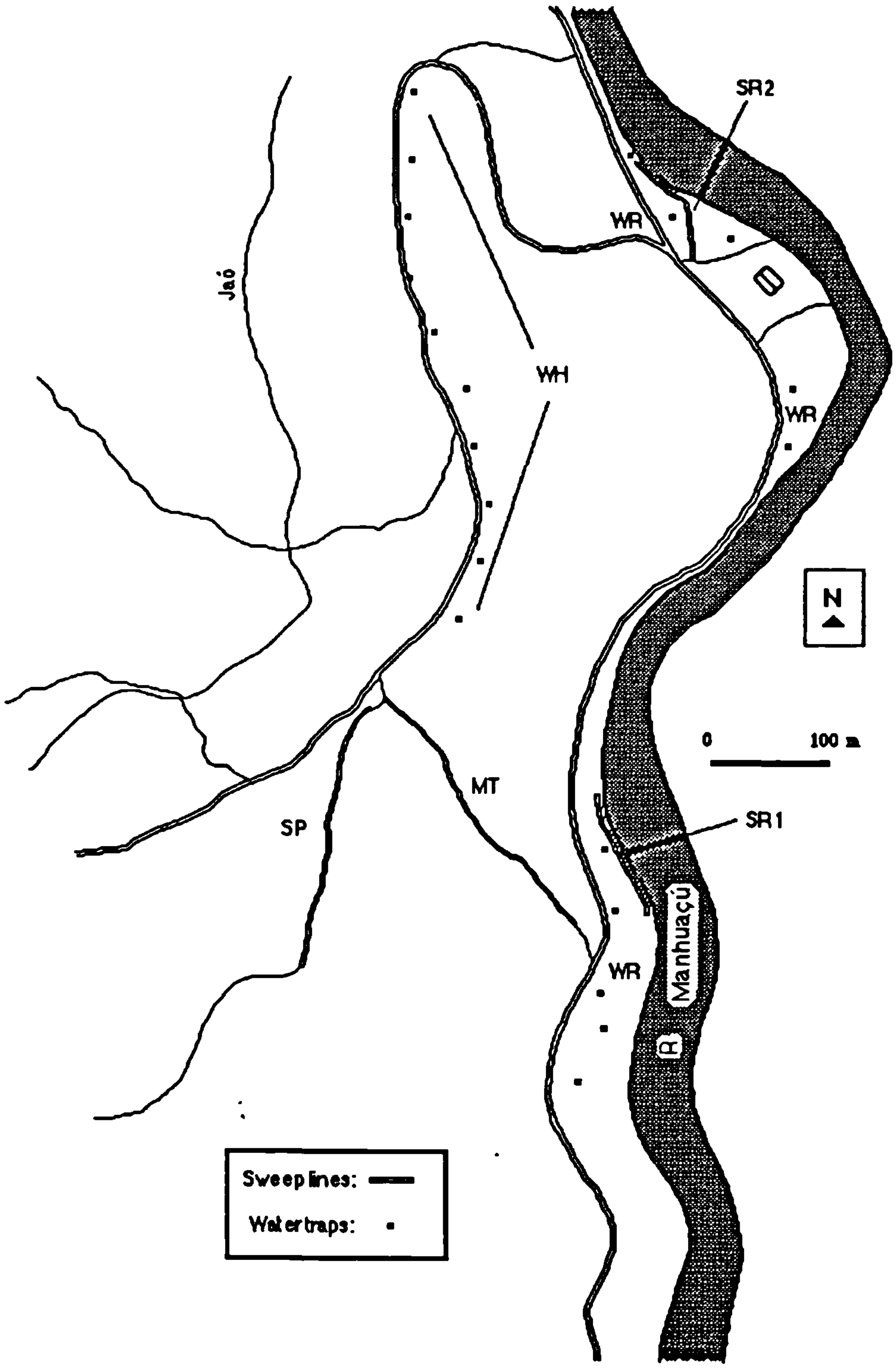
Animal material, insects in particular, is the third main component of marmoset diets. Insect trapping, in contrast with the more passive observation of plants, is open to a wide range of possible biases and random effects. One problem arising from the use of most methods, for example, is that the animals are killed during their capture, effectively reducing overall abundance. This can, in turn, have a direct and perhaps disproportionate influence on measured abundance in subsequent months. In this case, an attempt to increase the reliability of the measurement of changes in abundance through time by increasing the numbers of traps used (and arthropods collected) may actually have the opposite effect. Similarly, while trapping within the study group's home range may reduce the abundance of available prey and thus have some influence on its behaviour, trapping at another location, even within the same forest, would not necessarily provide a reliable measure of the abundance of insects available to that group [see *e.g.* Janzen & Schoener, 1968]. This may be especially important in the case of marmoset groups, whose preference for certain forest types, as discussed in chapter 1, may be partly determined by arthropod abundance.

In choosing the methods used, the emphasis was placed firmly on simplicity. As the primary function of the trapping was the measurement of changes in abundance through time, it was felt that relatively simple methods would be most reliably replicated from one month to the next. Two methods were chosen; water traps and sweep netting. While water traps are most easily and reliably replicated from month to month, they tend to capture disproportionate numbers of certain orders of insect, notably dipterans [Henshaw, 1984], which are only rarely, if ever, preyed on by marmosets. On the other hand, while sweep netting is less reliably replicated, it was felt that it would provide a better measure of the types of insect eaten by the study group as it does, in some ways, imitate their foraging behaviour (*i.e.* in that it effectively "searches" the leaves of the understorey). The use of these two different methods also allows the cross-checking of results. Preliminary trials were carried out to assess the numbers of traps (or sweeps) to be used, and these indicated that an adequate measure could be made without deleterious effects on abundance. As for the measurement of the availability of plant material, trapping was carried out in the middle of each "observation month", at an interval of approximately 30 days.

The water traps consisted of ten yellow plastic bowls 30 cm in diameter and 10 cm deep containing approximately 2 cm of a salt and detergent solution (100 g of salt and the same amount of detergent in 5 l of water). The traps were set at 50 m intervals along trail lines within JG1's home range and collected 24 hours later. Two lines of trails were used (WH and WR, see figure 2.4) and were set on consecutive days each month during the course of the main study. The traps were set and collected in the same order each month, and care was also taken to ensure that the quantity of water in each trap and the concentration of the solution used was constant. It was thus

Figure 2.4

Distribution of Insect Trapping Lines at the Jaó Study Site



hoped that the samples obtained in these traps each month would be consistent and comparable measures of actual arthropod abundance at the study site. The body length of all arthropods was measured and the order to which the insects belonged was recorded, as far as possible.

Sweep sampling followed methods similar to those used by Janzen [1973a, 1973b] with a sweep net approximately 0.4 m in diameter with a mesh of 1-2 mm. Preliminary trials along the trail grid proved unsatisfactory as the newly-cut vegetation tended to catch the net frequently, causing an irregularity in the flow of the sweeping. It was thus decided to follow sweep lines along the western edge of the forest between trails 17 and 13 (SP on figure 2.4), along "mosquito" trail (an established path used by local residents to pass through the forest (MT on figure 2.4) and on the riverbank between trails 16 and 14, and 05 and 02 (SR1 and SR2, figure 2.4). SP and MT consisted of 200 sweeps, while SR1 and SR2 consisted of 100 each. Great care was again taken to ensure consistency between the samples; the sweeps were carried out in the same order and at roughly the same time of day (between 08:00 and 09:00) each month, and an attempt was made to follow the same pattern of sweeps. All insects were measured and identified as for the water trap samples.

It was felt that the considerable variation in elevation within the range of JG1 may have had an influence on the humidity of different parts of the forest, especially during the dry season, and that these differences might be reflected, in turn, in the distribution of arthropods at the site during different times of year. It was felt that the distribution of the monthly trapping would allow, in addition to a measure of overall abundance, some assessment of possible seasonal changes in the distribution of arthropods within the group's home range. Thus, while WH and SP are situated at the highest altitudes habitually frequented by the study group, WR, SR1 and SR2 are located along the riverbank which is, naturally, the lowest part of its range. The sweep line at MT cuts down from one level to another and should represent, in theory, an intermediate measure.

Chapter 2

Behavioural Observations and Analysis of Bias

As original plans for the capture and marking of marmoset groups, and the use of radio telemetry, were abandoned, planned methods for the sampling of behaviour were re-assessed and altered. Without marked animals or radio telemetry, the close accompaniment of either individuals or groups through the dense vegetation of the secondary forest at FMC was seen as being extremely difficult, if not impossible. Under these conditions, the use of a method such as focal animal sampling would have been unsatisfactory [see Aldrich-Blake, 1970]. Scan samples were seen as being the most reliable alternative [Altmann, 1974]. This sampling method has been used successfully in many studies of primate ecology, including those of *Callithrix* species [Rylands, 1982], and may, in fact, be as reliable as focal animal sampling for the assessment of characteristics such as time budgets [Clutton-Brock, 1974a, 1977; Chivers, 1974]. After some preliminary testing of schedules with JG1, it was decided that the schedule used by Rylands in the study of both *C.h. intermedius* and *C.p. kuhlii* would not only provide an adequate sample of the study group's activity, but also a data set which would be reasonably comparable with these previous studies.

The schedule used consisted of a one-minute scan sample every five minutes. On the 125 "full" observation days (when the group was followed from one night's sleep-tree to the next) which make up the main data set, scan samples were conducted every five minutes according to the main divisions of the clock, *i.e.* 05:00, 05:05 and so on. The first scan of the day took place according to this schedule from the time the group was seen to be active. On the rare occasions when the group was visible in the sleep tree, it was defined as being "active" from the moment the first animal left the characteristic night-time huddle. Scans were then conducted at these regular intervals throughout the day until either no group members were visible or, on the same rare occasions, the group was seen as having taken up its night-time huddle and had thus ceased to be active.

The following details were recorded for the first sighting of each group member coming into view during each scan:

a) height above the ground in metres (estimated as the height above the base of the main support),
b) diameter of support in centimetres,

c) orientation[1] and "posture", *i.e.* head up or head down,
d) activity,
e) vocalisation,
f) identity of individual,
g) type of support *i.e.* tree, climber etc. (from November onwards),
i) additional details *e.g.* type of prey consumed, other individuals involved in recorded social behaviour, *etc.*

The time at which each scan was carried out and the position of the group were also recorded. The latter was an estimate of the central point of the group [again, following Rylands, 1982] and, with the help of the trail system, was usually judged to be accurate to within five or ten metres, except when it was spread over a relatively large area or in the extreme west of its home range, where there were fewer trails. Great care was taken to ensure that animals were recorded only once in each sample. As it was possible to distinguish most individuals (although not necessarily possible to identify them in every case) and as the group was usually in relatively close proximity to the observer, it seems unlikely that group members were included more than once in any one sample.

The behavioural categories used in the recording of individual activity are described in table 2.3. One problem with the definition of categories is the interpretation of an animal's activity by the observer, and the reliability of these categorisations both as a representation of the observed animal's activity and in comparison with results obtained in other studies. A major difficulty with the interpretation of marmoset foraging behaviour, for example, is that a great deal of time is spent systematically scanning the environment, often in a sitting position, for signs of prey. While it is usually relatively easy to decide whether a seated animal is engaged in such activity or is resting, there is an inevitable "grey area" between the two categories. An intermediate "rest/forage" category was included during preliminary observations, but complicated observations without improving the interpretation of these behaviours and was not used in the main study. While a small number of misinterpretations may have been made during the course of the study (the

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[1] *Three categories were used: "vertical" (orientation of animal judged to be within 10° of the vertical), "diagonal" (animal judged to be between 15° and 75° of the vertical) and "horizontal" (animal judged to be between 80° and 90° of the vertical).*

Table 2.3

Behavioural Categories Used in Scan Sample Records

Category (notation)	Activity of animal at first sighting
Travel (TR)	Walking, climbing, leaping (non-vertical supports) or falling.
Rapid travel (TR R)	Running or "galloping".
Vertical cling and leap (TR V)	Leaping between vertical supports.
Forage (FO)	Searching for and/or capturing prey[1].
Rest (RS)	At rest, sitting or lying, and not engaged in other activities.
Self scratch (RS S)	At rest, scratching self.
Self groom (RS G)	At rest, autogrooming.
Invertebrate prey (INS)	Consuming insect or other invertebrate prey[2].
Vertebrate prey (VERT)	Consuming vertebrate prey[2].
Acacia gum (RG)	Consuming gum known to be from *A. paniculata*.
Angico gum (AP)	Consuming gum known to be from *A. peregrina*.
Gum (GUM)	Consuming gum from unknown source, or source other than *A. paniculata* or *A. peregrina*[2].
Fruit (FT)	Consuming fruit[2].
Seed (SD)	Consuming seed[2].
Nectar (FLO)	Consuming nectar[2].
Scent marking (SM)	Sniffing support, gouging, face rubbing, or scent marking with circumgenital, suprapubic or sternal glands.
Social (SOC)	Social interaction[3].

[1] Foraging sub-categories (used between December 1985 and August 1986):

Scan (FO SK)	Intense scanning of environment.
Scan ground (FO SKO)	Intense scanning of ground.
Manipulate (FO MP)	Manipulation of object/substrate.
Break open (FO BKO)	Breaking open object/substrate.
Bite open (FO BIO)	Biting open object/substrate.
Grab (FO GB)	Grabbing object/substrate with one or two hands.
Pounce (FO PO)	Pouncing on possible prey.
Follow (FO FO)	Pursuing mobile prey.

[2] The prey item or source of plant material was identified, whenever possible.

[3] For social sub-categories, see appendix II.

usual close proximity of the animals again probably minimised such possibilities), it is hoped that the data set is large enough to ensure that this has not had a significant overall effect on its results.

Additional details of the group's behaviour and movements were recorded during the course of scan sampling in *ad libitum* fashion [Altmann, 1974]. All occurrences of behaviours such as prey feeding, allogrooming, scent marking and so on, were also recorded during all observation periods. Detailed records of vocalisations were also made, whenever possible. It was not possible, on the other hand, to collect systematic data on group dispersal due to the density of the vegetation in most areas, although some notes were made, particularly when the group seemed exceptionally well spread out.

Observations were carried out with the aid of a pair of Nikon 10 x 40 binoculars, and field notes were made in spiral-bound note books using codes developed both during preliminary observations of the study group and the observer's previous work with captive *C. jacchus* (table 2.3). Copies of all records were made, usually on the same day (whenever possible), when they were checked for possible errors. This also permitted the addition of observations which were not noted down at the time of their occurrence, although only when the observer was reasonably certain of their accuracy.

It was also possible, using detailed notes of the group's movements, to map its daily path on a plan of the area and trail grid. Estimates of path lengths were made from this mapping, and were double-checked to ensure consistency. For the analysis of the group's use of space (see chapters 5, 6 and 7), quadrat occupation records were used. The 50 m x 50 m quadrat (based on the trail system, see figure 2.3) in which the estimated centre of the group was located at the beginning of each scan sample was recorded. A quadrat occupation record was thus collected at five-minute intervals throughout the day. Partial quadrats bordering the river or the pasture were scored to the nearest quarter quadrat (see range maps, chapters 3 and 5). No reductions in range estimates were made with regard to other peripheral quadrats as these appeared, in most cases, to be a minimum estimate of the extent of the group's ranging (see chapter 5). Given the level of accuracy of the measurements, all calculations of range size are made to the nearest 1000 square metres (0.1 ha).

This method is a little different from that used in other studies, in which all the quadrats occupied by one or more group members were recorded for each scan [*e.g.* Struhsaker, 1975; Waser, 1977; Rylands, 1982]. While the number of quadrats entered by the group during any particular period may thus be slightly under-estimated relative to these studies, it was felt that this gave a more accurate measure of the group's use of space, given that it was rarely dispersed over a distance of more than 30 m. From the records of the group's movements, it was possible to calculate occupation records for the 25 m x 25 m quadrats formed by dividing each of the larger quadrats into four quarters. According to this method, day ranges were consistently between 50% and 70% of the values obtained using the larger quadrats. Qualitatively, it was felt that an accurate measure of the group's use of space probably lay somewhere between these two estimates, *i.e.* at approximately 80% of the values estimated using the 50 m x 50 m quadrats.

It should be borne in mind, nevertheless, that, while the quadrat size was the same, the method of range estimation used in this study was slightly different from that used by Rylands [1982]. It seems unlikely, however, given its usually narrow dispersal and the quadrat size used, that the range use of the *C. flaviceps* group was significantly under-estimated relative to the latter study. The larger day ranges of the *C.h. intermedius* group, for example, are more or less as would be expected, given its longer average daily path length. The most relevant comparisons between these studies are, in fact, unaffected by these differences as they deal with contrasts in the proportions of ranges used during any period, *e.g.* the proportion of the monthly range used each day (see chapter 5).

In addition to the 125 full observation days (14435 scan samples containing 70786 records) of the main study period, ten full observation days were carried out in July 1985, although the observer was not fully satisfied with the results and these data were not included in the main set for analysis. Scan samples were also collected during periods of up to seven hours on as many as four days each month during the main study, and the group was followed and observed in *ad lib.* fashion on as many as a further ten days each month. Focal animal sampling of foraging behaviour was also carried out intermittently during the latter half of the main study, once individuals could be consistently identified, although these data are relatively few and have not been analysed here. Observations of other groups, due to their timidity, were generally restricted to *ad lib.* sampling.

While great care was taken to ensure the accuracy of the observations, in their assessment both of individual behaviour and of the patterns of activity of the group as a whole, some bias seems inevitable, given the methods used and the general conditions under which observations were carried out [see Clutton-Brock, 1977]. Given the low levels in the forest at which the group was normally active and its usual close proximity to the observer, it is felt that such bias probably had a relatively minor influence, overall, on the results of this study, possibly far less than in comparable field studies of arboreal primates. This appears to be confirmed by a direct comparison with the study of *C.h. intermedius* (chapter 4, appendix III), in which the same observational methods and schedules were used [Rylands, 1982].

Rylands [1982: pp. 40-43] presents a detailed analysis of the direction of possible biases affecting the recording of different types of behaviour in the case of the *C.h. intermedius* study group. He argues that activities such as locomotion and fruit feeding were particularly conspicuous, and that there was a strong bias favouring their observation. Factors affecting the visibility of other major behavioural categories, such as foraging and rest, were judged to even out overall, although this implies that they would be under-represented, in relative terms, in the data as a whole. In the case of the *C. flaviceps* group, on the other hand, it seems unlikely that any marked contrasts in the visibility of different behaviours would have a significant effect on the results of the study, given the usually close contact maintained by the observer. While the density of the vegetation did restrict visibility on occasion, this seemed to apply equally to all activities, and is probably cancelled out, overall, given the relatively large number of records collected each month. Certain minor differences in the visibility of specific behaviours were noted, however, such as that between feeding on different types of gum and on insects of different sizes (these are discussed in chapters 4 and 6, respectively). This seems to have been the result of the sampling methods used, rather than of absolute differences in the visibility of these behaviours.

Scan sampling may also be open to biases resulting from the differential representation of different age/sex classes [Clutton-Brock, 1977]. Testing for such bias in the present study is, however, problematic. Certain individuals, such as Bo and BM, were known to be more easily identifiable than others, while individuals such as BJ and Ma were relatively less easily identified. Systematic identification of all group members was only possible after the third month of the study, while the "status" of some changed during the course of the year *e.g.* BJ became less easily identifiable as she matured to adult size. In addition, the actor was only positively identified in 56.2% of the records collected during the main study (including records for which the actor was identified only as "adolescent" or "infant/juvenile"). Any analysis of the records would thus have to assume that the group members are represented in similar proportions in the remaining 43.8%, an assumption which clearly does not hold if some were more easily identifiable than others.

Analysis of the records confirms these more qualitative observations (table 2.4a/b). Bo and BM were clearly identified more frequently than other adult group members during almost all months, while Ma was always among those recorded least frequently during any month. Similarly, the identification of BJ falls steadily throughout the course of the year (the contrast between August 1985 and August 1986 is particularly marked). While a significant bias is apparent in most months, the evidence seems to indicate that this is due to differences in the observer's ability to identify specific individuals rather

Table 2.4a

Identification of Individuals in Scan Samples

Individual	Percentage of records for which the actor was identified each month: Aug 85	Sept	Oct	Nov	Dec 85	Jan 86	Feb
Bo	15.3	11.1	9.2	9.2	8.0	8.4	6.8
BJ	15.6	12.4	8.5	6.6	5.8	4.5	5.1
BM	11.7	10.1	9.4	7.5	8.1	10.5	8.2
Di	2.1	1.9	5.5	6.6	4.9	5.3	5.0
FS	0.0	0.0	3.0	7.3	6.1	7.2	6.6
Go	2.3	7.5	6.7	6.2	6.4	6.0	5.9
Ma	0.0	0.0	2.3	5.5	3.9	2.8	3.8
Pa	0.0	0.0	0.0	0.0	0.0	1.7	3.8
PF	0.0	0.0	0.0	0.0	0.0	1.4	3.4
Si	1.8	7.6	8.3	6.7	6.8	6.3	6.2
Sm	0.3	2.3	6.6	8.8	7.2	7.5	6.3
Sp	0.0	3.0	7.2	5.7	4.8	4.5	5.5
WJ	12.3	11.8	7.6	6.5	5.9	5.7	4.9
"Adolescent"[1]	1.6	0.4	0.2	0.0	0.0	18.3	9.5
"Infant/juvenile"[1]	1.0	14.1	18.4	19.3	24.3	0.0	6.0

[1] N.B. category represents two or more individuals in any month.

Table 2.4b

Identification of Individuals in Scan Samples

Individual	Percentage of records for which the actor was identified each month: Mar 86	April	May	June	July	Aug 86
Bo	7.5	8.7	7.4	10.2	10.2	12.3
BJ	4.7	4.2	3.7	5.1	5.9	6.0
BM	9.8	8.0	8.3	10.0	11.5	13.4
Di	5.8	5.2	6.1	2.3[2]	0.0[1]	0.0[1]
FS	5.9	6.3	5.8	2.2[2]	0.0[1]	0.0[1]
Go	4.9	4.7	4.2	6.2	6.5	7.5
Ma	4.8	4.0	4.6	4.8	6.2	5.4
Pa	3.4	4.5	4.5	6.0	6.7	5.2
PF	2.4	4.3	4.4	5.8	6.2	4.7
Si	5.7	6.2	6.1	0.0[1]	0.0[1]	0.0[1]
Sm	3.8	4.2	5.3	7.0	7.8	8.7
Sp	5.3	5.1	4.2	1.7[2]	0.0[1]	0.0[1]
WJ	4.6	5.1	5.9	7.0	8.4	6.8
"Adolescent"[3]	8.8	2.9	2.2	26.0	29.2	25.5
"Infant/juvenile"[3]	17.0	22.1	23.9	0.0[1]	0.0[1]	0.0[1]

[1] Individual/category not present in group.

[2] Individual present in group for only half total observation days.

[3] N.B. category represents two or more individuals in any month.

than to differences in the visibility of different age/sex classes or the behaviours in which they are characteristically involved. A sub-set of the data was thus tested in order to find out if this conclusion could be confirmed.

To do this, the records for four individuals of each sex (BJ, Di, FS, Go, Si, Sm, Sp and WJ) collected during the months when all were both present in the group and systematically identified (November to May) were analysed. The analysis was based on the assumption that all individuals would have been recorded with equal frequency. The "expected" proportion of the total records collected for each individual in each month is thus 12.5%. A Chi-squared test was used to find out if the observed values differed significantly from this (see table 2.5). Significant deviations were not observed in any of the seven months . The difference appears to be smallest, in fact, when all seven months are taken together, which seems to confirm that there was relatively little bias overall, in terms of the differential visibility of different age/sex classes, operating on the data collection. Rylands [1982] found a similar pattern in the data collected on the *C.h. intermedius* study group.

Table 2.5

Analysis of Possible Differential Observability of Age/Sex Classes

	Percentage of records for which these individuals were identified:							
Individual	Nov	Dec 85	Jan 86	Feb	Mar	Apr	May	Nov-May
BJ	12.2	12.1	9.6	11.2	11.6	10.2	8.9	10.1
Di	12.2	10.1	11.2	10.9	14.2	12.7	14.8	12.2
FS	13.4	12.7	15.3	14.5	14.4	15.3	14.1	14.2
Go	11.3	13.4	12.8	13.0	12.0	11.5	10.1	12.1
Si	12.4	14.2	13.4	13.8	13.9	15.2	14.7	13.8
Sm	16.3	15.0	15.9	13.9	9.4	10.3	12.9	13.7
Sp	10.5	10.1	9.6	12.0	13.1	12.5	10.1	11.1
WJ	11.9	12.4	12.2	10.7	11.3	12.3	14.4	12.0
Chi-squared analysis for each sample period:								
Expected frequency	12.5	12.5	12.5	12.5	12.5	12.5	12.5	12.5
X^2	1.67	1.77	3.07	1.24	1.68	2.14	3.25	0.85
d.f.	7	7	7	7	7	7	7	7
p	0.98	0.97	0.88	0.99	0.98	0.95	0.86	>0.99

Overall, then, it appears that there was very little bias operating on the data collection, due principally to the observer's ability to maintain close contact with the group throughout the day. An analysis of the numbers of records collected in scan samples both during the course of the year and during the course of each day appears to further confirm this (appendix III). While this does seem to indicate, on the one hand, that the behavioural data are adequately objective, it also implies, on the other, that comparisons with most previous studies of marmosets and tamarins may, equivocally, be impaired (see chapter 4). Further details of all methods used, and a fuller discussion of possible bias, will be given, as appropriate, where the data are presented and analysed in the following chapters.

Data Analysis

It was felt, given both the comparatively large number of scan samples and records collected and the apparent lack of bias influencing the collection of behavioural data, that the relative frequencies at which different activities were recorded were a good measure of the actual frequencies in which they were engaged by the group. All analyses of the group's behaviour were thus based on the numbers of records collected rather than on the proportions of each activity recorded in each scan sample, a method suggested by Altmann [1974] and Clutton-Brock [1977] as a means of compensating for certain biases in the data collection. While the latter method may not produce significantly different results from the former [Strier, 1986], it was thought that its use in the present study may, in fact, have led to over-estimations of important, but rarely-recorded behaviours such as prey feeding. As this method was used for the analysis of the data on *C.h. intermedius*, *C.p. kuhlii* and *L.r. chrysomelas* [Rylands, 1982], its application to the present analysis again allows direct comparisons to be made with these studies.

All data analysis was carried out using the Apple micro-computers and statistical packages available at the Anthropological Institute of Zürich University. Overall, the organisation of the data and the analyses used were kept relatively simple, as far as possible, in order to facilitate both the interpretation of the results and their comparison with those from other studies. Standard statistical tests for the biological sciences [Siegel, 1956; Sokal & Rohlf, 1981] were used in all analyses. Please note that all statistical tests are two-tailed, unless stated. Details of the organisation and analysis of the results are given in the relevant chapters.

Summary

General information on the study site, the *Callithrix flaviceps* study group and the methods of data collection used are presented. The main points are:

1. The study site is located within the tropical zone, in the *Serra da Mantiqueira* of southeastern Brazil, lying at an altitude of between 318 and 682 m. The reserve is a 880 ha remnant of the Brazilian Atlantic coast forest, containing a varied vertebrate fauna which includes four primate species and numerous potential predators of marmosets, birds of prey in particular. No accurate measure of the *C. flaviceps* population was made, although eleven groups were known to be present and a population density of up to 40 individuals per square km was thought possible.
2. The study group contained between 11 and 15 members during the course of the main study period. Three births of twins were recorded, all offspring of the same reproductive female. A major change in group composition took place between the months of May and June when an adult male and three adult females emigrated. The latter individuals formed a new group with two adult males from a neighbouring group.
3. The availability of arthropods, reproductive plant parts, leaves and *Anadenanthera peregrina* exudate was measured on a monthly basis throughout the main study period. Temperature and precipitation were measured daily.
4. Behavioural observations were based on scan sampling (a minimum of eight full days each month), although numerous *ad lib.* records were also made. During standard sampling, a one-minute scan was carried out every five minutes throughout the day. This schedule was based on that used successfully in previous ecological studies of *Callithrix* species [Rylands, 1982], allowing systematic comparisons to be made. Due to the habituation of the group and the low levels at which they were normally active, observational bias appears to have had a minimal influence on the accuracy of the behavioural record.

3

Ecological Variables

The behaviour of primate groups in the wild is closely linked to and affected by the physical environment in which they are found. Most primates can adapt to a wide variety of habitat types and groups of the same species may exhibit very different patterns of ranging, activity, feeding and social organisation in different areas [*e.g.* Dawson, 1979, Cheney, 1987]. This variability can be a major problem in studies of primate ecology, and great care is needed in order to draw meaningful conclusions on the ecology of a species when only one group or population has been studied. As the first detailed work on *Callithrix flaviceps*, the present study is faced with such a problem. While the data collected on the behaviour of a single group may be characteristic of the behaviour of that group, it may not necessarily be representative of the species as a whole.

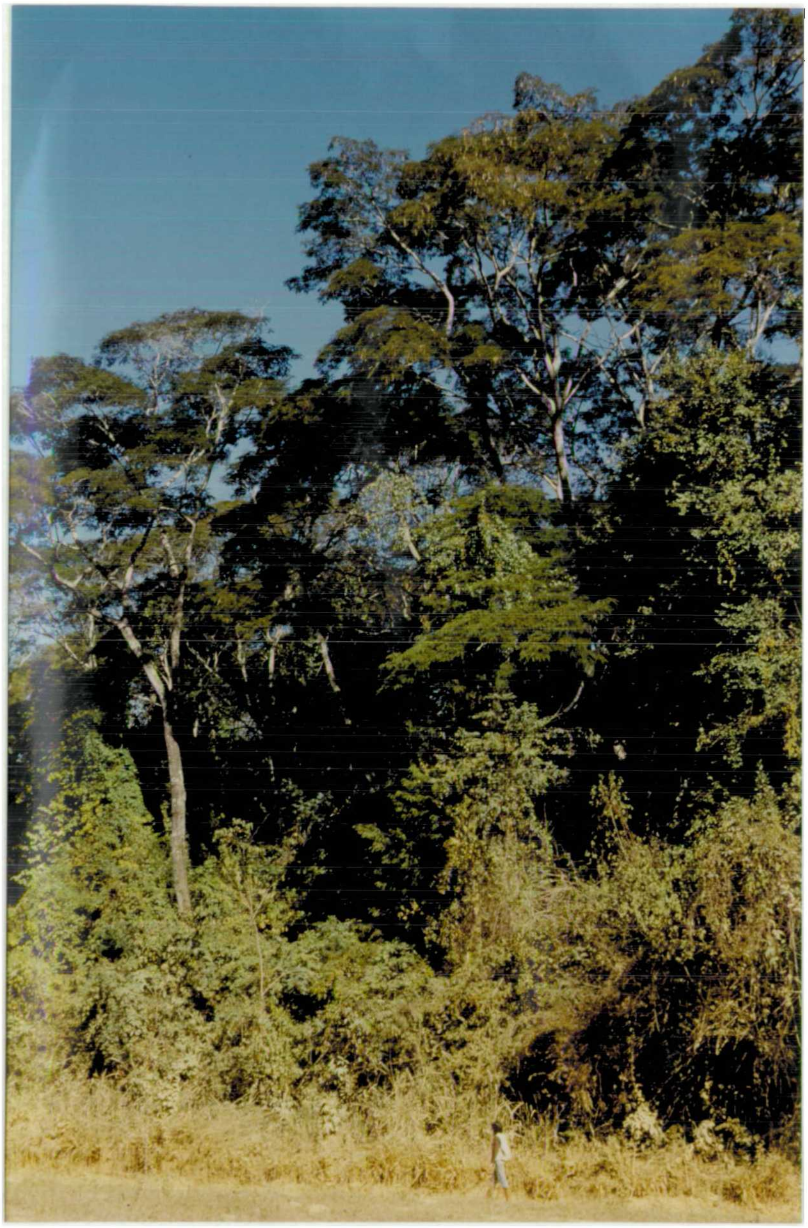
It was felt, however, that a detailed study of certain important ecological variables would both provide a framework for the analysis of the group's behaviour and form a basis for systematic comparisons with other studies. This framework will hopefully also provide an important basis for further studies of *C. flaviceps*, in particular, and of *Callithrix* species in general. Within the scope of the present study, therefore, it is hoped that this "ecological framework" can be used, through systematic comparisons with studies of other marmosets and tamarins, to investigate the basis of observed interspecific differences in behaviour patterns.

This chapter presents the data collected on a number of ecological variables. The first part deals with what might be called "spatial" variation and presents a detailed description of the home range of the study group JG1. The second part deals with the "temporal" variation within that range of climate, the abundance of arthropods and the availability of fruit, leaves and gum. The

Plate 2

View of the Jaó study site taken from east of the river Manhuaçú in August 1986. The abandoned house (AH in fig. 3.1) can be seen on the opposite bank of the river. Note the large numbers of leafless trees, mainly angicos, *and the relatively lush nature of the vegetation on the riverbank.*

Plate 3



View of the forest at Jaó, looking west from the abandoned house. Note the dense undergrowth and the height of the canopy trees, all of which are angicos.

Chapter 3

Plate 4

View of phenology quadrat 8 (see fig. 2.3) taken from the northeast corner in August 1986. Note the steepness of the terrain and the relatively dry, open nature of the forest.

choice of these variables was based on both the information available from previous studies of marmoset ecology and the preliminary observations of JG1. This choice, and the methods used, obviously restrict the scope and detail of this aspect of the study, but it is felt that an adequate and reliable framework for the analysis of the behavioural data was compiled, given the available time and resources. It is also hoped that the relative simplicity of the methods used for the collection of arthropods, for example, will facilitate their possible replication in future studies of marmoset ecology.

The concluding part of this chapter will integrate the two main aspects of the data collected to provide a source of reference for the following chapters. In retrospect, the unexpected importance of vertebrates in the diet of JG1, particularly during certain dry season months, does suggest that some measure of their abundance should have been included. This will be discussed more qualitatively in order to complete the overall picture of the "ecological framework".

The Home Range of the Jaó Study Group

As described previously, the study group, JG1, occupies a home range of approximately 35.5 ha at the northernmost extreme of the forest at FMC (see figure 2.2, plates 2-4). This part of the forest is bordered by the Manhuaçú river to the east and open pasture to the north and the west in two places (figure 3.1). The dirt road which links the two nearest towns, Caratinga and Ipanema, runs north to south through the forest along the riverbank and a second smaller track cuts across the forest on its way to the Jaó valley. An abandoned house is situated on the riverbank in the north of this area, creating a discontinuity in the forest cover here. Apart from a relatively flat area in the vicinity of this house, the land in this area presents a slope varying between approximately 1 in 3 and 1 in 2, and is almost vertical at a number of points. The group's home range varies in altitude between 318 m at its most northerly point and approximately 480 m in the southwest. The land slopes upwards from east to west in all areas except in the area between the Jaó stream and the "valley track" (VT, figure 3.1). The majority of the vegetation can be

Figure 3.1 (facing page)

Features of the Jaó Study Site

This map shows a number of the features mentioned in the text, such as the abandoned house (AH), the Caratinga-Ipanema road and the Valley Track (VT). Measurements of altitude at the lowest and highest points of this area are also shown. For the forested areas, the predominant slope of the land is indicated (see key).

Forested areas located on:

⧅ *Land sloping downwards from west to east*

⧄ *Land sloping downwards from east to west*

▤ *Flat ground*

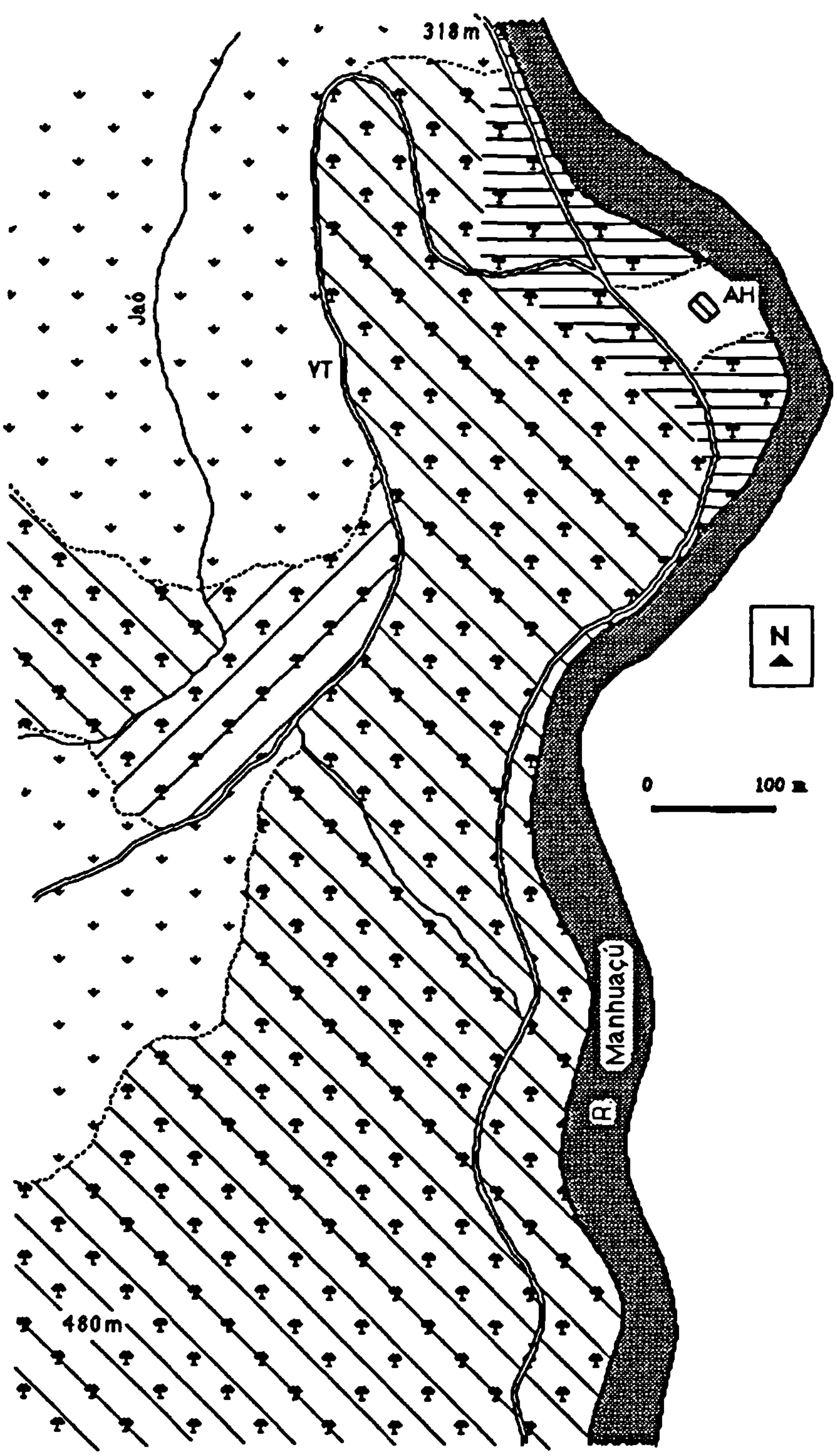

318m
AH
Jaó
YT
N
0
100 m
R. Manhuaçú
480m

Figure 3.2 (facing page)

Distribution of Forest Types at the Jaó Study Site

Figure 3.2 shows the distribution of the vegetation at the study site. It should be noted that the vegetation at this site is patchily distributed (see text) and that the distribution of forest types shown here is a broad generalisation.

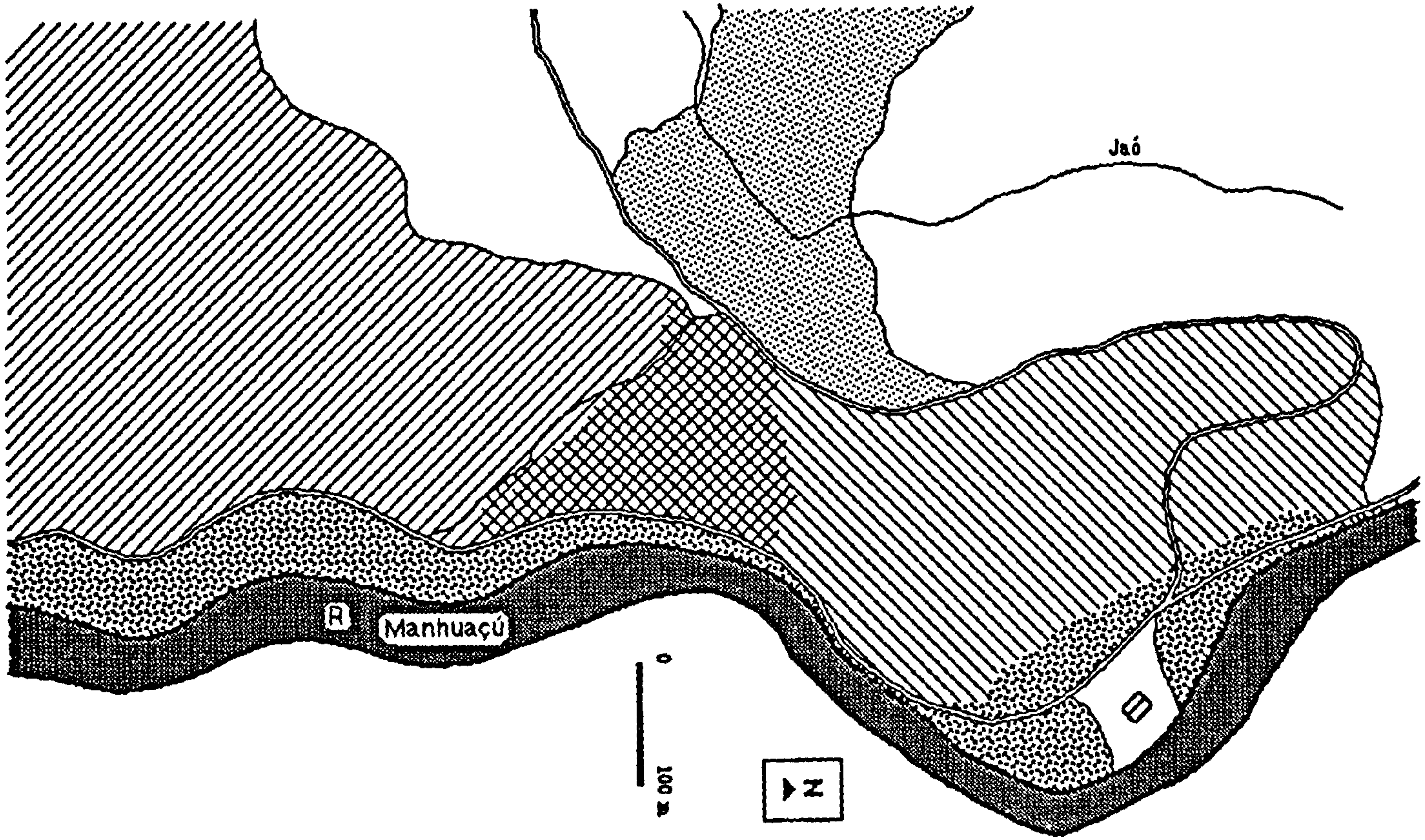
Forest types:

▨ *Type 1: tall, two-layered secondary forest dominated by* angico prego *trees*

▧ *Type 2: tall, two-layered secondary forest with some more mature areas*

▓ *Type 3: tall secondary forest with relatively dense, less deciduous vegetation*

░ *Type 4: young regenerating forest, less than 20 years old*


Jaó
R
Manhuaçú
B
0
100 m
N

described as two-layered tall secondary forest, corresponding with type III of the classification of Hatton *et al.* [1983]. The area of the group's range immediately to the west of the valley track, however, corresponds with type IV (young regenerating forest 10-15 m high) while the area in the very south and southwest of the range appears to correspond with type II (disturbed primary forest with many clearings).

The vegetation in the home range of JG1 can be divided into four main types (figure 3.2). The *"capoeira"* or young (less than 20 years old) regenerating forest situated in the Jaó valley to the west of the main area was visited infrequently by the group, and forms a somewhat uncharacteristic appendage to its range. The vegetation here is patchy, interspersed with scrub and even grass in places, and is dominated by *"embaúba"* trees (*Cecropia* spp.), particularly on the steep banks of the stream. Further to the west, however, this vegetation merges into more mature forest, although still highly disturbed and interspersed with open patches. The main area of the group's range consists of tall secondary forest more than 25 years old (according to both qualitative observations and information from local residents). Overall, the main body of the forest exhibits a continuum from north to south of increasing preservation, increasing species diversity and decreasing density of climbing plants. There is a similar continuum of decreasing humidity from east to west, corresponding with elevation and the distance from the river Manhuaçú, which is reflected in average tree height.

The eastern limit of this area forms the bank of the river. The vegetation here exhibits characteristics related to increased humidity and is thus seen as slightly different from the main body of the forest (type 3), although the north/south continuum is still apparent, to a lesser degree. The remaining forest shows a major division between the area to the north, dominated by *"angico prego"* (*Anadenanthera peregrina*) trees and the area to the south (types 1 and 2 respectively). Large *angico* trees reaching 25 m and more form an almost continuous canopy in some parts of the type 1 forest, while they are comparatively rare in the type 2 forest. The type 1 forest is also characterised by a higher density of climbing plants (reflecting the overall continuum outlined above) which includes large quantities of *Acacia paniculata*, the group's main source of exudate.

In addition to qualitative observations, all numbered trees in the phenology quadrats were measured and identified (when possible), and plotless sampling was used to collect data on the sizes and densities of trees along transects within the areas of vegetation types 1 and 2. These quantitative data tend to support the more qualitative observations on the whole, although some discussion is needed with regard to specific aspects of the findings.

Phenology Quadrats

The eight phenology quadrats each contained between 109 and 189 live trees over 3 m in height at the end of the study (1301 trees in all, averaging 162.6 trees per quadrat or 2602 per ha). The average height of all trees was 6.7 m and mean diameter at breast height, or dbh[1], was 6.5 cm (table 3.1). If a minimum dbh of 10 cm, rather than tree height, is used as a criterion for selecting trees, average tree height in all quadrats is 11.5 m (335 trees, equivalent to 670 per ha). Of the 1329 trees originally marked (a number died or were cut during the course of the study), 997 were identified to at least familial level by the time of writing this thesis, and 505, or 50.65%, of these were individuals of just six species (see appendix I). Overall, the sample of the vegetation provided by the phenology quadrats is characteristic of secondary forest, with relatively small trees on the one hand and low species density on the other.

One problem with this method, however, is that the vegetation is very patchy throughout this area and the relatively small number of quadrats selected, while providing an adequate picture of the vegetation as a whole, may not, due to purely random factors, provide a good measure of differences within the area and between vegetation types. In retrospect, a larger number of smaller quadrats may have provided a more accurate picture, although, as the problem is of a random nature, this is not be certain. In addition to the measurement of trees in the phenology quadrats, then, the vegetation was

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[1] *"Breast height" is taken as being approximately 1.5 m. This is the standard measurement of trunk diameter and can be measured directly with a forester's tape on which one scale shows the linear length (circumference) divided by Π.*

Table 3.1

Height Classes of Trees in Phenology Quadrats

	Number of trees in each quadrat (percentage of total):								
Tree height (m)	1	2	3	4	5	6	7	8	Total
3-5	76	86	101	62	89	70	105	95	684
	(68.5)	(48.9)	(56.1)	(45.9)	(50.6)	(39.5)	(56.8)	(50.3)	(51.5)
5.5-10	24	65	58	55	71	90	36	83	482
	(21.6)	(36.9)	(32.2)	(40.7)	(40.3)	(50.8)	(19.5)	(43.9)	(36.3)
10.5-15	10	9	11	12	8	14	21	7	96
	(9.0)	(5.1)	(6.1)	(8.9)	(4.5)	(7.9)	(11.4)	(3.7)	(7.2)
15.5-20	1	9	6	3	3	2	14	2	40
	(0.9)	(5.1)	(3.3)	(2.2)	(1.7)	(1.1)	(7.6)	(1.1)	(3.0)
20.5-25	0	5	4	2	1	0	8	1	21
	-	(2.8)	(2.2)	(1.5)	(0.6)	-	(4.3)	(0.5)	(1.6)
25+	0	2	0	1	0	0	1	1	6
	-	(1.1)	-	(0.7)	-	(0.6)	(0.5)	(0.5)	(0.4)
Mean height (m):	**5.7**	**7.4**	**6.5**	**6.8**	**6.3**	**6.8**	**7.7**	**6.2**	**6.7**
Mean dbh/trunk (cm):	**5.5**	**6.3**	**6.5**	**6.2**	**7.2**	**6.5**	**7.5**	**5.9**	**6.5**

assessed using the "quadrant" method in which trees are sampled along the length of a transect, rather than within the plot of a quadrat (see below). It was felt that this would provide an adequate complementary measure of the vegetation, given the time available.

Tall trees are rare in the phenology quadrats. Only 27, or 2%, of the trees marked were over 20 m in height, and only six of these (0.4% of the total) were more than 25 m tall (see table 3.1). More than half (51.5%) of the trees marked were between 3 m and 5 m in height, and 87.8% were less than 10 m in height. Certain apparently systematic differences between the quadrats were noted. Quadrat 7, situated on the riverbank and at the lowest altitude, had the largest proportion of trees with a height of more than 10 m (23.8%) while quadrat 8, the quadrat situated at the highest altitude, had the lowest

(6.8%). 15% of all trees in the four quadrats situated at the lowest altitudes (1, 5, 6 and 7) were above 10 m in height, while only 9.7% of those in the quadrats at the highest altitudes (2, 3, 4 and 8) were above this height. An average tree in the lower quadrats was 0.6 m taller than in the higher quadrats (7 m and 6.4 m respectively), and the average trunk 0.9 cm thicker (6.8 cm and 5.9 cm respectively). These results reflect the pattern seen throughout the forest at FMC [Hatton *et al.*, 1983].

Of the 997 trees identified so far, 778 (78%) belong to six families and 547 of these (54.9% of the total identified) belong to just three: Flacourtiaceae, Leguminosae and Meliaceae (appendix I). Two exotic species were also observed in these quadrats. A single mango tree (*Mangifera indica*) was recorded in quadrat 6 and coffee trees (*Coffea* sp.), while too small to be included with the marked individuals, were observed in a number of quadrats. The latter were, in fact, quite common in some parts of the study group's home range (particularly in the north). None of the other 21 families identified so far is represented by more than 43 individuals. Unexpectedly, *angicos* are relatively uncommon in the phenology quadrats as a whole, although they do consitute a major proportion of the larger trees (see transect data). *Angicos* were absent from quadrats 1 and 3, where, according to qualitative observations, they would be most expected, and no more than eight individuals were found in any of the other quadrats. This apparent anomaly is most probably due to the random factors outlined above. Quadrat 1, for example, is situated in an area in which *angicos* are particularly common, but is in fact dominated by individuals of the family Meliaceae which constitute 57% of the total identified (32 of these, 37.2% of those identified, belong to a single species, *Guarea guidonia*, which is found in only one other quadrat).

Taking the quadrats as a whole, it is possible to discern certain characteristics in the distribution of the most common species. The species most frequently observed in the quadrats as a whole was *Carpotroche brasiliensis*. This species was far more common in the four higher quadrats (84% of individuals were recorded in quadrats 2, 3, 4 and 8) than in the lower ones and seems to be adapted to a drier environment. The second most common species, *Trichilia pallida*, on the other hand, was more ubiquitous, and its distribution within the quadrats shows no such obvious pattern. The third and fourth most common species (*Allophyllus* sp. and *Siparuna* sp.)

found in the quadrats were the study group's most important sources of plant material, other than exudate (see chapter 6). *"Sessenta pau"* (*Allophyllus*) is characteristic of the more disturbed forest at FMC and was more common, in accordance with the observed continuum outlined in the previous section, in the northernmost quadrats (65.7% of individuals were recorded in quadrats 1 to 4). *"Negramina"* (*Siparuna*), on the other hand, was found almost exclusively in the lower quadrats (93.2% of individuals are found in quadrats 1, 5, 6 and 7) and is presumably adapted to a relatively humid environment.

The absence of certain types of plant is also of interest. There are no Melastomataceae in the phenology quadrats, although the study group did use the fruit of at least two species (see chapter 6). The species used were small bushes, however, and it thus seems likely that most individuals would have been excluded from the records through their small size. The lack of *Cecropia* spp. trees in the quadrats (only 2 were recorded), while reflecting the observed abundance in the main body of the group's home range, is also notable as this easily recognised genus is characteristic of secondary forest throughout the neotropics and was abundant in the Jaó valley itself (vegetation type 4, figure 3.2).

Transects

As a complementary measure of tree size and density, plotless sampling along transect lines (chosen from the trail system) was carried out within the areas of vegetation types 1 and 2 (see figure 3.2). The methods used were similar to those described in "Subcommittee on Conservation of Natural Populations" [1981: chapter 3]. More than 100 points were randomly selected along the lines of each of the two sets of transects. At each of these points, the observer drew an imaginary line perpendicular to that of the trail, thus forming four "quadrants". In each quadrant, the nearest tree with a total dbh of 10 cm or more (for individuals with multiple trunks, this was the sum of the dbh of all trunks) was located. For each tree thus selected, its distance from the intersection of the quadrants, total dbh and species, where appropriate, were recorded. The method was chosen for its relative simplicity as a complementary measure for the data collected in the phenology quadrats and the identification of all trees was not a major goal. As the sampling was carried out towards the end of the main study, a number of common species could be easily identified, although it was ultimately decided to record only the ***angicos*, *sessenta paus*** and ***Cecropia*** spp. individuals occurring in the quadrants (***negraminas*** were generally too small to be recorded using this method).

Table 3.2

Results of Quadrant Sampling

Variable	Sample representing: Vegetation type 1	Sample representing: Vegetation type 2
Number of trees recorded	399	407
Of which:		
Allophyllus sp.	85	6
A. peregrina	46	1
Cecropia spp.	4	3
Mean distance of trees from sampling point (m)	4.2	4.3
Mean trunk dbh (cm)	12.6	12.7
Number of individuals with:		
1 trunk	266	328
2 trunks	70	58
3 trunks	24	14
4 or more trunks	39	7

Table 3.2 presents the results of the quadrant sampling. Overall, the results show little difference between the two areas in tree density (in terms of the average distance of trees from the measurement points) or in mean trunk diameter. While both these values are slightly larger for the type 2 sample, as might be expected, they are not markedly different from those recorded for the type 1 sample. One possible confounding variable is that of altitude. More than a third of the trees included in the type 2 sample are situated at higher elevations than any of the trees in the type 1 sample. As the data from the phenology quadrats indicate that trees at higher altitudes tend to have thinner trunks, differences in the elevations of the two samples may have had an important influence on these results. Other differences between the two samples are much clearer. *Sessenta paus* and *angicos* together make up almost

a third (32.9%) of the trees recorded in the type 1 sample, but only 1.7% in type 2. The marked concentration of *sessenta paus* in type 1 vegetation (21.3% of trees recorded) supports the records from the phenology quadrats. *Angicos* are not only more common in the type 1 forest, but they also make up almost 40% of the trees with at least one trunk with a dbh greater than 20 cm, and almost 70% of trees with at least one trunk more than 30 cm in diameter. This supports the earlier observation that large *angicos* dominate this part of the forest. *Embaúbas* (*Cecropia* spp.), on the other hand, are rare in both types (7 out of a total sample of 806 trees), reflecting the results of the phenology quadrats.

Exactly half of the *angicos* recorded in type 1 vegetation have at least one trunk with a dbh of greater than 30 cm and these constitute 69.7% of trees in this category (average trunk diameter for all *angicos* was 29.7 cm). If *angicos* are removed from both samples, the number of trees with at least one trunk of dbh greater than 30 cm is 9 in vegetation type 1 and 7 in type 2. Large *angicos* also commonly have more than one trunk, almost a third (29.8%) of individuals recorded in both vegetation types had two or more. Calculating mean trunk dbh for all trees excluding *angicos* gives a value of 10.8 cm for vegetation type 1 and 12.7 cm for type 2, so it seems that their relatively high density in type 1 has an important influence on the difference in trunk diameter between the two types. Whether this is a valid manipulation of the data, however, is uncertain as excluding the relatively small *sessenta paus* from the samples would have the opposite effect.

Of the 806 trees recorded, 222 (27.54%) had two or more trunks, again reflecting the relatively early stage of growth of the forest in this area, although the frequent cutting of small trees by the local residents may also have an influence here. If multiple trunks are seen as an indication of younger or more disturbed forest, then the difference between the samples of vegetation types 1 and 2 again support the observed differences between them. Exactly one third (133) of the trees in the type 1 sample had two or more trunks, while only 89 or 21.87% of trees in the type 2 sample had more than two, and there were exactly three times as many trees with three or more trunks (63) in the type 1 sample than in the type 2 sample (21). Much of this contrast is due to the much higher frequency of both *angicos* and *sessenta paus* in vegetation type 1, as both of these species frequently produce multiple trunks (69.2% of all *sessenta paus* recorded had more than one trunk).

In general, then, these samples support both the qualitative classification of the forest within the study group's home range and some of the broader trends outlined in the quantitative records of the trees in the phenology quadrats.

Seasonal Change

Climate

The latitude (19°50'S) and the location of FMC in the eastern rainshadow of the Mantiqueira mountain range have major influences on its climate, and the degree of seasonal change in particular. In general terms, the climate has two major divisions into a hot wet season (from October to March) and a cool dry season (from April to September). Records from Caratinga, 50 km to the west of the study site, show a mean annual temperature of 22.1° C and an average of 1146.3 mm of rainfall annually. The amount, timing and duration of rainfall during the wet season have important consequences for both the fruiting phenology of many of the plant species found in the FMC forest (see below), and the fauna which depends on these resources. As for any location, the climate can vary considerably from year to year, and the total rainfall recorded during the six months of the 1984/85 wet season (1605 mm) contrasts markedly with that of the same period in 1985/86 (774.6 mm). In some years the rains may be delayed until late October, in others they may continue into April, although the months of November, December and January contain a marked peak in most years.

Precipitation was recorded daily with an "All-Weather" rain gauge situated at the station building in the Matão valley (figure 2.2). Temperatures were also recorded daily, using a Taylor maximum-minimum thermometer situated within the forest in the Matão valley adjacent to the station building. While no such measures were made at the home range of JG1, it is possible that daily temperatures, and their rates of change during the course of the day, were slightly different from those recorded in the Matão valley due to such factors as the type of vegetation, the orientation of the hillside and the proximity of the river Manhuaçú. We might expect, for example, that the relatively open nature of the canopy of the secondary forest at Jaó would allow greater penetration of sunlight than that of the primary forest of the Matão valley and hence that daily temperatures would be slightly higher overall. Temperatures within the forest may also rise more quickly during the course of the day, although the more open nature of the forest would have the opposite effect during the night, when temperatures may be slightly lower and fall more quickly.

The most obvious influence of the river is the thick mist produced during the night and early morning on colder days (principally during the dry season months). This may persist until well after 08:00, and is noticeably thicker and more persistent at lower altitudes, that is, closer to the river, whereas it is normally absent at higher altitudes and along the hilltops. On such mornings, ambient temperature is noticeably affected by the covering of mist and the degree of its penetration by the sun, so that the highest altitudes are generally the warmest. During the night, however, the proximity of the relatively warm body of water of the river and the insulative properties of the mist may mean that the lowest altitudes, and the riverbank in particular, are the warmest. As marmosets are particularly sensitive to extremes of temperature, the behaviour of the study group may have been influenced by such factors, particularly in comparing the warmer wet season and cooler dry season months. One expected difference would be in the choice of sleeping sites *i.e.* sleep trees at lower altitudes may be more consistently chosen during cold months than during warm ones.

Figures 3.3 and 3.4 show the monthly means of temperature and rainfall recorded at FMC during the past four years (including the period of the present study) and the averages measured during a ten-year period (1972 to 1982) at the nearest meteorological station, at Caratinga. These figures present the records according to the methods of Walter & Leith [1967] in order to show periods of drought when plant growth may be retarded. The only "transitional" months in the averages from Caratinga are February and April, although the former, with an average rainfall of 98.5 mm and its position between January and March, should quite clearly be included with the wet season months. April has a much higher average than the following dry

Figure 3.3

Monthly Means of Precipitation and Temperature Recorded at the Field Station, Fazenda Montes Claros (July 1983 to June 1987)

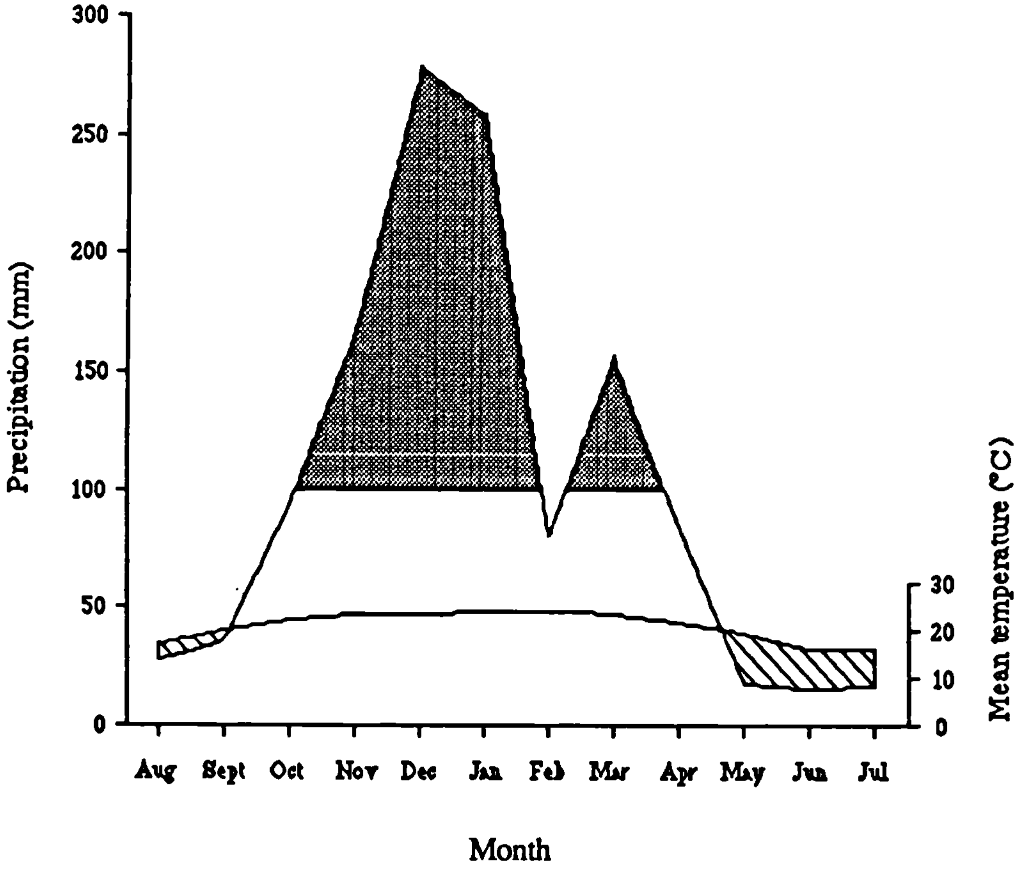


Figure 3.3 shows the mean monthly precipitation and daily temperature recorded at FMC during the period between July 1983 and June 1987. The records are presented according to methods adapted from Walter & Leith [1967]. The ordinates are scaled so that 20 mm of precipitation on the left corresponds with 10° C on the right. Periods of drought, during which plant growth may be retarded, are indicated when the precipitation curve falls below that of temperature (diagonal shading). "Wet" periods are seen as those during which precipitation exceeds 100 mm (grey shading). Months which fall between these two extremes are considered as "transitional" between wet and dry, according to this method.

Figure 3.4

Monthly Means of Precipitation and Temperature Recorded at Caratinga, Minas Gerais (1972-1982)

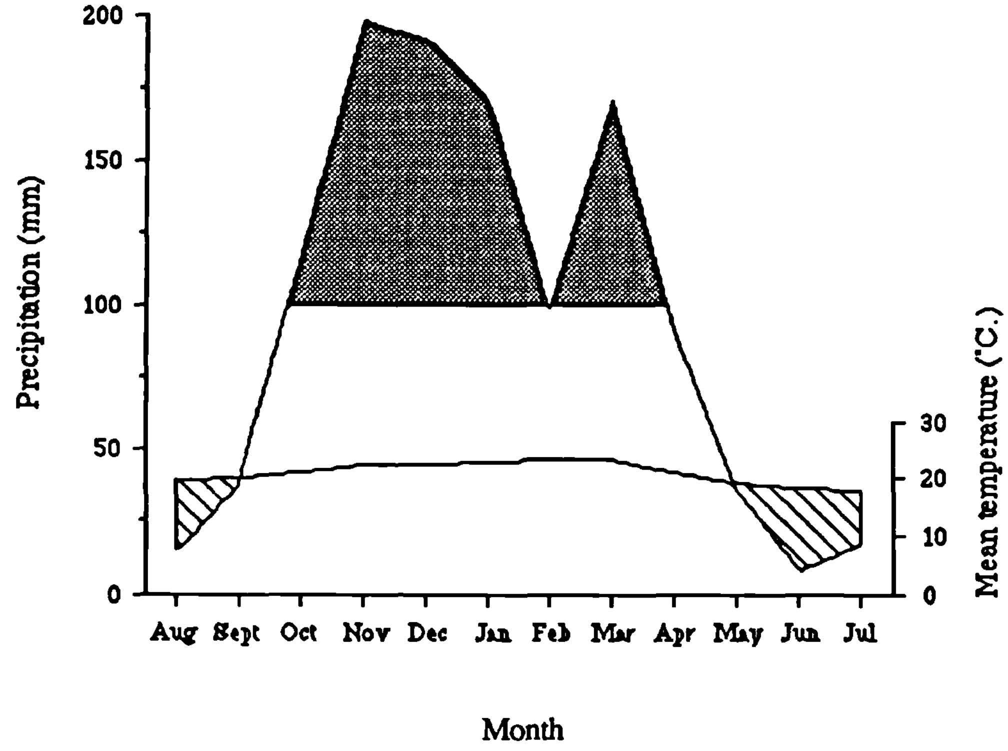


Figure 3.4 presents mean monthly temperature and precipitation recorded at the meteorological station in Caratinga, Minas Gerais (50 km west of FMC). The results are presented according to the methods described in figure 3.3.

season months (89.6 mm), reflecting the variation in the duration of the rains in different years, and its inclusion in the dry season is thus somewhat equivocal.

While the general pattern is the same, the situation is slightly different at FMC (figure 3.3). These records show a more marked concentration of precipitation in the wet season months of November, December and January, while months such as October and February fall well below the 100 mm "threshold" to become transitional months. The sample period is much shorter than that from Caratinga, however, and it seems likely that the apparently exceptional years covered by the present study period have had a major influence on this pattern. Whether records from a longer period would clarify this situation is not known, but it seems reasonable to accept the Caratinga sample as more indicative of average trends.

While the mean values for longer periods are useful for the definition of broad climatic trends, the actual values recorded during the course of the study are clearly most relevant to the present discussion. Monthly means of temperature and total rainfall for the period from October 1984 to August 1986, covering the period of the main study and the preceding wet season, are given in table 3.3. Precipitation levels during this period are also shown in figure 3.5. During the thirteen months of the main study, the highest temperature recorded was 33° C (in October 1985) and the lowest was 8° C (in June and July 1985). The values for the period preceding that of the main study are included here because the exceptional amount of precipitation, and, in particular, its contrast with that of the following wet season, undoubtedly had an influence on certain aspects of the study. There is little doubt that April 1986 should be included with the dry season months in this particular year. In fact, the relatively low rainfall of the 1985/86 wet season places both October and February as transitional months and March quite clearly in the dry period.

Despite the relative lack of rain in March, however, this month was grouped, for a number of reasons (including qualitative observations), with the wet season months for the analysis of other ecological variables and the behaviour of the study group. One assumption in making this categorisation is that the lack of rain would not have had an immediate and direct effect on variables influenced by humidity during this month because of the relatively high humidity of the preceding months. In contrast, a relatively dry March

Figure 3.5

Monthly Precipitation Recorded at FMC, October 1984 to August 1986

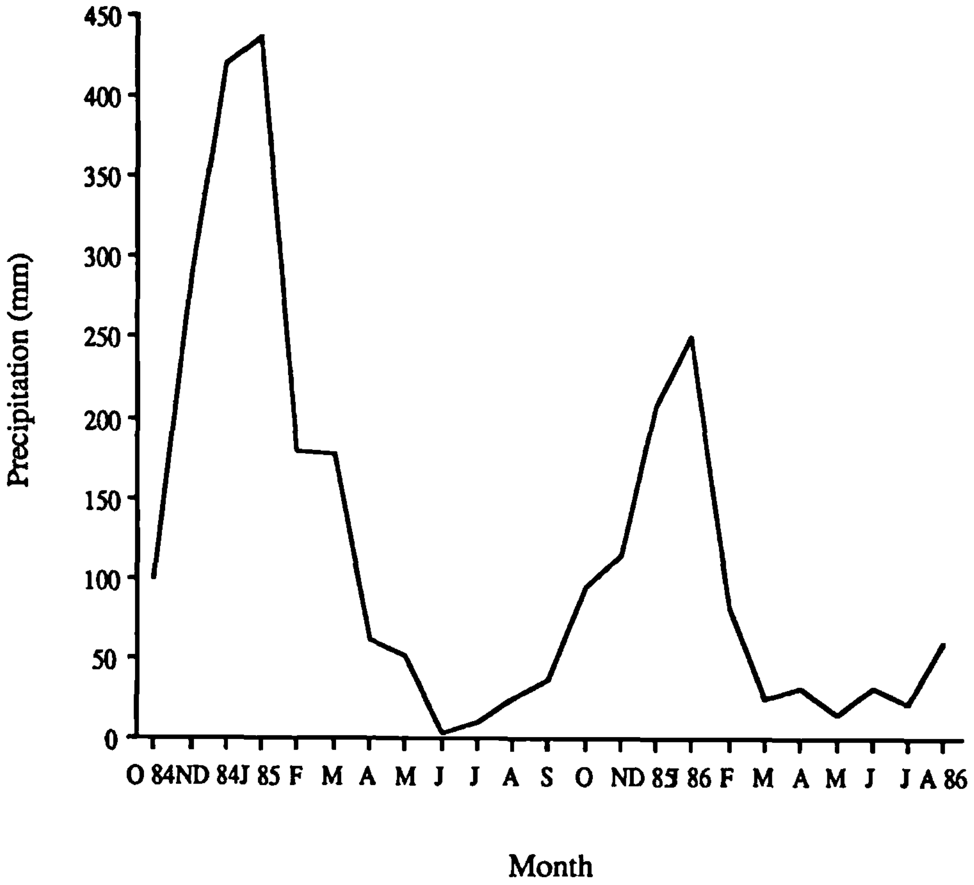


Figure 3.5 shows the total precipitation recorded at the field station, FMC during each month between October 1984 and August 1986.

Table 3.3

Climatic Records from FMC, October 1984 to August 1986

	Temperature (°C):			
Month	Mean minimum	Mean	Mean maximum	Rainfall (mm)
October 1984	17.7	21.9	26.0	100.3
November	18.5	22.7	25.8	291.2
December 1984	20.6	23.1	25.6	419.8
January 1985	20.7	22.8	24.8	437.0
February	20.3	23.8	27.2	178.6
March	20.8	23.1	25.3	178.1
April	18.6	21.1	23.7	61.8
May	16.3	18.6	21.0	51.6
June	9.5	13.8	18.1	3.3
July	11.3	15.2	19.1	10.2
August	13.5	17.4	21.3	24.3
September	14.2	19.1	24.0	36.5
October	18.3	22.6	26.9	95.4
November	18.6	23.0	27.2	113.8
December 1985	19.4	22.7	25.9	208.1
January 1986	20.5	23.8	27.1	250.1
February	21.1	24.1	27.0	81.8
March	20.3	24.2	28.0	25.4
April	18.4	22.0	25.7	31.5
May	16.5	19.9	23.2	14.9
June	13.2	16.7	20.3	30.9
July	11.9	16.5	21.0	21.3
August 1986	14.7	19.1	23.5	60.6

would have an emphatic effect on a subsequently dry April. Whether this assumption is generally applicable is not clear: insect populations, for example, may be particularly sensitive to minor fluctuations in rainfall levels [Wolda, 1978; Tanaka & Tanaka, 1982]. It does seem, however, to apply to the year in question at FMC. The mean temperature recorded during March was in fact the highest for any month during the study, and clearly places it with the hotter wet season months (the mean temperature for April, on the other hand, was lower than that of any wet season month). Similarly, overall insect abundance measured in March (see below) was the same as that recorded in February, but almost three times that recorded in April.

Chapter 3

Plant Phenology

The physical characteristics of the phenology quadrats have been outlined above. Here we look at the temporal variation in the abundance of flowers, fruit and leaves in these quadrats (according to the methods described in the previous chapter). Records of the leaf cover of the separate sample of *angicos* are also included here as a further measure of leaf abundance. As we have seen, trees in the quadrats are relatively small in general and a relatively large proportion belong to a small number of species. These are characteristic features of secondary forest formations, although 126 tree species have been recognised so far in this half hectare sample (appendix I), far more than would be found in a similar area of temperate forest [Myers, 1985].

While many of the small trees are mature specimens of species characteristically found in secondary or disturbed forest, many larger trees are immature specimens of typically much larger species. Thus, while many small individuals may produce fruit, many of the larger ones do not, so there is no clear correlation between tree size and the production of fruit. Continued human activity in the forest has also had an effect on the results. The continued cutting or copsing of small trees means that similarly-sized individuals of the same species may be of different ages and while one may produce fruit, the other may not. The palm hearts of the *"brejaúba"* (*Astrocaryum aculleatissimum*) were regularly removed by the local residents, which prohibited fruit production by this species.

Forty-two trees which produced flowers were identified as male individuals and, as they do not produce fruit, they are removed from the overall total for the analysis of fruit production. Of the remaining 1260 trees which survived to the end of the study, only 222 (17.62%) were recorded producing fruit at any time during the fourteen months between July 1985 and August 1986. An additional 77 (6.11% of the total) produced flowers during the course of the study, but were not observed bearing fruit in subsequent months. Thus, in all, 956 or 75.95% of the surviving trees were non-reproductive during the course of the study. More than three-quarters of the species recognised did not fruit during the study (see appendix I), although many of these were represented by only one or a few individuals. Fruit production was recorded relatively rarely, even for the most common species, although *Allophyllus* and *Siparuna* were exceptions. As trees of these two species made up almost one third (73 out of 222) of the total number of those which did produce fruit, they have a major influence on the pattern of fruit abundance. Only 21 of the 125 specimens of the most common species (*C. brasiliensis*), on the other hand, bore fruit. Overall, the picture is one of fruit being produced by a relatively small proportion of the trees, and by a similarly small proportion, in general, of the total number of any particular species.

According to the number of trees in the phenology quadrats bearing fruit each month, the abundance of fruit shows a clear relationship with the rainfall levels recorded during the study period (figure 3.6). Only around 5% of the trees were recorded bearing fruit during most of the year, although this proportion doubled during the wet season months between November and February. The numbers of trees recorded bearing fruit during the wet season months as a whole were significantly different from those recorded during the dry season (Mann-Whitney U test: $U = 4$, $p = 0.014$). A similar trend is apparent if the number of species, rather than individual trees, bearing fruit is considered. Between 11 and 21 species were recorded bearing fruit during any single wet season month, but only 6 to 17 different species bore fruit during any dry season month, although there is no significant difference between the seasonal samples, according to monthly records (M-W U: $U = 7.5$, $p > 0.05$).

These trends are somewhat diluted by the fact that certain trees were recorded bearing fruit over relatively long periods (throughout the whole of the study period in a few cases). While this seemed to be linked to the types of fruit in some cases, the lack of rain towards the end of the wet season may have an important influence in others. Most of the trees in the latter case bore immature fruits whose development appeared to have been inhibited by the lack of rain (see below). Hence, more species were recorded bearing fruit at the end of the 1986 dry season than in the equivalent months of the previous year. There is thus no significant correlation between the presence of fruit and monthly rainfall in terms of either the number of individual trees (Spearman Rank Correlation: $r_s = 0.424$, $n = 13$, $p = 0.149$) or the number of species (SRC: $r_s = 0.351$, $n = 13$, $p = 0.239$). There is, however, a highly significant correlation between the numbers of new trees recorded bearing fruit every

Figure 3.6

Monthly Variation in the Number of Phenology Quadrat Trees Bearing Fruit

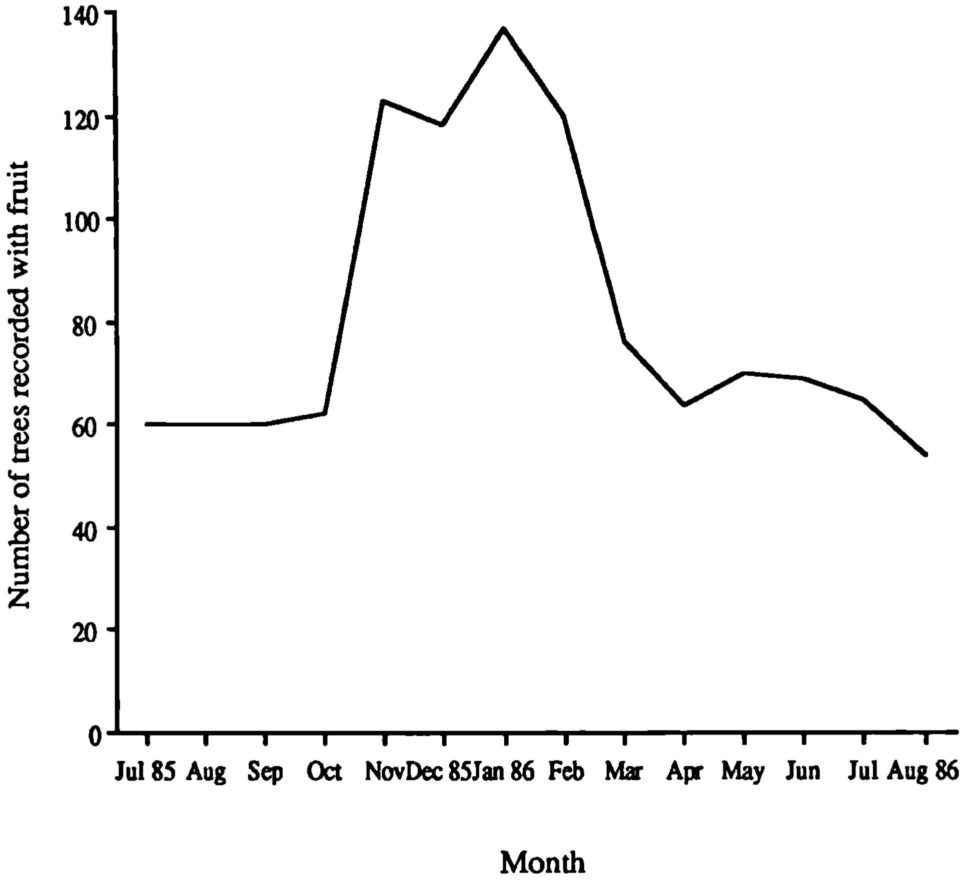


Figure 3.6 shows the number of marked trees in the phenology quadrats recorded bearing fruit in each month between July 1985 and August 1986.

month and rainfall (SRC: $r_s = 0.725$, $n = 13$, $p = 0.005$).

A number of observations support the idea that the relative lack of rainfall between the months of February and May had a significant influence on the reproductive processes of many of the trees species found in the phenology quadrats. *C. brasiliensis*, for example, begins fruiting towards the end of the wet season. While in the first year this species produced numerous large (maximum dimension approximately 12 cm) green fruits, the vast majority of the small numbers produced in the second year were small (around 5 cm long), dry and dark brown in colour. Of the 77 trees bearing flowers but no subsequent fruit, 41 were recorded in February. Only one new species fruited in each of the months of February, March, April and May, and only one of these was represented by more than 10 individuals. Only two *T. pallida*, which fruited in April, were observed with fruit in the second year whereas 36 individuals bore fruit in the same period of the previous year. A few species, on the other hand, seem to fruit only during drier years (*e.g. Erythrina* sp.). For these, the relatively abundant rainfall of the first year seemed to inhibit the reproductive process. Other tree species have complex fruiting patterns, some fruiting on a longer than annual cycle, and still others fruiting more than once in the same year, in addition to being affected by ongoing weather conditions. While the overall situation is complex, the evidence clearly suggests that the relatively low levels of rainfall during the study period led to abnormally low levels of fruiting being recorded, in terms of either the numbers of trees or the number of species.

While approximately thirty different tree species were recorded fruiting during the course of the study, the fruits or seeds of only three were known to have been eaten by the study group (*Siparuna*, *Allophyllus* and *Acantinophyllum ilicifolia*), although the latter was only rarely consumed (see table 6.2). The fruit of *Sorocea guilleminia* was also occasionally consumed by the marmosets, but this species was only represented by male individuals in the quadrats. The majority of the remaining fruits either had relatively thick or hard cases, or were dry seed pods or fleshless winged seeds. Most of these were judged to be inedible for small primates not specialised morphologically for the predation of seeds.

Thus, while the phenology records not only present a picture of a relatively small proportion of the trees of a relatively small number of species

Figure 3.7

Monthly Variation in the Leaf Cover Recorded in the Phenology Quadrats

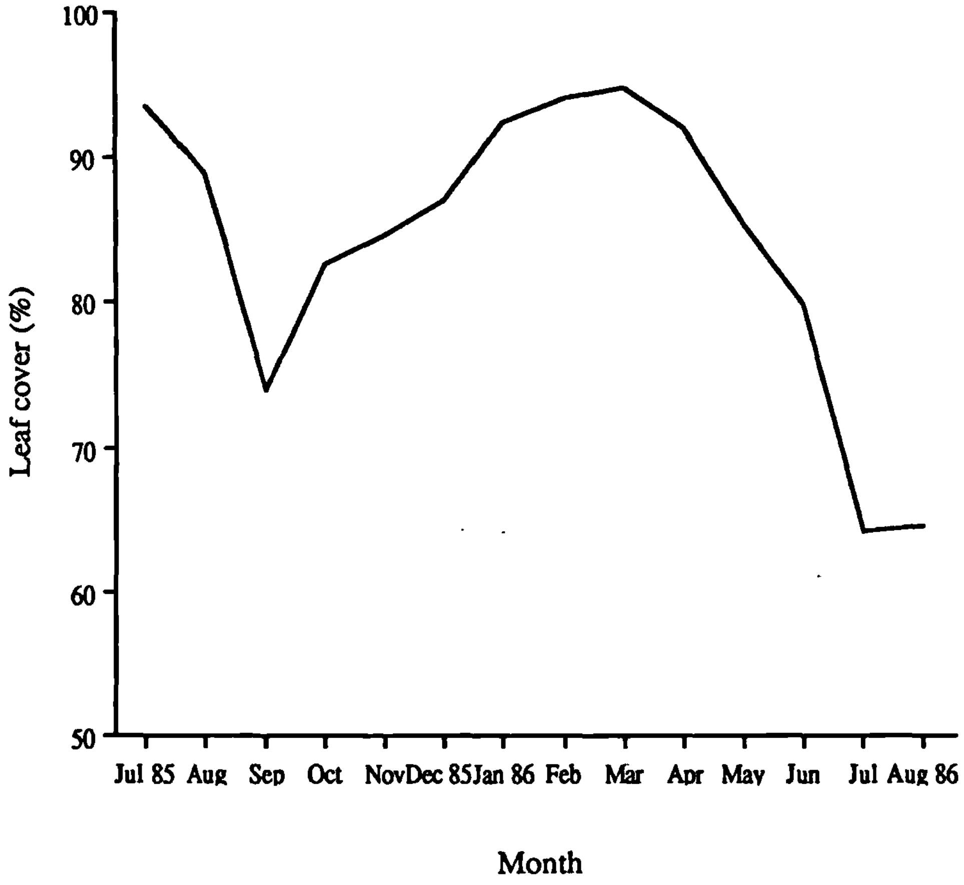


Figure 3.7 shows the estimated leaf cover recorded in phenology quadrats in each month between July 1985 and August 1986. Leaf cover is shown as a percentage of the total crown volume of the marked trees in the quadrats selected each month. Please note that values are not directly comparable as different quadrats were selected in different months (see text).

bearing fruit, most of the types of fruit which were produced were probably inedible as far as the study group was concerned. This reflects qualitative observations both of the study area and of the group's feeding behaviour during most periods (see chapters 4 and 6). It does seem from preliminary observations carried out in the phenology quadrats, however, that the early dry season of 1986 was characterised by unusually low numbers of both fruiting trees and species, and that this may also have been the case during the latter half of the preceding wet season. While more edible fruits may be available during this period in more "normal", wetter years, the picture presented by the phenology records is probably a faithful one, not only of the abundance of such fruits during the year studied, but also during most, if not all, months of most years.

While the fruiting phenology of the trees in the quadrats presents a complex picture with a large number of variables to be taken into account, the patterns of leaf fall and growth are relatively simple. All live trees usually have some leaf cover and thus, even though the total sample contains a mixture of apparently deciduous, semi-deciduous and evergreen species, the overall numbers are large enough to allow the appearance of broad trends. The accurate assessment of leaf cover is a more difficult, time-consuming task than recording the presence of fruit and so, as the abundance of leaves did not appear to have a direct influence on the group's activities, these data were collected less systematically than those on fruiting patterns. Leaf cover was, however, measured in at least two quadrats every month and the results seem, given the difficulties involved, to be a good representation of the general patterns observed at the site.

Putting together the records from all quadrats measured each month between July 1985 and August 1986 gives some idea of the total leaf cover of the forest during this period (figure 3.7). The curve produced by summing all the data is perhaps unexpectedly smooth, considering the fact that quadrats measured in consecutive months were different from each other in terms of elevation and apparent humidity. The values for the late dry season months are, however, probably least representative of the sample as a whole. For example, the August 1986 value is the sum of the cover measured in all four of the quadrats at lower altitudes, but in only two of the higher ones, and this may explain the flattening of the curve from the previous month whose value was taken from two of the higher quadrats only.

Overall, leaf cover rose throughout the wet season months to reach a maximum in March and then decreased through the following dry season months. This pattern does not correlate with that of rainfall (SRC: $r_s = 0.341$, $n = 13$, $p = 0.255$), but this seems to be due more to a delay in the loss of cover rather than in production (see below). Differences were also noted between the quadrats at higher altitudes (quadrats 2, 3, 4 and 8) and those lower down (1, 5, 6 and 7). While the lowest value recorded for total leaf cover in any of the latter quadrats was 76%, the lowest value recorded in any of the former was less than half of this (37%). The quadrats at lower altitudes clearly suffer much less leaf fall during the dry season months than those at higher altitudes, although leaf cover seemed to be similar in all quadrats during the wet season. One anomaly was quadrat 2 which, despite being at a higher altitude than most of the others, apparently suffered no more leaf fall in the dry season than the lower quadrats. This quadrat was situated in a small area whose vegetation was noticeably more luxuriant during the dry season than the surrounding areas at a similar altitude (and with similar vegetation), suggesting local differences in humidity due either to soil physiology or deeper geological characteristics. As trees in this quadrat were, on average, more than 0.5 m taller than those in the other higher quadrats, such differential humidity may have had an influence on the physical structure of the vegetation in this quadrat as well as on its seasonality (although this may have been due to differences in the tree species present). It thus seems that local differences in soil type and topography both contribute to and emphasize the patchy nature of the forest within the study group's home range.

Figure 3.7 also indicates that leaf fall was greater overall during the 1986 dry season than during the same period of the previous year. Here again, quadrats at different altitudes exhibit different trends. Quadrats 3 and 8 had 98% and 92% leaf cover respectively in July 1985, but only 76% and 56% in July 1986. Exactly the same values, on the other hand, were recorded for the lower quadrats 1 and 5 in the later month of August in both years (92% and 83% respectively). The higher quadrat 4 was recorded as having 64% leaf cover in September 1985, while it had just 37% in the earlier month of August in the following year and would presumably, judging by the trends of the previous year, have had even less cover by September of that year. Figure 3.8

Figure 3.8

Seasonal Variation in Leaf Cover, Quadrats 4 and 6

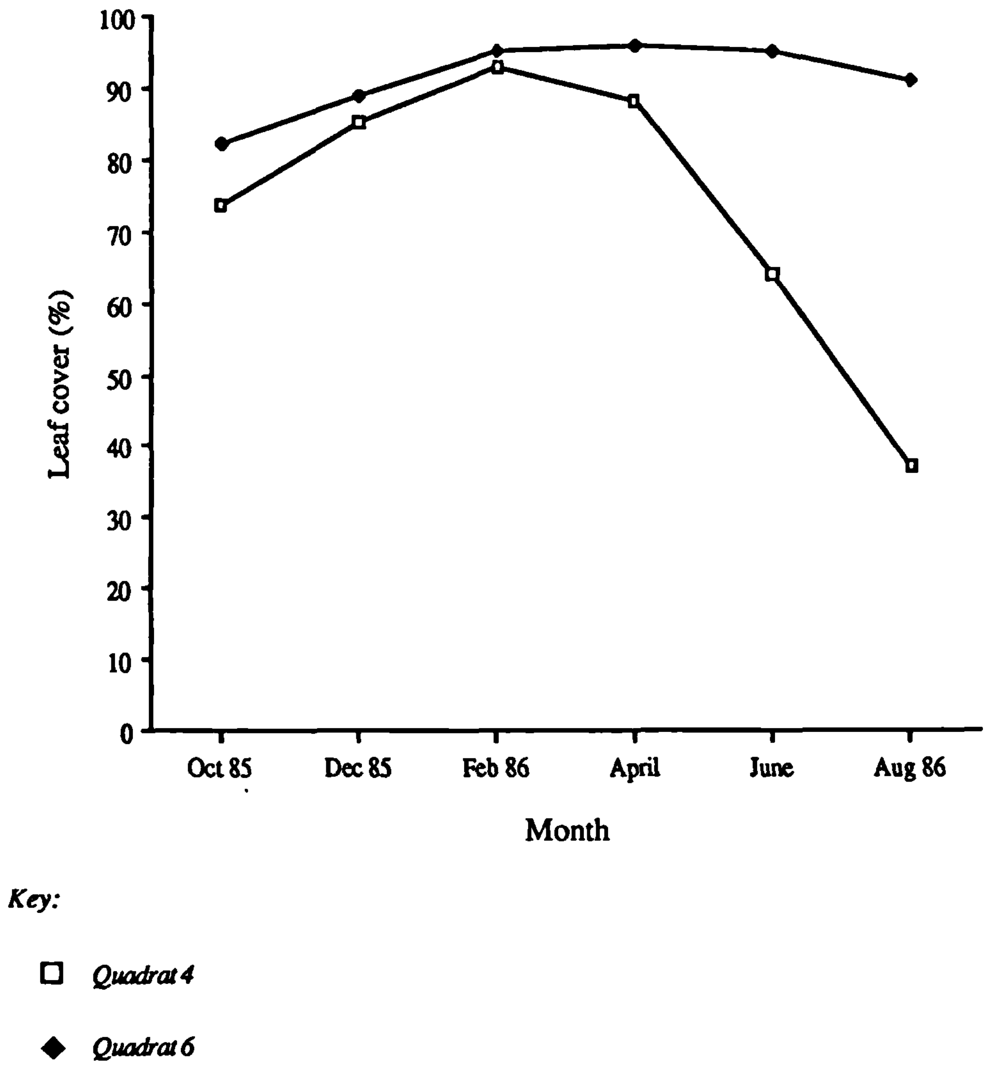


Figure 3.8 compares the seasonal variation in the leaf cover recorded in quadrats 4 and 6, representing the vegetation at the highest and lowest elevations, respectively (see fig. 2.3).

Figure 3.9

Monthly Variation in New Leaf Cover Recorded in the Phenology Quadrats

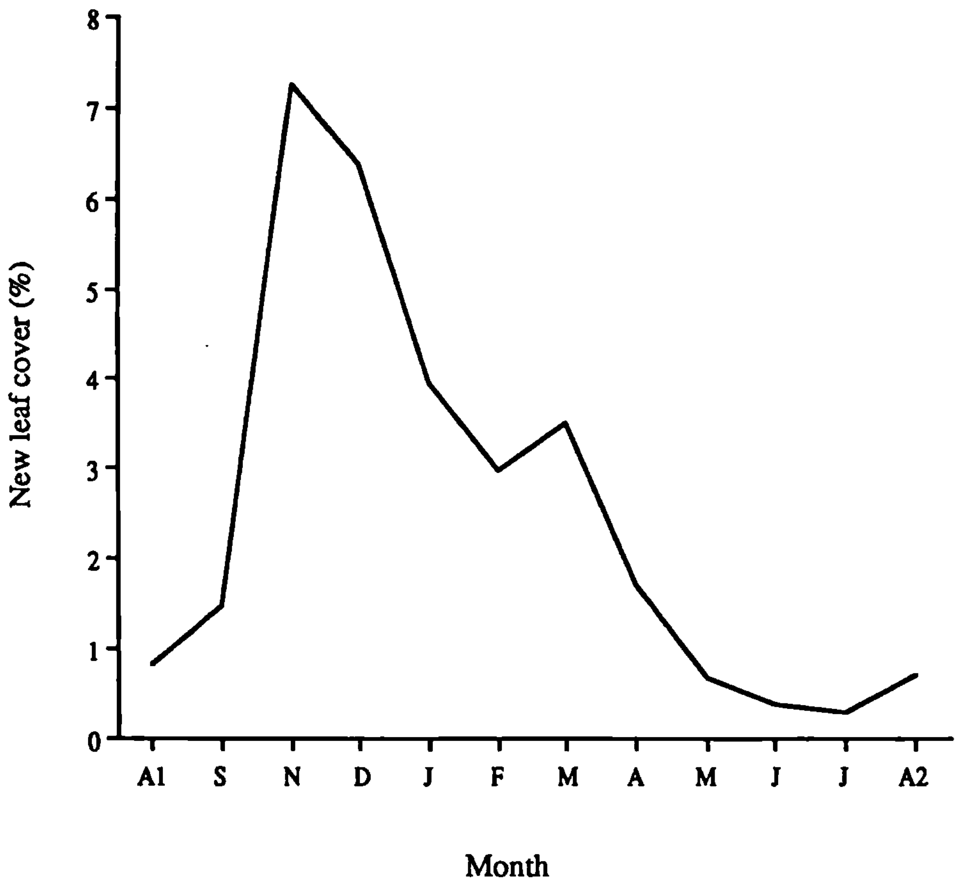
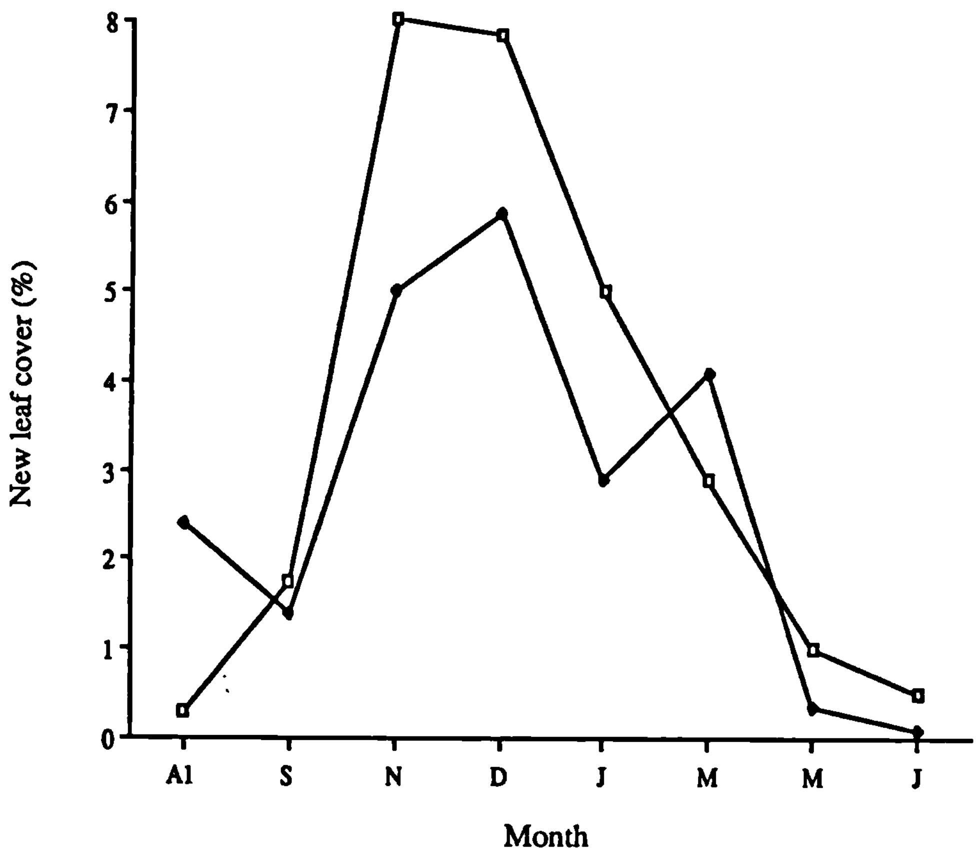


Figure 3.9 shows the estimated new leaf cover in phenology quadrats in each month during the study period. New leaf cover is shown as a percentage of the total crown volume of the marked trees in the quadrats selected each month (see figure 3.7).

Please note: The different months of the year are represented by their capital letters in this and all following graphs showing monthly variation during the main study period. A1 thus represents August 1985 and A2 August 1986.

Figure 3.10

Seasonal Variation in New Leaf Cover at Different Elevations



Key:

□ *Quadrats at lower altitudes (quadrats 1, 2, 6 & 7)*

◆ *Quadrats at higher altitudes (quadrats 3, 4, 5 & 8)*

Figure 3.10 compares the estimated new leaf cover recorded in phenology quadrats at lower and higher elevations in different months during the study period (see text). New leaf cover is shown as a percentage of the total crown volume of the marked trees in the quadrats selected each month.

Figure 3.11

Monthly Variation in the Leaf Cover of Anadenanthera peregrina *Trees*

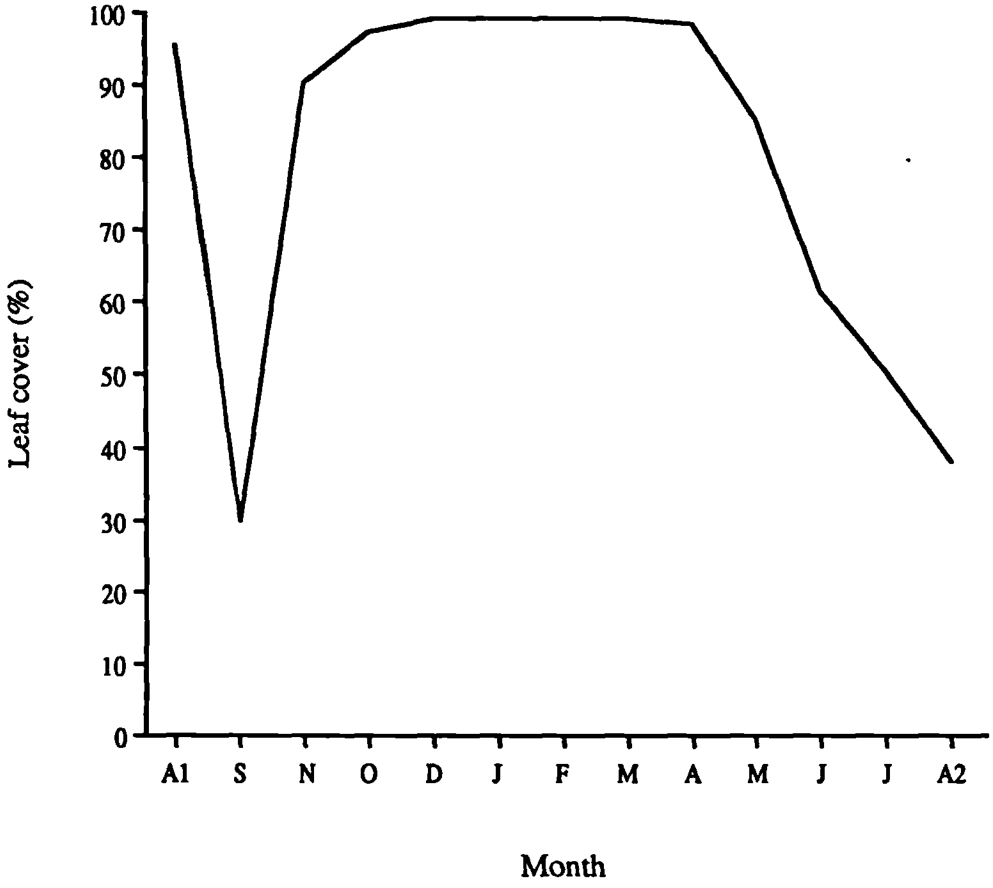


Figure 3.11 shows the estimated leaf cover of the **A. peregrina** ***sample trees each month during the study period. Leaf cover is shown as a percentage of the total crown volume of the sample trees.***

compares the values for quadrats 4 (hilltop) and 6 (riverbank) through the course of the study year. The lower quadrat is clearly more stable and relatively more luxuriant throughout most of the year, while the hilltop quadrat undergoes far more variation.

The proportion of new leaves recorded in the quadrats peaked during the early wet season (figure 3.9) when all quadrats exhibited marked increases in their production of new leaves. New leaf production shows a correlation with rainfall (SRC: $r_s = 0.648$, $n = 13$, $p = 0.017$), and the cover recorded in wet season months was clearly differentiated from that recorded during the dry season (M-W U: $U = 0$, $p = 0.001$). While we might expect leaf production to have been greater in the quadrats at higher altitudes during the dry season, given their more marked seasonal variation in total leaf cover, such a pattern is not clear from the data (figure 3.10). One major problem here is the data collection itself. While the assessment of total leaf cover is a difficult task, the accurate measurement of new leaf cover is doubly so. New leaves not only make up a relatively small proportion of the total cover but are also difficult to categorise and identify as they take different forms on different species, so the data are subject to even more possible random biases and fluctuations.

However, while the quadrats at higher altitudes underwent increases in total leaf cover of between 10 and 30% between the end of the dry season and the middle of the wet in the study year, increases in the lower quadrats were less than 10% during the same period. This alone implies that new leaf production was much greater in the quadrats at higher altitudes during the wet season. The relative stability of cover in the lower quadrats in comparison with those at higher altitudes similarly implies that, while some new growth may continue during the dry season in the former, it may cease in the latter.

Records of the leaf cover of the separate sample of *angicos* show a similar trend. Most, but not all, of the trees were deciduous (see plates 2 and 3). The sample as a whole showed a similar pattern to that of the phenology quadrats, with maximum leaf production and cover coming during the wet season, and declining steadily during the course of the dry (figure 3.11). The results also indicate that leaf loss was more rapid and extensive during the 1986 dry season than in 1985. Total leaf cover was already less in May 1986 than it had been in August of the previous year, and had reached the level of the previous September by August.

Overall, the records of plant phenology during the year studied indicate a number of patterns. Fruit, flowers and leaves were all far more abundant during the wet season than during the dry. Only a small proportion of individual trees or species, however, produced fruit during the course of the year, and most types of fruit were judged to be inedible for marmosets. The records also suggest marked differences in the abundance of resources between the dry season of 1985 and that of 1986, which appears to be linked to differences in the levels of rainfall between these two years, and during their respective dry seasons in particular. Differences in the temporal fluctuation of leaf production and cover were also noted between quadrats at different altitudes.

Arthropod Abundance

The methods used for the measurement of arthropod abundance have been described in chapter 2. As stated previously, such methods are subject to many possible biases. The recorded estimates of arthropod abundance did, however, prove to be consistent with data collected at other tropical sites [Janzen & Schoener, 1968; Janzen, 1973a, 1973b; Smythe, 1974; Bigger, 1976; Wolda, 1978; Denlinger, 1980; Tanaka & Tanaka, 1982] and corresponded well with observations of the study group's consumption of this type of prey. Overall, sweep sampling produced the most adequate measure of the types and sizes of insects most commonly preyed on, although the water traps did show similar overall trends in most months. One factor here is that dipterans are usually over-represented in water traps [Henshaw, 1984]. The sweep sampling also seemed to provide a better measure of differences within the group's home range, and this was again probably related to the types of insect usually collected. Other arthropods collected in the traps, mostly spiders, were also counted and measured and do, in fact, provide a complementary measure which seems to support the accuracy and validity of the methods used.

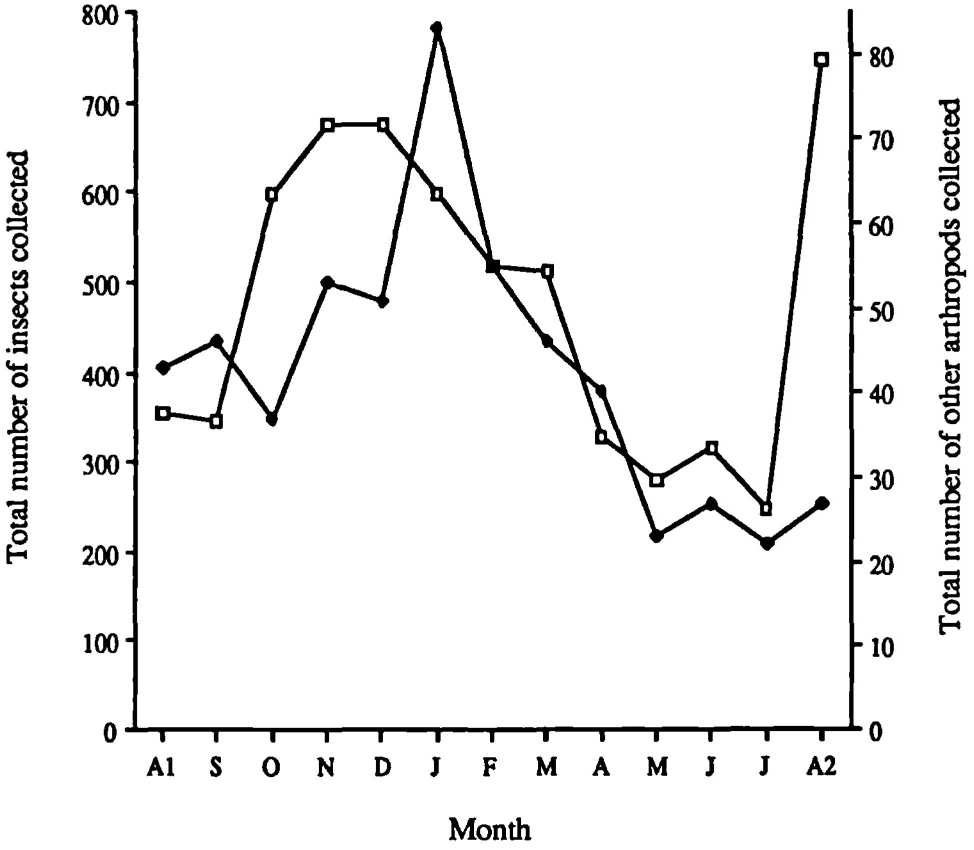
Only in August 1986 did apparently random local fluctuations in the abundance of a certain type of insect seem to have a significant effect on the collection. This month's sample contained an unusually large number of a single small dipteran species (body length less than 2 mm), which boosted the total to beyond that of any other month during the study period, in marked contrast with the overall trend shown in both the previous months and in the same period of the previous year. It is not impossible that this exceptional sample was in fact a true reflection of overall insect abundance during this month, although it seems most likely, both from the evidence of the group's prey feeding in this and previous months (see chapter 6), and from qualitative observations of insect abundance at the study site, that this was an anomalous result. What this sample does seem to reflect, then, is the temporary local super-abundance of a single small dipteran species which coincided with that month's insect trapping, rather than a systematic increase in the abundance of insects in general. Please note that, while more rain fell in this month than during the preceding ones (table 3.3), it came at the end of the month, more than ten days after both the insect trapping and the collection of behavioural records. As such, this would be unlikely to have had any great influence on the foraging behaviour of the group during this month, although the abundance of these insects might have had an indirect effect on its behaviour if this species attacked gum-producing trees, for example.

The elimination of insects with a body length of less than 5 mm from the sample not only seems to compensate for this and other random effects, but also removes a category of insect which marmosets probably only rarely, if ever, consume. Such a manipulation of the data, however well justified, may disguise certain trends or, in fact, misrepresent specific aspects of the measurements. Large-bodied insects, for example, may be relatively more abundant in drier periods or habitats than small-bodied ones [Janzen & Schoener, 1968; Tanaka & Tanaka, 1982]

One potential problem with the samples collected is that the larger insects most often consumed by the study group (*i.e.* of body length greater than 10 mm) are relatively poorly represented. This makes them most subject to possible random fluctuations in their capture from one month to the next, although this can be compensated for by taking the mean values for longer periods. While the methods could have been adapted during the study to provide a better measure of the types of insect consumed by the study group, this would not necessarily have been satisfactory (see chapter 2). Selecting the

Figure 3.12

Monthly Variation in Arthropod Catches



Key:

☐ *Insects*

◆ *All other arthropods*

Figure 3.12 compares the total monthly catches of insects and other arthropods. Values are the total number of individuals collected in all traps each month.

types of insects captured may have had adverse effects on both the assessment of the group's behaviour and, through the depletion of the populations of specific types of insect, on that behaviour itself. Ultimately, the validity of the methods used can be assessed by cross-checking with records of the group's behaviour and in particular the consumption of arthropods by its members.

The numbers of arthropods collected each month are presented graphically in figure 3.12. As discussed previously, the sample for August 1986 is markedly different from those of all other dry season months, including the previous August, although there is still a significant difference between the wet and dry season catches (M-W *U*: $U = 6, p < 0.035$). This contrast is even more apparent if we take only those insects with a body length greater than 10 mm (M-W *U*: $U = 4, p < 0.014$). Insect abundance peaked in the early wet season months, just before rainfall in the study year, and there is a highly significant correlation between measured abundance and monthly rainfall (SRC: $r_s = 0.791, n = 13, p = 0.001$). The fact that insect abundance does not decline rapidly in the abnormally dry March suggests that a late wet season peak, corresponding with that of rainfall (see figures 3.3 and 3.4), may be more apparent in more normal, wetter years. Other arthropods were also more abundant during the wet season months, as might be expected for insect predators such as spiders, again correlating with monthly rainfall (SRC: $r_s = 0.722, n = 13, p = 0.005$).

New leaf production, rather than total leaf cover, appears to be an important factor determining the abundance of certain herbivorous insects [Wolda, 1978], so it is interesting to note that this is a pattern also found in the present data. While not significant, the total monthly catches of insects are clearly more closely linked to new leaf cover (SRC: $r_s = 0.505, n = 13, p = 0.078$) than to total leaf cover (SRC: $r_s = 0.115, n = 13, p = 0.707$). This pattern is clearer, however, if we take the monthly catches of insects with a body length greater than 10 mm, a subset which contains a much larger proportion of leaf-eating insects such as grasshoppers. Monthly catches of large insects thus correlate significantly with new leaf cover (SRC: $r_s = 0.718, n = 13, p = 0.006$), but not with total leaf cover (SRC: $r_s = 0.52, n = 13, p = 0.069$).

It is also interesting to note that the catches of the two dry season months from 1985 are larger than the samples of all 1986 dry season months except August. While it is possible that these differences may be due to random effects in the case of the relatively smaller 1985 sample, the consistency between the two months sampled suggests that this is not the case. If we exclude the smallest insects, the August 1986 sample also falls well below that of either of the dry season months of the previous year. For insects of body length greater than 5 mm, for example, the August 1985 sample is 131 insects while that of the following August is only 90. The catch of larger insects (body length > 10 mm) actually fell by 44.1% from one August to the next (from 34 to 19 insects), which seems to suggest that their abundance in the preceding months may also have been less than in the same months of the previous year. The mean catch of insects with a body length greater than 5 mm in the 1985 dry season months was 129.5, but only 92 in 1986. For insects of the larger category (> 10 mm), the means were 30.5 and 22 respectively. Larger insects were not only more abundant in absolute terms during August and September 1985, but also made up a larger proportion of the total catch (whether August is included in the 1986 sample or not). Insects greater than 10 mm in length constituted 8.7% of the total catch during the 1985 dry season, 7.8% in June and July 1986 and only 5.7% when August is included.

Abundance, as we have seen, was closely related to rainfall and it thus seems somewhat inconsistent that the later dry season months of 1985 should exhibit greater insect abundance than the earlier months of the 1986 dry season, especially as the rainfall in June and July 1985 was much less than for any month during the following year. We might thus conclude either that the relatively greater abundance of insects in the late dry season of 1985 reflects factors other than rainfall or that insect abundance was much greater throughout the 1985 dry season and may, in fact, have been less in the later months than it would have been if June and July had been warmer and more humid. The marked difference in the quantity of rain falling during the wet seasons of the two years (figure 3.5) seems to support the latter hypothesis. The relatively greater abundance of insects, and large insects in particular, in the previous dry season may have been due both to the greater abundance and reproductive success of the insect population during the wet season as a whole

Table 3.4

Total Catches, All Traps, August 1985 to August 1986

	Body length (mm):				
	Insects:			Other arthropods:	
Sample	≤5	>5-10	>10	≤5	>5
August 1985	222	97	34	34	9
September	217	101	27	39	7
October	477	89	33	32	5
November	512	120	44	42	11
December 1985	520	123	31	27	24
January 1986	480	85	32	56	27
February	340	148	29	22	33
March	367	104	42	33	13
April	229	77	21	31	9
May	163	92	26	16	7
June	236	53	27	24	3
July	174	57	17	13	9
August 1986	655	71	19	23	4

and to the greater humidity of the later months of February, March and April (and possibly also May) in particular.

While insects seem to have been more abundant during the dry season months of 1985 than during the same period of 1986, they were consistently less abundant in all dry season months than during the wet season (table 3.4). The mean catch in all traps during the six wet season months (October to March) was 596, while it was 349 in August and September 1985 and 383.4 in the dry season months of 1986, although it is only 293 if we exclude August. For insects with a body length greater than 5 mm, the mean catch for the wet season months was 146.7, and for those greater than 10 mm in length it was 35.2. While these means are again consistently greater than those for either dry season, they do represent a smaller proportion of the total catch (5.9% of the total wet season catch had a body length of more than 10 mm). Such a difference is comparatively small, however, when compared with the absolute numbers of these larger insects captured during different seasons, the average catch of the wet season months was 59.9% larger than that of the 1986 dry season months, although it was only 15.3% larger than that of the 1985 dry season. With regard to the quantities of larger insects collected, therefore, the 1985 dry season sample seems more similar to that of the wet season than to that of the 1986 dry season.

The abundance of different types of insect also shows considerable variation through the course of the study period (see figures 3.13a-f). While the monthly samples of some orders are rather small (only seven were, in fact, numerous enough to be analysed here), most show quite clear and consistent trends of abundance during the course of the year. Dipterans were the most abundant insects in all months and exhibit a clear peak during the early wet season and a smaller peak in March, although they were, of course, more abundant in August 1986 than in any other month. Dipteran abundance also shows the strongest correlation with monthly rainfall (SRC: $r_s = 0.709$, $n = 13$, $p = 0.007$). After the dipterans, hymenopterans and homopterans were captured most often. The catches of hymenopterans show no clear patterns, and only a weak correlation with monthly rainfall (SRC: $r_s = 0.358$, $n = 13$, $p = 0.23$). Catches of this order appeared to be most subject to random fluctuations because of the social habits of many ant species. Homopterans, on the other hand, were more abundant during the wet season, showing a significant correlation with monthly rainfall (SRC: $r_s = 0.654$, $n = 13$, $p = 0.015$). Hemipterans were caught in relatively small numbers in most months, and their abundance exhibits the most unusual trend, with a marked peak at the end of the wet season and beginning of the dry season. In accordance with this, the abundance of this order shows a weak negative correlation with monthly rainfall (SRC: $r_s = -0.207$, $n = 13$, $p = 0.498$).

The remaining three orders averaged only 20 to 30 individuals in the monthly catches, but these were the orders most frequently preyed on by the study group and so their abundance should be analysed in more detail. Whereas the Coleoptera and Orthoptera exhibit marked peaks of abundance during the wet season, the Lepidoptera presents a somewhat equivocal picture. Apart from an unusually large catch in the first month of sampling, lepidopterans did not seem to be subject to systematic fluctuations in abundance during the course of the year and did, in fact, exhibit a negative correlation with monthly rainfall (SRC: $r_s = -0.264$, $n = 13$, $p = 0.383$). The average catch of lepidopterans in the six wet season months (20.5) was, in fact, slightly smaller than that of the dry season months combined (21.9), although removing the August 1985 sample gives a slightly lower dry season average of 19 individuals per month. Lepidopteran larvae were more frequently captured than those of any other type of insect. Although this may have had some influence on the results, the numbers are too small to show any specific patterns.

Coleopterans, on the other hand, show the most marked variation in abundance during the year. The main peak of coleopteran abundance came at the beginning of the wet season (figure 3.13d), with a smaller peak in March. The largest number of individuals captured in any dry season month was 19 (May), four less than the smallest catch in any wet season month (23 in February). The average catch in the wet season months was 39.8, more than double that for the dry season, which was 15.3, and there was a significant correlation between coleopteran abundance and monthly rainfall (SRC: $r_s = 0.619$, $n = 13$, $p = 0.024$). For larger coleopterans (body length > 5 mm), the difference is even more striking, the mean catch during the wet season months (15.7) being more than three times that of the dry season months (4.6). The average catch of these larger coleopterans in the 1985 dry season was also remarkably consistent with that of the 1986 dry season months, being 4.5 in the former and 4.6 in the latter.

While orthopterans are clearly more abundant during the wet season months than during the dry season, the differences are not quite as marked as for coleopterans (although the late wet season peak is more pronounced, see figure 3.13f). This is due in part to the relatively large catches in the dry season months of 1985. Wet season catches were nevertheless significantly different from those of the dry season (M-W U: $U = 3.5$, $p < 0.012$). While there is a correlation between orthopteran abundance and monthly rainfall, it is not quite significant (SRC: $r_s = 0.488$, $n = 13$, $p = 0.09$), although it is if we remove the samples from August and September 1985 (SRC: $r_s = 0.612$, $n = 11$, $p = 0.045$). Taking the larger forms (body length > 10 mm), the average catch in the wet season months was 9.2 individuals, 5.5 in the 1985 dry season and 5.6 in the 1986 dry season. Thus, although the numbers are small, there does seem to be a considerable and consistent difference in the abundance of these larger forms between wet and dry seasons.

It is also interesting to note that the abundance of both coleopterans and

Figure 3.13

Monthly Variation in the Catches of Insects of Different Orders

(a) Dipterans

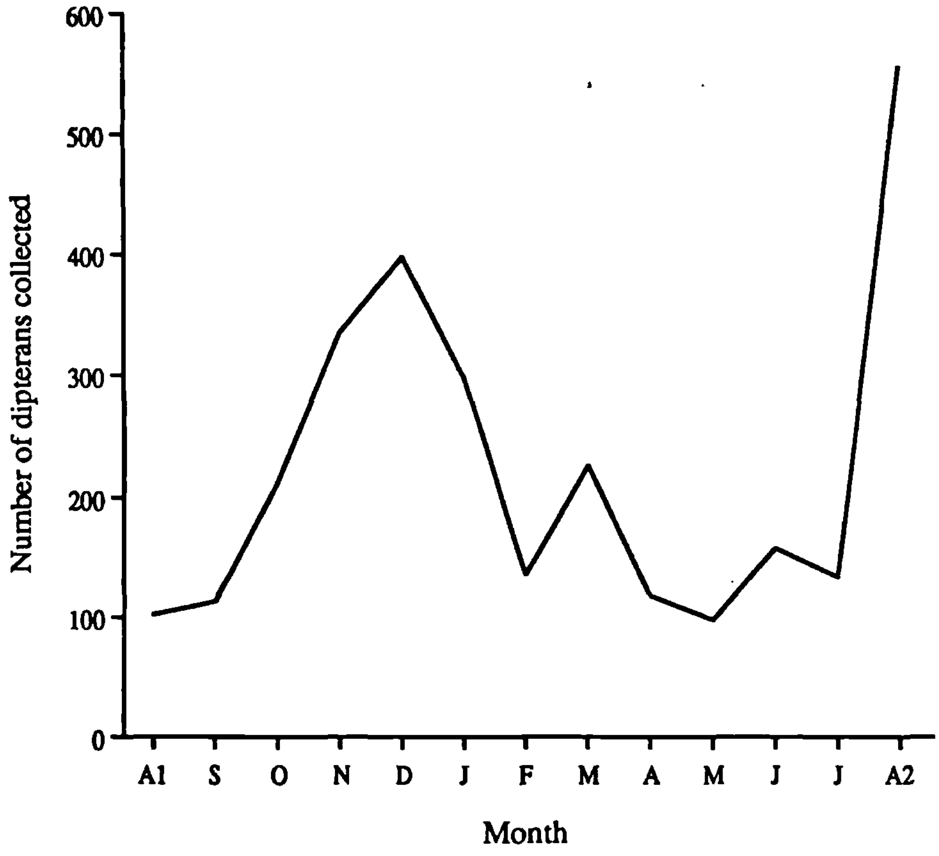


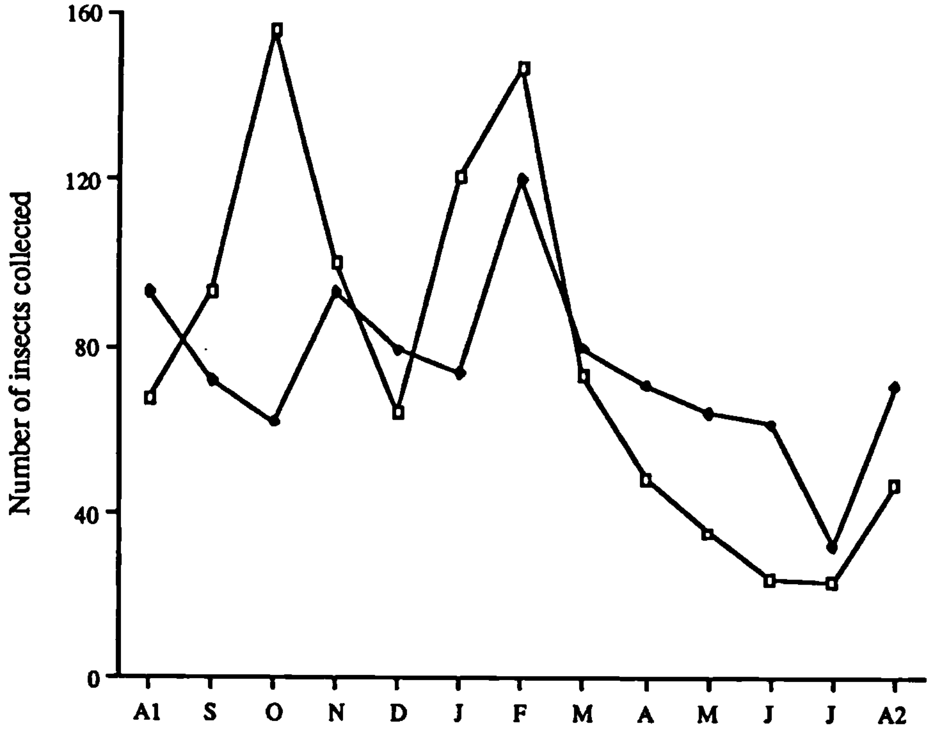
Figure 3.13 compares the monthly catches of the seven insect orders encoutered most frequently in the traps. Values are the numbers of individuals of each order collected in all traps each month.

Key for fig. 3.13b (facing page):

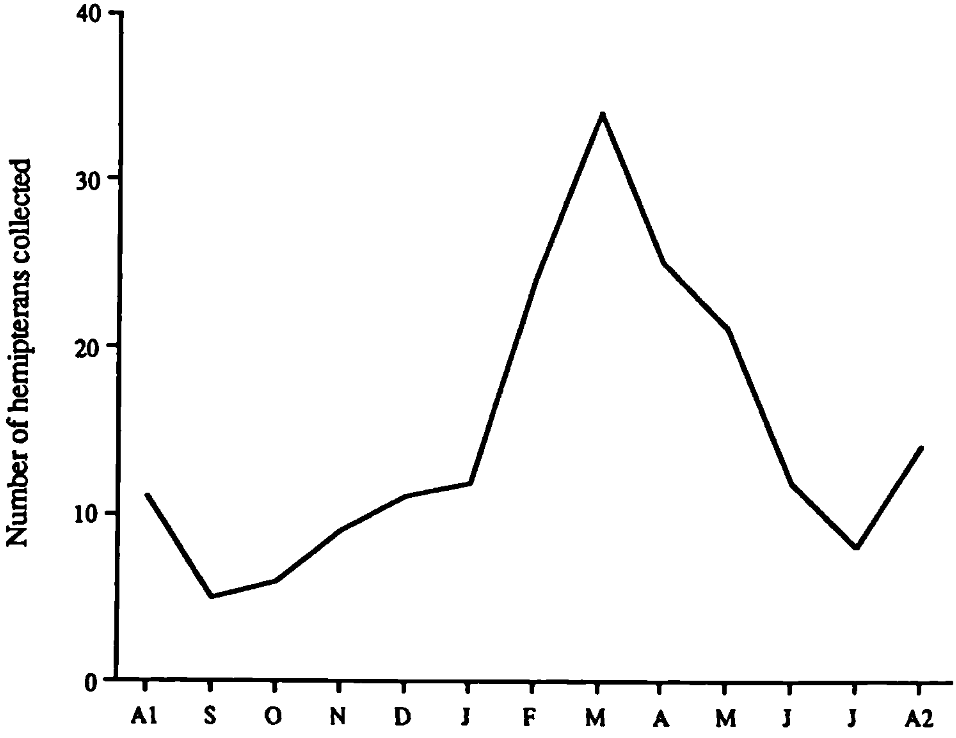
☐ *Homopterans*

◆ *Hymenopterans*

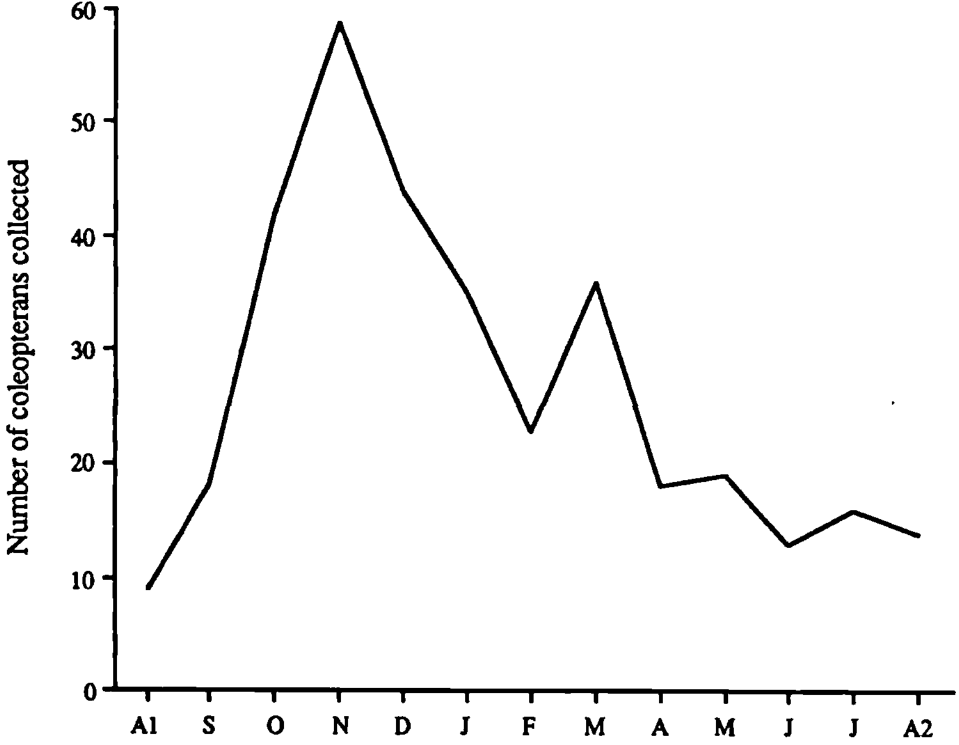
(b) Homopterans and Hymenopterans



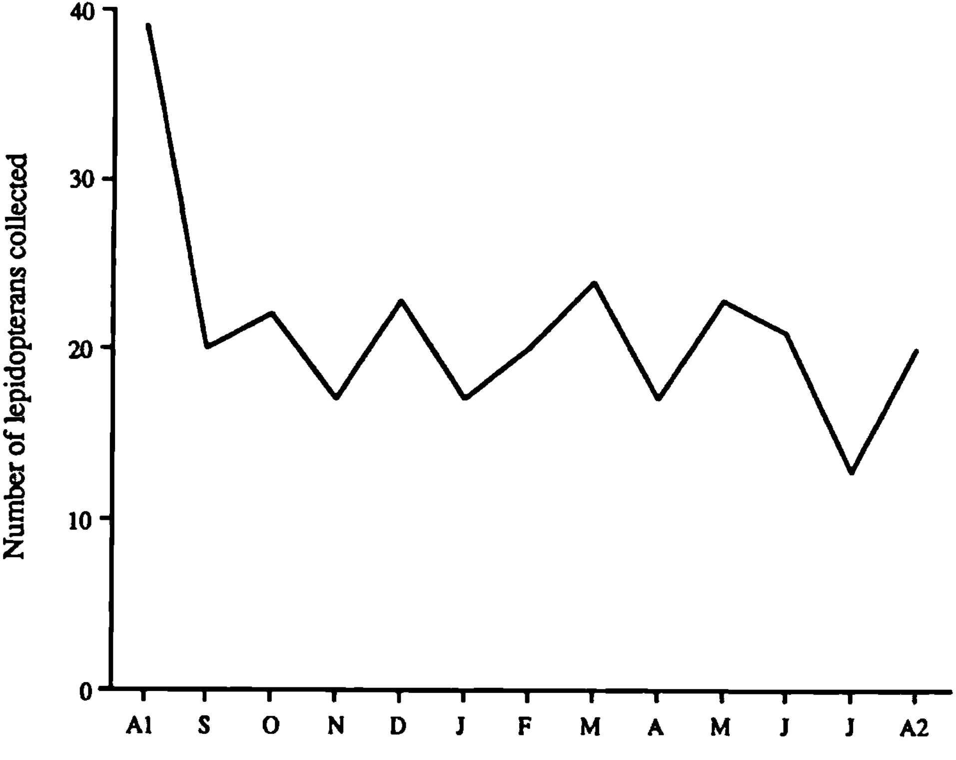
(c) Hemipterans



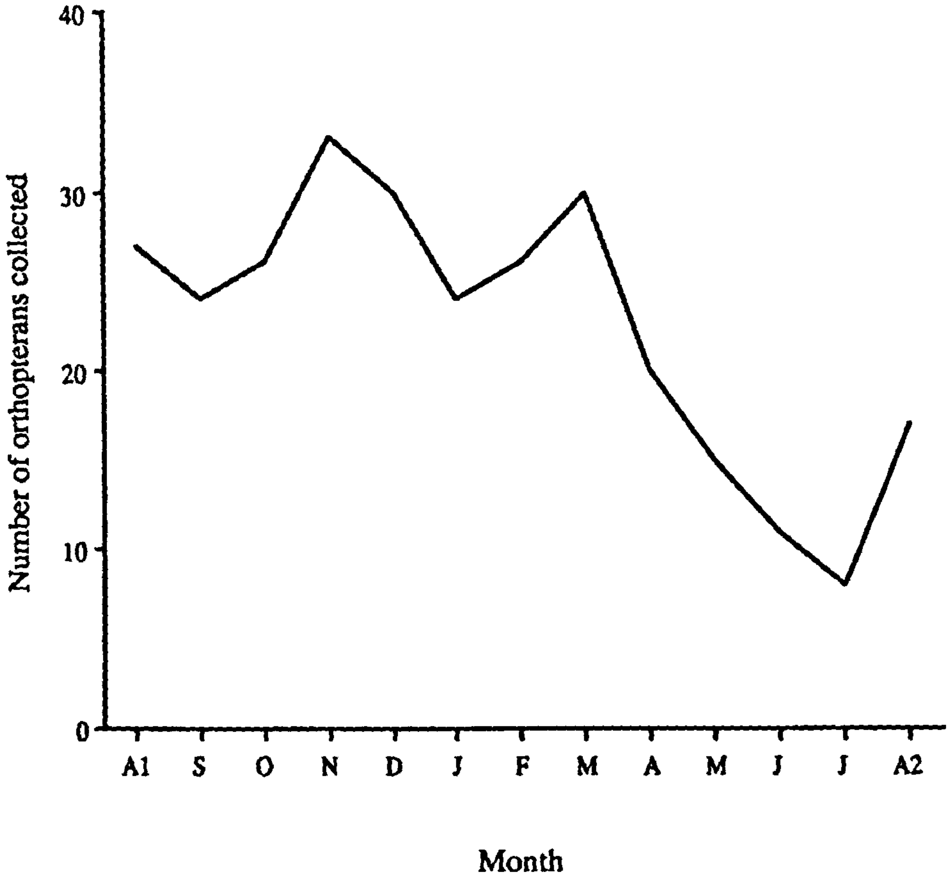
(d) Coleopterans



(e) Lepidopterans



(f) Orthopterans



orthopterans appeared to be closely related to new leaf production, rather than to the overall availability of leafy material. The patterns are even more marked than for the insect catches as a whole (see above), as might be expected for these predominantly herbivorous orders. The monthly catches of coleopterans were, in fact, less closely related to total leaf cover than those of the large-bodied insects as a whole (SRC: $r_s = 0.355$, $n = 13$, $p = 0.234$), but their correlation with new leaf cover was even more significant (SRC: $r_s = 0.823$, $n = 13$, $p = 0.001$). Similarly, the catches of orthopterans were far less closely related to total leaf cover (SRC: $r_s = 0.53$, $n = 13$, $p = 0.063$) than to new leaf cover (SRC: $r_s = 0.767$, $n = 13$, $p = 0.002$).

As well as fluctuating through time, insect abundance within the home range of the study group appears, according to the results of the trapping, to show different patterns in different areas. Janzen & Schoener [1968] found systematic variation in the dry season abundance of insects in adjacent Costa Rican lowland forest habitats of differing altitude and humidity, with insect numbers being very much greater in more humid habitats. Populations in lower, more humid habitats may thus be far more stable than those in drier, more seasonal environments. The proximity of the river Manhuaçú and the marked variation in altitude within this area have been seen as indications of overall variations in the humidity of the soil. Average tree size, both here and in the forest at FMC in general, decreases with increasing elevation. In addition, the results of the measurement of plant pheneology indicate that leaf fall is far greater in quadrats at higher altitudes during the dry season, and that the degree of leaf fall is more closely related to the amount of rain falling during the course of the year.

As insect abundance shows a clear correlation with rainfall, it seems reasonable to expect that the differential humidity within the forest has an influence on the abundance of insects in different areas. As the types of insect most commonly preyed on by the study group are, in general, folivorous, it seems likely that the availability of leaves in any given area will have a direct influence on the abundance of these insects in particular. In order to test these possibilities, the records of insect abundance can be divided into two comparable samples. The ten water traps and 200 sweep sample taken at the highest point of the group's range can be directly compared with the ten traps and two 100 sweep samples taken along the riverbank. Two smaller sweeps were carried out on the riverbank only because of the lack of an appropriate continuous trail, and there seems to be no reason to suppose that the two sweeps, taken together, are not comparable with that of the hillside. The complementary sweep sample taken along trail MT, while of the same number of sweeps, is probably not directly comparable with the others because of the sparser undergrowth existing along this trail.

Table 3.5

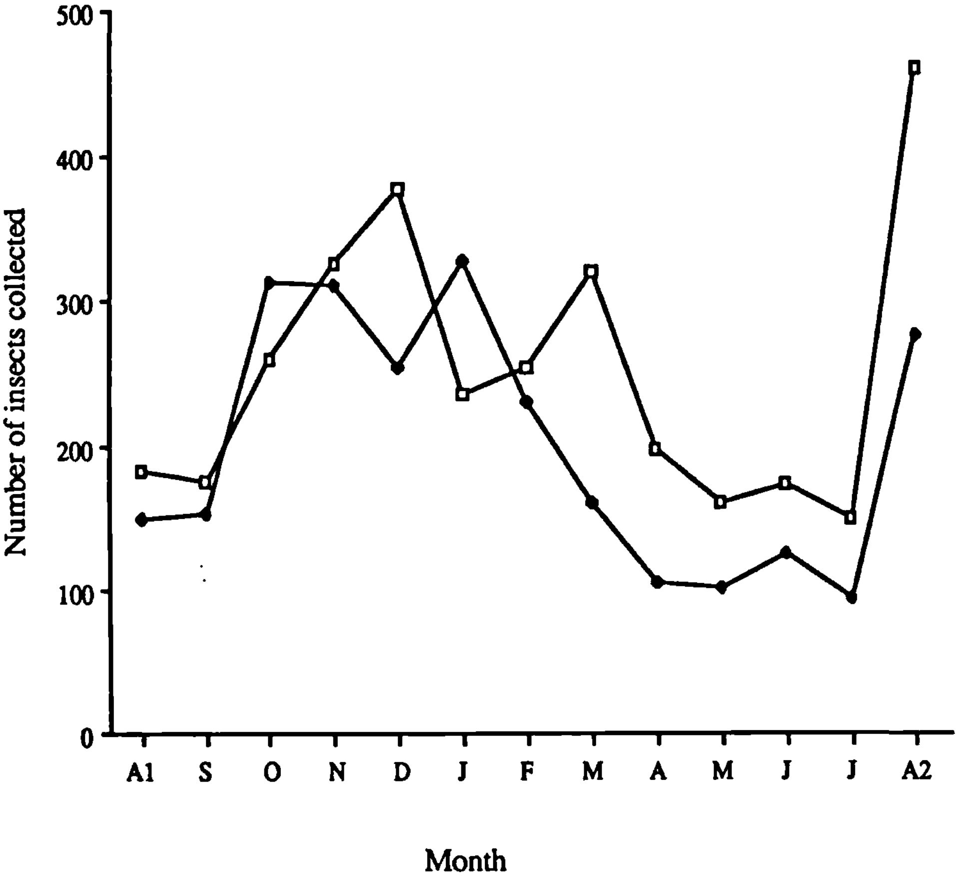
Seasonal Variation in Hilltop and Riverbank Catches of Insects

	Average number of insects collected per month:			
	Hilltop traps:		Riverbank traps:	
Sample	All insects	Body length >10 mm	All insects	Body length >10 mm
Late dry 1985	152.0	18.5	178.5	11.5
Early wet 1985	293.0	21.3	321.7	13.7
Late wet 1986	240.3	13.0	270.7	21.7
Early dry 1986	104.0	8.5	179.0	12.0
Late dry 1986	165.7	6.3	261.0	13.7
All dry season catches:	144.1	10.4	214.0	12.6
All wet season catches:	266.7	17.2	296.2	17.7
All catches:	**200.7**	**13.5**	**252.0**	**14.9**

Comparing the catches at the two altitudes (table 3.5 and figure 3.14), we can see that both locations exhibit the characteristic increase in abundance during the wet season seen in the total catches (figure 3.12). The major difference between the two locations is that, whereas the hilltop sample is very similar to or even exceeds the riverbank sample during most wet season months, it is consistently smaller during the dry season months. While the monthly hillside samples thus show a highly significant correlation with rainfall (SRC: $r_s = 0.879$, $n = 13$, $p < 0.001$), the riverbank samples show a less marked relationship (SRC: $r_s = 0.676$, $n = 13$, $p = 0.011$). It also appears, from the available evidence, that these differences in abundance were

Figure 3.14

Monthly Variation in "Hillside" and "Riverbank" Catches



Key:

□ *Riverbank catches*

◆ *Hillside catches*

Figure 3.14 presents a comparison of the monthly catches from the "hillside" traps (the sweep netting ar SP and the water traps placed on WH, see fig. 2.5) and the "riverbank" traps (the sweep netting at SR1 and SR2 and the water traps placed on WR). Values are the numbers of individual insects collected at the different sites each month.

greater during the 1986 dry season than during the 1985 dry season. March is exceptional here, showing the most marked difference between catches for any month except August 1986. As we have seen, rainfall was markedly less than average during the later wet season of 1986 and during March in particular. Assuming that the results of the data collection were not subject to significant random variation, these results seem to confirm not only that humidity is one of the major factors influencing insect abundance, but also that the insect population in the higher, drier part of the forest may be far more sensitive to seasonal fluctuations in rainfall.

For larger insects (body length > 10 mm), the riverbank catches show more differentiation between the wet and dry seasons (figure 3.15). Average monthly catches were very similar at the two locations during the wet season (see table 3.5). The dry season catches, on the other hand, show considerable differences. Correlations with monthly rainfall were not as strong for these larger forms as for the total catches, although there is again a marked difference between the two locations. Thus, while the abundance of large insects on the riverbank showed no relationship with monthly rainfall (SRC: $r_s = 0.028$, $n = 13$, $p = 0.929$), there appeared to be some correlation with rainfall in the hillside catches (SRC: $r_s = 0.45$, $n = 13$, $p = 0.123$).

These results appear again to have been influenced by the relatively large catches in the dry season of 1985. While the average riverbank catch during the 1985 dry season months was actually slightly smaller (11.5) than that of the 1986 dry season, that of the hilltop approached three times the average of the following year (18.5). Thus, while the abundance of these larger insects on the riverbank was more or less the same in both dry seasons, it differed considerably from one year to the next on the hilltop and was possibly even greater than on the riverbank in 1985. Removing the first two months from the analysis gives a significant correlation between the hillside abundance of large insects and monthly rainfall (SRC: $r_s = 0.644$, $n = 11$, $p = 0.033$) and a negative correlation for the riverbank samples (SRC: $r_s = -0.138$, $n = 11$, $p = 0.687$). This evidence seems to confirm previous conclusions about the influence of humidity on insect abundance, and in particular the influence of the quantity of rain falling during the wet season on dry season abundance.

Figure 3.15

Monthly Variation in "Hillside" and "Riverbank" Catches of Large Insects (Body Length > 10 mm)

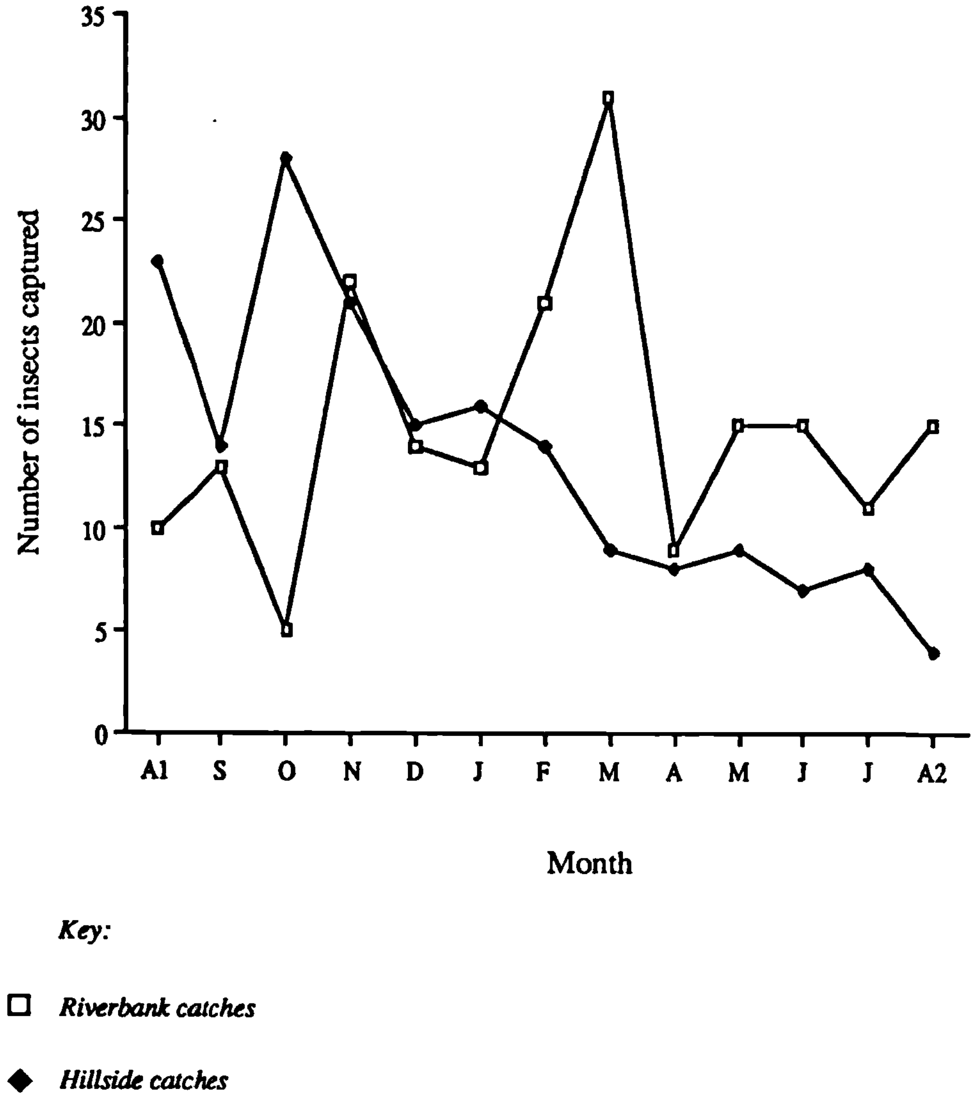


Figure 3.15 compares the hillside and riverbank catches (see fig. 3.14) of insects with a body length of 10 mm or more. Values are the numbers of individual insects of this body size collected at the different sites each month.

As certain orders (Coleoptera, Lepidoptera and Orthoptera) were more important as prey for the study group than others, analysing their abundance in different locations will provide a useful reference for the interpretation of its ranging and foraging behaviour. While the numbers of individuals of these orders collected are small, there are quite distinct patterns in their abundance at different altitudes. As we have seen, coleopterans were considerably more abundant during the wet season than during the dry. This trend is reflected in the numbers collected both on the riverbank and on the hilltop (figure 3.16a). Coleopterans were, however, far more abundant on the the riverbank during all seasons. In the 1985 dry season, the mean riverbank catch was twice that of the hilltop (8 and 4 respectively) and these proportions were very similar in the wet season (24 and 12.2 respectively). In the 1986 dry season, coleopterans were almost non-existent in the higher traps (average catch 1.6), in very marked contrast to the mean riverbank catch of 14.2. Thus, while the riverbank catches were actually larger in the second dry season, they were much reduced on the hilltop. As for overall abundance, lepidopterans exhibit no obvious trends at the different locations (figure 3.16b). They were, in general, around 50% more abundant in riverbank catches.

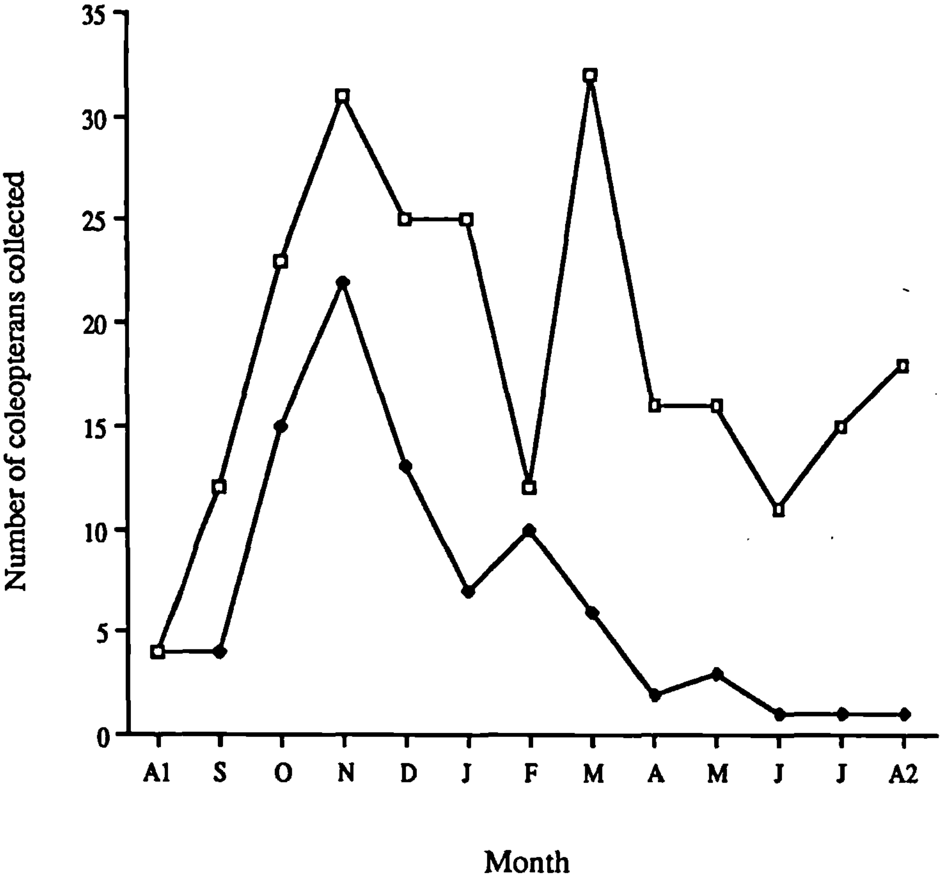
The abundance of orthopterans at the different locations exhibits the most interesting trends (figure 3.16c). The total number captured during the thirteen months at the different locations was exactly the same (129 individuals), but their distribution through time is completely different. The riverbank catches are remarkably consistent, given the small numbers involved, the average catch being 9.5 in all wet season months and 10.3 in all dry season months, and there is no correlation between the monthly catches and rainfall (SRC: $r_s = 0.261$, $n = 13$, $p = 0.39$). On the hilltop, on the other hand, the abundance of orthopterans fluctuated considerably between seasons (average monthly wet and dry season catches were 15.3 and 5.3 respectively), and did correlate with monthly rainfall (SRC: $r_s = 0.589$, $n = 13$, $p = 0.034$). It also seems, although the numbers are again small, that they were more abundant on the hilltop during the 1985 dry season than during the following year.

While the overall patterns of abundance can be easily related to differences in humidity and the availability of the principal orthopteran foodstuff (leaves) at the two locations, the significantly greater abundance

Figure 3.16

Monthly Variation in "Hillside" and "Riverbank" Catches of Coleopterans, Lepidopterans and Orthopterans

(a) Coleopterans



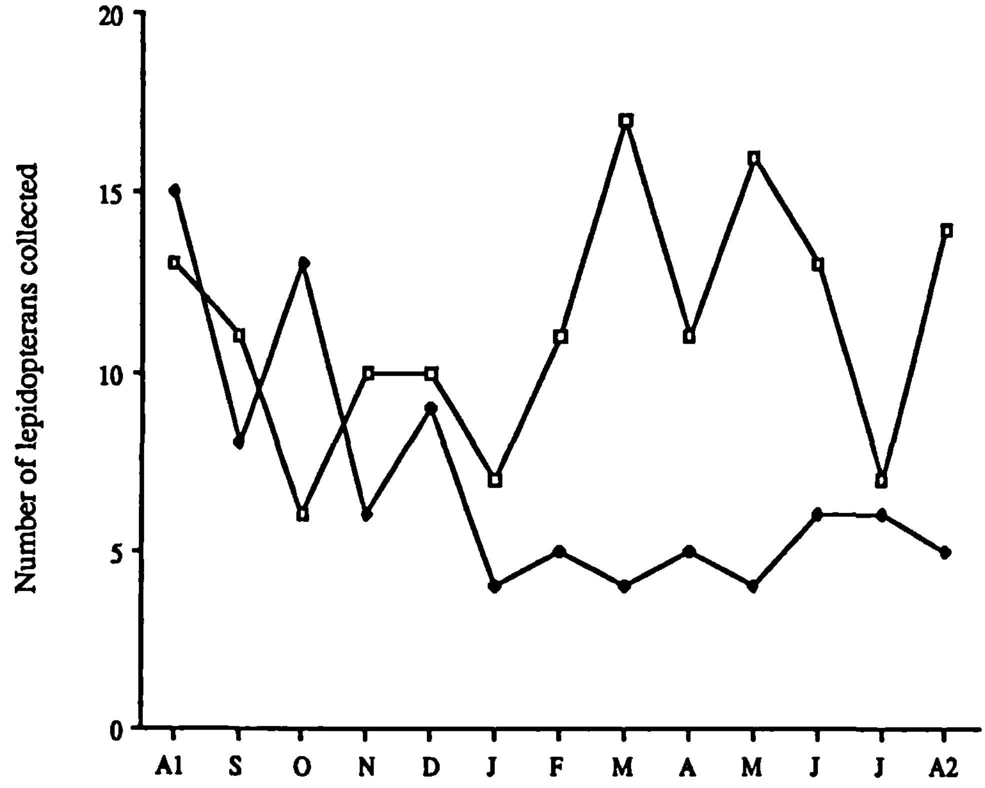
Key for figs. 3.16a-c:

□ *Riverbank catches*

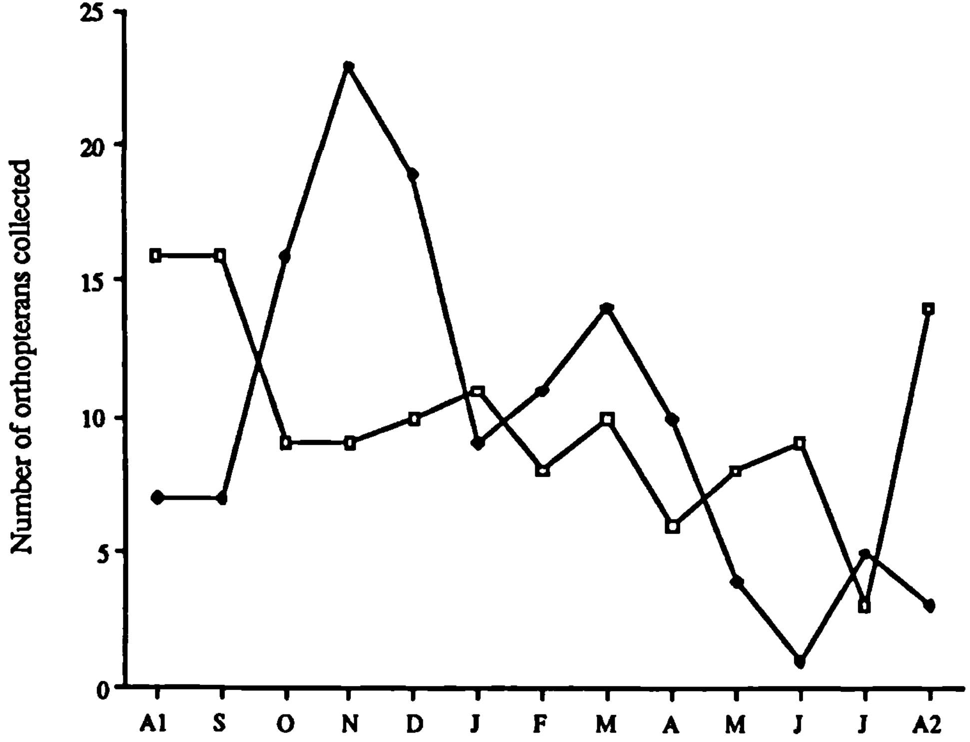
◆ *Hillside catches*

Figure 3.16 presents a comparison of the hillside and riverbank catches (see fig. 3.14) of the three insect orders most frequently consumed by study group members (see chapter 6).Values are the numbers of individuals of each order collected at the different sites each month.

(b) Lepidopterans



(c) Orthopterans



(61% more, on average) of orthopterans at higher elevations during the wet season is not so easily accounted for. One possible explanation is that, while leaf fall is much greater at higher altitudes during the dry season, these leaves are replaced during the wet season. So, even though leaves may be equally abundant at both locations, the availability of more nutritious young leaves, as confirmed by the phenology records, is greater over a longer period. In support of this, there is a slight peak in abundance on the riverbank at the beginning of the wet season when new leaves are apparently most abundant. Wolda [1978] found a clear relationship between leaf production and the abundance of certain folivorous insects on BCI, Panama. Trees at higher altitudes may thus support a larger orthopteran population during the wet season than those in lower, more humid locations, although this situation would be reversed (doubly so according to these records) in the dry season.

Arthropod abundance has been shown, according to the collections carried out in the study group's home range, to be correlated with and influenced by humidity, both through time and at different locations within this range. Insects of all sizes and most types are significantly more abundant during the wet season months and, in general, at lower, more humid altitudes. These trends are also shown by the types of insect most commonly preyed on by the study group and we might thus predict that its foraging, ranging and feeding behaviour would exhibit specific seasonal patterns related to those of the abundance and distribution of arthropods.

The Availability of Exudate

The study group's extensive use of plant exudate produced in response to damage caused by insects and other phenomena indicated that some measurement of this "naturally" available exudate would contribute to the understanding of its behaviour. *Angico* trees not only appeared to be by far the most important source of such exudate during preliminary observations, but are also especially abundant throughout most of the group's home range. It was thus felt that the measurement of the availability of exudate produced by a sample of these trees would provide the most useful records. A sample of 22 *angicos* was randomly selected (see figure 2.4), and gum availability was measured according to methods derived from those used by Bearder & Martin [1980] for the study of *Acacia karroo*, as described in chapter 2. All deposits observed on the sample trees were apparently produced in response to damage caused by insects. One of the trees had died during the early part of the study year, so the records from only twenty-one are included in this analysis.

Angico gum is usually light in colour, and soft and sticky in texture, when it is first produced by the tree. Left undisturbed, this gum will usually become much harder, and darker in colour, as it ages. There is, however, a good deal of variability in the colour and texture of gum of any particular age, even among deposits found on the same tree. This variability may depend on a number of factors such as how its production was stimulated, weather conditions and so on [see Bearder & Martin, 1980: pp. 123-124]. As gum remains soft longer when it is wet, we would expect, if gum production was more or less constant throughout the year, that soft gum would be more available during periods when rainfall is more frequent, *i.e.* during the wet season. We might also expect that the group would consume more of the available *angico* gum, including that on the sample trees, during the dry season, given the relative scarcity of dietary resources of all kinds outlined above. While such feeding would initiate some additional flow of gum, it is likely that the overall abundance on a particular day (*i.e.* when measurements were made) would be slightly reduced. Numerous additional random factors must be taken into account, but it does seem probable that gum, and soft gum in particular, would be, assuming production to be relatively constant, slightly more abundant during the wet season.

Three main types of gum formation were recognised, for the purposes of measurement; globules, casts and streaks or tendrils. No obvious "pools" of gum, as observed on the acacias at Mosdene, South Africa in Bearder & Martin's study, were observed. Colourless gum and crystalline formations were rarely observed on *angicos*, presumably also reflecting differences in the type of gum produced by this species from that of acacias. Newly-produced gum was usually yellow or amber in colour, although it was even black in certain cases. Darker-coloured gum was recorded more frequently than on the acacias at Mosdene.

Figure 3.17

Monthly Variation in the Availability of Anadenanthera peregrina *Gum Produced in Response to Damage Caused by Insects and Other Media*

(a) Type of Deposit

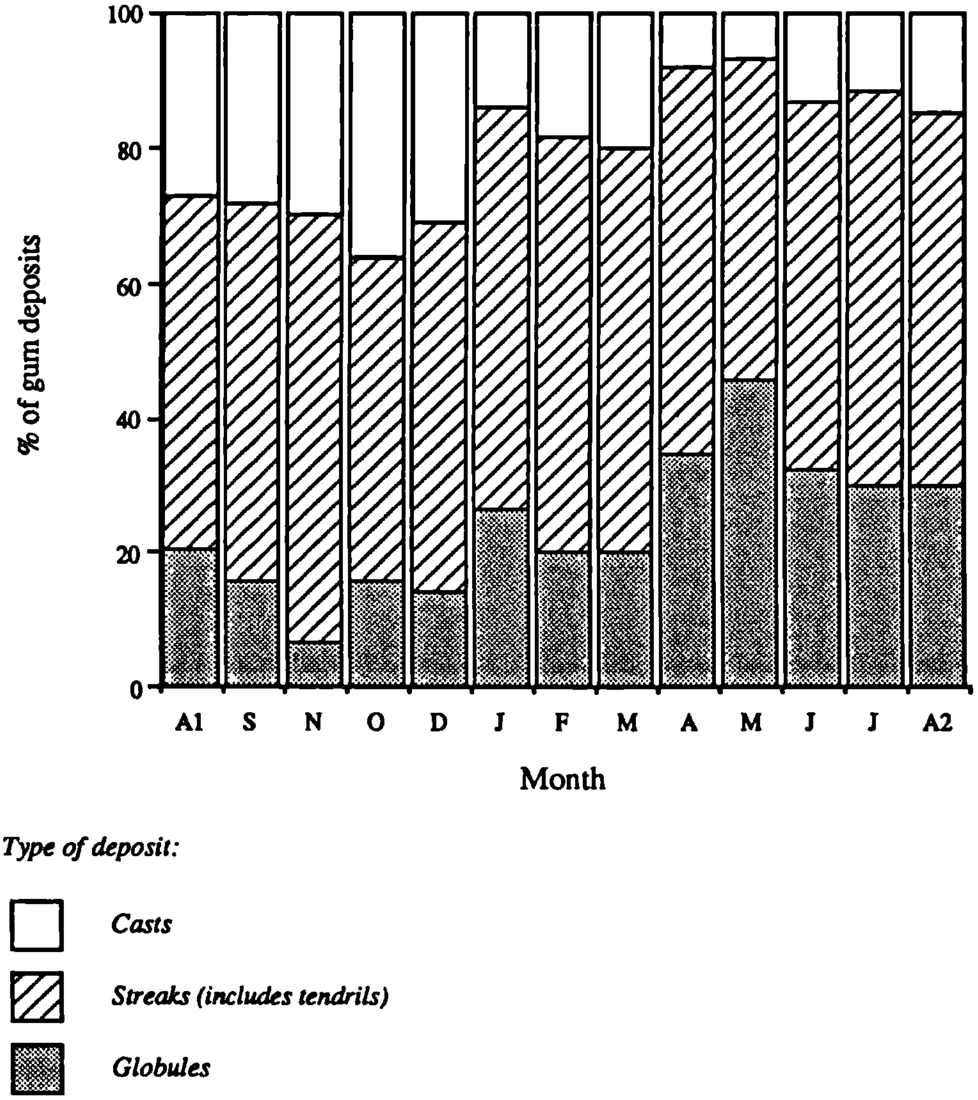


Figure 3.17a compares monthly changes in the availability of different types of gum deposit on the A. peregrina *sample trees. Values are percentages of the total number of deposits.*

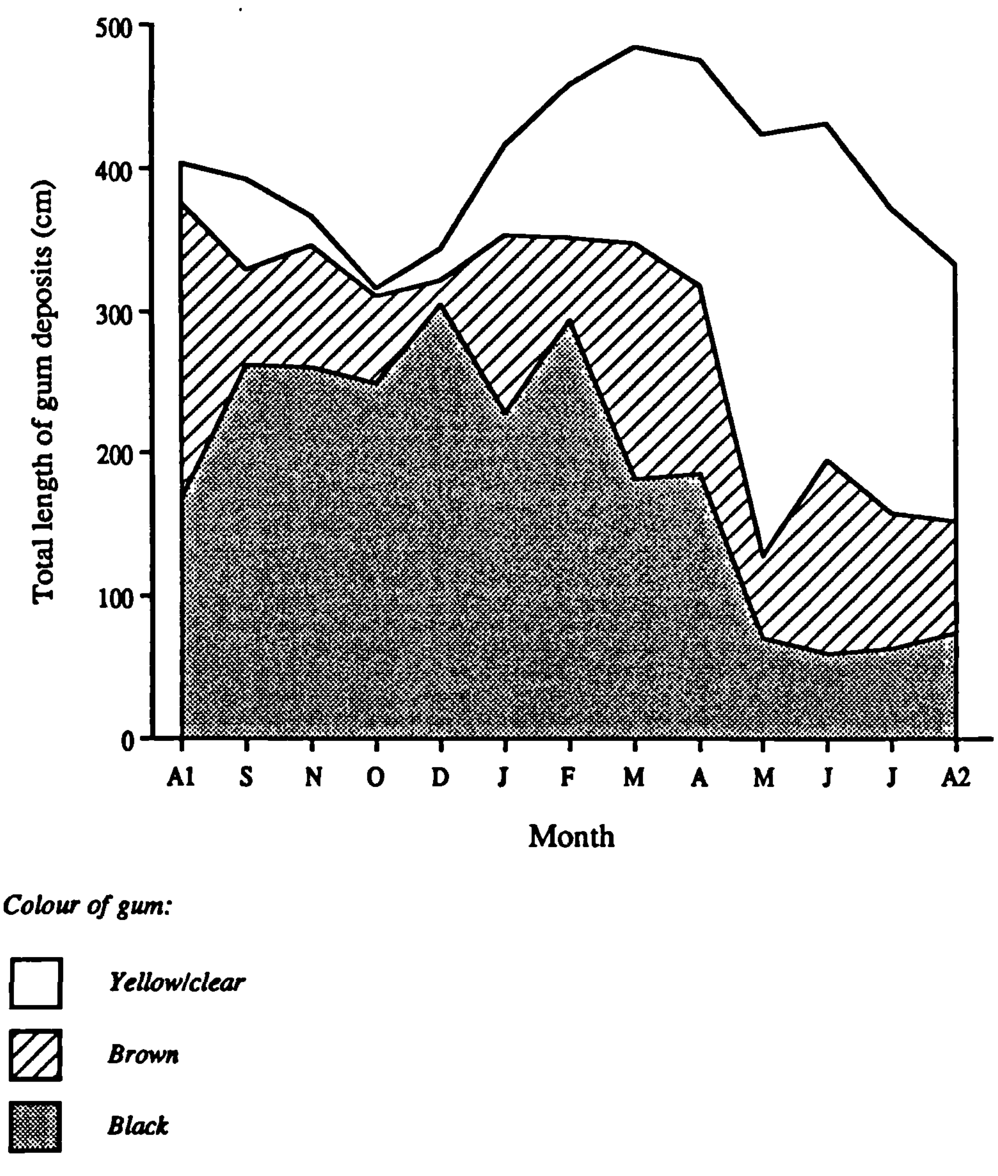

(b) Gum Colour

Figure 3.17b shows monthly changes in the availability of gum of different colours on the A. peregrina *sample trees. Values are the sums of the lengths of the deposits of each colour recorded each month.*

(c) Gum Consistency

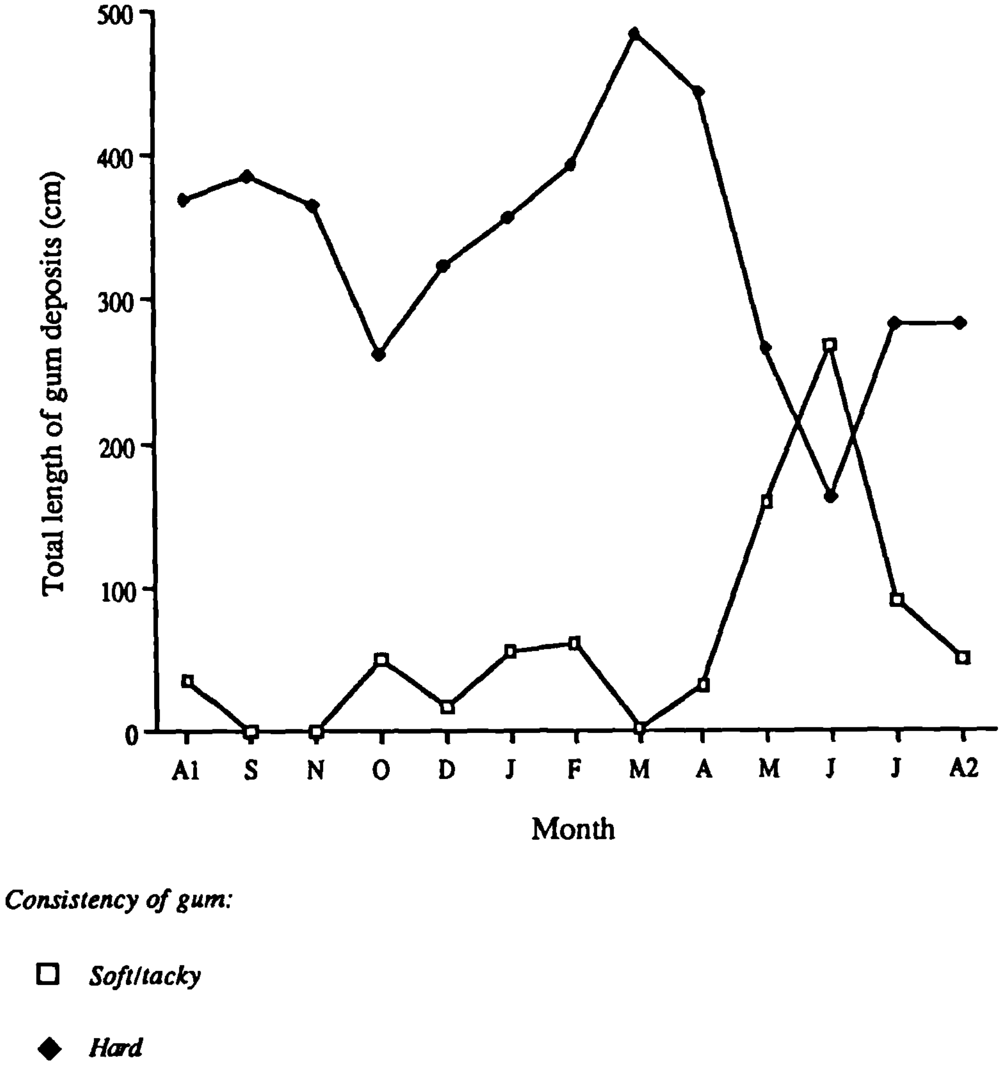


Figure 3.17c compares monthly changes in the availability of gum deposits of different consistencies on the A. peregrina *sample trees. Values are the sums of the lengths of the deposits of hard and soft gum recorded each month.*

The results of the measurement are presented in figures 3.17a to 3.17c. A number of trends indicate that gum production and availability were, in fact, greater during the dry season than during the wet. The abundance of gum, as measured by the total length of deposits, showed a negative, but not significant, correlation with monthly rainfall during the course of the year (SRC: $r_s = -0.412$, $n = 13$, $p = 0.162$). There was, however, a significant negative correlation between rainfall and the number of deposits recorded each month (SRC: $r_s = -0.591$, $n = 13$, $p = 0.033$).

Similar trends are apparent in other aspects of the measurements. While streaks and tendrils constituted a reasonably similar proportion of the deposits in all months, globules were more common during the dry season. Globules usually contain the soft gum first produced in response to insect damage [*ibid.*], and were apparently the type of deposit most commonly consumed by the study group. The numbers of these deposits recorded each month show a significant negative correlation with rainfall (SRC: $r_s = -0.642$, $n = 13$, $p = 0.018$). The measured abundance of light-coloured gum was also inversely related to monthly rainfall (SRC: $r_s = -0.698$, $n = 13$, $p = 0.008$). While the abundance of soft and tacky gum did peak during the dry season (figure 3.17c), the values recorded do not show such a clear relationship with rainfall (SRC: $r_s = -0.303$, $n = 13$, $p = 0.314$). While there may be random factors involved, given the comparatively small values recorded in most months, it seems likely that the lack of rainfall during the dry season, and in particular the relatively hot early months, may have contributed to the more rapid hardening of newly-produced gum at this time of year.

It is also interesting to note that the level of insect attack (estimated by the number of deposits recorded each month) was inversely related to the measured abundance of insects (SRC: $r_s = -0.608$, $n = 13$, $p = 0.027$). This is as would be expected, given both that the traps effectively measured the abundance of mature insects and that immature insects appear to be the chief cause of such damage. Bearder & Martin [1980] found that the majority of the deposits on acacia trees in southern Africa were produced in response to damage caused by coleopteran larvae. Qualitative observations at the FMC study site indicated that coleopterans are also responsible for much of the damage caused to trees at this site. In accordance with this, the number of gum deposits recorded each month shows an even more significant negative correlation with the measured abundance of mature coleopterans (SRC: $r_s = -0.758$, $n = 13$, $p = 0.003$). Similarly, the apparent increase in the production of gum coincides with the decline in the coleopteran population when, presumably, many species are found in their destructive larval form (compare figures 3.13d and 3.17b/c).

Table 3.6

Gum Sites on A. peregrina *Sample Trees, August 1985 to August 1986*

		Number of gum sites recorded on:		
Sample	Number of trees with gum sites	All sample trees	Top 3 trees[1] (% of total)	Top 7 trees[2] (% of total)
August 1985	13	63	24 (38.10)	53 (84.13)
September	13	57	27 (47.37)	48 (84.21)
October	11	44	24 (54.55)	38 (86.36)
November	11	50	29 (58.00)	43 (86.00)
December 1985	11	49	26 (53.06)	44 (89.80)
January 1986	10	64	39 (60.94)	57 (89.06)
February	9	55	30 (54.55)	47 (85.46)
March	9	55	39 (70.91)	50 (90.91)
April	10	60	41 (68.33)	52 (86.67)
May	10	76	43 (56.58)	63 (82.89)
June	12	78	34 (43.59)	62 (79.49)
July	11	70	29 (41.43)	52 (74.29)
August 1986	11	67	29 (43.28)	48 (71.64)
All records:	**18**	**788**	**414 (52.54)**	**657 (83.38)**

[1] More than 100 sites recorded during study period (one seventh of sample trees).
[2] More than 50 sites recorded during study period (one third of sample trees).

As discussed previously, the trees sampled for the measurement of gum production showed a marked loss of leaf cover during the dry season. While this can be linked to the lack of rainfall during this period, given the data from the phenology quadrats, it does seem possible that the damage caused to the sample trees by insect attack had some influence on their leaf loss, although the fact that the degree of loss appeared to be much greater during the second, drier year implies that humidity was the major factor. One further characteristic pattern of this natural gum production by *angico* trees was that a

Plate 5

Adolescent male "Paxo" feeding on the gum of an insect-damaged angico *tree located in quadrat M09 (see fig. 5.1) in May 1986. Note the characteristic thorns clearly visible on the left of the trunk.*

large proportion, usually more than two-thirds, of the sample trees would generally exhibit either a very few gum deposits or none at all, while the remaining trees would contribute the majority of the deposits measured. This pattern was seen throughout this area of the forest, *i.e.* insect damage was minor or absent from the majority of trees while a few exhibited evidence of very extensive insect attack (table 3.6, plate 5). Thus, while large *angico* trees are particularly abundant in this area, it seems that only a small proportion constituted a possible "major resource" for the study group at any one time and that their frequent use of the gum of this species is mostly related to its abundance within its home range in general, and in its core area in particular (see chapter 5).

The records of the abundance of "naturally-formed" gum deposits on the sample of *angico* trees indicate that both the production of gum and the availability of the types of gum usually consumed by the study group increased significantly during the dry season. This increase was contrary to the expected pattern, assuming relatively constant production and the much lower humidity observed during this period. It did, however, correlate with the observed decrease in the abundance of mature insects at the study site, a pattern which would be expected if immature insects were the primary agents causing gum production. This pattern does, however, contrast with that exhibited by *A. karroo* at Mosdene [Bearder & Martin, 1980] which showed no systematic seasonal variation in the production of gum. While the factors involved are probably too complex to be understood without further study, it does seem to indicate the probable variability of these patterns at different sites and/or for different plant species.

Chapter 3

The Ecological Framework

As we have seen, a number of the characteristics of the home range of the study group exhibit important variation. Topographically, the terrain is mostly very steep and altitude varies considerably over short distances. The close proximity of a relatively large body of water, the river Manhuaçú, is also relevant to a number of features, both physical and seasonal. The vegetation, while being patchy throughout, is clearly less disturbed, or more mature, in some areas than in others.

All the ecological variables measured exhibited marked fluctuations through the course of the year. Much of this variation is apparently linked to observed climatic changes, and rainfall levels in particular. Such changes may occur not only between different seasons, but also between years, depending on absolute differences in the climate (and rainfall in particular) from one year to the next. The degree and nature of this variation also seemed to be different in different parts of the forest. These characteristics appear to be closely linked to differences in elevation and humidity. Overall, with the exception of the plant exudate produced in response to insect damage, the group's principal dietary resources were more abundant during the wet season months between October and March than during the dry season months spanning the period from April to September. It also seems possible that a number of resources were exceptionally scarce during the dry season of 1986, including the fruit of plant species whose reproductive output was modified or cancelled by the unusual lack of rain during the preceding wet season months. Similarly, the records from the late dry season months of 1985 hint that the opposite was the case in the previous year, a situation which can be linked directly to the equally abnormal excess of rain during the preceding wet season.

The phenology records show that a small proportion of the marked trees were reproductive and that most of the fruits available were not only inedible for the marmosets but were also mostly ignored by other animals inhabiting the forest (*e.g. Carpotroche brasiliensis*). Two of the most common species (*Allophyllus* and *Siparuna*), however, not only produced fruit or seeds which were edible but were represented by large numbers of reproductive individuals, both in the phenology quadrats and throughout the forest. With regard to fruit, then, there is a very small number of "major resource" species, represented by a relatively large number of individuals which bore mature fruit during a short period of the wet season.

Leaves were more abundant overall during the wet season, although the reduction in leaf cover during the dry season was mainly due to leaf fall at higher, drier altitudes. On the other hand, new leaf production seems to have been greater at higher elevations during the wet season. While these characterisitcs do not directly affect marmosets, many of the insects they commonly prey on are folivorous, and these fluctuations in the abundance of leaves seem to be related to observed fluctuations in the insect population at different altitudes.

Insects of all types and sizes, including those most commonly preyed on by the study group, were also far more abundant during the wet season, and the earlier months in particular, than during the dry season. Insects also appeared to have been more abundant during the dry season of 1985 than they were during the same period of the following year, which again may be linked to the exceptionally humid wet season preceding, and the relative abundance of leaves (and other resources) during, the former period. Insect abundance and diversity at higher altitudes also apparently underwent more extreme fluctuations, which correlate with observed fluctuations in leaf cover and growth. Orthopterans present the most interesting and relevant case here, maintaining a relatively stable population at the lowest elevation, but undergoing major fluctuations at higher levels.

Unlike other variables, the production of *angico* gum in response to insect damage was greatest during the dry season months of May, June and July. This does, however, correspond with the dry season decline in the abundance of mature insects, and, presumably, with an increase in the abundance of immature forms, apparently the main cause of the damage stimulating the flow of gum.

While the abundance of the main types of vertebrate prey (lizards and frogs) consumed by the study group was not measured in any way at the site during the course of the study, it seems possible that this may also have undergone changes during this period (see chapter 6). As vertebrates were the most highly desired food for all group members, it seems unlikely that they would be procured principally as an alternative during periods when insects were scarce. There is also little evidence to suggest that there were changes in the group's foraging behaviour during such periods which would have made the capture of vertebrates more likely (see chapter 7). If these vertebrates were equally abundant throughout the year, on the other hand, the seasonal changes outlined in this chapter may have had an influence on their vulnerability to predation. For example, during the hot wet season when insects are more abundant these vertebrates (lizards in particular) would not only have to spend less time engaged in foraging activities which expose them to the possibility of predation, but would also be more likely to take shelter either from the rain or the relatively hot sun.

Observed differences in the group's predation of vertebrates may also reflect fluctuations in their abundance through time. The life cycle of most frogs and lizards is longer than that of most insects and we might thus expect fluctuations in their abundance taking place over a longer time scale. Most of the lizards eaten by the study group, for example, appeared to be iguanids, which reach sexual maturity, on average, at the age of approximately 15 months [Stearns, 1984]. Many of the species usually captured by marmosets probably reproduce on a more or less annual cycle, corresponding with peaks in the abundance of insects. Relatively large vertebrates would in this case be more abundant later in the year, during the dry season, and would also, for the reasons outlined above, be more vulnerable to predation.

In addition, the relatively high levels of rainfall during the 1984/85 wet season and the probable super-abundance of insects during this and the following period may have led to greater reproductive success for, and a greater abundance of, most of these small vertebrate species. In this case, relatively large numbers of individuals would have reproduced during the 1985/86 wet season leading to an abundant population which would then have been faced with an increasing scarcity of insect prey from the beginning of the dry season onwards. During the 1986 dry season, then, the study group would have encountered an abundant vertebrate population facing, like itself, increasingly serious shortages of insect prey. These small vertebrates would thus have been not only relatively abundant, but also more vulnerable to predation through their loss of physical condition, the relative paucity of protective leaf cover throughout much of the forest, and so on.

To conclude, the study of ecological variables indicates that there were considerable variations in the availability of the study group's principal resources during the course of the study year. Fruit (edible fruit in particular) was, in general, relatively scarce except in the mid wet season and, assuming that some vegetable material is an obligatory component of marmoset diets, we would expect exudates to have been an important resource for the study group throughout most of the year. While able to induce exudate flow themselves, the study group also consumed large quantities of gum produced naturally by plants (particularly *angicos*) in response to insect damage. Estimates of the availability of this gum indicate that it was more abundant during the dry season months. The abundance and diversity of arthropods also varied considerably, both through time and in space, and seemed to correlate both with humidity and leaf production, particularly in the case of those types most commonly preyed on by the study group. The results suggest that the group was faced not only with a scarcity of arthropod prey during the dry season, but also with more marked differences in its distribution.

As well as directly influencing its foraging behaviour, the observed variations in the abundance of the study group's resources, in both time and space, have wider implications for many aspects of its behaviour, including reproduction, territoriality and group stability. In the following chapters, the results of the complementary studies of ecological variables presented here will be drawn on for the analysis and interpretation of the behavioural data.

Summary

A detailed description of the study area and of the complementary study of ecological variables is presented. The latter has outlined the major temporal fluctuations in the abundance and distribution of the study group's principal dietary resources. These fluctuations are most apparently linked to seasonal changes in climate, especially rainfall. The major findings are as follows:

1. The main study area is a steeply-sloping hillside bordering a river. The vegetation consists of heterogeneous secondary forest approximately 25 years in age. The area to the north is dominated by large *Anadenanthera peregrina* trees and is characterised by a higher frequency of climbing plants than the area to the south whose vegetation seems, on the whole, to be slightly less disturbed. Trees at higher altitudes are generally smaller than those lower down, a feature which is characteristic of the forest at FMC and indicates, along with complementary observations, a gradient of humidity falling from east to west from the river to the higher altitudes.
2. The climate at FMC shows a marked division between a period of hot, wet weather occurring between the months of October and March in most years and a cooler, markedly dry period between April and September. The climate during the main study period was characterised by exceptionally low levels of rainfall during the wet season, and during the months of February, March and April in particular. During the previous year, however, the weather was abnormally wet, this seems to have had a number of influences on the variables measured and, in turn, on the study group's behaviour.
3. A small proportion of the trees of most species in the phenology quadrats bore fruit during the study period, and more than half of the species recognised did not produce fruit. In addition, most of the types of fruit observed were judged to be inedible for marmosets. Fruit was most available during the main wet season months. There is some indication that the level of fruit production between February and May was lower than in average years, and that the maturation of much of the fruit that was produced was delayed or halted. This was thought to be linked to the abnormally low levels of rainfall during the late wet season months.
4. Leaf cover in the phenology quadrats underwent marked changes during the course of the year. It was most sparse during the late dry season and

densest towards the end of the wet season. The results indicate that leaf fall was greater during the 1986 dry season than during the previous year, although this was principally in the quadrats at higher altitudes. Quadrats at lower altitudes were more stable throughout the year. The production of new leaves was most marked during the early wet season months in all quadrats, but was more sustained in the quadrats at higher altitudes.

5. Arthropods of all types were considerably more abundant during the wet season than during the dry. As for the other variables, it seems likely that insects may have been less abundant than usual at the end of the wet season and in at least the earlier part of the following dry season. Populations at lower altitudes were both more abundant throughout most of the study period and more stable than those at higher elevations. The abundance of the types of insect most commonly preyed on by the study group correlated well with humidity and leaf cover, both through time and in different areas of the range.

6. The production of gum by *A. peregrina* trees in response to damage caused by insects increased during the dry season, correlating with an assumed increase in the abundance of immature insects, given the observed decrease in the abundance of mature forms.

7. The results of these complementary studies also suggest that the small vertebrates most commonly preyed on by the study group were both unusually abundant during the 1986 dry season, and facing a critical scarcity of resources.

4

Activity patterns

The main factors constraining the activity patterns of an animal species are its size and its diet. These features are usually closely inter-related. Most mammalian obligate insectivores (except those specialised for feeding on social insects), for example, weigh less than 100 g [Emmons *et al.*, 1983], while strictly herbivorous mammals are generally much larger. The primate order as a whole exhibits a gradation from small, highly insectivorous forms such as the tarsier to the large herbivorous gorillas, with the proportion of animal (essentially arthropod) material in the diet being inversely related, in general, to body size [Gautier-Hion, 1978; Hladik, 1979; Kay & Simons, 1980]. These characteristics seem to be related closely to such features as social organisation and life history strategies [Clutton-Brock, 1974b; Harvey *et al.*, 1987], as well as to activity patterns [Clutton-Brock & Harvey, 1977a, 1977b, 1983]. This gradation is also reflected within the platyrrhines in general [Terborgh, 1983] and at FMC, where the relatively large, herbivorous *Brachyteles* and *Alouatta* exist alongside the smaller, more omnivorous *Cebus* and *Callithrix*.

Cebuella pygmaea, the smallest marmoset is, at 100 to 120 g, larger than most obligately insectivorous mammals and, as we might expect from body size alone, no callitrichid species appears to be wholly insectivorous. We would also expect, in general, that the larger species would be, proportionately, the least insectivorous, although there are too few data, at present, to uphold such an assumption with certainty (the situation is complicated by the gum-feeding specialisation of the marmosets). However, there is good evidence from two studies of sympatric primate species [Charles-Dominique, 1974, 1977; Terborgh, 1983] that obtainable arthropod prey increases negligibly, and far less than metabolic requirements, as primate body size increases [see also Kay & Covert, 1982]. For animals utilising similar foraging techniques in the same habitat, the time spent foraging for insects would thus have to increase at a rate approaching the three quarters power of that of any increase in body weight [*cf.* Kleiber, 1961] in order to maintain the insect proportion of their diets. In practice, most larger species seem to spend relatively more time both foraging for insects and feeding on plant material, with the net effect of reducing the proportion of animal material in their diets.

The results of Terborgh's study are perhaps the most relevant to the present discussion. There is a relatively clear-cut division between the two tamarin species and *Cebus* and *Saimiri*, in terms of the proportion of the activity budget devoted to insect foraging. In addition, while the larger *Saguinus imperator* (body weight *ca.* 500 g) devoted 34% of its time to insect foraging, the smaller *Saguinus fuscicollis weddelli* (body weight *ca.* 400 g) spent only 16% of its time in this activity. The difference between these values is possibly exaggerated by the behavioural sampling methods used. The more concentrated bursts of foraging characteristic of *S.f.weddelli* may have led to this type of activity being less well represented, in the data than the more continuous foraging behaviour of *S. imperator*. Despite this possible bias, the data clearly demonstrate the degree of variation that can occur between similar species inhabiting the same environment and feeding on the same types of prey. Some of this difference may be accounted for by the respective sizes of the two species, but much more is probably due to differences in foraging behaviour (both in absolute terms, and with observational bias in mind).

It is interesting to note that the foraging behaviour of *S.f. weddelli* at Manu seems to be different from that recorded at two other sites where this species is sympatric with other callitrichids. Pook & Pook [1982] found that a group of *S.f. weddelli* in Bolivia formed mixed associations with both *Saguinus labiatus* and *Callimico goeldii*. In this case, *S.f. weddelli* foraged in dense vegetation, primarily at levels of between 5 and 10 m (corresponding with *S. imperator* at Manu), while *S. labiatus* tended to forage at higher levels, and *C. goeldii* lower down. Castro & Soini [1978] also report that *Saguinus fuscicollis nigrifrons*, in northern Peru, travelled and foraged at lower levels than *Saguinus mystax*.

In addition to differences constrained by body size and attributable to different foraging strategies, the abundance of dietary resources, both in space and through time, will have a major influence on the activity patterns exhibited by a primate species during any particular period. It seems that body size may again be the major factor influencing strategy choice, in particular during periods when resources are scarce. When food is difficult to obtain, animals may spend more time resting or sleeping (or even hibernating), or devote relatively more time to foraging and/or broaden the variety of foods included in their diet. With their relatively higher metabolic expenditure and proportionately smaller reserves of fat [Calder, 1984], small animals are, in general, both relatively less resistant to periods of scarcity than larger animals and less able to make use of the less nutritious resources utlised by larger animals. In general terms, therefore, we would expect smaller animals to be less likely to follow a strategy of reducing activity during periods of resource scarcity than larger ones [Harvey, 1985]. This has been shown to be the case for shrew species of different sizes [Hanski, 1985]. In an experiment where individuals of the smaller species *Sorex minitus* and *Sorex caucutiens* increased their activity in response to food deprivation, individuals of the larger species *Sorex araneus* and *Sorex isodon* increased the amount of time they spent resting.

A study of two closely related prosimian species found in similar habitats in southern Africa and feeding on virtually the same diet of *Acacia* spp. gum and insects also reported marked interspecies differences in behavioural responses to periods of scarcity [Harcourt, 1980, 1986]. Much of the observed differences appear to be attributable to differences in the body sizes of the two species. *Galago senegalensis* weighs *ca.* 200 g while *Galago crassicaudatus* may weigh as much as 1800 g [Harcourt, 1986]. During the hot, wet summer, when insects were judged to be significantly more abundant and acacia gum more edible at both study sites, a relatively small proportion of the total activity time of both species was spent searching for and feeding on gum. During the dry winter period, however, the two species greatly increased both the amount and proportion of their time devoted to these activities.

Seasonal variation in the insect-foraging behaviour of the two species was, however, very different. The *G. senegalensis* individual studied reduced the time she spent insect foraging and feeding only very little during the winter. In contrast, the *G. crassicaudatus* individual greatly reduced the proportion of time spent in these activities, from 35% in summer to 1.5% in winter. Estimates of prey ingested, calculated from faecal samples, show that the quantities of prey consumed by *G. senegalensis* changed very little between the summer and the winter (111 and 97 "units", respectively) while the amount of prey consumed by *G. crassicaudatus* during the winter was greatly reduced, from 525 to 95 "units". Both species preyed on much larger arthropods during the summer. However, while *G. crassicaudatus* took significantly larger prey than *G. senegalensis* during the summer, there was no difference in the size of their prey during the winter. It also seemed, from an analysis of the types of arthropod preyed on, that both species were being far more selective of their prey during the summer.

Overall, given that there may be differences between the study sites [see Harcourt, 1986, for discussion], the results show that markedly different strategies were adopted in response to the annual period of resource scarcity. The larger *G. crassicaudatus* was able to follow a strategy in which it concentrated on gum feeding and reduced other activities (including insect foraging) to a minimum, without suffering weight loss. Under similar conditions, the optimal strategy for *G. senegalensis* seemed to be both an increase in gum feeding and the maintenance of its insect-foraging activities. Observations of *G. senegalensis* by Bearder & Martin [1980] at the same site during a much colder winter support this. In this case, *G. senegalensis* was apparently forced, by a much greater reduction in insect availability, to adopt a strategy involving an increase in both gum feeding and rest, similar to that of *G. crassicaudatus*. Unlike the latter, however, this strategy involved a marked loss of condition and body weight for the smaller species.

The forest at FMC, as we have seen, is also subject to marked seasonal changes during the course of the year, although probably less severe than those at the bushbaby study sites in southern Africa. These changes are reflected in significant fluctuations in the abundance of the principal resources used by the *Callithrix flaviceps* study group (chapter 3). The larger primates at FMC, *Brachyteles arachnoides* and *Alouatta fusca*, both include significant proportions of new or mature leaves in their diets during the dry season or at other times of the year when fruit is scarce [Mendes, 1985; Strier, 1986]. *C. flaviceps* is unable to do this and must, like the bushbabies, subsist on a diet of insects and gum. Unlike the prosimians, however, *C. flaviceps* is able, with its specialised dentition, to induce regular flows of fresh gum throughout the dry season. It is also likely, given the relatively milder climate at FMC, that insects are more abundant during the dry season than during the winter at either of the bushbaby study sites. Nevertheless, the degree of seasonal change, and dry season scarcity of resources in particular, facing the marmosets at FMC is probably more similar to that encountered by the two prosimians than by the only other marmoset which has been the subject of a long term study, *Callithrix humeralifer intermedius*, at Aripuanã [Rylands, 1982]. Thus, while we would expect most aspects of the behavioural ecology of *C. flaviceps* to be similar to those of *C.h. intermedius*, we might predict, given the similarities of their diets, that *C. flaviceps* follows similar feeding strategies to those of the bushbabies during periods of scarcity.

With a body weight of approximately 350-400 g, *C. flaviceps* is intermediate in size between the two prosimians, although much more similar to *G. senegalensis* than to *G. crassicaudatus*. From this, we would predict that *C. flaviceps*, like *G. senegalensis* and most other small-bodied mammals, should be less able to follow a strategy of reducing activity during periods of resource scarcity than larger animals utilising similar diets. Such a comparison is not necessarily straightforward, however. In addition to possible metabolic adaptations (see chapter 1), energy-saving strategies such as the characteristic night-time huddle are more effective for the more gregarious marmosets. The fact that bushbabies are inactive during the warmer daylight period may also have certain implications. It is clear that a number of factors must be taken into account in making comparisons or predictions, but the results of the bushbaby study will form a useful frame of reference for the present analysis of the activity patterns of the *C. flaviceps* study group.

The Time Budget of the Study Group

The annual time budget recorded for JG1 falls within the range of values recorded for most behaviours in similar studies of other marmoset and tamarin species (table 4.1). Most of the quantitative studies of marmoset and tamarin species have utilised different sampling methods to collect data on groups of different compositions in a variety of habitats, so detailed comparisons are obviously subject to a number of possible random influences and biases. In addition to differences in the methods used, there may be considerable differences between studies in the nature and degree of observational bias operating on behavioural observations (see chapter 2). In the case of the *C. flaviceps* study group, it seems likely that behaviours which are relatively less visible at higher levels in the forest are over-represented in the data, in comparison with most other studies. The actual period of JG1's activity was also much shorter, on average, than those of other species, so that comparable proportions refer to shorter absolute periods of time. While these sources of possible bias must be kept in mind, the general patterns of activity exhibited by the study group do seem similar enough to those reported in other studies to allow broad comparisons to be made.

Table 4.1

Activity Budget of the C. flaviceps *Study Group, August 1985 to August 1986*

Activity	Scan sample records	Percentage of total records
Feeding on animal material	1884	2.66
Feeding on plant material	7537	10.65
Insect foraging	17060	24.10
Resting	17582	24.84
Travelling	18529	26.18
Miscellaneous[1]	8192	11.57
Total	**70786**	**100.00**

[1] Including all social and scent-marking activities.

Overall, during the course of the study period JG1, like most other callitrichid groups, spent a relatively small proportion (26.76%) of its daily activity period engaged in insect foraging and feeding, and a relatively large proportion resting (24.84%). One major influence on the comparability of the data is the relatively large proportion of the study group's time spent in "miscellaneous", predominantly social, activities. Many of these activities, such as allogrooming and play, are indicative of rest, and have been included in this category in other primate studies [as they are, for example in Rylands, 1982]. The fact that the group seemed to spend a relatively large proportion of its time travelling (26.18%) is somewhat equivocal as records show (see table 1.2) that it ranged over very similar, if not shorter distances daily than other species (except *C. jacchus*). This may partly be accounted for by the shorter daily activity period of *C. flaviceps*, although Terborgh's study shows that records of ranging and travelling time are not necessarily comparable, even when the same methods are applied to groups of similar size inhabiting the same environment. Thus, while the mean daily path length of *S. imperator* was more than 15% longer than that of *S.f. weddelli*, the former spent only 5% more of its activity time travelling (note, however, that their daily activity periods may be different).

The most appropriate data for direct comparison with the present study are those available for *C.h. intermedius* [Rylands, 1982]. However, while the observational methods used in the two studies were similar, there is good evidence to suggest that differences in observational bias may have been as important a determinant of most observed differences (and the degree of these differences in particular) between the two studies as more fundamental ecological differences. As the same sampling schedule was used (chapter 2), we would expect, other things being equal, the number of records collected to have been roughly similar. A comparison of the two studies shows, however, that far more records were collected during scan samples in the *C. flaviceps* study than in that of *C.h. intermedius* (77.5% more, on average, per scan sample, see appendix III). This contrast cannot be accounted for by differences in the size of the study groups as that of the former was, on average, only 5.6% or 0.7 individuals larger than that of the former. There seems to be little doubt, from this comparison, that there were very marked differences in the visibility of group members at the two sites. The most important factor seems to have been the structure of the forest habitat and the levels utilised by the two study groups.

As discussed in chapter 2, the height above the ground of an arboreal primate has a considerable effect on its visibility. This is particularly the case for activities which involve little or no movement, such as prey feeding or rest (and associated social activities such as allogrooming). When engaged in the former activity, in fact, marmosets may attempt to minimise their conspicuousness in order to avoid the attentions of other group members

[Ferrari, in press]. The *C.h. intermedius* study group utilised an area of mixed primary and disturbed primary forest whose canopy and equivalent strata were, on average, much further above the ground than those available within the home range of the *C. flaviceps* study group. While both groups preferred relatively lower levels in the forest than most other primates, such levels were considerably higher above the ground, in absolute terms, for *C.h. intermedius* (see appendix III). While the latter spent a majority of its time at between 8 m and 15 m above the ground, JG1 spent 67% of its time at or below 5 m. At low levels in dense vegetation, in fact, a stationary animal may be at least as visible as one which is moving, if not more so in some cases, and there may even have been, in fact, some relative bias *towards* the recording of rest and social activity in the *C. flaviceps* study.

It seems very likely, therefore, that the observational biases operating were very different, if we assume that the discrepancy between the numbers of records collected in the two studies is directly related to the different heights at which the two groups were normally active. While it is not possible, or necessary in this context, to judge which study produced the better estimate of activity budgets, the evidence suggests quite clearly that there was a significant difference between them in the propensity for different types of behaviour to be recorded. As these budgets are based on the proportions of total activity time devoted to different behaviours, a bias against the recording of one category will increase the values recorded for others. In this case, if the levels of resting and social behaviour were under-estimated in the *C.h. intermedius* study relative to that of *C. flaviceps*, others, foraging and travelling in particular, would have been overestimated.

One piece of evidence which does support this comes from a closer analysis of the movements of the two groups. The average path length of the *C.h. intermedius* study group is estimated [from monthly averages given in Rylands, 1982] to have been 1450 m, approximately 18.5% larger than that of the *C. flaviceps* group (table 1.2). The former also utilised a proportionately larger area each day, on average (see chapter 5). Given both that the methods used in the two studies were the same and that the daily activity periods of the two groups were relatively similar (see below), we would expect the difference in the proportion of time devoted to travel each day by the two groups to be roughly similar to that of the difference in path length *i.e.*

between 15% and 20%. However, while the *C. flaviceps* group spent 26.18% of its time travelling, on average, each day, *C.h. intermedius* spent 38.26% of its time in this activity, a difference of 46%, more than two and a half times that expected. As foraging activities are normally associated with travel, it seems reasonable to assume that this category was also over-estimated for *C.h. intermedius* relative to *C. flaviceps*.

Despite the similarities of the methods used, then, some caution is required in the comparison of these two studies. While it is likely (according to path length values) that the *C.h. intermedius* study group spent more of its time travelling than the *C. flaviceps* group, the degree of difference apparent between the two studies is probably exaggerated. If the same degree of exaggeration applies to foraging behaviour, the *C.h. intermedius* group would have actually spent less of its time foraging for insects than JG1. According to the evidence, the opposite may have been the case for rest, social activities and prey feeding. Only the values recorded for plant feeding, based on the months during which fruit was a significant component of the *C. flaviceps* group's diet (see below), appear to be consistent with those recorded in other studies [*e.g.* Rylands, 1982; Terborgh, 1983].

Even if we ignore such bias, *C. flaviceps* and *C.h. intermedius* are more similar to each other in the proportion of their time spent foraging each day than either is to *S. imperator*. The fact that the latter spends a good deal more of its time foraging is as would be expected according to respective differences in body size, given that all three species utilise reasonably similar "scan-and-pounce" foraging techniques. *S.f. weddelli* is excluded from this comparison because of its different technique which, as we have discussed, may also be subject to bias in comparison with the others. The other primate in Terborgh's study which forages in a roughly similar way, although it "gleans" rather than "scans", is *Saimiri sciureus*, approximately twice the size of *Saguinus imperator*. As we might expect, this species spends a much greater proportion of its time foraging for insects [Terborgh, 1983], although this may also be related to other factors, such as differences in prey size (see chapters 1 and 6).

In addition to spending a greater proportion of its time in foraging activities, *S. imperator* also devotes approximately 50% more of its budget to feeding on plant material than *C. flaviceps*. The proportion of time spent in this activity by*S.f. weddelli* is very similar to that of its congenor, as is that of *C.h. intermedius* (17.49%). While *C. flaviceps* did feed predominantly on gum rather than fruit, it seems that the characteristics of the typical plants used, *i.e.* common species providing "piecemeal" resources, permits a direct comparison between these species. As expected, then, the larger species devote more of their time to feeding on plant material. In contrast, however, *Saimiri sciureus* devoted much less of its time to plant feeding than either of the tamarins at Manu, or *C.h. intermedius*. This may be accounted for by the fact that *Saimiri* exploits very different types of resources, their visits to large *Ficus* trees presumably being equivalent to and subject to the same biases, in terms of the sampling methods used, as the foraging technique of *Saguinus fuscicollis*.

Activity Budget by Season

As FMC lies almost 20° south of the equator, it experiences differences in day length of almost two hours during the course of the year. Unlike other primates, but like most callitrichids, the *C. flaviceps* study group was active during a relatively short period each day at all times of the year. The group was usually active at between ten and thirty minutes after full light, unless it was raining, in which case the start was delayed for anything up to one hour (and even more than this, on two occasions). At the end of the day, the group would usually retire to a sleep tree between one and two hours before dusk, and even earlier than this on many days (retiring before 14:00 on one occasion). Activity would often start relatively later on cold mornings, and the group did, in general, roost earlier during the dry season. Thus, while not directly correlated with the difference in day length between seasons, the average period of daily activity during the dry season (9 hours and 14 minutes) was more than 10% shorter than during the wet season (10 hours and 21 minutes).

While the fact that *C. flaviceps*, like other marmosets, is particularly sensitive to extremes of temperature may account for the group's shortened activity periods during the cooler dry season, it is not absolutely clear why the activity period was not increased more than it was during the hot wet season. As discussed in chapter 1, the idea that the daily activity cycle of callitrichids is closely related to the vulnerability of their large-bodied prey [Dawson, 1979] is not supported by most other detailed studies. The foraging activities of most species appear to remain at more or less constant levels throughout the day and may even, in fact, peak in the late afternoon rather than in the early part of the day. While Dawson's argument may still be partly valid, it does seem that other factors are involved.

Rylands [1982], on the other hand, proposed that, as many of the types of insect most commonly preyed on are nocturnal, the marmoset activity cycle is scheduled to coincide with the diurnal period of inactivity of these insects. Dawson's own data [in Garber, 1984a] show, in fact, that the insects consumed most commonly by *S. geoffroyi* were large grasshoppers of the family Tettigonidae, which are uniformly nocturnal and mostly rely on camouflage to escape predation. Large, diurnal grasshoppers (Acrididae) were, however, also frequently consumed both by *S. geoffroyi* [Garber, 1984a] and the *C. flaviceps* study group.

Here again, the size of the primates themselves is probably one very important factor. As we have already discussed, smaller primates are relatively more efficient at foraging for insects, in relation to their dietary requirements, than larger ones. Callitrichids also generally capture much larger insect prey than the larger-bodied cebids. The former may thus be able, during periods when insects are super-abundant, to capture prey well in excess of their minimum dietary requirements, particularly if some plant material is a necessary component of the diet. While this does not present a particular problem, they are unable, because of their small body size, either to ingest relatively large amounts of food during the course of a single day or to accumulate significant reserves of fat. As the capture of prey seems to require, on average, the expenditure of more energy than most other activities, a point must be reached when returns to continued foraging are, at best, nil. This would especially be the case if, as Dawson suggests, insects are less easily captured later in the day. Feeding on plant material (particularly fruit, when available) may then offer better "returns" than insect foraging and rest, with the possibility of saving energy, may be more rewarding. Overall, then, when

Figure 4.1

Seasonal Variation in the Activity Budget of the Study Group

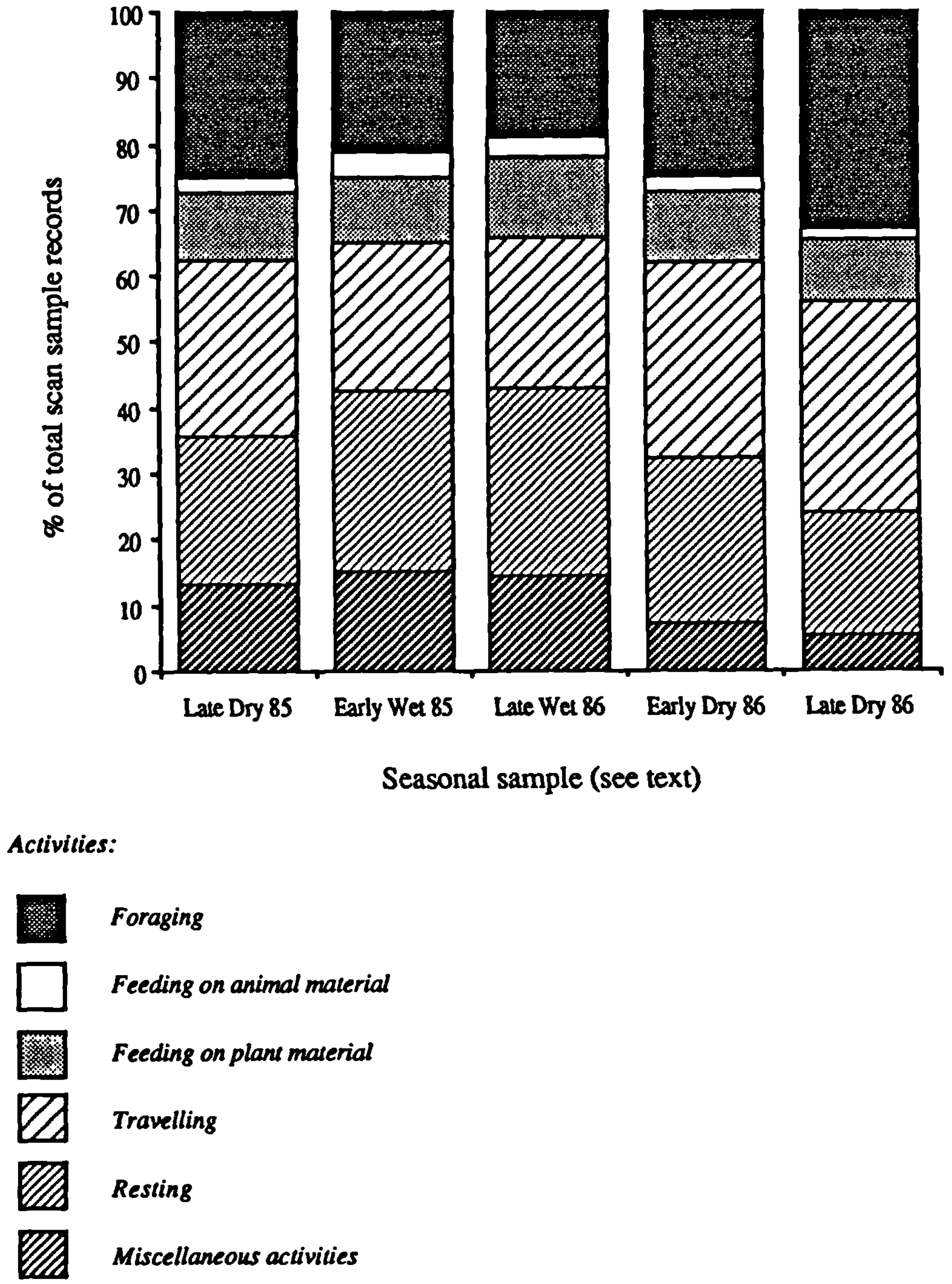


Figure 4.1 presents a comparison of the activity budgets of the study group during the five main seasonal divisions covered by the study period. Values are the percentages of total scan sample records attributed to each behaviour.

insects are abundant, we might expect an early cessation of activity preceded by a peak in feeding on plant materials, with a concomitant reduction in insect foraging.

In this context, the typical wet season activity period can be seen as being too long rather than too short, especially as a one to two hour period of inactivity, or siesta, is commonly taken during the middle of the day, and rest may take up a large proportion of the total activity period. It has been generally assumed [*e.g.* Dawson, 1979; Stevenson & Rylands, in press] that the relatively high ambient temperatures and intense sunlight at midday effectively prohibit activity during this period, but these siestas may also be, in part, another concession to small body size and the inability to ingest large quantities of food during a short period. JG1 exhibited a marked variability in the timing of its daily siesta during the hot wet season months, which suggests that the avoidance of the more intense midday heat is not necessarily the major influence on this type of behaviour. If siestas are also seen as a necessary break from foraging activities, a number of possible influences can be identified. One of these may be motivational, *i.e.* a relatively full marmoset may be far less motivated to pursue additional prey, especially in high temperatures. Their relatively small gut volume would also be important here [Calder, 1984]. It is possible that the concentration of foraging into a shorter continuous period followed by an even earlier cessation of activity is either not feasible, or is not the most effective strategy. Such strategies would also be dependent on the vulnerability of insect prey, and suggest that insects would not be significantly less vulnerable to predation during the later, hotter parts of the day. The relevant data, and the study group's prey feeding in particular, will be analysed in more detail in both this and the following chapters.

Bearing in mind the absolute differences in the length of the study group's daily activity period during different seasons, a number of patterns are evident (figure 4.1). In general, the group's activity in the wet season is marked by a relatively high proportion of time spent resting and socialising (essentially play and allogrooming), and a relatively small proportion spent insect foraging and travelling. In the dry season, the opposite trends are apparent. The group spent far more time insect foraging and travelling, and far less resting. The proportion of the group's time spent feeding on insects was also 65% greater during the wet season than during the dry. In contrast to other activities, however, the proportion of its time spent feeding on plant material is remarkably constant throughout the year. The only real deviation from this trend came during the months of January and February, when fruits and seeds contributed more than 50% of feeding records (see chapter 6). In these two months, feeding on plant material accounted for 13.5% of the group's activity whereas it consituted between 9.7% and 10.4% during all other periods of either the wet or the dry season.

Analysis of these results must also take differences in the length of the daily activity period into account. The average period during the wet season was 1 hour and 7 minutes, or 12%, longer than during the dry season, so similar proportions actually represent slightly different periods of time, in absolute terms, during these two periods. The actual period of time spent plant feeding during the wet season was thus greater, on average, than during the dry season, even if we exclude the exceptional months of January and February. Similarly, the difference between the two seasons in the actual amount of time spent in miscellaneous activities and feeding on prey is greater than the difference between their proportions suggests. The difference in the actual amount of time spent foraging and travelling in the two seasons is, on the other hand, not as great as suggested by the time budget data. Despite this, it still seems possible to state that the group spent approximately 20% more time travelling and 25% more time foraging during the dry season.

Rest is a somewhat equivocal category, because the shorter the daily activity period, the longer the period of inactivity between days, *i.e.* when the group is in its sleep tree. If we assume that it spends 100% of its time resting during this period (not strictly true as some grooming, at least, probably does take place) we may calculate the amount of time spent at rest each day directly from the activity budgets. This gives a period of 16 hours and 31 minutes at rest each day during the wet season and 16 hours and 46 minutes at rest each day during the dry season. In absolute terms, then, it seems that group members spent a roughly similar amount of time at rest during each 24-hour period in the two seasons. While a similar amount of time was spent at rest each day throughout the year, a greater proportion of this rest took place during the active period in the wet season. The relative increase in daytime resting and related social activities is, in fact, much greater than the increase in the daily activity period, which in turn relates to the reductions in the time spent both foraging and travelling, either in absolute or in relative terms.

Looking at the data in more detail, further trends are apparent. The group devoted the smallest proportion of its daily activity to foraging during January and February (table 4.2), the only months in which fruit was consumed in large quantities. Prey feeding also decreased relative to the previous wet season months, correlating with the decline in measured abundance. As the average daily activity period decreased by more than 20 minutes between the early and late wet season samples, these reductions also represent decreases in the actual amount of time spent in these activities. Feeding on plant material, on the other hand, took up more of the group's activity budget during January and February than in the other wet season months except November (the only other month during which fruit made up more than 10% of the group's diet). While this was partly due to the increased consumption of reproductive plant parts, it was also due to the fact that the group reduced their consumption of gum by a relatively small degree.

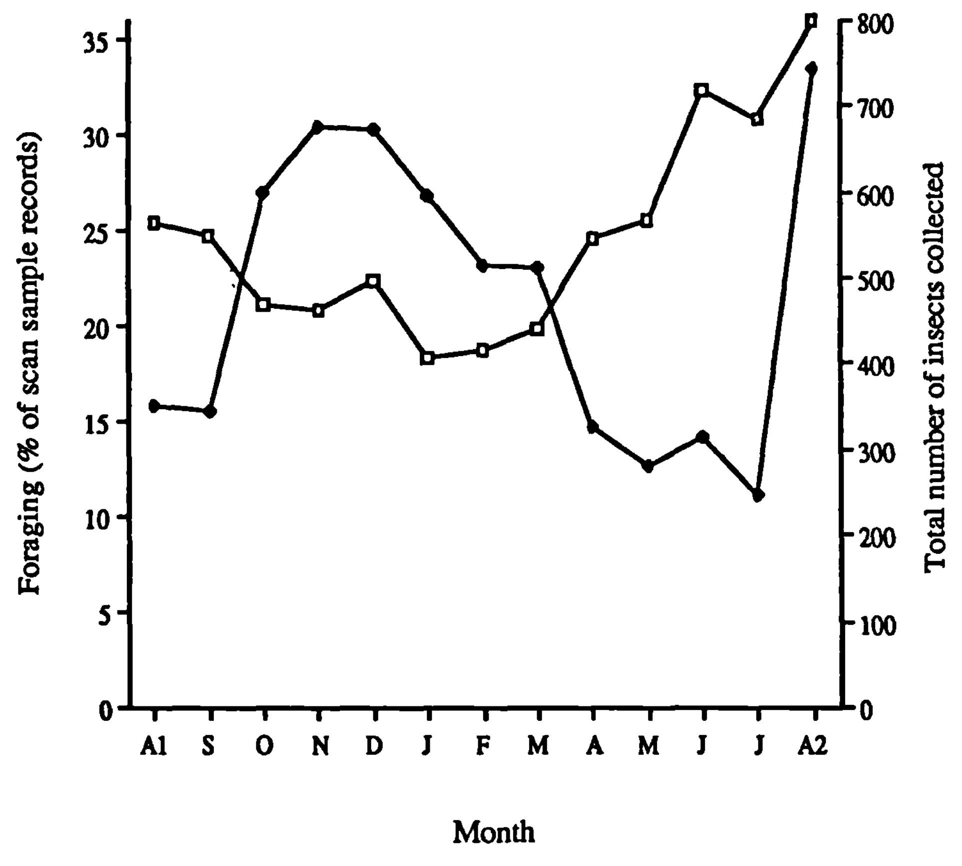
Table 4.2

Monthly Activity Budgets of the C. flaviceps *Study Group*

	Percentage of total monthly scan sample records:						
	Feeding on:						
Sample	Plant material	Animal material	Insect foraging	Resting	Travelling	Miscell-aneous	*N*
August 1985	9.59	2.15	25.38	22.80	25.06	15.02	4421
September	10.89	2.55	24.70	22.49	27.83	11.54	4740
October	8.40	2.95	21.13	29.22	22.02	16.28	6095
November	11.84	4.31	20.75	25.88	23.33	13.89	6129
December 1985	9.01	4.18	22.45	26.49	22.37	15.50	4851
January 1986	15.84	3.33	18.38	26.18	20.46	15.81	6192
February	11.15	2.50	18.75	28.52	21.95	17.13	6374
March	10.06	2.86	19.85	29.38	25.39	12.46	6301
April	10.43	2.05	24.58	26.20	28.12	8.62	5953
May	11.12	2.25	25.64	24.16	31.27	5.56	5737
June	7.78	1.92	32.46	18.79	31.96	7.09	5370
July	12.54	1.29	30.88	20.02	31.26	4.01	4786
August 1986	8.16	1.38	35.99	15.82	32.66	5.99	3837
Study period:	**10.65**	**2.66**	**24.10**	**24.84**	**26.18**	**11.57**	**70786**

Figure 4.2

A Comparison of the Monthly Variation in the Study Group's Foraging Behaviour and the Abundance of Insects



Key:

☐ *Insect Foraging*

◆ *Insects Collected*

Figure 4.2 compares monthly variation in the intensity of the study group's foraging activities and insect abundance, as recorded in the traps. The values for foraging behaviour are percentages of the scan sample records collected each month. Values for insect abundance are the total numbers of insects of all sizes collected.

Looking at the year as a whole (figure 4.2), we see that the group's insect foraging was inversely related, in general, to the measured availability of insects, while its prey feeding was directly related. In other words, the group devoted more time to foraging when insects were less abundant, but nevertheless captured less insects. While insect abundance declined during January and February, however, the group both foraged less and was less successful (note that March was more similar to the early wet season months). This would not be expected for a number of reasons, not least that twins were born into the group towards the beginning of the first of these months, an event which has the effect of increasing the group's total dietary requirements relative to its ability to forage. As insects were still reasonably abundant, in comparison with the dry season months, we would have expected the group to have at least maintained the foraging levels of the previous months. It seems likely, therefore, that the edible fruits and seeds which became abundant during this period constituted a partial alternative for animal material. Despite the fact that the fruits concerned were both extremely abundant and not utilised by other animal species, gum remained an important component of the group's diet (35.27% of the plant material consumed during January and 47.26% during February). While motivational factors may have been involved [see *e.g.* Wirth & Buselmaier, 1982; Kirkwood, 1983], the mineral-balancing function of the gum may have been equally important (see chapter 6).

In addition to differences between the two main seasons, differences between the dry season period of 1985 and that of 1986 are also apparent. August and September are at the end of the dry season period, as defined in chapter 3. It seems, from the results of the complementary studies of ecological variables, that the late dry season is the period during which the majority of resources are least available. While insects may be least available during the month of June, the coldest month in most years, this may be linked more to a reduction in their activity than of their abundance.

For the analysis of the group's activity patterns during the 1986 dry season, June is grouped with July and August as the late dry season period on the grounds of a number of similarities which are not shared with the previous months of April and May. The fact that the group also lost a number of its members at the beginning of June (see chapter 2) also makes it more comparable with the following months than with the preceding period.

Overall, we would, with caution, expect the activity patterns during the late dry season samples of both 1985 and 1986 to be reasonably comparable, assuming that the group was faced with a similar abundance of resources during the two periods.

The data analysed in chapter 3 show, however, that resources were not equally abundant during the dry seasons of the two years. In 1986, the relatively low levels of rainfall during the wet season, in particular the later months, seem to have led to a relative scarcity in the abundance of resources during the dry season of that year. Whether resources were significantly less abundant than average during this dry season is not known. Observations during June and July 1985 indicate that edible fruits were equally scarce and as rarely consumed by the group during this period as in the same period of the following year, so they appear to be comparable in this sense. We can see this lack of fruit in its diet during this and other periods as being the normal situation both for this group and, seemingly, for most other *C. flaviceps* groups at FMC. The relative abundance of gum is less easily assessed but, while the proportions of gum from different sources in the group's diet may have changed, it seems unlikely that the consumption of gum would have been affected by changes in its abundance (due to the super-abundance of *Acacia paniculata*). The amount of gum consumed may, however, be related to other factors, such as its composition. It may also be an alternative resource when others are scarce [Harcourt, 1986].

It is with regard to the abundance of insects, then, that we might expect the most significant differences between the group's activities patterns during the two periods. Apart from the small dipterans collected in August 1986, the abundance of insects during the late dry season of 1986 appears to have been much lower than it had been during the equivalent period of the preceding year. In accordance with this, the proportion of the group's time spent feeding on animal material was also much lower (1.6% as against 2.4%). The average daily activity period was only negligibly shorter during the late dry season of 1986 (by 3 minutes, or less than the period separating two scan samples), so these percentages are directly comparable. The proportion of time spent feeding on insects was in fact even lower, as a larger proportion of the group's prey was vertebrate (43.1% in 1986 compared with 12.6% in 1985).

The relative scarcity of insects is thus reflected in and confirmed by the group's consumption of animal material during this period. How, then did it react to this scarcity? As we have seen above, it spent more time foraging and travelling during the dry season months as a whole than during the wet season. As insects became progressively scarcer through the course of the 1986 dry season (according both to the numbers trapped and the group's prey feeding), the time spent foraging each day increased (figure 4.2). In July and August, 1986, an average of only 4 records of feeding on insects were collected in scan samples per day. This average was 8.3 records per day in August 1985, for the same number of independently-locomoting individuals, and activity periods of similar length. The consumption of vertebrates shows the opposite trend, but they were much less frequently consumed, overall, so that there were still almost 45% more records of prey feeding per day during August 1985 than during the same month of the following year (9.5 and 6.6 respectively). A comparison of the prey-feeding records between the two late dry season periods as a whole shows a similar contrast, with an average of 0.95 records per (independently-locomoting) individual per day during August and September 1985, and 0.67 records per individual per day during the period June to August 1986.

Table 4.3

Seasonal Variation in the Foraging Success of the Study Group

Sample	Percentage of total scan sample records: Insect foraging	Percentage of total scan sample records: Feeding on animal material	Index of foraging success (IFS)[1]
Late dry 1985	25.03	2.36	9.42
Early wet 1985	21.37	3.79	17.73
Late wet 1986	19.00	2.89	15.21
Early dry 1986	25.10	2.15	8.55
Late dry 1986	32.89	1.56	4.74
All dry season records	28.21	1.97	6.97
All wet season records	20.12	3.32	16.48
All records:	**24.10**	**2.66**	**11.00**

[1] IFS = (Number of records of feeding on animal material/records of insect foraging) x 100.

While apparently consuming less animal material, the group spent far more of its time both foraging for prey and travelling during the late dry season of 1986, and less time resting (see table 4.2). If we calculate a crude index of the group's foraging "success" (IFS) by dividing the number of records of prey feeding by the number of records of foraging during each period (table 4.3), it is evident that the group received significantly greater returns to its foraging efforts during the late dry season of 1985. This "success rate" fell in every month between April and August 1986, correlating with the pattern in the measured abundance of arthropods. During the same period, however, the time devoted to foraging increased every month. This quite clearly indicates that group's reaction to a decrease in the abundance of its prey was to increase its foraging efforts. *C. flaviceps* thus appears to have followed a similar feeding strategy to that of *G. senegalensis* during periods of insect scarcity.

Table 4.4

Monthly Variation in Temperature and the Average Length of the Daily Activity Period

Sample	Mean daily activity period (hrs:mins)	Mean temperature recorded at FMC (°C)
June 1985[1]	8:08	13.8
July	8:50	15.2
August	8:50	17.4
September	9:14	19.1
October	10:21	22.6
November	10:49	23.0
December 1985	10:28	22.7
January 1986	10:20	23.8
February	10:05	24.1
March	10:09	24.2
April	9:46	22.0
May	9:39	19.9
June	8:50	16.7
July	9:09	16.5
August 1986	9:20	19.1

[1] Only 4 complete days recorded. Sample may not be directly comparable with other months because of observer's lack of experience (see chapter 2).

It is interesting to note, in this context, that the length of the daily activity period during the dry season months seemed to be more consistently related to ambient temperature than to the abundance of insects. Daily activity periods were much shorter, on average, during the later dry season months than during the earlier months, correlating with the relatively lower ambient temperatures during this period (table 4.4). The average daily activity period was also consistently shorter during June, July and August of 1985 than it was during each of these months in 1986, again correlating with the lower temperatures recorded in these months during the former year.

This suggests that the strategy of the study group involved more than a simple increase in foraging activities when insects were scarce. Given that the group was only active for a portion of the daylight period during all seasons, it could easily have increased the time it was active each day. During the late dry season, it could have increased this period by at least two hours each day, which, if levels were maintained, would have increased the time spent foraging by more than 20%. *Saimiri oerstedii* has been observed to continue foraging after dusk during periods of insect scarcity [Baldwin & Baldwin, 1981], so such a strategy does seem to be feasible for this insectivorous cebid, at least. The smaller body size of *C. flaviceps* may, along with physiological adaptations to reduce energetic requirements, be a major influence on the feasibility of such a strategy for this species. It was suggested in chapter 1 that marmosets are able to reduce their metabolic expenditure during the nightly period of inactivity through both a condition of torpor and the huddling of group members. In this case, a reduction in activity may often be more beneficial to the group, in energetic terms, than continued foraging. When insects are scarce and ambient temperatures low, the net energetic gains of foraging may, in fact, be both negative and less than those of ceasing activity altogether, especially if energetic requirements can be further reduced through torpor. The intensification of foraging activity into a shorter period each day, with a minimum of rest (and a maximum of gum feeding, see below) would, in this case, be the optimal strategy for the group.

As discussed previously, gum was, in theory, equally available to the group throughout the year, so any changes in its consumption is likely to have been the result of changes in the availability of other foods. Studies of *G. senegalensis* and *G. crassicaudatus* [Bearder & Martin, 1980; Harcourt, 1986] have shown that both these species may significantly increase their gum feeding when insects are scarce. Apart from the wet season months of January and February (when edible fruits were abundant), however, gum feeding took up a remarkably consistent proportion of the study group's time (table 4.5). Taking into account the difference in the length of the daily activity period between the two periods, the proportion of time spent feeding on gum during the early wet season sample (8.8%) is almost directly comparable with the mean for all dry season samples (9.6%). As animal material was consumed in greater quantities during the early wet season, it makes up a much larger proportion of the feeding records during this period (27.8%, table 4.6) than during the dry season months as a whole (16.1%). During the late wet season, on the other hand, when large quantities of fruits and fewer insects were being consumed, levels of prey feeding were more similar to those of the dry season.

Looking more closely at the dry season samples, a degree of difference both within and between years is again apparent, although not as marked as for activities such as foraging. As for most other characteristics, the late dry season sample of 1985 is more similar to that of the early dry season of 1986 (April and May) than to the later months (table 4.5). Gum feeding took up 9.4% of the study group's activity during the late dry season of 1986, slightly

Table 4.5

Seasonal Variation in the Feeding Behaviour of the Study Group

	Percentage of total scan sample records spent feeding on:			
Sample	Inveretbrates	Vertebrates	Plant exudate	Fruit, flowers or nectar
Late dry 1985	1.89	0.47	9.85	0.42
Early wet 1985	3.54	0.25	8.84	0.97
Late wet 1986	2.60	0.29	6.81	5.52
Early dry 1986	1.55	0.59	10.05	0.38
Late dry 1986	0.89	0.67	9.51	0.21
All dry season records:	1.38	0.59	9.78	0.43
All wet season records:	3.05	0.27	7.77	3.36
All records:	**2.23**	**0.43**	**8.76**	**1.92**

Table 4.6

Seasonal Variation in the Composition of the Study Group's Diet, According to Scan Sample Records

Sample	Percentage of total feeding records collected in scan samples: Invertebrates	Vertebrates	Plant exudate	Fruit, seeds or nectar	*N*
Late dry 1985	14.96	3.72	78.03	3.29	1156
Early wet 1985	26.06	1.81	64.99	7.14	2322
Late wet 1986	13.59	1.49	56.12	28.80	2871
Early dry 1986	12.05	4.57	77.82	5.56	1600
Late dry 1986	7.86	5.96	84.34	1.84	1578
All dry season records:	11.29	4.85	80.30	3.56	4334
All wet season records:	21.11	1.85	53.80	23.24	5193
All records:	**16.69**	**3.20**	**65.72**	**14.39**	**9527**

less than during both the earlier months of the 1986 dry season and the 1986 late dry season months.

This may, in fact, be a random consequence of observational bias due to the relatively greater consumption of *angico* gum during this period than at other times of the year (see chapter 6). The patterns of behaviour involved in the consumption of *angico*and *Acacia* gum were generally quite different. When feeding on *angico* gum, the group would typically enter a single tree all together and feed rapidly on the deposits, which were usually readily available on the surfaces of trunks and branches. As most of these trees are relatively tall and open-canopied, the greater exposure to possible predation probably encourages rapid feeding. The group was often, in fact, visibly nervous when feeding on this type of gum on high, exposed boughs. Deposits of *Acacia* gum, on the other hand, were generally less accessible, being scattered through the dense undergrowth. The group may not only have required more time to consume the same amount of this type of gum, but would also have been relatively less exposed to possible predation. It is interesting to note a parallel with the observational biases proposed earlier in this chapter, *i.e.* that

Plate 6

Adult male "Smell" sprawl-resting on a Sessenta pau (Allophyllus *sp.) branch.*

of the possible under-estimation of the amount of time spent foraging by *Saguinus fuscicollis* in comparison with *Saguinus imperator*, and of the time spent fruit feeding by *Saimiri sciureus* [Terborgh, 1983].

Even taking into account the effects of possible bias, these results clearly indicate that the group did not increase its consumption of gum at times when insects were most scarce. As the consumption of prey fell considerably, however, the proportion of gum in the group's diet rose (table 4.6). In relative terms, then, gum constituted a much larger proportion of the group's diet during this period that at any other time of the year. Overall, the pattern of its consumption of gum indicate not only that gum may provide a less adequate substitute for animal material, but also that its composition may place specific limitations on its use. This is discussed in detail in chapter 6.

Apart from the period during which edible fruits were abundant, the study group spent more of its time foraging for insects when they were less available, but captured fewer. Gum, in addition, constituted a larger proportion of its diet during the periods when insects were least available, although it was not consumed in significantly greater quantities than at other times. Given the considerable differences between the species studied and the conditions facing them, these results seem to suggest that *C. flaviceps* was following a feeding strategy more similar to that of *G. senegalensis* than to that of *G. crassicaudatus* [Harcourt, 1986], as predicted by their more similar body size. The strategy of the *C. flaviceps* study group did, however, seem to be more complex, involving a complementary increase in the time spent at rest in the night-time huddle. This type of rest is functionally very different from that of the daytime siesta which involves much sprawling (plate 6), in response to high ambient temperatures. As discussed above, a strategy involving such an energy-saving component may be more feasible for *C. flaviceps* than for *G. senegalensis* for a number of reasons.

The *C.h. intermedius* study group at Aripuanã [Rylands, 1982] showed little change in its consumption of animal material in different seasons, which probably reflects less marked fluctuations in the abundance of insects at this site in comparison with FMC. Unexpectedly, however, the feeding records indicate that insects were less available at Aripuanã than they were during most of the year at Jaó. According to a direct comparison of the data from the two studies, the *C.h. intermedius* group spent more of its time foraging for

Table 4.7

Seasonal Variation in the Foraging Success of the C.h. intermedius *Study Group*[1]

Sample	Percentage of total scan sample records: Insect foraging	Percentage of total scan sample records: Feeding on animal material	Index of foraging success (IFS)[2]
Wet season (December to February)	27.15	1.52	5.60
Dry season (June to August)	27.87	1.97	7.07
All records:	**27.85**	**1.85**	**6.65**

[1] Data taken from Rylands, 1982: table 21.

[2] IFS = (Number of records of prey feeding/number of records of insect foraging) x 100.

insects during the course of the year, but less feeding on them, than the *C. flaviceps* group. Calculating the IFS for the *C.h. intermedius* group during different seasons (table 4.7), it is apparent that its foraging was far less successful, on average, than that of the *C. flaviceps* group. It also seemed to be slightly more successful during the dry season months, in marked contrast with the pattern observed for the *C. flaviceps* group.

While this difference may be partly accounted for by the differences in observational bias outlined previously (as well as others, such as a difference between observers in the interpretation of specific behaviours), this contrast between the two groups may be a realistic reflection of certain basic differences in the ecology of the two species. One important factor may be the competition for resources from other primate species. If *Aotus* and *Callicebus* are accepted as being at least partly insectivorous, there are 5 such species at Aripuanã, while there is only one (*Cebus apella*) at FMC. While marmosets probably avoid such competition to a certain extent by utilising different foraging techniques, there is a considerable overlap in the types of prey consumed [Terborgh, 1983]. Thus, while we might assume, given the higher levels of rainfall and less pronounced seasonality of this site, that insects are generally more abundant at Aripuanã, greater competition from other primates (in particular) may make them less available to the *C.h. intermedius* group.

If, in addition, animal material is a less important component of the diet of the *C.h. intermedius* group, as seems likely from the composition of its diet (table 4.8), this group may forage less systematically for prey. This is possibly a consequence, among other factors, both of the greater abundance of edible fruit throughout most of the year at Aripuanã, relative to FMC, and of the competition for prey from other primate species. If the *C.h. intermedius* group's movements (in both the horizontal and vertical planes) were more strictly determined by the distribution of fruiting trees than by that of arthropods, it may have have been foraging in areas containing a smaller abundance of insects, on average, than those visited by the *C. flaviceps* group. Comparisons of both the ranging patterns of the two groups (chapter 5), and the levels used during their foraging activities (appendix III), appear to support these ideas.

Table 4.8

Composition of the Diet of the C.h. intermedius *Study group*[1]

Sample	Percentage of total feeding records collected in scan samples: Animal material	Plant exudate	Fruit, flowers or nectar
Wet season (December to February)	6.74	8.24	85.02
Dry season (June to August)	9.79	11.38	78.83
All records:	**9.57**	**15.56**	**74.87**[2]

[1] Data from Rylands, 1982: appendix III, table 17.
[2] Includes 0.26% "leaf shoots".

Gum was a relatively unimportant component of the *C.h. intermedius* group's diet in most months, but it was also never absent, averaging 11.7% of plant feeding records during the total wet season sample and 22% during the dry season [Rylands, 1982]. While many variables, such as the chemical composition of the fruits commonly consumed by this group, are not known, this evidence does seem to suggest that gum is an important, if not obligatory, component of its diet. This further supports ideas on the importance of the calcium content of gums for highly insectivorous primates [Bearder & Martin, 1980; Garber, 1984a].

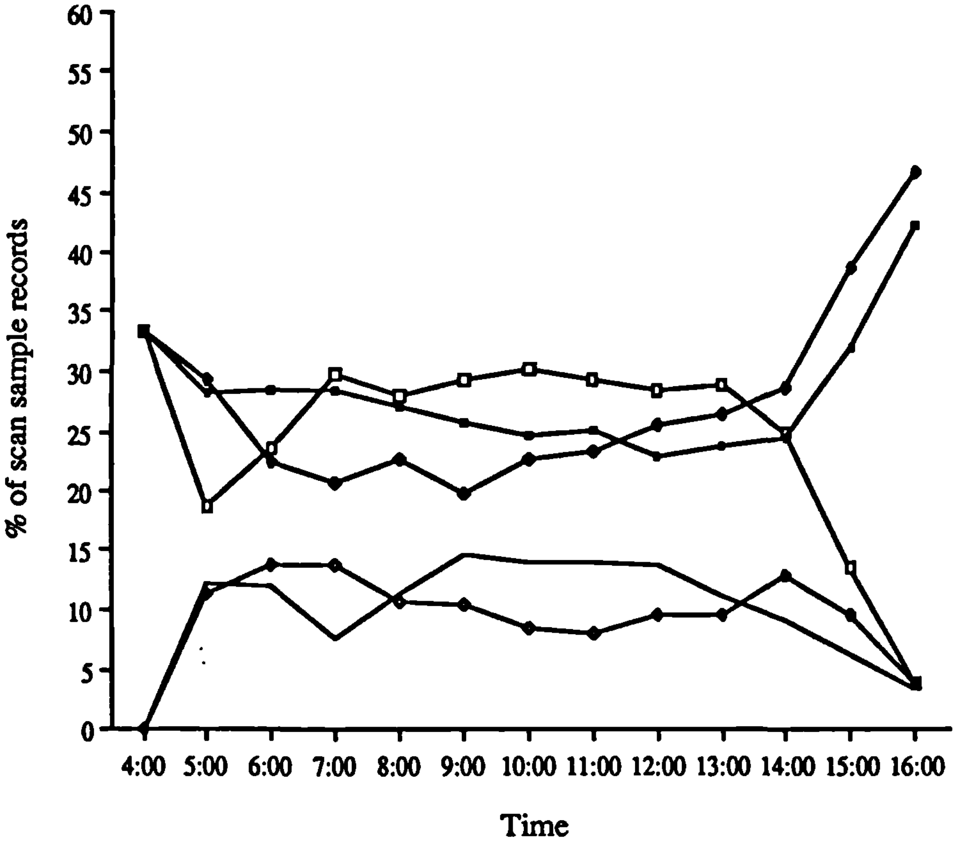
The Daily Activity Cycle

The daily cycle of marmoset groups, like those of most other diurnal primates, normally includes a substantial period of inactivity, during the middle of the day [Sussman & Kinzey, 1984; Stevenson & Rylands, in press]. As well as a midday siesta, marmoset groups may often take shorter periods of rest during the course of the day [Rylands, 1982; Soini, 1982]. Another common pattern of the activity cycles of primate species appears to be early morning and late afternoon peaks in feeding on plant material [Clutton-Brock, 1977; Raemaekers & Chivers, 1980], a bimodal pattern which has also been recorded in studies of both marmosets and tamarins [Rylands, 1982; Terborgh, 1983; Soini, in press]. *S. geoffroyi* has been reported to forage and travel most intensively during the early part of the day [Dawson, 1979] which, it has been suggested, corresponds with the greatest vulnerability of its insect prey, although other long-term studies have not recorded such patterns, and alternative reasons have been proposed [*e.g.* Rylands, 1982].

It is likely that patterns in the daily activity cycle of the *C. flaviceps* study group will reflect these, among other, factors. The records for the whole of the study period combined (figure 4.3), however, appear to indicate that the values for the main categories are relatively constant through the main part of the day. Records from the earlier (04:00 to 06:00) and later (14:00 to 16:00) parts of the day are influenced by the fact that the group was either leaving or retiring to sleep trees at these times, and at different times in different seasons. This reduces the overall number of records relative to other times of the day (see appendix III), and tends towards a bias for recording rest and travel, particularly at the end of the day when the characteristic "creeping" approach to and ascent of sleep trees usually excluded other activities. These problems are less pronounced when the data are analysed by season, when the

Figure 4.3

Daily Activity Cycle, All Records



Activities:

□ *Foraging for and Feeding on Animal Material*

■ *Travelling*

◆ *Resting*

◇ *Feeding on Plant Material*

—— *Miscellaneous Activities*

Figure 4.3 shows the daily cycle of the study group's activities for all records collected during the main study period (125 full observation days). Values are percentages of the scan sample records collected during each hourly division of the clock, i.e. *values for 10:00 are taken from all scan samples taken between 10:00 and 10:55. This division is used throughout this thesis for the discussion of daily patterns.*

N.B. *in this and figs. 4.4 to 4.10, sample sizes for the earliest and latest parts of the day are invariably much smaller than at other times and are thus not necessarily directly comparable.*

times of commencement and cessation of the group's activities were more narrowly distributed.

With this problem in mind, a number of trends are apparent in the records as a whole. The group spent progressively less of its time travelling through the course of the day (apart from the final two hours) and progressively more of its time at rest. There is, however, no clear-cut peak of resting at any time during the main part of the day. This contrasts with the pattern shown by *C.h. intermedius*, which had a very marked peak of rest at 12:00 throughout the year (more than double the levels recorded at other times during the main part of the day), when the propensity to rest was similar to that of *C. flaviceps* during the wet season months [Rylands, 1982]. A similar pattern has been reported for *S.f. illigeri* [Soini, in press]. The grouping together of the records for the *C. flaviceps* study group may have partly obscured such peaks, as long siestas were common during the wet season months as a whole, but were relatively rare during the dry season months. Such siestas were, in addition, taken at varying times of the day, even during the same month or on consecutive days.

Foraging for prey, on the other hand, remained at remarkably constant rates between 07:00 and 14:00, before declining rapidly towards the end of the day. It is interesting to note here that foraging activities also increased relatively slowly during the early hours of the day. Rylands noted a similar pattern for *C.h. intermedius*, except that there was a distinct depression of such activity at midday, coinciding with the peak in rest [see also Soini, in press]. The pattern of feeding on plant material does show a trend towards bimodality, but this might just as easily be seen as a slight depression of plant feeding during the middle of the "marmoset day" (*i.e.* at around ten o'clock). A similar trend is apparent in the data for *C.h. intermedius*, although this was very much more marked during the wet season [Rylands, 1982]. As the majority of the group's miscellaneous activities, such as allogrooming and play, were usually associated with rest, we might expect some correlation between these two categories. Apart from the earliest part of the morning, however, this is not the case.

We have already seen that there were marked differences overall in the activity patterns of the study group during different seasons. These differences will obviously be reflected in the proportions of its activity during

Figure 4.4

Daily Activity Cycle, All Wet Seasons Samples

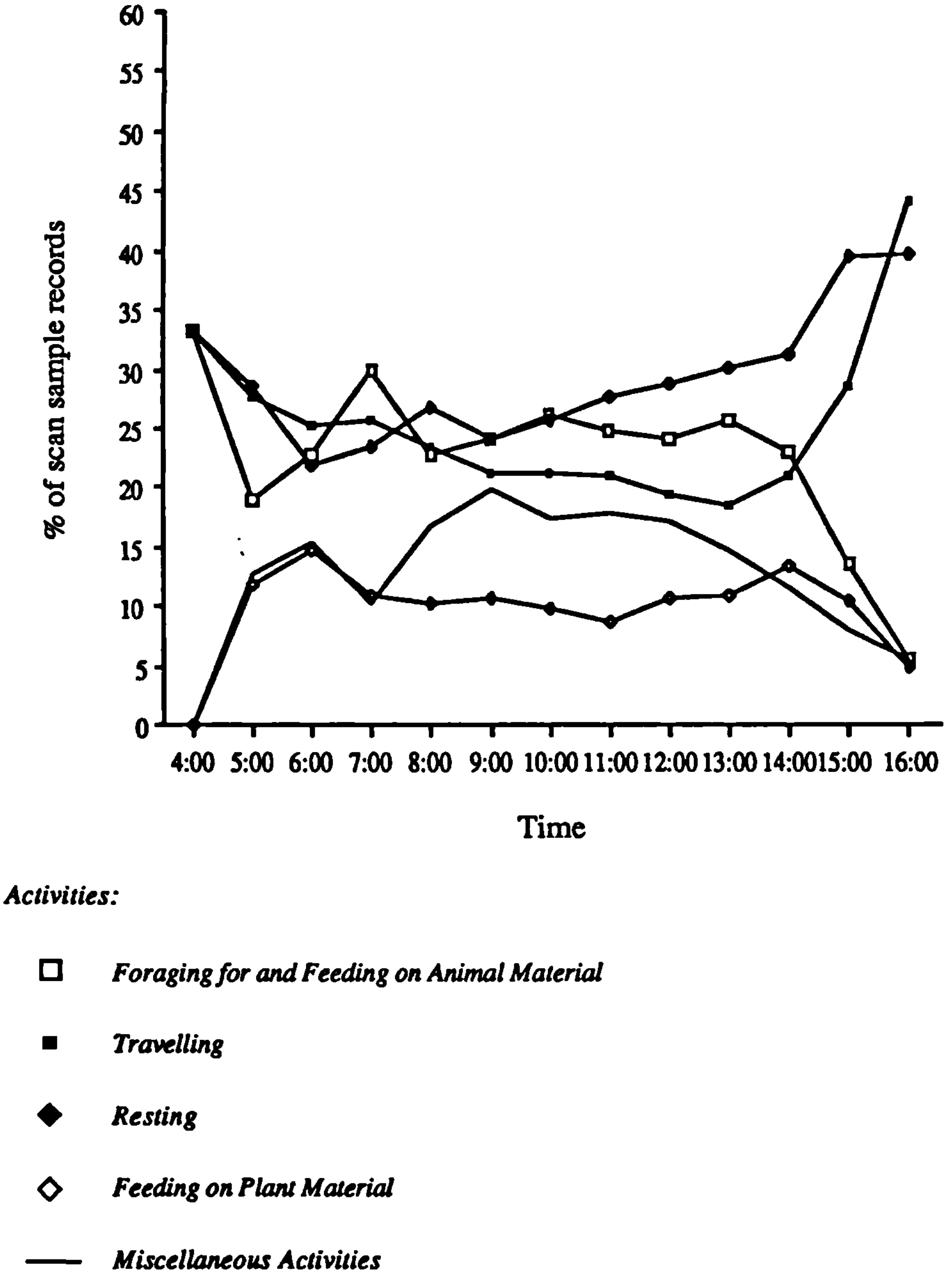


Figure 4.4 presents the daily cycle of the study group's activities recorded during all scan samples taken during the 1985/86 wet season (58 observation days). Values as for fig. 4.3.

the course of the day. In addition to this, we might expect different patterns in the daily activity cycle, correlating with observed variation in the abundance of resources, ambient temperatures and so on. The most obvious of these differences is in the length of the daily activity period in different seasons.

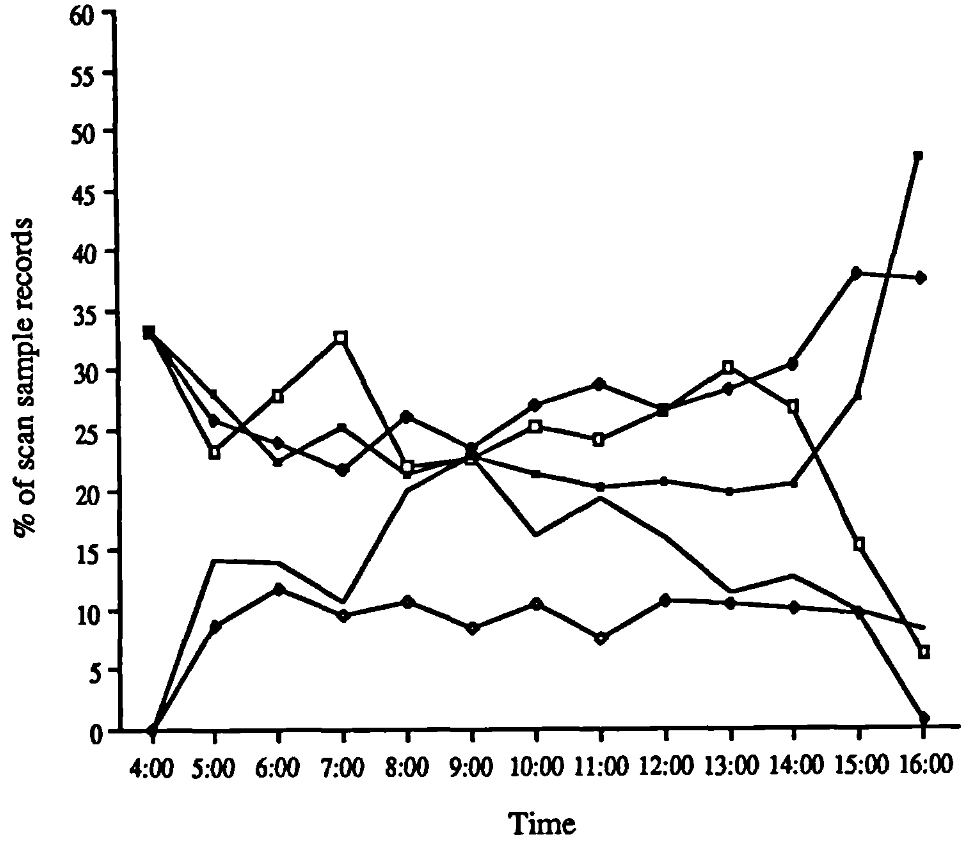
Looking first at the wet season sample (October to March, figure 4.4), we can see that the patterns of the group's travelling, resting and plant feeding are relatively similar to those found in the records as a whole (figure 4.3). The bimodality in the group's plant feeding is, however, less pronounced, whereas the patterns of a progressive decrease in travel and increase in rest through the course of the day are slightly more pronounced. There is a marked peak of foraging at 07:00, when approximately 20% more of the group's time was spent in this activity than at other times of the day. Otherwise, the pattern is little different from that of the year as a whole (figure 4.3), picking up slowly at the beginning of the day, remaining at more or less constant rates until 14:00 and then falling off rapidly at the end of the day. The miscellaneous category again exhibits no clear-cut pattern, although it does make a considerable contribution to the budget at this time of year, constituting as much as one fifth of the group's activities at certain times of day.

If we divide the wet season records into the early months of October to December (figure 4.5) and the late months of January to March (figure 4.6), further differences are apparent. Some trends, such as the increase in rest and the decline in travel through the course of the day, are common to both periods. The most interesting differences are in the group's insect foraging and plant feeding. In the early wet season sample, feeding on plant material remains at fairly constant levels throughout the day, while insect foraging shows a marked bimodality, peaking at 07:00 and 13:00. During the late wet season, on the other hand, foraging declines systematically through the course of the day while there are characteristic bimodal peaks in plant feeding at the beginning and end of the day.

With regard to feeding on plant resources, the most obvious difference between the two periods is the importance of fruit and seeds in the group's diet during the late wet season. The two most important tree species involved are particularly abundant in some parts of the group's home range, providing dense concentrations of resources for which it did not, apparently, compete

Figure 4.5

Daily Activity Cycle, Early Wet Season Samples



Activities:

□ *Foraging for and Feeding on Animal Material*

■ *Travelling*

◆ *Resting*

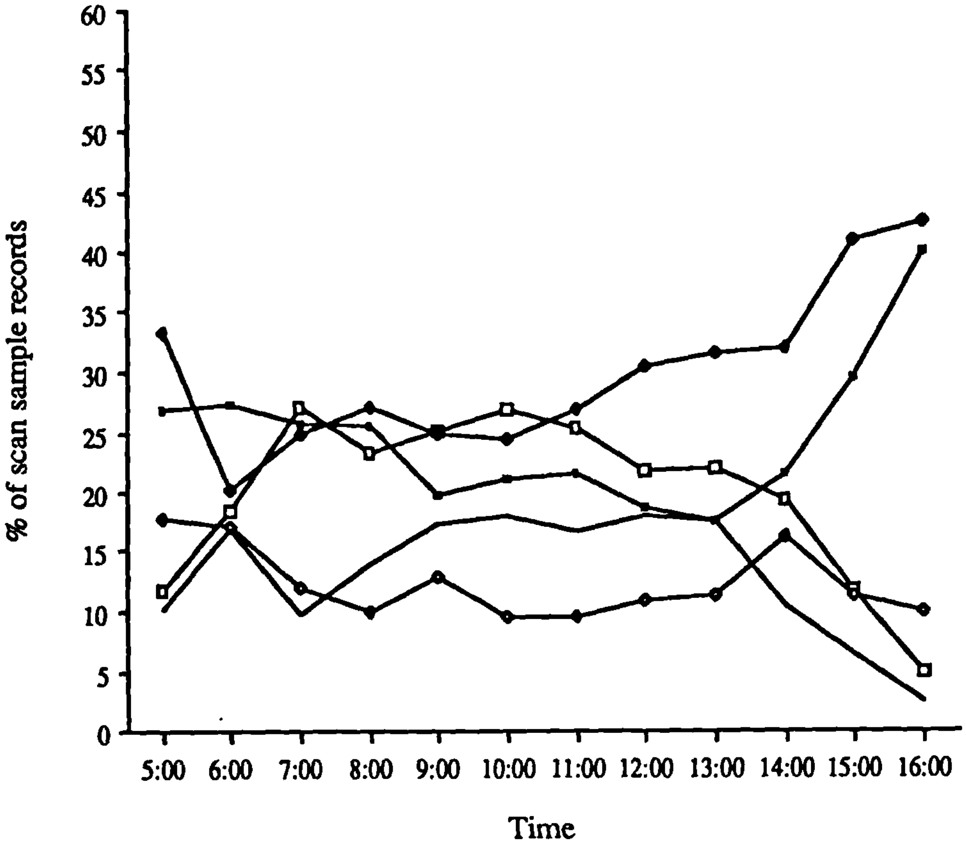
◇ *Feeding on Plant Material*

—— *Miscellaneous Activities*

Figure 4.5 shows the daily activity cycle recorded in scan samples taken during the early wet season months of 1985 (Oct. to Dec., 28 observation days). Values as for fig. 4.3.

Figure 4.6

Daily Activity Cycle, Late Wet Season Samples



Activities:

□ *Foraging for and Feeding on Animal Material*

■ *Travelling*

◆ *Resting*

◇ *Feeding on Plant Material*

—— *Miscellaneous Activities*

Figure 4.6 shows the daily cycle of the study group's activities recorded during the late wet season of 1986 (Jan. to Mar., 30 observation days).

with other animals[1]. In January, for example, the group frequently chose sleep trees surrounded by dense stands of *Allophylus* and fed intensively on their fruit both prior to retiring for the night and first thing in the morning. A decline in the availability of animal material, along with its partial substitution in the group's diet by fruit and especially seeds, may have been factors reducing the motivation of its members to continue foraging during the later part of the day. Somewhat equivocally, however, foraging was far more successful during the later part of the day, showing the most marked contrast of any period (see below).

It seems likely that the situation in the early wet season is derived from the relative abundance of insects during this period. If insects were super-abundant, in terms of the study group's requirements, it may have been able to utilise this resource as it feeds on plant material at other times of the year. Its foraging activities were, in fact, more than three times more successful during this period than they were in most dry season months, reaching almost one prey-feeding record for every four records of foraging, on average, during the later part of the day. Whether this, along with the relatively smaller amount of time devoted to foraging activities, is conclusive evidence of a super-abundance of prey is not known, but it does seem to support this idea.

Insects may thus have approached being as easily-acquired a source of nutrients during this part of the year as gum was throughout the year. In this case, with prey being preferred over gum and edible fruits being generally unavailable, the group would have utilised prey in the same way as it exploited plant material at other times of the year. Following on from this, plant feeding would have become a relatively unimportant complementary activity spread more or less evenly throughout the day as the group encountered gum sources during the course of its other activities. In the middle of the day, then, the group devoted most of its time to resting and associated activities. "Recreational" resting activities such as play and

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[1] Allophyllus *fruits were seen to be ignored, in general, by frugivorous animals such as parakeets, and the fruit of one tree standing in open pasture eventually rotted.* Siparuna *seeds were also generally ignored by other animals. Ants would rapidly take seeds placed on the ground, but would not take them from the trees, seemingly deterred by the pungent scent of both trees and fruit.*

allogrooming predominate during the early part of this period, and rest during the later, hotter part. Equivocally, the afternoon peak in foraging activity comes at a time (between 12:00 and 14:00) when ambient temperatures were highest, although travel was reduced.

Contrasting characteristics are evident in the dry season records as a whole (figure 4.7). The most striking feature is the relatively small proportion of time spent at rest throughout most of the day, and the relatively large proportions spent travelling and foraging. Consistent with other periods, however, these records show that rest increased through the day, while travel decreased, although the latter trend is less marked than at other times. Feeding on plant material exhibited a clear-cut bimodality, even more pronounced than that observed during the wet season, with the early morning peak being greater and more sustained than that of the late afternoon. While insect foraging took up a much larger proportion of the budget throughout the day, the pattern was fairly similar to that seen during the wet season as a whole. The dry season samples, as we have already seen, are even less homogeneous than those of the wet, reflecting variations both within and between years.

All three periods covered by the records do, however, exhibit the characteristic bimodality in plant feeding (figures 4.8 to 4.10). This is most distinct in the late dry season sample from 1986, and least marked in the sample from 1985. Comparisons are complicated, to a certain extent, by the presence of dependent infants during the 1985 sample. This has contributed to the relatively large proportion of miscellaneous activities during this period, and probably to the somewhat lower levels of rest in comparison with, for example, the early dry season of 1986. Terborgh [1983] noted that both pregnant females and the presence of dependent infants in the tamarin groups at Manu had a marked effect on group mobility and activity. This was not the case, however, for JG1, nor for *C.h. intermedius* [Rylands, 1982]. Both groups were much larger than those of the tamarins and there were thus not only more infant carriers available for more frequent changes, but infant carriers were a much smaller proportion of the group and would thus have a less marked influence on the behavioural records. In addition, the mobility of BM, the *C. flaviceps* group's reproductive female, was apparently unaffected by pregnancy.

Figure 4.7

Daily Activity Cycle, All Dry Season Samples

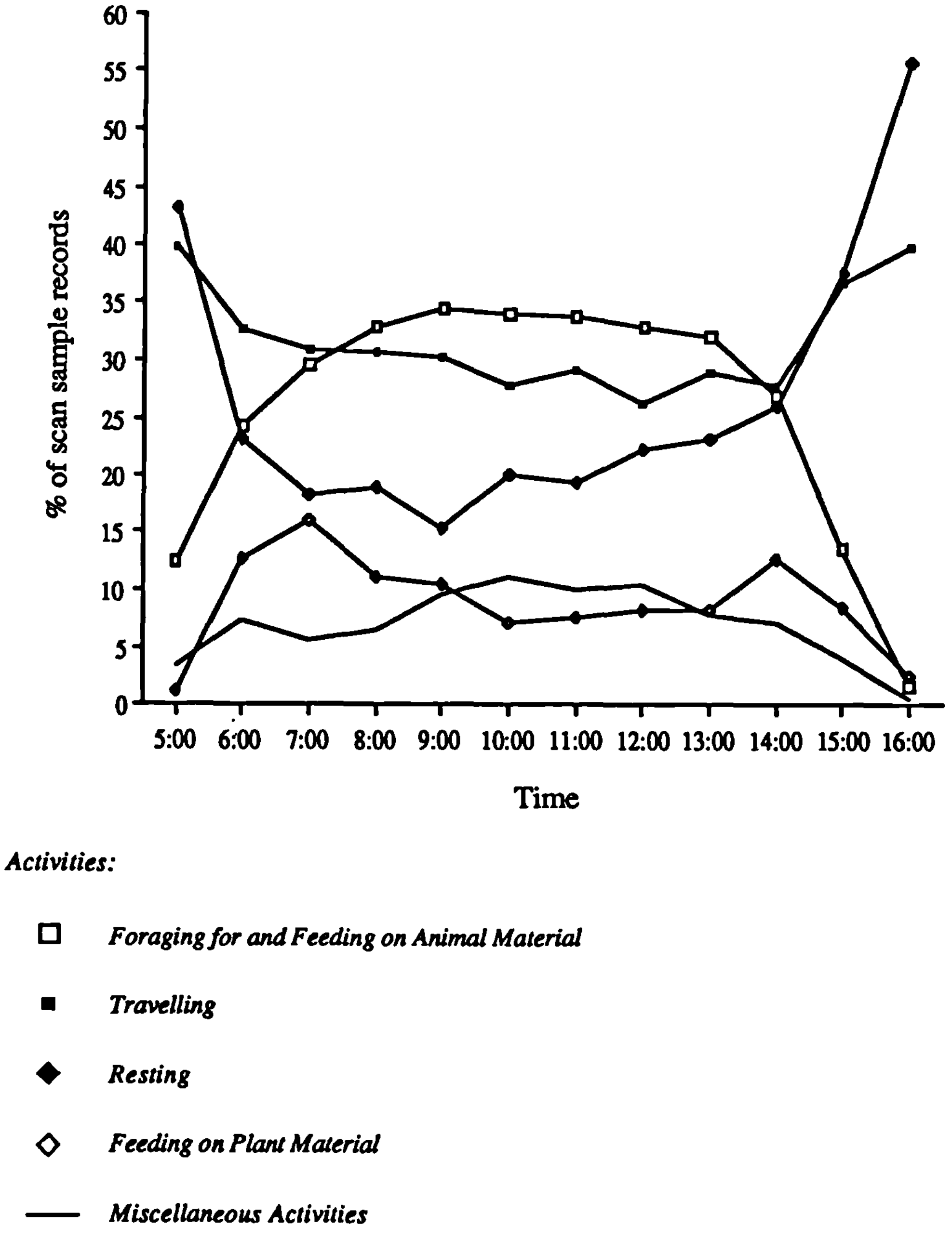
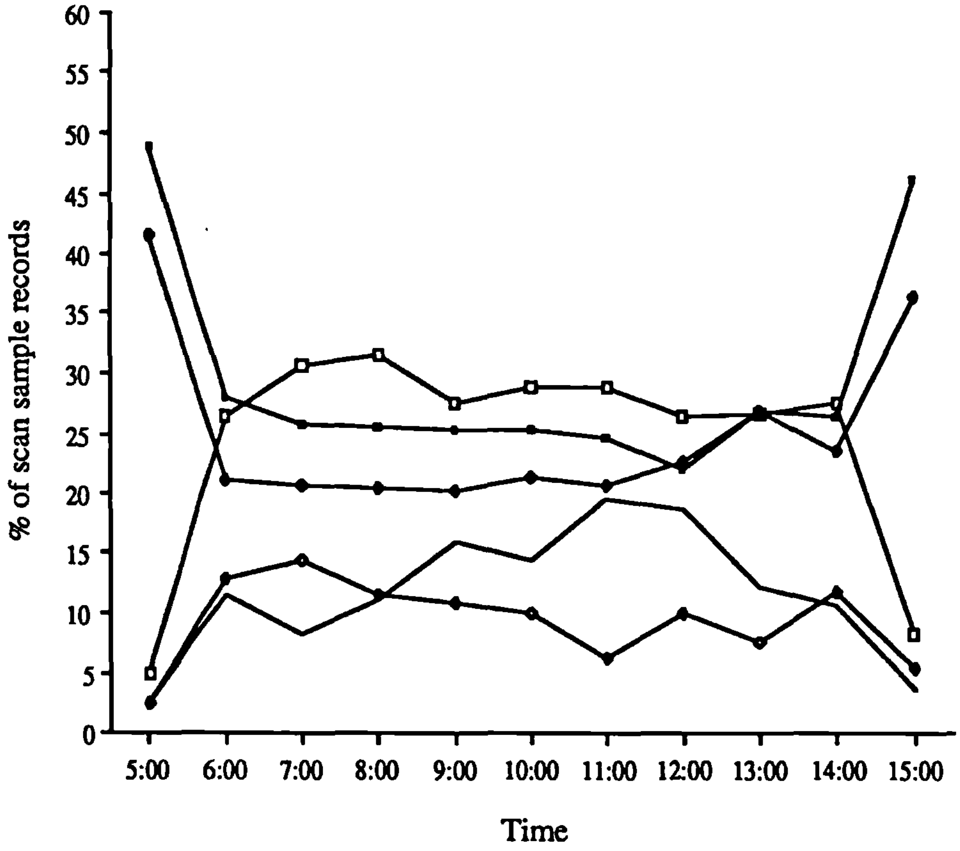


Figure 4.7 shows the daily cycle of the study group's activities during all dry season samples (67 observation days). Values as for fig. 4.3.

Figure 4.8

Daily Activity Cycle, Late Dry Season 1985



Activities:

□ *Foraging for and Feeding on Animal Material*

■ *Travelling*

◆ *Resting*

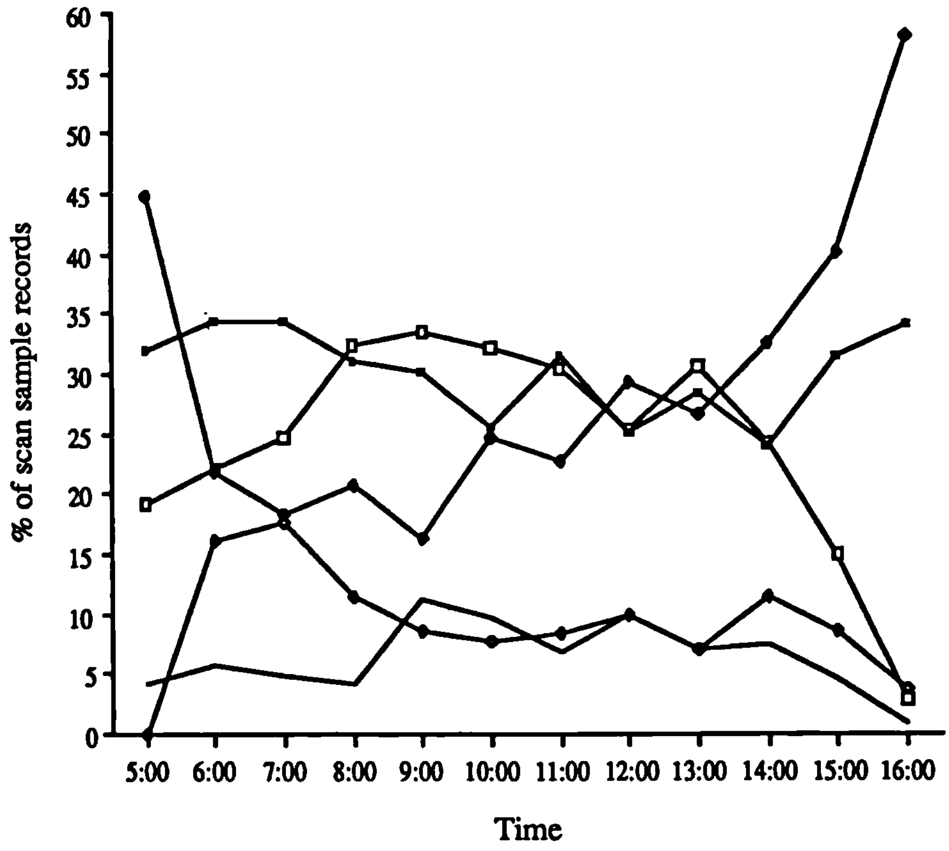
◇ *Feeding on Plant Material*

—— *Miscellaneous Activities*

Figure 4.8 shows the daily cycle of the study group's activities for scan samples taken during the late dry season of 1985 (Aug. & Sept., 19 full observation days). Values as for fig. 4.3.

Figure 4.9

Daily Activity Cycle, Early Dry Season Samples



Activities:

☐ *Foraging for and Feeding on Animal Material*

■ *Travelling*

◆ *Resting*

◇ *Feeding on Plant Material*

—— *Miscellaneous Activities*

Figure 4.9 shows the daily cycle recorded for the early dry season of 1986 (Apr. & May, 20 observation days). Values as for fig. 4.3.

Figure 4.10

Daily Activity Cycles, Late Dry Season 1986

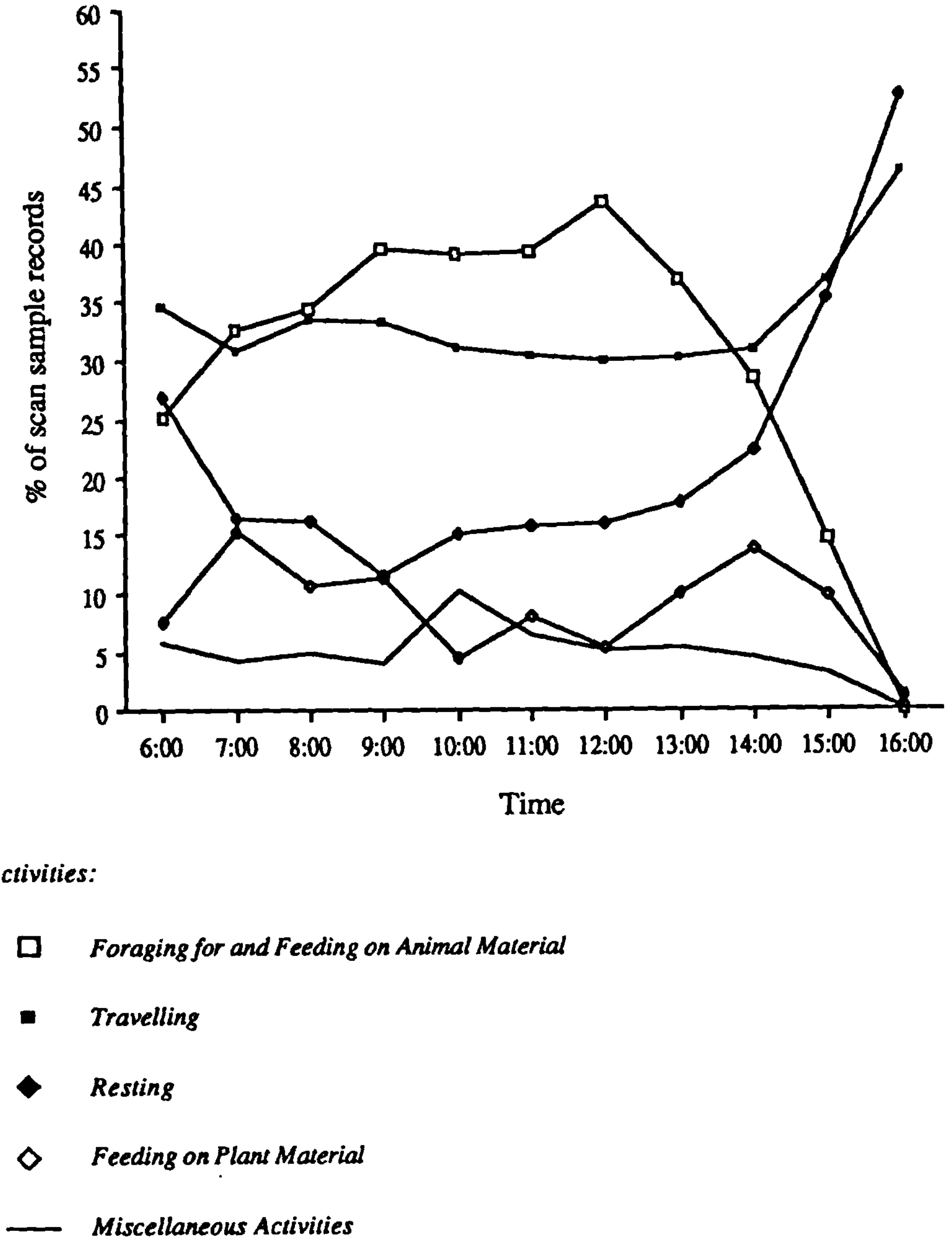


Figure 4.10 shows the daily cycle recorded during the late dry season of 1986 (Jun. to Aug., 28 observation days). Values as for fig. 4.3.

All three periods also show the characteristic trends of increasing rest and decreasing travel through the course of the day, although they are far less well defined than they are in the wet season samples. The clearest difference between the dry season periods is in the group's foraging behaviour. The 1985 sample shows a relatively rapid start to foraging activities followed by a very gradual decline through the course of the day. On the other hand, the early 1986 dry season sample shows a relatively slow start, correlating with high levels of feeding on plant material. This is also followed by a more or less gradual decline through the course of the day, with a minor peak at 13:00, before declining rapidly at the end of the day. Foraging patterns during the late dry season of 1986 are the most distinctive. By 07:00 the group was already, on average, spending more time foraging than at any time during any other period, an intensity which increased progressively up until 12:00, reaching a peak of almost 45% before declining towards the end of the day (note that the value for 14:00 is still almost 30%).

The group also travelled at relatively high and constant rates throughout the day during this part of the dry season, and the overall impression is one of its reducing all other activities, apart from feeding on plant materials during the early morning and late afternoon, to a minimum. The marked bimodality of its plant feeding may, in fact, be related to the other trends, given the idea that such a pattern is apparently related to the easy acquisition and consumption of this type of food [Raemaekers & Chivers, 1980; Terborgh, 1983]. In this case, we might see the group using this type of resource as a ready source of energy in the early morning and then in compensation for the small quantities of animal material acquired by the end of the day. In the early dry season months of 1986, on the other hand, while the early morning peak in feeding on plant material is relatively more marked, there is no equivalent peak at the end of the day. Apart from the late wet season, when other factors apply (even so, the pattern was not as marked as it was in most of the dry season), this bimodal trend was generally most distinct during the periods when insects were least abundant.

It is interesting to note that, while the group's foraging activities were relatively constant throughout the main part of the day (figure 4.3), the proportion of time spent feeding on animal material tended to increase. This is clearly demonstrated in the measurement of foraging success (IFS) at different times of day (figure 4.11). The study group, as we have seen, spent progressively less time travelling through the course of the day (apart from the final two hours). Thus, if travel is seen either as a major component of or complement to foraging, the difference in the returns to total foraging effort, *i.e.* foraging and travelling combined, between the earlier and later parts of the day would be even more apparent. The situation is not quite so simple, however, as the group's movements are clearly related to other activities, such as feeding on plant material in particular (see chapter 5).

Looking at the situation in different periods (figure 4.12a-e), we can see that this pattern is even more pronounced in the wet season samples, but not particularly clear in those from the dry season. Success during the late dry season of 1986 is particularly low, and oscillates about the 5% mark throughout the day. The late dry season sample of 1985 also shows more or less similar overall levels of success between the early and late parts of the day, although in this case there are distinct peaks of success at 07:00 and at midday. While a number of factors should be taken into account in the assessment of these results, it seems unlikely that observational bias would have influenced these patterns, given the low levels used by the group during such activities at all times of the year (see chapter 7). Even if foraging behaviour was more visible to the observer at some times of day than at others, there seems to be no good reason to assume that foraging and prey-feeding activities were subject to differing relative visibility.

These patterns in the study group's foraging success, along with those of its foraging activities as a whole, seem to contradict the hypothesis that a concentration of foraging into the early part of the day corresponds with the greatest vulnerability of large insects [Dawson, 1979]. Like *S. geoffroyi*, the *C. flaviceps* group did travel more during the early part of the day, but this did not correspond with any peak in foraging and might just as easily be accounted for by the early-morning peak in feeding on plant material. Even in periods, such as the late wet season, when foraging activities tended to decline during the later part of the day, this seems to have been compensated for by increasing success. Even in the exceptional late dry season period of 1986, the midday peak in foraging activities was accompanied by the highest IFS.

Figure 4.11

Daily Variation in the Foraging Success of the Study Group

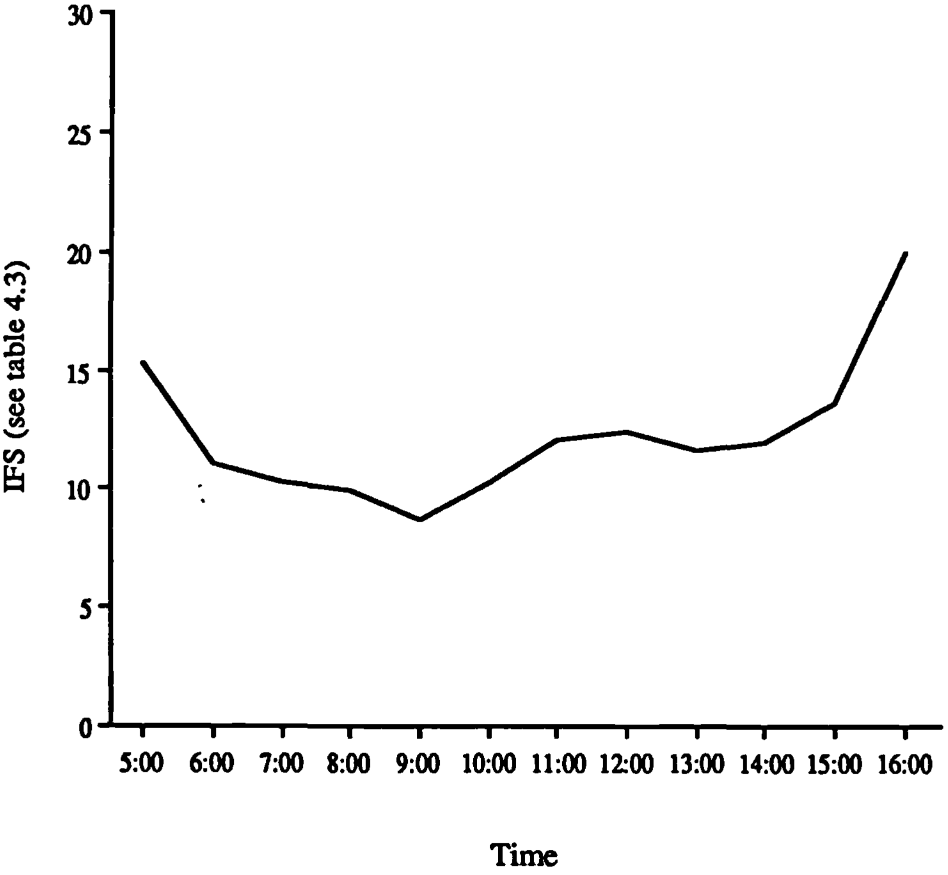


Figure 4.11 shows the daily variation in the study group's foraging success recorded in scan samples during the whole of the main study period. The Index of Foraging Success (IFS, see table 4.3 for formula) has been calculated for the foraging and feeding records collected during each of the hourly divisions of the day throughout the study period (125 observation days). Note that a value for 4:00 is absent due to the lack of records collected.

Figure 4.12

Seasonal Variation in Daily Patterns of Foraging Success

(a) Late Dry Season 1985

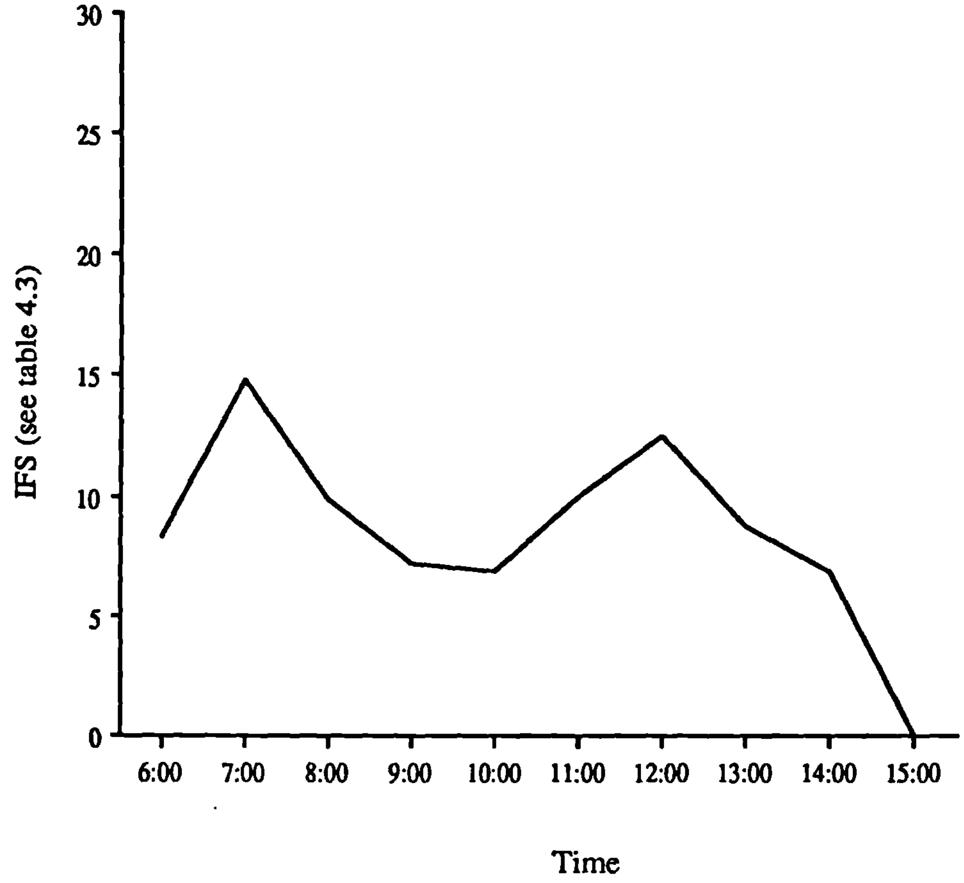
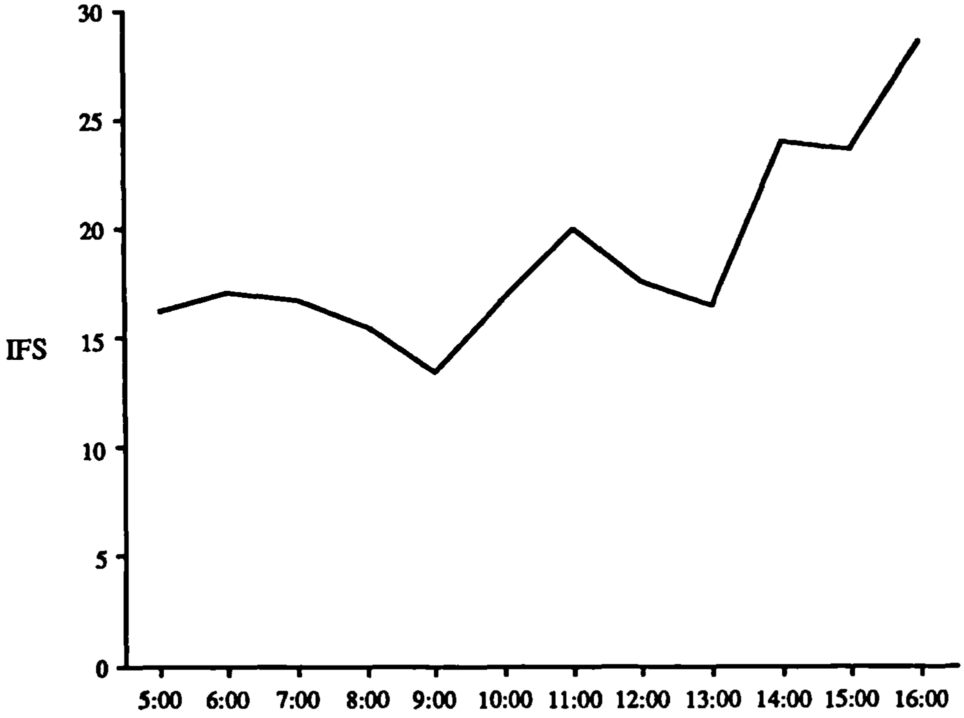
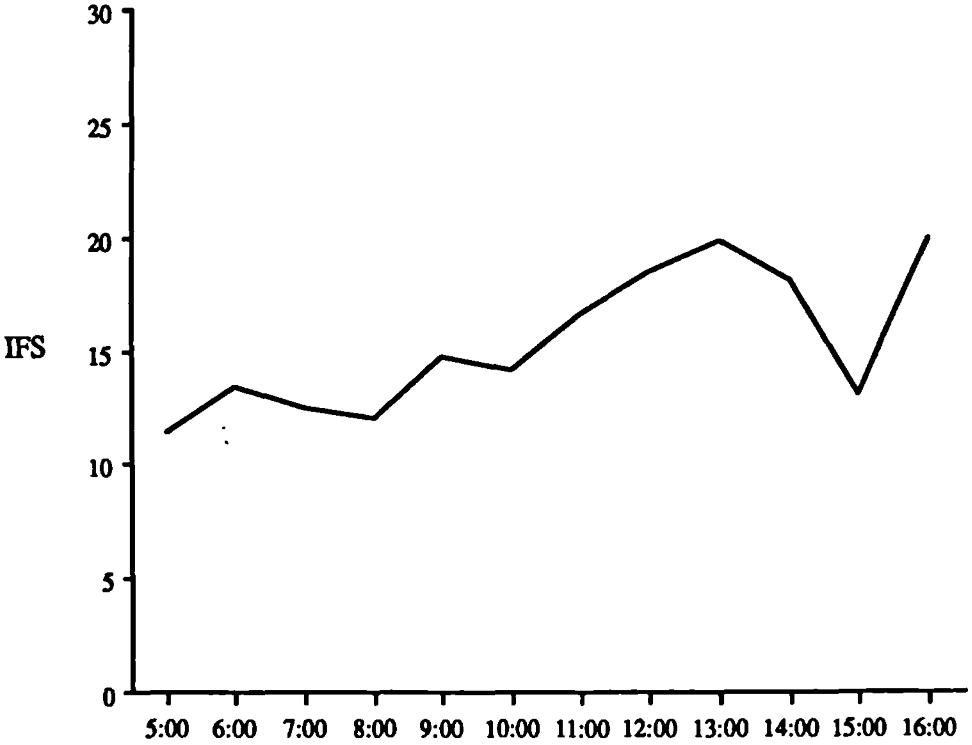


Figure 4.12 presents a comparison of the daily variation in foraging success recorded during each of the five main seasonal divisions covered by the main study period. Values as for fig. 4.11. Note that values for the earliest and latest parts of the day are excluded where records are lacking.

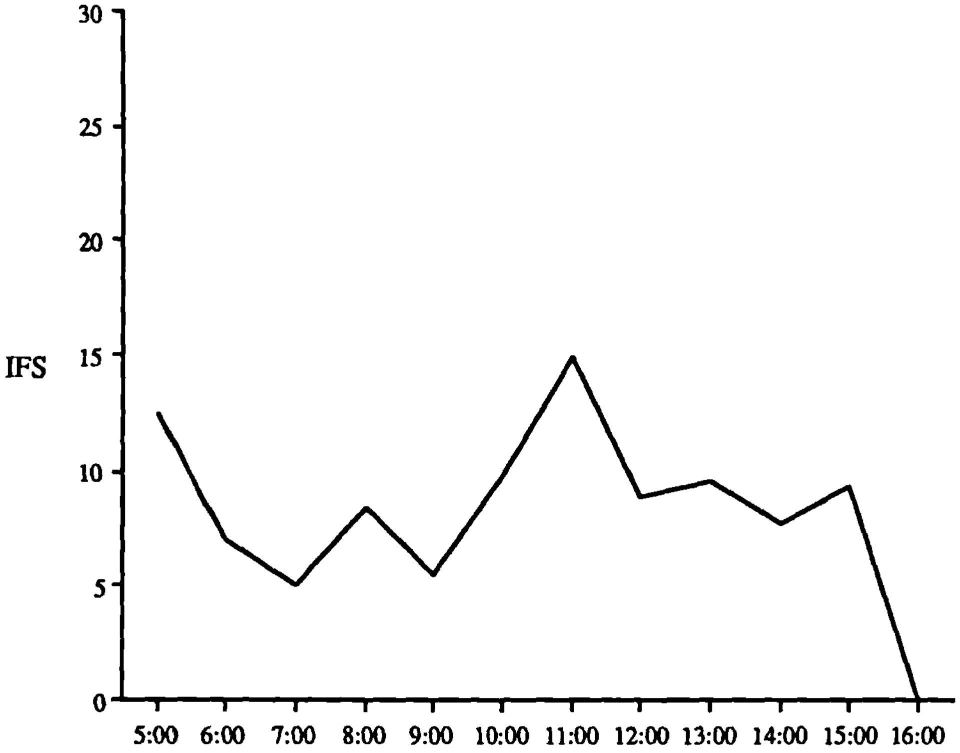
(b) Early Wet Season



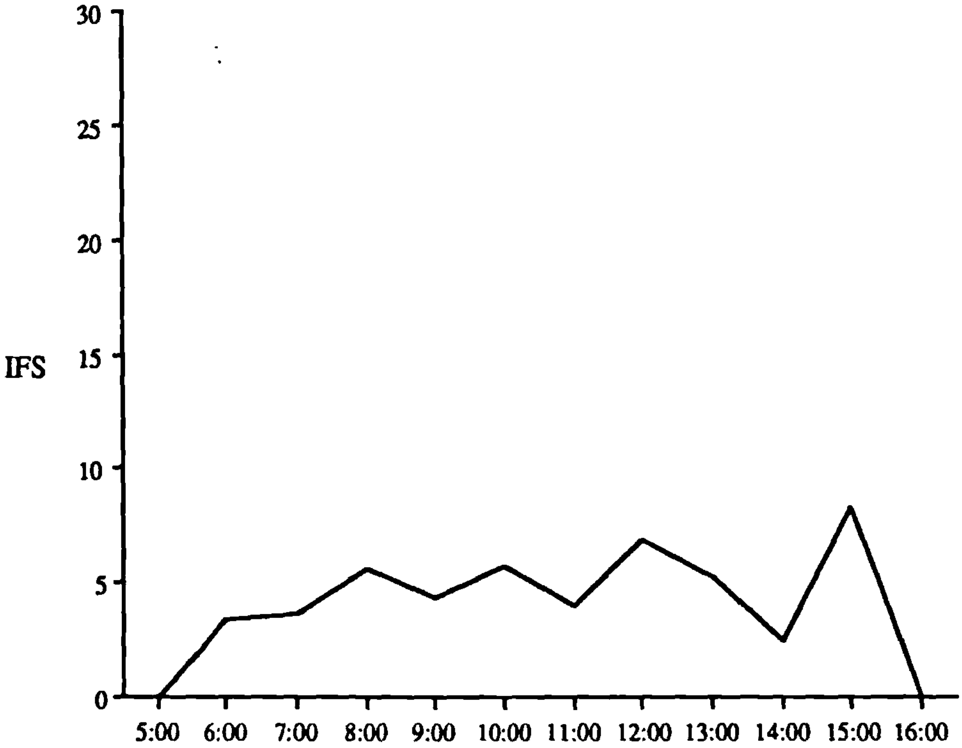
(c) Late Wet Season



(d) Early Dry Season



(e) Late Dry Season 1986



These trends also seem to have been influenced by fluctuations in the availability of different types of prey during different seasons (see chapter 6). The group's foraging behaviour must also be analysed more closely with regard to factors such as ranging and the techniques of search and capture (see chapters 5 and 7). All of these may, in turn, have had an influence on observational bias, through differences in the visibility of activity at different levels in the forest, for example. However, the numbers of records collected at different times of the day varied very little (appendix III), and it seems reasonable at this stage, given the relatively consistent rates of foraging recorded during most seasons, to assume that these results have not been influenced by major observational bias.

The results presented here represent average trends in the group's activity patterns through the course of periods of a number of months. This use of compounded data obscures, to a certain extent, the variability of its behaviour, not only on a monthly but also on a daily basis. All features of the group's activity were subject to frequently considerable fluctuations in their timing, rates, and so on, from one day to another. While some of this variability was attributable to climatic factors, notably rainfall, it appeared, on the whole to be relatively random. Some of this variability was, however, "deliberately" random, as in the case of its approach to and ascent of sleep trees, for example. A degree of randomness on a day to day basis may also be a functional characteristic of the group's foraging behaviour, as we shall see in the following chapters.

While this presentation of the data may have obscured, to a certain extent, the variable nature of the group's activity on a daily basis, it does seem to have very clearly shown a number of distinct patterns through the course of an "typical" day, both throughout the study period and during different seasons. The relatively smooth and consistent nature of the patterns shown, and their general similarity to observed patterns in other studies, again suggest that the data were not subject to significant observational bias. This is probably a direct result of the large number of records collected during the study period. This, in turn, seems to confirm the reliability of these records for the comparison of time budgets between seasons.

Summary

The activity patterns of the *Callithrix flaviceps* study group were similar to those recorded for other marmoset and tamarin species, although a high degree of variability was observed, both in different seasons during the same year and during the same season in different years. These patterns seem to have been systematically related to observed fluctuations in both climate and the abundance of the group's principal resources. Changes in activity during periods of scarcity appeared to be similar to those recorded for *Galago senegalensis*, a prosimian of similar size and dietary preferences. A number of patterns are of particular interest:

1. The study group was active for a relatively short period each day. Activity began at least twenty minutes after full light and was usually terminated more than one hour, sometimes more than two hours, before dusk. The average period of daily activity recorded during the wet season months (10 hours, 21 minutes) was more than one hour longer than that recorded during the dry season (9 hours, 14 minutes). This correlates with differences in the average length of the daylight period. The length of the activity period was also influenced by ambient temperatures and rainfall.
2. The group spent a relatively small proportion (26.8%) of its daily activity period foraging for prey, and a relatively large proportion resting and engaging in miscellaneous, mainly social, activities (24.8% and 11.6% respectively). It did, however, spend a smaller proportion (10.6%) of its time feeding on plant material than expected. This is thought to have been a consequence of the relatively large proportion of gum in its diet during most of the year.
3. Major seasonal changes in the group's behaviour was recorded. In general, it devoted more of its time to foraging for prey when insects were less abundant, but was apparently far less successful. It also spent more time travelling during periods when insects were scarce, and less resting and socialising. Feeding on plant material was, on the other hand, a relatively stable feature of the group's activity throughout most of the year.
4. The only exception to this general pattern was recorded during the late wet season months when edible fruits were abundant. During this period, the

group devoted a relatively large proportion of its time to feeding on plant material, and a relatively small proportion to insect foraging, even less than during the previous months when insects were more abundant.

5. The daily activity cycles of the study group were similar to those recorded for other marmoset and tamarin species. The group travelled more, on the whole, during the early part of the day, and rested more during the afternoon, although there was no distinct reduction of foraging or travelling at midday. Foraging activities were relatively constant throughout the main part of the day, although feeding on plant material exhibited noticeable peaks during the early morning and late afternoon.

6. These patterns were relatively constant through the different seasons, although some variations were observed. The degree of bimodality in feeding on plant material was most marked when insects were least available and least obvious during the early wet season when insects were most abundant. Foraging activities showed distinct early morning and late afternoon peaks during the latter period.

7. Foraging was more successful in general, according to the records of prey consumed, during the later part of the day. This pattern was most obvious during the wet season months when prey was more abundant and the group's foraging was more successful overall.

5

Ranging Behaviour

In the previous chapter, the use of time by the *Callithrix flaviceps* study group was considered in relation to constraining factors such as fluctuations in the abundance of resources. In this chapter, we go on to analyse the spatial dimension of the group's behaviour in relation to other aspects of its ecology. Its home range has been described in detail in chapter 3. The location is characterised by hilly, often steeply inclined terrain and patchy secondary forest in various stages of regrowth. Seasonal changes in variables such as leaf cover and insect abundance also appear to follow distinctly different trends in different areas. We would expect these, among other features, to have a major influence on the group's use of its home range.

The use of space by primate groups is, like their activity patterns, influenced by a variety of factors, including body size and dietary adaptations. Larger animals can travel greater distances than smaller ones and are thus able to exploit much larger ranges, although they may only utilise a very small area on any specific day *e.g.* the home ranges of *Brachyteles arachnoides* groups at FMC exceed 150 ha, but they sometimes "camp out" in large fruiting trees for a number of days, utilising far less than 1% of this area [Strier, 1986]. The ability of larger-bodied primates to utilise more abundant, poorer quality foods allows them to achieve much greater biomasses on the whole and, often, much higher population densities than smaller species [Martin, 1981; Terborgh, 1983; Pitchford, 1986]. Folivorous primates such as *Alouatta* may achieve particularly high population densities, utilising smaller home ranges and travelling very much shorter distances each day than many smaller platyrrhines [Mendes, 1985; Crockett and Eisenberg, 1987].

Most callitrichid species, including *C. flaviceps*, not only have relatively large home ranges (see tables 1.2 and 5.1), but also travel relatively long distances each day. It seems likely, from comparisons with other primates, that the major factor influencing these characteristics is the relatively large insect component of their diets. Unlike the plants which bear edible fruit, leaves or exudate, insects and other prey animals are highly mobile. While wholly folivorous/frugivorous primates utilise relatively stable resources between which they can usually travel directly (although some monitoring of seasonal resources is probably necessary), marmosets and tamarins are faced with the additional problem of locating and capturing small, cryptic prey animals dispersed randomly through the environment. Ranging behaviour clearly depends on a complex interaction of a variety of factors. A review of the information available on the ranging patterns of other marmoset and tamarin species will provide an important frame of reference for the detailed analysis of the patterns recorded for the *C. flaviceps* study group.

Table 5.1

Ranging Data for Selected Neotropical Primate Species

Species	Adult body weight (kg)[1]	Home range (ha)	Mean daily path length (m)	Source
Alouatta palliata	6.5	31.0	443.0	Milton, 1980
Alouatta fusca	5.0	8.0	523.0	Mendes, 1985
Aotus trivirgatus	0.8	10.0	710.0	Robinson *et al.*, 1987
Ateles paniscus	7.5	220.0	-	van Roosmalen, 1980
Brachyteles arachnoides	12.0	168.0	1282.0	Strier, 1986
Callicebus personatus	1.2	4.7	695.0	Kinzey & Becker, 1983
Callithrix flaviceps	0.4	35.5	1222.5	Present study
Cebus albifrons	2.8	>150.0	1820.0	Terborgh, 1983
Cebus apella	3.2	81.0	2070.0	Terborgh, 1983
Chiropotes satanus	3.0	>200.0	2500.0	van Roosmalen *et al.*, 1981
Saimiri sciureus	1.0	>250.0	-	Terborgh, 1983

[1] Estimates adapted from various sources.

Chapter 5

Ranging Patterns of Marmoset and Tamarin Groups

Groups of marmosets and tamarins, like those of most other arboreal primate species, usually have relatively well-defined and fixed home ranges, from which they rarely migrate or "wander erratically" [*cf.* Brown and Orians, 1970]. Specific patterns of home range use are influenced, to a greater or lesser extent, by many factors, including the distribution of resources, the needs of territorial defence and climatic conditions. Field studies have demonstrated the adaptability of marmosets and tamarins to a wide variety of habitat types, a characteristic which is reflected in the variability of the use of space by individual groups. While there is, as for most other aspects of their ecology, relative little detailed information available on ranging patterns, it does seem possible to identify certain general trends.

Many arboreal primates are territorial by nature, with groups actively defending specific areas for their exclusive use. Territoriality is, however, a relatively poorly defined and highly variable aspect of primate behaviour. The howler monkeys (genus *Alouatta*) are a good example of this problem. Their distinctive howling choruses, directed at neighbouring groups, appear to be a clear expression of territorial behaviour. In practical terms, however, the home ranges of howler groups may overlap considerably with those of neighbouring groups [up to 63%, Sekulic, 1982], and some authors have argued that this indicates that these animals are not, in fact, territorial [see Crockett and Eisenberg, 1987]. While a species may thus exhibit "actual or ritualized agonistic encounters" [Sussman and Kinzey, 1984: p. 440], the maintenance of areas of exclusive use by individual groups can be extremely variable. A number of factors may determine this variability, including home range size, the distribution of resources, population density and possibly also the relatedness of the members of neighbouring groups.

It seems that most callitrichid species exhibit behaviours indicative of territoriality [Sussman and Kinzey, 1984]. The actual defence of an area of exclusive use by marmoset groups does, however, appear to be highly variable, even for groups of the same population [Lacher *et al.*, 1981; Hubrecht, 1985; Stevenson and Rylands, in press]. Tamarins exhibit even more variability, from the almost total exclusion of neighbouring groups from a well-defined territory [Terborgh, 1983; Terborgh & Stern, 1987] to the defence "of the area around the group at a given point in time" [Dawson, 1979: p. 280]. Tamarin groups may also even merge for short periods [Castro and Soini, 1978; Izawa, 1978]. It is likely that the degree of home range overlap between groups has been under-estimated in most studies due to the relatively short periods of observation involved in most cases. Overall, this variability, while suggesting that callitrichids are not strictly territorial, seems to further emphasize their adaptability to and use of a wide range of habitats, even within the same area.

When such behaviour is feasible, most marmoset and tamarin groups appear to defend an area of "exclusive use", whether the area actively defended is virtually the whole of the group's home range [Terborgh, 1983; Dawson, 1979] or a single tree [Maier *et al.*, 1982]. Rylands [1982] noted that the *C.h. intermedius* study group temporarily shifted its territorial boundary in order to include access to a stand of *Inga thibaudiana* trees bearing fruit, although its ability to do this may have been directly related to the presence of the observer, as the group whose territory was encroached was unhabituated.

The specific nature of territorial defence may also differ according to factors such as the size of the group's territory. Terborgh [1983], for example, noted that, while virtually exclusive territories of 30 ha were maintained by the *Saguinus* groups studied, the peripheral parts were only rarely visited. At Tapacura, on the other hand, *C. jacchus* groups entered the peripheral quadrats in which intergroup encounters were observed far more frequently than others, although their territories were less than 2 ha [Hubrecht, 1985]. The "lowland" group of *S. geoffroyi*, on the other hand, both maintained a large territory (26 ha) and devoted a large proportion of its time to the patrolling of boundaries [Dawson, 1979]. *Saguinus oedipus* may utilise home ranges half this size, but with overlap in excess of 20% [Neyman, 1978]. These contrasts may be related both to differences in feeding ecology and competition for resources from other groups.

Terborgh [1983] has suggested that the minimisation of the distance travelled each day is a more important determinant of the ranging patterns of the two tamarin species at Manu than the patrolling of territorial boundaries.

The maintenance of a relatively large territory in this way may only be feasible, however, where there is relatively little competition for resources from neighbouring groups. Such a strategy does not appear to be feasible for the "lowland" group of *S. geoffroyi* at Rodman [Dawson, 1979]. In the case of *C. jacchus* at Tapacura, on the other hand, the use of relatively tiny territories does appear to allow both the minimisation of daily travel, and the maintenance of exclusivity through the regular patrolling of peripheral areas. It has been suggested that the density and distribution of marmoset species are directly related, in general, to those of exudate-producing trees [Ramirez *et al.*, 1978], although Terborgh [1983] believes that other factors may be equally important for the distribution of *Cebuella pygmaea* at Manu. Data on the ranging patterns of the eastern Brazilian marmosets are, however, far from complete, being based on relatively short-term studies in more or less altered habitats.

The only other marmoset for which there are good long-term data is *C.h. intermedius* [Rylands, 1982]. The home range of the study group overlapped with those of its neighbours by 22%, although, as indicated above, access to specific resources was actively defended. *C.h. intermedius* also appears to be much more frugivorous and much less gummivorous than the *C. jacchus* group species. It is thus interesting to note that the size of the *C.h. intermedius* group's home range was more similar to those of most tamarin species than to those of most other marmosets. This situation may be related to differences between the two species groups either in their morphological adaptations for gum feeding (see chapter 1) or in the abundance of exudate-producing plant species in the types of forest they inhabit, or both. The latter may also explain the relatively low densities of *Cebuella* usually encountered in the wild [Ramirez *et al.*, 1978; Terborgh & Stern, 1987]. Assessment of the importance of these, and other, factors for the ranging and territorial behaviour of different marmoset species is especially difficult. The fundamental problem is again the general lack of adequate long-term data.

The results of the present study of *C. flaviceps*, however, seem to contradict whatever trends are apparent in the data. With an area of approximately 35.5 ha, its home range was far larger than that recorded for any other marmoset, including *C.h. intermedius*. While the *C. flaviceps* group was relatively large, it was not significantly larger than the averages recorded at Aripuanã or Tapacura (table 1.1), so it seems unlikely that this difference can be accounted for by that of group size. Equally unlikely as a determinant of the large size of its range is the availability of edible exudate which appears to have been especially abundant throughout much of its range (see chapter 3). This group's range was not only exceptionally large, but also overlapped to a considerable degree with those of its neighbours (87.5%). It did appear, however, to recognise boundaries in peripheral areas of its range where long calls were usually given before it progressed (figure 5.1).

While marmoset population density and home range size are undoubtedly influenced by the density and distribution of exudate-producing trees, it is possible that there are other, perhaps more important, determinants. The available data on the home range size of the *C. jacchus* group species are far from adequate, but it does seem to be possible to draw certain limited conclusions on possible influences, bearing in mind the overall contrast between the humid coastal sites and the drier, more seasonal forest habitat available further inland (see chapter 1). *Anacardium occidentale* trees, found in high densities at the humid Tapacura site, not only produce edible gum, but also large succulent fruits. A number of other types of tree which produce edible fruits, including *Cecropia* spp., *Inga* spp. and the exotic *Arctocarpus integrifolia*, also appear to be abundant at this site [Hubrecht, 1985]. The fragmented nature of the forest cover, with relatively much larger areas of optimal edge habitat, may also be an important factor. In the drier, more seasonal forest at Barreiro Rico, São Paulo, on the other hand, a 100 ha area was found to contain "the full home range of two groups [of *Callithrix aurita*] and part of the home ranges of two other[s]" [Stevenson and Rylands, in press]. Groups at this site were also smaller than those at Aripuanã, FMC or Tapacura [*ibid.*]. In the light of the findings of the present study, it seems likely that the population density and typical home range size of *C. aurita* at Barreiro Rico is similar to that of *C. flaviceps* at FMC.

While there are no quantitative data on the relative density of exudate-producing trees at any of these study sites, the results of the present study appear to confirm that the abundance of such plants is not the only influence on home range size. Secondary forest, a preferred marmoset habitat, is characterised by concentrations of single tree species. Many typical colonising trees and lianas are members of the family Leguminosae, most of

Figure 5.1 (facing page)

The Distribution of Long Calls Recorded during Scan Sampling

The distribution of the study group's long calling is shown according to the number of months in which long calls were recorded in quadrats during scan sampling.
The 50 m x 50 m quadrats used for the analysis of the group's ranging are shown schematically in this figure. The marginal quadrats whose dimensions were less than the standard size are represented by the regular polygons (square, rectangular or L-shaped) which most closely reflect their actual form. All standard-sized quadrats are represented by squares. This schematisation is used in all following figures which present details of the study group's range use.

Key:

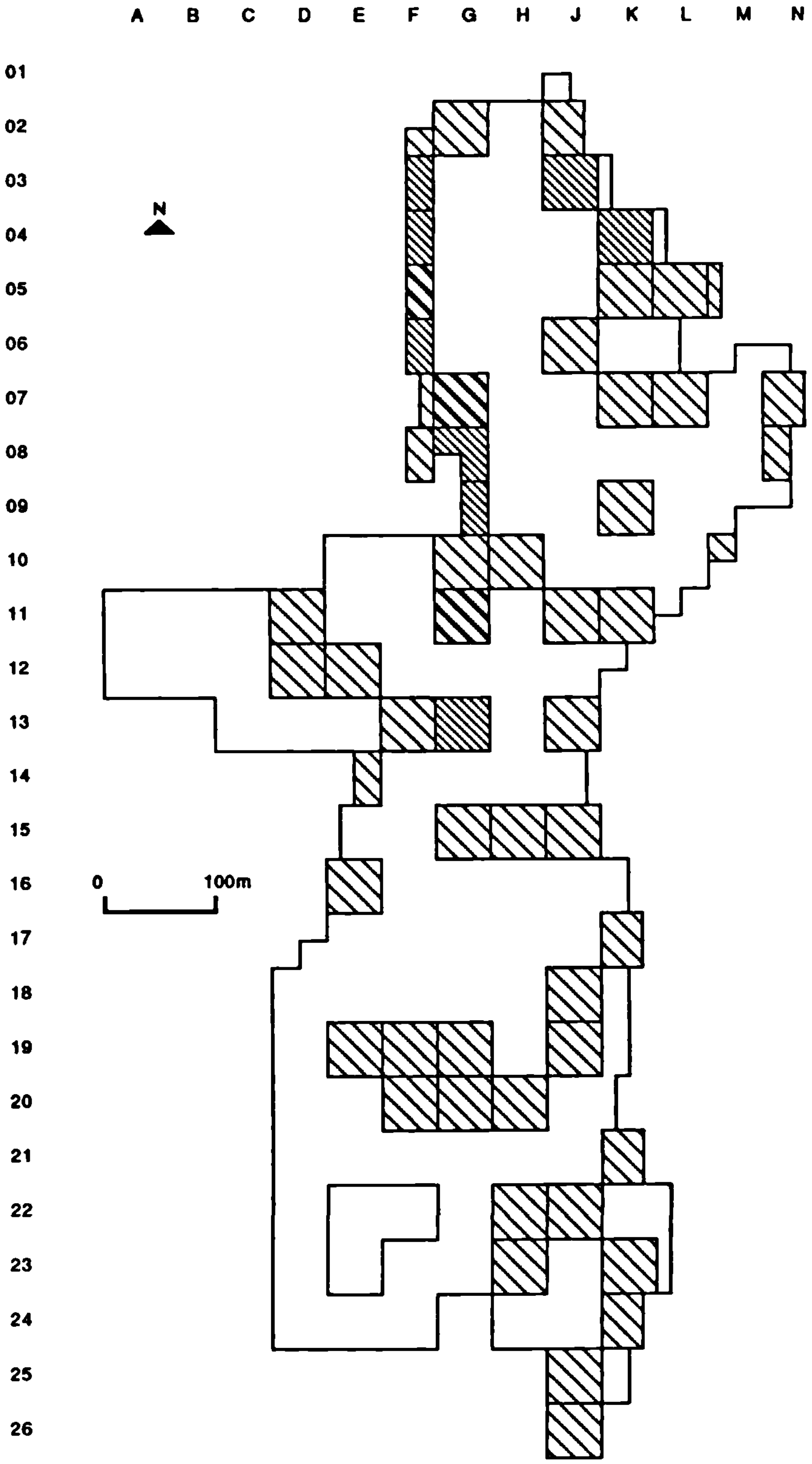
☐ *Long calls not recorded*

Long calling recorded in quadrat during:

▧ *1 or 2 months*

▨ *3 or 4 months*

▧ *5 or 6 months*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which appear to produce edible exudate. Other forest types, such as gallery forest within the *cerrado*, may also contain relatively high densities of gum-producing trees [Santos de Faria, 1984b]. In addition, marmoset groups appear to require only a relatively small number of gum trees to survive [Maier *et al.*, 1982], even in the long term [Stevenson and Rylands, in press].

While there are again no quantitative data, there is circumstantial evidence to suggest that there are considerable differences in both the abundance of insects and their availability to marmoset groups at the different study sites (see chapter 4). In addition to absolute differences in their numbers, the direct competition of other insectivorous primates for the available insects may be an important factor, as it seems to be where *Galago senegalensis* and *Galago crassicaudatus* occur sympatrically [Harcourt, 1986].

At Tapacura, and other study sites in northeastern Brazil, *C. jacchus* is not sympatric with other primate species. Other eastern Brazilian marmoset populations are usually sympatric with *Cebus apella*, and also often with *Callicebus personatus*, although insects are a relatively unimportant component of the diet of the latter [Kinzey, 1981]. *Callithrix penicillata kuhlii* is also sympatric with *Leontopithecus rosalia chrysomelas* at Una [Rylands, 1982]. As we have seen, *C.h. intermedius* is sympatric with five possible competitors at Aripuanã. While marmosets may avoid competition with these other species to a certain extent through different foraging techniques, there appears to be a considerable degree of overlap in the types of prey consumed by different insectivorous platyrrhine species [see Terborgh, 1983: table 6.5, p. 106]. Such overlap is likely to be greatest at sites where insects are least abundant, and during periods of scarcity in particular.

While it may be argued, then, that the high density of *A. occidentale* trees at Tapacura is the primary determinant of the small ranges of *C. jacchus* groups at this site, the available evidence does not contradict the possibility that insect availability is a major, if not the primary factor. An important assumption underlying this idea is that marmosets require a mixed and balanced diet of animal and plant material, and that a diet consisting entirely of gum would not support dense populations in the long term. This does not seem unreasonable, given evidence of the dietary requirements of captive *C. jacchus* [Hearn *et al.*, 1975].

As we have seen, both Tapacura and Una enjoy humid, relatively stable climates. It thus seems reasonable to expect that the abundance of arthropods is relatively similar at these two sites. Simplistically, we might see the relatively larger home ranges of *C.p. kuhlii* (table 1.2) as a consequence either of a difference in the density of exudate-producing trees, of the competition from other primates for insect prey, most significantly *L.r. chrysomelas*, or of some combination of both. Interestingly, Rylands [1982] noted that *L.r. chrysomelas* captured larger prey than *C.p. kuhlii.* While the *Callithrix flaviceps* study group at FMC did have abundant supplies of gum, it seems likely that it was faced with far greater seasonal fluctuations in the availability of arthropods. It also faced competition for this prey from *Cebus apella.* The far greater contrast in home range size between *Callithrix flaviceps* and *Callithrix jacchus* thus appears to support the idea that the availability of arthropod prey may be the most important determinant of home range size.

The distribution of the two principal resources utilised by marmosets (insects and plant exudates), both in time and space, is clearly very different. Folivorous insects, and other types of prey animal, appear to be relatively evenly distributed throughout the forest, although their populations, as we have seen in chapter 3, undergo significant fluctuations during the course of the year. Exudate-producing trees, on the other hand, are not only fixed, and often clumped, in space but also provide marmosets with a relatively constant supply of nutrients throughout the year. It is thus probably the stability, rather than the overall abundance, of the supplies of nutrients provided by gum-producing trees which allows some marmoset species to maintain such comparatively small ranges. Terborgh & Stern [1987], for example, suggest that the dependence of *S.f. weddelli* on the nectar of *Combretum assimile* and *Quararibea cordata* during the dry season at Manu is the major determinant of this tamarin's use of ranges as large as 120 ha. While the availability and distribution of insects may thus be the major determinant of home range size, the distribution of exudate-producing trees will probably have the greatest influence on the territorial behaviour of marmoset groups.

A further important influence on the distribution of resources, and of ranging patterns, is that of habitat types within a group's range. Almost all studies, including the present one, have recorded distinct preferences for disturbed or secondary forest, low levels in the canopy and edge habitat [Sussman and Kinzey, 1984]. Regeneration of the forest on BCI in Panama has been seen as the primary cause of the decline in the numbers of *S. geoffroyi* at that location [Moynihan, 1970]. Most authors have explained this preference in terms of the more abundant vegetation in such forest, at or near its edges in particular, in comparison with less disturbed or primary forest. It has also been assumed that this comparatively abundant vegetation supports significantly larger populations of insects, on average, than that of primary forest, although there seems to be no good quantitative evidence, as yet, to support either assumption.

While samples from understorey vegetation have shown a particular abundance of insects [Janzen and Schoener, 1968; Janzen, 1973a, 1973b], this is not necessarily greater than that of the upper canopy of an undisturbed primary forest, as assumed by Sussman and Kinzey [1984]. The main problem here is the taking of directly comparable samples of the insect populations present in both types of vegetation. Without such evidence, there seems to be no good *a priori* reason to assume that there is any significant difference in the abundance of insects in the two types.

As we have seen in chapter 3, much of the habitat within the home range of JG1 underwent marked fluctuations in both leaf cover and arthropod abundance during the course of the year. Qualitatively, most of the secondary forest was more deciduous than any equivalent area within the less disturbed and primary forest of the FMC reserve. This seems to imply that, during the dry season months at least, much of the secondary forest at this location probably supports fewer insects than an equivalent area of primary forest. In contrast, both the leaf cover and insect populations of the part of the forest bordering the river Manhuaçú were relatively abundant throughout the year. Clearly, neither secondary forest nor edge habitat is homogeneous, and it would seem that there are a variety of factors to be taken into account in the interpretation of the influence of habitat type on the ranging patterns of marmoset groups.

Seasonal fluctuations in the abundance of resources appear to have a considerable influence on both ranging and territorial behaviour. At a very basic level, the home range of any primate group must be large enough to provide an adequate supply of resources throughout the year, and through the period when resources are least abundant in particular. As we saw in chapter 4, periods of scarcity frequently stimulate major changes in primate activity patterns, according to factors such as body size and dietary habits. The most obvious seasonal influence on the ranging of most species is the fruiting of trees. The patterns of seasonal change in the ranging of some callitrichine species have been interpreted as being directly determined by the distribution of fruiting trees [Rylands, 1982; Terborgh, 1983; Soini, in press].

Less obvious factors, such as the distribution of arthropods, seem, on the whole, to be ignored, possibly because they are only poorly understood. While the utilisation of fruit or exudate obviously requires that a group visits a number of specific locations during the course of its daily ranging, its movements between these fixed points may be far more significant with regard to the interpretation of foraging strategies and the optimal use of available resources. As we have seen, insects were not only often more abundant in some areas than others, but the degree of difference fluctuated considerably during the course of the year. Looking at the situation in even finer detail, it seems reasonable to assume that the distribution of arthropods (especially the relatively less mobile forms) will be affected by a group's foraging activities on a day-to-day basis. In this case, an area visited on a certain day may contain significantly fewer arthropods on the following day than a similar neighbouring area which was not visited. Home range use may thus reflect both long- and short-term fluctuations in arthropod abundance.

As the *C.h. intermedius* and *C.flaviceps* study groups were of similar sizes, it seems reasonable to make direct comparisons between their ranging patterns. The *C.h. intermedius* group utilised a total area of 28.25 ha during the course of the year [Rylands, 1982], although an area of only 12.5 ha accounted for 90% of quadrat occupation records. This was defined as its "core area" [*cf.* Kaufmann, 1962]. The *C.h. intermedius* group ranged over a larger area during each of the wet season months than it did during any dry season month, but never used an area of more than 21.5 ha in any one month. The size of its core area was, however, relatively constant. It tended to utilise a larger area, on the whole, when more plant species were included in its diet, although there was no correlation with daily path length. In this study, the group's use of its home range, and of specific forest types, was seen as being related primarily to plant food density.

S. imperator and *S.f. weddelli* groups at Manu appeared to utilise their territories in a similar way, concentrating their activity into a relatively small central area and using marginal areas only lightly [Terborgh, 1983]. Both these species were also highly frugivorous, and the areas used most intensively corresponded with the distribution of the most important fruiting trees. Seasonal patterns are not clear due to the nature of the data collection.

Very different patterns have been recorded for *S. geoffroyi* [Dawson, 1979]. This contrast appears to be based on those of habitat type and seasonality, and related differences in feeding ecology. The available habitat at Rodman appears both to be far more degraded than that at sites such as Aripuanã or Manu and to undergo far greater fluctuations in the availability of resources, corresponding with a more marked dry season. The ranging of *S. geoffroyi* groups at this site appeared to be more closely related to the distribution of edge habitat rather than to that of fruiting trees [Dawson, 1979]. The ranging patterns exhibited by groups occupying characteristically different areas at this site also differed considerably.

In an area with relatively stable resources, the "lowland" group defended most of its home range as a territory [Dawson, 1979]. The intensive use of peripheral parts of the territory appeared to be directly determined by the needs of territorial defence. The range of the "upland" group, on the other hand, located in an area where resources were both relatively scarce overall and fluctuated markedly during the course of the year, overlapped considerably with those of its neighbours and was not defended in any way. While the home range of the former group remained stable throughout the year, that of the latter increased by more than one third during the dry season. Both groups travelled relatively greater distances and used a much larger portion of their home ranges each day (approximately one third), on average, than other tamarins. These patterns appear to be related to the importance of insects in the diet of this species [Garber, 1984a]. Assuming that fruit is scarce during the dry season at Rodman (according to its marked seasonality), insects may form the basis of the diet of this species at this time of year, given its inability to systematically exploit plant exudates. This seemed, however, to lead to a severe loss of physical condition in many individuals [Dawson, 1979], a pattern not noted in the present study, despite the fact that the group appeared to be faced with at least as severe a scarcity of both prey and fruit during the dry season at FMC.

The variability exhibited by all species should, however, be borne in mind when making comparisons of ranging behaviour, especially when only a few groups have been studied, often during only short periods. Data on a *S. oedipus* population inhabiting an equally seasonal type of forest in Columbia indicate much smaller home ranges, although groups were generally smaller and even less stable than those at Rodman [Neyman, 1978]. The forest cover may also have been more mature and there is some indication that *S. oedipus* was more frugivorous than *S. geoffroyi*. Probably most important, however, is the difference in the observational methods used in the two studies. Whereas Dawson's study of *S. geoffroyi* utilised radio tracking, the *S. oedipus* study was dependent on less systematic methods. In the latter, the most detailed data on ranging were collected on comparatively small groups occupying easily accessible ranges on the margin of the forest, which is also optimal habitat. This is particularly so in the case of group UB which occupied a thin, isolated strip of gallery forest. Comparatively few data were collected on groups occupying apparently much larger ranges away from the forest margins [see Neyman, 1978: figure 7, p. 57].

The wider ranging of the "upland" group of *S. geoffroyi* during the dry season may have been specifically related to a strategy of increasing insect foraging activities, similar to that followed by the *C. flaviceps* study group (chapter 4). It is also interesting to recall, in this context, the nature of the tamarin group's territorial defence. It defended the integrity of the area around it at any point in time, but no fixed geographical space, demonstrating its priorities in clear contrast to those of the *C. jacchus* group in a similarly extreme situation which vigorously defended only its principal gum tree from neighbouring groups [Maier *et al.*, 1982].

While the distribution of resources seems to the major determinant of ranging behaviour, other factors may also have some influence. Predator avoidance, including the choice of sleep trees, seems to be particularly important. The preference for low levels in the dense vegetation of disturbed forest may be partly due to the protection offered against aerial predators, a factor which should also be borne in mind when considering the evolution of marmoset foraging strategies (chapter 7). Marmosets and tamarins generally utilise specific types of tree, usually those whose crowns are densely overgrown with lianas, for night-time roosts, and seem reluctant to utilise open-crowned trees. Dawson [1979] also saw predator avoidance as a factor in the avoidance of areas of open forest and grass by *S. geoffroyi*, particularly the latter, which not only usually borders preferred edge vegetation but probably also contains relatively dense populations of orthopterans.

As these small primates are particularly sensitive to extremes of ambient temperature, their movements may also be related to the needs of thermoregulation. In the case of high ambient temperatures, the additional shade provided by dense vegetation would further emphasize its preferential use, particularly during the middle of the day. For some species, such as *C. flaviceps*, low ambient temperatures may also be a problem, during certain times of the year. In this case, exposure to rather than shelter from direct sunlight would be the characteristic influencing habitat choice during certain times of day, from a thermoregulatory viewpoint.

Overall, while the available data are relatively few and should be treated with caution, it does seem possible to identify a number of characteristic traits on which we can draw for the present detailed analysis of the ranging of the *C. flaviceps* study group. As we might expect, the distribution of resources seems to have the most significant influence on group movements. The distribution of food plants and prey animals appear to have contrasting influences, however, the degree of which seems to be linked to their relative availability to or consumption by a group. Whereas *C.h. intermedius*, with relatively abundant supplies of plant material throughout the year, used a smaller proportion of its range during the dry season months when resources were assumed to be least available overall, the more insectivorous "upland" group of *S. geoffroyi* significantly expanded its range during the equivalent period.

Thus, while the relatively fixed and stable distribution of food plants enables groups to exploit their resources in a systematic way with a minimum of travel, foraging for prey requires far more flexibility and movement. The facultative nature of their territoriality seems to be, in part, a reflection of this contrast in the distribution of resources, with the access to plant resources being more easily defended from other groups, on the whole, than prey. The degree of territorial behaviour exhibited will also depend on factors such as the size and topography of the home range, population density and the distribution of habitat types. While the density of exudate-producing trees in a particular area may have a direct influence on the population density and range size of marmoset groups, there seems to be good evidence to support the idea that the availability of insect prey is at least as important an influence on these variables. While the presence of an abundance of exudate-producing trees within an area may provide the basis for stable and systematic ranging, the availability of arthropods may ultimately determine minimum possible home range size. As for all other aspects of their ecology, the omnivorous diet and adaptability of the marmosets and tamarins contribute to the exhibition of a wide variety of ranging and territorial behaviour both by different species and by groups of the same species.

Ranging Patterns of the Study Group

While the *C. flaviceps* study group occupied a total area of 35.5 ha during the course of the main study period, it did not use this area evenly (figure 5.2). It showed a clear preference for the northern and eastern parts of its range, except for the area directly to the south of the abandoned house (L-M at 06-08). Reasons for the relatively infrequent use of this area are not clear, but it may be related to the predominant type of vegetation, which consists of tall, relatively well spaced trees with few climbing plants and little undergrowth. Local residents extracted small trees, other plants and firewood from this area far more frequently than they did from others, probably because of its originally greater accessibility, and have thus further contributed to these characteristics of the vegetation.

According to the complete and partial 50 m x 50 m quadrats entered, the study group utilised a total area of 20.5 ha on at least one observation day in every ten, of which 11.7 ha was used on at least one day in five. Only one quadrat was entered on more than half of all observation days during the main study period. The group's clear preference for the north and east of its range correlates with a number of factors, including an absence of contact with neighbouring groups and the greatest concentrations of gum-producing plants and edge vegetation (see chapter 3).

If we take the amount of time, in terms of occupation records, spent by the group in each quadrat (figure 5.3), it is clear that it spent a comparatively

Figure 5.2 (facing page)

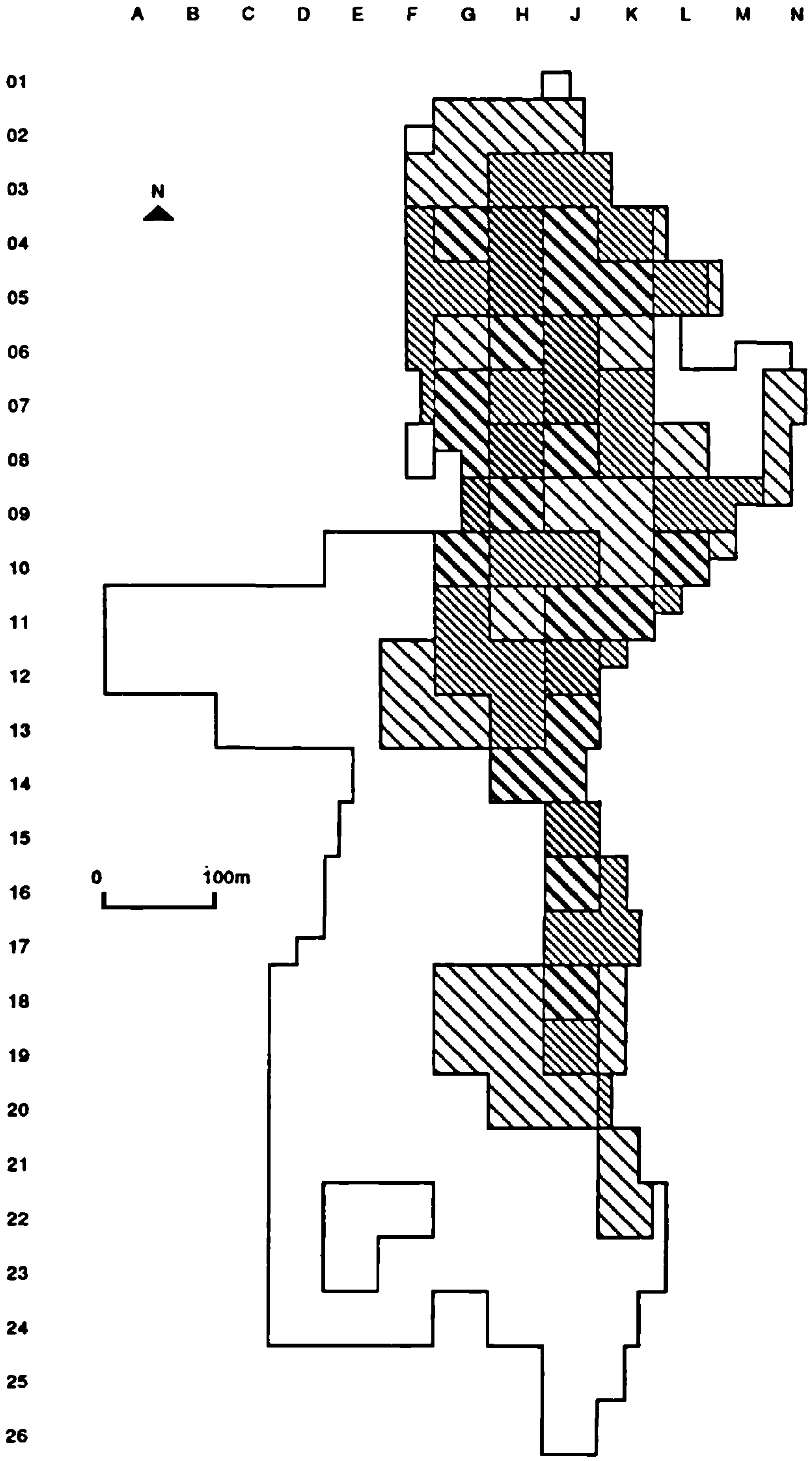
Home Range Use by the Study Group According to Observation Days

The group's use of its home range is shown in this figure according to the number of observation days on which it was recorded in each of the quadrats consituting its range during the course of the main study period (125 days).

Key:

Quadrats entered by the group on:

□	*1-12 days (less than 10% of observation days)*
▧	*13-25 days (10-20% of observation days)*
▧	*26-37 days (20-30% of observation days)*
▧	*38-50 days (30-40% of observation days)*
▧	*More than 50 days (more than 40% of observation days)*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small amount of time in some of the quadrats it visited relatively frequently, and stayed for longer periods in some it visited less frequently. This is particularly evident in the case of the southernmost quadrats, and is related, as we shall see, to differences in the group's activities in different parts of its range. The area enclosed by the quadrats whose occupation records contribute more than 50% of the total number of records for all quadrats during the course of the study period is just 6.6 ha, and the group's core area (90% or more of occupation records) covered just 18.6 ha. This represents 52.3% of the total area used during the course of the study (figure 5.4). The 12.5 ha core area of the *C.h. intermedius* study group similarly consituted only 44% of its total home range [Rylands, 1982]. The area used most intensively by the *C.flaviceps* group is roughly equivalent to that visited most often (the 20.5 ha visited on at least one day in every ten), and further emphasizes the fact that the group regularly utilised little more than half of its home range through the course of the study period.

Despite the relative isolation of the study group's home range, more than 80% of its area overlapped with those of neighbouring groups (figure 5.5). Much of the area used most intensively by the study group was thus actually located within the ranges of neighbouring groups, although it does seem likely, from observations of these groups, that they used these areas relatively infrequently. The total area of overlap did, in fact, increase following the division of the study group at the beginning of June, when neighbouring groups were observed within its range far more frequently (see figure 5.5). Much of this change is probably attributable to the formation of the new neighbouring group JG4, 60% of whose members were originally in the study group, although JG3 was also observed to encroach further into the study group's range at this time. There was no obvious increase in territorial behaviour by any of these groups. Thus, while the study group's ranging can be seen as being indicative of a minimisation of travel by the concentration of activity into a relatively small "central" area, the high degree of overlap with the ranges of neighbouring groups suggests a very different situation from that of the tamarins at Manu.

Of the 15 ha area visited infrequently (on less than one day in ten) by the group, a total of 16.5 quadrats (4.1 ha) were entered on only one day during the study period, and 20 others (5 ha) were entered on either two or three days. The value of 35.5 ha is nevertheless a conservative estimate. Three quadrats (0.75 ha) which the group was not recorded entering during the study period form a lacuna within the total area of its range, while an additional area of 9 quadrats (2.25 ha) to the north of the westernmost part of the range were visited by the group on one day in July 1985. Preliminary observations also indicated that the group ranged beyond the southern and western limits of the area used during the main study period.

The actual limits of the group's home range thus appear to have been flexible, and a good deal of care is needed in the interpretation of the data. Chance factors, for example, seem to have had an significant influence on the estimate of the total area of its home range during the study period. Judging from the factors outlined in the previous paragraph alone, this estimate could have varied between 30 ha and 40 ha. Without any strictly defined territorial boundaries, the nature of the mechanisms spacing groups and changes in their expression through time, are difficult to assess. In addition to seasonal fluctuations in resources, changes in population density, and in the size and composition of groups must have some influence on the amount of space they require. A major problem with the interpretation of the data in such broad terms, then, is the lack of any good information on how the size and shape of the group's range may have been changing through time.

Figure 5.3 (facing page)

Home Range Use by the Study Group According to Quadrat Occupation Records

The group's use of its home range is shown here according to quadrat occupation records (see chap. 2).

Key:

□	***Quadrats contributing less than 1% of total occupation records***
▧	***Quadrats contributing more than 1% and less than 2% of total occupation records***
▩	***Quadrats contributing more than 2% of occupation records to the total***

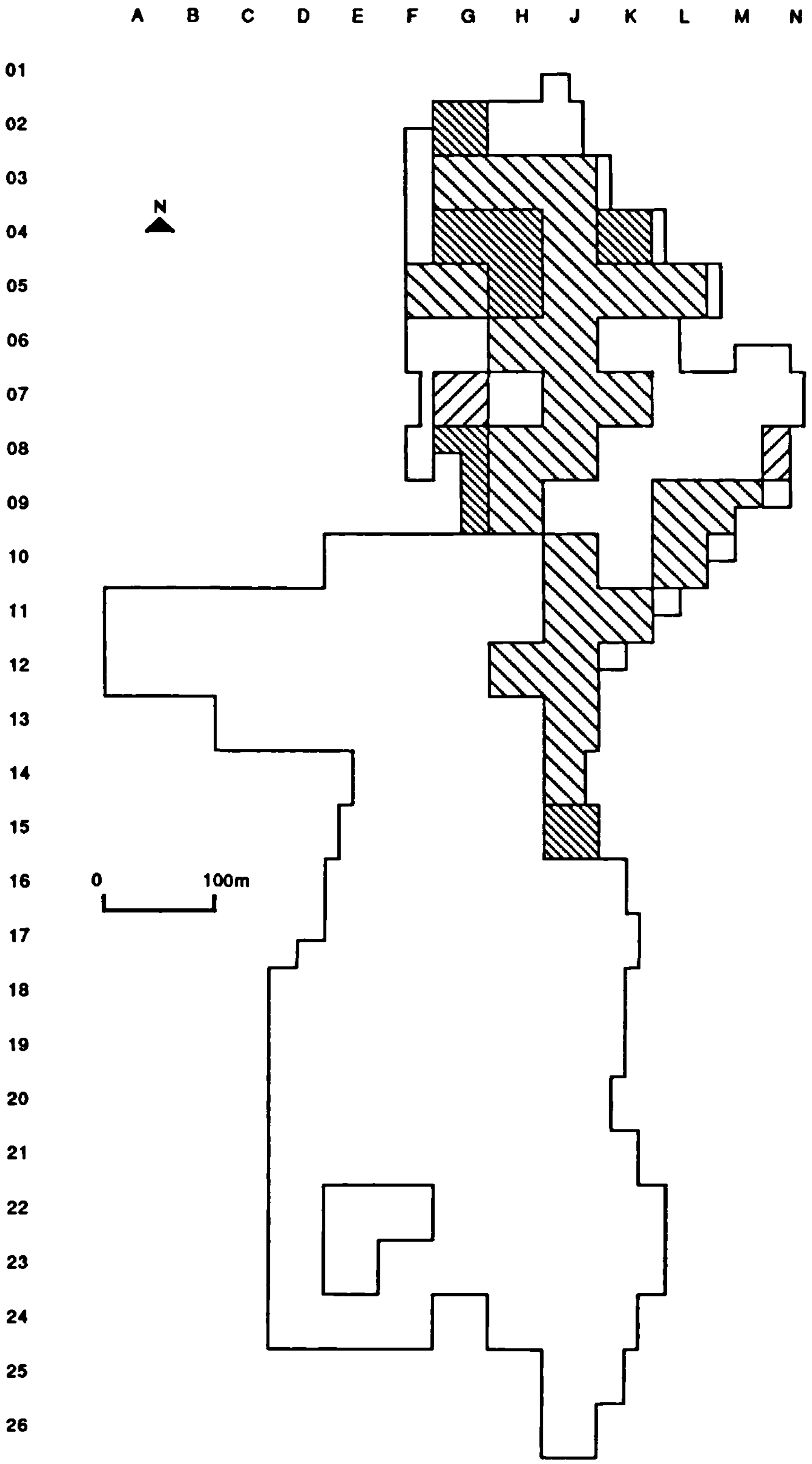
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Figure 5.4 (facing page)

The Core Area Used by the Study Group

The area contributing the first 90% of quadrat occupation records is outlined and shaded in figure 5.4. The area contributing the first 50% of records is indicated by the darker shading.

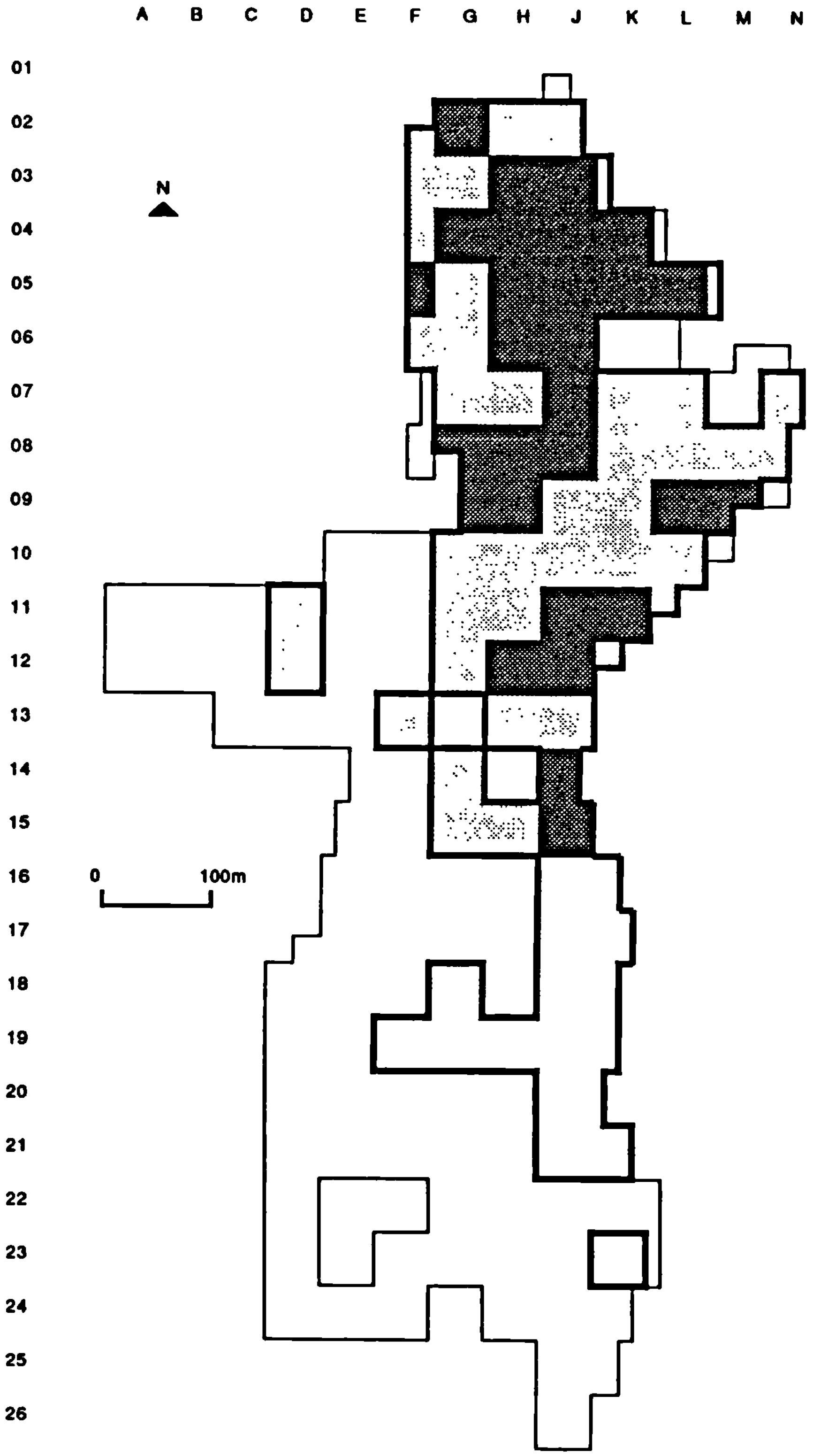
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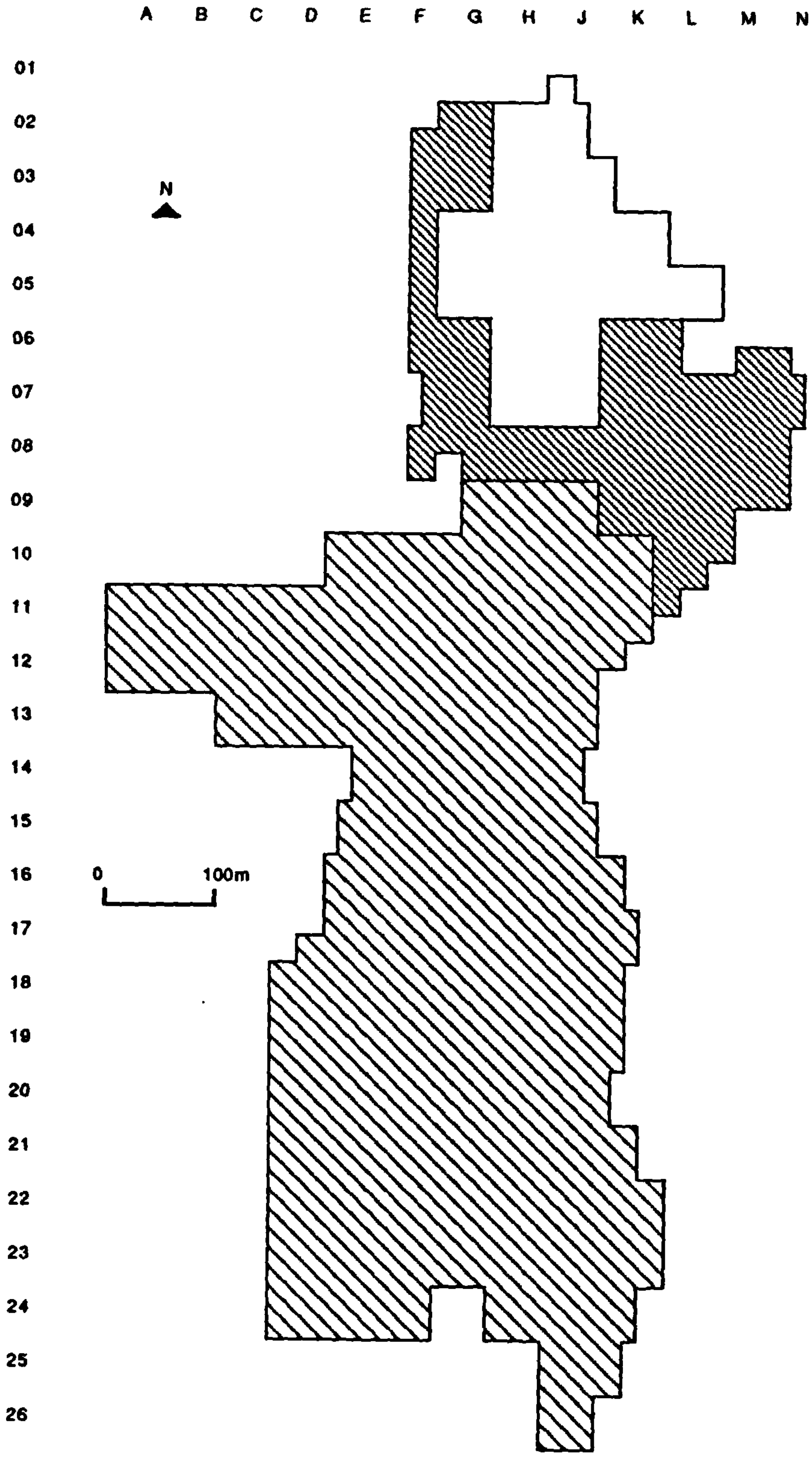
Figure 5.5 (facing page)

The Overlap of the Study Group's Home Range with those of Neighbouring Groups

Figure 5.5 shows the estimated area of overlap of the study group's home range with those of its neighbours. It should be noted that, while the northern, eastern and southern limits of the area of overlap are defined according to recorded sightings of neighbouring groups, the inclusion of some areas in the west and southwest is based on the assumption that neighbouring groups occupied the whole of these outlying areas. While this assumption seems reasonable, given both the topography of the range and the extensive ranging of marmoset groups at this site, it is not entirely impossible that some of the quadrats included have never been visited by these groups.

Key:

□	*Area used exclusively by the study group*
▨	*Area of overlap up to the beginning of June 1986*
▧	*Additional area of overlap following the formation of JG4*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Chapter 5

Seasonal Patterns

The group not only exhibited a marked and consistent preference for the northern and eastern portions of its home range throughout the study period, but also utilised areas of relatively similar size, on average, during equivalent periods (daily, monthly and so on) of the different seasons. For some features, there is more variation between the months of the same season than between the months of different seasons. There is, however, some important seasonal variation in home range use, in terms of the specific area utilised by the group and the distribution of its time within that area. This variability seems to be systematically related to fluctuations in the abundance of resources during the course of the year, as well as to factors such as the changes in activity patterns outlined in the previous chapter.

Day Range

The *C. flaviceps* group travelled an average of 1222.5 m per day during the study period, with a minimum path length of 650 m, recorded in February, and a maximum of 2670 m[1], recorded in May. The distance travelled by the group each day, even on consecutive days, was highly variable, as reflected in the standard deviations for different months which were as high as ± 479.6 m in the wet season month of October and ± 539.5 m in the dry season month of May (table 5.2). There was, in fact, an apparent, but not strictly consistent, alternation between shorter and longer daily paths on consecutive days. Taking the first six observation days of June 1986 as a random example, the distances travelled on consecutive days were 1470 m, 1860 m, 1020 m, 1165 m, 1915 m and 860 m.

While the group did forage above army ant swarms on occasion, this did not seem to have any noticeable effect on path length, as it did in the case of *C.h. intermedius* [Rylands, 1982]. Monthly averages varied between 1022.2 m and 1455 m, with both these extremes occuring in the wet season

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[1] *This was an exceptional value (the next largest was 2200 m), probably associated with subsequent changes in the group's composition.*

(table 5.2), and there was no significant difference between the values for the dry season months as a whole and those of the wet season (Student's t test: $t = 1.021$, d.f. = 123, $p = 0.309$). Overall, the values recorded are comparable to those recorded for species such as *S. nigricollis*, *S. fuscicollis*, *S. imperator* and *C.p. kuhlii*, although they are consistently smaller than those recorded for *S. geoffroyi*, *S. oedipus* and *C.h. intermedius* (see table 1.2).

The mean values for the area used by the group each day (calculated from the quadrat occupation records) varied between 4.6 ha and 6.2 ha each month (table 5.2). While these values were slightly larger, on average, during the wet seasons months, there was again as much variability within as between seasons, and no significant difference between the values for the dry and wet season months as a whole (t test: $t = 0.989$, d.f. = 123, $p = 0.324$). These values are, overall, far more consistent than those recorded for *C.h. intermedius* [Rylands, 1982], whose average day range varied between 5 ha and 8.9 ha in different months and showed significant differences between

Table 5.2

Monthly Variation in the Daily Ranging of the Study Group

	Daily path length (m):		
Sample	Mean	Range	Mean day range (ha)[1]
August 1985	1073.5 ± 166.5	755-1335	4.9 ± 0.8
September	1245.6 ± 370.0	760-1805	5.1 ± 2.0
October	1217.0 ± 479.6	745-2200	5.7 ± 1.8
November	1455.0 ± 294.0	950-1920	6.2 ± 1.2
December 1985	1350.6 ± 261.9	1045-1905	6.2 ± 1.2
January 1986	1338.5 ± 343.8	845-1870	5.5 ± 1.6
February	1022.2 ± 221.4	650-1380	4.7 ± 0.9
March	1140.0 ± 226.8	840-1540	4.8 ± 1.4
April	1160.0 ± 266.4	800-1655	4.8 ± 0.9
May	1230.0 ± 539.5	815-2670	5.6 ± 2.8
June	1302.5 ± 382.7	790-1915	5.9 ± 1.7
July	1109.0 ± 160.7	945-1965	4.6 ± 0.9
August 1986	1264.4 ± 282.4	820-1665	6.1 ± 1.8
All months:	**1222.5 ±331.3**	**650-2670**	**5.4 ±1.6**

[1] Calculated by the number of full or partial 50 m x 50 m quadrats entered (see chapter 2).

Table 5.3

Seasonal Variation in the Daily Ranging of the Study Group

Sample	Daily path length (m): Mean	Daily path length (m): Range	Mean day range (ha)[1]
Late dry 1985	1155.0 ± 287.2	755-1805	5.0 ± 1.5
Early wet 1985	1340.2 ± 365.8	745-2200	6.0 ± 1.4
Late wet 1986	1166.9 ± 285.2	650-1870	5.0 ± 1.3
Early dry 1986	1195.0 ± 415.7	800-2670	5.2 ± 2.1
Late dry 1986	1222.5 ± 292.9	790-1965	5.5 ± 1.6
All dry season samples:	1195.1 ± 328.8	755-2670	5.3 ± 1.7
All wet season samples:	1250.6 ± 334.0	650-2200	5.5 ± 1.6

seasons, with both day range and path length values being larger during the wet season. In addition, whereas the *C.h. intermedius* group visited more than one third, and as much as 44%, of its monthly range during the course of an average day, the *C. flaviceps* group visited only between 22.5% and 29.7%. This is consistent with both the relatively smaller day ranges and the larger monthly ranges of the latter (these were 16.8-26.1 ha for *C. flaviceps*, compared with 11.5-21.5 ha for *C.h. intermedius*).

The consistency between seasons in the group's daily ranging is somewhat surprising, given the marked changes in activity patterns noted in chapter 4. While the group did spend a larger proportion of its time travelling during the dry season, however, it was active for a shorter period each day, and the two factors appear to have cancelled each other out overall, in terms of the distances travelled. Differences within seasons again seem to be as relevant as those between seasons (table 5.3).

The group ranged, for example, over an average area of 6 ha per day during the first three months of the wet season, but this value fell significantly to just 5 ha during the second half (*t* test: $t = 2.812$, d.f. = 56, p=0.007). The average path length also fell, from 1340 m to 1163.5 m, but this was not such a marked difference (*t* test: $t = 1.902$, d.f. = 56, p=0.062), although this may have been due, in part, to the concomitant reduction in the daily activity period and perhaps also the presence of dependent infants in the group. At least two studies have shown, on the other hand, that the daily path length of primate groups can be directly, and significantly, correlated with the number of independently-locomoting group members [Waser, 1977; Kinzey, 1981]. If such a correlation is based, in part, on the nutritional requirements of the group, we would expect to have observed some increase in the daily ranging of the *C. flaviceps* group (given its larger size), or perhaps at least a maintenance of the levels recorded during the early wet season.

While a number of other factors may obviously have influenced these changes, they are correlated with both a reduction in the abundance and predation of insects, and with a significant increase in the proportion of fruit in the group's diet. If fruit partially replaced animal material in the group's diet, either preferentially or in response to a decrease in its availability, or both, this reduction in the area visited by the group each day can be seen as a reflection of a concomitant shift in its foraging activities. It is relevant to recall that the group's fruit feeding concentrated on two common tree species with a distinctly clumped distribution within their range. This pattern is thus similar to that recorded for *C.h. intermedius* during the dry season at Aripuanã, when the resources of a relatively small number of plant species were utilised. Individuals of the plant species commonly used at this time also had a typically more clumped distribution within than those of the species used during the wet season. The smaller values recorded for path length and day range size during the dry season months was seen as being directly related to these factors [Rylands, 1982].

This pattern seems to have been particularly marked during the exceptional month of February, when the *C. flaviceps* group, as we shall see, completely shifted its core area to coincide with the distribution of *Siparuna* trees in the south of its home range. *Siparuna* seeds may, in fact, provide a much richer source of nutrients, in particular proteins, and may thus be a more feasible substitute for animal material than the *Allophyllus* arils consumed during January (when insects were also, incidentally, more abundant). This is further emphasized by the contrast in the group's ranging between these two months (table 5.2).

While the group tended to range further during periods when it spent more time foraging in the dry season, this was *inversely* related to both arthropod abundance and the length of the daily activity period during the main divisions of the dry season (table 5.3). While there are no significant differences between the samples (one major problem in making comparisons is the group's division in June, see below), they do seem to reflect certain basic trends. While the exact influence of the size of the group on its ranging is not easily assessed, it may be significant that it was smaller (and younger), on average, during the late dry season of 1986 than it was at other times during the study period in general, and the preceding months in particular. The observed differences within the dry season is thus even greater if path length or range size is calculated per group member, but this may not be a valid manipulation of the data, and is probably best omitted from the present discussion.

Monthly Range

The study group utilised a slightly larger portion of its home range during the wet season months, on average, than during the dry season (table 5.4), but there was again almost as much variation within as between seasons. The differences between seasons are, in fact, less than we might expect when differences in group size, for example, are taken into account [see above, and Clutton-Brock and Harvey, 1977a, 1983]. As we have seen, the group was found in only 52.3% of its home range during more than 90% of the time. Similarly, while it utilised a range of between 16.8 ha and 26.1 ha each month, the core area was usually much smaller, represent between 54.3% and 80.2% of their respective monthly ranges.

Comparing these values with those available for *C.h. intermedius*, we see that the *C. flaviceps* study group not only utilised a much larger area each month, on average (approximately 30% more), but used that area less intensively (table 5.5). While the *C.h. intermedius* study group only utilised a core area larger than 9 ha during three months (the largest being 12.75 ha), the smallest used by the *C. flaviceps* group in any one month was 10.2 ha. The latter was, in fact, almost double the size of the smallest used by *C.h. intermedius* (6.25 ha) which, as suggested in chapter 2, is possibly at least slightly over-estimated, relative to the results of the present study. It is interesting to note that, while the group's monthly range was smallest in July, its core area was not the smallest used, and that the month with the largest

Table 5.4

Monthly Ranges used by the Study Group

Sample	Total area used (ha)[1]	Core area (ha)[1,2]	Core area as % of monthly range	Group size[3]
August 1985	18.8	10.2	54.3	13.0
September	19.7	15.8	80.2	13.0
October	20.8	12.6	60.6	13.0
November	26.1	14.9	57.1	13.0
December 1985	20.8	14.6	70.2	13.0
January 1986	21.0	14.5	69.0	14.0
February	20.8	13.7	65.9	15.0
March	19.9	12.4	62.3	15.0
April	18.6	13.1	70.4	15.0
May	25.0	13.9	55.6	15.0
June	22.5	16.1	71.6	12.5
July	16.8	11.4	67.9	11.0
August 1986	23.5	14.3	60.9	11.0
Main study:	**35.5**	**18.6**	**52.3**	**13.4**

[1] Calculated by the number of full or partial 50 m x 50 m quadrats entered.
[2] 90% of quadrat occupation records.
[3] Average number of group members per observation day (including dependent infants).

Table 5.5

Monthly Ranges used by the C.h. intermedius *Study Group*[1]

Sample	Total area used (ha)[2]	Core area (ha)[2,3]	Core area as % of monthly range	Group size[4]
September 1978	11.50	6.25	54.4	11
October	14.75	7.50	50.9	11
November	18.50	11.25	60.8	11
December 1978	20.50	12.75	62.2	10
January 1979	16.75	8.25	49.3	11
February	17.75	8.75	49.3	13
March	17.50	8.75	50.0	13
April	21.50	11.75	54.7	13
May	14.00	6.75	48.2	13
June	15.50	7.50	48.4	13
July	15.25	8.50	55.7	15
August 1979	14.00	8.00	57.1	15
Main study:	**28.25**	**12.50**	**44.25**	**12.4**

[1] Adapted from Rylands, 1982: figure 85 and appendix V, table 20.
[2] Calculated by the number of 50 m x 50 m quadrats entered.
[3] 90% of quadrat occupation records.
[4] Number of group members present (including dependent infants).

core area (September) had one of the smallest total ranges.

It is thus apparent that while the *C. flaviceps* study group did not travel as far or use such a large proportion of its range each day as the *C.h. intermedius* group, it distributed its movements more evenly, and over a much larger area, during the course of each month. This contrast may be directly linked to overall differences in the foraging strategies of the two groups, and seems to be consistent with the relative importance of fruit and insects in their diets. This hypothesis is based on the evidence presented in chapter 4, which indicates that the marmosets of the *C.h. intermedius* study group were both less insectivorous (and gummivorous) and far more frugivorous than those of the *C. flaviceps* group.

While the *C.h. intermedius* group may thus have been travelling relatively widely to visit a large number of fruiting trees each day, it seems to have done this within a relatively small area during the course of any specific period of time. This would be consistent with the idea that the distribution of fruit, rather than of insects, had the greatest influence on this group's range use, and that its insect foraging, as suggested in chapter 4, was less systematic than that of the *C. flaviceps* study group. In this case, *C.h. intermedius* would not only have been foraging in less optimal habitats than might be available within its range, it would both be visiting these areas with greater frequency and/or remaining in them for longer periods. Such behaviour would tend to diminish the group's foraging success, which seems to have been generally far lower than that of JG1 (see table 4.6), even taking possible bias into account.

The *C. flaviceps* group, on the other hand, was able to utilise a relatively small number of the abundant gum-producing plants available within its home range during any one day and thus minimise its path length, on average. It did seem to maximise, on the other hand, the area over which it travelled during the course of any particular period. As insects appear to be far more evenly dispersed through the forest environment than fruiting trees, this is consistent with the idea that the distribution of insects had the greatest influence on this group's ranging. In this case, it was not only selective of the habitats within which it forages for prey (evidence to support this idea will be presented below), but also distributed its time more evenly through such areas, minimising the depletion of resources at any particular location. Such factors would obviously tend to increase its foraging success.

The data available for other species do not allow such detailed comparisons, but they do seem to support these ideas. The tamarins at Manu, as we might expect, appear to be similar to *C.h. intermedius*, with a relatively small area used intensively during any particular period. Daily path length is slightly smaller (for *S.f. weddelli* in particular), but this may be related to habitat differences or particularly the much smaller size of the tamarin groups themselves. *S. geoffroyi*, on the other hand, not only travelled over relatively large distances, but also covered approximately one third of its home range each day [Dawson, 1979]. While somewhat different from the patterns shown by the *C.flaviceps* study group, this does not contradict the basic trend if it is borne in mind that *S. geoffroyi* may not only be far more insectivorous but also lacks the ability of the marmosets to systematically exploit gum sources.

Two months deserve closer attention. February was unique in the marked concentration of activity into the southern part of the group's home range, in an area situated well within the range of the neighbouring group JG2, although the preference for the easternmost quadrats was maintained (figure 5.6). The other feature which distinguishes February from all other months was the group's feeding on *Siparuna* seeds. *Siparuna* trees did appear, qualitatively, to be far more common in the south of its range, although the quantitative data appear to offer only equivocal evidence of a causal relationship between their distribution and that of the group's movements. As we have seen, 93.2% of *Siparuna* trees were located in the four phenology quadrats situated at the lowest altitudes, indicating a preference for more humid habitats. This does correspond with the concentration of the group's activity in the eastern part of its range, but this is also, of course, little different from other months. Only 54.1% of the 74 trees were located in the southernmost four of the eight quadrats, on the other hand, and there was no obvious difference in the proportion of individuals bearing fruit at different latitudes (73% in the southern quadrats and 67% in the north). A much larger sample of the vegetation would obviously be necessary to confirm the qualitative observations.

While other, more subtle factors may be involved, it does seem possible to conclude, tentatively, that this uncharacteristic ranging behaviour was part of a major shift in the emphasis of the group's activities in relation to the

Figure 5.6 (facing page)

Range Use During February 1986

The group's use of its range during February 1986 is shown here according to the number of days on which the different quadrats within its total range for the month were visited.

Key:

Quadrats enetered on:

▨ ***1 day***

▨ ***2 or 3 days***

▨ ***4 or 5 days***

▨ ***6 or 7 days***

▨ ***8 or 9 days***

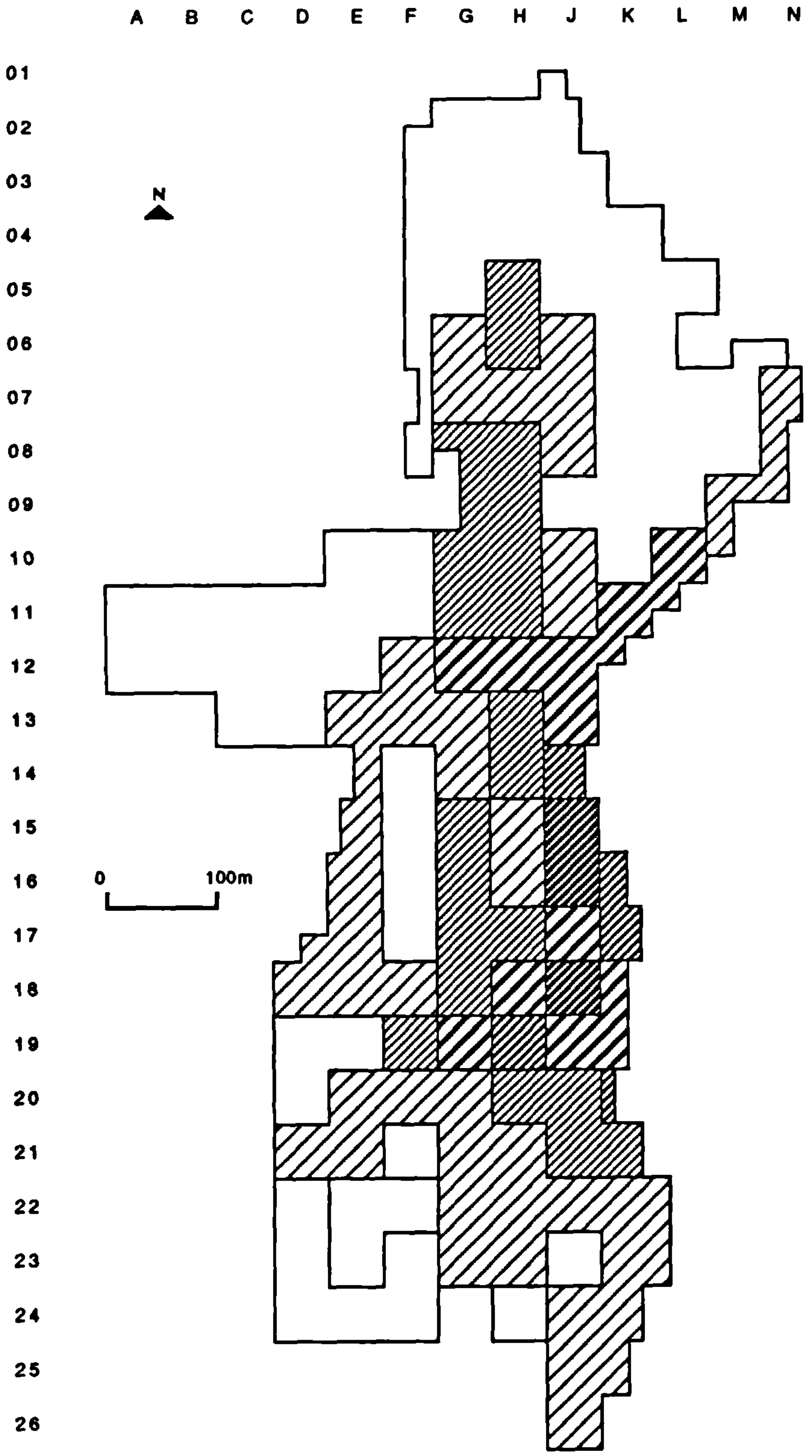
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Figure 5.7 (facing page)

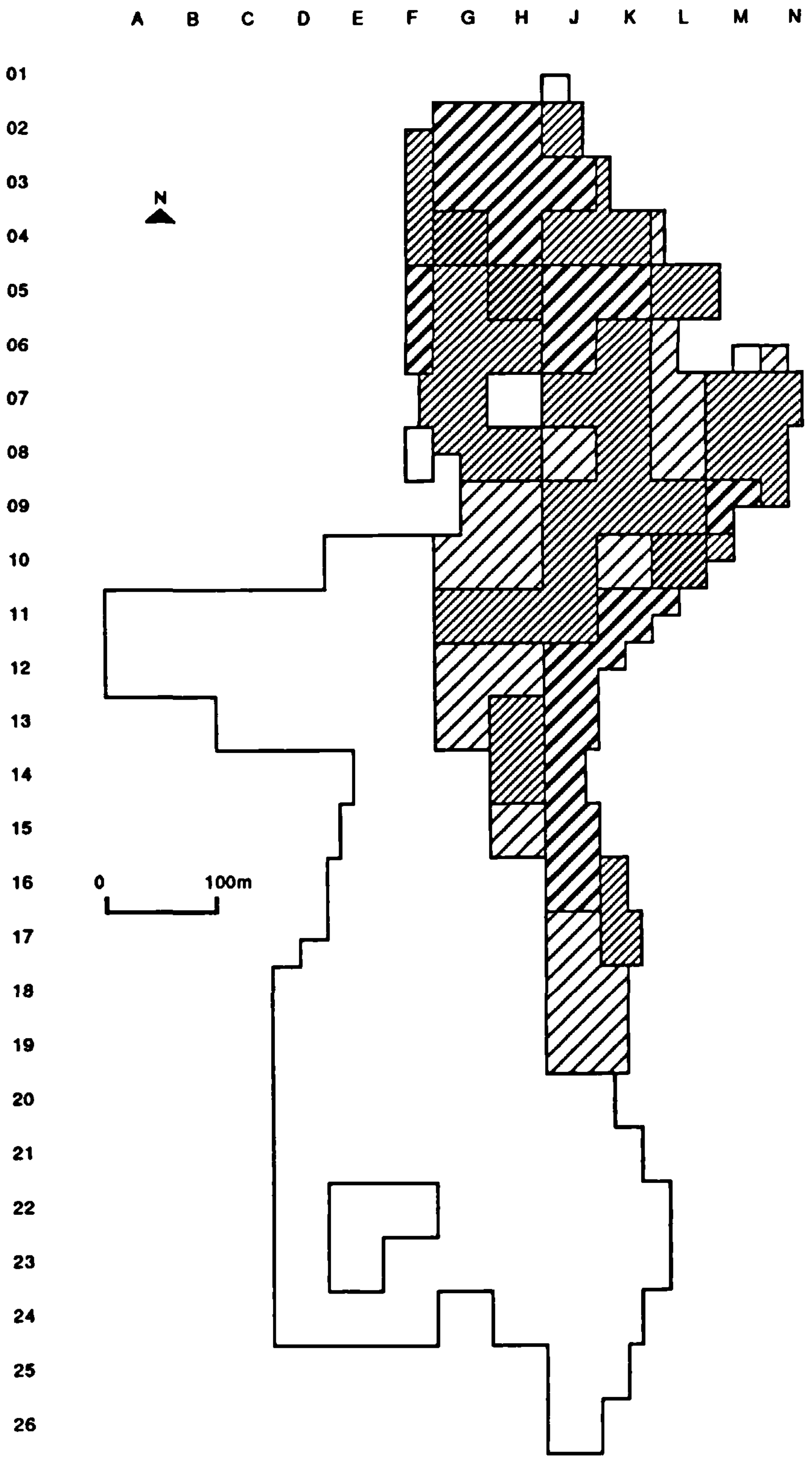
Range Use during July 1986

The group's use of its range during July 1986 is shown here according to the number of days on which the different quadrats within its total range for the month were visited.

Key:

Quadrats enetered on:

- ▨ *1 day*
- ▨ *2 or 3 days*
- ▨ *4 or 5 days*
- ▨ *6 or 7 days*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abundance of these edible seeds during this period. Foraging for insects was a less important part of its activity than during other months, especially when the abundance of arthropods is taken into account (see chapter 4). If the group's preference for the northern part of its range is related primarily to insect foraging, a concentration of *Siparuna* trees in the south would thus have made this area relatively more attractive during this month, despite the fact that it might have been foraging for insects in less than optimal habitats, on average (although insects were relatively abundant at this time).

In contrast to February, records of the group's movements during July show a marked concentration of activity in the northern part of its range, and an exceptionally small monthly range, more than 2 ha less than the next smallest recorded during the course of the study (figure 5.7). The small size of this range contrasts with those of the neighbouring months of June and August in particular, both of which were more than one third larger. Such a marked contrast is particularly anomalous as the overall trend throughout the dry season is one of an increase in the area used each month. This exceptional pattern does not appear to be closely linked to any obvious differences in the availability of resources in comparison with neighbouring months. Feeding on fruit was as rare an activity as it was in the other late dry season months, and prey was consumed less frequently than during June and only slightly more often than in August, reflecting the overall decline in the abundance of prey through the course of the dry season.

The only factor which may be important is the relative abundance of *angico* gum at this time of year, and its consumption by the group (see chapters 3 and 6). *Angico* trees are, as we have seen, particularly common in the northern part of the range. The importance of this type of gum in the group's diet during July might thus be seen as a major influence on its ranging during this month. The group consumed *angico* gum in similarly large quantities in the preceding months, however, which appears to contradict this hypothesis. In this case, the relatively large quantities of *angico* gum consumed in July can be seen as a consequence, rather than a determinant of the group's use of the northern part of its range.

The division of the study group in mid June, and in particular the formation of a new group, JG4, may be far more relevant. This event seemed to have the effect of increasing the extent of the group's ranging during the preceding months of May and the early part of June, when contact with neighbouring groups was more common than it was at other times during the study. In the second half of June (exactly half the observation days were carried out following the group split), on the other hand, the group also ranged almost exclusively within the area of its July range. It seems most likely, from the evidence, that the concentration of the group's activity into the northern part of its range was closely linked to both its reduction in size from 15 to 11 individuals and the presence of a new neighbouring group.

While the study group did not actively defend a specific geographical area as a territory, its behaviour in the extreme south and west of its range (in particular, the giving of long calls before advancing) suggests that there may be more subtle mechanisms controlling the spacing between groups at Jaó. If the study group encountered signs of a neighbour in an outlying part of its range (usually through long calls), for example, it would normally not advance further into that area. In this case, the intensive use of the preferred northern part of the group's range during the period following its division can be seen as a form of defensive behaviour. This may also have been important for the redefinition of existing "boundaries".

Range Use

As we have seen, the *C. flaviceps* study group exhibited a clear preference for the eastern portion of its home range throughout the study period, and for the northern part in all months but one. These preferences correlate with a number of characteristics of topography and forest cover, which seem, in turn, to be related to the availability and distribution of specific resources. The forest cover is, however, both somewhat uniform and yet also patchy. While it is possible to recognise some variation in the types of vegetation present within this area (figure 3.1), this is more a question of degree than of the more clearly demarcated differences apparent at some sites [*e.g.* Dawson, 1979: p. 262; Rylands, 1982: figure 59]. As we have seen, relatively random features, such as the distribution of *Siparuna* trees, can have a marked effect on the group's use of its range. Caution must again be emphasized in the interpretation of the data.

Thus, while the group's preference for the northern part of its range does correlate with denser concentrations of gum-producing plants and edge habitat, it is not necessarily certain that such resources were available in sufficiently greater quantities to determine such a preference. Gum-producing plants, for example, did appear to be generally less common in the southern part of its range, but a large number of potential sources in both areas were ignored by the group. The fact that the northern part of the range is also relatively isolated from the rest of the forest, and especially from intrusions by neighbouring groups, may be a more important determinant of this preference. The group's presence in this area appeared to ensure the exclusion of its neighbours. While such groups are not necessarily important competitors for resources such as gum, the relative exclusivity of access to sites in the northern part of its range may have been an important determinant of the study group's preference for this area.

The presence of its neighbours did appear to have, as we have seen, some influence on the study group's movements. The westernmost area of its home range is a case in point. The forest cover here is at an earlier stage of regrowth than in most other areas, with dense stands of gum-producing plants such as *Acacia paniculata* and *Piptadenia gonocantha*, a high density of *Allophyllus*, and abundant edge vegetation (probably at least as abundant as in the area to the north). Such habitat appears to be as well suited for marmosets as other areas at this location, if not more so. *Acacia* was particularly abundant in quadrat G09, for example, and this was one of the most frequently visited by the group throughout the study period (see figure 5.3). The group usually seemed reluctant, however, to progress further to the west of this point, and it did not enter this area at all during the period of observation in January (22 full and part days), for example, when *Allophyllus* was in fruit.

Long calling was a frequent feature of the group's behaviour in this and neighbouring quadrats (see figure 5.1), and a possibly aggressive intergroup encounter has been observed in this area [M.C. Alves, pers. comm.]. On one occasion during of the present study, the western neighbouring group, JG3, spent the night in the region of quadrat G03 while the study group utilised a sleep tree in quadrat H05. The following morning, on perceiving the presence of JG3, the study group moved rapidly to the northwest to meet it. While there was no overt aggression involved, JG3, along with a number of the adult members of the study group, then moved rapidly southwards. On reaching quadrat G09, JG3 crossed the valley track and continued westwards. The accompanying study group members turned back at this point and returned to the northwestern corner of their range.

The exceptional abundance of plants which produce edible exudate throughout the study group's range does, in fact, make the interpretation of the effects of their distribution on its movements particularly difficult. It seemed, qualitatively, that the group was selective in its use of gum-producing plants, and that such sites were usually chosen in relation to factors other than their distribution, as a complement, in effect, to the group's ranging rather than an important determinant of it. The systematic utilisation of exudate trees over the long term does seem to be a feature of marmoset behaviour [Soini, 1982; Stevenson and Rylands, in press], and there is no good reason to believe that *C. flaviceps* would not behave in a similar way.

Thus, while the group used a relatively small number of sites regularly and frequently throughout the study period, these sites were used less intensively during some periods than in others. In August 1985, for example, quadrat G09, containing a dense stand of *Acacia*, was visited almost every day, was then visited less than half as frequently during September and October, but was again used intensively during November and December. Quadrat J15, which also contained a dense stand of *Acacia* was again visited very frequently in some months, but not so often in others. A severely insect-damaged *angico* situated in quadrat M09 (see plate 5) was visited frequently during the period between April and July, although this quadrat was never used as intensively as those, such as G09, H05 and J16, which contain dense concentrations of *Acacia*. This probably reflects the group's more opportunistic use of *angico* gum, which is dependent on more widely-distributed, generally less productive sites.

The group's preference for the eastern portion of its range does, on the other hand, appear to be relatively independent of the presence of neighbouring groups. Quadrats on the riverbank between 06 and 09, for example, were visited less frequently than areas either further to the north or further south. Some of the quadrats used most intensively by the study group, such as J15, lie on the riverbank well within the area of overlap with the home range of JG2 (see figure 5.5). Factors such as the presence of neighbouring groups cannot be ignored, of course, but it does seem likely that the more intensive use of the eastern part of the range was related to its lower altitude and higher humidity in comparison with other areas, and to related factors such as the relative abundance of insects in particular.

The data on leafing phenology (chapter 3) have shown that the leaf cover at lower altitudes both fluctuated far less during the course of the year and remained at much higher levels during the dry season than that at higher elevations. The results of the insect trapping show similar, seemingly correlated, seasonal trends in the abundance of the types of insects most commonly preyed on by the group. If its preference for the eastern part of its range is directly related to the abundance of these insects, we would expect to observe, in the light of observed fluctuations in the availability of insects, similar fluctuations in the intensity of the use of this area.

In addition to their relationship with changes in insect abundance, fluctuations in leaf cover may influence the group's movements in their own right. Relatively dense vegetation offers protection both from aerial predators and direct sunlight, and may also have an important thermoregulatory function for marmosets during periods when ambient temperatures are low, particularly at night. The relatively more abundant leaf cover at lower altitudes during the dry season would, therefore, further encourage the use of the eastern part of the range.

In order to assess whether these fluctuations did have some influence on the group's movements, and the relative intensity of its use of the eastern part of the range in particular, the quadrat occupation data were analysed in further detail. For this, only those quadrats constituting the "main body" of the range were considered. The westernmost quadrats, between coordinates A and F, and 09 and 13 were not only visited relatively rarely, but form a "somewhat uncharacteristic appendage to its range" (chapter 3). As they also do not form a uniform west-east slope, they were excluded from the analysis. All the peripheral quadrats whose area was less than 10,000 m^2 were also excluded, leaving an area of 27.5 ha, made up of 110 50 m x 50 m quadrats (details are given in appendix IV). This area was then divided into two equal halves by a line running north-south through the middle of each east-west line of quadrats. The eastern or "riverbank" half thus represents the part of the group's home range lying at the lowest altitude, while the western or "hillside" half represents the part lying at the highest. While this is not a precise division based on altitude, it is related to the distance of the quadrats from the riverbank and the east-west width of the range at any point.

Records of the group's use of the quadrats of the eastern and western halves of this main body of its range show a number of trends (table 5.6). In general, as we would expect, the group used the eastern half more than the western. During the study period as a whole, it was recorded on the riverbank during 55.6% of the quadrat occupation records, and entered 23.2% more riverbank quadrats than hillside quadrats, on average, during any season. The only exception was the early dry season during which the group actually entered more quadrats on the hillside, although the records show that it did,

Table 5.6

Seasonal Variation in the Distribution of the Study Group's Ranging

			Percentage of time spent:		
Sample	Quadrats entered	Quadrat occupation records	In quadrats[1]	Insect foraging[2]	Feeding on plant material[2]
Late dry 1985:					
Hillside	31.5	622.5	43.4	45.4	43.5
Riverbank	42.5	811.5	56.6	54.6	56.5
Early wet 1985:					
Hillside	40.5	1295.0	49.1	46.2	49.8
Riverbank	50.5	1342.0	50.9	53.8	50.2
Late wet 1986:					
Hillside	43.5	1209.0	43.4	41.8	38.6
Riverbank	48.5	1576.0	56.6	58.2	61.4
Early dry 1986:					
Hillside	39.5	727.5	47.6	45.0	54.9
Riverbank	35.5	800.5	52.4	55.0	45.1
Late dry 1986:					
Hillside	30.0	875.5	38.6	36.2	56.9
Riverbank	51.0	1394.5	61.4	63.8	43.1

[1] Percentage of total quadrat occupation records.
[2] Percentage of records collected during scan samples.

Table 5.7

Chi-squared Values for Comparisons of the Observed Distribution of Quadrat Occupation Records with Expected Values[1]

Sample	χ^2	p
Late dry 1985	24.91	<0.001
Early wet 1985	0.84	0.360
Late wet 1986	48.36	<0.001
Early dry 1986	3.49	0.062
Late dry 1986	118.66	<0.001

[1] Values of Chi-squared for a comparison of the observed distribution of quadrat occupation records (see table 5.6) with the values expected assuming an equal distribution of records between the hillside and riverbank quadrats.

in fact, spend more time on the riverbank. Nine of the hillside quadrats, more than the difference between the two areas, contributed only one or two occupation records during this period. This seems to have been more related to the group's movements during May, prior to its division, than to its foraging activities. As for many other aspects of the group's ranging behaviour, there seem to be a number of complicating factors to be taken into account and, again, as much variation within as between seasons.

While the group did spend more time in the eastern half of its range throughout the year, the difference was generally greater during the dry season, and in the late dry season of 1986 in particular (table 5.7). During the latter, in fact, the group spent almost 60% more time in the eastern half of its range than it did in the western half. The results do show some anomalies, however, such as the fact that the group spent a larger proportion of its time in the eastern half of its range during the late wet season than it did during the following early dry season. It seems from the records, however, that this was probably more closely related to the distribution of fruit than to that of insects (table 5.8). This was the only season during which the group spent significantly more time than expected feeding on plant material in the riverbank quadrats, whereas in all but one of the other samples, there was a significant tendency to feed on plant material in the hillside quadrats. The group also fed on plant material in almost 20% more riverbank quadrats than hillside quadrats during the late wet season sample. This correlates well with the records of the group's fruit feeding during this period. Its activity was concentrated at low altitudes during February in particular (figure 5.6), corresponding with the distribution of the *Siparuna* trees whose seeds it was exploiting. The overall trend is, in fact, even more accentuated if March (during which fruit was not a significant part of the group's diet) is removed from the analysis and it is recalled that the group spent more time feeding on plant material during this period than at other times (see chapter 4).

It is again interesting to note that the records for the late dry season period of 1985 (August and September) are more similar to those from the early dry season of 1986 than they are to those from the more equivalent late dry season of 1986. For example, while the group spent 54.6% of its foraging time on the riverbank during August and September 1985 and 55% during the early dry season of 1986, 63.8% of the relevant foraging records

Table 5.8

Chi-squared Values for Comparisons of the Distribution of Insect-Foraging and Plant-Feeding Records with Expected Values[1]

Sample	χ^2	p
Late dry 1985:		
Insect foraging	0.02	0.876
Plant feeding	1.10	0.294
Early wet 1985:		
Insect foraging	0.04	0.843
Plant feeding	5.67	0.017 (hill)[2]
Late wet 1986:		
Insect foraging	2.66	0.103
Plant feeding	16.76	<0.001 (river)
Early dry 1986:		
Insect foraging	0.99	0.319
Plant feeding	17.13	<0.001 (hill)
Late dry 1986:		
Insect foraging	9.45	0.002 (river)
Plant feeding	102.58	<0.001 (hill)

[1] Values of chi-squared for a comparison of the observed distribution of foraging and feeding records (see table 5.6) with the values expected according to the distribution of scan sample records between the hillside and riverbank quadrats.

[2] "Direction" of difference for significant values of Chi-squared. "Hill" indicates that significantly more records than expected were collected in the hillside quadrats and *vice versa*.

were collected in riverbank quadrats during the late wet season of 1986. These similarities reflect observations both of the availability of resources within the group's home range and of its activity patterns during these two periods (see chapters 3 and 4). Discrepancies between these two periods are probably due more to the division of the group and random factors, such as changes in the use of gum sites, than to any marked overall differences in the distribution and abundance of resources. Even so, they are far more similar to each other than either is to the late dry season sample from 1986.

The fact that the group spent significantly more of its foraging time than expected on the riverbank during the late dry season sample from 1986, in direct contrast with its plant-feeding activities, seems to lend most support to the idea that the distribution of insects was the primary factor influencing its preference for the eastern portion of its range throughout most of the year. This corresponds not only with observed fluctuations in both leaf cover and arthropod abundance, but also with the exceptional intensity of its foraging activities during this season. Similarly, while the group entered fewer hillside quadrats than during any other sample period (even though it was spending significantly more of its plant-feeding time there), it also entered more riverbank quadrats than at any other time.

As we have seen a number of times in this chapter, many aspects of the group's ranging behaviour exhibit equally marked, or sometimes even greater, variability within seasons as between them. The group ranged most widely during the periods when insects were both most and least abundant (*i.e.* the early wet season of 1985 and the late dry season of 1986). The present analysis of its ranging, however, has shown that these two periods are at opposite ends of a continuum of the intensity of use of the eastern part of the range. During the former period, in fact, the group spent virtually equal proportions of its time in these two halves of its range, and devoted only very slightly more of its foraging time to the eastern quadrats (in which its foraging was, as we shall see in chapter 6, relatively less successful). Plant-feeding records are also evenly distributed between the two areas. The evidence suggests that, while the group ranged more widely each day than at other times, it spread its time far more evenly over its range than it did during other periods.

It thus seems that the group was, in fact, following very different strategies during these two periods of contrasting arthropod abundance, even though both involved relatively larger day and monthly ranges (and core areas), on average, than at other times during the same seasons. When arthropods were most abundant, these patterns of range use were associated with a more or less even distribution of the group's time within its range. When arthropods were least abundant, on the other hand, these patterns underpinned a marked concentration of activity, especially insect foraging, at lower altitudes.

Sleeping Sites

The study group utilised 45 different sleep trees during the course of the main study period (figure 5.8), and at least another 4 different sites at other times during the field study. The group returned to the site it had used on the previous night on only one occasion during more than 140 full observation days. The distribution of sleeping sites again reflects its preference for the north and east of its range, with only a quarter (11) of the sites located to the south of trail 12 and one third (15) in the western half of its range. There were no sleeping sites in vegetation type 4, nor in the southwestern corner of the range.

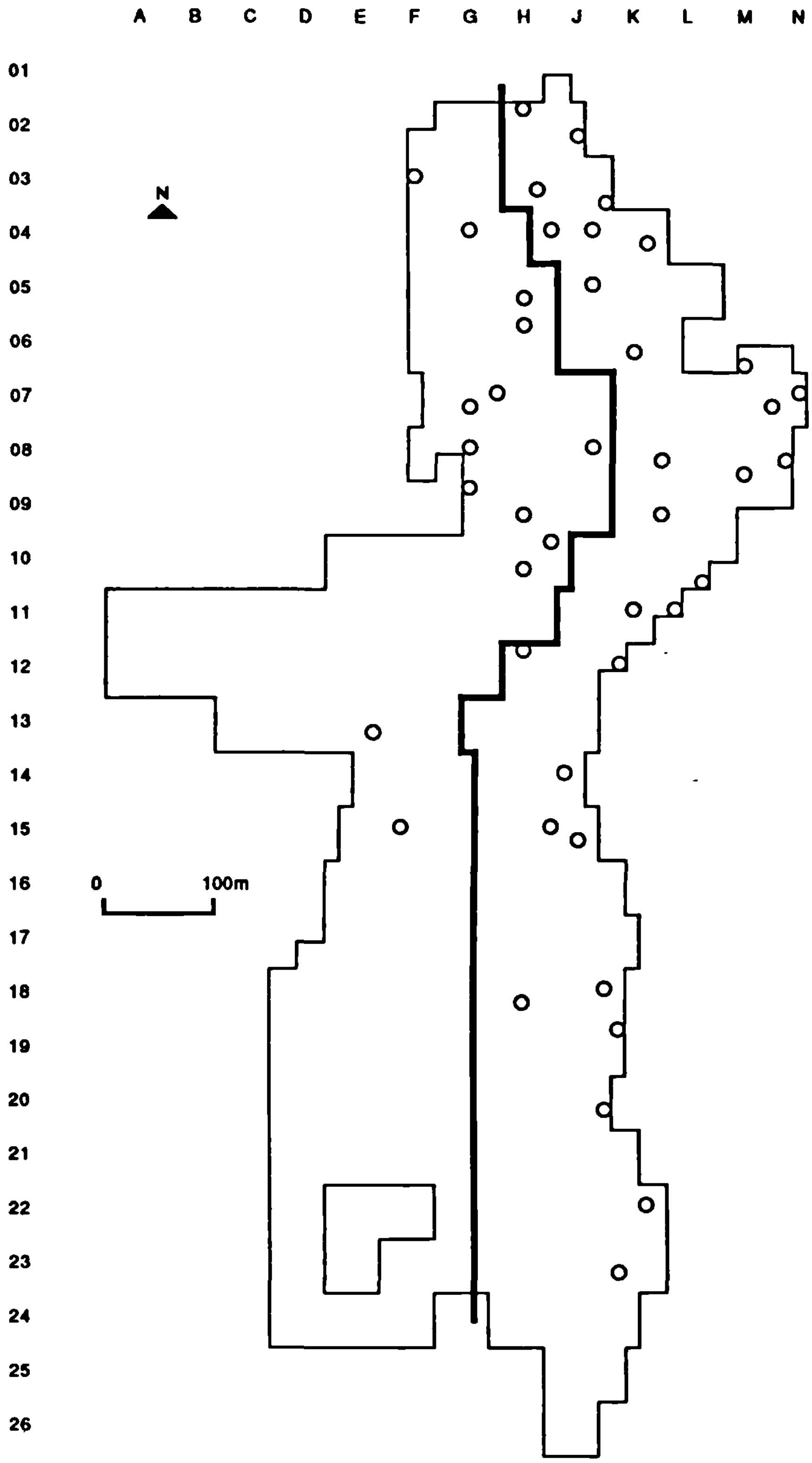
The *C.h. intermedius* study group at Aripuanã utilised a similar number of sleeping sites (46), although *C. jacchus* groups at Tapacura repeatedly use either one or a few sleep trees, presumably because there are so few available within their small territories [Stevenson and Rylands, in press]. The *C.p.kuhlii* study group at Una utilised 14 sleep trees within its 10 ha home range during the course of a three-month study [Rylands, 1982]. It thus seems that the number of sleeping sites utilised by marmoset groups is directly related to the availability of appropriate sites which is, in turn, related to range size. Predator avoidance appears to be the primary factor influencing the choice and use of sleep trees by marmosets.

The sleeping sites of the *C. flaviceps* group were mostly located at between 10 and 20 m above the ground in relatively isolated trees densely covered in tangles of lianas and other climbing plants, although on one occasion a leafless *Genipa americana* was used, the group forming three

Figure 5.8 (facing page)

Distribution of Sleeping Sites

Figure 5.8 shows the distribution of sleeping sites used by the study group during the course of the main study period. The heavy line indicates the division between the "hillside" and "riverbank" sites used for the analysis of their distribution (see text).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huddles in branch forks at 12-14 m. There seemed, qualitatively, to be an abundance of suitable trees throughout most of the group's range and its choice of sites appeared to be determined by its movements (and possibly also its preference for certain sites) rather than *vice versa*. Following from this, the abundance of sites in the north and east of the range is a reflection of the group's general preference for these areas rather than the distribution of appropriate sites.

When approaching a sleeping site, the group would normally adopt a characteristic silent "creeping" style of locomotion, with all members following each other in line and frequently stopping to scan the surrounding area. While this same behavioural pattern was followed on almost all occasions, the actual approach to the sleep tree was extremely variable on consecutive days, sometimes direct and relatively rapid, on other occasions involving complicated detours and double-backs. The use of different trees on consecutive nights seems to be a further aspect of this variability, all of which appears to be systematically linked to the avoidance of detection by potential predators. One further feature of this behaviour was the use of decoy sleep trees, which the group would ascend in normal creeping fashion only to descend again and continue on to another tree. Some, but not all, of these decoy trees were never seen being used as sleeping sites either during the main study period, or at other times during the field study. The group was observed ascending six decoy trees on one occasion before settling for the night in a seventh. A.B. Rylands [pers. comm.] reports similar behaviour for *C.h. intermedius*, and it seems most probable that such patterns of behaviour are again related to predator avoidance.

While the *C. flaviceps* group "systematically" utilised different sleeping sites on consecutive nights throughout the study period, it used some sites far more than others. It began using a large *angico* tree in quadrat H05 in January, after the crown fell from a frequently-used sleep tree in the neighbouring quadrat J05 (the latter was used on more occasions than any other during the early wet season months). The *angico* was used another 15 times in the following seven months of the study, and was also the only site used on consecutive nights. Other sites, mostly those in the south of the range, on the other hand, were only observed being used once during the whole of the field study.

As we have already seen, the group spent a larger proportion of its time in the eastern part of its range during all seasons, and during the late dry season in particular. Analysis of the use of sleeping sites in this context is complicated by a number of factors, not least that the relatively small number of records (154) may be subject to random influences. While the vegetation at lower altitudes supported more leaf cover than that at higher altitudes during the dry season, for example, this was not a uniform, definitive trend and certain patches of vegetation, or individual trees, at higher altitudes lost no less of their cover than the majority located on the riverbank (*e.g.* phenology quadrat 4, see chapter 3). The apparent shift from the site in quadrat J05 to that in quadrat H05 in January probably had a significant effect as the latter, while situated at only a slightly higher altitude than the former, is actually located to the west of the line dividing the range for this analysis (see figure 5.8). According to the number of sleeping sites located in the two halves of its range, the group would be expected to have spent one night in every three (51 of the 154 records) in the western half of its range. While it did actually spend slightly fewer nights than this in the western half (45), this was not greatly different from the expected value. The site located in quadrat H05 had a major influence on this, however, contributing more than a third of the records for the western half of the range. Removing this one site from the analysis (probably not invalid, considering its altitude) would give a value of 29, or 21% of the remaining records.

While excluding this site would also give values of 2 and 26 nights, respectively, in the western and eastern halves of the range during the late dry season of 1986, this may not be a realistic picture. This period is unique, however, in the fact that the group did not utilise any sleeping sites located at the very highest elevations, *i.e.* along the western edge of the main body of its range, and none, in fact, further west than trail H (the tendency to use sites this far west was greatest during the wet season). There does seem, then, to be a trend for the group to utilise sleeping sites at lower altitudes during the late dry season, but there are too few records to make meaningful comparisons between seasons. The relatively denser vegetation at lower altitudes would favour the use of sleeping sites in the eastern part of the range throughout the year, especially as the group spent a majority of its time in this area during all seasons. Its range is also relatively narrow in an east-west direction and the preferential use of such sites would not normally require a significant amount of extra travel.

Other Factors Influencing Range Use

The topography of the study group's home range may, in fact, have had a more important influence on its movements than many other factors, apart from the distribution of resources. As suggested previously, the relative isolation of the northern part of its range from those of neighbouring groups may have contributed to the observed preference for this area, although this would also contribute, in turn, to the marked degree of overlap between ranges. Thus, while the relatively narrow east-west dimension of this area may allow the study group easy access to sleeping sites at the lowest altitudes no matter where it is, the relatively long north-south dimension allows neighbouring groups relatively free access to the apparently optimal riverbank habitat in the south.

Drinking water was one resource which may have had some influence on the group's movements, especially during the late dry season. The narrow east-west dimension of its range again means, however, that it was rarely more than 200 m either from the river or the Jaó stream. The group could travel this distance in far less than one hour, although this does represent a relatively large proportion of its average daily path. If such a detour was obligatory, it would have a significant effect on day range size, on certain days at least. The fact that the group spent a majority of its time in relatively close proximity to the river during the periods when it was most important as a source of water makes the assessment of its influence on the group's movements rather difficult. In addition, there was usually some water available at other sources for a number of days following even light rain, and the group would preferentially use these whenever possible.

Similar factors apply to the assessment of the influence of adequate cover, for both the avoidance of predation and thermoregulation. The group's preference for the denser vegetation available at lower altitudes can obviously be linked to such factors, at least in part. The marmosets never completely avoided exposed tree crowns or even travelling across open ground, however, so the anti-predator function of their use of dense vegetation is again a question of degree rather than a definitive factor controlling habitat use. The importance of dense cover for the regulation of body temperature is similarly relative, apparently dependent on the time of day or the group's activity. Qualitatively, dense patches of vegetation appropriate for a midday siesta were never absent from the higher elevations during any part of the year and its distribution was likely to have had only a minor effect, on a daily basis.

Territorial defence did not appear, as we have seen, to be a major feature of the study group's behavioural repertoire. It thus seems unlikely, considering the degree of overlap of its own range with those of neighbouring groups, that its relations with them had any great influence on its movements, except during the period preceding and following the formation of the new group, JG4, in mid June. It nevertheless seems possible that the presence of neighbouring groups did influence its use of the southern and western parts of its range. As we have seen, the study group recognised the presence of specific boundaries between its range and those of neighbouring groups (see figure 5.1), and there seemed to be some systematic spacing of the groups on a temporal basis. The study group's infrequent, but regular, movements through the southern and western portions of its range may thus have been related, in part, to such spacing mechanisms. The degree of influence of such factors is again difficult to assess, and the use of the southern and western portions of the range can just as credibly be attributed to the monitoring of resources, for example (see chapter 7).

Overall, then, it seems reasonable to assume that the distribution of resources within the study group's home range had the major influence on the patterns of its use. While the inter-relationship of the distribution of different resources creates a number of problems for the detailed analysis of their influence on ranging, this may also form an important basis for the understanding of marmoset foraging strategies, as we shall discuss in the following chapters.

Summary

The patterns of home range use recorded for the *Callithrix flaviceps* study group were similar, in general terms, to those recorded for most other marmoset and tamarin species. The area utilised during any given period and the distances travelled daily were relatively larger than would be expected for a primate of this body size. Despite the considerable seasonal fluctuations recorded in activity patterns, there was relatively little seasonal change, in quantitative terms, in the group's use of space. More detailed analyses of the data reveal patterns which seem to be systematically related to the abundance and distribution of resources. The main findings are as follows:

1. The group utilised a total area of 35.5 ha during the course of the main study period, although observations indicate that this is an underestimate of the total area used by the group. Monthly ranges were much smaller than this, varying between 16.8 ha and 26.1 ha. The core area (90% of occupation time) in any month varied between 10.2 ha and 16.1 ha. The group thus utilised much larger areas than has been recorded for other *Callithrix* species. No significant overall differences between the areas used during different seasons were found.
2. The group's range overlapped considerably (87.5%) with those of its neighbours. This was thought to have been related, at least in part, to the topography of its range and the relative isolation of most areas of intensive use. It did appear, however, that the group perceived specific boundaries in the peripheral areas of its range. There was also evidence to suggest that some form of spacing mechanism exists in order to minimise contact and overlap between groups.
3. On average, the group travelled 1222.5 m each day and utilised an area of 5.4 ha. On a monthly basis, mean day range size varied between 4.6 ha and 6.2 ha. The group visited less than 30% of its monthly range on an average day. Mean daily path lengths varied between 1022.2 m and 1455 m in any one month. Both these values were recorded during the wet season, and there were no significant differences between the values in the wet and the dry seasons samples.
4. Intra-seasonal differences in daily ranging were noted, however. The group ranged over a significantly larger area each day during the early wet season

than during the late wet season. A similar, less significant, pattern was observed in a comparison between the late dry season of 1986 and other dry season samples. The situation during the wet season correlated with the contrast in the relative importance of insects and fruit, in particular, in the group's diet during the two periods. The factor most obviously correlating with the longer day ranges during the late dry season, on the other hand, was a marked reduction in the abundance of arthropods.

5. The study group exhibited a marked preference for the northern and eastern portions of its range during all months. This correlates with a number of features, such an abundance of more disturbed vegetation and edge habitat, lower altitudes and higher humidity. The relative isolation of the northern part of the range from neighbouring groups may have been an additional factor in the group's preference for this area.

6.It was found that the group's preference for the east of its range was most marked during the late dry season when insects were disproportionately more abundant at lower altitudes than they were at other times of the year. While more time than expected was spent foraging for insects in the eastern half of the range during this period, far less than expected was spent feeding on plant material. During the early wet season, when insects were most abundant overall and least abundant, in relative (but not absolute) terms, in the east of the group's range, it distributed its time and foraging far more evenly between the two halves of its range than at any other time.

7. Detailed comparison with the study of *C.h. intermedius* indicate that differences in ranging patterns correlate with the relative importance of fruit, gum and insects in their diets. While the *C.flaviceps* study group ranged over a relatively smaller area each day, it utilised a much larger area during the course of a month, and distributed its time much more evenly over that area, than the *C.h. intermedius* group. This seems to be related to the relative importance of insect foraging for the former.

8. The influence of factors other than the distribution of dietary resources, such as that of appropriate cover or water sources, is not obvious and seems to be related, on the whole, to that of other resources.

6

Feeding behaviour

All marmoset and tamarin species are omnivorous, eating a wide variety of prey, reproductive plant parts and exudates in the wild [Coimbra-Filho & Mittermeier, 1973a; Soini, 1982, in press; Rylands, 1982, 1984; Terborgh, 1983; Stevenson & Rylands, in press]. While the consumption of new leaves and buds has been reported for some species [but not unequivocally in the case of *Callithrix*: Stevenson & Rylands, in press], such foliage is consumed relatively rarely, and mature leaves do not seem to be a component of marmoset diets. The diet of the *Callithrix flaviceps* study group was similarly varied, including plant exudates, fruit, seeds, nectar, invertebrates and vertebrates, although the group was never observed feeding on flowers or foliage. In spite of the apparent variety of its diet, however, the records show that the group's feeding activities concentrated on a few plant species and certain types of prey. Through the course of the main study period, for example, the gum, fruit or seeds of just four plant species (*Acacia paniculata*, *Allophyllus* sp., *Anadenanthera peregrina* and *Siparuna* sp.) accounted for 92.5% of the records of feeding on plant material. Similarly, 64.3% of the invertebrate prey items identified during the main study were orthopterans (93.6% of these were grasshoppers).

Gum was a far more important component of the study group's diet than it appears to be for species such as *Callithrix humeralifer intermedius* and *Callithrix penicillata kuhlii* [Rylands, 1982]. But it does seem that other eastern Brazilian forms of the genus, *e.g. Callithrix penicillata penicillata*, occupying more seasonal forest and open woodland, are probably as dependent on gums as *C. flaviceps* [Lacher *et al*, 1984; Bouchardet da Fonseca & Lacher, 1984]. The *C. flaviceps* group was exceptional, however, in the degree of its use of gum produced in response to insect damage. This contributed more than half of the gum-feeding records in at least two months. The systematic consumption, or predation, of seeds (as opposed to their incidental ingestion during fruit feeding) is also unusual, and has not been previously recorded for other marmoset species. The large numbers of vertebrates captured and consumed by study group members, particularly during certain dry season months, again appears to have been exceptional.

These characteristics are linked most obviously to constraints such as the relative availability of resources at different sites and during different times of the year. It is also possible, however, that they represent specific behavioural or physiological adaptations which, along with other factors such as the types of habitat normally available to members of this species, differentiate *C. flaviceps* from other marmosets. While a number of speculations about such adaptations might be made at this stage, the lack of detailed long-term data for most other species precludes any definitive conclusions. The present study itself focussed on a single group during the course of a thirteen-month period. The results are thus not necessarily representative of the behaviour and ecology either of the study group itself or of the species as a whole, given the marked variability observed in the abundance of resources both during different years and in different habitats.

It is possible, on the other hand, to analyse the group's feeding behaviour in the context of theories on optimal diet [Schoener, 1971; Pulliam, 1974, 1975; Pyke *et al.*, 1977; Altmann & Wagner, 1978; Stephens & Krebs, 1987]. The models formulate predictions on the composition of an animal's diet according to the availability of different resources and the expenditure of time and energy necessary for their acquisition [see *e.g.* Richard, 1985, pp. 200-205]. Such models, like those of traditional economic theory on which they are based, are validated by "common-sense" notions of how animals should behave. It is thus assumed, for example, that if two foods have the same composition, an animal will preferentially feed, other things being equal, on the one whose acquisition requires the least expenditure of energy. However, while the simplicity and apparent logic of such models encourage their application to the analysis of feeding behaviour, they are not necessarily realistic representations of the phenomena they attempt to explain [see *e.g.* Post, 1984; Pierce & Ollason, 1987].

One problem for many omnivorous animals, and small omnivores such as marmosets in particular, is the need to acquire or balance specific nutrients contained in different types of food. The problems have been outlined in chapters 1 and 4. Taking a broad perspective, the most easily-acquired types of food, such as leaves (or gum in the case of marmosets), usually demand physiological or behavioural specialisations, or both, for their exploitation [Milton, 1980]. While gum is a good source of carbohydrates and is easily acquired by marmosets, with their specialised dentition, it provides only very small quantities of protein [Bearder & Martin, 1980; Garber, 1984a; Nash, 1986]. It thus seems likely, assuming no specific physiological adaptations, that a diet consisting entirely of gum would be inadequate in the long term for a primate of this size.

Insects and other types of prey, on the other hand, are a high quality resource providing large quantities of protein and fats in particular [Uvarov, 1966; Martin *et al.*, 1976; Hladik, 1979]. While easily digested, the acquisition of animal material requires the expenditure of relatively large amounts of time and energy. In terms of optimality models, then, feeding on prey is characterised both by high benefits and high costs, while gum feeding can be seen as providing medium or low benefits at low costs. The relative costs involved in prey feeding may, however, fluctuate in accordance with factors such as the availability of prey, in general, and the relative abundance of prey items of different types and sizes, in particular [*e.g.* Richard, 1985]. In chapter 4, for example, we saw that the success of the study group's foraging activities varied considerably during the course of the year, apparently correlating with fluctuations in the abundance of arthropods at the study site. This indicates that animal material was more easily acquired when it was most abundant. In this case, we might have expected the group to devote more time to foraging for prey, and to have included more animal material in its diet, during these periods.

A number of other factors must be taken into account in assessing or predicting the group's use of such resources. It seems reasonable to assume, for example, that the "costs", or foraging effort involved in the acquisition of prey will never be as low as those of acquiring plant material. As the latter also contains relatively much larger quantities of certain nutrients than animal material, a theoretically optimal feeding strategy would always include both in the group's diet. In addition, the relative quantities of specific nutrients available in different types of material may actually limit their inclusion in the animal's diet. One such factor in the case of the marmosets appears to be the relatively high phosphorus and low calcium content of their insect prey. In this case, we would expect its feeding behaviour to follow patterns similar to those outlined in "nutrients as constraints" models [Pulliam, 1975; Altmann & Wagner, 1978].

The optimal calcium:phosphorus ratio in the diet of most mammals lies between 1:1 and 2:1 [Robinson, 1980] and imbalances can have serious consequences, particularly for skeletal development [Maynard & Loosli, 1969]. Some grasshopper species of the family Acrididae (a preferred marmoset prey) have been recorded as having a calcium:phosphorus ratio as high as 1:70 [Uvarov, 1966], although most vary between 1:2 and 1:4, values similar to those recorded for other insects such as *Tenebrio molitor* [Martin *et al.*, 1976]. Analysis of the content of a number of types of gum, on the other hand, have shown calcium:phosphorus ratios of between 31:1 and 142:1 [Bearder & Martin, 1980; Garber, 1984a]. These authors have suggested that the gum consumed by many highly insectivorous primates has an important function in balancing the calcium:phosphorus ratios of their diets. Nash [1986] has pointed out, however, that the absorption of minerals in the gut may be inhibited by other chemicals, such as uronic acids, which are also present in gums.

The leaves and leaf buds of many tropical forest plants also contain relatively large quantities of calcium and may have a calcium:phosphorus content as high as 14:1 [Coelho *et al.*, 1976; Hladik, 1977]. Hladik [1977], for example, found that the frugivorous/folivorous *Presbytis entellus* and *Prebytis senex* at Polonnaruwa, Sri Lanka, generally consumed three to eight times as much calcium as phosphorus. *Saguinus oedipus*, for example, has been reported to feed on leaves, stems and buds [Neyman, 1978] and such material may be an important resource for tamarins when gum is not available, although such a strategy would be limited by the ability of these relatively small-bodied primates to digest leafy material.

Gum is invariably available to most marmoset groups, on the other hand, and it seems possible that they may sometimes be faced with the reverse problem of relatively too little phosphorus in their diets during periods when insects are particularly scarce. Assuming that a relatively close balance of calcium and phosphorus is required for an adequate diet, the relatively high calcium content of most gums may in itself place certain limits on their consumption. Other components may also place specific limitations on the use of gum, especially as a substitute for other types of material. Tannins in the gum of *Acacia tortilis*, for example, appear to greatly inhibit its consumption by vervet monkeys, *Cercopithecus aethiops* [Wrangham & Waterman, 1981]. The low protein content of most gums probably also restricts their use as a source of this nutrient, especially when the small body size of the marmosets themselves is considered. The consumption of large quantities of gum during periods when prey is scarce might also inhibit the digestion of animal material when it is at a premium, especially if tannins, which may inhibit the digestion of proteins [Scheline, 1978], are present.

There are, then, a wide range of factors to be taken into account when considering the study group's diet in terms of its feeding strategies. This chapter will thus both document changes in the composition of its diet during the course of the study and analyse this variation in the context of factors such as fluctuations in the availability and distribution of different resources. This will, in turn, both continue the development of themes outlined in the previous chapters and provide the basis for further discussion. Comparison with the data available from studies of other marmoset and tamarin species will again permit a more detailed analysis of the group's feeding behaviour.

Components of the Study Group's Diet

The study group's diet has been discussed previously, in particular in chapter 4. In this chapter we shall consider this aspect of its ecology in more detail, looking at the variety of resources used, and fluctuations in their consumption during the course of the year. Gum was consumed in by far the largest number of feeding records during the year (see table 4.6), although feeding on fruit and seeds constituted the largest component of the records in January and February, respectively. Fruit was a minor component of the group's diet during all other months except November, although even in this month it constituted only 12.9% of feeding records. As we would expect, animal material forms a smaller component of the group's diet than plant material throughout the year, according to the behavioural records, although, as suggested previously, this may underestimate its importance to a certain extent. Nevertheless, prey-feeding records did contribute between 26% and 31.3% of the totals during the three early wet season months.

Plant Exudates

Marmosets are, arguably, the most specialised of the primates which include a significant proportion of exudates in their diets (see chapter 1). Their gouging dentition allows them to systematically exploit sources of both gum and sap which are only randomly available, if at all, to most other primates, including the tamarins [Coimbra-Filho & Mittermeier, 1978; Sussman & Kinzey, 1984]. Marmosets, but not tamarins, may also have specialisations of hind-gut morphology related to their more intensive use of gums [Coimbra-Filho *et al.*, 1980], similar to those seen in a number of prosimian species [Chivers & Hladik, 1980; Nash, 1986]. Unlike species such as *Euoticus elegantulus* and *Phaner furcifer* [Charles-Dominique & Petter, 1980; Bearder & Martin, 1980], there appears to be no related specialisation of the tongue. However, if the relatively long and roughened tongues of most exudate-eating prosimian species is an adaptation related to the accessibility of gum produced in insect bore holes [Bearder & Martin, 1980], the ability to induce exudate flow through tree gouging would probably avoid the need for any such specialisation.

Marmosets appear to use a large number of different gum-producing plant species, those belonging to the families Anacardiaceae, Leguminosae, Meliaceae and Vochysiaceae in particular (see Appendix V). A number of studies of *Callithrix* species [Rylands, 1982; Lacher *et al.*, 1984; Bouchardet da Fonseca & Lacher, 1984; Santos de Faria, 1984a; Stevenson & Rylands, in press] have reported aspects of the systematic use of gum-producing plants by marmosets. The almost universal preference for gouging many small holes rather than a few large ones, for example, appears not only to ensure maximum gum flow, but also to have a less deleterious effect on the plant itself [Stevenson & Rylands, in press]. The number, form and location of the gouge holes may also differ with the type of tree or liana and features such as the thickness of its bark. Gouge holes on trees with hard or thick barks, for example, are often less numerous, larger and deeper than those on trees with softer bark. Rylands [1982] noted that the *C.h. intermedius* group concentrated their gouging at the first fork of *Didimopanax* sp. trees, and suggested that this was related to the relatively hard bark of this tree and the need for horizontal supports for the gouging of holes.

Stevenson and Rylands [in press] note features such as the concentrated use of only a few individuals of any one species and the apparent rotational use of such individuals, *i.e.* the presence of old gouging scars on plants which were not being used at the time of the study. This appears to be similar to the use, on a different scale, of exudate-producing trees by *Cebuella pygmaea* groups which utilise "lifetime" ranges [Soini, 1982], abandoning not only the gum-producing trees, but the territories which encompass them as well, in moving to new sites. Bouchardet da Fonseca & Lacher [1984] also report the apparent monitoring of trees by *Callithrix penicillata*. Holes were gouged in trees of three species which did not appear to produce exudate, and these had been abandoned. A number of studies, including the present one, however, have recorded tree gouging by marmosets in association with scent-marking rather than exudate-feeding activities, so it is possible that such behaviour was related to the former rather than the latter type of behaviour.

Gum, as we have seen, was the major component of the *C. flaviceps* group's diet during the main study period. Two types of gum-feeding behaviour were observed, one of which involved the typical gouging behaviour seen in all other marmoset species [Coimbra-Filho & Mittermeier, 1976, 1978]. The second involved the consumption of gums produced in response to damage caused by other media such as insects (in particular) and falling branches. While all marmosets probably feed on a certain amount of gum in this latter, opportunistic fashion, it seems to be a relatively unimportant aspect of their gum-feeding behaviour as a rule. It was, on the other hand, a major component of the gum-feeding activities of the *C. flaviceps* study group during much of the study period (see below). Only in the case of *A. paniculata*, in fact, did the group induce gum flow through the gouging of holes. Even so, much of the feeding on the gum of this species appeared to be opportunistic. The gum of all other plant species was also obtained opportunistically. While the feeding activities of the marmosets may have frequently stimulated further gum flow during such feeding, characteristic bark gouging behaviour was only observed in connection with scent-marking activities. Group members were sometimes observed superficially gouging the upper surfaces of horizontal branches of *angico* trees, for example, but no gum deposits were observed at such sites and this appeared to be linked solely to scent-marking behaviour.

In all cases except *A. paniculata*, it was clear that the type of exudate consumed by group members was, in fact, gum [according to the definition of Bearder & Martin, 1980]. Gums of a variety of colours (ranging from "colourless" or very pale yellow to black) and consistencies were consumed, although softer, more lightly-coloured deposits were preferred, and hard deposits were frequently ignored. While much gum was consumed *in situ* (*i.e.* eaten while still attached to the plant), large pieces, often more than 10 cm in length, were eaten while held in the hand. The latter were sometimes carried over distances of more than 20 m and even transferred between individuals [Ferrari, in press]. In the case of the *Acacia* exudate produced in response to the gouging activities of the study group, it seems likely that some sap was also consumed, although quantitative observations suggest this would have been only a relatively small proportion of the material ingested.

Despite these apparent differences, the group's gum-feeding behaviour was similar to that of other marmosets in terms of the concentrated use of a small number of individuals of a few species during any particular period. Gum from just two plant species (*Acacia paniculata* and *Anadenanthera peregrina* - these will be referred to as "major sources") was consumed during more than 90% of the gum-feeding records collected in any one month (table 6.1). This was frequently the only plant material consumed during the course of a day. As the source of the gum being eaten in some samples was not identified, it is likely that these figures under-estimate the actual consumption of gum derived from these two species. This concentrated use of the gum of only a very few plant species has also been recorded for marmosets such as *Callithrix jacchus* and *C. penicillata*, although the opposite seemed to be the case for *C.h. intermedius*, particularly during periods when gum was an important component of its diet [Rylands, 1982]. This contrast is probably

Table 6.1

Monthly Variation in the Use of Plant Exudate Sources by the Study Group

	Percentage of exudate feeding records attributed to:		
Sample	*Acacia paniculata*	*Anadenanthera peregrina*	All other sources
August 1985	78.7	16.7	4.6
September	79.8	12.5	7.7
October	83.9	12.3	3.8
November	70.9	27.6	1.5
December 1985	74.1	22.9	3.0
January 1986	79.2	18.2	2.6
February	94.9	4.2	0.9
March	81.9	16.9	1.2
April	60.0	38.0	2.0
May	30.1	67.1	2.8
June	55.9	42.9	1.2
July	33.7	61.8	4.5
August 1986	64.2	29.7	6.1
All records:	**66.4**	**30.5**	**3.1**

most closely related to differences in the abundance of gum-producing species at the different study sites, although it is interesting to note that the latter, as a member of the *Callithrix argentata* species group, may be less specialised for the exploitation of gum sources (see chapter 1).

Acacia and *angicos* are, as we have seen, particularly abundant throughout much of the study group's home range. Its concentrated use of the gum of just two species is nevertheless somewhat puzzling. Many of the plant species whose gum was consumed opportunistically, for example, not only had much softer bark than that of *angico* trees but were also relatively abundant within certain parts of the group's range. Group members regularly gouged many plants solely for scent marking, so it does not seem likely that the avoidance of such activities would be a determinant of their gum-feeding behaviour. It also seems unlikely that the gum of all such species contains significantly less nutrients than the two principal ones used. A number of the more common species such as *Piptadenia gonocantha*, for example, are closely-related members of the family Leguminosae. In addition, while *C.h.*

intermedius was also observed to feed on the gum of *A. paniculata* [Rylands, 1982], it was only consumed during seven of the 12 months of that study. While it is possible that there were important differences in the composition of the available gums, either favouring the use of that of *Acacia* and *angico* or inhibiting the exploitation of others, we might still have expected the marmosets to have utilised the gum of other plant species more frequently than they did. It thus seems likely that the concentrated use of *Acacia* and *angico* exudate reflects factors other than the abundance of these plants.

Most of the other types of plant used by the study group for their gum were also members of the family Leguminosae (Appendix V), although the gum from trees and lianas belonging to the Rubiaceae, Nyctaginaceae and Elaeocarpaceae (among others) were also certainly used. Identification of many of the individual plants used by the group was hampered by the fact that they were either non-reproductive during the study period or were, in fact, in so badly damaged a condition as to be completely leafless, which usually meant that it was impossible to identify even the family to which the tree belonged. The two major sources were easily recognised, however, *Acacia* by the colour and form of its bark and *angicos* by the distinctive thorns around the base of the trunk (see plate 5).

Apart from this concentrated use of the gum of a few plant species, a number of features of the group's use of exudate sources suggests that its gum-feeding behaviour was systematic rather than random. In the previous chapter, we saw that it would frequently visit quadrats containing major gum sources during some months, but would apparently ignore such locations at other times. It is possible that such behaviour indicates a rotational use of gum sources, similar to, but apparently on a different time scale from that described for *Callithrix jacchus* [Stevenson & Rylands, in press] and perhaps also the "lifetime ranging" of *Cebuella pygmaea* [Soini, 1982].

If the group was highly selective in its choice of gum sites, on the other hand, it appears that such choice was relatively independent of the distribution of its insect foraging activities. As we saw in the previous chapter, the group concentrated its insect foraging at lower altitudes during the dry season months of 1986, but spent relatively more time feeding on gum in the higher part of its range. This may, in fact, be closely related to the distribution of the gum sites used, and to the importance of *angico* gum in the group's diet during this period in particular (table 6.1). The percentage of gum-feeding records attributed to *angico* gum each month does, in fact, correlate closely with its availability on the sample trees, whether measured by the number of deposits (Spearman Rank Correlation: $r_s = 0.605$, $n = 13$, $p < 0.05$, one-tailed) or the proportion of the total amount made up of soft gum (SRC: $r_s = 0.718$, $n = 13$, $p < 0.02$, one-tailed). In this case, it seems that the group was preferentially feeding on "naturally" available gum when it was most abundant (or rather, when newer, softer deposits were most available) and would thus have been minimising its use of gum from gouged sources, *i.e. Acacia*. This would presumably, in turn, both ensure higher, more prolonged productivity from the latter and perhaps also entail some reduction in the energetic costs of feeding, assuming that tree gouging requires the expenditure of a significant amount of energy, at a time when other resources were scarce.

Fruit, Seeds and Nectar

Unlike exudate, the reproductive parts of plants constituted a relatively minor component of the group's diet during most of the study period, and fruits were, in fact, only observed being consumed on 78 of the 125 observation days of the main study period. This correlates with the apparent lack of edible fruits within the group's range throughout most of the year (chapter 3). Surprisingly, however, the group was observed consuming the reproductive parts or nectar[1] of what was estimated to be at least 29 different plant species, from at least ten different families, during the study (table 6.2). During February, for example, the group was observed feeding on the fruits or seeds of at least nine different plant species, although in some months only one type of fruit was eaten. In the majority of cases, however, only very small numbers of the fruit were eaten. The fruit of 14 species was recorded being eaten five or less times during scan samples and feeding on the fruit of 27 of the 29 species utilised constitutes only 25.4% of all fruit-feeding records.

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[1] *For ease of reference, "fruit feeding" will be used in this chapter to refer to the consumption of fruit, seeds and nectar.*

Table 6.2

Sources of Fruit, Seeds or Nectar Exploited by the Study Group

Family: species (habitus)[1]		Feeding records	Seasons in which feeding was recorded[2]
Boraginaceae:	*Tournefortia bicolor* (C)	33	EW
Chrysobalanaceae:	*Hirtella sprucei* (T)	21	EW, LW
Erythroxylaceae:	*Erythroxylon subracemosum* (S)	5	LW
Euphorbiaceae:	*Mabea fistulifera*[3] (T)	43	ED
Guttiferae:	Unidentified sp. (T)	5	EW
Leguminosae (Mim.):	*Inga* sp. (T)	1	EW
Melastomataceae:	Unidentified sp. (T)	2	LW
	Unidentified sp. (T)	5	EW
Monimiaceae:	*Siparuna* sp.[4] (T)	380	LW
Moraceae:	*Acantinophyllum ilicifolia* (T)	2	EW
	Sorocea guilleminiana (T)	8	EW, LW
Myrtaceae:	Unidentified sp. (S)	3	LD
	Unidentified sp. (T)	66	EW
	Unidentified sp. (T)	12	EW
Palmae:	Unidentified sp. (T)	19	ED, LD
Rubiaceae:	*Coffea* sp. (T)	15	ED
	Coussarea sp. (T)	1	LW
Sapotaceae:	*Pouteria* sp. (T)	6	LW
	Unidentified sp. (T)	2	ED
Sapindaceae:	*Allophyllus* sp. (T)	605	EW, LW
Theophrastaceae:	*Clavija spinosa* (S)	51	ED, LD
Unidentified family:	Unidentified sp. (T)	5	ED, LD, EW
	Unidentified sp.	4	LD
	Unidentified sp. (C)	8	EW, ED
	Unidentified sp.	2	LW
	Unidentified sp.	1	LW
	Unidentified sp. (S)	23	EW, LW
	Unidentified sp. (T)	2	LW

[1] T = tree, C = climber, S = shrub.

[2] Early Wet (EW), Late Wet (LW), Early Dry (ED), or Late Dry (LD).

[3] Nectar only consumed.

[4] Seeds only consumed.

Almost all the fruits consumed were small and relatively sweet, and many were brightly coloured (most were yellow, red or black). The largest consumed, the sticky, fibrous fruit of a palm, was a little over 2.5 cm in length, although the maximum dimension of most did not exceed 1 cm. The majority of plants used were either shrubs, climbers or small trees, and fruit feeding thus most commonly took place on thin supports at low levels in the forest and even on the ground (see appendix III). This was probably most closely related to the availability of fruit rather than to any specific preference for these types of plants, although it does correspond with the low levels most frequently used during foraging (see chapter 7). While the numbers of records involved are generally small, it is apparent that the group tended to concentrate its feeding on only one or two species during any particular month. In February, for example, when the fruits of at least nine different species were consumed, *Siparuna* seeds contributed 95.2% of the fruit-feeding records. Similarly, 93% of the records in January were provided by *Allophylus*.

In the only other two months in which fruit feeding was recorded more than 40 times in scan samples (November and April), just two species again contributed the material consumed in 75% and 86.7% of fruit-feeding records, respectively. As for the group's gum-feeding behaviour, whether this reflects the preferential use of the fruits of a just a few species, or simply the relative availability of different fruits within its home range, is not known. This trend may be partly related to the small size of the marmosets themselves [Clutton-Brock & Harvey, 1977b], although the relatively large values recorded for both the group's home range and its daily movements appear to be contradictory. Similarly, the relatively low density of plant species normally found in secondary forest may be an equally important factor to consider when making comparisons with other primate species.

Fruit-feeding behaviour was similar to that described for *C.h. intermedius* [Rylands, 1982], and included a variety of postures, including hanging by the hind limbs, frequently adopted when feeding on the nectar of *Mabea fistulifera*, for example. The smallest fruits were usually eaten whole, but the seeds and/or peel were often discarded, especially in the case of larger fruits. In the case of *Allophyllus*, however, the seeds (approximately 1 cm in length) were occasionally swallowed whole, but appeared to be passed undigested. The smaller (approximately 5 mm long) seeds of *Siparuna*, on the other hand, were masticated completely before swallowing. Access to these seeds was dependent on the splitting and opening of the small (1 cm-1.5 cm), round fruits, which presumably occurs for seed dispersal (the fruits were never broken or bitten open). The marmosets would then pluck the seeds with their mouths from the exposed inner surfaces of the fruits. In feeding on the nectar of *M. fistulifera*, they would often pull the flowers up to their mouths while suspended by their hind limbs. The nectar was then licked directly from the inflorescence and it was frequently apparent that pollen was left on the facial hair. It thus seems likely that *Callithrix flaviceps*, like *Cebus apella* and *Brachyteles arachnoides* [Torres de Assumpção, 1981; Strier, 1986], is a pollinating agent for this species.

As for the species used for their exudate, the identification of the plants whose reproductive parts were used for food by the group was frequently problematic (see table 6.2). In many cases, as we have seen, a small number of fruits were eaten, often the only ones available on the plant, and the only material available for identification consisted of the discarded remains of consumed fruits. Identification of at least the genus was possible, however, for most of the fruits most commonly consumed by the group (*i.e.* those represented in at least 1% of the fruit-feeding records). These included a non-indigenous plant, *Coffea* sp., which is cultivated on the surrounding farms and whose seeds may have been introduced into the forest by birds.

Interestingly, some types of fruit which have been seen being eaten by other marmosets and tamarins were ignored by the group. On one occasion, group members were observed passing through the crown of a large *Ficus* sp. tree in the southernmost part of their range. Small, apparently ripe fruits were abundant, but were ignored by the marmosets. Unfortunately, the group did not return to this area during subsequent observations, so it is not known with certainty that this fruit was never consumed nor if it was, in fact, ripe at that time. The group did, on the other hand, regularly pass close to or through the crowns of *Cecropia* spp. trees, which are present in most parts of its home range, throughout the year. The fruit of these trees was also never observed either being investigated or consumed by group members, even though it has been observed being eaten regularly by marmosets such as *C.h. intermedius* [Rylands, 1982] and *C. jacchus* [Hubrecht, 1985]. In the case of *Passiflora alata*, the abundant ripe fruits observed at a number of locations were ignored not only by the study group, but also by the other primates in this area. This may have been related to their composition (the juice is used medicinally as a calmant), although *C.h. intermedius* [Rylands, 1982] and *Cebus albifrons* [Terborgh, 1983] apparently do eat *Passiflora* fruit.

Chapter 6

Animal Material

As we have seen, foraging for insects and other prey was the most prominent feature of the study group's activity throughout the year. Even though animal material did not always appear, from the feeding records (see table 4.6), to be a major component of its diet, it is likely that it was an important, if not essential, resource for the study group. Thus, while the marmosets consumed virtually no fruit during much of the year, prey-feeding records constituted at least 9.1% (and as much as 31.3%) of the total feeding records during any one month. It is also possible that the observational methods used tend to under-estimate the consumption of prey relative to that of plant material. While not necessarily comparable, analyses of the stomach contents of wild *Saguinus geoffroyi*, for example, have shown that animal material constituted between 30% and 64% of the volume of material consumed by this species [Hladik & Hladik, 1969; Garber, 1984a]. Fluctuations in the abundance and distribution of arthropod prey, as we have seen, appear to have had a major influence on the group's behaviour. In addition, whereas a scarcity of fruit (*i.e.* throughout most of the year) was compensated for by the consumption of relatively larger amounts of gum, a similar strategy during periods of low arthropod abundance did not seem feasible.

As for all other marmosets and tamarins, the study group preyed most frequently on orthopterans, particularly large grasshoppers and stick insects. Other invertebrates commonly consumed were coleopterans, lepidopterans (mainly caterpillars), snails and spiders (table 6.3). Group members were also observed feeding on insects of the Hemiptera, Homoptera, Hymenoptera and Odonata, although far less frequently. Many prey items were not identified, however, usually because of their small size or their immature form, so it is quite possible that other types of arthropod were consumed. It does seem unlikely, however, that these other types of prey would have made a significant contribution to the group's diet, either in terms of the numbers of individuals or the amount of animal material consumed.

It was far easier to identify vertebrate prey, on the other hand, except in a few cases where the item was first observed when most of the animal had already been consumed. The group fed relatively frequently on this type of

Table 6.3

Identified Prey Captured by the Study Group during the Field Study

Type of prey	Number of items captured	Percentage of total identified
Invertebrates		
Coleoptera	75	6.5
Hemiptera	3	0.3
Homoptera	28	2.4
Hymenoptera	17	1.5
Lepidoptera		
Caterpillars	52	4.5
Others	23	2.0
Odonata	1	0.1
Orthoptera		
Grasshoppers	593	51.8
Others	39	3.4
Snails	87	7.6
Spiders	33	2.9
Vertebrates		
Birds/eggs	3	0.3
Frogs	107	9.3
Lizards	85	7.4
Total	**1146**	**100.0**

prey. In the months apart from those between November and January, vertebrates contributed at least 10% (and as many as 49.5%) of the prey-feeding records, and 16.2% of the total during the study period (see table 6.4). Almost all the vertebrate prey were either tree frogs or lizards (mainly iguanids, nut scincids were also seen being captured). Group members were twice observed feeding on the eggs of a small bird (*Zonotrichia capensis*) and on a fledgling, possibly *Cacicus haemorrhous*, on another occasion.

This type of prey appears to have been a more important resource for the study group than for most other marmosets and tamarins. It is possible, however, that vertebrate prey is consumed as frequently by *S.f. weddelli* [13% of the total prey items identified, Terborgh, 1983: table 6.5, p. 106], although this was a much smaller sample (31 items), and probably not directly

Table 6.4

Monthly Records of Feeding on Vertebrate Prey Collected in Scan Samples

Sample	Total prey-feeding records	Records of feeding on vertebrate prey: Number of records	Percentage of total prey-feeding records
August 1985	95	12	12.6
September	121	31	25.6
October	180	20	11.1
November	264	21	8.0
December 1985	199	1	0.5
January 1986	206	13	6.3
February	153	19	12.4
March	178	22	12.4
April	122	21	17.2
May	128	48	37.5
June	103	51	49.5
July	63	22	34.9
August 1986	53	21	39.6
Total	**1865**	**302**	**16.2**

comparable for a number of other reasons. Terborgh suggests that the relatively large numbers of vertebrates captured by *S.f. weddelli* in contrast with *S. imperator* is due to differences between the two species in foraging techniques. While the former spent a great deal of time foraging on the surfaces of the trunks of large trees, the latter spent most of its time on small supports, searching among leaves. The insect foraging techniques utilised by the *C. flaviceps* study group, however, were far more similar to those of *S. imperator*, which suggests that other factors (differences in the abundance of such prey, for example) are involved.

In capturing and feeding on prey, the behaviour of study group members was similar to that observed in other marmosets both in captivity [Stevenson & Poole, 1976] and in the wild [Rylands, 1982]. Mobile prey was pounced on rapidly and usually gripped with both hands, although small immobile items were sometimes bitten directly from a substrate such as a dead leaf or a twig. Feeding on large animals almost invariably began at the head (there was sometimes obvious confusion over which end of a stick insect feeding should begin at), which was presumably mainly in order to immobilise the prey. In the case of large insects, the wings and distal portions of the legs were frequently, but not invariably, discarded, although vertebrates were consumed completely. In feeding on snails, group members would usually bite the tip from the shell (all the snails eaten had long, pointed shells) and extract the soft body with the teeth, although small snails were sometimes consumed whole. The marmosets were also often observed attempting to bite open (and sometimes licking) snails with slightly thicker shells than the ones usually consumed. On failing to open the shell, it would be discarded. Curiously, while spiders were occasionally observed being taken from their webs, they were generally ignored by the group, even during periods when insects were scarce.

As well as apparent preferences for certain types of insect prey, such as orthopterans, the study group generally consumed relatively large items. Some estimate of the size (in terms of body length) of the invertebrates consumed was possible for 1177 (76.3%) of the 1542 items captured during scan sampling. 59.8% of these were judged to have been more than 1.5 cm in length, and almost half of these were "large", that is, 4 cm or more in length

Table 6.5

Numbers of Prey of Different Estimated Sizes Consumed during Scan Samples

	Body length:				
Prey	≤1.5 cm	>1.5 cm-<4 cm	≥4 cm	Body size estimated	Body size not estimated
Invertebrates	473 (40.2)[1]	381 (32.4)	323 (27.4)	1177 (100)	365 (31.0)
Vertebrates	31 (21.5)	47 (32.6)	66 (45.8)	144 (100)	31 (23.4)
All prey	**504** **(38.2)**	**428** **(32.4)**	**389** **(29.4)**	**1321** **(100)**	**396** **(30.0)**

[1] Values in parentheses are percentages of the total records of each type of prey for which body size was estimated.

(table 6.5). Table 6.5 also shows that "small" vertebrates were rarely consumed, as we might expect. These small vertebrates were mostly frogs. Marked seasonal differences in the sizes of prey were also apparent, as we shall see later on.

The proficiency of these small-bodied primates at the capture of large mobile prey has important implications for a number of aspects of their behaviour and ecology. Terborgh [1983], for example, proposed that *Saguinus* is far more able, through its relatively small body size (and that of its foraging groups), to be selective of its prey than primates such as *Cebus* and *Saimiri*. While the tamarins may capture fewer prey items each day, these items are much larger on average, so they are able not only to consume more animal material in proportion to their body size but also to maintain a larger proportion of such material in their diet while spending far less time each day foraging for prey. The *C. flaviceps* study group did, in fact, capture an even greater proportion of large prey than *S.f. weddelli* (59.8% of the prey items consumed by *C. flaviceps* had a body length of more than 1.5 cm, while only 42% of those of *S.f. weddelli* were 1 cm or more in length). However, while it seems quite clear that *C. flaviceps* captured a larger proportion of large prey than *S.f. weddelli*, it is difficult to tell from the available data whether there are significant differences in other important variables, such as the numbers of prey captured.

Seasonal and Spatial Patterns

Seasonal fluctuations are apparent in both the abundance of the resources exploited by the study group and in much of its behaviour. Marked variations in the composition of its diet were also observed during the study period. This variation, in particular that of the plant material consumed, has already been briefly discussed. Here we shall look more closely at these patterns, paying particular attention to the animal component of the group's diet with a view to further discussion of its insect foraging behaviour. The spatial distribution of its feeding behaviour will also be considered, both in terms of seasonal variation and in relation to other aspects of its activity.

Chapter 6

Seasonal Variation

In chapter 4, we saw that the group spent a relatively similar proportion of its activity time feeding on plant material throughout most of the year, while the consumption of prey fluctuated from a high point during the early wet season to its lowest levels at the end of the dry season. These trends are reflected in the composition of the group's diet, according to the feeding records (see table 4.5). It is clear that the diet contained a far larger proportion of animal material during the early wet season (27.8%) than during any other period. The value for the late wet season (18.8%) is slightly higher than for any of the dry season samples, but not as large as we might expect, given the relative abundance of insects during these different periods. The abundance of fruit during January and February probably had the major influence on this. Thus, while animal material contributed 17.5% of the feeding records during these two months, the value was 22% during March. Reflecting other aspects of its behaviour, the composition of the diet during the late dry season of 1985 is again more similar to that of the early dry season of 1986 than to the later months of this year. Thus, while animal material contributed 18.7% of the feeding records during the 1985 sample and 16.6% during the early dry season of 1986, this value fell to 13.9% during the late dry season of 1986.

Plant Exudates

Exudates were consumed in large quantities throughout the year, and were only eaten less frequently, both in relative and absolute terms, during the months of January and February, when fruit feeding was more important. If we remove March from the late wet season sample, the proportion of feeding records involving the consumption of exudates falls to just 33.2%, while the value for fruit feeding rises to almost half of the total (49.2%). The group's diet in March was, in many ways, more similar to that of the early wet season months than to that of the other late wet season months.

Acacia gum was, by far, the type consumed most often, contributing 4118, or 66.4%, of the gum-feeding records during the course of the study period (table 6.6). *Angico* gum was consumed less frequently, on the whole (30.5% of gum-feeding records), although it was a relatively larger component of the group's diet than *Acacia* during both dry season periods in 1986, when new deposits were apparently most abundant (figure 6.1). During the latter periods, then, it is quite clear that a majority of the gum consumed by the group was obtained in an opportunistic fashion rather than through bark gouging. The more intensive use of *angico* gum during this period also correlates, as we have seen, with the apparent abundance of this type of gum, and represents one aspect of the group's systematic use of sources.

The use of gum-producing plants other than these two major sources shows no systematic seasonal patterns or trends, which reflects the infrequency of the records and the apparently random use of such sources by the group. Discounting the records of gum feeding for which the source was not observed (which, as suggested previously, may frequently have been either *Acacia* or *angico*), minor sources contributed just 2.3% of all gum-feeding records collected during the main study period. Between two and six different minor sources were estimated to have been used during any one month (table 6.7). Such sources frequently (42% of all cases) contributed

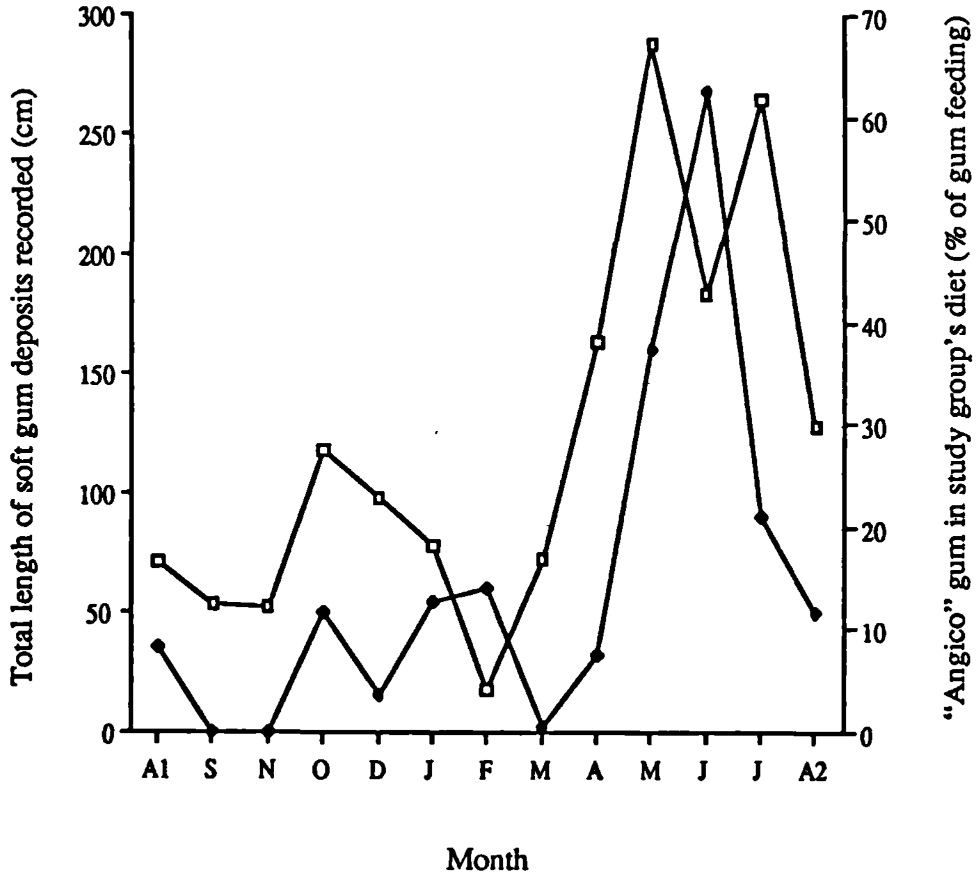
Table 6.6

Seasonal Variation in the Composition of Exudate Consumed by the Study Group

	Percentage of exudate feeding records attributed to:		
Sample	*Acacia paniculata*	*Anadenanthera peregrina*	All other sources
Late dry 1985	76.2	14.4	6.4
Early wet	76.1	21.2	2.7
Late wet	84.6	13.9	1.5
Early dry	45.3	52.3	2.4
Late dry 1986	47.7	48.5	3.8
All wet season records:	80.0	17.9	2.1
All 1986 dry season records:	46.6	50.3	3.1
All dry season records:	55.2	40.8	4.0

Figure 6.1

Monthly Variation in the Availability of Soft Angico *Gum and its Use by the Study Group*



Key:

□ *Feeding on* angico *gum*

◆ *Availability of* angico *gum*

Figure 6.1 compares the monthly variation in the study group's consumption of angico *gum and the availability of soft gum on the sample trees. Values for gum availability are the sums of the lengths (in cm) of soft deposits recorded on the* angico *sample trees each month. Values for gum feeding are percentages of the scan sample records of gum feeding attributed to* angico *gum each month.*

Table 6.7

Estimated Number of "Minor" Gum Sources Utilised by the Study Group each Month

Total of "Minor" gum sources utilised	Months in which this total was recorded
2	October, March
3	January, February, June, July, August 1986.
4	September
5	August 1985, November, December April
6	May

N.B. Due to the difficulties of plant identification, these values may have been over-estimated in some months.

only a single feeding record to the monthly total and passed ten records on just three occasions. These latter cases are attributable to the group's use of trees which had suffered severe insect damage. In fact, 30.3% of the records of feeding on minor sources derive from the use of a single *Alseis* sp. tree on four days in September and October. The tree appeared to have died at this time, and was not used as a gum source again.

Rylands [1982] found that *C.h. intermedius* used a much larger number of gum-producing plant species during periods when other resources were scarce and gum was a relatively more important resource for the study group. In April, for example, when gum was consumed by this group during 58.8% of feeding records, 18 different species were used (compared with a maximum of eight used by the *C. flaviceps* group during any one month). The *C. flaviceps* group did not, however, utilise a significantly greater variety of sources during the dry season. Overall, 18 different minor sources were utilised during the seven dry season months and 16 during the six wet season months of the main sample. Rather than increasing with the decline in other resources, the variety of gum sources actually decreased during the course of the 1986 dry season. Thus, whereas five and six minor sources were used during April and May respectively, only three sources were used during each of the later months (see table 6.7). During June, for example, each of the three sources used contributed just one record to the total, exactly as in February when other resources were far more abundant. The evidence clearly indicates that the group's use of minor gum sources was related to random encounters during the course of other activities rather than to their systematic exploitation.

While the group did reduce its gum feeding slightly during the late wet season, presumably in response to an increase in the abundance of edible fruit, we might perhaps have expected such a reduction to be much greater than it was. Captive studies have shown that both marmosets and tamarins consume larger quantities of food when a more varied diet is available [Wirth & Buselmaier, 1982; Kirkwood, 1983], so it could be argued that the group's consumption of gum during January and February merely represents the preferential use, at a behavioural level, of this type of food. The fact that it continued to feed on relatively large quantities of gum, however, supports the idea that other factors are involved, such as the balancing of the calcium:phosphorus ratio in its diet [Bearder & Martin, 1980; Garber, 1984a]. Similarly, while gum was a much smaller component of the *C.h. intermedius* study group's diet overall, it was never absent, contributing between 6.3% and 58.8% of monthly feeding records.

We might also have expected the *C. flaviceps* group to have increased its use of gum during the times of year when both arthropods and alternative resources such as fruit were least abundant. However, while the proportion of gum in its diet was much larger during the dry season months, especially in the late dry season of 1986, this appears to have been the result of the reduction in the use of other resources (see chapter 4) rather than of any increase in gum feeding. The apparent decrease in the variety of gum sources used during the course of the dry season also supports the idea that there was no systematic increase in the use of gum during the later months and, in turn, that certain factors place specific limits on such a strategy.

Thus, while the group's optimal feeding strategy during periods of abundance may include some reduction in its consumption of gum, there may be specific limits on the compensatory use of gum when other resources, particularly animal material, are scarce. This appears to support a "nutrients as constraints" model for the understanding of the group's feeding behaviour [Pulliam, 1975; Altmann & Wagner, 1978]. As discussed previously, a number of factors may be involved. Whether, and to what extent, the quantities of substances such as tannins, uronic acids, minerals and proteins in the gum influence the observed patterns remains unclear at this stage. When other resources are especially scarce, however, an increase in gum feeding may be the only available alternative, as it seems to be for *G. senegalensis* in bad years [Bearder & Martin, 1980; Harcourt, 1986], although this option would seem to be of the last resort as it appears to involve a severe loss of physical condition for this species. It seems likely, however, that *C. flaviceps* will only very rarely be faced with such severe conditions as those which regularly occur within the southern African distribution of *G. senegalensis*.

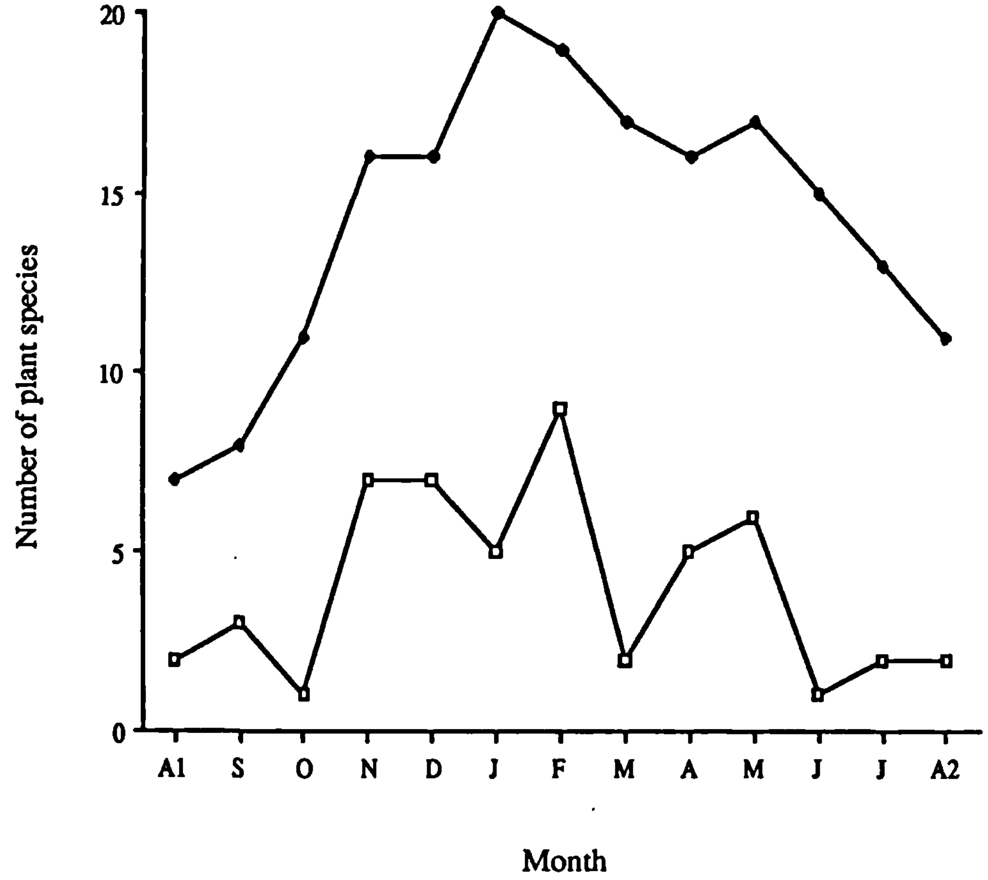
Fruit, Seeds and Nectar

In contrast with gum feeding, the study group's use of reproductive plant parts (referred to as "fruit feeding" here) underwent extreme fluctuations during the course of the main study period, both in terms of its contribution to the group's diet and the number of plant species utilised (table 6.2). While never absent from the group's diet during any month, fruit was a relatively rare component during most of the year, and during the late dry season in particular. Fruit feeding was, in fact, recorded only 28 times in the 28 observation days of the late dry season of 1985 (1.8% of feeding records), but was the largest component of the group's diet during January and February. The number of plant species utilised during any month varied between one and nine, although in all cases but one (December), either one or two species contributed more than 70% (and up to 100%) of the fruit-feeding records. As for gum feeding, however, the number of records involving "minor" fruit sources is generally too small to permit much detailed analysis.

Despite this, some correlation between the group's fruit-feeding behaviour and the availability of fruit, as measured in the phenology quadrats, is apparent from a comparison of the records (figures 6.2 and 6.3). There is a significant correlation between the number of species exploited each month and the number bearing fruit in the phenology quadrats (SRC: $r_s = 0.596$, $n = 13$, $p < 0.05$, one-tailed). The proportion of fruit in the group's diet (according to feeding records) shows an even clearer relationship with the number of phenology quadrat trees bearing fruit each month (SRC: $r_s =$

Figure 6.2

Monthly Variation in Fruit Feeding and Fruit Availability by Species



Key:

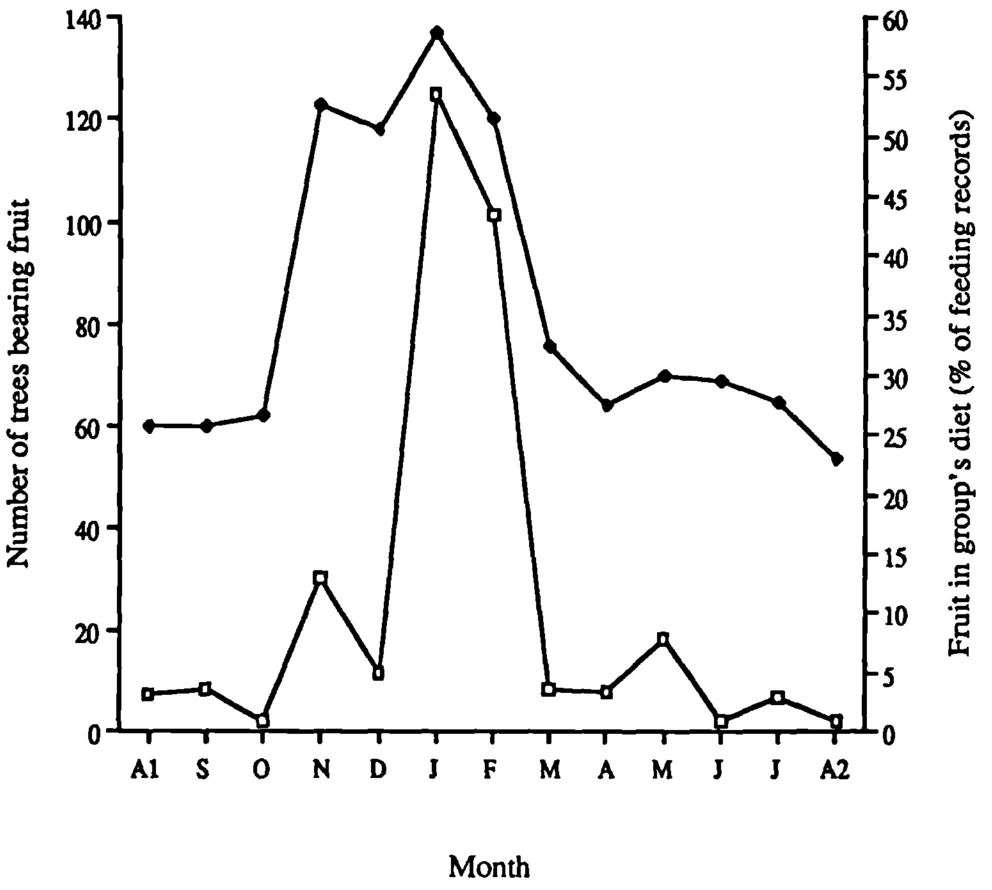
☐ *Plant species fed on by the study group*

◆ *Tree species bearing fruit in the phenology quadrats*

Figure 6.2 compares the monthly variation in the numbers of different plant species exploited for their fruit, seeds or nectar by the the group and of tree species recorded bearing fruit in the phenology quadrats.

Figure 6.3

Monthly Variation in Fruit Feeding and Fruit Availability by Number of Trees



Key:

□ *Fruit-feeding records*

◆ *Phenology quadrat trees bearing fruit*

Figure 6.3 presents a comparison of the monthly variation in the "fruit" (including seeds and nectar) component of the study group's diet and the number of trees in the phenology quadrats recorded bearing fruit. The values for fruit feeding are percentages of total feeding records collected in scan samples each month.

0.812, $n = 13$, $p < 0.01$, one-tailed). This is as we might expect, given the large numbers of *Allophyllus* and *Siparuna* trees present in these quadrats. However, while the records show that the group consumed the reproductive parts of more than twice as many species during the wet season as it did during the dry (22 and 9 respectively, see table 6.8), there was no significant difference between the numbers of species used each month during the two main periods (Mann-Whitney U test: $U = 12.5$, $p > 0.2$).

Table 6.8

Estimated Number of Plant Species Exploited for their Fruit, Seeds or Nectar by the Study Group during Each Season

Sample	Plant species utilised
Late dry 1985	4
Early wet	13
Late wet	12
Early dry	7
Late dry 1986	3
All dry season records:	9
All wet season records:	22
All records:	**29**

Overall, the results do seem to present a realistic picture of the group's fruit feeding. During all months except January and February, it was usually restricted to the random use of small, rare and widely-dispersed sources. The main influence on this pattern appears to have been the abundance and distribution of such resources within the group's home range. This also correlates, albeit indirectly, with the evidence from the phenology quadrats. During January and February, on the other hand, fruit and seeds were exploited in a systematic way, becoming the major component of the group's diet. It seems likely, from this and other marmoset studies, that fruit is preferred over gum, when available in sufficient quantities. *C.h. intermedius*, for example, only consumed large quantities of gum when fruit was relatively scarce [Rylands, 1982]. The evidence from both these studies similarly suggests that marmosets may spend relatively less time foraging for and consuming prey when edible fruit is more abundant.

It is worth remembering, on the other hand, that neither group excluded gum from its diet at any time during the year. While it is possible that fruit was never sufficiently abundant at either site to allow the groups to exclude gum completely from their diets, this seems unlikely. Gum constituted as little as 6.3% of the diet of the *C.h. intermedius* group during any one month. The mature fruit of *Allophyllus* and *Siparuna* appeared to have been available in sufficient quantities at Jaó to have allowed the study group to have excluded gum completely from its diet in January and February (and at least eleven other species were used during this period). These observations again appear to indicate the importance for marmosets of the mineral-balancing functions of gum, as discussed above.

The *C. flaviceps* study group fed on the resources (whether fruit or exudate) of far fewer plant species than *C.h. intermedius*, both in overall terms and during equivalent periods (daily, monthly or by season). The major factor influencing this difference between the two groups appears to be the characteristic differences in plant species density in the environments they inhabit. Other factors may also influence these contrasts, such as differences in the foraging strategies of the two groups which, it has been suggested, are reflected in the relative importance of animal material in their diets. There may also be related differences in the ecological adaptations of the two species. Much more information on the ecology of these, and other marmoset species will be necessary before definitive conclusions can be drawn.

It does seem possible to conclude from the evidence presented here, however, that fruit is a preferred food for marmosets while plant exudate may be an obligatory component of their diets. It also seems that both are utilised in a systematic or "optimal" way according to their availability, both in the short and in the long term. The concentration of feeding upon a small number of species during any period is probably a further reflection of this and may be an integral part of the study group's overall foraging strategies, as will be discussed below.

Chapter 6

Prey Types

In many ways, seasonal patterns in the study group's consumption of animal material reflect those in their use of plant resources. Overall, the group consumed larger quantities of more diverse prey items during the wet season months, although if we consider vertebrate prey alone, larger numbers were consumed during the dry season months as a whole, and in May and June in particular (table 6.4). While 1094 prey items were identified during the thirteen months of the main study (records taken from all observation periods), most of the categories are represented in the records relatively infrequently, which restricts the detailed analysis of seasonal variation in the proportions of these categories in the group's diet (table 6.9). The categories involved are also much broader than those for the types of plant utilised, and include a much larger proportion of items for which no identification of any sort was made (approximately one quarter of all prey items consumed during any period). It is nevertheless possible for a far more detailed analysis of this component of the group's diet to be made than those of other behavioural studies, and the following analysis of the data on prey size, in particular, will make an important contribution to the understanding of the group's foraging behaviour.

As we have seen, the proportion of feeding records attributed to animal material during any month varied considerably, from less than 10% to over 30%. In general, animal material constituted a much larger portion of the group's diet during the wet season months than during the dry season. Foraging was also far more successful, overall, during the wet season, correlating with the availability of arthropods at this site (see chapter 4). In addition to these trends, closer analysis of the prey-feeding records shows that the composition of this part of the group's diet also varied considerably during the course of the study period.

One characteristic of all the samples is the predominance of orthopterans in the group's diet. During July, in fact, grasshoppers were the only invertebrate prey identified, and this type of insect made up 85.7% of insect prey identified during the late dry season months of 1986. They constituted a relatively smaller proportion of the group's prey during other periods, but never constituted less than 45%, and usually made up over 60%, of the

Table 6.9

Seasonal Variation in Prey Captured during Main Study Period

Type of prey	Percentage of all prey items identified during each season: Late dry 1985	Early wet	Late wet	Early dry	Late dry 1986
Coleoptera	1.1	8.7	7.4	5.9	2.1
Lepidoptera	8.9	9.9	5.0	2.6	3.1
Orthoptera	55.6	51.8	64.4	52.6	31.0
Snails	0.0	11.1	6.5	7.2	7.3
All other arthropods[1]	2.2	11.7	6.6	3.4	2.3
Vertebrates	32.2	6.8	10.1	28.3	54.2

[1] See table 6.3.

Table 6.10

Orthopteran Component of the Study Group's Insect Prey

Sample	Percentage of insect prey items identified as: Orthopterans	Grasshoppers
August 1985	85.7	78.6
September	81.3	75.0
October	52.1	45.2
November	61.0	56.8
December 1985	73.4	71.8
January 1986	93.3	86.5
February	76.6	73.4
March	80.7	75.0
April	89.3	83.9
May	81.1	75.7
June	83.3	83.3
July	100.0	100.0
August 1986	77.8	77.8
All dry season records:	85.1	80.3
All wet season records:	72.9	68.1

insects identified during any one month (table 6.10). These values are similar to those given for the proportion of insect material identified as orthopteran in the stomachs of *S. geoffroyi* captured at different times of the year [65.7% to 77.3%, Garber, 1984a].

It must be remembered, however, that these proportions represent considerably different numbers of insects in different months. Comparing November 1985 and July 1986 (during which the sample periods were approximately equivalent), for example, the predation of grasshoppers was recorded 83 and 8 times respectively, although these records corresponded with 49.4% and 100% of the invertebrate prey items identified during these months. The proportion of insect prey items made up by orthopterans each month does, in fact, correlate negatively with the measured abundance of this type of insect (SRC: $r_s = -0.596$, $n = 13$, $p < 0.05$, one-tailed). This appears to be the result of changes in the relative abundance of other types of prey, and supports the qualitative observations of changes in prey diversity.

Prey such as cicadas (Homoptera) and flying ants (Hymenoptera) were consumed during the early wet season months, but were never seen being eaten at other times of the year (except for two cicadas captured during March). The predation of bugs (Hemiptera) was similarly only recorded during the wet season, although on only three occasions. The only type of prey exclusive to the dry season, on the other hand, was a single dragonfly (Odonata) captured in September. Overall, the group's capture of such "minor" prey types was strikingly similar to that of its use of minor plant food sources. The most interesting seasonal contrast is perhaps that of the vertebrate proportion of the identified prey, which was only 6.8% during the early wet season, but 54.2% during the late dry season of 1986.

Most of these specific features of the group's prey feeding seem to be closely related to observed fluctuations (both quantitative and qualitative) in the abundance of arthropods at the study site. Mature medium/large cicadas, for example, were so abundant during October that the group's vocalisations were frequently inaudible, although they had become very much less common by November. It is, in fact, somewhat surprising that cicadas were not consumed more frequently than they were during these months, although this may be related to the specific nature of the group's foraging behaviour, as we shall discuss in the following chapter.

The majority of the records of feeding on flying ants were made on a single day during which the group came across a leaf-cutter (*Atta* sp.) nest from which a large number of winged males and females were emerging. Here again, the marmosets consumed fewer of the ants than might have been expected, possibly because this incident occurred in the late afternoon when they were most likely to have been satiated (especially as this was during the insect-abundant month of November). In addition, most of the group members, especially the younger ones, appeared reluctant to capture and eat the ants, possibly because of their unfamiliarity with this type of insect. No records of the abundance of snails at the study site were collected, although their predation by the marmosets almost invariably took place during rainy periods, when these animals were active. The fact that they contributed a larger proportion to the group's prey during the early wet season than at other times is thus to be expected. Please note that the absence of snails from the late dry season sample of 1985 is probably due to the inexperience of the observer at that time, rather than their complete absence from the group's diet. The large numbers of spiders in the group's diet during the late wet season is also as we would expect, given their relative abundance during this period (see chapter 3).

The patterns of the group's predation of vertebrates are perhaps the most difficult to account for, although it may be that these trends are related, indirectly, to the relative abundance of insects both during and preceding the study period. In this case, the apparently extreme scarcity of insects during the dry season of 1986 would have had deleterious consequences for the populations of the mainly insectivorous vertebrates (lizards and frogs) which predominate in the group's diet. Facing severe shortages of their insect prey, these animals would have been more vulnerable to predation by marmosets for a number of reasons (see chapter 3). This pattern is mainly due, in fact, to fluctuations in the group's predation of lizards (see table 6.11). Frogs were preyed on more frequently than lizards, both during the course of the field study as a whole and in each month between August 1985 and May 1986. During each of the following three months, however, lizards were consumed more frequently than frogs, whose capture tended to decline. The lizards consumed were also generally much larger than the frogs (see below), and they thus consituted an even larger component of the group's diet during this

Table 6.11

Monthly Variation in the Composition of the Vertebrate Prey Captured by the Study Group

	Individuals captured:	
Sample	Frogs	Lizards
August 1985	4	3
September	13	9
October	7	5
November	12	2
December 1985	1	0
January 1986	8	2
February	7	4
March	10	4
April	11	5
May	16	11
June	7	17
July	5	8
August 1986	3	12
All observations (12/84-08/86):	**107**	**85**

period in terms of the quantity of animal material consumed.

One further prey category which is of interest is that of immature arthropods (other than caterpillars which were included in the preceding analysis). During July and August 1985, the group was frequently observed eating small (body length < 5 mm) homopteran nymphs found in foamy secretions on the leaves of *Sorocea guilleminia*. During the same months of the following year, however, these nymphs were not observed in the group's range and were thus not included in its diet. This seems to be a further reflection of the overall difference in the abundance of insects at the study site during the two years. The detailed identification of other immobile, immature arthropods (predominantly eggs, egg cases and pupae) was usually not possible, although these items were recorded under the general category of "immatures". The proportion of immatures in the group's prey fluctuated considerably during the course of the year.

Feeding on immatures was recorded infrequently during the wet season samples (making up 1.2% of invertebrate prey items), and only once during each of the months between December and February. Overall during the dry season months, however, the proportion of invertebrate prey made up of immatures was more than ten times larger (12.6%). Here again, the late dry season of 1985 is remarkably similar to the early dry season of 1986 during which immatures made up 7.4% and 7% of the invertebrate prey, respectively. During the late dry season of 1986, on the other hand, immatures constituted 28.7% of such prey (this value was 43.6% in July). This pattern correlates inversely both with that of the consumption of animal material and measured arthropod abundance, that is, of the predominantly mature, mobile forms (chapter 3). The influence of possible changes in the group's foraging behaviour and/or of the abundance of these forms will be discussed below and in chapter 7.

Prey Size

An estimate of the size of the prey was made for 1321 of the items consumed in scan samples during the main study period (76.3% of the invertebrates and 82.3% of the vertebrates captured by the group). The data were grouped in three classes: "small" for those whose body length was estimated as ≤ 1.5 cm, "medium" for those whose body length was estimated as > 1.5 cm but < 4 cm and "large" for those with an estimated body length of ≥ 4 cm (see table 6.5). A majority of the group's prey had a body length of 2 cm or more, and much larger prey was captured, on the whole, than has been reported for other neotropical primates including *Saguinus* [Terborgh, 1983], although there is little detailed quantitative evidence available for most other species. It seems likely, from the fact that the *C. flaviceps* study group most commonly consumed the types of prey most frequently recorded in other studies (*i.e.* large orthopterans in particular), that the values in table 6.5 are characteristic, rather than exceptional, of the prey usually consumed by marmosets and tamarins.

The relative proportions of the different size classes underwent marked changes during the course of the year (table 6.12). Overall, the group consumed larger prey during the wet season months than it did during the dry season. The only exception to this general pattern came during the late dry

Table 6.12

Seasonal Variation in the Relative Proportions of Prey of Different Estimated Sizes Consumed during Scan Samples

Sample	Body length of prey item (percentages of total prey for which an estimate of size was recorded):		
	≤1.5cm	>1.5cm - <4 cm	≥4 cm
All invertebrates:			
Late dry 1985	55.8	13.1	31.1
Early wet	34.0	41.5	24.5
Late wet	35.5	30.7	33.8
Early dry	39.5	31.8	28.7
Late dry 1986	70.2	18.1	11.7
All vertebrates:			
Late dry 1985	39.1	8.7	52.2
Early wet	24.0	40.0	36.0
Late wet	10.0	43.3	46.7
Early dry	25.0	34.4	40.6
Late dry 1986	14.7	32.4	52.9

season of 1986 when 14.7% of the group's vertebrate prey was recorded as small, compared with 24% during the early wet season sample. Here again, the late dry season of 1985 is similar to the early dry season of 1986, while the late dry season period of 1986 is exceptional, especially for the large proportion (70.2%) of small invertebrate prey consumed. During the wet season, then, the group not only captured much larger quantities of prey than during the dry season, but was usually consuming much larger items. This indicates that the difference in the quantity of animal material consumed during the two seasons was even greater than suggested by the numbers of prey captured. It is also likely that larger insects contain proportionately greater quantities of nutrients than smaller ones [Dawson, 1979], which would further accentuate this difference.

One complicating factor is that relatively larger numbers of vertebrates were captured during much of the dry season. These were, as might be expected, generally larger than their invertebrate prey (see table 6.12), and probably also contain larger quantities of more easily-digested nutrients than arthropods of the same body length. Vertebrates were, however, captured in relatively much smaller numbers during most of the study period, and it seems unlikely that their more frequent capture would have compensated for the scarcity of arthropods during the dry season. For example, while the group captured twice as many large vertebrates during the late dry season of 1986 as it did during the early wet season of 1985 (directly comparable samples of 28 observation days), this represents an overall difference of only 9 prey items. On the other hand, the group captured more than ten times as many large invertebrates during the wet season sample, a difference of 107 items. For every "extra" vertebrate captured during the late dry season sample, then, the group captured almost 12 large invertebrates during the equivalent late wet season sample. This contrast was even more marked in the case of medium-sized prey, further emphasizing the idea that the group was obtaining much smaller quantities of animal material during dry season months, and in the late dry season of 1986 in particular.

One further factor influencing the interpretation of the data is the problem of the differing observational biases affecting the visibility and recording of the capture of different types of prey (see chapter 2). The consumption of larger prey items usually took much longer than that of smaller prey and was thus relatively more likely, overall, to be recorded in scan samples. The consumption of larger items (vertebrates in particular) also attracted more attention from other group members, especially infants, who would frequently attempt to take them from the feeder. Such behaviour further increased the probability of recording large prey in scan samples, both by attracting the attention of the observer and increasing the time necessary for the consumption of the item. It was thus felt possible that these biases may have had an important influence on comparisons between seasons, according to the relative importance of the different size classes during different periods. In this case, we might expect the scan samples records to under-estimate the number of prey captured, and thus both the animal material consumed and the group's foraging success, during periods when a larger proportion of the prey was small.

In order to assess the effects of possible biases, the early wet season records and those for the late dry season of 1986 were considered in more detail. These were the periods during which small items constituted the smallest and largest proportions, respectively, of captured prey. All observed events of prey feeding were recorded throughout the study in *ad lib.* fashion (chapter 2) and so a comparison of these records with those from the scan samples provides some idea of the degree of bias. The records show, in fact, that the capture of small prey was recorded relatively less frequently in scan samples than would be expected according to all observed instances of prey feeding during the same periods (table 6.13). Unexpectedly, however, the difference was more marked in the wet season sample, both in relative and in absolute terms. According to this comparison, then, the capture of small prey was actually under-estimated to a slightly greater extent in scan samples recorded during the wet season than in those of the dry season.

Table 6.13

Relative Proportions of Invertebrate Prey of Different Sizes Consumed in all Observations Carried out during the Early Wet Season of 1985 and the Late Dry Season of 1986

	Body length of prey item (percentages of total invertbate prey for which an estimate of size was recorded):		
Sample	≤1.5 cm	>1.5 cm - <4 cm	≥4 cm
Early wet	42.5 (34.0)[1]	35.7 (41.5)	21.8 (24.5)
Late dry 1986	75.2 (70.2)	17.0 (18.1)	7.8 (11.7)

[1] Values in parentheses are those recorded in scan samples for the same categories of prey (see table 6.12).

A number of factors may have influenced this contrast. One possibility is that small items attracted much more attention from other group members during periods when prey was scarce than during those when it was abundant. In this case, feeding on small prey would have been relatively more likely to have been recorded in scan samples during the dry season. The considerable difference in the numbers of records involved may also have had an important influence. Whatever the factors involved, the evidence indicates that there was no major difference in the under-estimation of the group's capture of small prey during the two periods, and that the scan sample data are adequate for comparisons of seasonal trends in prey size.

Bearing this in mind, the evidence indicates quite clearly that the study group was capturing much larger prey items, on the whole, during the wet season, when arthropods were most abundant. The records of arthropod availability show, however, that larger individuals made up a smaller proportion of the total during periods of abundance (table 3.4). According to this, we would have expected the group, all things being equal, to capture a larger proportion of smaller prey during the wet season. While the size classes are different, a comparison of the insects captured by the group with those trapped each month indicates quite clearly that this was not the case (figure 6.4). As for other size classes, the number of large insects captured by the group each month correlated with their measured availability (SRC: $r_s = 0.77$, $n = 13$, $p < 0.01$, one-tailed). There is a slight negative correlation, on the other hand, if we compare the values of these categories as proportions of their respective totals (SRC: $r_s = -0.291$, $n = 13$, $p > 0.3$, one-tailed). While the group thus captured more large insects when they were more available, it was not capturing them in proportion to their availability. This seems to support the idea that factors other than the relative availability of arthropods of different sizes were influencing their predation by the group.

Overall, then, the study group, like those of other marmosets and tamarins, tended to capture relatively large prey and certain types, such as orthopterans, more frequently than others. It thus exhibited clearly-marked preferences for specific categories of relatively scarce types of prey while more or less ignoring others (small dipterans, for example) which were far more common. It will be argued in the following chapter that such selectivity can be seen as an integral part of a complex of behavioural adaptations related to insect foraging.

In these terms, the study group appears to have been progressively less selective of its prey, in terms of size, during the dry season, as arthropod abundance declined. This correlates with other features, such as the increase in the time spent foraging each day during the dry season and the concomitant reduction in foraging success. Overall, these features appear to confirm that the group was experiencing a marked, perhaps severe, shortage of prey

Figure 6.4

Monthly Variation in the Relative Abundance of Small Insects and Their Consumption by the Study Group

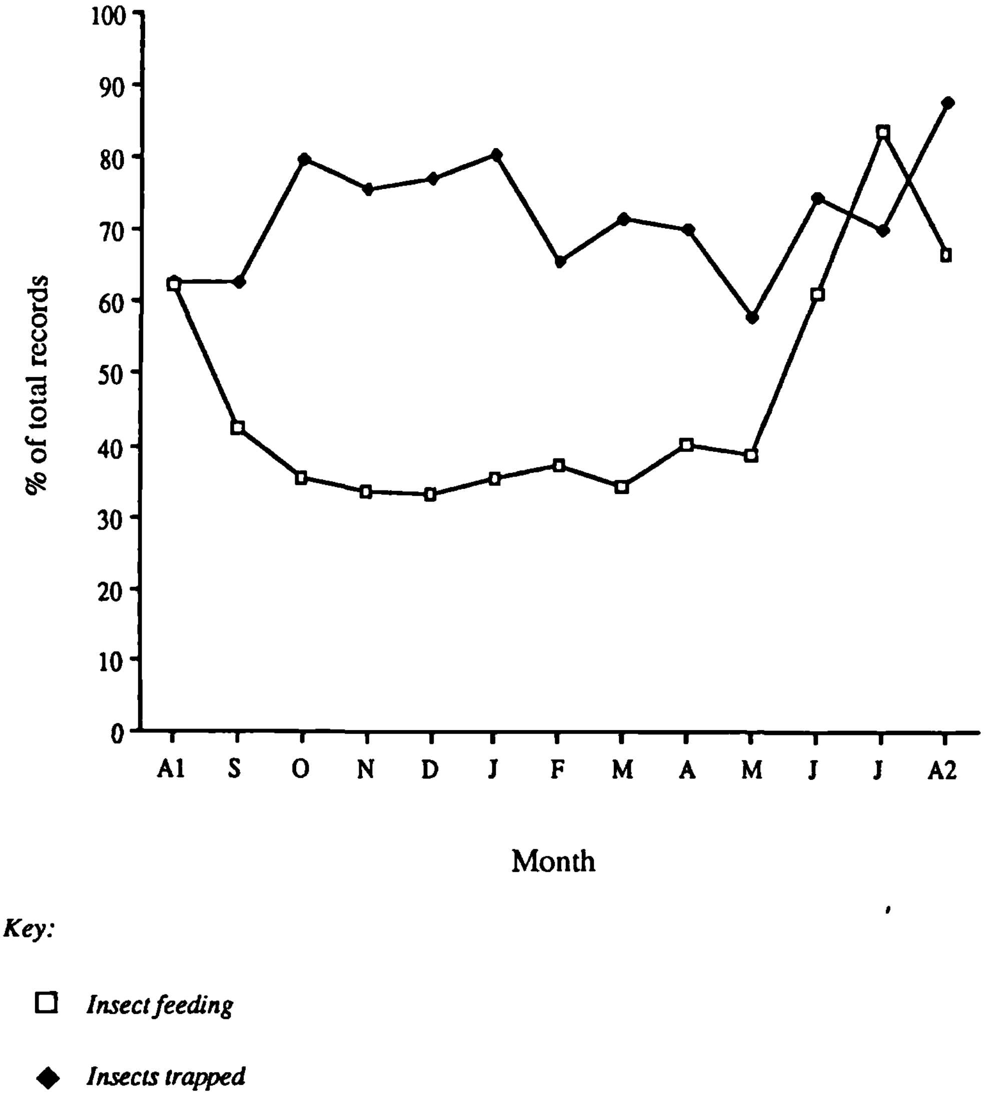


Figure 6.4compares the monthly variation in the study group's consumption of small insects and their relative availability. Values for feeding are the percentages of the group's insect prey made up of small individuals (body length ≤1.5 cm)each month. Values for availability are the percentages of the insects trapped each month made up of small individuals (body length ≤5 mm). Note that the size classes are not directly comparable (see text).

during the late dry season of 1986. The pattern is broadly similar to that recorded for the two *Galago* species which also preferentially consumed much larger items when prey was apparently more abundant, and then became far less selective when it was scarce [Harcourt, 1986]. This was accompanied by marked changes in both the behaviour of these species and the composition of their diets (see chapter 4).

Analysis of these patterns in terms of theories on optimal diet is useful, but somewhat complicated. Assuming that the capture (and "handling") of large prey does not usually require the expenditure of significantly more time or energy than that of small prey, in relative terms, we would expect the study group to have preferentially captured larger prey as far as possible. Prey of all sizes was both far more abundant and more easily acquired (according to the IFS), during the wet season. The group captured far more prey of all sizes during this period, and proportionately more larger prey, even though it was relatively less abundant. As the same foraging techniques were apparently applied to the capture of prey of different sizes, however, these findings imply that the group was actively ignoring large numbers of the smaller items it was presumably encountering during the course of its foraging activities. In this case, decisions on whether to "pounce" on a prey item, for example, may have been based on its perceived size in relation to a number of other factors, varying from the age and experience of the individual to the time of day and its previous foraging success. Thus, while the evidence does indicate that the group was far more selective of its prey during the wet season in comparison with the dry, detailed analysis of the complex set of variables which probably influence such selectivity appear to be beyond the scope of the present study.

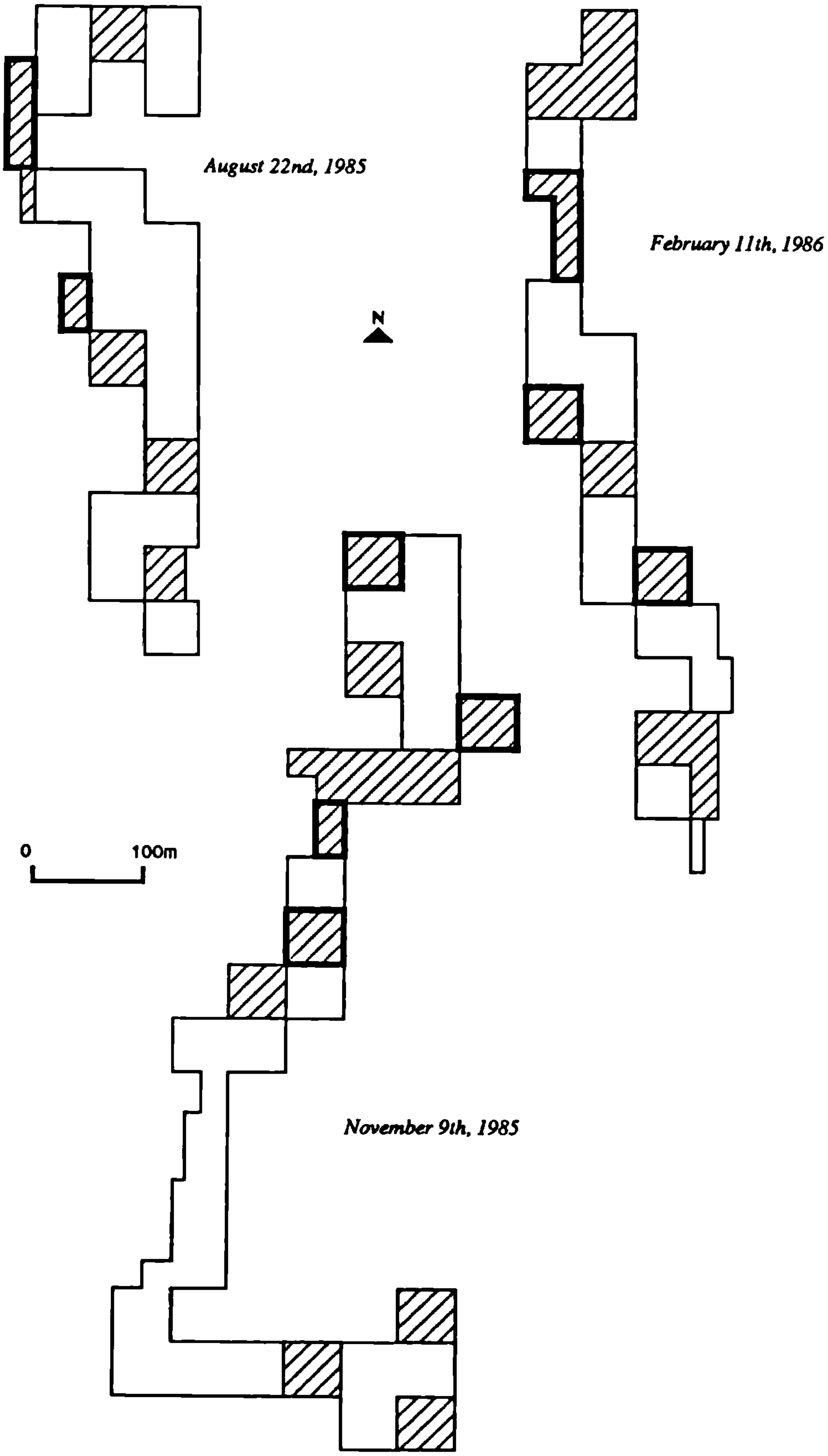
Spatial Patterns

In the previous chapter, we saw how the group's use of space varied during the course of the year in apparent response to observed changes in the availability and distribution of resources. Here we shall analyse two aspects of the group's feeding behaviour in relation both to the use of space and to its other activities. The discussion of prey feeding follows on from the analysis of ranging behaviour presented in chapter 5. This, along with the analysis of plant feeding will be developed further in the more detailed discussion of the group's foraging strategies in chapter 7.

Feeding on Plant Material

While the group's use of plant resources was closely linked, overall, to their distribution within its home range, it was apparent that a relatively small number of sites (in the case of both fruit and gum) were selected for intensive use during any particular period. This, as suggested previously, appears to be an integral part of the group's systematic use of its available plant resources and may, in turn, be closely related to other aspects of its activity, foraging in particular. This pattern also correlates with the tendency for the group to concentrate its plant feeding during certain times of the day, *i.e.* the early morning and the late afternoon (see chapter 4). The use of accumulated data from periods of a month or more tends, however, to obscure patterns which were apparent to the observer in qualitative terms at the daily level. The relatively simple analysis presented here aims at providing some quantitative measure of these patterns in order to support, hopefully, these more qualitative observations.

Days were selected at random from each of the five seasonal divisions of the main study period (*i.e.* late dry, early wet, *etc.*). For each of these five days, the "day range" (see chapter 5) was mapped out and the quadrats in which plant feeding was recorded during scan sampling were marked (figure 6.5). On none of the days selected was plant feeding recorded in more than half of the total number of quadrats entered. The plant-feeding "core area" (defined as 80% or more of the total records) constituted between three and six quadrats each day, representing no more than 22.9% of the day range (table 6.14). The overall pattern is quite clearly one of intense plant-feeding activity at two to five separate sites during the course of the day, with little or no such activity taking place within the remaining areas of the day range. This analysis thus appears to support the qualitative observations of the group's behaviour. This theme will be developed further in the following chapter.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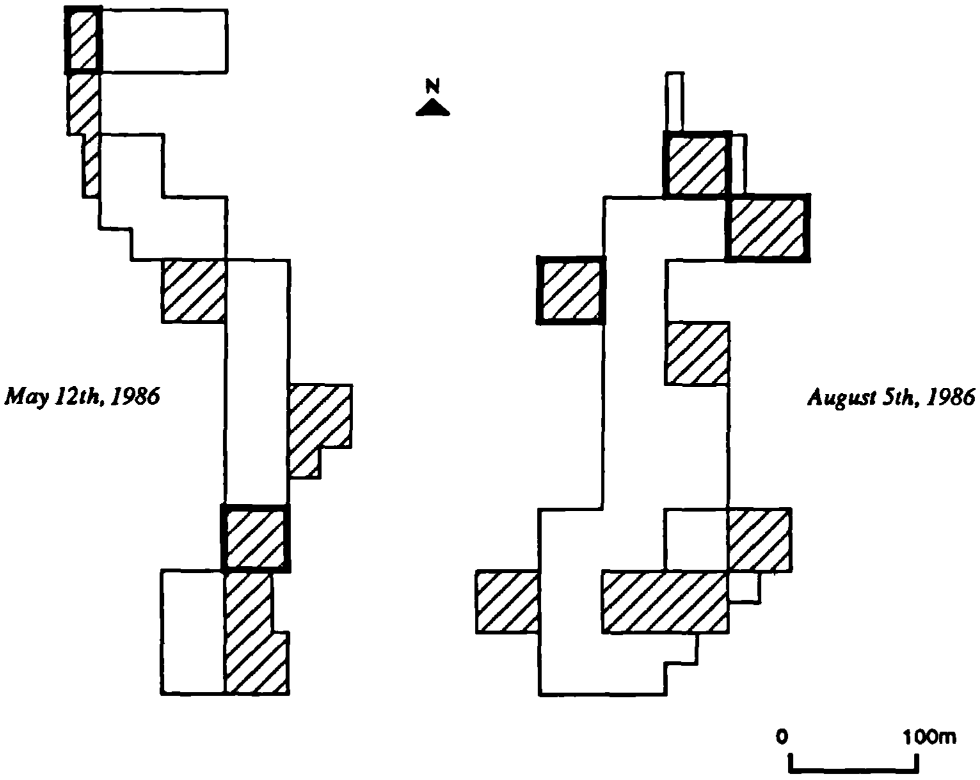


Figure 6.5 (and facing page)

Day Ranges Used for the Analysis of the Distribution of the Study Group's Plant Feeding

The five day ranges used for the analysis of the distribution of the group's plant feeding (see text) are shown. Quadrats in which feeding on plant material was recorded in scan samples on the selected days are indicated by diagonal shading. The plant-feeding "core areas" (the quadrats in which 80% or more of the plant feeding records were collected on the relevant sample day) are outlined.

Table 6.14

Day Range Samples: Areas Used and Distribution of Plant-Feeding Activities

Ranging variable	22/08/85	09/11/85	11/02/86	12/05/86	05/08/86
Day range (ha)[1]	5.4	7.7	4.8	4.3	5.8
All plant feeding records:					
Number of quadrats[2]	8	12	11	9	9
Total area of quadrats (ha)	1.4	2.8	2.4	1.6	2.1
Area of plant-feeding quadrats as a percentage of day range	25.9	36.4	50.0	37.2	36.2
Plant-feeding "core area"[3]:					
Number of quadrats	3	6	5	4	5
Total area of quadrats	0.4	1.3	1.1	0.7	1.1
Percentage of day range	7.4	16.9	22.9	16.3	19.0

[1] Calculated by the number of full or partial 50 m x 50 m quadrats entered.
[2] Number of full or partial 50 m x 50 m quadrats.
[3] Area in which 80% or more of plant feeding was recorded on sample day.

It was also apparent that the group tended to utilise these sites on consecutive or nearly consecutive days (quantitative evidence for this will be presented in the next chapter). This regular use of "known" sources of both fruit and gum probably allows the group to minimise the time it spends feeding on such material. This would be most advantageous in the case of gum, as regular feeding would also stimulate further flow and ensure the presence of fresher, more easily ingested, deposits at these sites. Such behaviour has further important implications for a number of other aspects of the group's daily life, especially its foraging activities. While the need to monitor the availability of the plant resources within its home range would be greatly reduced, on the one hand, its ranging could be more systematically related to its insect foraging activities, on the other. In regularly feeding at a few sites, then, the study group appears to have been following a strategy which effectively minimises its expenditure of time and energy on the locating of and feeding on plant resources. This seems to be, in turn, both an important and integral part of its foraging behaviour.

Chapter 6

Prey Feeding

Locating and capturing mobile prey presents very different logistical problems from those of plant feeding. The group's strategies for insect foraging appear to include a degree of irregularity in the use of its home range. We also saw in chapter 5 that the spatial distribution of the group's foraging behaviour appeared to have been directly related to fluctuations in the distribution of prey animals within its range. The group spent significantly more of its insect foraging time than expected at lower altitudes during the late dry season months of 1986, when such prey was scarcest at higher levels. A similar analysis of the distribution of the group's prey-feeding behaviour may permit further insights into this aspect of its behaviour. It seems reasonable to expect, for example, that the distribution of prey feeding would reflect that of its foraging behaviour to some degree. In this case, the distribution of the group's foraging activities may be determined, to a greater or lesser extent, by some form of feedback mechanism based on the differing levels of foraging success experienced by the group within its range.

Taking the same divisions of the range as those used for the analysis of the distribution of the group's activtity in the previous chapter (appendix IV), it is possible to analyse the distribution of its prey-feeding behaviour during

Table 6.15

Seasonal Variation in the Distribution of the Study Group's Prey-Feeding Activities

	Proportion of prey-feeding records recorded in sample quadrats (percentage of total records):	
Sample	Hillside quadrats	Riverbank quadrats
Late dry 1985	37.4	62.6
Early wet	47.5	52.5
Late wet	41.0	59.0
Early dry	39.2	60.8
Late dry 1986	29.5	70.5
All dry season records:	35.6	64.4
All wet season records:	44.4	55.6
All records:	**41.2**	**58.8**

Table 6.16

Chi-squared Comparison of Observed Distribution of Prey Feeding with Expected Values[1]

Sample		X^2	p	d.f
Late dry 1985:	*vs.* all records[1]	9.13	0.003 (river)[2]	1
	vs. foraging[1]	4.80	0.028 (river)	1
Early wet 1985:	*vs.* all records	2.38	0.123	1
	vs. foraging	0.22	0.641	1
Late wet 1986:	*vs.* all records	1.58	0.209	1
	vs. foraging	0.40	0.526	1
Early dry 1986:	*vs.* all records	4.67	0.031 (river)	1
	vs. foraging	3.52	0.061	1
Late dry 1986:	*vs.* all records	7.29	0.007 (river)	1
	vs. foraging	4.38	0.036 (river)	1

[1] Values of Chi-squared for a comparison of the observed distribution of prey-feeding records (see table 6.14) with the values expected according to the distribution of either all scan sample records or foraging records (as indicated) between the hillside and riverbank quadrats.

[2] "River" indicates that significantly more records than expected were collected in the riverbank quadrats.

different periods. Reflecting the distribution of its movements, the group captured a larger proportion of its prey at lower altitudes at all times of the year (table 6.15). There are clear differences between the seasons, however, especially when these records are compared with the values expected according to the distribution of its other activities (table 6.16). The distribution of prey feeding was essentially the same as that of other activities, including foraging, during the wet season samples. During all dry season samples, on the other hand, the group spent significantly more time than expected, according to the distribution of scan sample records, feeding on prey in the riverbank quadrats. While the differences were less marked in comparison with the distribution of its foraging activities, they were still significant in the two late dry season samples, and there was, again, a very clear contrast with the patterns recorded in the two wet season samples (table 6.16).

These trends are confirmed by the distribution of foraging success (table 6.17). Foraging was, in fact, slightly more successful in the *hillside*

Table 6.17

Seasonal Variation in the Distribution of the Study Group's Foraging Success

	Index of Foraging Success (IFS)[1]:		
Sample	Hillside quadrats	Riverbank quadrats	Difference in success between riverbank and hillside (%)[2]
Late dry season 1985	7.1	10.0	40.8
Early wet	17.4	16.7	-4.0
Late wet	14.0	14.9	6.4
Early dry	7.1	9.4	32.4
Late dry 1986	3.3	4.8	45.5
All dry season records:	5.5	7.1	29.1
All wet season records:	15.7	15.7	0.0
All records:	**9.9**	**10.6**	**7.1**

[1] IFS=(Foraging records/prey-feeding records) x 100.
[2] Difference as a percentage of hillside success.

quadrats during the early wet season, contrary to the pattern recorded in all other periods. There is similarly little difference in the records from the late wet season sample. During the dry season, on the other hand, foraging was between 32.4% and 45.5% more successful at the lower altitude of the riverbank quadrats than it was higher up. This evidence appears to confirm conclusions made in the previous chapter. On the one hand, the comparatively large proportion of its time spent at lower altitudes during the late wet season appears to have been related to the group's plant-feeding activities rather than to the distribution of prey. The uneven distribution of its foraging activities during the dry season, on the other hand, seems to have been directly related to that of the arthropods it was procuring. It is somewhat surprising, in fact, given the considerable differences in foraging success during the dry season, that the group did not devote an even larger proportion of its foraging time to the lower part of its range.

A number of factors can be seen as limiting the potential for such a strategy. It seems reasonable to assume, for example, that the group's foraging activities will have a deleterious effect on the abundance of prey within an area, in either the short or the long term. Increasing its foraging at lower altitudes would thus have the effect of reducing success in overall terms and, according to the idea of a feedback mechanism based on experienced foraging success, encourage a more even distribution of these activities. In addition, while the returns to foraging at higher altitudes may be much lower during the dry season, the group may benefit from the use of this part of its range in a number of other ways. The systematic monitoring of the availability of both animal and plant resources in this area may be particularly important, considering that their distribution appears to have the major influence on the group's movements. According to the evidence of the previous chapter, the regular use of the southern and western part of the range would also allow the group to discourage the encroachment of its neighbours. This may have been particularly important during the dry season. These influences are analysed in more detail in the following chapter.

Chapter 6

Summary

The *Callithrix flaviceps* study group consumed a variety of animal and plant material during the course of the study period. In broad terms, its diet was similar to those of other marmoset species, with the emphasis on plant exudates and insects. The intensive use of a few plant resources and the predation of specific types of insect were also characteristic. A number of features of its feeding behaviour were unusual, however, such as seed predation, the frequent opportunistic use of gum and the large numbers of vertebrate prey captured. Marked seasonal changes in feeding behaviour correlated with those observed in other activities and, in turn, with the abundance of resources. The major features of the group's feeding behaviour were:

1. According to feeding records, the group's diet consisted of 65.8% exudates, 19.8% animal material and 14.4% fruit (and other reproductive plant parts) over the course of the main study period. These proportions varied considerably during the course of the year. This was mainly due to fluctuations in the consumption of fruit and animal material, while gum feeding was relatively less variable.
2. The gum of no more than 8 plant species was used during any one month, although that of just two (*Acacia paniculata* and *Anadenanthera peregrina*) contributed 97.6% of the gum-feeding records for which the source was known. While the bark of *Acacia paniculata* was gouged in order to stimulate exudate flow, all other gum was consumed opportunistically when made available through damage caused by insects or other agents. While difficult to estimate, it was certain that more than half of the group's gum feeding was opportunistic during some periods.
3. While a wide variety of prey was captured during the study, certain types were captured far more commonly than others. Almost two-thirds (64.3%) of the invertebrate prey were orthopterans, mostly grasshoppers. Vertebrate prey was also captured relatively frequently, contributing 16.1% of prey-feeding records. The group usually captured relatively large prey items, 61.1% of those observed in scan samples having a body length of 1.5 cm or more.
4. Plant material other than exudate (fruit, seeds and nectar) was a relatively

minor component of the group's diet. Here again, while it utilised at least 30 different plants, two species (*Allophyllus* sp. and *Siparuna* sp.) contributed 74.6% of the total records. The seeds, rather than the fruit, of *Siparuna* were consumed.

5. *Acacia* gum was the type most frequently eaten (66.4% of gum-feeding records). During the 1986 dry season, however, *angico* gum was consumed slightly more frequently than *Acacia* gum.This increase in the consumption of *angico* gum correlated with the increase in the availability of new deposits. The use of minor sources of gum was relatively rare, and showed only random variation.

6. Animal material was not only a considerably larger component of the group's diet during the wet season (and the early wet season in particular), but a wider variety of generally larger prey items was consumed. The patterns correlate well with observed fluctuations in the availability of arthropods. The increased capture of vertebrates during the dry season is thought to have been due to an increase in their vulnerability to predation at this time of year.

7. Seasonal changes in fruit feeding also appeared to be correlated with the availability of such material. This material only made an important contribution to the group's diet during January and February. The evidence indicates that the consumption of gum, and perhaps also animal material, was reduced during this period, possibly in response to changes in the availability of certain nutrients.

8. Spatial patterns in feeding behaviour were also apparent. Feeding on plant material tended to be concentrated at certain regularly-used points during specific periods. Prey feeding was more frequent at lower altitudes during all seasons, correlating both with the distribution of both foraging activities and arthropods. This trend was more marked during the dry season, however, and foraging success was distributed far less evenly.

7

Foraging Behaviour

Searching for food, or foraging, is the most important aspect of the daily lives of almost all animal species, and in particular for those depending on resources whose abundance fluctuates seasonally. The exact nature of an animal's acquisition of an adequate diet during any particular period will be influenced by the inter-relationship of a number of factors, ranging from its body size and dietary adaptations to the availability and distribution of resources. The evidence presented so far in this thesis indicates that most aspects of the *Callithrix flaviceps* study group's behaviour were not only oriented towards the problem of obtaining an adequate supply of food (in both quantitative and qualitative terms), but were also influenced to a considerable degree by fluctuations through time in the abundance and distribution of resources. In this chapter, we shall examine its foraging behaviour in more detail and attempt to integrate the patterns outlined in previous chapters. It is hoped that this analysis will provide useful insights into the behavioural adaptations for foraging exhibited not only by the group itself, but also by this and other marmoset and tamarin species.

Efficient foraging for foods of different types demands appropriately different patterns of behaviour, depending on their nutritional value, abundance and distribution. Seasonal fluctuations in these variables present additional problems which may demand some provision for the longer term. Broad categories of apparently homogeneous resources, such as leaves, may also conceal variation in composition either at the level of the species or even of the individual plant, which may, in turn, demand relatively more complex foraging behaviour than might otherwise have been expected [Milton, 1980]. While omnivory has the advantage of a much wider range of potential foodstuffs for relatively unspecialised animals, there may be additional problems stemming from the need to balance specific nutrients (see chapter 6).

As we have seen, marmosets and tamarins are omnivorous, including a variety of plant and animal material in their diets. These two types of food present characteristically different foraging problems. Edible plant material is generally found concentrated into "patches", such as fruiting trees, which provide resources through periods ranging from a few days to a number of months, or even longer in the case of gum sources. Small animals such as insects, on the other hand, are usually more evenly distributed both within a particular area and through time. While faunivory thus demands a systematic process of searching on a daily basis, the exploitation of plant material requires the monitoring of potential sources, effectively over much longer periods of time. As the process of insect foraging appears to involve systematic searching throughout a group's range, it seems likely that the monitoring of plant sources will be a subsidiary, and complementary, aspect of this behaviour. Thus, while many herbivorous primates, such as *Alouatta palliata* [Milton, 1980], may be obliged to search systematically for new sources of plant material, it seems that this would rarely be necessary for most marmoset groups.

A number of features of the plant feeding behaviour of marmosets and tamarins imply a further reduction of the need for systematic foraging for plant material. Most studies have shown that they tend to concentrate their feeding on the resources of a few common plant species [*e.g.* Terborgh, 1983; Rylands, 1982; Soini, in press; Stevenson & Rylands, in press; this study], which are usually highly clumped in their distribution, a general characteristic of secondary forest habitats. Many of the species utilised for their fruit bear their crops in "piecemeal" fashion [Opler *et al.*, 1980], providing a regular, although usually small, supply over periods often extending to a number of months. The relatively small amount of material available at any one time effectively excludes the systematic exploitation of such plants by larger-bodied primates [Terborgh, 1983]. The tree-gouging adaptation of the marmosets entails a further advantage, enabling them to stimulate a regular supply of plant exudates at the same site for periods which can extend to more than a year, as observed in the present study.

The preference for secondary forest, along with characteristics such as their relatively small body size, may thus guarantee marmosets and tamarins a more regular supply of plant material, on average, than is available to groups of most other primate species. This will depend, of course, on the presence and distribution of certain plant species, and it is possible that some areas of secondary forest would not support callitrichine groups in the long term. The gum-feeding adaptation of the marmosets gives them an even greater advantage, and it seems likely that they are able to exploit habitats in which tamarins could not survive. Overall, the evidence indicates that these primates, especially the marmosets, are normally able to gather sufficient information about the availability of plant resources during the course of their insect foraging activities and would thus rarely be obliged to forage systematically for such resources.

An alternative interpretation would be that insect foraging is, in fact, a subsidiary activity taking place during systematic foraging for plant resources. This seems highly unlikely, however, given the apparent importance of animal material in marmoset diets, on the one hand, and the difficulty of its acquisition, especially for young individuals, on the other [Ferrari, in press]. Marmosets also appear to be almost constantly attentive to signals of prey [Rylands, 1982]. What seems more likely, in fact, is that searching for prey will be the major component of foraging activities even during periods when systematic foraging for plant resources is a necessity. This is emphasized by the fact that the periods of scarcity of both types of resource are correlated at most study sites. While the need to monitor plant resources may obviously have an important influence, it seems reasonable to assume that marmoset foraging activities, at a behavioural level in particular, are usually oriented primarily towards the capture of prey (that is, specifically, animal prey).

Following on from this interpretation, we might expect the exploitation of plant resources to be influenced directly by a group's insect foraging activities. An important assumption here is that the group has a detailed knowledge of the distribution of such resources within its range. Studies of baboons, for example, indicate that ranging and foraging behaviour may be based on the use of a "mental map" [Altmann & Altmann, 1970; Sigg & Stolba, 1981]. Studies of both marmosets and tamarins have also indicated that group movements are systematically, rather than randomly related to the distribution of plant resources [*e.g.* Terborgh, 1983; Rylands, 1986].

The *C. flaviceps* study group appeared to know the exact locations of its principal gum sites, to which it would normally move directly and rapidly.

Its behaviour at the end of the day also indicates that the locations of the most frequently used sleep trees were well known (chapter 5). The group often moved in its distinctive creeping posture over distances of more than 50 m, sometimes directly from a late afternoon rest period. On one occasion, it travelled in this way towards a sleeping site, only to discover that it had become unuseable (the crown of the tree had collapsed, leaving a bare trunk). The marmosets were visibly confused by this situation, and spent some time in retreating and moving on to what appeared to be a makeshift site nearby. The typical "double-backs" and use of decoy trees further support the idea that these marmosets had a mental map of these locations.

Given the assumption that the activities of a marmoset group may be determined, at least in part, by a knowledge of the distribution of its "fixed" resources, certain patterns would be expected. While a large herbivorous primate such as *Brachyteles arachnoides* might "camp out" at the site of a large fruiting tree during the course of a period of a number of days [Strier, 1986], this would probably not be a good strategy in most cases for the omnivorous marmosets if animal material is a necessary component of their diet. As its prey is relatively evenly distributed within the forest, it seems likely that an insectivorous primate will need to forage within a minimum area during the course of any given period. Foraging for prey repeatedly within the same area, that surrounding a fruiting tree for example, would probably tend to reduce the availability of prey in the short term, at least. While a group might concentrate its activities at a central point, such as a fruiting tree, it would probably experience increasingly smaller returns to its foraging efforts and would thus be forced to range progressively further from that point. If we assume that other factors, including territorial vigilance, resource monitoring and the avoidance of predation, will further encourage the extension of its movements, the concentrated use of a single plant source would be an even less feasible strategy.

Thus, while a single source might provide adequate supplies of plant material for a marmoset group [as it does for *Callithrix jacchus* at João Pessoa, Maier *et al.*, 1982] we would predict that a number of sites, if available, will be used during any period. In the case of gum feeding, the regular use of sources may also be important not only for the maintenance of an adequate supply but also for the minimisation of the time spent gouging holes. Both gum and gouge holes harden with time, so the more regularly visited the site, the less time and energy will be necessary both for the ingestion of gum and the gouging of holes. The regular use of sources distributed throughout a group's range is probably also an important strategy in the long term, especially as it would probably be complementary to insect foraging activities. According to the present discussion, then, the main orientation of marmoset foraging activities is the capture of prey, while searching for plant resources can be seen as both a subsidiary and complementary activity. This view was followed both in the collection (*i.e.* the category "forage" referred specifically to prey foraging activities) and in the analysis of the behavioural data.

While the typical plant resources available in secondary forest have important implications for marmoset foraging behaviour, other characteristics of these habitats may have similarly important implications in terms of the capture of prey. There is some evidence that the dense vegetation usually present in such areas may support relatively higher densities of arthropods, particularly folivorous insects, than primary habitat [Janzen, 1973a, 1973b; Cates & Orians, 1975; Opler, 1978]. Whether this is in fact the case, or true of all such habitats, is not known. Rylands [1986], for example, noted that the *Callithrix humeralifer intermedius* study group tended to avoid one area of secondary growth within its range, possibly because of a relative lack of plant resources. The present study has also shown that the abundance of arthropods within the secondary forest habitat occupied by the study group was not only far from homogeneous [see also Janzen & Schoener, 1968], but fluctuated considerably during the course of the year. Comparisons between different habitats obviously require a great deal of care.

Whether arthropods are more available or not, a number of features of secondary and edge habitats may favour the insect foraging behaviour of most marmosets and tamarins. Their preference for these habitats might be seen as part of a broader adaptive strategy based on characteristics such as their small body size and including specialisations of foraging technique and prey type. One important factor may be the avoidance of competition from larger-bodied primates such as *Cebus*, whose foraging activities are inhibited by the dense vegetation and relatively thin supports which characterise these types of forest. In this case, the availability of prey in these habitats would effectively be greater for the smaller-bodied primates, even if the absolute density was similar to that of primary forest. Other features of these habitats which may be important are the normally low levels of the canopy and the proximity to the ground of dense vegetation. The relatively large size of the typical prey animals, along with their characteristic predator avoidance behaviour may, in fact, favour their predation by marmosets and tamarins in these habitats.

In this chapter, then, a number of aspects of the foraging behaviour of the *C. flaviceps* study group will be discussed, and analysed in the context of the patterns recorded in previous chapters and for other primate species. This analysis will attempt to draw on predictions from foraging theory [*e.g.* MacArthur & Pianka, 1966; Schoener, 1971; Pyke *et al.*, 1977; Stephens & Krebs, 1987]. In doing this, the discussion will both investigate the adaptive significance of the observed behavioural patterns and test the efficacy of such theories for the analysis of primate foraging behaviour. A central theme of the analysis will be that of a proposed specialisation for secondary and edge habitats based on both the characteristics of marmoset insect foraging behaviour and their exploitation of plant resources.

A major problem in this discussion, however, is the identification of causality in the determination of proposed foraging strategies. Caution is necessary in order to avoid circular arguments drawn from apparently logical patterns [Gould & Lewontin, 1979; Pierce & Ollason, 1987], particularly as the data themselves are far from complete. The adaptive significance of apparent specialisations in behaviour (as opposed to those of morphology, for example) is particularly difficult to assess, especially as there may be significant differences between individuals in their ability to make foraging or feeding decisions [Ross & Bras, 1975; Post, 1982]. Information on many other variables, such as the availability of resources and their composition, is also far from complete. It is hoped, however, that a cautious and systematic analysis of the information available on the study group's foraging behaviour will create useful insights into both its foraging strategies, and those of other primate species.

Habitat, Prey and Insect Foraging Techniques

In the scan samples of the study group's behaviour, any activity which was interpreted as involving "searching for and/or capturing prey" was recorded in the category "forage". This category included a number of specific types of activity, ranging from an intense scanning of the environment for signs of prey to biting or breaking open substrates (table 2.3), although scanning was by far the activity most commonly recorded as foraging behaviour (table 7.1). As the category "forage" was applied to activities primarily related to the capture of prey, this behaviour has been frequently referred to more specifically as "insect forage" in this thesis in an effort to minimise possible confusion in comparisons with other studies in which foraging behaviour is defined differently.

Group members appeared to be continually attentive to possible signs of prey in their immediate surroundings, and seemed to remarkably perceptive. There is some evidence, in fact, that marmosets have better depth perception than other primates, especially when their small size is taken into account [Glaser, 1980]. As well as helping in the location of prey, this perceptiveness

Table 7.1

Relative Frequency of Different Foraging Behaviours Recorded in Scan Samples between December 1985 and August 1986

Behavioural category	Percentage of total foraging records collected in scan samples (Dec 1985-Aug 1986)[2]
Visual scanning (FO SK)[1]	82.0
Scanning ground (FO SKO)	7.2
Manipulating substrate (FO MP)	6.1
Grabbing prey/substrate (FO GB)	2.1
Biting substrate (FO BI)	0.9
Pouncing on prey (FO PO)	0.9
Following potential prey (FO FO)	0.7
Breaking substrate (FO BKO)	0.1

[1] Categories defined in table 2.3.

[2] N = 11737

is probably also important for the detection of possible predators. While actively scanning for signs of potential predators may occupy a significant proportion of the time budget of primates such as *Cebus olivaceus* [de Ruiter, 1986], this behaviour was rarely observed in the *C. flaviceps* group, usually only when stimulated by some incident such as an alarm call. Perception of potential danger from aerial predators was very common, however, judging from the frequency of alarm calls given by group members, which were even stimulated by falling leaves. Snakes, almost invisible to the observer because of their camouflage, were regularly perceived and investigated by the group. If scanning for both prey and predators can be effectively combined, more time would be made available for other activities (including rest) and the adaptive significance of this type of foraging behaviour for marmosets would be even greater. These two types of scanning behaviour appear to be well differentiated in the larger *Cebus olivaceus*, on the other hand [de Ruiter, pers. comm.]. It is interesting to note that whereas marmosets seem to be most vulnerable to predation by aerial raptors, the scanning of *Cebus olivaceus* was apparently related to the danger from terrestrial predators.

Rapid pouncing normally followed the perception of a possible prey item by group members, with the target usually being grabbed forcefully with both hands and brought to the mouth. Similar "scan-and-pounce" behaviour has been recorded for other marmosets and tamarins [*e.g.* Rylands, 1982; Terborgh, 1983]. Variations on this technique mainly involved the pursuit of mobile prey which had been disturbed, either by that individual or by other group members. The rapid pursuit of prey which had fallen to the ground was frequently observed, with the marmosets often travelling vertically down the trunks of trees or climbers. Group members would forage systematically for prey on the ground, usually scanning from vantage points at 0.5 to 3 m before coming down and searching in the leaf litter. Such behaviour almost invariably resulted in the capture of the desired prey.

Apart from scanning for and pouncing on or pursuing prey, group members spent only a relatively small proportion of their time manipulating and opening substrates. This invariably involved relatively easily-opened substrates such as leaves and peeling bark. The majority of this behaviour appeared to be directed at the capture of immature insects found in rolled-up or dead leaves, although some mature forms were also captured in this way.

Taking the substrate in both hands, the marmoset would break or bite it open until it was possible to extract whatever prey might be present inside. While group members would sometimes pull at peeling bark, the biting or breaking open of branches [as reported for *Cebus* by Terborgh, 1983] was never observed.

Terborgh noted that the larger-bodied primates at Manu generally utilised techniques which involved strength and stamina, and concluded that the use of stealth in the capture of prey was more feasible for the tamarins because of their small body size [see also Garber, 1984b]. These differences in technique have a number of consequences for the types of prey captured by the different primate species. Marmosets and tamarins, as we have seen in the previous chapter, most frequently capture large, mobile prey, usually orthopterans. For the larger cebids, on the other hand, smaller, usually immobile forms are the most common prey [Terborgh, 1983: pp. 104-107]. Being small-bodied and capturing large prey appears to enable the tamarins at Manu to spend relatively less of their time foraging for prey each day, while maintaining a larger animal component in their diet, characteristics which also seem to apply to marmosets, in comparison with larger-bodied insectivorous primates (see also chapter 4).

As most mature insects are able to fly, their predation presents a major problem for flightless arboreal animals. Disturbances will put the prey to flight, and thus beyond the reach of the predator. In addition to the size of the primate, other factors, such as the size of the group, may have an important influence on the degree of prey disturbance, another factor which may favour the marmosets and tamarins, with their normally much smaller groups than *Cebus*, and *Saimiri* in particular. It has been suggested, on the other hand, that the relatively large foraging groups of *Saimiri* may serve to increase capture rates through the disturbance of insect prey [Klein & Klein, 1975], although this has not been supported by more detailed studies [*e.g.* Terborgh, 1983].

While mature insects are usually far more mobile than their immature forms, the degree of agility, and vulnerability, varies considerably with the type and size of insect and possibly even the time of day [Dawson, 1979]. Whereas all these neotropical primates tend to prey on the same types of mature insect, the foraging of the smaller species appears to be far more successful. While the body size of a primate species may be the most important factor determining its relative foraging success, others, such as habitat type, may also have an important influence.

Rather than depending on their agility to escape predation, these less mobile insects rely on other forms of defence, such as noxious chemicals or camouflage. Generally unable to fly over long distances, most orthopterans rely heavily on camouflage to escape predation. The most extreme example is that of the flightless stick insects, family Phasmidae, although many grasshopper species, the nocturnal Tettigonidae in particular, also rely on elaborate systems of camouflage to avoid predation. While the former rely on their similarity to twigs to escape detection, the latter often take the form of leaves and are thus almost undetectable in dense tree-tops, as long as they remain motionless. Once disturbed, however, they may attempt to escape. In the case of grasshoppers, this involves the use of the well-developed hind legs which spring the animal into the air through which it is able to fly, or rather "glide", over relatively short distances. This distance tends to be further reduced by obstructions, such as those of the dense vegetation of a forest canopy. On coming to a halt, the insect returns to a motionless state until disturbed again. Having reached the ground, however, many larger orthopterans may be unable to initiate further flight (this would be impossible for the flightless stick insects, of course). In this case, their only defence is to remain motionless, even if disturbed. Insects in this position are extremely vulnerable to predation.

Apart from orthopterans, the types of prey most commonly captured by the *C. flaviceps* study group were coleopterans, caterpillars, snails, spiders, frogs and lizards (table 6.4). Together with the orthopterans, these categories constitute 94.1% of the prey items identified during the course of the field study. While very different in many ways, the majority of the animal species in these categories utilise camouflage as their principal means of defence against predation. Observations of the study group also show that all these prey animals use rapid escape as a defence of the last resort when disturbed by predators. In almost all cases (even for the coleopterans, which are mostly slow to take flight), this rapid escape is similar to that of the orthopterans, *i.e.* leaping or simply falling out of the tree and then remaining motionless. Other types of insect consumed by the study group were captured only rarely, on the whole (table 6.4), and much less than might be expected, given their apparent abundance. Most of these types of insect, such as cicadas and butterflies, do not use camouflage to escape predation, relying instead on their flying abilities. Group members were observed as being inept, on the whole, at the capture of such prey.

This evidence supports the idea that factors other than the small body size of the marmosets and tamarins influence their success at the capture of large, mobile prey animals. Instead of capturing a wider variety of mobile prey than the larger cebids, as we would expect if stealth alone was the factor determining their success, these smaller primates appear to be simply more adept at the capture of the same types of prey. This, in turn, would permit them to ignore the smaller, less "economic" types of prey (except when all prey is scarce, see chapter 6) which the larger primates seem obliged to capture in order to acquire an adequate supply of animal material. While accepting the greater potential of the smaller primates for stealth, it will be argued here that their preference for specific types of habitat is a major factor determining their greater success in the capture of these types of prey.

The apparent preference of marmoset and tamarin species for disturbed and edge habitats has been discussed in both this and preceding chapters. Most authors have explained such a preference in terms of the abundance of resources and the greater protection against predation offered by the dense vegetation, including suitable sleeping sites [Dawson, 1979; Rylands, 1986]. While there is some evidence to suggest that arthropods are more abundant in such habitats, it is far from conclusive. What may be more important are the types of prey and their methods of predator avoidance, in relation to foraging techniques. In this case, the critical factor is the height of the vegetation. While the small-bodied marmosets and tamarins may be able to capture much of their prey by stealth and surprise, such prey is also frequently disturbed, judging from qualitative observations of the *C. flaviceps* study group. Disturbed prey will attempt to escape by leaping away rapidly and, in the case of most grasshoppers, "gliding" to a new position.

The efficacy of such behaviour will be directly related to the height above the ground of the escaping animal. The higher the animal when initiating escape, the greater the distance it will probably travel, both vertically and horizontally, and the greater its chance of falling into vegetation at lower levels in the forest, rather than to the ground, from which further escape is impossible. Doubling the height from which escape is initiated would have the effect of doubling the horizontal distance over which the animal travels, assuming the same angle of descent (figure 7.1). The scope for escape is likely to be further reduced in secondary forest by the density of the vegetation, which may be most important in the case of the gliding orthopterans. It thus seems that such an animal falling from the crown of a canopy tree at 30 m in primary forest will have a far greater chance of avoiding detection by its predators than one falling from an "equivalent" tree at 10-15 m in secondary habitat. We would thus expect the success of marmoset foraging activities to be greater the lower the canopy of the forest, assuming the same abundance of arthropods.

Table 7.2

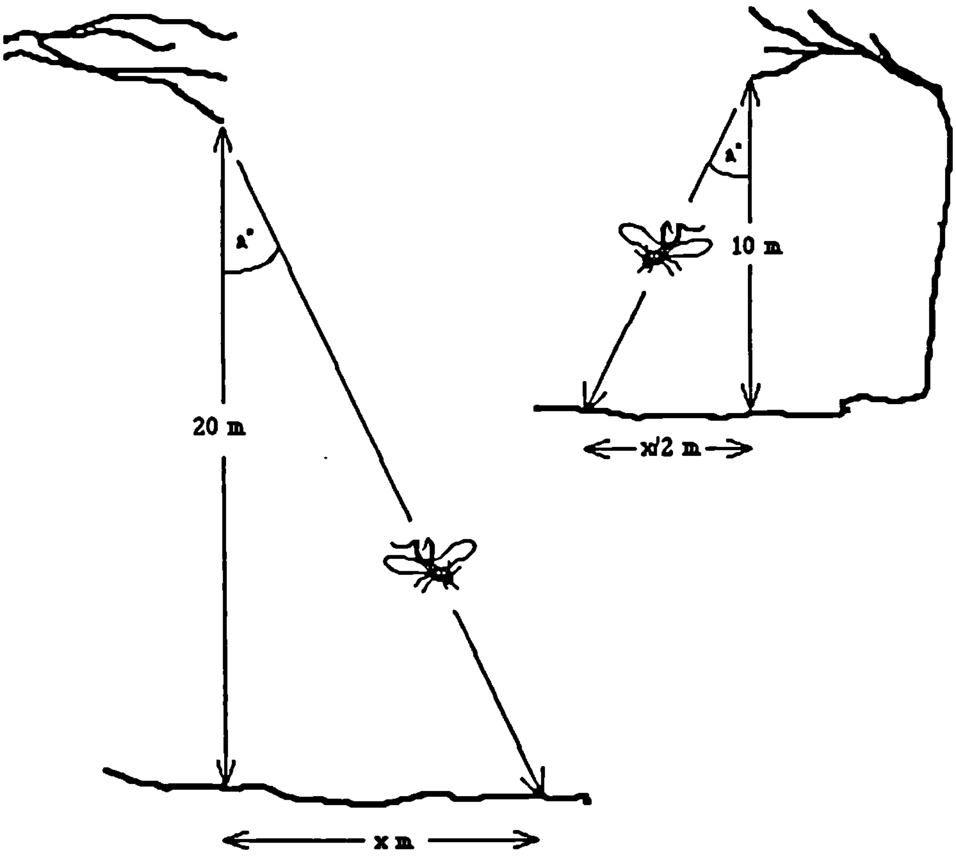
Heights at which Foraging was Recorded in all Scan Samples

Height of activity (m)	Percentage of total foraging records
≥16	2.0
10-15	6.8
6-9	21.0
4-5	20.2
2-3	35.5
0-1	14.5

This hypothesis is based on detailed observations of the foraging behaviour of the *C. flaviceps* study group. In addition to preferring secondary and edge habitat, the group foraged for prey at relatively low levels in the forest throughout the year, spending exactly half of its time at or below 3 m (table 7.2). Small animals were frequently observed being disturbed by group members, which would react rapidly to any movements, often following such prey down to or near the ground. Detailed estimates of the importance of this type of capture for the foraging success of the study group are difficult to make, given the usual rapidity of such events and the observational methods used, but it did seem to make a considerable contribution to the capture of prey, during certain periods in particular.

Figure 7.1

Differences in the Horizontal Distance Travelled by an Insect Falling at the Same Angle from Different Heights



When falling from 20 m at angle a°, the insect falls x m. Halving the vertical distance fallen halves the horizontal distance travelled (x/2 m), given the same angle of descent, a°.

The study group was observed foraging on or near the ground at the front of swarms of army ants (*Eciton burchelli*) on five occasions during the field study, a type of behaviour also recorded for *C.h. intermedius* and *Callithrix penicillata kuhli* [Rylands *et al.*, unpubl.]. This did not appear, however, to be as intense or prolonged an activity as that recorded for *C.h. intermedius* [Rylands, 1982], a contrast which may have been linked to the different levels at which these two groups normally foraged. In this case, such behaviour may have been relatively less advantageous for the *C. flaviceps* group, in terms of increasing its success, given that it generally foraged at very much lower levels and frequently captured prey on the ground. It is nonetheless possible that this difference was more closely linked to absolute differences in the abundance of arthropods at the two sites.

A number of tentative conclusions are possible. According to the scan samples taken between December 1985 and August 1986, for example, group members were recorded as searching for signs of prey on the ground in 8% of "scanning" records. This is probably an underestimate of the actual frequency of this type of behaviour as it was only recorded if the observer was certain that the animal was scanning the ground at the moment of its sighting. Similarly, and despite the usual rapidity of such events, group members were recorded as being on the ground during 2.3% of all foraging records. Almost one tenth of all the recorded foraging behaviour can thus be linked unequivocally with the pursuit of prey on the ground. This is again probably an underestimate of the true frequency of this type of behaviour, given the fact that half of all foraging took place at or below 3 m above the ground. As both scanning the ground and foraging there were almost invariably stimulated by the movement of potential prey, and can thus be seen as a "pursuit" rather than "search" type of foraging behaviour [*cf.* MacArthur & Pianka, 1966], their significance for the group's foraging success is again probably much greater than this value suggests.

This is reflected in the records of prey feeding, despite the fact that captures which took place on the ground were usually even less likely to be recorded in scans than animals foraging there. Nevertheless, 4.2% of all prey items recorded during scans were being consumed on the ground at first sighting. This is almost twice what might be expected, given that 2.3% of foraging took place on the ground. There was also a major difference between seasons, which seems to correlate with the capture of different types of prey (this will be discussed in more detail in the following section). Thus, while similar proportions of the group's foraging took place on the ground during all wet and dry season scan samples (2.2% and 2.4%, respectively), only 2.7% of prey items were recorded being consumed on the ground during the dry season while this value was 5% during the wet season.

Stick insects and vertebrates were observed being captured on the ground very frequently, more so than other types of prey, especially flying insects. This may have been a consequence of observational bias, however, as these larger prey items not only usually required more handling time on the ground, but attracted more attention from other group members. Prey which was captured on the ground was almost never consumed there. The marmosets would usually pounce down and then leap rapidly back up to a perch, often in the same movement, in order to feed. They would rarely, in fact, feed on prey at the location of its capture, especially when large, desirable items were consumed, when the feeder would frequently avoid other group members attempting to initiate food transfer [Ferrari, in press]. The height of prey feeding is thus not necessarily a good measure of the height of capture, although such feeding normally took place, like foraging, at relatively low levels in the forest (see appendix III).

While the evidence is not conclusive, given the lack of detailed quantitative data, it does seem possible to postulate that their preference for secondary forest habitats has an important influence on the relative success of marmosets and tamarins at the capture of large mobile prey such as orthopterans and vertebrates. This idea is supported both by the seasonal variation in the study group's foraging behaviour (see below) and in comparison with the data from other studies. While again not conclusive, there does seem to be good evidence that marmoset and tamarin groups inhabiting more disturbed habitats forage more successfully and include a larger proportion of animal material in their diets. It worth noting, in this context, that the small, highly insectivorous tarsiers (*Tarsius* spp.) also prefer secondary or disturbed habitats in which they both forage at the very lowest forest strata and capture a relatively large proportion of orthopteran prey [Niemitz, 1977, 1984; MacKinnon & MacKinnon, 1980; Crompton & Andau, 1987].

One point of interest is the preference of *Saguinus geoffroyi* for the "vicinity of edge" [Moynihan, 1976] rather than the edge of the forest itself. Prey falling outwards from the very edge of the forest will be beyond the reach of marmosets reluctant to expose themselves on open ground. Disturbed insects were sometimes observed escaping out into the open pasture when the *C. flaviceps* group was foraging at the edge of the forest. While group members would pounce rapidly on such prey if it had fallen relatively close to the forest edge (within 2 m), the ability of large grasshoppers to glide away usually put them beyond reach.

The home range of the *C. flaviceps* study group has been described in chapter 2. While much of the forest reaches between 10 and 20 m in height, this stratum is generally made up of open-crowned trees forming a discontinuous canopy, interspersed with lower patches of more continuous and much denser vegetation. The type of habitat used most often by the *C.h. intermedius* study group at Aripuanã, on the other hand, was defined as "disturbed primary forest", characterised by a more or less continuous canopy at 20-25 m [Rylands, 1986]. While this group tended to be active at lower levels than this, and was observed occasionally coming to the ground to capture prey, it generally foraged at much higher levels than the *C. flaviceps* study group (appendix III). As discussed previously, the foraging activities of *C.h. intermedius* appeared to be far less successful than those of *C. flaviceps*. While this is probably also a function of a number of other factors (chapter 4), it is not inconceivable that differences in the structure of the forest available to the two groups has a major influence on this contrast. It is interesting to note that *S. imperator*, while inhabiting "mature high ground forest" at Manu, usually foraged at lower levels than *C.h. intermedius*, at "between 3 and 10 m above the ground" [Terborgh, 1983: p. 112]. Comparable data on the success of this group's foraging activities are lacking, however.

The secondary and edge habitats preferred by *S. geoffroyi* at Rodman, on the other hand, appear to be far more similar to that utilised by *C. flaviceps* at FMC [Dawson, 1979]. Animal material is, in addition, the major component of the diet of this species [Garber, 1984a], and here again it appears to be more similar to *C. flaviceps* than to *C.h. intermedius* at Aripuanã. In addition, a severe decline in the *S. geoffroyi* population on BCI has been linked to the regeneration of the forest there [Moynihan, 1976]. While none of this evidence is incompatible with the possibility of significant differences in the abundance of arthropod prey at the different sites, and in different types of forest, it does appear to support the hypothesis that the structure of secondary forest habitats has important implications for marmoset foraging behaviour.

Other factors can be seen as being complementary to the preference for secondary and edge habitats in their implications for foraging success. One factor is body size which, it has been suggested, is an important aspect of the ability of marmosets to approach prey undetected. While this may be the case, to a certain degree, what may be more important is the ability of these relatively small primates to move efficiently in the typically dense, fine-limbed vegetation of these habitats [Garber, 1984b]. Whether or not stealth is a factor, marmosets and tamarins appear to have access to prey in locations which are inaccessible to most larger primate species, thus not only avoiding competition, but possibly also gaining access to different types of prey. A further factor may be the cohesiveness of the group. The *C. flaviceps* study group members were rarely distributed over more than 20 m, and individuals were normally within 1 to 5 m of one another. If it is assumed that the capture of disturbed prey is a major feature of their foraging behaviour, this cohesiveness would further enhance its success by maximising the chance of at least one individual observing the movement of disturbed prey. Group members were, in fact, frequently observed reacting to and capturing prey disturbed by other individuals, which were usually prohibited from doing so themselves by the dense vegetation in which they were foraging.

While it is possible that the preference for secondary habitats is determined by the presence of significantly higher densities of typical marmoset prey animals, there is relatively little evidence available to confirm this. The evidence presented here supports the idea that such a preference may be related to a far more complex interaction of the characteristics of the foraging behaviour itself and the predator avoidance mechanisms of the prey. In this case, higher capture rates would be related to the greater foraging efficiency of marmoset groups in such habitats, rather than the greater availability of prey, and we would thus expect such a preference regardless of the relative abundance of arthropods in this type of habitat (as long as it was not prohibitively lower than in primary forest).

The preference for secondary and edge forest habitats can thus be seen as having important benefits for these small-bodied primates, especially when considered as an integral part of a "time-minimising" foraging strategy. Able to move easily and stealthily through dense vegetation at low levels, they gain access to large prey animals in an environment which favours their foraging techniques. Whether or not arthropods are more abundant in absolute terms, competition from other primate species appears to be reduced. Overall, then, marmosets and tamarins are not only likely to encounter more prey animals in such environments, but are also more likely to capture them, on average. This implies that the acquisition of animal material requires the expenditure of less time and energy than in undisturbed habitats. Foraging efficiency, in terms of the ratio of benefit to cost, thus appears to be increased by this habitat preference. In terms of a time-minimising strategy, this increase in efficiency effectively reduces the expenditure of time necessary for the acquisition of an adequate diet on a daily basis. This appears to be reflected in both the relatively small amount of time spent foraging by marmosets and tamarins each day and the generally short duration of the daily activity period (see chapter 4).

It seems that the characteristics of the plant resources available in secondary forest would also have important implications for a time-minimising strategy. As we have seen, the exploitation of plant resources by callitrichine groups, and marmosets in particular, generally involves the regular use of a number of sites over long periods. A knowledge of the distribution of these relatively fixed resources (assuming a "mental map"), would allow groups to minimise the time necessary for the monitoring of plant resources. This, in turn, would allow them to maximise their foraging efficiency in relation to the abundance and distribution of prey. As we have seen in the case of the *C. flaviceps* study group, this may involve very different patterns of activity, range use and prey feeding during different times of the year.

Overall, then, the available evidence seems to support the idea that an inter-relationship between habitat preferences, foraging techniques and the typical prey of the marmosets and tamarins promotes the foraging efficiency of these small-bodied primates. The evidence indicates the following of a time-minimising strategy, especially when comparisons are made with larger primates, such as *Cebus* and *Saimiri* [Baldwin & Baldwin, 1981; Terborgh, 1983]. One additional aspect of such a strategy is the apparent ability of marmosets to physiologically reduce their metabolic expenditure, and hence their dietary requirements, during periods of rest [Morrison & Simões, 1962; Morrison & Middleton, 1967; Hetherington, 1978]. The systematic changes recorded in the activity patterns of the *C. flaviceps* study group during the course of the year support the idea that this is an important, integral feature of a time-minimising strategy (see chapter 4). In reducing dietary requirements, this adaptation would also contribute to the reduction of the expenditure of time for a forager following a time-minimising strategy.

Spatial Patterns

As we have seen, there was considerable variation in most aspects of the study group's behaviour during the course of the year. This variation appears to have been systematically related to concomitant fluctuations in the abundance and distribution of resources at the study site. The distribution of the group's foraging activities during the course of the year, for example, appeared to be closely related both to that of arthropods and to its foraging success. The proportion of activity time devoted to foraging during the different seasons was, on the other hand, inversely related both to the abundance of arthropods and the group's overall foraging success. Here we shall look at a number of aspects of its foraging behaviour in more detail, with the emphasis on seasonal variation.

Foraging and Range Use

A number of aspects of the study group's use of space have been outlined in previous chapters. In general terms, most features of its ranging behaviour were similar to those recorded for the majority of other marmoset and tamarin species. More detailed analysis of the data has shown that range use appeared to correlate with the distribution of the group's principal resources, especially that of its arthropod prey. Evidence has also been presented to show that the group was selective in its use of plant resources, concentrating its feeding at certain points within its range, while apparently ignoring, to a greater or lesser extent, the majority of available sites during any particular period (chapter 6). All these features have been seen as being closely related to the systematic use of both time and space, and the maximisation of foraging efficiency in particular. Here we shall look more closely at the distribution of the group's ranging on a day to day basis in order both to characterise this aspect of its behaviour and to assess the validity of these conclusions.

It was apparent, both from following the group's movements over a period of more than sixteen months and in mapping its ranging, that it never followed the same path on consecutive days, although some overlap was inevitable. The final location of the group on one day was invariably its first location on the following day, for example. In addition, the more or less obligatory use of specific arboreal pathways for crossing major gaps in the vegetation (those formed by the road in particular) tended to channel the group's movements through certain areas. The concentrated use of a few sites for feeding on plant material also tended to influence the overlap of its movements, as might be expected.

On the other hand, the systematic avoidance of areas visited (and foraged in) on previous days may be important for the group's foraging efficiency, assuming at least some short-term depletion of the available prey within these areas. While there seems to be no information on the short-term effects of predation on insect populations, there is good evidence that avian predators may significantly deplete local arthropod populations over longer periods. This has been shown for Acrididae in temperate grasslands [Joern, 1986] as well as for arthropod communities in the tropical forest understorey [Gradwohl & Greenberg, 1982; Rypstra, 1984]. The majority of the group's prey were relatively slow-moving arthropods and seem unlikely to be able to respond rapidly to localised changes in population density. Such variation in its movements would have additional advantages for the study group, including the monitoring of both plant and animal resources and the presence of neighbouring groups, which would presumably reward the use of new areas on consecutive days regardless of the depletion of prey in areas visited previously. The expression of such a strategy would depend ultimately on the overall distribution and abundance of resources within its range, factors which, as we have seen, are subject to considerable seasonal change.

In order to analyse the nature of the overlap of the group's ranging on consecutive days, two samples of five days were selected from both the early wet season month of November 1985 and the late dry season month of

August 1986. These two months were chosen as representative of the two extremes of the availability of arthropod prey at the study site, according to both the results of the insect trapping and the records of the group's feeding and foraging success (chapters 3, 4 and 6). The area used each day, according to the quadrats entered, was plotted for each of the four pairs of consecutive days chosen from the two months (figures 7.2 and 7.3). Excluding the quadrat in which the sleep tree was located, the maximum area of overlap between any two consecutive day ranges was 1.9 ha, while the minimum was 0.5 ha (table 7.3). The average area of overlap was approximately one fifth of the average daily range for each of the sample periods (17.5% during November and 21.7% during August). Day ranges were relatively large during both of the samples, so the group visited, on an average day, an area of more than 5 ha which it had not visited on the previous day.
A more detailed analysis of the data is presented in appendix VI.

Table 7.3

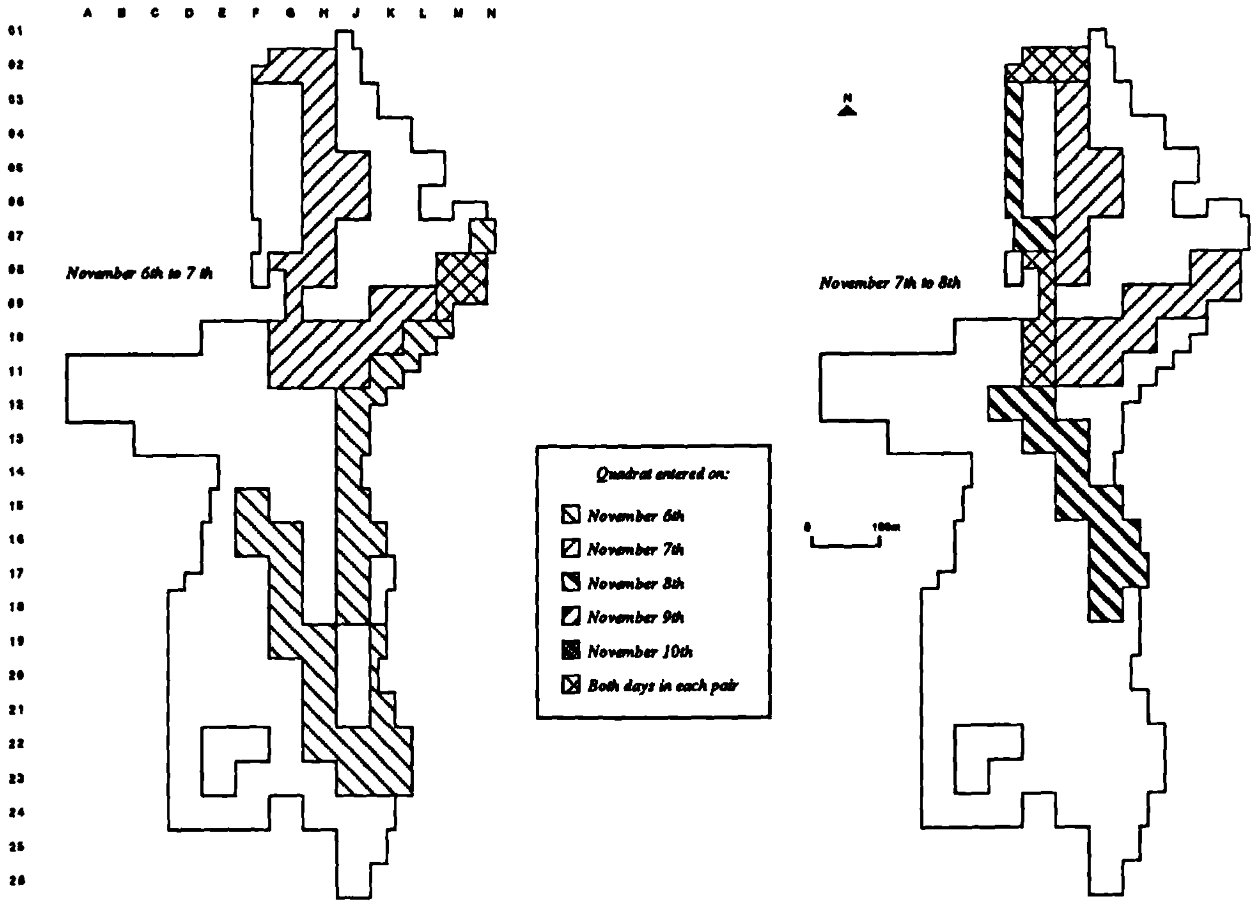
Area of Overlap between the Ranges of Sample Days

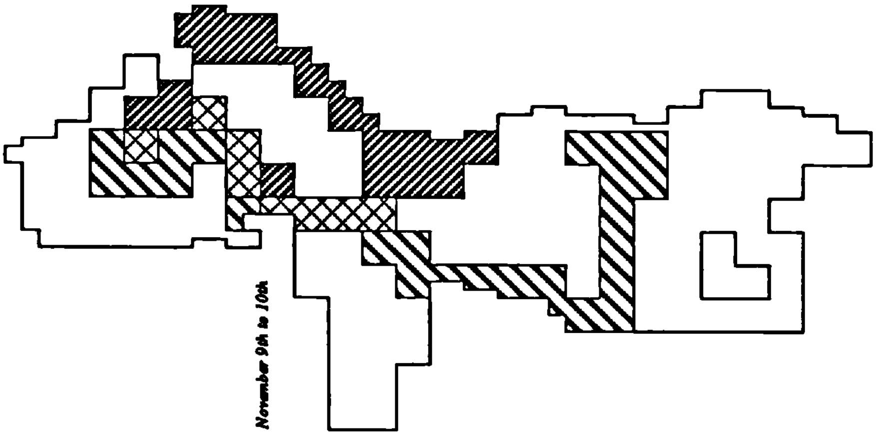
Sample	Area of overlap[1]: Area (ha)	Area of overlap[1]: Percentage of average day range[2]
November:		
06/11-07/11	0.5	7.7
07/11-08/11	1.1	17.5
08/11-09/11	1.4	21.5
09/11-10/11	1.6	24.6
Average:	**1.1**	**17.5**
August:		
03/08-04/08	1.5	22.6
04/08-05/08	0.9	13.3
05/08-06/08	1.8	27.3
06/08-07/08	1.9	28.8
Average:	**1.4**	**21.7**

[1] Excluding quadrat in which sleep-tree was located.
[2] Average day range for each five day sample.

Figure 7.2

Day Ranges, November 6th to 10th 1985




November 9th to 10th

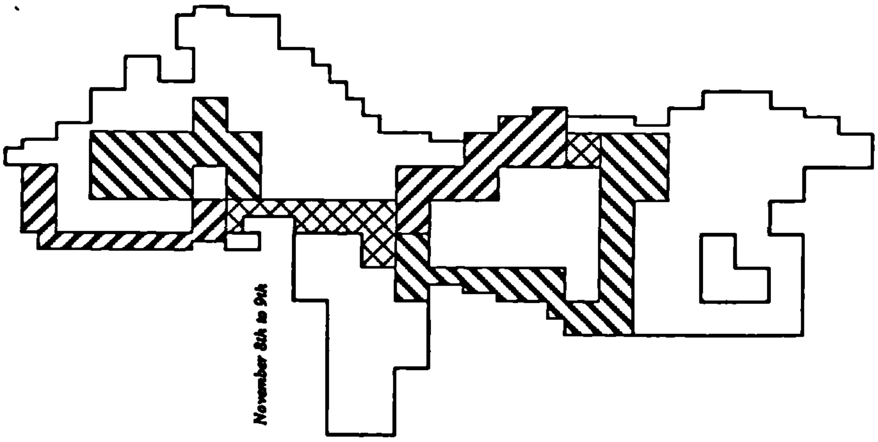
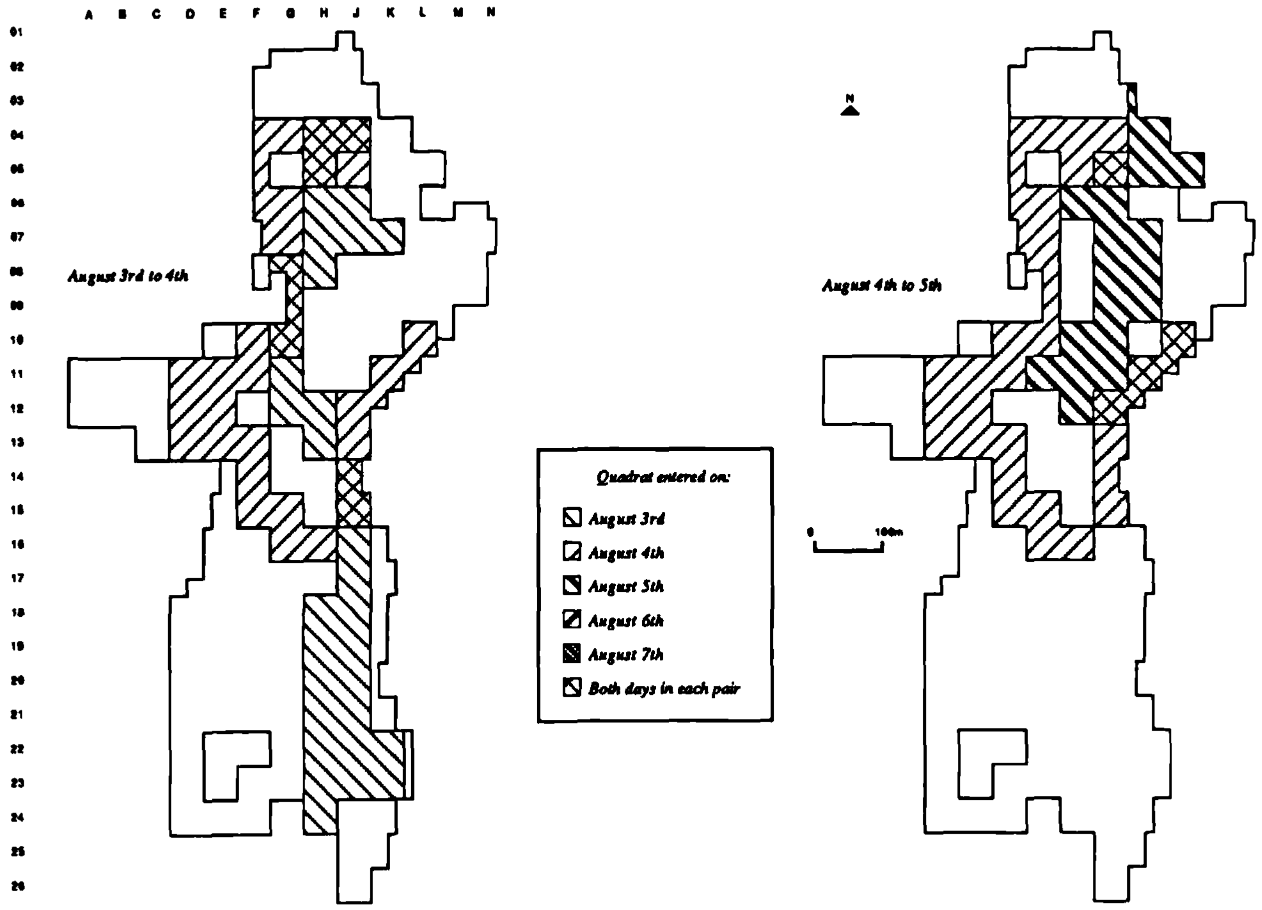
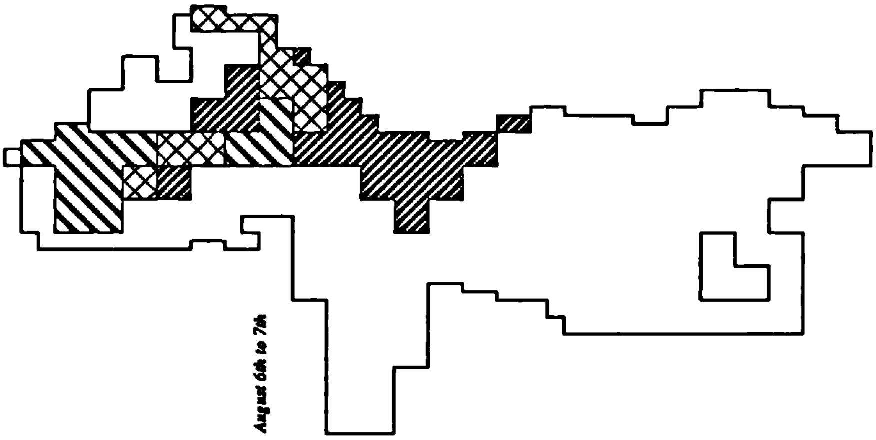

November 8th to 9th

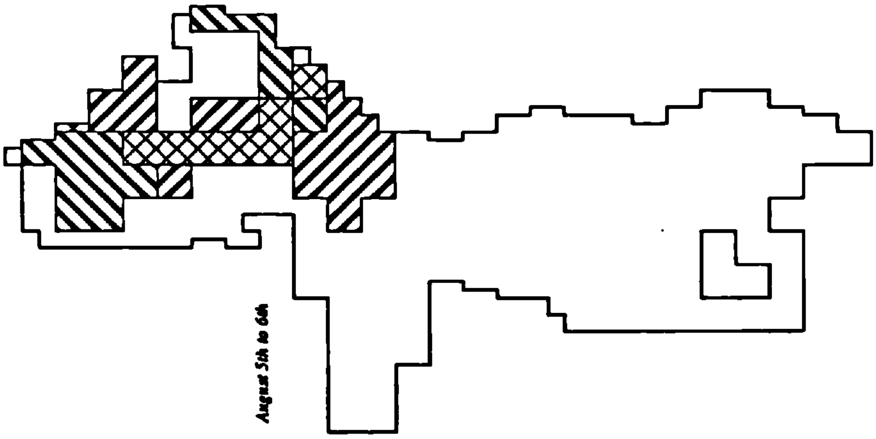
Figure 7.3

Day Ranges, August 3rd to 7th 1986





August 6th to 7th



August 5th to 6th

This appears to confirm that the group tended to avoid overlap between its movements on consecutive days, although this was progressively less apparent over longer periods. This also correlates with the patterns observed in chapter 5, *i.e.* while this group tended to travel over shorter distances than *C.h. intermedius* each day, it utilised much larger monthly ranges. Thus, by apparently systematically avoiding overlap between its movements on consecutive days, the *C. flaviceps* group was covering a much larger area than the *C.h. intermedius* group during the course of each month, while actually travelling less each day. This again seems to support the hypothesis that this contrast in the ranging behaviour of the two groups was related to differences in the importance of animal material in their diets. Confirmation of this depends, however, on the relative distribution of their plant resources which, it has been suggested, was the primary determinant of the use of space of the *C.h. intermedius* group.

As we saw in the previous chapter, the *C. flaviceps* group tended to concentrate its plant-feeding activities at certain regularly-used sites within its range. While the two sample periods presented here show relatively similar patterns of overlap between daily ranges, the patterns of the distribution of their plant feeding are somewhat different. These differences appear be related to seasonal trends in foraging and feeding activities as a whole.

During the November sample, all the "overlap quadrats" between consecutive days were either those in which plant feeding was recorded on both days or directly adjacent to these, implying that such overlap was primarily determined by plant-feeding activities, and their regular use of certain sites. During these five days, in fact, 84.3% of the group's plant feeding activities were recorded in quadrats in which feeding on plant material was recorded on two or more days during the sample period (table 7.4). This appears to further confirm the idea that the avoidance of overlap was a systematic pattern related to the group's insect foraging.

During the August sample, on the other hand, while the overlap between consecutive day ranges was proportionately greater, there was much less overlap in the distribution of plant-feeding activities (table 7.4). While plant feeding was recorded in fewer quadrats (35 compared with 40) and was less scattered in its distribution (figure 7.4) in the August sample, only 55.6% of plant feeding took place in quadrats in which such activity was recorded

Table 7.4

Overlap in Plant-Feeding Activities during Sample Periods

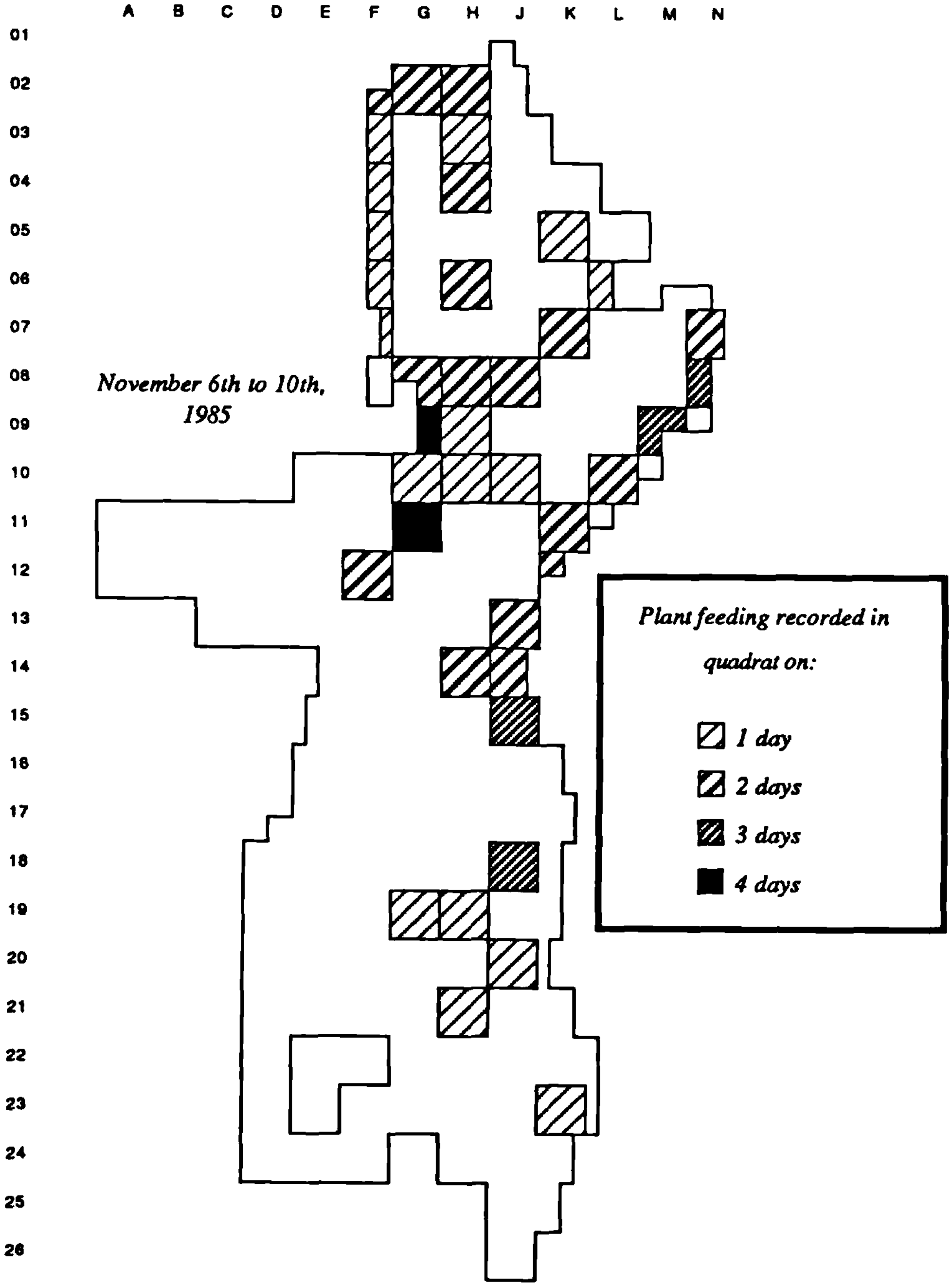
Observation	Sample: November 6-10, 1985	Sample: December 3-7, 1986
Number of quadrats in which plant-feeding was recorded	40	35
Total plant-feeding records	344	187
Quadrats in which plant feeding was recorded on 2 or more days	22	14
Plant-feeding records collected in overlap quadrats	290	104
Feeding in overlap quadrats as a percentage of total records	84.30	55.61

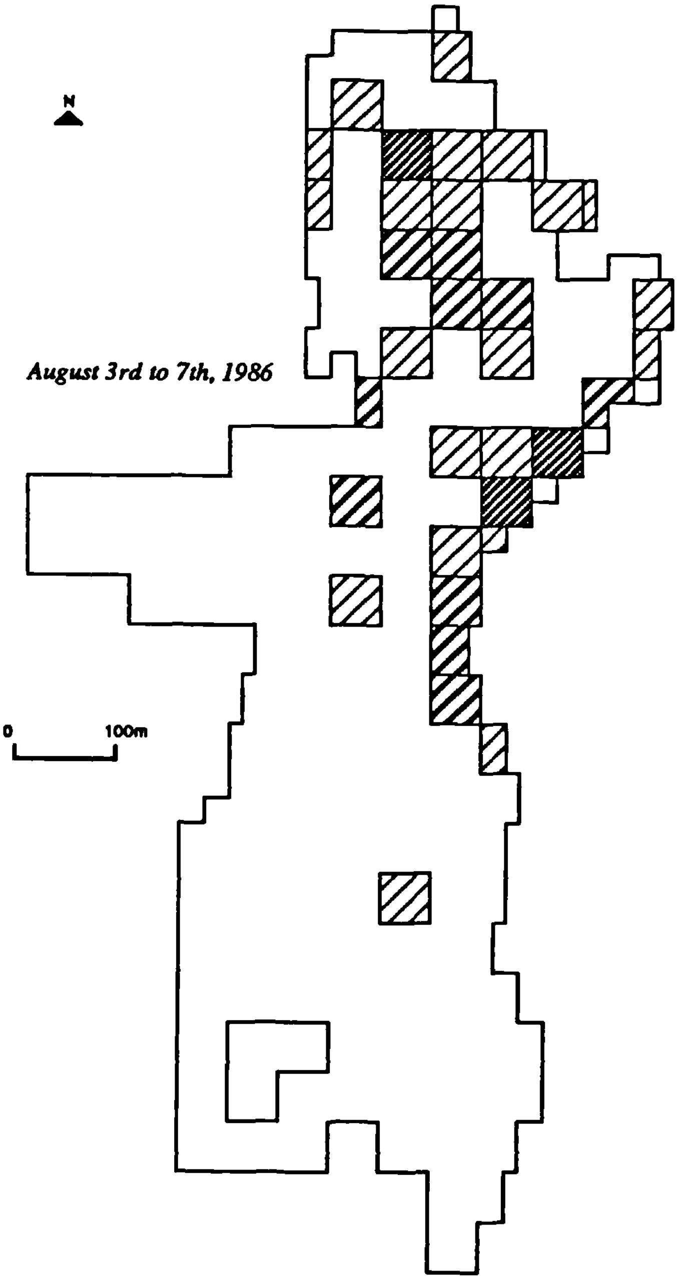
on two or more days. During this period, then, overlap did not appear to be directly related to the use of plant resources. This pattern may have been determined by a number of factors, including the possible influence of variables such as group size and random differences in observational bias. Far fewer plant-feeding records were, for example, collected during the August sample (table 7.4). However, as these two months were characterised not only by very different patterns of the abundance and distribution of resources but also by concomitant differences in the patterns of the group's activity and range use, it seems reasonable to expect that these variables had the most important influence on this aspect of its ranging.

While the group's arthropod prey was most abundant and apparently most evenly distributed during the early wet season months, the opposite was the case towards the end of the 1986 dry season. We saw in chapters 5 and 6 that while the group travelled, foraged and captured prey fairly evenly within its home range during the former period, there was a significant tendency to use the eastern part of its range during the latter, where its foraging success was also greater. As much of the overlap between consecutive days during August occurred in quadrats lying in the east of its range (figure 7.3), it seems

Figure 7.4 (and facing page)

Distribution of Plant Feeding, November 6th to 10th 1985 and August 3rd to 7th 1986





August 3rd to 7th, 1986

likely that this pattern was related to the group's more intensive use, for foraging in particular, of this part of its range during this month. While avoiding overlap between days was probably still an effective strategy during this month, the relative scarcity of prey in the west of the range would probably have reduced its benefits to certain extent.

However, while more time was spent foraging in the east of the range during the late dry season, more plant feeding was recorded in the western half (table 5.6). A major aspect of this appears to have been the larger contribution of *angico* gum to the group's diet during this period (see chapter 6). Its visits to *angico* trees in quadrats G03 and F05 on different days, for example, constitute 12.3% of the total records of plant feeding during this sample. These, and other factors, appear to have had a considerable influence on the observed patterns.

Despite these relatively minor differences between the two samples, the evidence clearly indicates that the group's day-to-day movements were not random, but were systematically inter-related with other aspects of its behaviour. Along with the broader trend in its range use, these patterns appear to be most closely related to the group's foraging activities. The regular use of a few plant-feeding sites and the even distribution of its ranging can thus be seen as strategies aimed at both minimising the time spent in such activities and maximising their overall efficiency, both in the short and in the long term. While there is no comparable data available for the *C.h. intermedius* group, this analysis of the *C. flaviceps* group's ranging does appear to further confirm the suggestion that the apparent differences in range use between these two groups were based on fundamental differences in both their use of plant resources and their insect foraging behaviour.

Seasonal Variation

The basic characteristics of the study group's foraging behaviour have been described in detail above. Most of the data presented in previous chapters have shown major fluctuations in general aspects of its behaviour and ecology, such as the intensity and distribution of its foraging behaviour and the composition of its prey. It would thus seem reasonable to expect significant variation in the basic patterns of the group's foraging during the course of the year, correlating with these broader fluctuations, and those in the relative abundance of different types of prey in particular. Further details of the group's foraging behaviour are analysed here in order to identify possible seasonal patterns and to assess their relationship with the changes observed in other variables.

The Foraging Milieu

The *C. flaviceps* study group occupied an area of secondary forest which was characterised by a relatively open canopy, abundant climbing plants and dense vegetation closer to the ground (chapter 3). As we have seen, it spent the majority of its time at relatively low levels within this habitat. It also appeared to prefer dense vegetation, particularly when foraging, and this is reflected in its marked tendency to utilise slender supports (table 7.5). A similar preference was recorded for most other activities (see appendix III). While trees were the main type of support utilised during foraging, climbing plants were also used very frequently, presumably again reflecting the preference for dense vegetation. Despite expectations to the contrary, very little variation was observed in the nature of support use during the course of the year. This situation does, however, reflect the relative lack of variation in the characteristics of its foraging behaviour, as we shall see below.

Table 7.5

Diameters of Supports Used during All Foraging Activities Recorded in Scan Samples

Diameter of support (cm)	Percentage of total foraging records
>20	1.6
11-20	4.7
6-10	5.5
4-5	5.3
2-3	16.6
0-1	64.2
Ground (support not used)	2.1

Foraging Levels

Foraging generally took place at slightly lower levels than most of the study group's other activities (appendix III). This pattern has also been recorded for *C.h. intermedius* [Rylands, 1982], *S. imperator* [Terborgh, 1983] and *S. geoffroyi* [Garber, 1984b], although the actual heights involved vary considerably. According to the scan sample records, the group spent exactly half of its foraging time at or below 3 m, and 91.2% of its foraging activities took place at levels below 10 m (table 7.2). While the group appeared to forage at very much lower levels than other callitrichids [except *Callimico goeldii*, Pook & Pook, 1982], it seems likely that this is principally due to differences in habitats and the availability of resources at the different study sites, rather than to specific differences in behavioural adaptations for foraging (see appendix III). The high degree of habituation of the study group may also have been an important factor. Whatever the influence of the available habitat on this feature of the group's foraging behaviour, however, it does appear to reflect a genuine preference for the vegetation occurring at such levels. While no detailed quantitative information was collected, it was quite clear that the majority of the forest reaches between 10 and 20 m in height, with many *angico* trees being even taller than this (see plates 2, 3 and 4). Most of the denser, more continuous vegetation, on the other hand, is found at much lower levels than this.

Apart from a few minor differences, this preference appeared to be equally strong throughout the year (figure 7.5). Only during the early wet season sample, in fact, did the group spend less than 90% of its foraging time at levels below 10 m, and even during this period the value was 87.7%. While the group utilised the very lowest levels slightly more during the late wet season and early dry season than at other times, this does not appear to indicate any major change in this aspect of its foraging behaviour. A similar lack of seasonal change in the levels at which foraging took place was recorded for *C.h. intermedius* [Rylands, 1982]. In this case, however, the lack of variation correlated with those apparent in both the group's foraging and prey-feeding activities. It is interesting to note that Harcourt [1986] found significant changes in the foraging levels used by both *Galago senegalensis* and *Galago crassicaudatus* at different times of the year. This correlated with the considerably different seasonal patterns in their foraging behaviour (see

Figure 7.5

Seasonal Variation the Levels used by the Study Group during Foraging

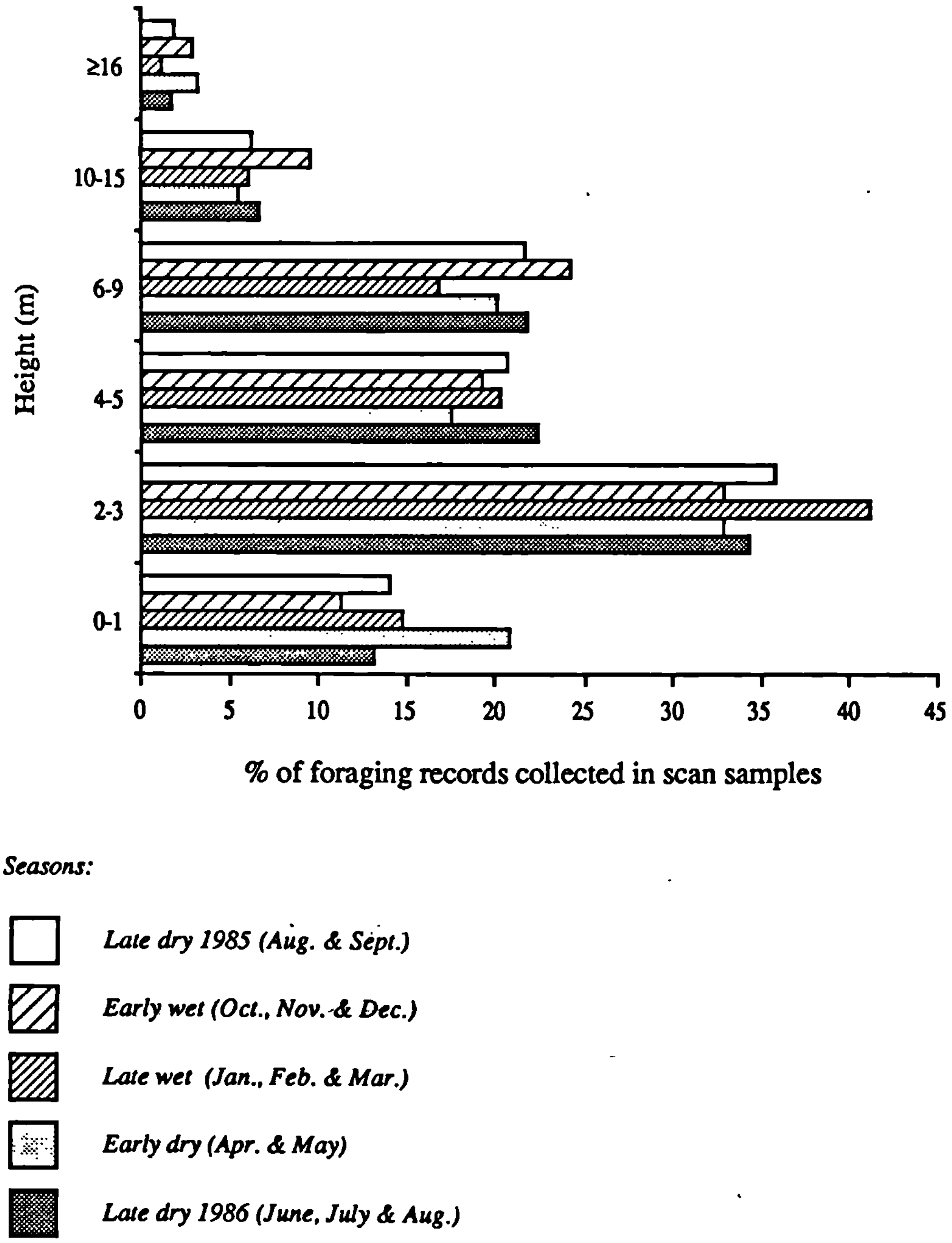


Figure 7.5 presents a comparison of the levels used for foraging by the study group during the five main seasonal divisions of the study period. Values are percentages of the records of foraging collected during each period

chapter 4). Seasonal variation, or the lack of it, in the levels used during foraging thus appears to have very different implications for different primate species.

One further pattern observed consistently throughout the study period was a tendency for the group to forage at relatively high levels during the earliest part of the day (figure 7.6). The overall trend during all seasons was one of decreasing levels until approximately 09:00 when the average height of foraging activities levelled off at between 3 and 5 m above the ground throughout the rest of the day, although there was a tendency for even lower levels at the very end of the day (figure 7.7). While a number of factors may have contributed to these trends, it does seem that the distribution of the group's prey, in the vertical dimension, may have been a primary determinant of this pattern. Most large insects, and the study group's other poikilothermic prey, are probably found at relatively high levels in the forest during the earliest part of the day, allowing them to absorb the sun's rays more efficiently at a time when their body temperature is at its lowest [Janzen, 1973b]. Such exposure would be disadvantageous during the later, hotter part of the day, however, when these animals are presumably forced to seek shelter at lower levels within the forest. In this case, the pattern of the vertical distribution of foraging during the course of the day can be seen as a being directly related to that of prey animals.

The only comparable data available are for the tamarins at Manu [Terborgh, 1983: figure 6.3, p. 113]. *S. f. weddelli* exhibited marked fluctuations in foraging levels during the course of the day, but this appears to have been related to its unique foraging technique (chapter 4). While the foraging behaviour of *S. imperator* was, on the other hand, comparable with that of *C. flaviceps*, this species appeared to forage at roughly similar levels (between 6 and 8 m) throughout the day. One factor which may have contributed to this contrast is the difference in the structure of the forest at the two study sites. The lack of shade provided by the apparently lower, more open canopy of the forest at FMC would force the group's prey to seek shelter at much lower levels in absolute terms.

These patterns provide further useful insights into the study group's foraging behaviour. As we have seen (figure 4.11), foraging success tended to be greater during the later half of the day. Taking all records of both

Figure 7.6

Daily Variation in Foraging Height, All Samples

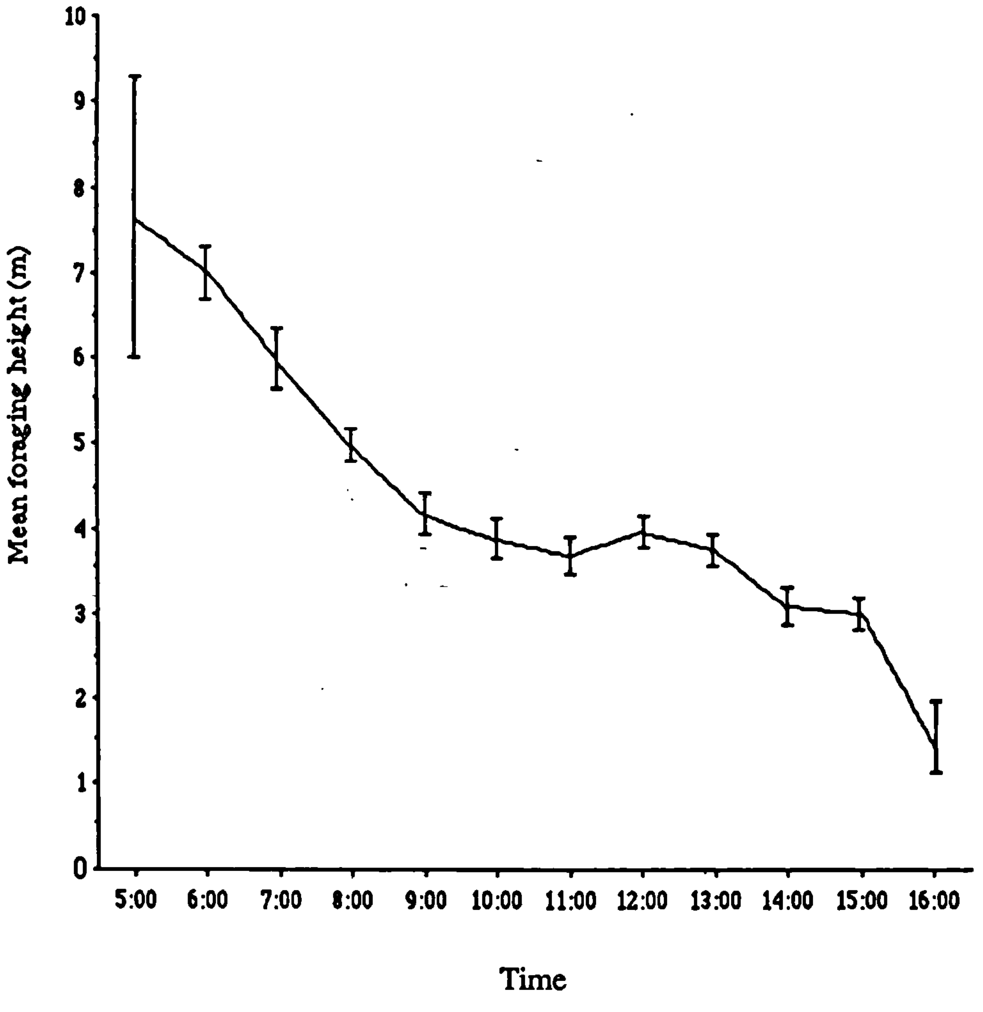


Figure 7.6 shows the daily variation in the heights at which the study group foraged. Values are the mean heights recorded for foraging during each hourly division of the clock in all scan samples (125 observation days). Bars show the standard errors calculated from the monthly means. Note that the value for 04:00 is excluded because of a lack of foraging records.

Figure 7.7

Seasonal Variation in Foraging Height by Time of Day

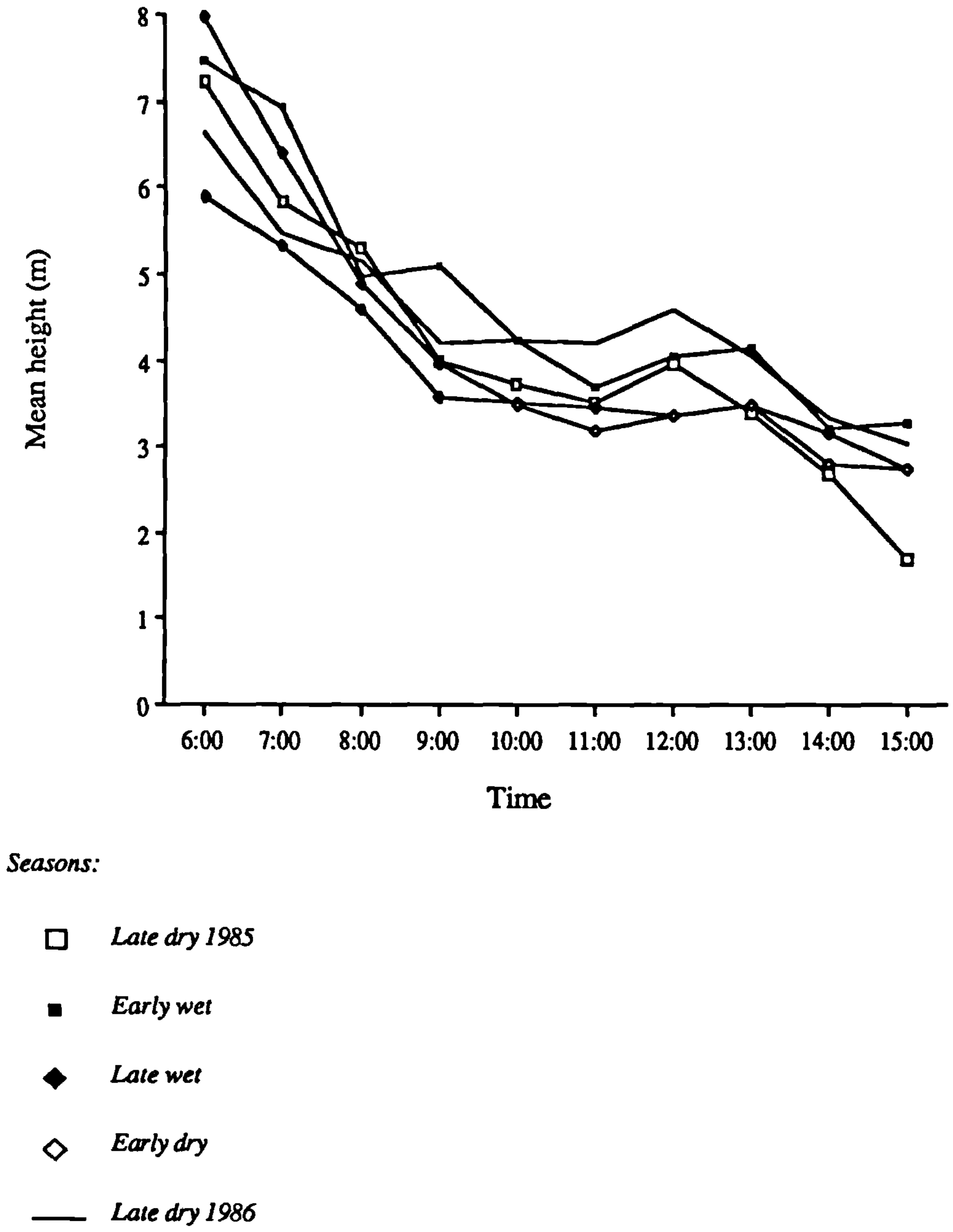
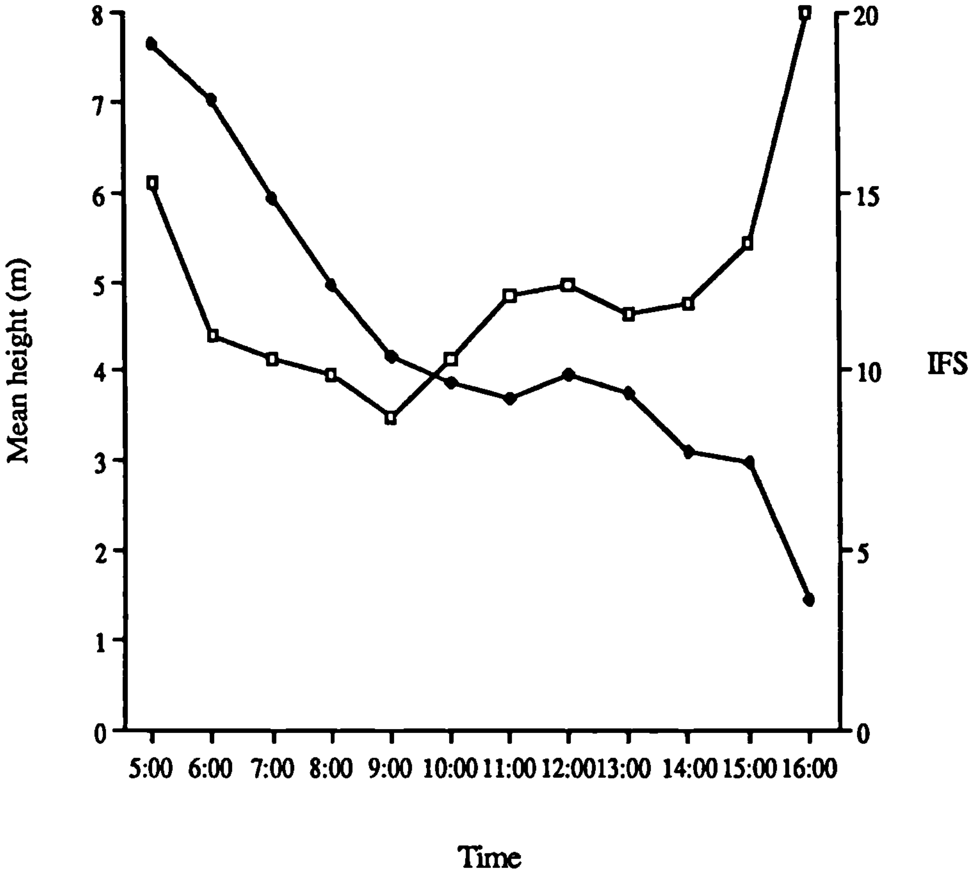


Figure 7.7 shows the daily variation in the levels at which foraging took place during the five main seasonal divisions of the study period. Values as in fig. 7.6. Note that values for 04:00, 05:00 and 16:00 are excluded because of the small numbers of records collected in most seasons.

Figure 7.8

Daily Variation in Foraging Height and Success, All Samples



Key:

☐ *Index of Foraging Success (IFS)*

◆ *Foraging height*

Figure 7.8 presents a comparison of the daily variation in the levels at which the study group foraged and its foraging success, according to the IFS (see table 4.3). Values for foraging height are as in fig. 7.6, those for the IFS are taken from fig. 4.11.

foraging and success together (figure 7.8), there is a strong, although not quite significant, inverse correlation between foraging levels and success (Spearman Rank Correlation: $r_s = -0.545$, $n = 13$, $p = 0.054$). While it could be argued that this correlation was partly an effect of differential bias acting on the observation of foraging and prey feeding, this seems unlikely, given that the average levels recorded during the early part of the day were mostly between 5 and 7 m. Evidence of changes in the visibility of the animals is similarly lacking, judging from the numbers of records collected (table III.vi, appendix III). The evidence appears to lend further support to the hypothesis that the group was able to increase the efficiency of its foraging by utilising lower levels in the forest, during the later part of the day at least. In this case, while it did experience lower returns to its efforts, in absolute terms, by foraging at high levels during the early part of the day, it would presumably have been even less successful at lower levels.

There are marked seasonal differences. While the daily pattern of foraging levels used was similar in all seasons (figure 7.7), those of foraging success were very different (figure 4.12a-e). A pattern of increasing success through the course of the later part of the day was relatively clear in the wet season samples, but not apparent during the dry season. Success shows a highly significant negative correlation with foraging levels during both the early (SRC: $r_s = -0.801$, $n = 13$, $p = 0.001$) and late (SRC: $r_s = -0.754$, $n = 12$, $p = 0.005$) wet season samples. Equivocally, there is a significant *positive* correlation between levels and success during the early dry season sample of 1985 (SRC: $r_s = 0.685$, $n = 11$, $p = 0.02$), although this appears to be an effect of the small numbers of records collected at the beginning and end of the day. The early (SRC: $r_s = 0.011$, $n = 11$, $p = 0.974$) and late (SRC: $r_s = -0.18$, $n = 10$, $p = 0.618$) dry season samples from 1986, on the other hand, show no correlations. The group's foraging was thus not only far less successful overall during the dry season months, but did not exhibit the clear relationship with height recorded in the wet season.

In the dry season, then, when the group's typical arthropod prey was scarce, its strategy of foraging at lower levels did not appear to increase its success. As large, mobile arthropods became scarce, "immatures" made up an increasingly large proportion of its prey (chapter 6). While foraging at low levels was probably an equally effective strategy for the capture of mobile prey during all seasons, it would probably not make the capture of immatures more likely. None of the ninety-seven immatures (excluding caterpillars) captured during scan sampling were, in fact, being consumed on the ground. While these records are admittedly small in number, they do support this idea, given that more than one in twenty of all other prey items were seen being consumed on the ground (see above). If immatures are generally distributed at higher levels in the forest, foraging at low levels during the dry season would only be the optimal strategy as long as large mobile prey are abundant enough to compensate for any decrease in the capture of immatures. Depending on the scarcity of mobile arthropods, a major shift in the orientation of foraging towards the capture of immatures might be a more effective strategy. As we shall see below, however, there is little evidence to suggest that such a strategy was followed by the study group during the period when prey was least abundant.

In general, then, there appears to have been very little seasonal variation in the levels at which the group foraged. Differences are small and appear to be relatively random, and it seems unlikely that they are systematically related to variations in foraging behaviour. There is, on the other hand, good evidence to support the idea that the effectiveness of foraging at these relatively low levels changed during the course of the year. This, in turn, may be systematically linked to changes in the availability of different types of prey rather than to any major changes in the group's foraging behaviour.

Supports Used during Foraging

During scan samples, the size (*i.e.* diameter) and orientation of the supports used by group members during all activities were recorded. The type of support was also recorded from November onwards..In preferring the dense vegetation of secondary and edge habitats, marmosets and tamarins tend to utilise relatively thin supports during their foraging activities [Garber, 1984b]. These types of vegetation are characterised by high densities of climbing plants, so their frequent use as a support during foraging would also be expected. Garber [1984b] found that *S. geoffroyi* mainly used oblique supports when foraging (52.7% of records), a pattern which would again be expected, given the use of thin supports, especially those of climbing plants, in dense vegetation.

The patterns of support use during foraging by the *C. flaviceps* study group again appear to be similar to those recorded for other callitrichines. While there is very little comparative information available, it does seem that the study group was exceptional in its use of relatively thin supports, with 82.6% of foraging recorded on supports with a diameter of 3 cm or less (table 7.5). In Garber's study of *S. geoffroyi*, for example, only 36.9% of foraging took place on supports of less than 2.5 cm in diameter, and this rose to only 62.8% for supports of less than 5 cm in diameter [Garber, 1984b: table 4.2, p. 120]. As for the levels at which foraging took place, the characteristics of the supports used by the *C. flaviceps* group exhibited very little variation during the course of the year. Here again, the small differences that were observed appear to have been randomly, rather than systematically related to other aspects of the group's foraging behaviour. One possible exception is the variation in the orientation of supports used during different seasons, as will be discussed below.

The group foraged on thin supports equally frequently throughout the year (figure 7.9), spending between 60% and 70% of its foraging time on supports with a diameter of 1 cm or less during all seasons. This value was just over 80% for supports with a diameter of 3 cm or less during all periods except the early dry season sample when it was slightly lower, at 78.7%. The remainder of the group's foraging time was distributed more or less evenly among supports of between 3 and 20 cm in diameter. These results correlate clearly both with observed foraging patterns and with the nature of the vegetation at the study site.

While trees were the type of support most commonly used during foraging throughout the period between November 1985 and August 1986, foraging frequently took place from climbing plants (figure 7.10). Curiously, these types of support were used in the opposite proportions by *S. imperator* [Terborgh, 1983: table 6.3, p. 104]. There is again virtually no difference between seasons in the use of different types of support during foraging, although trees were used slightly more during both dry season samples than they were during the wet season, and lianas slightly less. The significance of

Figure 7.9

Seasonal Variation in the Diameter of Supports Used by the Study Group during Foraging

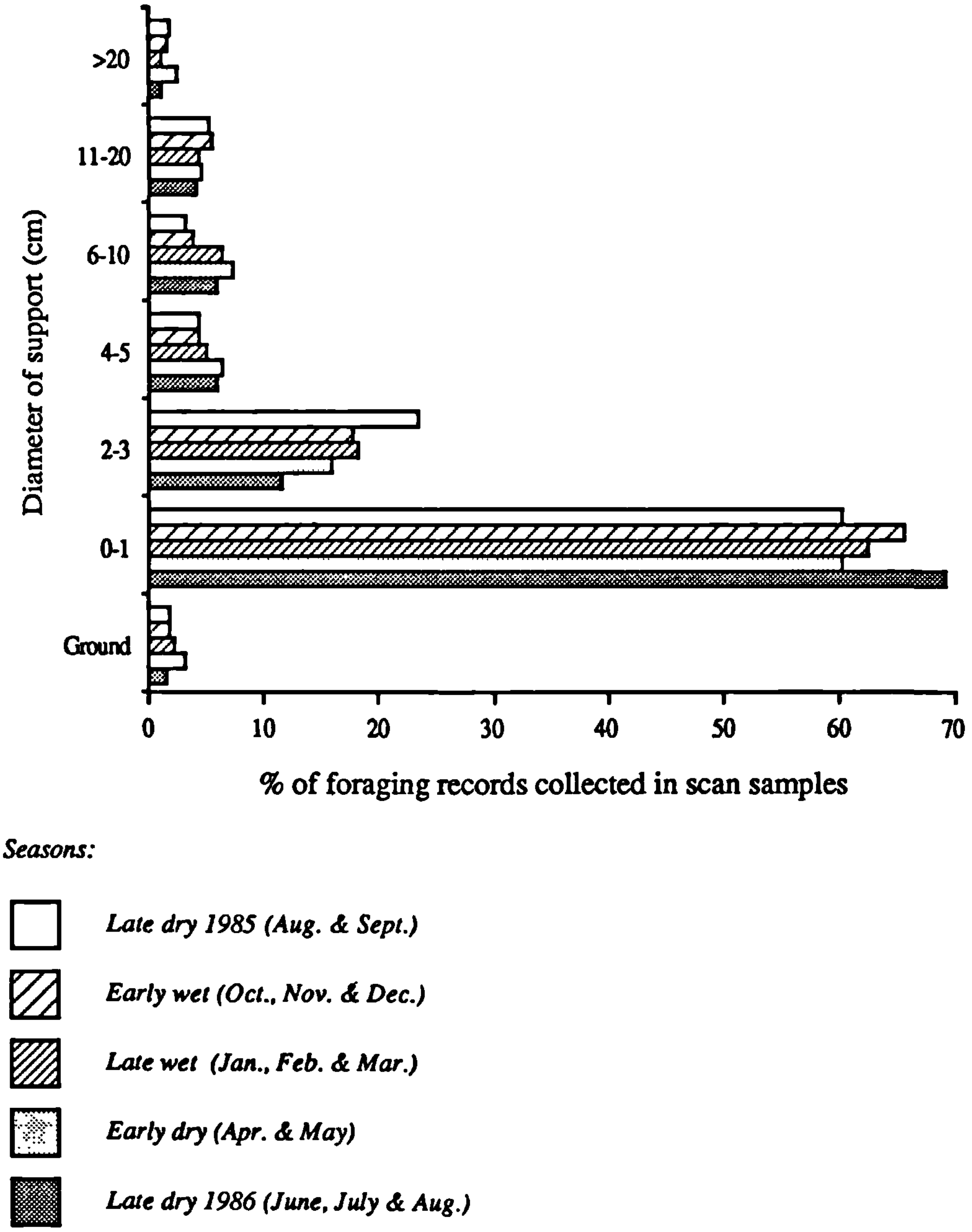


Figure 7.9 compares the study group's use of supports of different diameters for foraging during the five main seasonal divisions of the main study period. Values are percentages of the foraging records collected in scan samples during each of the five periods.

Figure 7.10

Seasonal Variation in the Study Group's Use of Supports of Different Types during Foraging

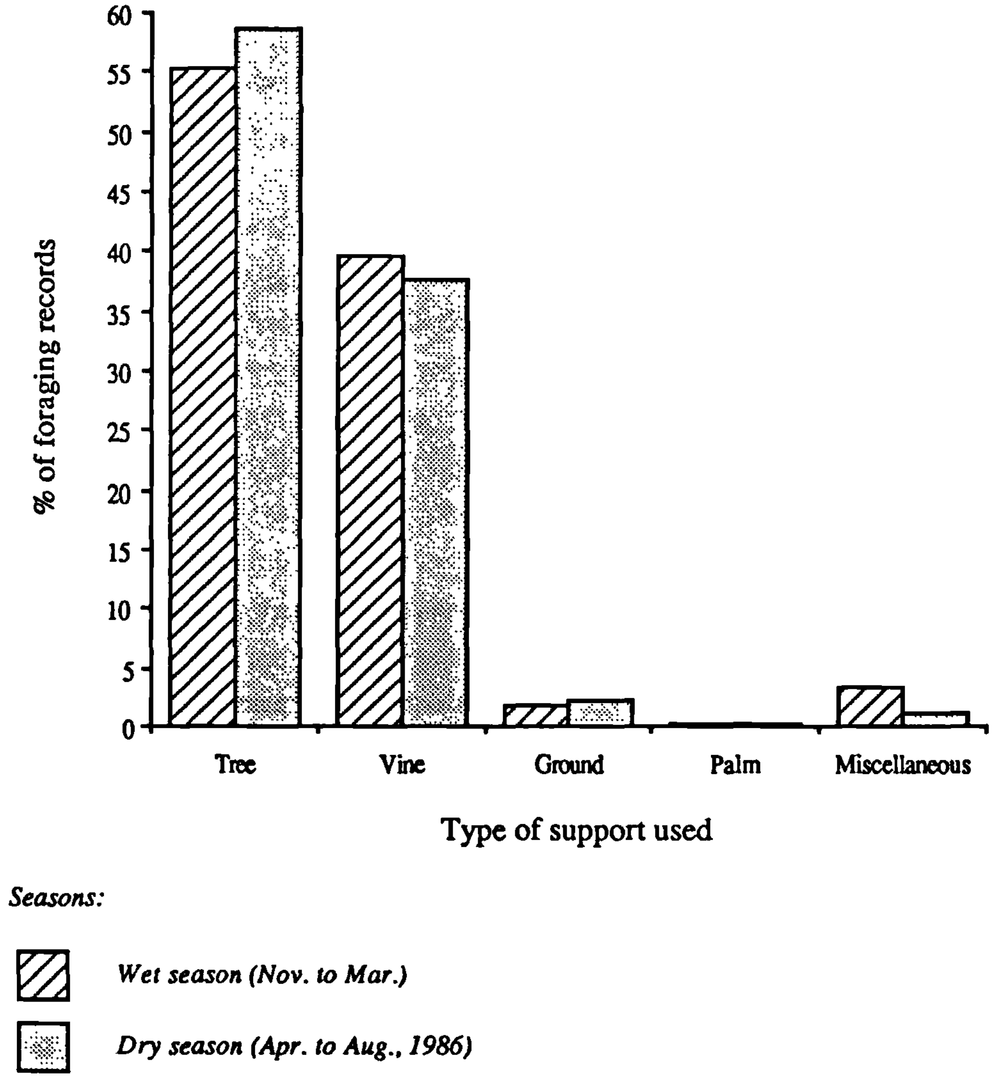


Figure 7.10 compares the use of supports of different types by the study group during the wet and the dry season. Values are percentages of the foraging records collected during the two sample periods (see key).

Figure 7.11

Seasonal Variation in the Orientation of Supports Used by the Study Group during Foraging

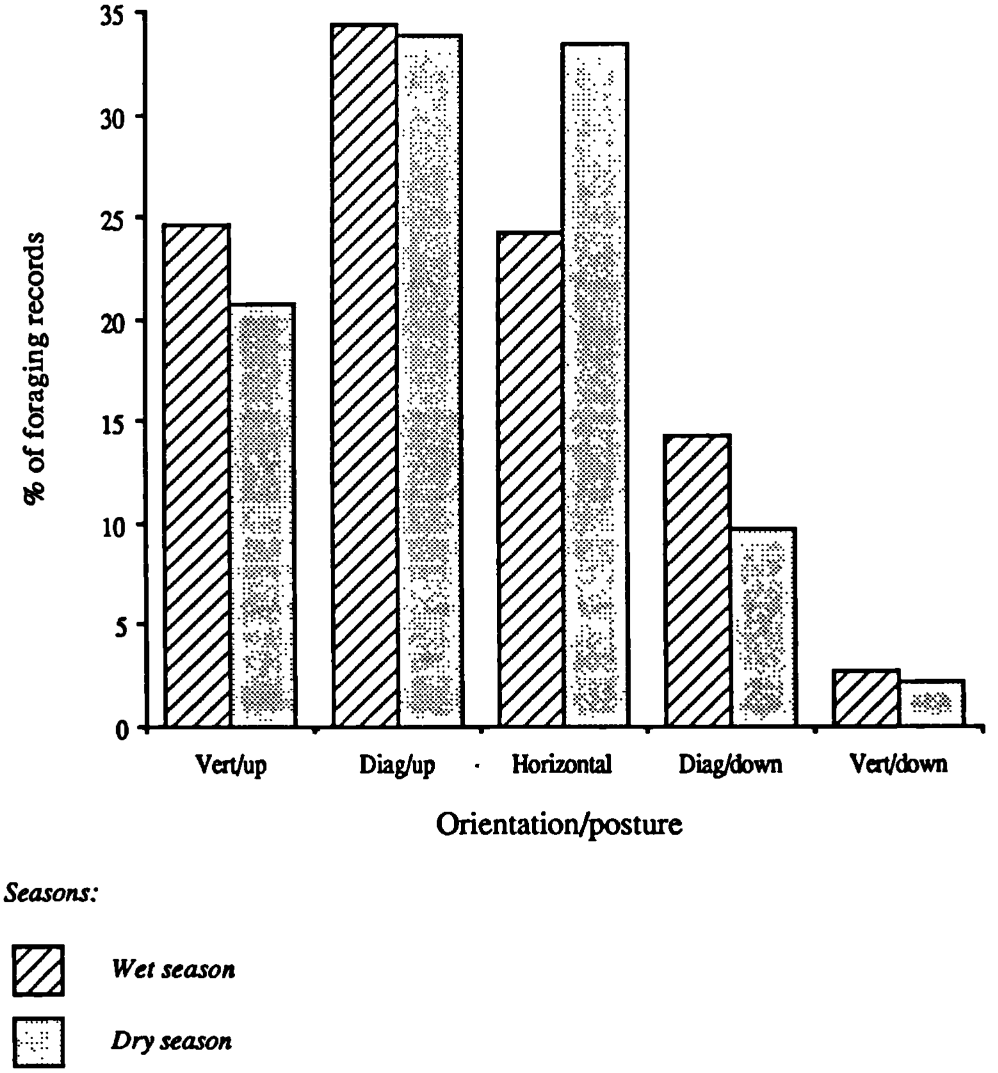


Figure 7.11 compares the orientation of supports used by the study group during foraging in the wet season and the dry season. Values are percentages of the total foraging records collected during scan samples in the two seasons.

this small difference is difficult to judge, but it does not appear to be systematically related to other factors. One point of interest is the virtual absence of foraging in palms, a characteristic also noted for *S. imperator* at Manu, in contrast with the other species studied [*ibid.*].

In contrast with these other variables, there are major differences in the orientation of supports used during foraging. Combining the data from all wet and dry season samples gives the clearest picture (figure 7.11). Upward postures on diagonal supports and downward postures on vertical supports were used with almost equal relative frequency in the two seasons. The main difference was in the use of horizontal supports, which accounted for just over a third of foraging records during all dry season samples, but for less than a quarter during all wet season samples. This difference was divided almost equally between upward postures on vertical supports and downward postures on diagonal supports.

While this pattern does correlate with the seasonal difference in the use of trees and climbing plants as supports during foraging (assuming that trees are more likely to offer horizontal supports), it seems likely that other factors were more important. As well as capturing far greater numbers of prey overall during the wet season, the group captured a larger proportion of mobile prey and appeared to capture prey far more frequently on the ground. In accordance with this, it spent a larger proportion of its foraging time engaged in "pursuit" activities such as scanning the ground and following or pouncing on prey. Scanning the ground, for example, frequently involved a vertical clinging posture on relatively small saplings, while following prey almost invariably involved downward movement on diagonal or vertical supports. During the foraging activities which were recorded more frequently during the dry season (*e.g.* "search" scanning and the manipulation of substrates), on the other hand, horizontal supports were more commonly used. These patterns will be discussed in more detail below.

Chapter 7

Seasonal Changes in Foraging Behaviour

The evidence presented so far has shown quite clearly, in apparent contradiction to the patterns outlined in previous chapters, that there was very little variation in most subsidiary features of the group's foraging behaviour during the course of the year. In spite of other changes, the group was apparently searching for prey in similar locations, in the vertical dimension of its environment, throughout the year. In this final section, the data are examined in further detail, with the emphasis again on seasonal patterns. As we have seen, the group's foraging was based on typical "scan-and-pounce" techniques. Others, such as the biting or breaking open of substrates were recorded much less frequently overall. Here again, however, while some variation in the use of different techniques is apparent during different times of the year, it seems to be far less than might be expected, given fluctuations in the availability of different types of prey in particular.

Scanning for signs of prey was by far the largest category recorded during all months (that is, between December 1985 and August 1986), making up 89.2% of all foraging records for which the type of activity was recorded (table 7.1). While other types of behaviour were frequently recorded, no single category contributed more than 10% of the records during any one month. For the purposes of the present analysis, the data were divided into three main classes, "scan", "pursuit" and "manual search" (see table 7.6). It is important to remember that the "scan" category used in this analysis includes all records of scanning for signs of prey *except* records of scanning the ground which, as argued previously, can be seen as a "pursuit" type of activity in the terminology of MacArthur & Pianka [1966]. While undirected or more random scanning is a "search" type of activity, it is kept separate here in order to clarify the analysis.

One small problem with the analysis is the inclusion of the data collected during December 1985. These data exhibit two exceptional characteristics in comparison with all other months; a relatively low level of scanning and very high levels of pursuit behaviour. December was the first month in which the systematic recording of these details was attempted, and it is thus possible that these exceptional patterns were primarily a result of the

Table 7.6

Classification of Foraging Behaviours Used in Present Analysis

Class	Foraging categories included
"Scan"	Intense scanning of environment (FO SK)[1].
"Pursuit"	Intense scanning of ground (FO SKO). Pursuing mobile prey (FO FO). Pouncing on possible prey (FO PO). Grabbing object/substrate with one or two hands (FO GB).
"Manual search"	Manipulation of object/substrate (FO MP). Biting open object/substrate (FO BI). Breaking open object/substrate (FO BKO).

[1] Abbreviations used in the collection of the data, see table 2.3.

inexperience of the observer at that time. One piece of evidence supporting this is the fact that, while these details were recorded for more than 90% of foraging records collected during scan samples in all of the other months, they were recorded for only 77% of foraging records collected during December. If it is assumed that group members were scanning during the majority of the records for which no details were collected in this month, the proportions of activities would have been similar to those recorded in the late wet season.

Whether this does, in fact, reflect the true situation during December cannot be ascertained, given the available information. December did, however, differ from the later wet season months in a number of important ways. Arthropods were apparently more abundant, and insect foraging was both a more important feature of the group's activities and more successful during this month than it was during January and February. During the latter two months, the availability of fruit may also have had an indirect influence on its foraging behaviour. While only speculations can be made, it is possible that the exceptional characteristics of the December sample reflect broader trends, so this month is included in the present analysis, with appropriate caution.

Given that the group was observed to search for prey in a number of different ways, we might predict certain patterns in its use of techniques from observed changes in the composition of its prey during the course of the year.

Figure 7.12

Seasonal Variation in the Foraging Activities of the Study Group, December 1985 to August 1986

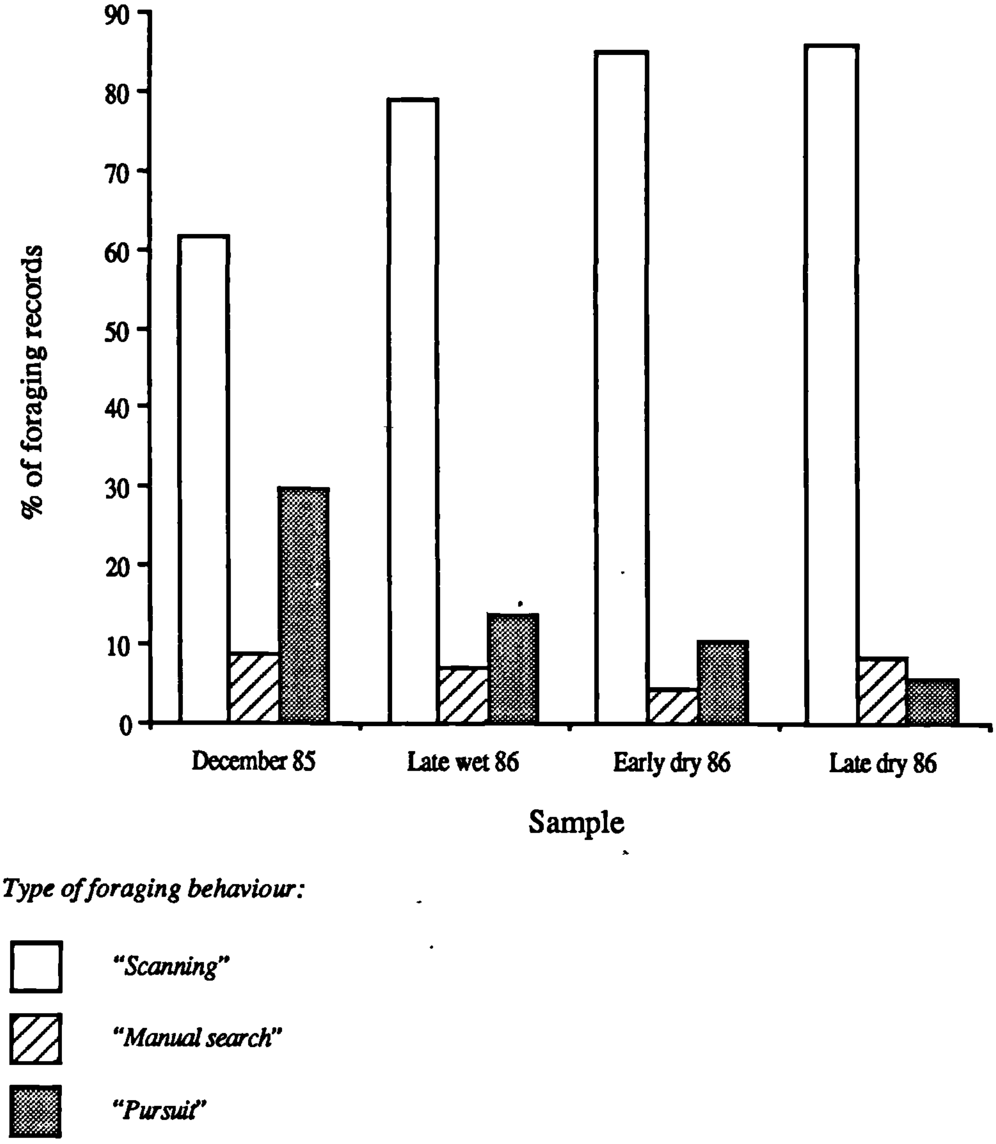


Figure 7.12 compares the foraging behaviour of the study group during different periods. Values are percentages of the scan sample records for which the type of foraging behaviour was identified.

As we have seen, arthropods were relatively scarce during the dry season and the group appeared to be far less selective of its prey at this time of year, especially in the late dry season of 1986. It captured smaller numbers of generally much smaller items and a relatively large proportion of immatures. During the dry season, then, we would expect it to be engaged in pursuit foraging much less than during the wet season, and in manual search foraging (which seems to be directed primarily at the capture of immatures) much more. Undirected scanning for signs of prey can be seen as an equally important complement to both types of foraging activity, although any major shift towards manual searching might be expected to result in a relative decrease in scanning.

While the data do show that the proportion of the group's foraging time devoted to pursuit activities fell considerably between the wet and the dry season (figure 7.12), this was balanced by an increase in scanning rather than in manual searching. Why the latter should make up such a small proportion of the group's foraging activities during the early dry season sample is not clear. One factor may be the overall increase in the numbers of foraging records collected during the dry season. Thus, while an average of 115 records (excluding those for which the activity was not identified) were collected each day during the late wet season, the average was 145 during the early dry season and 163 during the late dry season. For records except scanning, the averages were 24, 22 and 23 respectively (note that these values are not directly comparable because of differences in variables such as group size and day length). In terms of the numbers of these records collected each

Table 7.7

Average Number of Foraging Records Collected per Day, by Season

Sample	"Scan"	"Pursuit"	"Manual search"
Late wet	91.2	15.9	8.1
Early dry	122.8	15.1	6.6
Late dry	140.0	9.1	13.8

day, then, these two categories were almost the same in the late wet and early dry season samples, while the late dry season showed the opposite trend (table 7.7).

The overall pattern thus appears to be a general increase in scanning activities between the late wet and the late dry seasons, with a major increase in manipulatory searching being delayed until the late dry season. This seems compatible with observed trends in both the availability of prey and its capture by the group. While prey was less abundant during the early dry season, the group was still capturing relatively large quantities of large, mobile animals, compared with the late dry season (chapter 6). One important influence on these trends may have been the relatively large numbers of vertebrate prey captured during this period. June was, in fact, more similar to the early than to the later dry season months in this respect (table 6.5). It is thus interesting to note that pursuit records made up 6.8% of the total during this month, compared with 4.8% in July and August combined, while the manual search category contributed 6.6% and 9.7% of the respective totals.

While these trends do appear to correlate with those of both the availability of prey of different types and their capture by the group during the course of the year, there does not seem to be any indication that its foraging behaviour underwent any major systematic changes. The fundamental characteristic of this type of behaviour during all months was the intense scanning for signs of potential prey. The apparent decrease in pursuit activities through the course of the dry season correlates quite clearly with that of both the availability of mobile prey and its capture by the group (chapters 3 and 6). This also correlates with patterns such as the relatively larger proportion of prey apparently captured on the ground and the greater foraging success at lower levels during the wet season (see above). While the manual searching of substrates did appear to increase towards the end of the dry season, this pattern was not as clear.

One problem may have been at the level of the collection of data. It was not usually possible, for example, to distinguish precisely between manual searches directed at the capture of mobile prey and those directed at immobile prey. Thus, while manual searching may have been directed at different types of prey at different times of the year, this was not clear from the data collected. It is possible, however, to look more closely at two aspects of the manual search records in an attempt to identify possible seasonal changes in these activities. On the one hand, the relative proportions of the three distinct types of behaviour which constitute the manual search category (see table 7.6) may have exhibited seasonal variations indicative of changes in the emphasis of such behaviour. On the other, differences in the types of substrate searched during different times of the year may also point to underlying variations in the orientation of this type of activity.

Very little variation is apparent, however (tables 7.8 and 7.9). The breaking or biting open of substrates was an equally minor feature of manual search activities during all sample periods. In addition, leaves were almost invariably the type of substrate searched throughout the year, a pattern also recorded for *Saguinus imperator* and *Saimiri sciureus* at Manu [Terborgh, 1983: table 6.10, p. 116]. While there was a small increase in the manual searching of branches during the dry season samples, it was balanced by a decrease in the searching of miscellaneous substrates such as flowers. As both these categories make up a very small proportion of the total in all samples, these minor fluctuations do not appear to indicate any major shift in the orientation of this type of behaviour.

One final point concerns the observed variation in the orientation of supports used during foraging (figure 7.11). The different types of foraging behaviour differed considerably in their typical orientation (figure 7.13a-h). Upward postures on vertical supports were clearly preferred for scanning the

Table 7.8

Seasonal Variation in Manual Search Activities

	Percentage of total "manual search" foraging recorded as:	
Sample	Manipulate (FO MP)	Break open (FO BKO) or bite open (FO BI)[1]
December	84.3	15.7
Late wet	86.4	13.6
Early dry	88.5	11.5
Late dry	86.0	14.0

[1] FO BI was recorded only very rarely and is thus included in this column.

Figure 7.13

The Orientation of Supports Used by the Study Group during Foraging Activities of Different Types

(a) Scanning

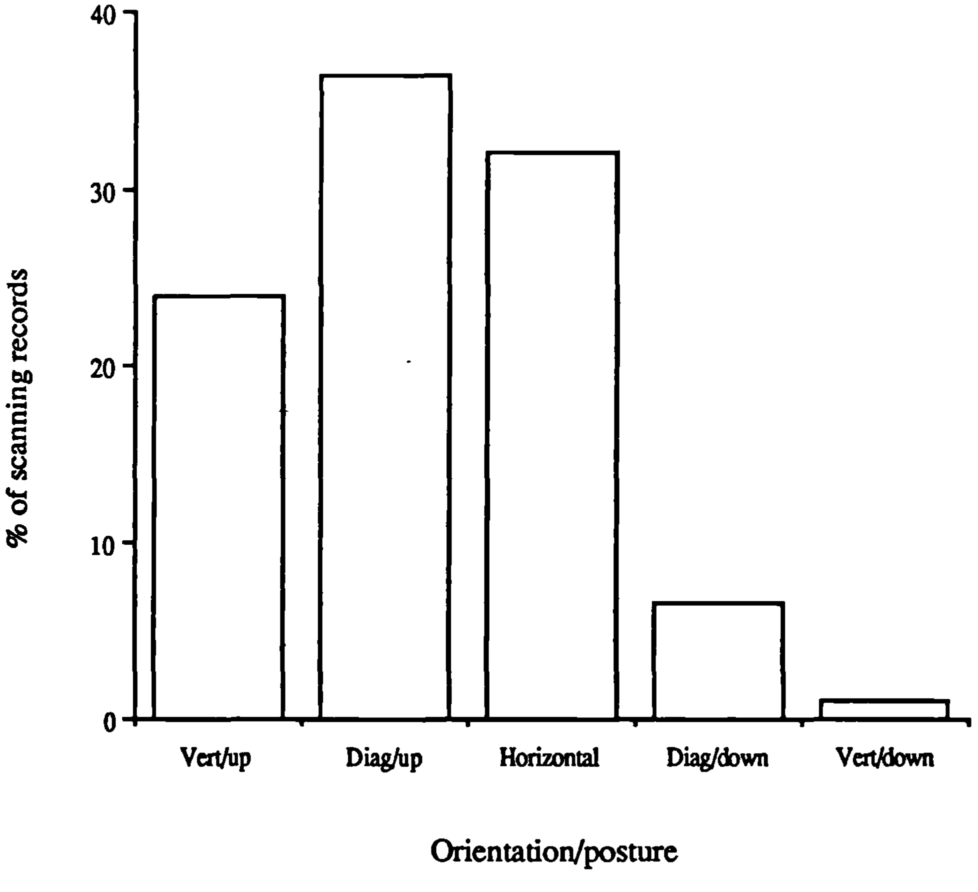
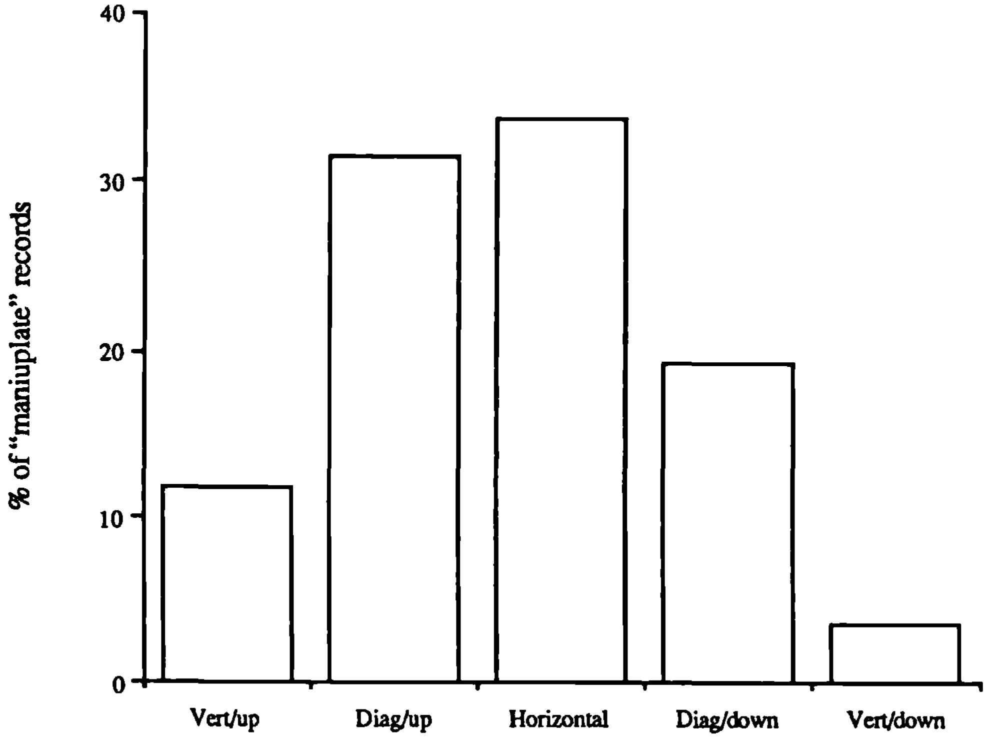
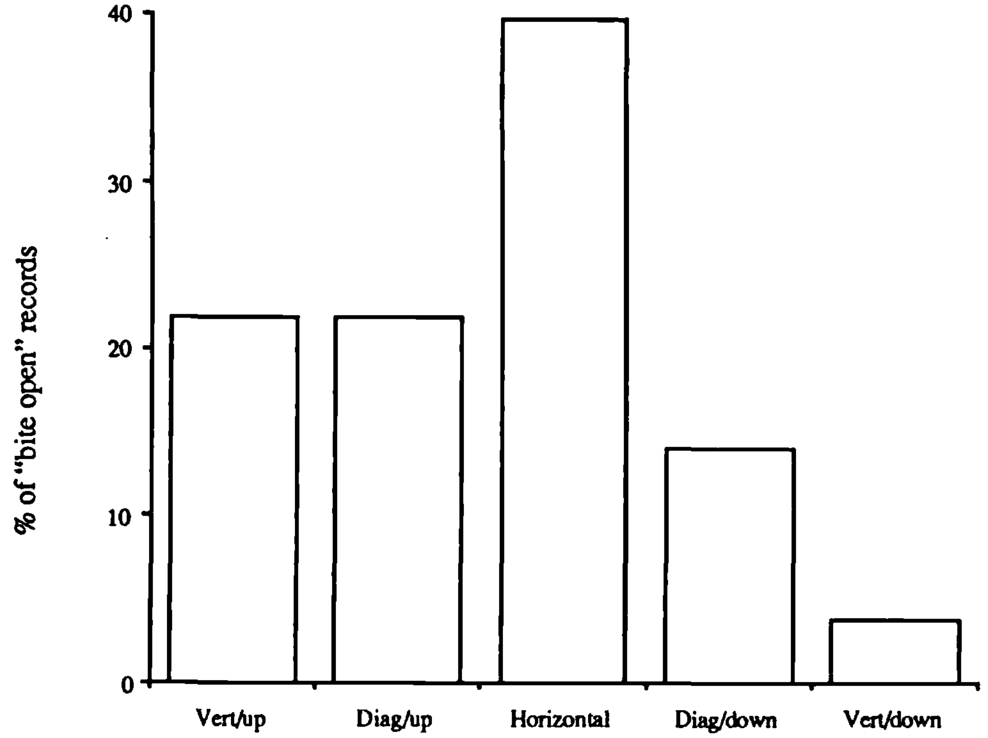


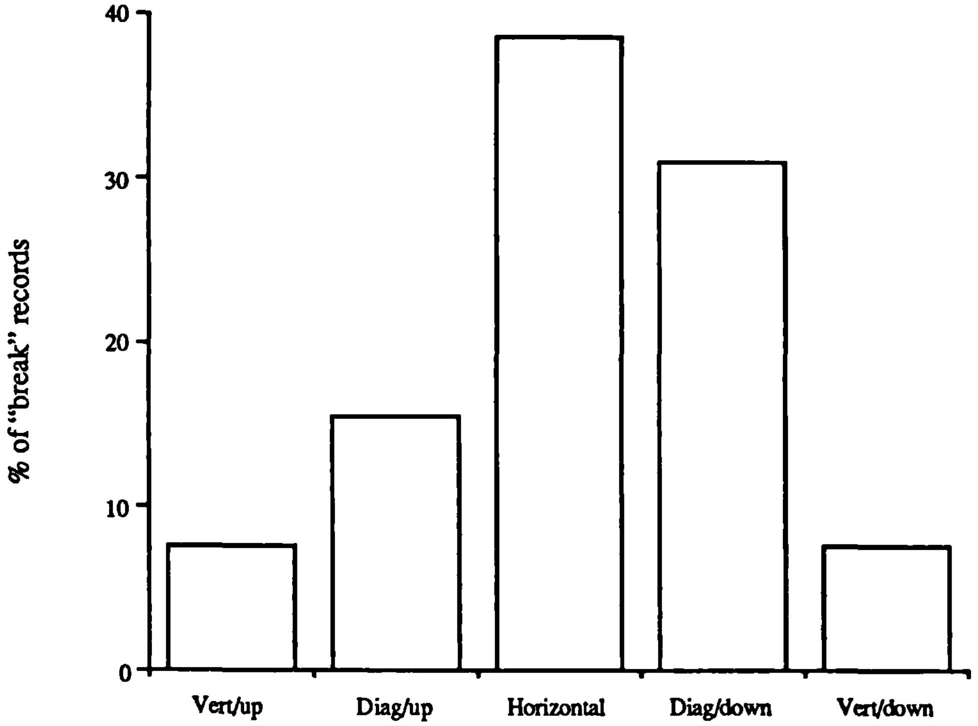
Figure 7.13 compares the orientation of supports used and the posture of the animals (i.e. *head up or head down) during foraging behaviours of different types. Samples taken from the period December 1985 to August 1986. Values are percentages of the total records of each type of behaviour. Note that the scale on graph (g) is slightly different from the others, in order to accomodate the high values for head-down postures on diagonal supports.*

(b) Manipulating Substrate/Object

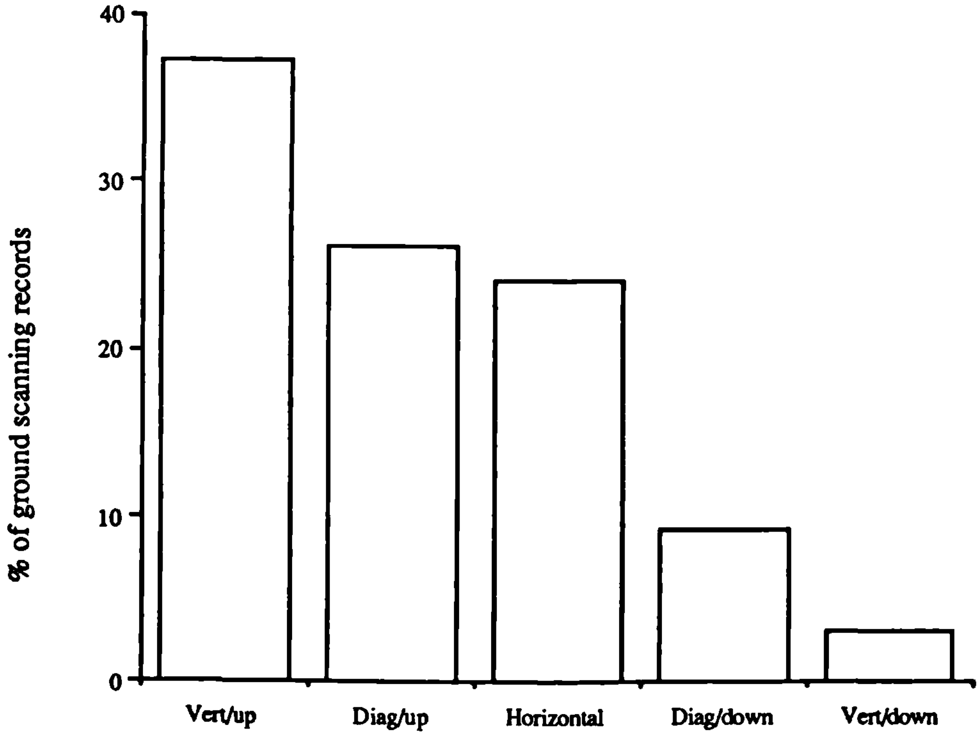


(c) Biting Open Substrate/Object



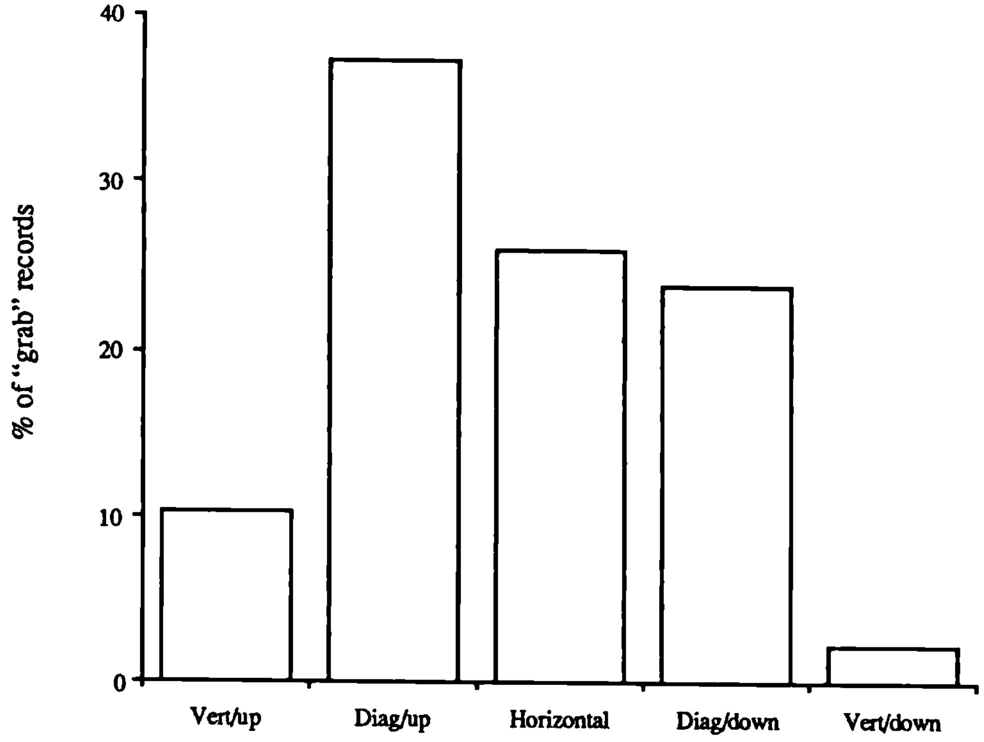


(d) Breaking Substrate/Object

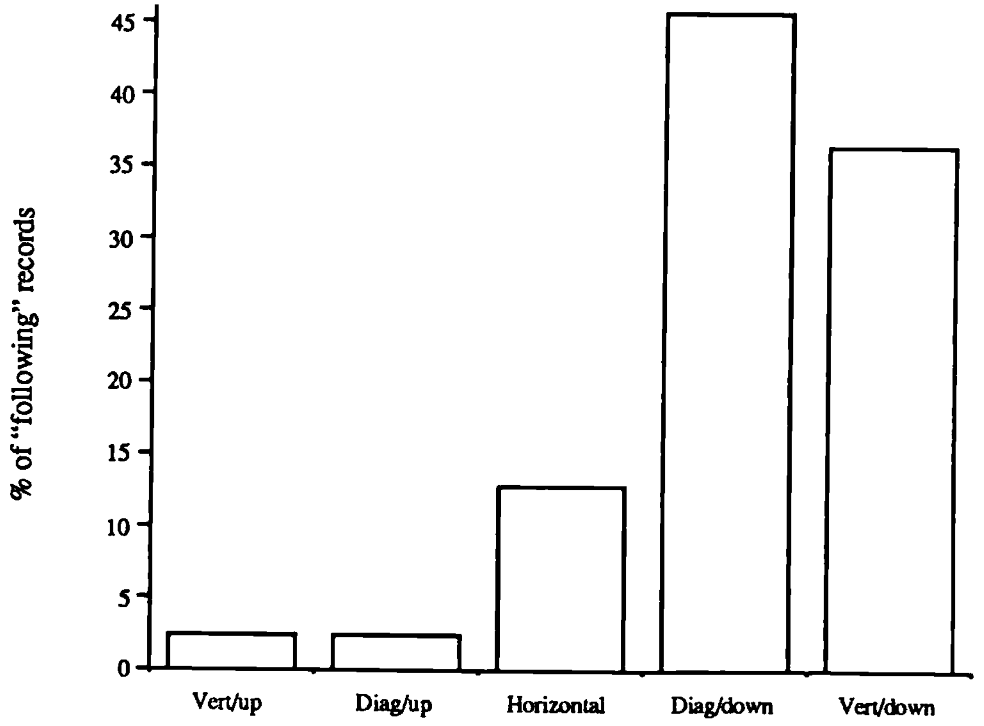


(e) Scanning Ground

(e) Grabbing Object



(g) Following Prey



(h) Pouncing

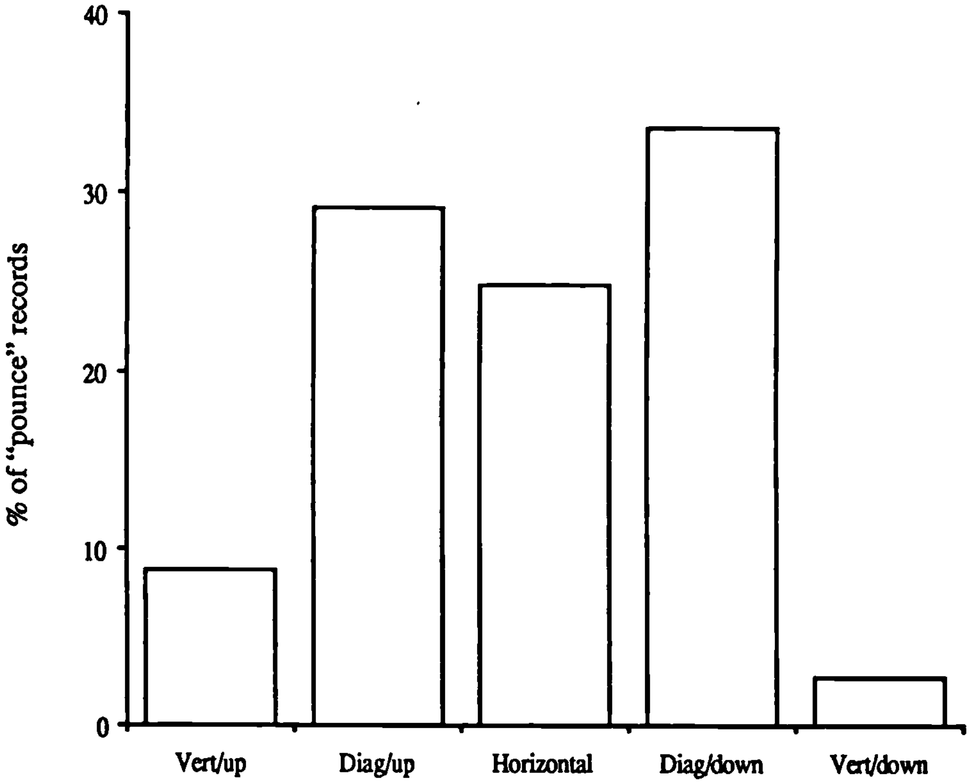

% of "pounce" records
0
10
20
30
40
Vert/up
Diag/up
Horizontal
Diag/down
Vert/down

Table 7.9

Substrates Searched during Foraging, by Season

Sample	Substrate searched during "manual search" activities (percentage of total records): Leaf	Branch	Other
December	94.2	1.4	4.4
Late wet	94.9	2.1	3.0
Early dry	92.5	5.6	1.9
Late dry	93.4	5.8	0.8

ground, while downward postures on diagonal supports were most frequently recorded during following and pouncing. For manual search categories, on the other hand, horizontal supports were preferred. While upward postures on diagonal supports were used most during scanning, horizontal supports were also used more frequently than they were during any of the pursuit activities. Overall then, this evidence supports the idea that the observed differences in the orientation of foraging activities between the two main seasonal samples was due primarily to changes in the frequency of these activities. This would especially be the case if the December sample is seen as representative of the preceding early wet season months.

Taken as a whole, then, the evidence presented here appears to show that the group was not only searching for its prey in similar locations throughout the year, but was also employing the same foraging techniques. This appears to imply that it was basically searching for the same type of prey, *i.e.* large mobile arthropods, throughout the year, even though the availability of such prey fluctuated considerably. The only seasonal variation which is apparent from the data seems to have been a consequence of changes in the types of prey encountered by the group, rather than of the nature or orientation of its foraging activities, at different times of year. Pursuit foraging was thus recorded relatively more frequently during the wet season, when mobile prey was more frequently captured, than during the dry, and so on.

These findings have a number of implications for the assessment of the group's foraging strategy. As we have seen, its response to an apparently severe scarcity of its large, mobile arthropod prey, *i.e.* during the late dry season of 1986, involved both a marked increase in the amount of time it devoted to foraging activities each day, and a concentration of these efforts into the parts of its range which appeared to contain the highest densities of mobile arthropods. It also appears to have been far less selective of its prey, capturing relatively much larger proportions of small items and immatures (chapter 6). Despite these responses, the group experienced an acute reduction in the quantity of animal material in its diet and an apparently considerable decrease in the overall returns to its foraging efforts.

The lack of any major modifications of foraging behaviour in response to apparent changes in the availability of prey of different types can be seen as somewhat equivocal, given the other changes. While the group did capture larger numbers of immatures during the dry season, this seems to have been a consequence of the greater abundance of this type of prey at this time rather than of any change in its searching patterns. Despite the small sample size, an analysis of the distribution of its feeding on immatures during the dry season supports this idea. While 64.4% of all prey feeding was recorded in the "riverbank" quadrats during the dry season samples (see table 6.15), only 50% of the records of feeding on immatures was collected at these lower elevations (methods as in appendix IV). This raises the question of whether the group was, in continuing to "scan-and-pounce" for large mobile insects at low levels in the forest at low elevations, making best use of the time available for its foraging activities during the dry season.

Assuming that immatures were relatively far more available than during the wet season, we would, for example, expect a shift in the orientation of the group's foraging behaviour towards the capture of this type of prey. A major increase in the manipulation of substrates is one change which might be expected. While broadly similar to *Saguinus imperator* in features such as the levels used and the substrates searched, much of the foraging behaviour of *Saimiri sciureus* at Manu involved the manipulation of leaves rather than scanning. This is reflected in the much larger proportion of immature prey items, predominantly lepidopterans, captured by the latter species [Terborgh, 1983: table 6.5, p. 106]. A shift towards this type of behaviour would not necessarily require major changes in the habitat use of the *C. flaviceps* group, so it would not conflict with its searching for large mobile insects. While it can be argued that such a change would have an adverse effect on the latter activity by disturbing mobile prey, the contrary has been argued in this chapter, *i.e.* that the disturbance of mobile prey at low levels in the forest increases the effectiveness of marmoset foraging behaviour.

One further option is the type of destructive foraging engaged in by larger primate such as *Cebus*, notably the breaking and biting open of branches to gain access to the eggs and brood of hymenopterans and isopterans [*ibid.*]. It seems likely, however, that the energetic demands of such behaviour would restrict the possibilities for the small-bodied marmosets, despite their strong gouging teeth. Ant colonies were nevertheless observed in hollow branches of only a few millimetres in diameter at FMC, which implies that they would be accessible to the marmosets, although they were never seen feeding on such insects.

One of the principal factors limiting the possibilities for such changes may, in fact, be the cognitive abilities of the marmosets themselves. Foraging behaviour appears to be somewhat stereotyped in small, insectivorous primate species and may be relatively inflexible. Terborgh [1983], for example, notes that young *Cebus apella* exhibit the same types of foraging behaviour as mature individuals throughout their development. This appears to be species-specific, rather than size-related, as young *Cebus* do not forage like *Saimiri sciureus* when they are of a similar body size. While, as we have seen, marmosets may have the ability to respond to gross changes, such as those in the abundance and distribution of their prey, they may be unable to respond effectively to more subtle fluctuations, such as those in the relative availability of prey of different types.

This assessment of the group's foraging behaviour depends, however, on a number of assumptions, principally that it was experiencing a deleterious scarcity of arthropod prey during the late dry season months of 1986. Whether this was the case is difficult to assess, but there is some evidence to suggest that it was not. Qualitatively, group members did not appear to suffer any loss of physical condition during the dry season, even though this has been recorded for tamarin species such as *Saguinus geoffroyi* and *S. f. weddelli* [Dawson, 1979; Terborgh & Stern, 1987]. Similarly, the birth and survival of twins at the end of September indicates a lack of any significant nutritional stress affecting the reproductive female, BM, during the preceding dry season months.

The reduction in the size of the group from fifteen to eleven individuals in June may also have been important, although this appears to have conflicting implications. While its absolute dietary requirements were reduced by this change, the much larger proportion of young individuals among the remaining group members implies that its foraging would have been less successful, given the same levels of arthropod abundance. Increases in both the number of neighbouring groups and the frequency of their encroachment into the study group's home range also imply an increase in competition for the available resources. While the pattern of the group's ranging during July suggests an increase in range "defence" at this time (see chapter 5), there does not seem to have been any obvious increase in territorial behaviour, which might have been expected if such competition had a serious effect on the availability of prey. Here again, the lack of such a change may simply reflect the difficulty of the defence of these resources [as for the "upland" group of *S. geoffroyi*, Dawson, 1979] rather than the absence of such an effect.

While other factors, such as the gum-feeding adaptations of the marmosets and their apparent ability to reduce metabolic expenditure, may be even more important, they are even less easily assessed. It does seem, however, that they do make an important contribution to the ability of marmosets to endure periods of scarcity. In this case, while the scarcity of arthropod prey at FMC during the late dry season of 1986 may have been severe, it does not seem to have been deleterious enough to have stimulated major changes in the study group's behaviour. One further aspect of its behaviour which supports this idea is that, while it greatly increased the intensity of its foraging activities during the late dry season of 1986, there was no obvious increase or decrease in the length of its daily activity period, relative to the values recorded during the previous year (see chapter 4).

Whether the apparent lack of change in the group's foraging behaviour during the course of the year is seen as result of a lack of either ability or necessity (or both), the data presented here do seem to complete the picture of its foraging activities and their emphasis on the capture of large, mobile arthropods at low levels in the forest. The implications of this, and other aspects of its behaviour are discussed in the following, concluding chapter.

Summary

The foraging behaviour of the *Callithrix flaviceps* study group is described in detail. Habitat preferences, together with factors such as the relatively small body size of these marmosets and the relatively large size of their typical prey, are seen as important integral features of an overall strategy of maximising foraging efficiency while minimising the expenditure of time. The marked seasonal variation recorded for other aspects of the group's behaviour and ecology were not, however, reflected in the finer details of its foraging behaviour. This suggests that, while it greatly increased its foraging efforts during periods of scarcity, this did not involve significant changes in searching behaviour. The main points are:

1. The study group's foraging behaviour appeared to be oriented primarily towards the capture of prey. Other needs, such as predator avoidance and the monitoring of both resources and neighbouring groups are seen as being integral and subsidiary aspects of this behaviour. As the expenditure of time in these activities is effectively reduced, this is seen as part of an overall time-minimising strategy.
2. Scanning for signs of prey was the major feature of the group's foraging behaviour, constituting 89.2% of the records collected between December 1985 and August 1986. This proportion was equally large in both dry and wet season sample periods, while other behaviours, such as the manual searching were consistently minor features of its foraging.
3. The group foraged at relatively low levels at all times, spending 50% of its foraging time at or below 3 m. "Pursuit" activities related to the capture of prey on the ground constituted approximately 10% of foraging, although this was thought to have been an under-estimate of such behaviour, given its nature. Prey feeding on the ground, despite a strong negative bias, was recorded almost twice as frequently as expected, given the proportion of foraging time spent there. However, while foraging took place at similar levels throughout the year, the effectiveness of this strategy declined considerably with the availability of typically large, mobile prey.
4. Analysis of the group's daily ranging shows that there was relatively little overlap between the ranges of consecutive days (approximately 20%, on

average). This pattern was recorded in both dry and wet season samples. This is interpreted as a systematic avoidance of areas in which the abundance of prey may be depleted in the short term, and contrasts with the pattern of feeding on plant material, which tended to take place at a few, frequently-used locations.

5. Very little seasonal variation in habitat use during foraging was noted. Similar levels were utilised at the same times of day throughout the year. While the diameters and types of support used remained constant, there was some contrast between the wet and dry seasons in their orientation. While horizontal supports were used more frequently during the dry season, upward postures on vertical and downward postures on diagonal supports were recorded far more frequently during the dry season.

6. Similarly little seasonal variation was noted in foraging techniques. While manual searching increased, and "pursuit" activities decreased towards the end of the dry season, these changes were relatively small and scanning remained the predominant behaviour. Again, no seasonal change was noted in the nature of manual searching, nor in the types of substrate searched, which were almost always leaves. The only changes that were recorded seem to have been related to differences in the types of prey encountered, rather than the foraging methods employed. Seasonal differences in the orientation of foraging activities correlate with those of the activities themselves.

8

An Ecological Overview

This thesis has presented the findings of the first detailed study of the behaviour and ecology of the buffy-headed marmoset, *Callithrix flaviceps*, which took place in the forest reserve at the Fazenda Montes Claros (FMC), Minas Gerais, Brazil between December 1984 and October 1986. In general terms, the main study group exhibited patterns of behaviour which can be seen as characteristic of marmoset species as a whole, and of the eastern Brazilian forms in particular. Some features of its behaviour did not, however, appear to be typical of other marmosets. While these differences may have been due, at least in part, to species-specific variations, there is at present too little information available to allow conclusions to be drawn. Analysis of the seasonal patterns recorded in both the group's behaviour and the availability of resources at the study site has nevertheless indicated some of the possible causes of such differences.

The present study has explored the ecology of the study group at three different levels. The base stratum of the investigation has been that of the "ecological framework", which has provided information on the abundance of resources at the Jaó study site and, through inference, their availability to the group. From this basic viewpoint, the group's behaviour has been analysed, first at the level of the general patterns of its activity and ranging, and then in finer detail. This analysis has shown that most of the variation recorded during the course of the year can be systematically linked to certain "fixed" constraints such as the body size of the marmosets themselves, on the one hand, and to fluctuations in the availability of resources, both through time and in space, on the other. While this linking of one observed pattern to another has been relatively successful, it has relied, to a greater or lesser extent, on certain "logical" expectations derived from a specific viewpoint, that of optimal foraging theory (OFT), a viewpoint that is not without some controversy.

The mathematical models on which OFT is based [see *e.g.* Schoener, 1971; Maynard Smith, 1974; Pyke *et al.*, 1977; Stephens & Krebs, 1987] allow predictions to be made about how animals will forage in different environments. The basic assumption underlying such models is that the foraging behaviour of a species will be moulded, through the forces of natural selection, by its efficiency (usually measured in terms of net energy gain). Reproductive success is seen as being related directly to foraging efficiency, so that an animal which maximises that efficiency will also be maximising its reproductive success, and its foraging behaviour will, in turn, be selected for. If evolution is seen as a strictly optimising process, foraging behaviour will also be optimised.

While OFT might be seen as being based on an apparently logical extension of the theory of natural selection, its underlying assumptions have frequently been challenged [*e.g.* Gould & Lewontin, 1979; Lewontin, 1983; Pierce & Ollason, 1987]. Most theorists acknowledge that the application of optimality models to the analysis of foraging behaviour is not only problematic in theory but often erroneous in practice [Stearns & Schmid-Hempel, 1987; Stephens & Krebs, 1987]. The main problem facing OFT lies at the interface between the relatively simple models themselves and the vastly complex physical and behavioural environments within which most animals evolve. Even if we accept the theoretical basis of the models, it seems unreasonable to expect all animals to forage optimally at all times, whether we take the animal as an individual [*e.g.* Ross & Bras, 1975; Post, 1982] or as a member of a species, whose "Fitness optima are inevitably moving as the environment and the gene pool change." [Pierce & Ollason, 1987: p. 113]. A systematic link between the short-term processes analysed in the models and the longer-term processes which underpin the phylogeny of such behaviour also seems to be missing [Stearns & Schmid-Hempel, 1987].

However, despite the fact that, as Post [1984: p. 299] points out, "There are many reasons why animals may forage suboptimally", the application of such models to both laboratory experiments and field studies has proved relatively successful in a majority of cases [Krebs *et al.*, 1983; Stephens & Krebs, 1987], including some studies of primate species [*e.g.*

Milton, 1979, 1980; Harcourt, 1980, 1986]. While optimality models may have a number of limitations, they do appear to provide important insights for the analysis of foraging behaviour. Such insights, as we have seen, form a useful basis for the interpretation of the behaviour and ecology of the *C. flaviceps* study group. The increase in the intensity of its foraging behaviour with the decline in the abundance of arthropods was one pattern predicted from the small body size of these primates, for example. The apparent decrease in prey selectivity which accompanied these changes was also expected. A number of the characteristics of the group's behaviour indicate, in addition, that a "time-minimising" foraging strategy was being followed. It is difficult to judge, however, whether, or to what extent, these findings support the general applicability of the models.

It is also difficult to judge, in fact, whether or not we can see the patterns of behaviour exhibited by the group as "optimal". While the behaviour of the animals under specific conditions may have conformed to that predicted from optimality models, there is no *a priori* reason for accepting the hypothesis that it was being optimised. Alternative hypotheses may be equally valid, especially given our partial or complete lack of knowledge of many of the variables which may have influenced the group's behaviour. While there is good evidence that insects were more abundant during the wet season, for example, the methods used gave only a crude measure of the availability and distribution of animal material at the site, especially when the patchy nature of the habitat is considered. Similarly, while evidence has been presented to support the idea that certain metabolic adaptations have significant implications for marmoset behaviour, in general, and for their foraging strategies, in particular, the exact nature and degree of the influence of these adaptations is not well known. Most other variables can be seen in a similar light.

Nevertheless, many of the patterns observed do appear to be consistent with the idea that strategies which tended to maximise foraging efficiency, not only at a certain point in time but also in the long term, were being followed, given constraining factors ranging from the small size of the marmosets themselves to the overall availability and distribution of resources. The evidence is particularly consistent with the view of marmosets as time-minimising foragers adapted for the exploitation of secondary and disturbed forest habitats. However, while most of the patterns observed indicate that foraging efficiency, in terms of both net energy gain and the minimisation of the expenditure of time, was being maximised, the apparent lack of flexibility in the foraging techniques utilised has raised one or two questions (see chapter 7). In this closing chapter, the main results of the behavioural study are reviewed and a number of general conclusions are drawn about the ecological adaptations of *C. flaviceps*, in particular, and of the marmosets and tamarins, in general.

General Characteristics of the Study Group's Ecology

In broad terms, the basic characteristics of the ecology of the study group can be seen as typical not only of the *C. flaviceps* population at FMC as a whole, but also of those of other marmoset species. All the *C. flaviceps* groups observed at FMC exhibited a clear preference for the dense vegetation of the secondary and edge habitats, the types which dominate the Jaó study area. Daily activity periods were not only relatively short (averaging only 9 hours and 45 minutes over the 125 days of the main study period), but were also characterised by relatively low levels of foraging and travelling, and high levels of rest and social activities. The main components of the group's diet were plant exudates and animal material, again typical not only of the marmoset population at FMC, but also of other species. In addition, it tended to both prey on characteristically large insects, predominantly orthopterans, and concentrate its feeding on the resources of only two or three plant species each month. The "scan-and-pounce" technique which dominated the group's foraging behaviour is also typical of that reported for other marmosets, such as *Callithrix humeralifer intermedius* [Rylands, 1982].

Other characteristics of the group's behaviour were less typical and may indicate possible differences between species, although many aspects of this contrast appeared to be systematically related to environmental factors and are thus difficult to interpret in terms of their implications for inter-species differences. The lack of detailed data for most other marmoset species, especially those inhabiting similarly seasonal environments, also prevents systematic comparisons. While the relatively large distances travelled by the study group each day are typical, for example, its home range is, at 35.5 ha, much larger than any recorded for other marmoset species, especially those of the *Callithrix jacchus* group. This relatively large range did appear, however, to be typical of the *C. flaviceps* groups at FMC. The lack of territorial behaviour and the degree of overlap of the study group's home range with those of its neighbours (87.5%) also appear to be unusual.

It has been suggested here that these differences may be systematically related to the marked seasonality at FMC, and to fluctuations in the abundance of arthropods in particular. This suggestion is based on the assumption that plant exudates are at least as abundant within the study group's home range as they are at other, less seasonal eastern Brazilian sites such as Tapacura and Una. As fruit is usually scarce in the secondary forest at FMC, it seems most likely that the relatively large home ranges which appear to be typical at this site are related to the abundance and distribution of arthropod prey. Similarly large home ranges may, however, be typical of another eastern Brazilian species, *Callithrix aurita* [Stevenson & Rylands, in press]. It is thus interesting to note that it may be even more insectivorous than other marmosets [Muskin, 1984a, 1984b]. Assuming that the availability of resources is the major influence on range size, we would predict that populations of *Callithrix jacchus* and *Callithrix penicillata* inhabiting more seasonal sites further inland would have relatively larger ranges, while those of *C. flaviceps* groups in more stable environments such as that at Nova Lombardia in Espírito Santo would have smaller ranges. We might also expect concomitant differences in territorial behaviour. If, when such data becomes available, other patterns are observed, this would contribute to the identification of inter-specific differences.

A number of aspects of the study group's feeding behaviour also contrasted with the patterns recorded for other marmoset species, although these features again appear to be related to the availability of resources at this site rather than to systematic inter-specific differences. As there is little evidence, apart from the levels used, to indicate that the group's foraging behaviour would have made vertebrates more accessible than for other marmosets, the capture of relatively large numbers appears to have been a consequence of both their abundance at this site and their vulnerability during the dry season (see chapter 3). The frequent use of gum produced in response to damage caused by insects and other media rather than by the marmosets themselves was also unusual, although the patterns of exploitation of these sources again appear to indicate that this was a direct consequence of the availability of such gum at this site. The predation of *Siparuna* sp. seeds was the first recorded case of such feeding behaviour for any species of marmoset or tamarin, but here again it seems that this was most probably related to the availability of this resource at FMC.

The systematic nature of the group's exploitation of the resources available within its home range provides a number of valuable insights into the foraging and feeding behaviour of the marmosets as a whole. The repeated use of a small number of gum sources from among those available was typical of the gum-feeding behaviour of other marmosets [Stevenson & Rylands, in press]. This seems to be one aspect of the long-term strategies underlying the exploitation of this type of resource, epitomised by the "lifetime ranging" of *Cebuella pygmaea* groups, which abandon not only their exudate trees, but also the territories which surround them, to move to new sites every few years [Soini, 1982]. In concentrating its feeding at a small number of sites (see chapter 6), the *Callithrix flaviceps* study group not only seemed to be minimising feeding time, but was also apparently able to systematise its movements with regard to the distribution of arthropods. On a day-to-day basis, its movements reflected this concentration of feeding on plant material, on the one hand, and the systematic avoidance of other areas which had been visited on the previous day, on the other (see chapter 7). The latter pattern is consistent with the idea that the abundance of prey in any part of the forest will be significantly depleted, at least in the short term, by the group's foraging, so that the regular avoidance of such areas on consecutive days would tend to maximise its foraging success in the long term.

There thus seems to be good evidence that the patterns of the group's movements within its range were an integral part of strategies aimed at the maximisation of the consumption of both plant and animal material and the minimisation of the expenditure of time and energy necessary for their acquisition. Given other aspects of its behaviour, this appears to equate with the maximisation of foraging efficiency within a time-minimising framework. The evidence also supports the idea that the group's movements were effectively guided by a "mental map" [Altmann & Altmann, 1970], an idea which is confirmed by the typical behaviour surrounding the use of sleeping sites (see chapter 5). Such a "map" appeared to have been influenced, at least in part, by a feedback mechanism operating between the group's current experience and its future behaviour. This was especially apparent in the seasonal patterns recorded (see below), which indicate that the distribution of its foraging activities was systematically determined by that of its foraging success. Along with other factors, this also indicates that the monitoring of the abundance and distribution of both plant and animal resources had an important influence on the group's ranging, although the degree of this influence is not easily assessed from the data.

In general, almost all characteristics of the study group's behaviour indicate that it was following a time-minimising foraging strategy. Such a strategy appears to be typical of marmosets and tamarins in general, and is as we might predict for such small animals which are, among other things, extremely vulnerable to predation (see chapter 1). Following a strategy which minimises the amount of time spent procuring food each day allows these animals to spend as large a proportion of their time as possible engaging in activities, especially rest, which, by their cryptic nature, reduce the chances of predation. The results of the present study, especially the seasonal patterns recorded, as we shall see below, also support the idea that the physiological regulation of metabolic expenditure is an important functional feature of this strategy.

Resource Availability and Behavioural Patterns

The major theme underlying the presentation of the behavioural data has been that of the seasonal fluctuations in the availability of resources. Rainfall appeared to be the main factor influencing seasonal variation at this site (see chapter 3). Arthropods, leaves and fruit were all generally more abundant during the wet season months (October to March in the study year) than they were during the dry season. The only resource which appeared to be more available during the dry season was the gum of *angico* (*Anadenanthera peregrina*) trees produced in response to insect damage. It seemed that the proximity of the relatively large river Manhuaçú also had, through its effects on the humidity of the soil, a major influence on the overall abundance and distribution of resources within the group's home range, during the dry season in particular.

In general terms, the yearly cycle at FMC is divided almost equally between distinct wet and dry seasons, which are respectively hotter and cooler, a pattern which was especially well-defined during the study period. For the analysis of the data, further divisions within each of the two main seasons were utilised, corresponding with the patterns observed in the principal variables. The wet season was thus divided into an early period (October to December) and a late period (January to March). The first two months of the main study period (August and September, 1985) were designated as the late dry season sample of that year. The division of the dry season months of 1986 was complicated by a number of factors, including the division of the study group, which took place at the beginning of June. April and May were thus defined as the early dry season of this year, and the following months (June to August) as the late dry season. These divisions were consistent with those observed in the study group's behaviour during the course of the year.

There were a number of indications, in particular from the rainfall levels during the study period and the evidence of the late dry season records from 1985, that most resources were abnormally scarce during 1986. While there is relatively little information on which to base such an assumption, it seems possible that the observed levels of scarcity represent the lower limits likely to be encountered by this marmoset species, at least in this particular region, in all but highly exceptional years. It is thus interesting to note that, while the group's behaviour did change significantly in accordance with seasonal changes in the availability of resources, there were no obvious indications, either from its behaviour or from the physical condition of its members, that this scarcity had any markedly deleterious consequences. This situation contrasts markedly with those facing certain tamarin species [Dawson, 1979;

Terborgh & Stern, 1987], which appear to experience less serious fluctuations in the abundance of fruit and arthropods than those recorded at FMC. It seems likely that the major feature underlying this contrast is the ability of the marmosets to systematically exploit plant exudates, which ensures a regular and stable supply of nutrients throughout the year. It has been argued that this has a number of benefits for the foraging and feeding strategies of the marmosets and important implications, ultimately, for their social organisation (see chapter 1).

Ranging, Foraging and Resting

Observed changes in the patterns of the group's behaviour during the course of the study appeared to correspond closely with those in the abundance of resources at the site. As fruits were scarce throughout most of the year, the major trends appeared to be most closely related to the abundance of arthropods. The relative abundance of fruits and seeds during January and February appeared, however, to have their own characteristic influence on the group's behaviour. During this period, it not only foraged less than "expected", given the observed abundance of arthropods, but also seemed to range over smaller distances each day, on average. The availability of *Siparuna* seeds during February also resulted in a major southward shift of the focus of the group's movements, while the northern part of its range was preferred in all other months (see chapter 5). The specific patterns which appeared to be related to the abundance of edible fruits and seeds during these months are considered in more detail in the following section.

Arthropods, especially the types most commonly preyed on by the study group, were clearly most plentiful during the early wet season. Taking this period as our baseline, we can see a continuum of systematic changes in behaviour through to the late dry season of 1986, when arthropods were apparently most scarce (table 8.1). The decline in arthropod abundance corresponded with a reduction in the mean daily activity period. Concomitant reductions were recorded in the amount of time spent feeding on animal

Table 8.1

Seasonal Trends in the Study Group's Behaviour in Relation to Arthropod Abundance

Behavioural variable	General trend with decreasing arthropod abundance
Daily activity period	Decrease
Foraging:	
As proportion of activity	Marked increase
Success/prey feeding	Marked decrease
Technique (support use, etc.)	Stable
Prey selectivity	Apparent decrease
Predation of vertebrates	Increase
Gum feeding:	
As proportion of activity	Stable
As proportion of diet	Marked increase
Use of gum produced by insect damage	Apparent increase
Ranging:	
Travel as proportion of activity	Marked increase
Daily path length	Stable
Range size	Stable
Distribution of group movements	Increasing concentration at lower altitudes
Daytime resting	Marked decrease
Social activities	Marked decrease

material, resting and engaging in social activities, on average, each day. There is a certain amount of ambiguity in this pattern because any reduction in the daily activity period results in an increase in the period spent roosting each day. An estimate of the amount of time spent at rest during each 24-hour period, based on the assumption that the group was resting during the whole of the time it was located in its sleep-tree, actually found very little difference between the wet and dry season samples (see chapter 4). What did change, however, was the nature, or function, of the rest itself. Daytime rest during the much hotter wet season frequently involved the characteristic "sprawling" (plate 6) which functions as an effective cooling mechanism. These siestas were also characterised by prolonged bouts of grooming and, often very energetic, play. In the night-time huddle, on the other hand, there was generally very little activity, and this type of resting can be seen as having an important energy-saving function for the marmosets, given their possible metabolic adaptations. In this case, the evidence does appear to indicate that the reduction of the daily activity period corresponding with the decline in insect abundance was closely related to an energy-saving strategy.

The time spent travelling and foraging each day, on the other hand, systematically increased with the decline in arthropod abundance. There is again a certain amount of ambiguity here because, as we saw in chapter 5, there was very little seasonal variation in the size of the day ranges used by the group. They were, if anything, slightly larger during the early wet season than at other times of the year. The increase in travelling actually appears to be a consequence of the reduction in the daily activity period rather than of other factors. While range size was relatively stable during the course of the year, there were significant changes in the distribution of the group's movements, which were progressively concentrated at lower, more humid elevations as arthropod abundance declined. These changes corresponded systematically with those in the distribution of arthropods, which declined at higher altitudes while remaining relatively stable lower down, but not consistently with the apparent distribution of plant resources. This further confirms the idea outlined above that, while the group was obliged to visit a certain number of sites to feed on plant material each day, its movements were basically determined by the distribution of its arthropod prey and thus primarily by the needs of its insect foraging activities.

A more detailed analysis of the spatial distribution of the group's foraging and feeding activities (see chapters 5 and 6) provides further confirmation of this pattern. This analysis also offers useful insight into the influence on the group's movements of what is seen as a "mental map". The analysis shows that the increasing differential in the foraging success experienced by the group within its range had the effect of systematically channelling the distribution of both its movements and its foraging activities towards the lower altitudes as arthropod abundance declined higher up. The evidence suggests the operation of a feedback mechanism, moulding the group's future behaviour on the basis of its present experience. As it experienced progressively lower returns to its foraging efforts at higher altitudes during the course of the dry season, so it devoted progressively and significantly more of its foraging time to the more humid riverbank habitat.

Other aspects of the evidence do, however, indicate conflicting influences on the pattern of the group's movements. The distribution of its gum feeding during the 1986 dry season is perhaps the most contradictory feature, although it does seem to be consistent with the overall patterns of the group's systematic long-term exploitation of gum sources, and the increase in its use of the more abundant *angico* gum during this period, in particular. The evidence for a feedback mechanism operating on ranging behaviour also suggests that the monitoring of resources was an important aspect of its behaviour, and may, in turn, have had a direct influence on the distribution of its movements. The monitoring of both resources and the presence of neighbouring groups have thus been seen as determinants of the continued regular use of the western half of the range during the 1986 dry season.

The systematic increase in foraging activities as arthropod abundance declined appears to offer one of the most important insights into the foraging strategies, not only of the study group, but also of the marmosets and tamarins in general. This increase in foraging corresponds with decreases in both foraging success and prey selectivity (see table 8.1), although the increase in the numbers of vertebrates captured is contradictory. As most of the vertebrates captured (predominantly tree frogs and lizards) were probably insectivorous, this may also have been related to the relative scarcity of arthropods during the dry season. Overall, the seasonal patterns observed in the foraging behaviour of the *C. flaviceps* group are very similar to those recorded for the small-bodied insectivore/gummivore *Galago senegalensis* [Harcourt, 1986].

It has been argued that this similarity is a function of the small body size of these primates (chapter 4), which appears to restrict the feasability of strategies involving increases in energy-saving behaviour. A time-minimising foraging strategy thus appears to make conflicting demands of marmosets during periods of resource scarcity, although their gum-feeding adaptations again seem to represent a significant advantage, in the context of this strategy, in comparison with the tamarins. It appears, in turn, that certain characteristics shared by these platyrrhines represent significant advantages in comparison with *G. senegalensis*. Underpinning these differences is the fact that the former are generally found in environments enjoying much milder climates than that of Harcourt's southern African study site.

Other things being equal, it seems likely that the night-time huddling of the social groups of marmosets and tamarins entails a significant reduction in energy requirements in comparison with *G. senegalensis*, which usually only nest in small groups of two or three individuals [Bearder, 1987; R.D. Martin, pers. comm.]. With their apparent ability to physiologically reduce metabolic expenditure during periods of rest [Morrison & Simões, 1962; Morrison & Middleton, 1967; Hetherington, 1978], marmosets, at least, would be able to redouble this advantage. More work is necessary before the exact nature of this mechanism, and its significance for their foraging strategies, is fully understood. It does seem possible to predict from the results of the present study, however, that a period of approximately 15 hours represents the upper limit for a "roosting strategy", under normal conditions. This conclusion derives from the fact that the length of the study group's average daily activity period was virtually the same in both late dry season samples, despite the very different conditions prevailing in the two years (see chapter 4).

The seasonal patterns in ranging, foraging and resting offer a number of insights into the behavioural strategies followed by both *C. flaviceps* and other marmoset and tamarin species. The maximisation of foraging efficiency and the minimisation of the expenditure of time on foraging and related activities, appear to be the principal goals motivating all such changes observed during the course of the year. A detailed and up-to-date knowledge of the availability and distribution of resources within its home range seems to have been an important determinant of the group's movements and, in turn, of the maximisation of its foraging efficiency in both the short and the long term. An ability to reduce metabolic expenditure during periods of rest, particularly at night, may also have significant implications for the following of time-minimising foraging strategies by marmoset and tamarin groups, especially given the small body size of the animals themselves.

From the opposite viewpoint, we can see that the minimisation of the amount of time spent active each day has important benefits for these small animals, particularly with regard to the avoidance of predation. The cryptic colouration and habits of these primates, their preference for the dense vegetation of secondary and edge habitats and their general alertness to signs of potential predators all indicate that predation pressure has had a significant influence on their evolutionary history (see chapter 1). It is interesting to note here that the typical "scan-and-pounce" technique which dominates the foraging activities of most species may also favour a time-minimising strategy by allowing these primates to reduce the expenditure of time necessary for predator vigilance (see chapter 7). The maximisation of foraging efficiency within a time-minimising framework can, in this context, be seen as the key-stone of the behavioural evolution of the marmosets and tamarins.

Feeding

One feature of the study group's ecology which deserves more detailed attention here is its feeding behaviour. As we have seen, the group's diet was typical of those of other marmoset species, being composed primarily of gum and animal material. Most of the seasonal variation in feeding behaviour appeared to be systematically related both to the overall availability of resources at this site and fluctuations in their abundance through time. Plants bearing edible fruit, for example, are relatively scarce in the secondary forest at this site, but the seasonal peak in their abundance correlated with a considerable increase in the consumption of fruit. The evidence indicates that it was the scarcity of fruit at this site, rather than a preference for gum, which determined its general absence from the group's diet. It seems reasonable to predict that fruit would be a much larger component of the diet of *C.flaviceps* groups at other sites, such as Nova Lombardia (see chapter 1).

While seasonal fluctuations in the abundance and distribution of arthropods appeared to have the major influence on the study group's behaviour and range use over the study period, the temporary abundance of edible fruit and seeds seemed to have a considerable influence in January and February. In general, the patterns observed (table 8.2) are contradictory to the trends accompanying the decline in arthropod abundance (see table 8.1). They do appear to be consistent, however, with those which characterise the differences between this species and *C.h. intermedius*, given the generally much greater importance of fruit in the diet of the latter. This also seems to support the idea that most types of fruit not only offer a more plentiful or concentrated supply of many important nutrients than gums, but also represent

Table 8.2

Influence of the Abundance of Reproductive Plant Parts on the Behaviour of the Study Group

Behavioural variable	Apparent effect of abundance of fruit and seeds[1]
Daily activity period	No effect
Fruit feeding	Marked increase
Foraging:	
As proportion of activity	Decrease
Success/prey feeding	No effect
Prey as proportion of diet	Decrease
Gum feeding:	
As proportion of activity	Decrease
As proportion of diet	Decrease
Ranging:	
Travel as proportion of activity	Decrease
Daily path length	Decrease
Range size	Decrease
Distribution of group movements	Correlated with distribution of plant resources
Daytime resting	Increase
Social activities	Increase

[1] This column shows the apparent deviation in the behavioural variable from the pattern expected according to the overall trends outlined in table 8.1, taking into account factors such as the presence of dependent infants.

a more feasible substitute for animal material (although see below). The diet of the *C.h. intermedius* study group included a far smaller proportion of animal material, on average, than that of the *C.flaviceps* group. Similarly, the diet of the latter during January and February included a much smaller proportion of animal material than "expected", given both the apparent abundance of arthropods at this time and the feeding patterns observed during all other months.

These comparisons allow us to predict that marmoset groups will, in general, reduce their foraging for and feeding on animal material when fruit is abundant. This is again as we might expect, given the suggested time-minimising foraging strategy of these primates. Plant resources, being relatively concentrated and stable in their distribution, are obviously acquired far more easily than animal material (this is particularly the case with regard to the types of plant usually exploited by marmoset groups). In turning to such resources, when available, as a partial substitute for animal material, the *C. flaviceps* study group appeared to have been able to acquire an adequate diet while further reducing its expenditure of time and energy on both foraging and travelling. This appears to confirm previous conclusions on the importance of the abundance and distribution of arthropods for the group's behaviour, given that fruit was generally scarce at this site throughout most of the year. These results also identify a number of the specific variables which must be taken into account in comparing the behavioural ecology of different marmoset and tamarin species, on the one hand, and of populations of the same species at different sites, on the other.

While the systematic exploitation of plant exudates by the marmosets does offer a stable source of nutrients throughout the year, a number of limitations are indicated by the study group's feeding behaviour. The latter, along with the available information on the composition of fruit and gum [Coelho *et al.*, 1976; Hladik, 1977; Bearder & Martin, 1980; Garber, 1984a], indicates that gum is less easily substituted for animal material in the marmoset diet. Similarly, while marmosets may have specialisations of the hind-gut which enable them to digest gum efficiently [Coimbra-Filho *et al.*, 1980], its composition probably places specific restrictions on its exploitation and inclusion in their diets (see chapter 6). The presence of substances, such as tannins and uronic acids, which inhibit digestive processes, may be particularly important [Nash, 1986]. It has also been suggested here that, while the high calcium content of gum may be advantageous as a balance for the high phosphorus content of arthropods, it may have the opposite effect when the arthropod component of the diet is reduced.

While much depends on the assumption that the composition of the group's diet was based on the "rational" exploitation of the available resources, there does seem to be good evidence to support these conclusions. On the one hand, despite the fact that the proportion of gum in the group's diet increased as the consumption of animal material declined, the records show that gum feeding itself did not increase. During the late wet season, when edible fruit was abundant, on the other hand, gum was never absent from its diet. As phosphorus-rich insects were still consumed in large quantities and, as gum appears to contain relatively much larger amounts of calcium than most types of fruit, its continued consumption during the late wet season may be directly related to its mineral-balancing function. Similarly, gum was never absent from the diet of *C.h. intermedius*, which was generally far more frugivorous than *C.flaviceps* [Rylands, 1982].

During the late dry season, when both arthropods and fruit were most scarce, however, the group did not increase its consumption of gum. This appears to indicate that certain components of gum itself constrain its substitution for animal material in the marmoset diet, given that gum was abundant throughout the year. Such constraints may include the presence of substances such as tannins and uronic acids, the high calcium:phosphorus ratio of most gums, and their low protein content. Whether, and to what extent, these factors influenced the observed patterns of gum feeding is difficult to assess, given the lack of information either on the composition of the gums consumed or the nutritional requirements of the marmosets themselves. The patterns of change observed in the composition of the study group's diet during the study period nevertheless correspond well with a "nutrients as constraints" model [Pulliam, 1975; Altmann & Wagner, 1978]. Further information is obviously required, however, before the exact nature of such constraints can be defined.

Seasonal changes recorded in the proportions of gum from the two "major sources" (*Acacia paniculata* and *Anadenanthera peregrina*) in the group's diet also support the idea of the "rational" exploitation of this type of resource, both in the short and the long term. *Anadenanthera* (*angico*) gum was consumed in relatively much larger amounts during the dry season months of 1986, when measurements indicate that softer, more easily-ingested deposits of this type of gum were most abundant. In turning to this newly-produced gum, when available, the group appeared to be reducing the expenditure of time and energy necessary for the acquisition of an adequate supply of this plant material. Similarly, the reduction in its use of *Acacia* gum would presumably ensure continued production of this type of gum in the long term, both at specific sites and within its home range as a whole. These patterns are consistent with those of the systematic exploitation of gum sources reported for other marmoset species [Stevenson & Rylands, in press].

Seasonal patterns in the study group's consumption of animal material were more complex than those recorded in its use of plant resources. Some aspects appeared, in fact, to contradict trends in other features of the group's ecology, such as the availability of arthropods and the lack of variation in foraging techniques. Thus, for example, while the variety and types of arthropods captured by the marmosets did appear to correlate, in general terms, with their abundance, the sizes of the prey captured were apparently inversely related to their availability (chapter 6). The evidence indicates that the group became far less selective, in terms of prey size, as the abundance of arthropods declined. The increase in the capture of immature insects during the dry season, while correlating with the relative increase in their availability, can also be seen as evidence of a reduction in selectivity, given that the foraging techniques used were apparently directed primarily at the capture of mature insects (chapter 7).

This decline in selectivity is, however, consistent with predictions drawn from the "prey model" of feeding behaviour [*e.g.* Schoener, 1971; Maynard Smith, 1974; Pulliam, 1974]. Thus, when arthropods were abundant, large prey items were preferred, even though they constituted a smaller proportion of the total available than at other times. During the periods when prey was scarce, on the other hand, the capture of items of different sizes corresponded far more closely with their relative availability. Selectivity thus declined with the abundance of prey, a pattern recorded for animals as diverse as insects, fish, birds and primates [Werner & Hall, 1974; Charnov, 1976; Snyderman, 1983; Rechten *et al.*, 1983; Harcourt, 1986].

A Broader View

As we have seen, the results of the present study of *C. flaviceps* have not only documented the main features of the behavioural ecology of this species, but have also produced considerable insights into the behavioural strategies of marmoset and tamarin species as a whole. While this does contribute to the information available for comparisons between species, there are at present too few data, particularly for the eastern Brazilian forms, to permit more than tentative conclusions on systematic inter-specific differences to be drawn. The results have nevertheless emphasized the important behavioural and ecological differences which exist between the marmosets and the tamarins, a difference which is based on the gum-feeding adaptations of the former (see also chapter 1). This difference is especially clear when comparisons of their apparent ability to endure periods of scarcity are made.

In general, most aspects of the study group's foraging and feeding behaviour support the idea of both marmosets and tamarins as "colonising" animals, specialised for the exploitation of the resources typically available in secondary and edge habitats. The evidence suggests that the marmosets, with their gum-feeding adaptations, can be seen as being more highly specialised for this colonising rôle than the tamarins. Their ability to ensure a stable supply of nutrients in environments which are frequently characterised by severe seasonal scarcities of resources such as arthropods and fruit has far-reaching implications for many aspects of their ecology, especially when seen in contrast with the tamarins. From an evolutionary perspective, it is interesting to recall, in this context, that marmosets are generally smaller in size than tamarins. Seeing the former as being significantly more specialised for a "colonising", secondary forest niche than the latter might thus be seen as support for the idea of small body size as a secondarily-derived characteristic in the callitrichine lineage (chapter 1).

While much of the study group's behaviour has been seen as reflecting a tendency towards the optimal use of time, space and resources in the short term, certain aspects can also be seen as integral features of longer-term strategies. This appears to apply in particular to the systematic use of gum sources, both by the study group and those of other marmoset species. The apparent postponement of reproduction by *C. flaviceps* groups at FMC during the second, more severe dry season covered by the study also supports this idea. The presence of a pregnant or lactating female and dependent infants in a group greatly increases its total nutritional requirements while usually reducing the overall efficiency of its foraging efforts, in terms of both returns (*i.e.* foraging "success") and the expenditure of time. The delay of births until the onset of the wet season can thus also be seen as a strategy aimed at the optimisation of foraging efficiency during the dry season. The facultative nature of birth seasonality exhibited by the groups at FMC again suggests a form of feedback mechanism determining future behaviour (reproduction) according to present experience. The relevant factor influencing this pattern may be the amount of rainfall during the late wet season, although the abundance of insects may also have been important. In the latter case, foraging success might again function as a determinant of the group's activities, overlapping with other aspects of its behaviour.

An integrating aspect of these strategies at all levels is the relative stability of the marmoset group. This characteristic can again be linked directly to their gum-feeding specialisations, particularly in highly seasonal habitats such as the secondary forest at FMC. Stability entails a number of advantages for the marmoset group, especially when seen in the context of kin selection [Hamilton, 1964; Axelrod & Hamilton, 1981]. Whether or not we invoke such a viewpoint, it seems reasonable to assume that a high degree of familiarity and cohesiveness would make a significant contribution to the foraging efficiency of the group as a whole. Advantages include not only the capture of prey disturbed by other individuals, but also the minimisation of the amount of time spent both travelling and exposed to possible predation. In addition to the benefits of familiarity with other group members, familiarity with the environment may also be important. Marmosets which remain in the same group over a number of years will obviously have a more detailed knowledge of their home range than those which have regularly transferred to new groups.

One obvious aspect of this is the knowledge of the locations of fixed resources such as gum-feeding sites which would again contribute to the minimisation of the necessary travelling time between sites. The evidence presented here on the cognitive abilities of marmosets (*i.e.* the "mental map" and feedback mechanisms) again suggests that the experience of animals which have spent a number of years in the same group will have significant benefits not just for those individuals, but also for the group as a whole. This would be important both in the context of seasonal variation and in that of long-term changes taking place in the secondary forest environment itself. As the forest regenerates, the availability and distribution of resources will undergo marked changes as, for example, plants reach reproductive maturity or patches of dense vegetation become more or less accessible to foraging marmosets. Here again, a detailed and up-to-date knowledge of such changes, and the long-term experience of foraging in the same environment will have considerable benefits for the marmoset group.

It is interesting to note, in this context, that groups may not only be extremely stable in the long term, but may sometimes contain three generations of related individuals. While the breeding female first observed in the *C.h. intermedius* study group was replaced in this rôle by a second female at the beginning of the study, both remained in the group throughout the twelve months of the study, although only the latter reproduced [Rylands, 1982]. The mature male assumed to have been the former's mate also remained in the group as an apparently non-reproductive member. This contrasts significantly with the observed inter-group transfer of parous and possibly even pregnant females recorded for a number of tamarin species [*e.g.* Neyman, 1978; Ramirez, 1984; Terborgh & Goldizen, 1985]. While the evidence is only circumstantial, it seems reasonable to postulate that the male Go was also a post-reproductive member of the *C. flaviceps* study group. While he did appear to be older than all other group members, he was never observed consorting or attempting to mate with the reproductive female BM, unlike the other adult males Si and Bo.

As both the *C. flaviceps* and *C.h. intermedius* study groups were relatively large, it seems unlikely that the presence of these individuals would have had any major benefits with regard to the carrying of infants. What does seem likely, on the other hand, is that both their detailed knowledge of the established home range and their foraging experience have a number of advantages for the group, and in particular the maximisation of its foraging efficiency. In broad terms, such individuals may not only guide group movements more efficiently with regard to the distribution of resources, but may also be the best judges of important variables such as "patch residence time" [Charnov, 1976]. At a different level, such older individuals also appear to be generally more adept at the capture of prey, which, given the typical food sharing behaviour observed [Ferrari, in press], would have the effect of reducing the necessary time spent foraging each day by the group as a whole. Qualitatively, Go did not only appear to be one of the most efficient predators, but was also usually the least reluctant to share food with infants. This may also be reinforced by the high degree of relatedness between individuals which appears to be a feature of marmoset groups, again a function of their long-term stability.

Here again, it appears that there are important differences between the marmosets and the tamarins. The relative stability of groups of the former entails a number of benefits which can be seen as translating ultimately into relatively more efficient foraging behaviour, particularly in terms of the time-minimising strategies proposed as a universal feature of callitrichine ecology. The gum-feeding adaptations of the marmosets can thus again be seen as a fundamental feature not only of their ecology, but also of their evolutionary history.

Much of the discussion in this chapter has focussed on the group as the principal foraging unit. This is mainly a function of the fact that the data collection concentrated on the estimation of the activity levels of the group as a whole rather than on the behaviour of specific individuals (see chapter 2). While this may be somewhat erroneous, especially if we accept that certain individuals may not forage optimally at all times [*e.g.* Post, 1984], there seem to be a number of good reasons for accepting the idea that the marmoset social group functions as a cohesive whole, and that its foraging efficiency is closely related both to its stability and that cohesiveness. While this does seem to be a reasonable conclusion from the available evidence on two groups of *C. flaviceps* and *C.h. intermedius*, much more information is needed before the wider implications of these findings can be fully understood. A number of useful criteria for the comparison of the marmosets with the tamarins have, however, been identified.

In general, the analysis of the results of the present study has shown that most aspects of the foraging behaviour of the *C. flaviceps* study group correspond with predictions drawn from optimality models, given both the small size of these primates and the assumption that the main emphasis of the strategies followed was the minimisation of the necessary expenditure of time for the acquisition of an adequate diet. There appears to be good evidence that the efficiency of these strategies was directly related to the cognitive abilities and behavioural flexibility of the marmosets themselves, given the availability and distribution of resources, in both the short and the long term. Whether or not we can see the behaviour patterns recorded as being the "optimal" strategies, however, is one question which must remain unanswered at the present time. Far more information on the ecology, behaviour and physiology of all marmoset and tamarin species, especially those under threat from extinction, is necessary for the detailed development of this discussion of their ecological adaptations and evolution.

Chapter 8

Summary

The results of the field study of *Callithrix flaviceps* are reviewed and general conclusions are drawn. A number of comparisons with other marmoset and tamarin species are outlined. Most features of the behavioural ecology of this species were similar to those recorded for other marmosets, and contrasts appear to have been due more to environmental factors than interspecific behavioural differences. The seasonal patterns observed in most aspects of the group's behaviour were also systematically related to fluctuations in the abundance and distribution of resources. Most trends appear to uphold predictions drawn from optimality models, and the results of this study generally support the use of the OFT viewpoint for the analysis of marmoset behavioural ecology.

1. Characteristics of the study group's behaviour which were typical of other marmoset species include:
    - (a) Short daily activity period
    - (b) Small proportion of time foraging/travelling each day
    - (c) Large proportion of time resting/socialising each day
    - (d) Relatively long distances travelled each day
    - (e) "Scan-and-pounce" foraging behaviour
    - (f) Plant exudates as a major component of the diet
    - (g) Apparent preferences for:
        - dense vegetation
        - secondary/edge habitats
        - low canopy levels
        - large arthropod prey, especially orthopterans
        - "piecemeal" plant resources
    - (h) Group stability
2. Characteristics of the study group's behaviour which were apparently atypical include:
    - (a) Large home range and degree of overlap
    - (b) Lack of territoriality
    - (c) Large proportion of the gum consumed derived from non-marmoset damage to plants

  - (d) Large numbers of vertebrates captured during foraging
  - (e) Seed predation

3. Patterns which correlated with the decline in arthropod abundance and appear to support predictions derived from optimality models:
  - (a) Increase in time spent foraging/travelling each day
  - (b) Decrease in daily activity period (*N.B.* assuming metabolic adaptation)
  - (c) Decrease in prey selectivity

4. Patterns which support the view of marmosets as "time-minimising" foragers:
  - (a) Short daily activity period/activity patterns
  - (b) Preference for large prey
  - (c) Partial substitution of animal material with fruit, when available
  - (d) Concentrated use of plant resources
  - (e) Preferential use of angico gum when soft deposits abundant
  - (e) Relationship between range use and distribution of arthropod prey

5. The group's consumption of gum indicates that its calcium content is important as a balance for the relatively high phosphorus content of the animal material consumed, even when fruit is available. This, and other components of gum may, on the other hand, inhibit its use as a substitute for animal material when other resources are scarce. The observed patterns are consistent with a "nutrients as constraints" model.

6. A number of features of the group's ranging behaviour indicate both that a "mental map" guides its movements and that the monitoring of the distribution of resources is an important determinant of its range use. There also appears to be a systematic feedback mechanism relating the group's present experience to its subsequent behaviour.

7. Longer-term strategies appear to underlie these other features of the group's behaviour, such as its systematic use of *angico* gum and the delay of reproduction during a relatively harsh dry season. The relative stability of marmoset groups may also be beneficial in terms of overall foraging strategies.

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Appendix I

The Identification of Tree Species Found in the Phenology Quadrats

A tropical forest environment, such as that found at FMC, typically contains a number of hundred tree species, presenting a major problem for their classification. Samples of the reproductive structures of most species are required for identification. In some cases, leaves, flowers and fruit are all necessary for the differentiation of closely-related species. As well as a characteristic variety of species, the structure of the forest at the Jaó study site presented its own problems for the identification of tree species.

As an area of relatively young secondary growth, many trees have not yet reached reproductive age, which obviously implies that the collection of reproductive parts is impossible. Another problem is the dense vegetation which restricts access to tree crowns in many places and makes the collection of samples virtually impossible without major alterations to the vegetation. Such alterations were avoided, given that they may have had some adverse influence on the behavioural observations. One further problem was the fact that many of the trees were deciduous, prohibiting the collection of leaves at the end of the study, which coincided with the late dry season. Leaves were nevertheless collected from all other marked trees which had not reproduced during the course of the study.

Despite these disadvantages, there are at least two factors which facilitate the identification of tree species at this site. The first is the fact that the flora at FMC has been studied in detail over the past five years [Hatton *et al.*, 1983; Strier, 1986; Moreira de Andrade & Lopes, 1987]. The species most frequently encountered are thus both well-known and easily-identified from the reference collection in the herbarium of the Department of Botany at the Universidade Federal de Minas Gerais (U.F.M.G.), Belo Horizonte. The second is again, equivocally, the structure of secondary forest itself. There are not only typically fewer species in a given sample than in undisturbed forest, but these species tend to be densely concentrated. Trees can thus frequently be identified through their obvious similarity with their neighbours.

From samples collected and prepared by the author, M.A. Lopes Ferrari and J. Gomes, the identification to at least familial level was thus possible for 997 of the marked trees in the phenology quadrats (table I). It was also possible, from observations at the study site and careful comparisons of the samples collected, to identify many individuals of species which were not classified formally. These anonymous species are represented in table I by the FMC serial number of the first individual encountered (the "type specimen"). 126 distinct species have thus been recognised in the quadrats. While a small proportion (14.3%) of the marked trees remains unclassified, either formally or informally, it seems likely that many were members of the other species recorded, given the problems with the collection of samples outlined above.

The FMC collection in the herbarium of the Department of Botany, U.F.M.G. was referred to for the identification of all botanical samples, from both the phenology quadrats and the plants exploited for their resources by the study group (see table 6.2 and appendix V). The classification of all samples was undertaken by M.A. Lopes Ferrari with the assistance of P. Moreira de Andrade. All samples have been deposited in the herbarium at U.F.M.G.

Table I

The Numbers of Trees of Different Species Found in the Phenology Quadrats and Their Reproductive Status

Tree species	Number of trees in phenology quadrats	Number of trees recorded bearing fruit
Anacardiaceae:		
Mangifera indica[1]	1	0
Annonaceae:		
Guatteria sp.	5	2
Rollinia sp.	4	3
Apocynaceae:		
Tabernamontana sp.	9	4
Aquifoliaceae:		
Ilex sp.	1	0
Araliaceae:		
5252	1	0
Bignoniaceae:		
Tabebuia sp.	8	0
Bombacaceae:		
Pseudobombax sp.	5	0
5934	3	0
Clusiaceae:		
5347	3	0
Elaeocarpaceae:		
Sloanea aunifolia	1	1
Euphorbiaceae:		
Alchornea sp.	2	0
Croton sp.	1	0
Croton sp.	1	0
Flacourtiaceae:		
Banara kuhlmannii	1	0
Carpotroche brasiliensis	125	21
Casearia mariquitensis	64	16
Casearia sylvestris	9	7
Casearia ulmifolia	2	1
Lauraceae:		
Endlicheria sp.	8	4
Nectandra rigida	2	0
5151	1	0
6013	1	0
6040	1	0
6206	1	0
6565a	1	0
Lecythidaceae:		
Eschweilera sp.	22	0

[1] Exotic species.

Table I (contd.)

Tree species	Number of trees in phenology quadrats	Number of trees recorded bearing fruit
Leguminosae (Caesalpinoidea):		
Apuleia leiocarpa	46	1
Hymnea sp.	2	0
Melanoxylon braunia	1	0
Leguminosae (Faboidea):		
Dalbergia nigra	11	0
Dalbergia sp.	1	0
Platycyamus regnelli	10	0
Leguminosae (Mimosoidea):		
Albizia polycephala	13	2
Anadenanthera peregrina	24	9
Inga sp.	1	0
Inga sp.	1	0
Piptadenia gonoacantha	5	0
Platymenia foliolosa	1	0
Leguminosae:		
5215	3	0
5364	18	0
5433	1	0
5556	2	0
5609	7	3
5737	4	0
5740	6	0
5996	2	0
6060	9	0
6520	2	0
6631	1	0
Meliaceae:		
Guarea guidonia	56	12
Trichilia pallida	119	22
Monimiaceae		
Mollinedia sp.	11	5
Siparuna sp.	74	52
Moraceae:		
Acanthinophyllum ilicifolia	11	2
Cecropia sp.	2	0
Sorocea guilleminiana	8	0
5222	7	0
5321	30	0
5891	4	0
Myrtaceae:		
5278a	1	0
5698	1	0
5926a	1	0
6580	1	0

Table I (contd.)

Tree species	Number of trees in phenology quadrats	Number of trees recorded bearing fruit
Palmae (Arecaceae):		
Astrocaryum aculleatissimum	14	0
5693	8	4
5699	21	0
Piperaceae:		
Piper amalago	4	4
Piper arboreum	2	0
Piper sp.	1	0
Rubiaceae:		
Alseis sp.	18	3
Coussarea sp.	3	1
Genipa americana	4	1
5248	1	0
5506a	2	0
5644	1	0
6066	1	0
6146	1	1
Rutaceae:		
Galipea jasminiflora	7	5
Zanthoxylum sp.	3	0
Sapindaceae:		
Allophyllus sp.	67	21
Toulicia aff. *reticulata*	17	12
Sapotaceae:		
5586	3	0
Solanaceae:		
Solanum sp.	1	0
5549	2	0
5970	2	0
Tiliaceae:		
Luhea sp.	13	2
Ulmaceae:		
Trema micrantha	1	1
Total identified to famliy:	977	222
% of marked trees:	75.5	16.7
Family unidentified:		
5110	2	0
5115	28	0
5116	2	0
5132	5	0
5134	2	0
5141	29	0

Table I (contd.)

Tree species	Number of trees in phenology quadrats	Number of trees recorded bearing fruit
Family unidentified:		
5146	7	0
5166	1	0
5167	2	0
5186	4	0
5213	7	0
5214	5	0
5229	1	0
5241	1	0
5259	25	0
5276	4	0
5304	2	0
5313	3	0
5343	1	0
5398	1	0
5531	3	0
5562	1	0
5585	1	0
5599	4	0
5601	3	0
5708	1	0
5816	5	0
5917	1	0
5921	2	0
6026	2	0
6064	1	0
6147	1	0
6154	1	0
6194	1	0
6564	1	0
6593	1	0
6624a	1	0
Total family unidentified:	162	0
% of marked trees:	12.2	0
Total categorised:	1139	
% of marked trees:	85.7	
Total uncategorised:	190	
% of marked trees:	14.3	

Species identified to family: 89
"Anonymous species": 27
Total species recognised: 126

Appendix II

Social Behaviour Sub-Categories Used in Scan Sample Records

While comprehensive records were made of the study group's social behaviour, they are not analysed in detail in this thesis. A study of these records is currently in preparation, however. Most categories of social behaviour used in the study are similar to those developed in other studies of marmosets, particularly *Callithrix jacchus*, and are more or less self-explanatory. More detailed descriptions are given in table II, where necessary.

Table II

Social Behaviour Sub-Categories Used in Scan Sampling

Category (notation)	Activity of animal at first sighting
Aggressive behaviours:	
Arch-back-walk (ABW)	Strutting with arched back, normally pilo-erected
Attack (ATT)	Attacking other individual(s) without physical contact
Bite (BI)	Biting second individual
Chase (CHA)	Aggressively chasing other individual(s)
Fight (FI)	Attacking other individual(s) with physical contact
Hit (HIT)	Hitting second individual
Threat (THR)	Threatening other individual(s), either by posture or facial expression
Non-aggressive behaviours:	
Approach (APR)	Approaching other individual(s)
Be groomed (BGM)	Being groomed by one or more individuals
"Box" (BOX)	Greeting second individual by standing on hindlimbs and pushing against it with the forelimbs
Follow (FLW)	Following other individual(s) in line
Groom (GM)	Grooming a second individual
Huddle (HD)	Coming into physical contact with other individual(s), usually in sitting beside them
Ignore (IGN)	Moving or looking away from individual attempting to initiate social interaction (usually grooming)
In huddle (IN HD)	In seated, physical contact with other individual(s)
Invite groom (INV)	Taking up a posture in order to stimulate grooming by a second individual
Proximity (PX)	Coming into close proximity with other individual(s)
Play (PL):	
Chase (PL CHA)	Rapidly chasing other individual(s) in play sequence
Hide-and-Seek (PL H+S)	Avoiding other individual(s) in play sequence
Wrestle (PL WRS)	Playfully wrestling other individual(s)[1]

[1] Wrestling was frequently recorded with open-mouthed facial expressions

Appendix III

Analysis of the Use of Forest Strata and Supports by the Study Group and Comparisons with Callithrix humeralifer intermedius

Most callitrichid species appear to prefer relatively low levels in the forest, especially in comparison with other neotropical primates. The low levels used by the *Callithrix flaviceps* study group appeared, however, to be exceptional. The group did, in fact, spend more than two-thirds of its time (66.97%) at or below 5 m above the ground (table III.i). It seems that only *Callimico goeldii* may use these lowest strata to such an extent [Pook & Pook, 1982]. Whether, and to what extent this situation is a function of the forest structure at Jaó is not clear at this stage, but the records indicate that this preference applied almost equally to all activities. Foraging did take place at the very lowest levels more than travelling and resting, as we might expect, given the foraging behaviour of these primates (see chapter 7), but the small amount of difference which is apparent between most activities does not seem to indicate any major contrasts in the use of forest strata for different activities. The records of feeding on plant material exhibit the most interesting pattern, which this activity being recorded more frequently than the others at both the lowest and the highest levels. This is discussed in more detail below.

Table III.i

The Time Spent by the C. flaviceps *Study Group at Different Levels, According to Activity*

	Percentage of the total scan sample records of:					
Height (m)	Travelling	Foraging	Feeding on animal material	Feeding on plant material	Resting	All behaviours
0-1	4.79	14.46	7.56	23.06	7.53	11.01
2-3	35.57	35.47	37.64	27.47	42.28	34.37
4-5	23.26	20.18	25.81	19.74	21.74	21.59
6-9	23.49	20.96	21.65	15.91	19.51	21.75
10-15	9.05	6.86	6.32	8.31	6.69	7.99
≥16	3.84	2.12	1.03	5.51	2.25	3.29

While the *Callithrix humeralifer intermedius* study group used much higher levels overall than *C. flaviceps* (table III.ii), the tendency to forage at relatively low levels is similar. Please note that, while this table excludes records of activity above 20 m, this category formed a very small proportion of the total (apparently *ca.* 3%) and does not appear to have an important influence on the comparisons made here. Rylands reports that the group spent approximately 56% of its time at heights between 8 and 15 m [1982].

Table III.ii

The Estimated Time Spent by the C.h. intermedius *Study Group at Different Levels below 20 m, According to Activity*[1]

Height (m)	Locomotion	Foraging	Feeding on plant material	Rest/social activities	Total
	Percentage of the total scan sample records of:				
0-1	1.82	4.99	-	1.68	2.40
2-3	4.97	6.65	0.70	2.67	4.31
4-5	7.41	10.35	4.24	3.96	7.14
6-9	28.45	30.17	16.61	25.58	26.34
10-15	41.71	37.70	49.38	52.22	43.55
16-19	15.64	10.14	29.07	13.88	16.25

[1] Values derived from Rylands, 1982: table 23a. The records are a combined total from three wet season and three dry season months.

The most obvious feature of these data is the tendency to use relatively high levels in the forest when feeding on plant material. There thus appears to be a clear differentiation between the levels used for foraging and plant feeding by this group which seems to reflect both the distribution of resources and the foraging strategies of the marmosets themselves. This also contrasts with the behaviour of the *C. flaviceps* group which, if anything, appeared to feed on plant material at lower levels than those at which it foraged, although it did also spend almost twice as much of its plant-feeding time at levels above 10 m than it did foraging.

A closer analysis of the data from the present study reveals that the contrasts between the two species probably indicate differences in the structure of the forest at the sites at which they were studied rather than in their ecological adaptations. The habitat utlised by *C.h. intermedius* at Aripuanã is more mature and less disturbed, in general, than that available at Jaó, and the equivalent strata at the two sites appear to be at very different heights above the ground (see chapter 4). Other things being equal, we can assume that a preference for foraging in the lowest forest strata at the two sites will be reflected in the use of different heights above the ground.

Another important influence seems to be the differences in the available plant resources at the two sites. The *C. flaviceps* group's intensive use of the gum of *Acacia paniculata* accounts for much of the plant-feeding activity recorded at levels of 3 m or less (table III.iii). While fruit feeding generally took place at higher levels than this, the two species (*Allophyllus* sp. and *Siparuna* sp.) which provided the bulk of the records were small trees typically no more than 8 m in height. This is also reflected in table III.iii. The exception to this general pattern was the group's use of *angico* (*Anadenanthera peregrina*) gum. In its opportunistic use of this gum, the group was generally feeding on the trunks of relatively large trees, at much higher levels. These contrasts, as we shall see, are also reflected in its use of supports of different diameters.

Table III.iii

Levels Used by the C. flaviceps *Study Group during Feeding on Plant Material*

	Percentage of the scan sample records of feeding on:			
Height (m)	*Acacia paniculata* gum	*Anadenanthera peregrina* gum	Gum from other sources	Fruit, nectar and seeds
0-1	39.01	5.18	9.23	2.57
2-3	32.59	19.85	33.85	21.97
4-5	13.64	17.98	15.90	40.71
6-9	8.96	21.72	23.59	27.33
10-15	4.36	17.29	17.44	6.32
≥16	1.44	17.98	0.00	1.10

According to the feeding behaviour of the *C.h. intermedius* study group, edible fruit was apparently far more abundant at Aripuanã than at Jaó. This may have had a number of influences on the levels used by this group, the most obvious being that it would probably have been feeding on fruit at higher levels in much larger trees, in general. There are further aspects of this situation which are of interest. One is the ability of the marmosets to systematically exploit gum sources through their gouging which would allow them, in theory, to coordinate gum feeding with their other activities. This may apply to the use of *Acacia* gum by *C. flaviceps*. As most of the larger *Acacia* lianas used by the group reached relatively high levels in the canopy, it seems possible that the consistent use of feeding sites at very low levels is directly related to its other activities, notably foraging. In this case, the higher levels recorded for feeding on fruit and, in this context, *angico* gum reflect their more opportunistic exploitation.

Conversely, the relative abundance of fruit at Aripuanã may itself have had an influence on the foraging activities of the *C.h. intermedius* group. As both study groups appeared to forage for and feed on animal material less when fruit was more available, it is argued in chapter 6 that fruit may partially substitute animal material in their diets, when available. The exploitation of fruit in relatively tall trees at Aripuanã would have conflicted with the use of low levels for foraging by the *C.h. intermedius* group. In this situation, the expenditure of time and energy necessary for moving between fruit-feeding sites and optimal insect-foraging habitat may be prohibitive. The group may thus have been following a strategy of foraging at higher levels in the forest where the lower returns to foraging effort would be more than compensated for by the access to fruit.

While the contrasts between these data are interesting enough in themselves, their importance to the present study is principally that of their influence on observational bias. The heights at which most arboreal primates are active are seen as inhibiting the visibility of many activities, especially those involving little or no movement (see chapter 2). It thus seems very likely that the considerable difference in the heights at which the groups were active is the major factor determining the difference in the numbers of records collected in the two studies (table III.iv), given that the sampling schedules used were the same

Table III.iv

A Comparison of the Numbers of Behavioural Records Collected in Scan Samples during the Field Studies of C. flaviceps *and* C.h. intermedius

	Study of:	
Variable	*C. flaviceps*	*C.h. intermedius*
Observation days:	125	115
Total number of scan samples:	14435	14064[1]
Total number of behavioural records collected in scan sample:	70786	38841
Average number of individuals in study group[2]:	13.12	12.42
Mean number of records collected per scan samples:	4.90	2.76
Mean number of records collected per individual per observation day:	43.16	28.33

[1] Calculated from the number of observation hours.

[2] Number of independently-locomoting individuals in the group, calculated from group composition per month.

(see chapter 2). While it can be argued that other factors, such as differences in the density of the vegetation at the two sites, may also have had an important influence on the contrast between the studies, it does seem likely, from this evidence, that height was the major factor.

Table III.iv shows that, while the *C. flaviceps* study group was only 5.6% larger than the *C.h. intermedius* group, on average, 77.5% more records were collected in scan samples. Similarly, 52.4% more records were collected per individual in the study of the former species, although this figure is less reliable as data on the number of individuals present in the *C.h. intermedius* study group per observation day are not available in Rylands' thesis. Please note that the apparent discrepancy between the two studies in the number of samples carried out per observation day is due to differences in the lengths of the daily activity period of the two groups.

The reliability of the observations carried out on *C. flaviceps* is further confirmed by an analysis of the numbers of records collected during different months (table III.v) and during the course of the day (table III.vi). Rylands [1982] found that the numbers of records collected each month increased during the course of his study, and suggested that this was a function of the increasing habituation of group members. The data from the present study indicate, on the other hand, that there was no such trend during the course of the year, and again emphasize the reliability of the behavioural data for inter-seasonal comparisons.

Table III.v

Monthly Variation in the Number of Behavioural Records Collected during Scan Samples in the C. flaviceps *Study*

Month	Mean number of individuals present per day[1]	Total number of scan samples	Total number of records	Records collected per scan sample	Records collected per individual per day
August 1985	11.0	847	4421	5.22	40.19
September	13.0	997	4740	4.75	40.51
October	13.0	1242	6095	4.91	46.88
November	13.0	1298	6129	4.72	47.15
December 1985	13.0	1005	4851	4.83	46.64
January 1986	13.0	1239	6192	5.00	47.63
February	15.0	1211	6374	5.26	42.49
March	15.0	1218	6301	5.17	42.01
April	15.0	1172	5953	5.08	39.69
May	15.0	1158	5737	4.95	38.25
June	12.5	1061	5370	5.06	42.96
July	11.0	1098	4786	4.36	43.51
August 1986	11.0	889	3837	4.32	43.60

[1] Mean number of independently-locomoting individuals calculated per observation day.

Table III.vi

Daily Variation in the Numbers of Records Collected in All Scan Samples Carried Out during the C. flaviceps *Study*

Time	Total number of behavioural records collected during scan samples
04:00	6
05:00	1892
06:00	6350
07:00	6981
08:00	7025
09:00	7282
10:00	7282
11:00	7233
12:00	7390
13:00	7182
14:00	7130
15:00	4565
16:00	468

Table III.vi similarly shows that there was very little difference in the numbers of records collected in scans during the course of the day. Please note that only the values for observations carried out between 08:00 and 14:00 are directly comparable because of incomplete sampling hours at the beginning and end of the day during different seasons.

The relative similarity in the use of forest levels during different activities by the *C. flaviceps* study group is reflected in its use of supports of different sizes, as might be expected (table III.vii). Supports of 3 cm or less in diameter were used with almost equal frequency for all types of activity, although travel, foraging and feeding on animal material generally took place on slightly smaller supports than resting and feeding on plant material. The use of larger supports during rest is as would be expected, given the observed preference of the marmosets for more substantial supports during prolonged rest periods and activities such as grooming. While thin supports were used very frequently, feeding on plant material is again exceptional in the use of relatively thick supports, with 16.5% taking place on supports greater than 10 cm in diameter. This contrasts considerably with other activities, for which supports of this size were used in between 2.6% and 6.8% of the records.

Table III.vii

The Time Spent by the C. flaviceps *Study Group on Supports of Different Sizes, According to Activity*

Diameter of support (cm)	Percentage of the total records of: Travelling	Foraging	Feeding on animal material	Feeding on plant material	Resting	All behaviours
Ground[1]	1.23	2.12	3.75	5.90	0.49	2.95
0-1	68.56	64.23	62.57	45.02	47.01	56.07
2-3	16.43	16.60	21.88	21.11	27.95	20.18
4-5	4.35	5.32	4.67	6.30	9.32	6.51
6-10	4.60	5.47	4.56	5.19	8.44	6.40
11-20	3.46	4.70	2.25	8.26	5.39	5.47
>21	1.37	1.58	0.32	8.22	1.40	2.42

[1] When no support was used.

A closer analysis of the plant-feeding data (table III.viii) shows that this situation again derives from the contrast between feeding on *Acacia* gum and fruit, on the one hand, and the remaining types of gum, on the other. While some feeding inevitably took place on supports other than the plant from which the material was derived, the patterns correspond well with qualitative observations of the group's behaviour. As the diameter of *Acacia paniculata* stems rarely exceeds 10 cm, the use of thin supports when feeding on its gum would be expected. The frequent use of the ground during feeding on *Acacia* gum also corresponds with the observed behaviour of the marmosets. Similarly, the almost invariable use of the thinnest supports during fruit feeding corresponds with the acquisition of these resources on the relatively thin branches of small trees such as *Allophyllus* and *Siparuna*. The use of relatively much thicker supports during feeding on other types of gum obviously corresponds with the opportunistic use of sources, particularly of *angico* gum on the trunks of relatively large trees.

Table III.viii

Diameters of Supports Used by the C. flaviceps *Study Group during Feeding on Plant Material*

Diameter of support (cm)	Percentage of the records of feeding on: *Acacia paniculata* gum	*Anadenanthera peregrina* gum	Gum from other sources	Fruit, nectar and seeds
Ground[1]	9.93	1.22	0.51	0.66
0-1	43.19	14.69	30.26	92.73
2-3	30.37	12.30	22.56	4.48
4-5	8.16	5.79	9.74	0.88
6-10	4.56	9.35	11.28	0.74
11-20	3.03	24.88	20.51	0.37
>21	0.75	31.78	5.13	0.15

[1] When no support was used.

Appendix IV

Methods Used for the Analysis of the Spatial Distribution of the Study Group's Activities

A relatively simple, but apparently effective method was chosen for the analysis of the distribution of both the study group's movements and its most important activities. The "main body" of the group's home range was defined as the area to the east of the Valley Track (VT, see figure 3.1), which exhibits a uniform downward slope from west to east, from VT itself to the bank of the river Manhuaçú. The decision to exclude the area to the west of VT was based on the fact that it was both used only very rarely by the group and does not form a uniform east'west slope. All the quadrats (those used for the analysis of ranging, see figure 5.1) in this area were marked, and those with an area of less than 2500 m^2, *i.e.* those which are not 50 m x 50 m, were excluded. All the quadrats excluded from the analysis are shaded in figure IV.i. This leaves an area of 27.5 ha containing 110 quadrats of equal size.

For the analysis of the group's use of this area, a north-south line was drawn through the quadrats, bisecting them (figure IV.ii). The quadrats in any one east-west line, *i.e.* the numbered co-ordinates, were thus equally divided between east and west, forming the "riverbank" and "hillside" quadrats, respectively. As the east-west dimension of the range was not the same in different areas, this did not systematically divide the quadrats according to their elevation, but they are separated according to their distance from the river and, presumably, their relative humidity. A more detailed analysis might, in fact, take altitude into account, although other variables, such as the presence of neighbouring groups or local habitat differences, may not only be equally influential but are far less easily assessed. While the methods may thus not present an accurate picture of the influence of these variables on the group's range use, it was felt that they were adequate for comparisons between seasons, given the information available. It is nevertheless felt that the analysis may, in fact, have under-estimated the degree of the overall trend towards the use of the forest at lower, more humid elevations with decreasing arthropod abundance.

Please note that the occupation and behavioural records deriving from quadrats which were bisected by the line (*e.g.* quadrat H03) were divided equally between the hillside and riverbank samples. This accounts for the half-quadrat values in table 5.1. It was felt that the choice between this and excluding these values altogether was somewhat arbitrary, especially given the relative simplicity of the methods used. While it might be argued that the inclusion of these values would tend to have reduced the degree of difference between the hillside and riverbank samples, their exclusion would almost certainly have the opposite effect of over-estimating this contrast. Given that these quadrats constitute a small proportion (10%) of the total, it seems likely that the overall effect on the analysis was small.

Appendix IV

Figure IV.i

Quadrats Excluded from the Analysis of the Distribution of the Group's Ranging

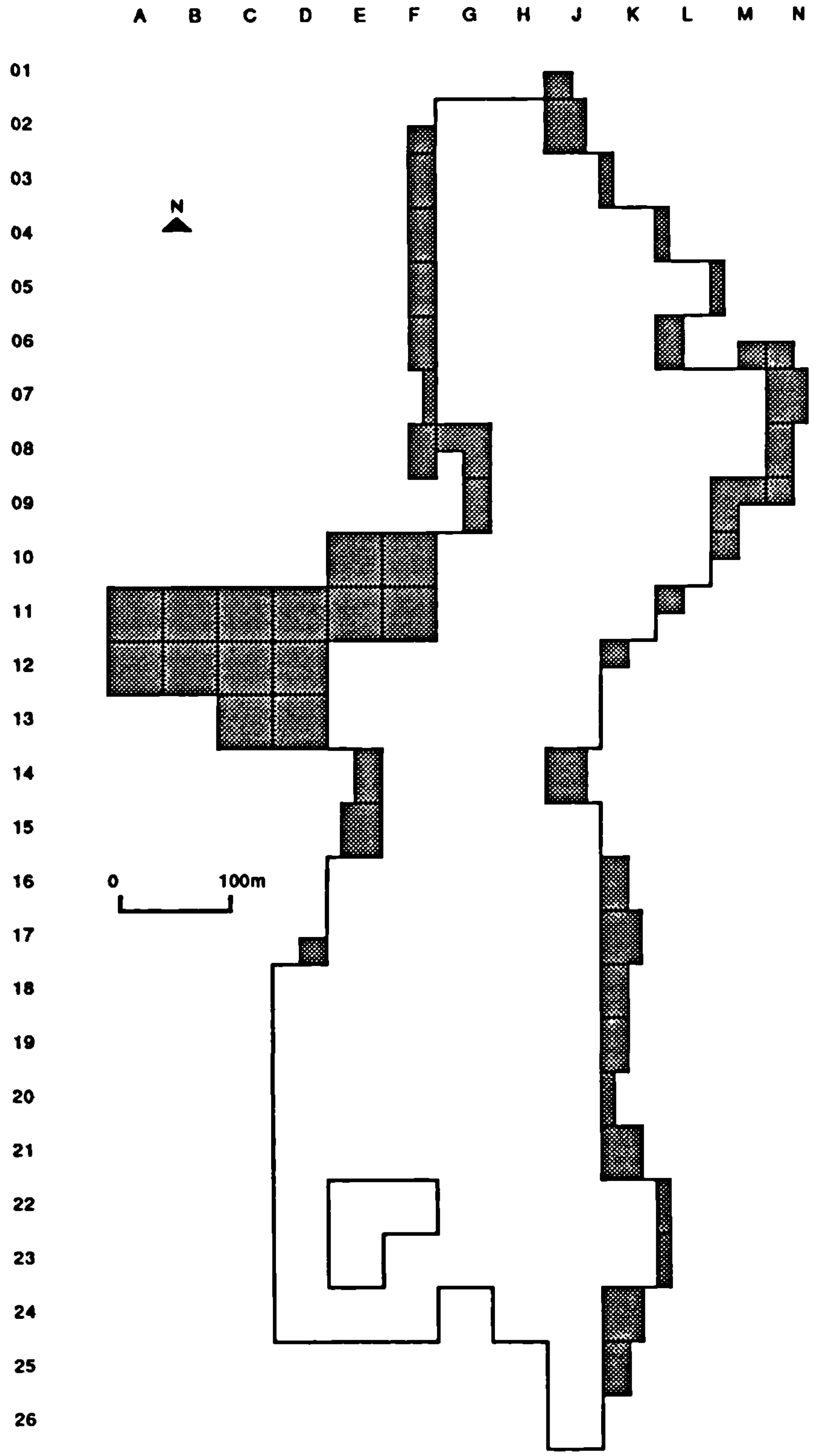
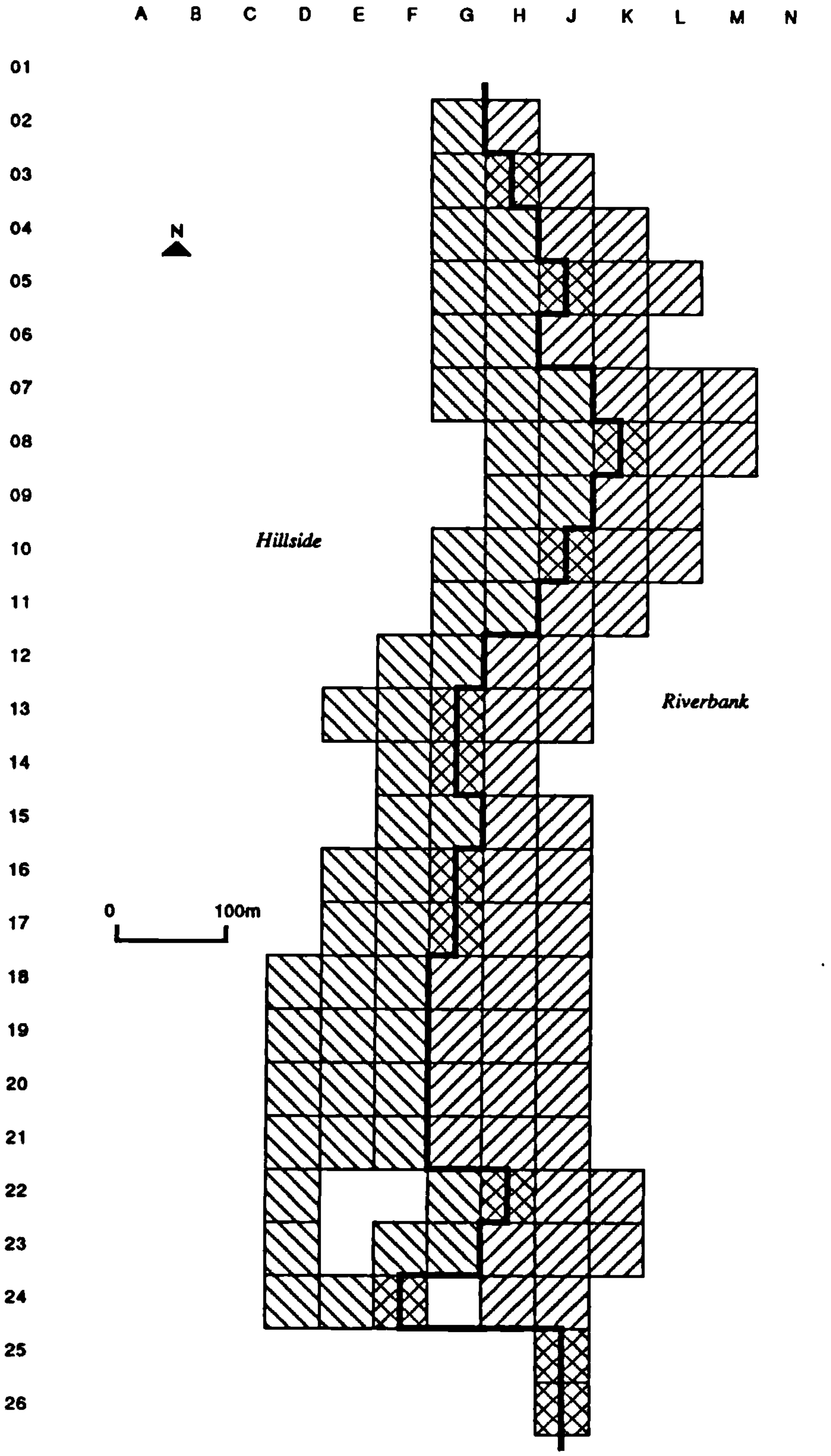


Figure IV.ii

Division of "Hillside" and "Riverbank" Quadrats



Appendix V

Gum Sources Utilised by the Study Group and Other Marmoset Species

Marmosets exploit the exudate of a wide range of plant species belonging to at least 25 different families, although the most commonly reported source appears to be the Leguminosae. This was especially the case for the *C. flaviceps* study group, which fed almost exclusively on the exudate of legumes, although plants belonging to other families were also used (table V.i). For reference and comparisons, the sources of exudate used by other marmoset species are given in tables V.ii to V.vi.

Table V.i

Plant Species Utilised for their Exudate by the Callithrix flaviceps *Study Group*

Family	Species	Number of scan sample records attributed to this species	Habitus
Elaeocarpaceae:	*Sloanea stipitata*	4	Tree
Euphorbiaceae:	*Croton* sp.	1	Tree
Leguminosae:			
(Faboidae)	*Dalbergia nigra*	3	Tree
	Dalbergia sp.	3	Tree
(Mimosoidae)	*Acacia paniculata*	4118	Liana
	Anadenanthera peregrina	1889	Tree
	Inga sp.	5	Tree
	Piptadenia gonocanthus	12	Tree
	Unidentified spp.[1]	30	
Nyctaginaceae:	*Bougainvillea spectabilis*	3	Liana
Rubiaceae:	*Alseis* sp.	47	Tree
Rutaceae:	*Zanthoxylum* sp.	1	Tree
Unidentified spp.		38	
Source unknown		48	

[1] Includes an estimated minimum of 3 different species.

Table V.ii

Gum Sources Used by Callithrix humeralifer intermedius *at Aripuanã, Mato Grosso*[1]

Family	Species
Anacardiaceae:	*Anacardium giganteum*
	Tapirira guianensis
	Tapirira sp.
	Spondias lutea
Apocinaceae:	*Forsteronia* sp.
Araliaceae:	*Didimopanax* sp.
Combretaceae:	*Combretum* spp. (2 species)
Dilleniaceae:	*Doliocarpus brevipedicellatus*
	Doliocarpus dentatus
Elaeocarpaceae:	*Sloanea* sp.
Meliaceae:	*Guarea* sp.
	Trichilia guianensis
	Unidentified sp.
Lacistemaceae:	*Lacistema* sp.
Leguminosae (Caes.):	*Swartzia* sp.
(Fab.):	*Diplotropis purpurea*
	Diplotropis sp.
	Hymenolobium sp.
	Unidentified sp.
(Mim.):	*Acacia paniculata*
	Acacia sp.
	Enterolobium maximum
	Enterolobium schomburgki
	Imga thibaudiana
	Inga sp.
	Parkia oppositofolia
	Parkia pendula
	Unidentified sp.
Rutaceae:	*Spathelia excelsa*
	Zanthoxylon sp.
Simarubaceae:	*Simaba* sp.
Sterculiaceae:	*Sterculia stipulifera*

[1] Data from: Rylands, 1982, table 29.

Table V.iii

Gum Sources Used by the Callithrix penicillata kuhlii *Study Group at Una, Bahia*[1]

Family	Species
Elaeocarpaceae:	*Sloanea* sp.
Flacourtiaceae:	Unidentified sp.
Leguminosae: (Mimosoidea)	*Inga* sp. *Parkia pendula*
Sapindaceae:	Unidentified sp.
Sapotaceae:	*Cupania* sp. Unidentified sp.

[1] Data from: Rylands, 1982, table 70.

Table V.iv

Gum Sources Used by Callithrix penicillata penicillata *in Brasília, D.F.*[1]

Family	Species
Anacardiaceae:	*Tapirira guianensis*
Araliaceae:	*Didymopanax macrocarpum*
Leguminosae:	*Sclerobium paniculatum*
Vochysiaceae:	*Calistene major* *Qualea grandiflora* *Qualea parviflora* *Vochysia pyramidalis* *Vochysia thyrsoidea*

[1] Data from: Bouchardet da Fonseca & Lacher, 1984, table 2, p. 445; Santos de Faria, 1984b

Table V.v

Gum Sources Used by Callithrix jacchus *at various sites*[1]

Family	Species
Anacardiaceae:	*Anacardium occidentale* *Tapirira guianensis* *Spondias* sp.
Combretaceae:	*Terminalia catappa* (exotic)
Leguminosae:	*Acacia* sp. *Piptadenia colubrina*
Moraceae:	*Artocarpus heterophyllus*[3]

[1] Data from: Coimbra-Filho & Mittermeier, 1978; Maier *et al.*, 1982; Hubrecht, 1985, table III, p. 540.

[2] The substance eaten was the latex produced by gouged fruit.

Table V.vi

Gum Sources Used by Cebuella pygmaea *at Río Maniti, Peru*[1]

Family	Species	Number of sources used
Anacardiaceae:	*Spondias mombin*	10
Combretaceae:	*Terminalia* sp.	1
Compositae:		1
Convolvulaceae:	*Maripa* sp.	6
Dilleniaceae:		1
Euphorbiaceae:	*Croton cuneatus*	2
Flacourtiaceae:		1
Gnetaceae:	*Gnetum* sp.	27
Hippocrataceae:	*Cheiloclinium* sp.	3
Leguminosae:	*Acacia riparia*	2
	Bauhinia sp.	1
	Campisandra laurifolia	6
	Cassia sp.	1
	Dioclea sp.	5
	Entada polystachys	9
	Inga spp.	8
	Parkia oppositifolia	4
	Swartzia sp.	7
Moraceae:	*Coussapoa* sp.	1
Polygonaceae:		2
Vochysiaceae:	*Qualea amoena*	1
	Vochysia lomatophylla	87

[1] Data from: Soini, 1982, table III, p. 15.

APPENDIX VI

ANALYSIS OF OVERLAP IN THE DAY RANGE SAMPLES FROM NOVEMBER 1985 AND AUGUST 1986

The day ranges examined in chapter 7 are considered in more detail here, in an attempt to confirm that the patterns observed support the idea that the group systematically avoided overlap in its movements on consecutive days. To do this, the observed degree of overlap between days is compared with that which would have been expected if the group's movements had been randomly distributed over time.

According to the records, the group entered a mean of 24.4 different quadrats each day over the course of the 125 days of the main study period. The group thus visited an average of 15% of the 163 quadrats encompassed by its home range each day. If these visits had been distributed randomly among these quadrats during the course of the year, the group would have returned to each quadrat every 6.7 days, on average.

The quadrats were not visited with equal frequency, however. While a number of quadrats were entered on only one day during the thirteen months of the study, quadrat H05 was visited on 67, or 53.6%, of the 125 observation days. In order to estimate the expected frequency of return to a specific quadrat, assuming a random distribution of visits, a crude index (r) of the likelihood of return to any quadrat on a given day can be calculated:

$$r = \frac{(\text{Number of days quadrat was entered} - 1)}{(\text{Total number of observation days} - 1).}$$

Quadrats which were entered only once were obviously not returned to at any time and are thus excluded from the present analysis. r values for each of the remaining 146 quadrats range from 0.008 for those which were entered on just two days during the year to 0.532 for the most frequently-visited quadrat, H05.

To calculate the expected degree of overlap for any day range, the r values for all the quadrats visited are summed and then divided by the number of quadrats to give an mean value which is used here as a crude index of the likelihood of return or overlap, R, for the day range as a whole. Where just two quadrats were entered, one with an r value of 0.25 and one with an r of 0.75, for example, the R value for that day would be:

$$(r1 + r2)/n \text{ quadrats} = (0.25 + 0.75)/2 = 0.50.$$

As for the analyses presented in chapter 7, the quadrat in which the sleeping site is located is excluded from the calculations, given that its occupation on the following day is guaranteed by the group's presence overnight.

The observed degree of overlap (V) between consecutive days is easily calculated by dividing the number of quadrats common to both days, after subtracting that containing the sleep-tree, by the number of quadrats in the first day's range. If the value of V is lower than that of R, the overlap between the two days is less than would have been expected if the group's movements had been randomly distributed. Where V values are consistently lower than those of R, the analysis would support the idea that the group was systematically avoiding overlap between consecutive day ranges.

While the method used to calculate the R value is relatively crude, there are at least two reasons for believing that it actually provides an under-estimate of the degree of overlap which might be expected, other things being equal. Firstly, the fact that the second day of each pair invariably begins in the same part of the group's home range as the first would seem to imply that overlap would be more likely, on average, than for any pair of days selected at random. Similarly, the influence of the distribution of the group's plant feeding behaviour, which is generally concentrated at just a few locations during most periods, on its day-to-day movements has not been taken into account. The analysis presented in chapter 7 does in fact show that much, if not most of the overlap between days is related to the group's plant feeding behaviour, especially during the November sample.

Even without taking these two factors into account, the results of the analysis presented here (table VI.1) both reflect the patterns outlined in chapter 7 and further support the idea that the group systematically avoided overlap between consecutive day ranges during the sample periods. The value of V is in fact only greater than R in one of the eight pairs of sample days, that of the 6th to the 7th of August. Observed values fall to as little as 44.3% of the expected value in the November sample (06/11 to 07/11) and to 62.3% of that expected in the August sample (04/08 to 05/08). Overall, the consistency, rather than the degree of the differences between observed and expected values lend most support to the idea that the group was systematically avoiding overlap from one day to the next. It seems likely from the preliminary analysis of the data presented in this thesis that a more detailed examination of the records, including both a wider range of variables and a larger sample of consecutive days, will further confirm the systematic nature of this feature of the group's ranging behaviour.

Table VI.i

Expected and Observed Degrees of Overlap Between Sample Days in November 1985 and August 1986

Sample	Index of Overlap: Expected	Index of Overlap: Observed
November:		
06/11-07/11	0.183	0.081
07/11-08/11	0.275	0.231
08/11-09/11	0.251	0.240
09/11-10/11	0.223	0.219
Average:	0.226	0.182
August:		
03/08-04/08	0.251	0.201
04/08-05/08	0.223	0.139
05/08-06/08	0.270	0.269
06/08-07/08	0.301	0.409
Average:	0.253	0.235