SPIDER MONKEY (*ATELES GEOFFROYI YUCATANENSIS*) TRAVEL PATTERNS IN A SUBTROPICAL FOREST OF YUCATAN, MEXICO

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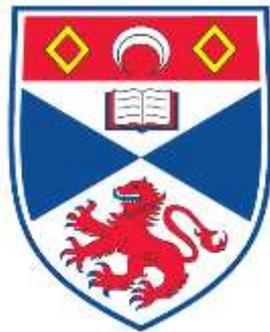
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"As he marches ahead he seems to be seeking his way. Does he in point of fact explore the country? Does he choose the most practicable places? (...) His subordinates follow very placidly, reassured by the cord which they hold between their legs; he, deprived of that support, is uneasy. ...Why cannot I read what passes under his black, shiny skull, so like a drop of tar to look at?"

Jean Henri Fabre (describing the behaviour of the Pine Caterpillar), In: *The Wonders of Instinct.*

to Jan Verpooten

ABSTRACT

A 12-month study of the ranging behaviour of 11 spider monkeys (*Ateles geoffroyi yucatanensis*) was undertaken at the Otochma'ax Yetel Kooh nature reserve in the state of Yucatan, Mexico. The aims were: 1) to evaluate the relationship between ranging patterns of the monkeys and ecological features i.e. climate and food distribution, 2) to assess the efficiency of ranging patterns, and 3) to test the hypothesis that spider monkeys navigate between important sources through spatial memory of key locations. A focal animal was followed daily for as long as possible and details of its ranging patterns recorded by entering positional fixes with a GPS receiver. Behavioural states were included in the observations to link them with the geographical information recorded simultaneously. The results revealed that the ranging patterns of spider monkeys at the study site were determined by the availability of key species of fruit in the area. Ranging was efficient, as evidenced by the fact that in most instances – particularly in the dry season when food was scarce - (1) spider monkeys moved in straight lines to distant food sources, (2) were able to orient their movement toward a food source at distances that could not have been in sight from the point where directed movement originated, and (3) the successive organisation of these linear segments was consistently forward, suggesting an ability to plan ahead of the next food source visited. I present these results as evidence of the use of spatial memory to move efficiently between important sources in their environment, and I argue in favour of higher-level spatial abilities in this species of New World monkeys.

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CHAPTER 1

INTRODUCTION

1.1 How do animals find their way in their environment?

In his 2003 television series "The Life of Mammals" naturalist and broadcaster Sir David Attenborough pointed out that, for many mammals, knowing where to find food or a safe refuge away from a predator could mean the difference between life and death. Attenborough's claim stresses the adaptiveness of the ability to orient in space, and places it in the same league as the ability to mate with a suitable partner, to ensure the survival of offspring through parental care, or to hide from a predator through simple camouflage. The aim of studies that take into account the relationship between animals' spatial cognition and foraging behaviours is to illuminate the behavioural mechanisms involved in this important aspect of survival.

In order to find food, almost all animals must travel within their ranges in search of mobile prey or stationary food sources. In addition, some animals may undertake "patrolling" trips to secure the boundaries of a territory from invasions, or may simply extend travel movements to explore previously-unvisited areas outwith the limits of a territory, while other wide-ranging movements may arise as a consequence of a motivation to emigrate. The efficiency with which these different kinds of ranging can be carried out affect an organism's chances of survival. Thus, from an evolutionary perspective, it is of particular relevance to investigate which factors contribute to variation in ranging behaviour and, in particular, what mechanisms enable an organism to range efficiently.

My thesis deals with the ranging behaviour of spider monkeys in forests, addressing both ecological and cognitive determinants of such behaviour, to provide insights into the relationship between environmental variables and ranging, and also into the cognitive mechanisms responsible for the ranging patterns observed. In it I attempt to provide an answer to the following questions: To what extent, if any, are spider monkey

movements between food sources efficient? And if so, what mechanisms underlie the efficiency of movements in spider monkey ranging?

1.2 Overview of the study

In the rest of Chapter 1 I will present an overview of the main topics that underlie my research. In Chapter 2 I introduce the forest environment where I carried out the research presented throughout this dissertation, by describing the ecological aspects (including anthropogenic impacts) of the habitat of the spider monkey group studied. In chapters 3 and 4 I provide a detailed explanation of data types used, data collection procedures, sampling methods, and data analyses. In Chapter 5 I present an overview of spider monkey movements between places throughout the year when I conducted the research work, while in Chapter 6 I address the mechanisms responsible for the spider monkey movements observed and place them within the framework of the spatial memory hypothesis. In Chapter 7 I extend the investigation into the spatial abilities of spider monkeys by introducing a novel statistical procedure to analyse animal movements and in Chapter 8, by providing an analysis of the movements of the study group to particular food resources through this novel test. Finally, in Chapter 9 I discuss the findings of my research in light of the current ideas on animal spatial cognition and draw conclusions about the use of spatial memory in the foraging movements of spider monkeys.

1.3 Ecological influences on ranging behaviour

Among other things, the Order Primates can be characterised by the diversity of habitats they exploit (reviewed in Chapman *et al.* 1999, Gupta and Chivers 1999, Peres and Janson 1999). Their distribution comprises a variety of environments and vegetation types, from montane humid forests at high altitudes in the mountain forests of Africa, bare deserts lined by dangerous rocky cliffs, riverine gallery forests and swamp forests in Asia (Gupta & Chivers 1999), and exhuberant tropical evergreen forests. These environments are challenging in terms of finding food and/or suitable places to refuge from environmental threats, e.g. predators. To face these challenges, primates must travel within their habitats every day.

Various factors may determine how far primates move around in order to satisfy their basic needs of food. The majority of primate biologists agree that the patterns of food abundance and distribution are crucial in understanding the variability in ranging behaviour within the Order Primates (Oates 1987, Strier 2000), but species-specific factors like dietary requirements and social structure may also be involved.

Food abundance is determined to some extent by abiotic features of the environment. The amount of rainfall in a year, the nutrient quantity in the soil and other specific features of soil (e.g. permeability, erosion), the intensity and degree of exposure to solar radiation, and variations in annual temperatures, all affect the phenological patterns of plants. In addition, the abundance of food competitors also influence the availability of food sources. The patterns of plant distribution and phenology may also directly influence their exploitation by primates. For example, if the main sources of food occur continuously in the environment and they are of high quality, consumers may benefit more from exploiting them in a random fashion than when they occur in patches and their quality is variable (Richards & de Roos 2001).

In addition to the variety of habitats exploited, the dietary requirements of primates also vary intra- and inter-specifically, therefore it is not an easy task to generalise their feeding preferences, and some authors have proposed that "eclecticism is the rule among primate diets" (Harding 1981). Most primate species eat fruits, leaves, insects, seeds/nuts, roots, grasses, gum and mud in variable proportions (reviewed in Harding 1981), although others have never been seen to consume some of these food types. Dietary variation depends on body size, types of food available in the environment (Harrison 1983), morphology of food-processing structures (mouthparts or hands) and of digestive systems (e.g. Chivers & Hladik 1980), and the costs and benefits of diverse locomotor adaptations and ranging behaviours (Steudel 2000).

Thus, the ranging patterns of a given species will reflect, to some extent, the availability and distribution of their preferred foods (including how often these become

available, i.e. their phenological patterns), their feeding preferences, and also the outcome of the intra-specific competitive interactions that shape social systems. For example, red colobus monkeys (*Colobus badius*) have home ranges of about 70 ha and this species is predominantly frugivorous, moving between fruit patches that are separated by a considerable distance from others. However, the folivorous black-and-white colobus monkey (*C. guereza*) has a smaller home range (15 ha,Clutton-Brock 1975) than the red colobus, and can find an abundant supply of food by moving over smaller distances.

The influence of biotic and abiotic factors on the ranging behaviour of primates falls in the general domain of primate ecology, where associations between environmental variables and behaviour are measured and analysed. The study of the mechanisms of ranging behaviour falls in the domain of ethology, however where the processes underlying behaviour are studied from observations of the animal.

1.4   Primate navigation

It has been hypothesised that, to navigate their environment in search of food and shelter, animals use information about the locations of important places in their environment, which is held within a mental representation of the environment, or a cognitive map (Tolman 1948). A central focus of my thesis concerns to what extent this claim is true for spider monkeys.

Some evidence suggests that primates use spatial memory to locate and move directly to many sites that provide food in their environments (Menzel 1973, MacDonald & Wilkie 1990, MacDonald *et al.* 1994, MacDonald 1994, MacDonald & Agnes 1999, Menzel *et al.* 2002). This evidence comes from studies of captive primates, which are housed in relatively small and predictable environments where visual access to landmarks and targets is available (Janson 2000). To date it is not known whether the abilities used by captive primates to navigate 'small-scale' environments (i.e. areas that can be visually inspected from a single point) are equivalent to those used while navigating 'large-scale' environments (i.e. areas where travel to out-of-sight locations is essential), such as the natural habitats of primates.

A number of studies have found that, even when faced with the difficulties of finding targets in a complex large-scale environment where visual access is limited, free-ranging primates move towards important targets in ways that suggests they use spatial memory. A one-year-long study was carried out in the Peruvian forest of the Amazon Basin where feeding sites occur in small, scattered patches and visibility in the canopy is highly limited (10-15 m Garber 1989). Nonetheless, moustached and saddle-back tamarin monkeys exploited food sources by trap-lining: they fed sequentially on trees of the same species bypassing even fruiting trees of other species, which suggests they hold a representation of the next target tree in mind before they set out to visit it. Moreover, rather than accessing 15 of the highest-ranking fruit trees through commonly- used pathways they used different routes to reach them, suggesting that they were able to map the location of a target tree with reference to virtually any place in the forest.

In other cases, primate movements in large-scale environments may reflect simple foraging principles, without the need for complex cognitive mechanisms. This point of view has been particularly adopted in the field of optimal foraging (see review in Pyke *et al.* 1977), and some of the concepts derived from such theoretical framework have been used to explain animal movement patterns. For example, a model of directional inertia (i.e. maintaining the same bearing throughout a bout of movement, cf. Cody 1971) could explain the straight-line, goal-oriented movements frequently observed in studies of primate behaviour. A different model justifies the increase in rate of sharp turns in the foraging patterns of an animal consuming items from a large food source (Chandler 1969 cited in Pyke 1977). Such strategy could maximise foraging efficiency at foods that occur in large patches by ensuring frequent encounters with food (for example, Mitchell 1963, cited in Pyke 1977).

These simple foraging rules may arise as a result of operant learning (stimulus-response) mechanisms, on a history of past feeding events. The result is a foraging strategy that appears to be rule-based, for example "continue searching for large bromeliads because over the past few days several have contained easily-caught small vertebrate prey" (cf. Garber 2000, p.270). Thus, the fact that some species navigate their

environments according to simple principles provided by optimal foraging theory does not conflict with the action of basic cognitive abilities (i.e. route memory, landmark detection and association with a particular direction) to aid efficient navigation. The behaviourist and cognitive traditions simply describe some common behaviours in different terms.

1.5   Spider monkey ecology and behaviour

Spider monkeys belong to the genus *Ateles*, the subfamily Atelinae and the family Cebidae. There is no marked sexual dimorphism in the genus, with both sexes weighing around 8 kg and the morphology of the genital area being the only sexually-distinctive trait (Robinson & Janson 1987), although this often lends itself to confusion since the female pendulous clitoris is in many cases mistaken for a penis. Most *Ateles* species live in tropical evergreen and semi-evergreen forests from southeast Mexico to northern Bolivia and Brazil (van Roosmalen & Klein 1988). Their diet is primarily frugivorous (83-90%) with the residual proportion dominated by leaves and flowers, and with occasional ingestion of bark, decaying wood, roots, honey, termites and caterpillars. Due to the scattered and patchy nature of the distribution of their main source of food, spider monkeys cover large areas of their habitat daily in order to secure a suitable amount of food in their diet. The high degree of prehension in their fingers, but most remarkably in their tails and the elimination of the thumb, allow them to brachiate from tree to tree with formidable agility and speed (Robinson & Janson 1987). As such, they spend most if not all the time in the upper canopy of the forest, where they engage in feeding, resting, moving and social activities.

Spider monkeys are unique among New World primates in that they show a social structure characterised by a high degree of flexibility in grouping patterns (Eisenberg & Kuehn 1968, Klein & Klein 1977). Groups of many individuals can be seen together in one place at the beginning or at the end of a day, but for the rest of it, parties of 3-4 animals (Klein & Klein 1977) are more common. The composition of these parties or subgroups varies throughout the day; individuals join and split from subgroups at many

times, and animals can also be solitary for some lengths of time. This unusual grouping structure of spider monkeys has been termed *fission-fusion* due to the dynamic nature of the grouping patterns; this system is characteristic of several Old World primates (e.g. *Papio hamadryas*, *Theropithecus gelada*, and *Pan troglodytes*), but in spider monkeys subgroup composition is more variable than in the baboon species (Symington 1990).

Diverse hypotheses for the adaptive nature of fission-fusion social systems have been put forward. It has been postulated that fission-fusion systems evolved as a response to increased levels of intra-group feeding competition due to the patchy distribution of food resources exploited by this frugivorous species (Symington 1988b; 1990). Other authors have argued differently, stating that intra-group feeding competition did not produce fission-fusion systems, but a highly-segregated social system of female subgroups and male-male alliances with a low level of interactions between the sexes (Eisenberg & Kuehn 1968; Fedigan & Baxter 1984). What is clear from spider monkey societies is the low level of social cohesion, suggesting that at least all adult individuals are highly independent from others, to the point where the individual may be the only source of information regarding knowledge of foraging routes (Milton 1981). This would suggest that in spider monkeys, individuals must probably rely on their own wayfinding abilities in order to forage efficiently.

This means that spider monkeys are a highly-suitable species to study individual spatial abilities of primates in natural environments. In order to satisfy their dietary demands both in quantity and in type, spider monkeys must forage for items that occur in food patches that are scattered in the environment. In addition, their environments are challenging, in that they offer limited amounts of food during the dry season, and visibility is limited in the canopy strata where they tend to search for food. Finally, the low level of social cohesion within adult individuals must impose an unusual degree of independence from other members of the group and may influence individual way-finding abilities.

CHAPTER 2

STUDY SITE AND SUBJECTS

2.1 Human populations in the site

About 1000 years ago, the area surrounding the study site was inhabited by traditional Mayan peoples. They erected stone houses and temples in the forest, which were later abandoned but are still standing today. Thirty years ago a few families from the nearby town of Chemax decided to settle down in the middle of the forest to establish a sustainable exploitation of the zapote tree (*Manilkara zapota*) for its gum. The gum from this tree has diverse industrial uses, and thus could be used as a basic form of subsistence for these groups. These families were the founders of what is now known as the Punta Laguna (PL) village and of the smaller Yodzonot village, 4km from the main road that leads to PL. There are 14 families and a total of 72 people living there today.

The people of PL subsist mainly on farming activities, growing corn, pumpkin beans and maintaining bee colonies to harvest honey. These products represent their most basic income, but most of the men also have jobs as tourist guides. Their life is intricately linked to the environment as they depend on the natural cycles in physical phenomena and abundance of resources in the area. This relationship with their environment has produced a community of men and women with detailed knowledge of the flora and fauna available to them, as well as of the natural phenomena that shape the ecosystem.

When asked about their motivation to contribute to conservation efforts in the area, the inhabitants of PL frequently claim that their fathers and grandfathers taught them the value of knowing and taking care of their environment. Thus, it seems likely that they have always been interested in finding ways to reach a balanced exploitation of the resources to meet their basic needs, as well as preserving the original biodiversity of the area. It was not until recent times, however, that this area gained official recognition as a nature reserve, after years of continuous struggle led by senior members of the PL

and Yodzonot communities along with representatives of a Mexican NGO that promotes conservation efforts throughout the Yucatan peninsula (i.e. PRONATURA, A.C).

Eco-tourism activities are carried out in the area in order to obtain support for conservation activities, and to promote conservation issues to a wider audience. As was mentioned above, the men work as tourist guides for the reserve. Groups of tourists visit the site almost daily to take guided walks in the forest. Most of the men have a small knowledge of the English language, so they are able to engage the tourists in conversations about the native flora and fauna of the reserve. The main attraction is the sight of the spider monkey group which, given the characteristics of the area (its small size, good visibility and easy-to-walk terrain), can be seen practically every day.

Formal ecological and ethological research projects in the study site began in the early 1990's, but it was until 1995 that the spider monkey community was studied in an effort led by David Taub and Laura Vick. By 1997 two of the spider monkey groups had been habituated and individual members of each group recognised and given a name. The men in the community whom today work as permanent research assistants, were trained in observational and data collection skills since 1995. They collect daily behavioural and ecological data for various research projects that take place in the reserve. Since habituation efforts started in 1995, the research assistants have accumulated a vast amount of knowledge of the monkeys' behaviour, their social relationships and the particular physical features that distinguish each of them from the other members of each group.

2.2   General description of the site.

2.2.1   *Location*

The study took place in the Otochma'ax Yetel Kooh (Home of Monkeys and Panthers) reserve (20°38' N, 87°38' W, 14m above sea level), adjacent to the Punta Laguna village, in the state of Yucatán (see map on Fig. 2.1), Mexico. It is located in the border between

the states of Yucatan and Quintana Roo, about 18km north of the archaeological site of Coba.
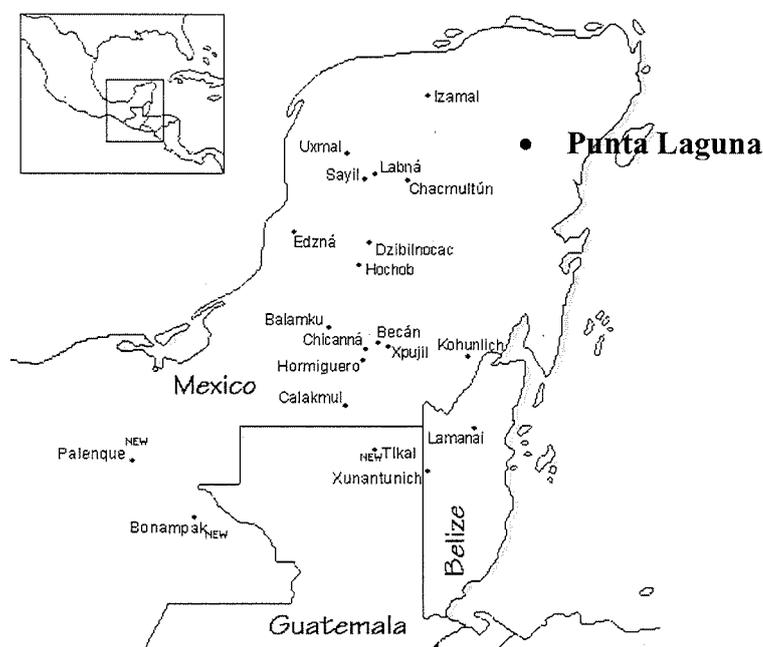
Figure 2.1. Location of the field site with respect to the Yucatan Peninsula and Mexico.

The data were collected in a portion of forested area surrounding a Lake (2 km x 0.75 km, fig. 2.2). The monkeys in the study group ranged over an area of 234.8 ha on the Southwest shore of the lake.

2.2.2 *Why study spider monkeys in Punta Laguna?*

The study site is particularly well suited for long- and short-term behavioural observations of spider monkeys for three reasons; good visibility on the ground, a well-designed trail system, and monkeys that are habituated to the presence of and use of scientific equipment (i.e. binoculars, GPS devices, loudspeakers, audio or video-recording devices, photographic equipment) by humans.

2.2.3 *Climate*

The climate is usually placed in the general category of tropical rain climates (*sensu* Lamb 1972, cited in Kalvova *et al.* 2003), under the specific label of savanna climate.

Since the driest month has a precipitation of less than 2cm, it is denoted as an Aw2 climate (*sensu* Koppen 1931, cited in Kalvova *et al* 2003). The bulk of precipitation falls in the months of May to October.

Figure 2.2. Aerial photograph of the lake next to the field site. The yellow and red contours enclose the approximate home ranges of the MX and EU groups, respectively (see text).*(Photo courtesy of Gabriel Ramos-Fernandez)*.

During the time I conducted the observations, annual rainfall at the study site was 2072 mm and mean annual temperature oscillated around 26 °C (fig 2.3), although the average annual rainfall reported for previous years was lower (around 1500 mm). The weather, specifically the rainfall, during the year in which this study took place was particularly different from previous years due to the tropical storm Isidore, which manifested itself during the early weeks of September 2002, close to the end of the study. September was thus the month with the heaviest rainfall (598 mm), while November was the driest (12 mm).
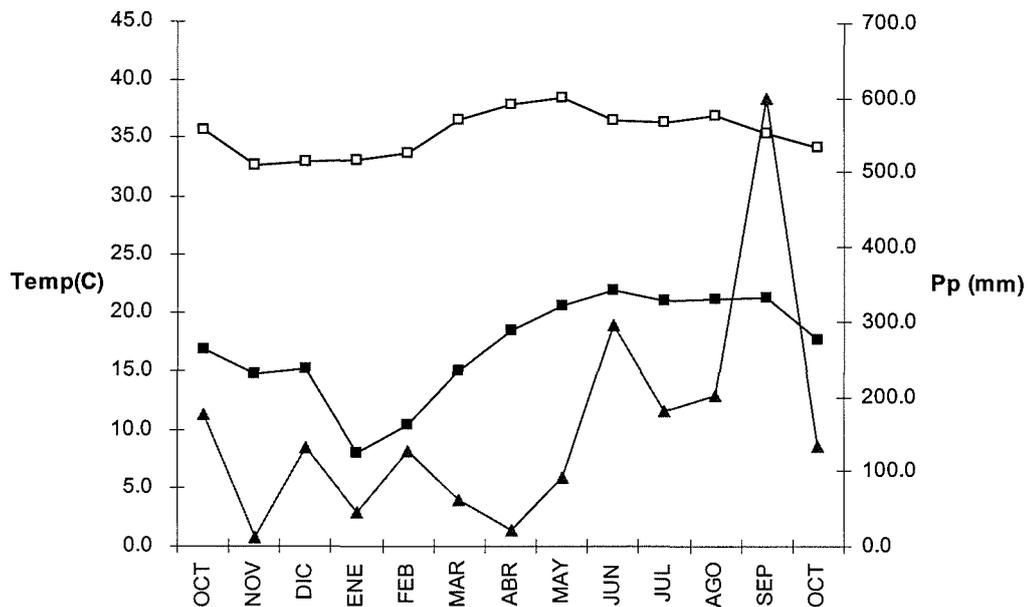
Figure 2.3. Annual weather readings during the year spanning from October 2001 to September 2002. The months of the year are shown on the horizontal axis; minimum and maximum temperature values (open and closed squares,vertical left axis) and precipitation values (closed triangles, vertical right axis) are displayed.

2.2.4 *Topography*

The study site is located on a plateau made of calcareous rock. There are no recent major episodes of mountain formation in the area, which makes the terrain fairly uniform with respect to the presence of elevated sites. On the other hand, there are several topographical depressions (called rejolladas) throughout the site; but these do not seem to represent a salient obstacle to the movement of the spider monkeys, as trees emerge from these depressions, allowing the continuation of arboreal paths through the canopy.

2.2.5 *Hydrology*

There are no superficial rivers or streams in the area. The main hydrological feature is the lake, which comprises 90 ha. It is composed by two depressions, each 10-20 m deep, interconnected by a shallow portion. The lake receives water that percolates from subterraneous streams, as well as by rainfall. These subterraneous streams also feed the rejolladas mentioned above, some of which are inundated periodically, forming shallow ponds (2-3 m deep). During the dry months these become a source of water for the

monkeys, but they may dry out, leaving only a few holes in the trees and bromeliads as sources of water.

2.2.6 *Flora and Fauna*

Medium semi-evergreen forest (Miranda and Hernandez 1964, cited in Cairns *et al.* 2003, Eyre 1968), interspersed with successional forest 30-50 years old predominates in the study site. The monkeys use both of these vegetation types on a daily basis (Ramos-Fernandez & Ayala-Orozco 2003). The edge of the lake is covered by typical aquatic vegetation, but the spider monkeys do not use this substrate. There are also a few portions of gallery forest near the boundaries of their home range, although the monkeys seldom travel that far. The nearby human communities have transformed the rest of the area into farming land where the spider monkeys do not venture at all.

The upper canopy (22-35 m) of the semi-evergreen forest is characterised by the abundance of two species, the ramon (*Brosimum alicastrum*) and the zapote (*Manilkara zapota*), both of which are an important food source for the monkeys in the study group. Other species also present in this stratum are the piich (*Enterolobium cyclocarpum*), koopo (*Ficus* spp), chakaj (*Bursera simaruba*), chee-chen (*Metopium Brunei*) and yaax'nik (*Vitex gaumeri*). In the medium stratum (12-22 m) the guano palm (*Sabal* spp) constitutes the main food source, while the lower stratum remains untouched. Epiphytes like bromeliads (*Aechmea bracteata*) and orchids (*Brassavola nevosa*) are also abundant and the spider monkeys use the bromeliads, in particular, as a source of water and food (specially the base of the leaves).

With respect to the fauna the site is rich and diverse in terrestrial animals, but systematic study has been sparse. At least 158 species of birds have been reported for the study site, 114 of which are resident and 44 are migratory (Berlanga & Wood 1997). The potential competitors of the spider monkey could be the toucans *Ramphastos sulphuratus* and *Pteroglossus torquatus*, or the parrots *Amazona albifrons* and *Amazonas xantholora,* as they feed on some of the same fruits that monkeys consume.

Mammals also seem to be well represented, with 39 species in a nearby site (Navarro 1990), although they were rarely seen during my study, except for the squirrels *Sciurus yucatanensis* and *Sciurus deppei*. A few small mammals that could be potential competitors to the spider monkey could be the coati *Nasua narica*, the tayra *Eira barbara*, and/or the howler monkey *Allouata pigra*, all of which I saw during the study. I heard howler monkey calls relatively close to the core area (minimum estimated distance: 500 m, maximum 1000 m, estimated by the field assistants) very frequently, but the spider monkeys encountered them only rarely. The coati and the tayra were seen feeding on the same trees as the spider monkeys on only two occasions throughout the study. Other mammals known to the study site that could potentially be predators of the spider monkey, are the puma *Felis concolor* and the jaguar *Panthera onca*. The puma was seen by a student who collected data for a different project on only one day; the jaguar was never seen as such, but the field assistants reported its presence from night-hunting exploration trips. In conclusion, the likelihood of an attack by any of these felids was remote.

2.3   The spider monkey group

The spider monkeys in the study site have been studied since 1995, providing the habituation necessary for individual identification and continuous observation of behaviour. About 80 individuals of the black-handed spider monkey (*Ateles geoffroyi yucatanensis*) live in the forested area surrounding the lake; three groups of monkeys are recognisable because their group members range together and hardly come into interaction with animals from other groups. The EU group is composed of about 45 individuals that range in the easternmost portion of the lake, on the best-preserved patches of forest. The MX group is composed of 20 individuals that range near the area used by the EU group (see fig. 2.2); this group's habitat contains some portions of well-preserved forest, discussed above, but it also covers a portion of logged forest in regeneration. Finally, the GA group (unknown composition or size) ranges in the northern shore of the lake, distinctively separated from the MX and EU groups by a road that is used by the local villagers and the tourists who visit the reserve. GA group's habitat has about the same degree of mixed vegetation as that of MX. The MX group

sometimes crosses this boundary and enters a portion of the GA territory in their daily ranging, but it is not known to what extent the GA and MX ranges overlap, nor if their interactions are pacific or agonistic. In this study I report observations made between October 2001 and September 2002 on the behaviour of the MX group. Composition of the MX group as of 8th of October 2001, when this study began, is shown in Table 2.1.

Table 2.1 Composition of independently-moving animals in the MX group.

Age-sex class	Number of animals	Name	Age (yrs)
Adult males	4	Pancho	?
		Benito	?
		Damian	?
		Archi	?
Adult females with newborn	3*	Claudia	?
		Flor	?
		Veronica	?
Adult females	2	China	?
		Cecilia	?
Sub-adult males	1	Licho	4.5
Sub-adult females	3	Pilar	3.5
		Lamat	3.5
		Kaban	3.5
Juvenile males	1	Jose	?
Juvenile females	1	Enriqueta	2.5
TOTAL	15		

*This number later became 5, as the other adult females gave birth at the end of October, after the study had begun.

Visibility on the ground was fairly good for most of the time. In about 70% of the time, a field assistant or I were able to approach any individual monkey to within 10 meters. Some of the individuals in the study group (3 out of the 15 that formed the MX group) were less wary of human observers and would let us approach up to 5 meters. In

the EU and the GA groups the habituation distance was larger (within 15 m). None of these distances changed considerably over the year. The monkeys usually moved in the canopy at 10-15 m distance from the ground, which facilitated their identification by the use of binoculars. This, along with the relative uniformity of the terrain and the existence of a clear-cut system of trails, facilitated locating, following and observing the monkeys for long periods of time.

In summary, the Otochma'ax Yetel Kooh reserve was an ideal place to undertake a study of the ranging behaviour of spider monkeys. Its general good visibility on the ground, the presence of a trail system connecting virtually every place within the core area of the group, and the habituated monkey group, ensured continuous observations of behaviour on many days during the study.

CHAPTER 3

GENERAL METHODS

3.1 Overview

This section provides a description of the methods used during fieldwork observations, and the subsequent chapters of this dissertation rely on to the methods outlined here for their data analysis. Detailed data handling procedures and statistical analyses are described separately in each chapter. Fieldwork was conducted from 8 October 2001 to 2 September 2002 at the Otochma'ax Yetel Kooh (Home of Monkeys and Panthers) nature reserve, with a brief interruption during December 2001 when I was absent from the site for nearly a month. During my absence the field assistants kept records for me of the monkeys' locations throughout the day and their feeding activities. In total, I observed the spider monkeys and collected data on their movement and behaviours, for 980 hours.

3.2 Contribution of the field assistants

I appointed two local men as field assistants to help me with the data collection. Each was a brother to the two senior field assistants who had been studying spider monkeys since 1995. At the beginning of this study they had minimal experience identifying monkeys and recording their behaviour, but were as experienced as the senior assistants at opening trails in the forest, identifying tree species, and moving quickly and directly through the trail system to keep pace with the monkeys' movements. I was accompanied by one of these men in the forest at all times during the study. In the first two weeks of the study the senior field assistants also accompanied us, effectively instructing the new recruits in identification of individual monkeys and in basic data collection, while I also collected data on my own. Although I had gained extensive experience identifying the members of the study group from a pilot study carried out between February and April 2001, the senior assistants instructed me in identifying new-borns and a few juveniles. At the end of the initial two weeks of training I was proficient at identifying individuals on my own, thus during the following two weeks, I supervised the new field assistants at this

task. On rare occasions, when we became confused about the identity of an individual, we communicated with the senior assistants to corroborate this information through walkie-talkies. Nevertheless, by the first month of fieldwork the new assistants had already acquired the ability to identify all the animals in the study group with little help from me.

A field assistant's role was to keep sight of the focal animal while it was moving or when I was occupied tagging trees or recording GPS and behaviour data. Because of their extraordinary hearing skills, they also helped me in estimating the direction and distance of distant calls produced by other spider monkeys and howler monkeys, and to open trails in the forest when needed. Throughout the study, they became colleagues and to this day their skills and advice are highly valued by the other researchers who are currently working in the study site.

3.3   Observation methods

3.3.1   *Observation schedules*

From 8 October 2001 to 31 March 2002 the field assistants and I followed a focal animal from dawn until dusk, or until we lost sight of the animal (schedule 1, or S1). On the 1st of April of 2002 the schedule changed: we began following a focal animal from 1600hrs to 1200 on the next day (schedule 2, or S2). The decision to modify the schedule of observations came after a few unsuccessful attempts at finding a desired focal individual at dawn. As soon as we started collecting data from the previous afternoon, the problem was minimised, and the morning observation time maximised. The focal individual was usually found quickly in the afternoon, followed until it entered the sleeping site, and found quickly again the next morning. Morning and evening observation times are an important source of movement and activity data, since spider monkeys are more active during these than at other times of the day (van Roosmalen & Klein 1988). The new schedule was used until the 2nd of September 2002 when fieldwork ended.

3.3.2 *Locating a focal animal*

To locate a desired focal individual we used two different strategies depending on whether we knew where the planned focal animal had spent the night or not. During S1 follows we never knew where the desired focal animal had slept the night before, so every morning upon entering the forest the field assistant and I would split up to walk down the trails looking for this individual. When either of us found it we would alert the other by whistling, upon which we would re-join and start data collection on that animal. If an hour had passed or we were not able to find the desired focal animal we would go to the sleeping site where the focal animal of the previous day had slept and follow the 1st or 2nd next individual on the list of scheduled individuals (see below). As the study progressed it became evident that spider monkeys spend a good deal of the morning at or near the sleeping site. Thus we began our morning search at the sleeping site where the focal animal of the previous day had slept; if we could not find the desired animal there, we would quickly go to any of the other sleeping sites that the monkeys used most frequently.

During S2 follows the field assistant and I would enter the forest at 1600hrs and walk down the trails until we found the desired focal animal. Observation and data collection started at that time and went on for the rest of the afternoon until the focal animal settled down at a sleeping site. The next morning the field assistant and I would go directly to that sleeping site, locate the focal animal and start data collection, continuing until 1200 or shortly after that. If we could not locate the animal in the sleeping site at dawn, the alternative method described for locating focal individuals during S1 follows was then used.

As the study progressed, the field assistants became better at estimating the locations of spider monkey calls that we heard near dusk, while we were still collecting data. If the next morning we could not locate the focal animal on its sleeping site, we could use the knowledge of other monkeys' sleeping sites and move quickly and directly to these sites in order to locate the desired animal or to start data collection with a different one.

If focal animals disappeared from view for more than one hour, as usually happened when they travelled at great speeds to far-off locations, the field assistant and I would walk back to the core area and start looking for a new focal animal.

3.4   Sampling methods

I used continuous recording of behaviour (Altmann 1974) of a single focal animal for an entire day (length of days for S1 follows: 10-11 hours; length of day for S2 follows: 8-9 hours), or for as long as I could be as close as possible to it.

An observation period started when the field assistant and I identified the desired focal animal. I punched the behaviour codes in a hand-held computer (see section 3.5) as they were taking place as well as the identity of individuals who participated in social (grooming or play) and aggressive exchanges with the focal animal. The timings of the behaviours were recorded automatically by the hand-held computer. If the focal animal was out of view I noted this too in the recording file and resumed behavioural notes as soon as I could see the animal again. The observation period ended when the focal animal entered a known sleeping site and assumed a sleeping posture, i.e. arms, legs and tail folded close to the body, head between shoulders with chin touching the chest. It also ended if the light inside the forest was too low to walk out safely, or if the focal animal was out of view for more than one hour. During S2 follows, when the observations were scheduled to finish at 1200, I made sure that if feeding was the last behavioural state in the record, the observation period continued until the animal had stopped eating.

As long as sampling durations are long, continuous recording of behaviour is particularly useful in obtaining reliable data on the duration of specific behaviours and on the sequence of behaviours performed (Altmann 1974). I chose this method to obtain reliable data on the duration of feeding bouts and to maintain an accurate record of GPS data for the description of movement patterns.

3.4.1 *Assigning focal individuals*

In an attempt to obtain equal numbers of samples on every individual in the MX group, I assigned each individual of the study group pseudo-randomly to one day of observation. I created a list with the names of the individuals that I would follow on each particular day, randomly picking out one card with the name of an individual from a shuffled pile of name cards, and continuing until all monkeys had been listed. This procedure was performed every time that all the monkeys in the group had been followed once. If on a given day I could not find an individual in the forest, I attempted to find the next one on the list. If that were not possible I would follow the first different individual that the field assistant or me could identify, ensuring that no individual was over-sampled as a result. In general, I made sure that all individuals in the study group had been followed once before assigning them to a new round of observations (Table 3.1). This condition was not met for some of the adult males who "disappeared" from the group for a few days. In this case, I kept a record of the number of "missed" samples/individual. If the number were 2 or higher, the next time that the under-observed individual was seen I would follow it instead of keeping up with my predetermined list. This might have produced biases in the context in which a few of the adult males were observed (i.e. mostly in the vicinity of the study group's location, instead of wherever they might be found). However, had I not overridden the order of observations in my predetermined list, those under-observed individuals would have been highly under-represented in the data.

Table 3.1. Distribution of day follows/focal individual throughout the year. *: indicates the month when that focal individual was last seen in the group. †: indicates the month when that individual died. **: indicates the month when that individual immigrated into the group.

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Total
Males													
Archi	2	2	1	1	2	0	2	1	2	0	1*†	-	14
Benito	1	2	0	1	1	2	1	1	1	0	1	2	13
Damian	1	1	0	1	1	1	0	1	1	1	1	1	10
Jose	2	0	0	1	0*	0	†	-	-	-	-	-	3
Licho	2	0	0	1	1	1	1	2	1	2	1	1	13
Pancho	2	0	0	1	1	1	1	1	0	2	0	0	9
Females													
Cecilia	1	1	0	1	0	1	1	2	1	1	1	2	12
China	3	0	1	1	1	2	0	2	1	2	1	2	16
Claudia	0	1	1	1	2	0	2	1	1	0	2	2	13
Flor	2	0	1	1	2	0	1	2	1	2	1	1	14
LaOtra	-	-	-	-	-	-	-	-	-	1**	1	0	2
Pilar	0	2	0	1	1	1	1	2	0	2	0	1	11
Veronica	1	2	0	1	1	1	1	1	2	1	1	1	13

3.5 Data collected and recording methods

The procedure for collecting data was not a simple one, since I had to record different aspects of two behaviours almost simultaneously. I describe these aspects separately by making reference to the particular device used to collect each type of data.

3.5.1 *Behavioural data on a Hand-held computer*

I used a Psion Organiser (model LZ64) hand-held computer with the software *The Observer 3.0* installed in it to record the behaviour of the focal animal. When the observation period began, the device's internal timer started running from 0 seconds, at which time I started recording behaviour. I entered the behaviour codes manually by tapping keys that I had established previously for particular behaviours on the Psion keyboard. I did not have to look at the keyboard when entering the codes, as I selected codes that would be easy to locate by touch instead of by sight. The device automatically links the codes to a time (seconds from 0) and the computerised output of this simple procedure (see below) allows for computations of behaviour duration. In some cases I also entered a separate code to characterise some aspects of the behaviour recorded. For example, if the focal animal Cecilia were grooming its daughter Pilar, I would enter the code for *grooming another individual* (GG) together with the code for *receiver of the action*, Pilar (PI). Table 3.2 shows a summary of behaviours recorded and their description.

3.5.2 *Movement data on a GPS receiver*

I used a Garmin 12CX GPS receiver to record the location of the focal animal at regular intervals throughout the day. I set a bleeper to go off at every 2-min, upon which I would walk until I got underneath the focal monkey, or as close as possible to this target. I then

set the GPS to record the co-ordinates of my current location. If the focal animal was feeding, I also recorded the location of the tree on which it fed. When the focal animal moved over long distances, the field assistant and I tried to keep close to it in order to get the most precise GPS data possible.

Table 3.2. Behaviours recorded in this study. "Additional notes" for that behaviour were input with the help of the hand-held computer too.

Individual Behaviour	Description	Additional notes
Feed	Picking food, putting it in the mouth, chewing it and ingesting it.	Food type and tag number or ID of feeding site
Move	Arboreal locomotion, including short and long translocations.	None
Rest	The default state, when no other behaviours were observed. Includes sleeping and self-grooming.	Tag number or ID of sleeping site.
Social behaviours	**Description**	**Additional Notes**
Play	Gentle biting on tail, arms, legs, or face, accompanied by chasing and by play calls. Usually reciprocated.	Identity of the partner(s).
Groom	Use of hands, mouth and teeth to remove dirt or parasites from a conspecific's hair/skin.	Identity of the partner(s).

During long-distance movements, I stopped to get the GPS data of the location that the focal animal had already passed by while the field assistant followed the focal animal so that it was never out of sight. As far as possible I kept visual track of the route that the focal animal followed while I was behind, so that the subsequent GPS data reflected the real trajectory of the focal animal's movements. This proved to be easy to accomplish in most cases.

If the focal animal remained in one location for a long time, which was common when it fed or when it rested, I suspended the collection of GPS data until it moved again. Whenever it was not possible to record data with the GPS due to poor satellite reception or other factors, I noted that down in the behavioural record, and described the location verbally for later conversion to spatial co-ordinates.

3.5.3 *Feeding site tag*

When the focal animal was feeding I also tagged the tree with a plastic tape on which I wrote an ID, made up of the common name of the tree and a consecutive number. To ensure tag permanence, I attached the tag around the trunk of the tree (for thin trunks) or to resistant branches that I considered would not be damaged or lost. Tree tagging allowed me to keep track of species that the monkeys visited repeatedly. The majority of these tags remained up on the trees until the last day of fieldwork.

3.5.4 *Notes on a Tape recorder*

From January 2002 I acquired a tape recorder that I used until September 2002 to make casual notes of unusual or 'new' behaviours and interactions between the monkeys, calls heard at a distance, weather conditions and/or phenological aspects that I noticed

spontaneously. I later transcribed these to A4 sheets to form a diary of casual observations.

3.6 Statistical data analysis

Each section describes the details of the specific statistical techniques employed. All tests were two-tailed with $\alpha=0.05$ or $\alpha=0.01$, but this is clearly stated in each case. The output from the Psion hand-held computer was a text file with times and codes for behaviours, without any information on the location of the focal animal at a particular time. To join behavioural and GPS data I used scripts that were programmed in the Perl language (see Appendix 1). The output of these was a text file that was converted into Excel spreadsheets (see following chapter for a detailed description of this procedure). Statistical analyses were conducted mostly in SPSS v.10 for Windows, but to a limited extent also in Excel, and some tests were done 'by hand' from computations outlined in (Zar 1996) and (Batschelet 1981). The ranging patterns were analysed using a novel statistical procedure devised by Dr Peter Jupp of the School of Mathematics and Statistics at the University of St. Andrews, but I report the details of this procedure in Chapter 7.

3.7 A word on the concept of visibility

Often field studies of primates provide an estimate of visibility conditions on the ground, aiming to provide an idea of the ease with which the researchers were able to identify and/or keep track of the study subjects. In a tropical forest like the one in the Taï National Park, Boesch and Boesch (1984) estimated that the visibility conditions on the ground would not allow a human observer to identify an individual chimpanzee if it were farther

than 20 m from her. In more open habitats like savannah, visibility can be up to 83 m (Noser 2004).

While such estimates are of use with respect to the visibility conditions experienced by semi or fully terrestrial species, they do not give a clear idea of the visibility conditions in the canopy – i.e. for arboreal species. However, Garber and Hannon (1993) modelled the foraging behaviour of tamarins in the rainforest of Northeastern Peru assuming a visual detection field of 17.5 m, based on their observations of this species' behaviour. It is reasonable to expect that visibility conditions on the ground will differ from those in the canopy. This would be particularly true of medium to highly dense forests (like the current study site) where the middle and upper strata can be thought of as an impenetrable mesh of branches and leaves that could decrease the ability of an animal to detect edible items.

Given that spider monkeys are arboreal, I did not attempt to measure visibility on the ground, and for safety reasons I did not measure visibility in the canopy. I base my predictions and conclusions on a highly conservative visibility estimate in the canopy, at 20-30 m above the ground – i.e. the stratum where spider monkeys move - taken from two independent field studies of arboreal primates. One is from a study of siamangs in the humid forests of Malaya, in which D.J Chivers (pers. comm) estimated visibility in the canopy, at 30 m from the ground, to be of 100 m if the view was unobstructed, but restricted to 30-40 m if a prominent tree was in the field of view. The other estimate is from an experimental study of capuchin monkeys in the subtropical forest of Iguazu National Park in Argentina where Janson (1997) measured the distance from a target tree to the periphery and to the centre of a group of travelling monkeys whenever a focal

individual showed clear signs of having detected such target. The maximum distance at which capuchin monkeys were able to detect a target tree from the centre of the group was 80 m, while from the periphery of the group it was 30 m (assuming an even group spread of 50 m). However, the ability of the monkeys to detect targets (feeding platforms) decreased dramatically if the group travelled fast. In order to be highly conservative in my interpretations of spider monkey foraging decisions, I estimate that the maximum distance at which the monkeys would be able to detect an edible item would be of 80 m.

CHAPTER 4

DATA USED AND DATA PREPARATION

4.1 Overview

This section is aimed at familiarising the reader with the type of data used in analyses performed in subsequent sections, as well as with the specific procedures carried out on the data in preparation for such analyses. Some of the tables and figures shown here may appear in further sections, but this section can be used as a general reference when in doubt about the types of data and data manipulations performed throughout the dissertation.

4.2 Computer procedures used in preparation of data for analyses

4.2.1 *Linking observational data from the Psion hand-held computer to GPS data.*

The information stored in the Psion hand-held computer was downloaded at the end of each day of work, into the software *The Observer 3.0* installed on a portable laptop computer, by connecting the hand-held computer to the portable computer with a cable. I then saved the observational data in a text file. To join each behavioural recording to a geographical record, I used a script developed in the programming language Perl (see Appendix 1 for a transcription of the script). Both the file generated in *The Observer* and the file of geographical co-ordinates contained information about the data and the precise time at which each behavioural record or GPS record was entered. Thus, the main task of the script was to align the information in both files to produce a list of behaviours with precise geographical information of the location where they were performed.

4.2.2 *Visualising daily travel paths in ArcView 3.2*

The GIS software package *ArcView 3.2* was used to display GPS data graphically, and to perform the movement simulations described in chapter 6. To visualise the geographical co-ordinates of a travel path in *ArcView*, I first created a file of geographical co-ordinates

from data stored in the GPS receiver. This information had to be downloaded from the GPS receiver into the computer package *Ozi Explorer 3.85*, which arranged all the geographical co-ordinates stored in the GPS receiver into a list in a text file for use with other software applications. This text file included a list of geographical co-ordinates and also information about the time and the date of each GPS record, but it did not separate co-ordinates by dates. In order to extract co-ordinates for each day, I used a script developed in the programming language Perl (see Appendix 1 for a transcription of the script) to create a daily list of geographical co-ordinates (see figure 4.1). Each of these text files that contained daily lists of geographical co-ordinates could then be used to visualise daily paths by opening them in Excel and converting them into a dBase (extension .dbf) file that *ArcView* was able to read and interpret.

4.3 Meteorological conditions throughout the year (October 2001 – September 2002)

The climate in the study site is usually classified in the general category of tropical rain climates (*sensu* Lamb 1972, cited in Kalvova *et al.* 2003), under the specific label of savanna climate. Since the driest month has a precipitation of less than 2cm, it is denoted as an Aw2 climate (*sensu* Koppen 1931, cited in Kalvova *et al* 2003). The bulk of precipitation falls in the months of May to October. The rainfall and temperature patterns shown here were taken from records kept by a meteorological station in the nearby town of Valladolid (70 km north of Punta Laguna), there being no suitable equipment in Punta Laguna village to record such data. During the time I conducted the observations, annual rainfall at the study site was 2072 mm and mean annual temperature oscillated around 26 °C (Fig 4.2), although the average annual rainfall reported for previous years was lower (around 1500 mm, data from the same meteorological station).

The rainfall in 2002 was different from previous years due to the tropical storm Isidore, which occurred during the early weeks of September 2002, close to the end of the study. September was thus the month with the heaviest rainfall (598 mm), while November was the driest (12 mm)

(a)

ID	UTMzone	Eastings	Northings	Date	Time
WP,UTM,T807	16Q	433994	2283090	**06-Jun-02**	06:13
WP,UTM,T808	16Q	433965	2283524	**06-Jun-02**	17:21
WP,UTM,T809	16Q	433864	2283580	**06-Jun-02**	17:28
WP,UTM,T811	16Q	434033	2283150	**11-Jun-02**	08:04
WP,UTM,T812	16Q	434005	2283170	**11-Jun-02**	08:15
WP,UTM,T813	16Q	434000	2283167	**11-Jun-02**	08:24
WP,UTM,T819	16Q	434118	2283049	**19-Jun-02**	08:04
WP,UTM,T820	16Q	433858	2282934	**19-Jun-02**	09:48
WP,UTM,T821	16Q	434031	2283088	**19-Jun-02**	17:03

(b)

ID	UTMzone	Eastings	Northings	Date	Time
WP,UTM,T807	16Q	433994	2283090	06-Jun-02	06:13
WP,UTM,T808	16Q	433965	2283524	06-Jun-02	17:21
WP,UTM,T809	16Q	433864	2283580	06-Jun-02	17:28

(c)

ID	UTMzone	Eastings	Northings	Date	Time
WP,UTM,T811	16Q	434033	2283150	11-Jun-02	08:04
WP,UTM,T812	16Q	434005	2283170	11-Jun-02	08:15
WP,UTM,T813	16Q	434000	2283167	11-Jun-02	08:24

(d)

ID	UTMzone	Eastings	Northings	Date	Time
WP,UTM,T819	16Q	434118	2283049	19-Jun-02	08:04
WP,UTM,T820	16Q	433858	2282934	19-Jun-02	09:48
WP,UTM,T821	16Q	434031	2283088	19-Jun-02	17:03

Figure 4.1. A small fragment of a list of geographical co-ordinates (a) before and after (b-d) application of a script that separated it into three different files (b-d) according to the desired date (see columns labelled 'Date' on all lists).
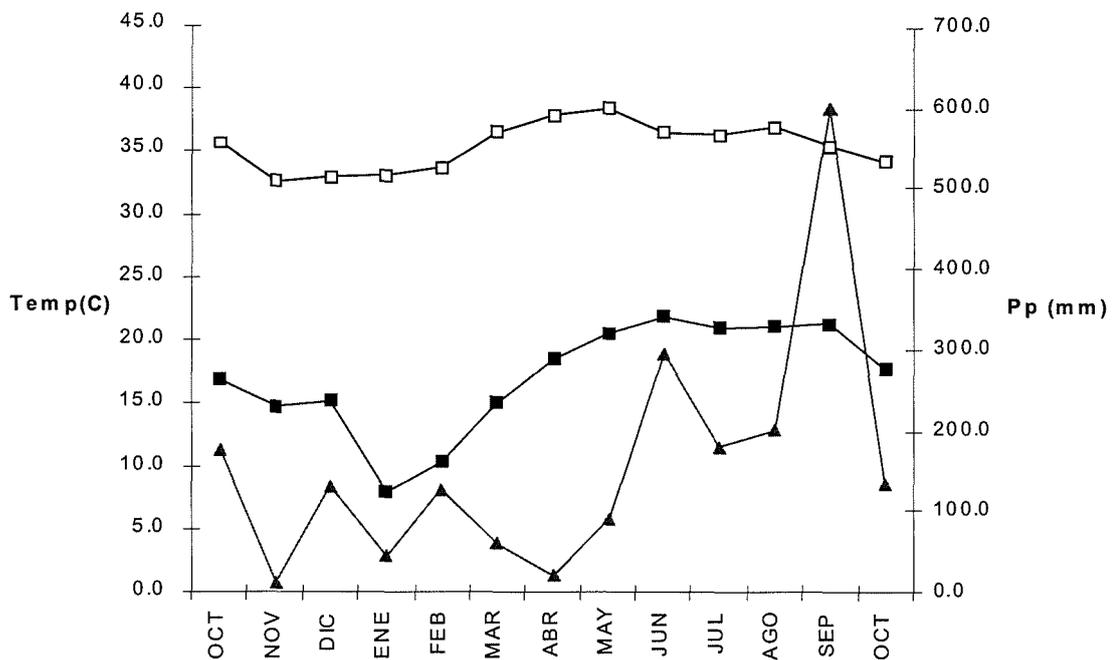
Figure 4.2. Annual temperature and precipitation readings during the year October 2001 - September 2002. The months of the year are shown on the horizontal axis; minimum and maximum temperature values (open and closed squares, vertical left axis) and precipitation values (closed triangles, vertical right axis) are displayed.

4.4 Diet of the spider monkeys throughout the year October 2001 – September 2002.

Data on species of food consumed by the monkeys in the study group come from behavioural observations made while single focal animals were being followed. Thus, it does not include all types of food that all members of a group fed on, but only the species that the focal animal fed on at a given time. However, a consistent effort was made to reach a balanced sample of focal animals (i.e. same number of focal observations for each member of the group) and therefore the data presented here should give a broad picture of the diet of spider monkeys from October 2001 to September 2002.

Spider monkeys fed on the majority of the species listed in Table 4.1 at limited times of the year. The proportion of time feeding that was spent on each type of fruit in each month when observations were made is listed in Table 4.2. The monkeys fed on

three fruit species consistently throughout the year (i.e *Brosimum, Ficus* sp, *and Ficus cotinifolia*) suggesting that these must have been readily available throughout that period of time. This cannot be confirmed for species that were not consumed in a given month, since it is not possible to know whether the monkeys did not consume them as a result of their ranging decisions (i.e. moving into areas where that particular type of food does not occur) or because they were not available.

Table 4.1. Proportions of the annual time spent feeding accounted for by each species consumed at stop sites. Species in bold make up 95% of the total time spent feeding.

Common name	Species	%
Ramon	**Brosimum alicastrum**	22
Alamo	**Ficus sp.**	16
NI	**Unidentified trees**	13
Copo	**Ficus cotinifolia**	8
LEAVES	**LEAVES**	5
Cheche	**Metopium brownei**	5
Zapote	**Manilkara zapota**	5
Pixoy	**Guazuma ulmifolia**	4
Pich	**Enterolobium cyclocarpum**	3
Kilim	**Spondias lutea**	3
Jujub	**Spondias mombin**	2
Huaya	**Talisia olivaeformis**	2
Sayaak	**NI**	2
Tsilil	**Diospyros cuneata**	1
Yaxnik	**Vitex gaumeri**	1
Caracolilllo	Sideroxylon capiri	0.6
Morax	NI	0.4

Table 4.1.(cont)

Common name	Species	%
Copal	*Bursera bipinnata*	0.2
Jirinich	*NI*	0.1
Ceiba	*Ceiba pentandra*	0.1
Ciruela	*Ziziphus jujuba*	0.1
FLOWERS	FLOWERS	0.1
Botox	NI	0.1
Tsitsmuk	*Dalbergia glabra*	0.1
Xuul	*Lonchocarpus yucatanensis Pittier*	0.1
Guarumbo	*Cecropia peltata*	0.1
Tatzi	*Hippocratea celastroides*	0.1
Pasache	*Simarouba glauca*	0.1
Toxtab	*Guettarda combsii*	0.1
Tohiu	*Coccoloba acapulcensis*	0.1
Cinche	*Caesaria nitida*	0.05
Isaki	NI	0.04
Kanaste	*Sideroxylon foetidissimum*	0.03
Anona	*Annona cherimola*	0.02

NI: Unidentified species

Table 4.2. Percentage of time spent feeding on different species each month. The 13 species in the left column are arranged as in table 4.1. Cells with >40% are highlighted.

Species	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Brosimum alicastrum	11.1	41.0	--	37.3	18.8	13.9	26.3	3.9	13.3	33.5	28.5	38.3
Ficus sp	15.9	4.6	2.3	11.9	32.3	7.8	5.4	46.7	2.7	--	6.0	3.3
Ficus cotinifolia	24.2	--	--	16.7	8.0	--	6.4	1.0	3.7	0.3	--	--
Metopium brownei	0.1	--	--	--	--	--	3.3	4.7	0.3	31.0	38.4	2.8
Manilkara zapota	0.1	13.7	--	1.8	8.6	19.4	18.6	2.4	1.4	--	--	--
Guazuma ulmifolia	--	3.5	--	12.4	12.4	17.9	--	--	--	--	--	--
Enterolobyium cyclocarpum	--	--	--	--	--	6.4	17.0	8.0	--	--	--	--
Spondias lutea	4.1	--	--	--	--	--	--	--	--	--	--	36.7
Spondias mombin	12.0	10.6	--	--	--	--	--	--	--	--	--	1.5
Talisia olivaeformis	--	--	--	--	--	--	--	--	42.8	9.6	--	--
Sayaak	11.2	--	--	--	--	--	--	--	--	--	6.0	--
Diospyros cuneata	--	6.1	71.6	2.4	2.1	--	--	--	--	--	--	1.3
Vitex gaumeri	--	--	--	--	--	--	--	--	--	--	5.6	9.2
Other*	0.6	1.1	9.5	0.4	5.6	3.6	1.7	1.0	5.8	3.2	4.3	1.2
Total % fruit	79.3	80.6	83.4	82.9	87.8	69	78.7	67.7	70	77.6	88.8	94.3
Total #spp eaten	10	7	3	8	12	7	8	8	10	6	8	8
Leaves	3.15	10.5	--	2.15	4.0	5.6	6.4	9.2	25.3	3.9	2.7	3.8

* refers to species that were not in the top 13 list

4.5 Spider monkey home range area estimation

Several analytical methods have been devised to measure the extent of space in which animals perform their daily activities. The "home range" of a species is a theoretical construct that has been defined and re-defined continuously over the last few decades, in order to fit it with development of new methods in home range area estimation. One definition that is widely accepted today, however, is that of Burt 1943 (cited in Seaman & Powell 1996) whereby the home range is

"...that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as part of the home range."

Burt's definition implies that the pattern of habitat use is the principal determinant of home range shape and area. I do not adopt Burt's full vision in this study, because I consider the home range of an animal to be a dynamic entity that has the potential to expand or contract as a result of the exploratory behaviour of the animal. In this view the 'concept' of home range is temporary instead of permanent, as it depends on the intensity of the observational work, i.e. on how much time the researcher allows for exploratory behaviours to emerge and be recorded as 'fixes' for inclusion in home range area estimation. In the case of theis study, the home range is defined as the area the monkeys in the study group were known to use during the study period October 2001- September 2002.

A treatise on methods of home range area estimation would constitute a dissertation in itself and goes well beyond the scope of the present study. Various authors have reviewed various selections of methods and put forward arguments to justify the efficiency of one method over another (for example Seaman & Powell 1996, Ostro *et al.* 1999). Here I will concentrate on describing the method I used to estimate the home range area of spider monkeys in Punta Laguna.

It is common procedure in studies of primate ranging behaviour to accumulate data of the location of one or a group of animals in their habitat for a given period of time

(fixes). These fixes are plotted on a map of the study area and the home range area calculated through either of two non-statistical methods, the minimum convex polygon (MCP, Kenward 2000) or the grid-cell analysis (or grid-cell count method, Kenward 2000).

Minimum Convex Polygon (MCP) Method - The MCP method consists of drawing the smallest possible convex polygon around the outermost 'fixes' and then computing the area of that polygon.

Grid-Cell Counts (GCC) Method - The grid cell analysis consists of superimposing a grid of same-size cells on top of a map of 'fixes' and then computing the area of the total number of cells that contain fixes.

4.5.1   *Data used*

The GPS readings recorded during individual follows (except those of two individuals, see below) throughout the study were used in the procedures described here. Three measures of MCP home ranges were computed:

1) Group home range:

All GPS readings generated during the study were included in the same file

2) Home ranges by sex.

The GPS readings of males collected throughout the study were collated into a single file. The GPS readings of females were collated into a single file, and treated independently from the males'.

3) Individual home ranges:

All GPS readings of any one individual collected throughout the study were collated into a single file. Since I followed 11 individuals throughout the study, I produced 11 measures of individual home ranges.

Two individuals – one juvenile male and an adult female - were excluded from these analyses. The juvenile male Jose was excluded, because I did not follow him as intensively as the other males, as a result of his isolation from the group after the other males attacked him in January 2002. This individual later died due to a final attack from the same males in April 2002, when he apparently attempted to re-join the group. The adult female LaOtra was excluded from the analyses because she joined the study group in July 2002, and I did not follow her as intensively as the other females.

4.5.2 Methods

I used the grid cell count method in order to be able to compare my results with those of other published studies at the level of group home ranges (see below). I also computed the area of the home range by the MCP procedure for group, individual, and males/females home ranges for qualitative comparisons of home ranges within the study group. Finally, I used the GCC method to compute the core area of the study group, which I defined as the area where the monkeys were observed, and GPS readings made in 9 or more months (i.e. 80% or more) of the year. Since individual follows were less frequent in the month of December, I considered the year to be composed of 11 months, therefore in order to be included in the core area, cells had to have GPS readings of at least 9 months.

4.5.3 Delineation of the home range by the GCC method.

A file with a list of GPS readings was entered in the computer package *ArcView 3.2* in order to display them graphically and to perform home range delimitation. In *Arc View 3.2* I created a grid of cells of the same size. This grid was then superimposed on a graphic representation of the fixes collected in the study, i.e. the GPS records. The size of the cells can greatly influence the accuracy of the estimation: a very fine grid will lead to underestimation of home range area, and a coarse grid will tend to overestimate it. Cell size should be determined by each study's particular objectives, although it has been recently proposed that this should not be smaller than "the resolution of the tracking technique" (Kenward 2000). However, other authors have proposed that the length of the study subject's movement step (i.e. its speed of movement) should determine cell size

(White & Garrot 1990), as this would ensure that subsequent records of movement fall in separate cells and independence of the data is reached. The drawback of this approach is that the assumption of constant speed of movement for all species at all times during their movements is not entirely realistic.

I chose to use a grid with cell size of 100m x 100m, as used in many studies of primate ranging behaviour. It is worth mentioning that from an extremely conservative point of view, the tracking technique I used would have given a resolution of 20x20m, which if compared to the size I chose here, does not contradict the advice proposed by Kenward (2000). I considered a cell as part of the home range if at least one GPS reading was within it, therefore blank cells enclosed by occupied cells were not counted in this procedure even though they are visible in figure 4.3, within the whole home range. To estimate home range area the occupied cells enclosed by the polygon were counted and since the cell size was known the total area was computed from these.

To delineate the home range, a contour was drawn around occupied cells (fig. 4.3). Occupied cells that were separated from other occupied cells by one or more empty cells were not included in the delineation nor in the final count, as their disconnection from the home range may have been due to them being unreliable GPS readings rather than true monkey sightings.

Results and Discussion

According to the GCC method, a total of 152 cells contained at least one GPS fix, therefore the home range of the spider monkeys between October 2001 and September 2002 had a total area of 152ha (Fig, 4.3). This estimate is consistent with what has been reported in other studies of spider monkey ranging behaviour (see Table 4.3). The method used to estimate home range area is given for only a few of these studies (grid cell count method: Chapman 1988; Symington 1988a, Nunes 1995; MCP method: Ramos-Fernandez & Ayala-Orozco 2003), and in all of them group home ranges were estimated.
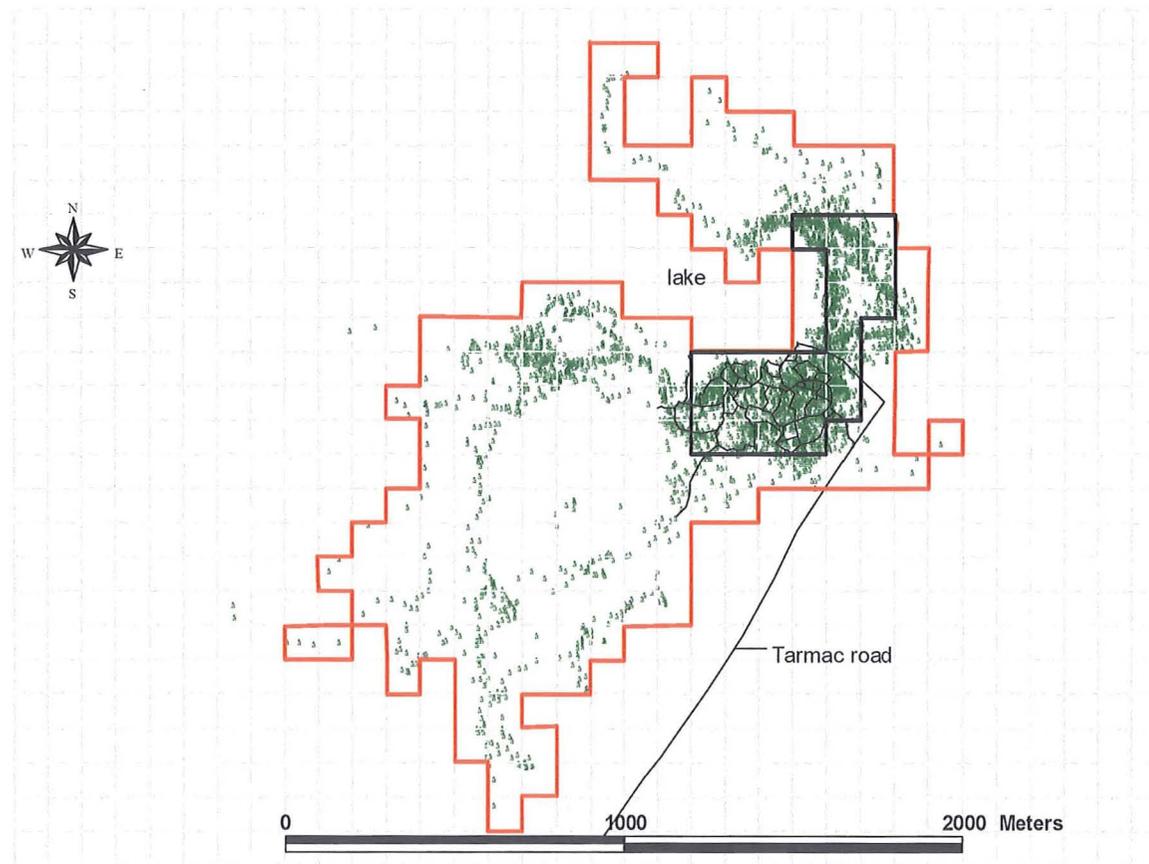
Figure 4.3. A grid of 100m x 100m cells was superimposed on top of the GPS readings (represented by points). The area delineated by the black contour is the core area of the study group. The red contour is the perimeter of the home range according to the procedure described in the text.

Table 4.3. Home range area for different spider monkey sites. The method used in each case is indicated: GCC = Grid cell count method; MCP = Minimum convex polygon method. ND = Data unavailable.

Location	Species	Daily Travel Distance (range in m)	Home range Area (km^2)	Reference, method used.
Suriname	*A. paniscus*	500–5000	2.5	van Roosmalen 1980, cited in (van Roosmalen & Klein 1988)*
Maraca Ecological Station, Brazil.	*A. belzebuth*	984-2460	3.2	Nunes 1995, GCC
Manu National Park, Peru	*A. paniscus*	465-4070	1.5, 2.3	Symington 1988a, GCC
North-eastern Bolivia	*A. paniscus*	ND	2.9	Wallace 1998*
BCI, Costa Rica	*A. geoffroyi*	ND	1.0-1.5	Dare 1975*
*	*A. geoffroyi*	ND	1.4	McDaniel 1994*
Santa Rosa, Costa Rica	*A. geoffroyi*	ND	1.4	Chapman 1988, GCC
Punta Laguna, Mexico	*A. geoffroyi*	1182-3872	0.95	Ramos-Fernandez & Ayala-Orozco 2003, MCP
Punta Laguna, Mexico	*A. geoffroyi*	398-3414	1.5, 2.2	This study, GCC, MCP

* Denotes results from PhD thesis cited in other texts, methods and/or location not mentioned in the citation.

Chapman's (1988) and Symington's (1988a) studies provide an average of individual home range areas that was consistently smaller than the group estimate. Their results led them to suggest that measuring group home range areas in this species is prone to overestimation due to the fission-fusion system of spider monkey social organisation. The group home range area reported here might be biased by observations of individuals which moved farther away than others, but this caution applies similarly to previous studies where the cell count method was used to estimate group home ranges, and it does not affect comparisons with such studies.

It is also interesting to note the discrepancy between my estimate and that of Ramos-Fernandez and Ayala-Orozco (2003) for the same study site. These authors estimated home range area from records of daily follows of all individuals in the group between 1997 and 2000, but used the minimum-convex-polygon (MCP) method instead. Thus a plausible explanation for the discrepancy would be that the two methods simply yield different results, but, as can be seen from my measure of group home range by the MCP method, the discrepancy persists. An alternative explanation is that the size of the home range of the study group in Punta Laguna has increased progressively over the years. This seems feasible, since group size has also increased from 1999 to 2002 (see Table 4.4).

As new independently-moving individuals are incorporated into the group (through development from infant to adult stages and/or through immigration of new individuals), the feeding needs of the group would also rise, thus affecting the size of the home range used. This has been confirmed previously for two populations of muriquis (*Brachyteles aracnoides*) studied in Brazil, where a small population of 7 individuals used a range area of 70ha, while the study population of 26 individuals used a larger area of 168ha (Strier 1987).

Table 4.4. Age and sex class of the study group over two different observation periods

Sex	1999[b]		2002	
	Females	Males	Females	Males
Infants	3	1	2	3
Juveniles[a]	2	2	3	1
Adults	5	3	5	5
Total	10	6	11	9

[a]Juveniles were independently moving animals that had not yet reached adult size.

[b]Data reproduced from (Ramos-Fernandez & Ayala-Orozco 2003) with permission from the authors.

Strier also observed an increase in home range of the study population over the course of the two years of fieldwork, which was attributed to the fact that their group size increased from 26 to 33 individuals. In the spider monkey group at Punta Laguna, something similar happened, as the adult cohort saw two "additions" over 3 years, from developing immatures rather than immigration, which might have been responsible for the larger home range area in 2002 than in 1999. Another possible explanation could be that a reduction in the availability of food sources in 2001-2002 forced the animals in the study group to look for alternative feeding sites outwith their usual ranging grounds. However, data on food availability from 1999 to 2002 do not exist; thus any conclusions regarding this issue can only be speculative.

Finally, according to the same method, a total of 22 cells contained GPS readings of at least 9 months, therefore the core area used by the monkeys in the study group had an area of 22 hectares.

4.5.4 *Delineation of home ranges by the MCP method.*

A file with a list of GPS readings was entered in the computer package *ArcView 3.2* in order to display them graphically and to perform home range delimitation. I used the program *Animal Movement*, which was installed in and accessed through the ArcView

platform. *Animal Movement* produced a MCP drawn around the outermost fixes entered (Figure 4.4A, B). I later manually adjusted this MCP to reflect the real area that the animals moved in, by excluding the lake from the final area computed (Fig. 4.4C). Another routine called *Area tools*, also installed in and accessed through ArcView 3.2 computed the area for the MCP automatically.

Results and Discussion

According to the MCP method, the group home range area (2.2 km^2) was 50% larger than calculated with the GCC method (See Table 4.5). Also, the measures of home ranges by sex indicated that males ranged over a larger area than females (1.9 km^2 and 1.4 km^2, respectively). However, when individual home ranges of males and females were compared, this difference was not significant (Mann-Whitney U = 18, N_1=5, N_2=6, p>0.05).

The results presented here are consistent with those reported by Chapman (1988), i.e. individual home range areas were smaller than the group home range area. An explanation for this discrepancy is that the individual home ranges exhibit a low degree of overlapping, and that some individuals range over a wider area than others, which results in an enlarged group home range area. The degree of overlap of individual home ranges was indeed very low (area of overlap zone: 0.13 km^2 or 5% of the group home range, fig. 4.5). Moreover, assuming maximum home range overlap, one would expect zero or only a small decrease in total shared area as each individual's data are added. Such a decrease was indeed small and stable, but it dropped abruptly when I added male home ranges into the computation (fig. 4.6). This suggests that males and females do not range in the same areas in the study site.
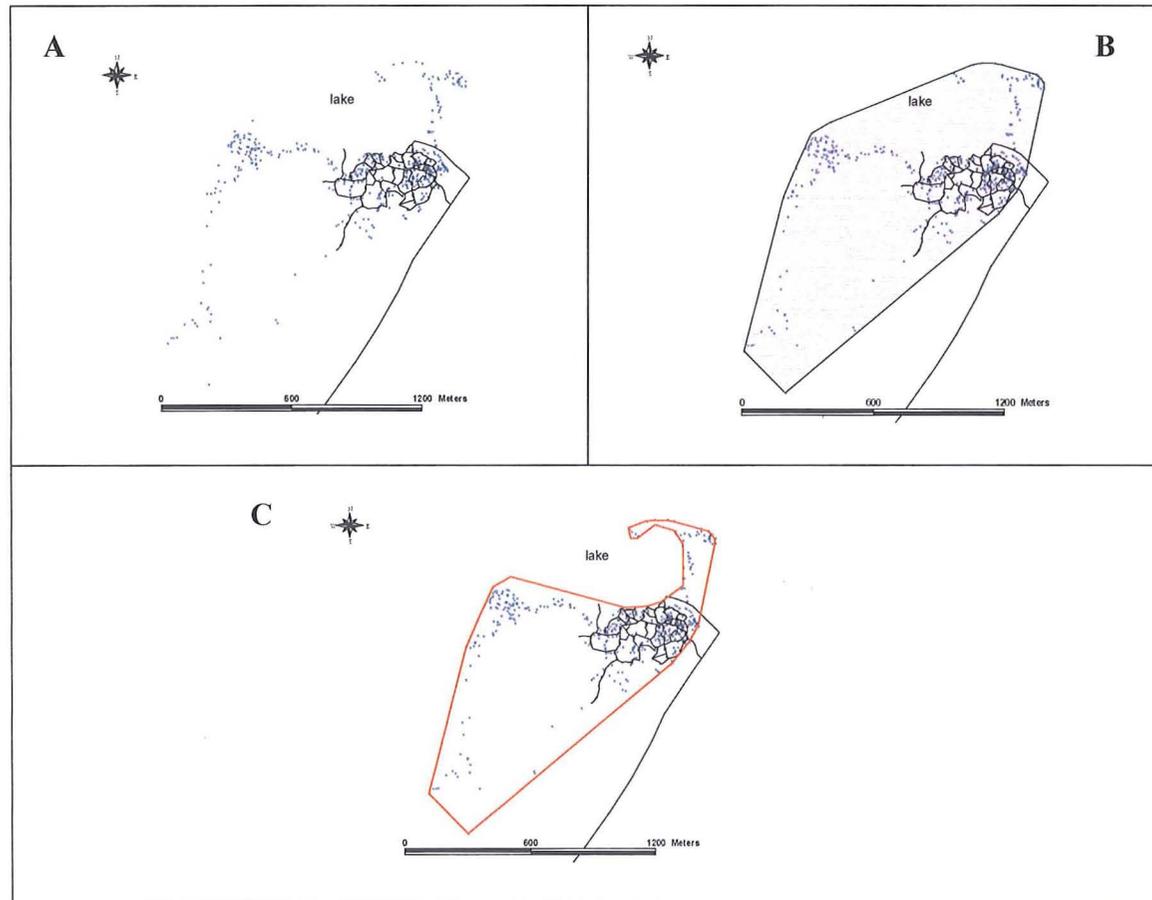
Figure 4.4. Example of an individual home range delineation by the MCP method. A: The GPS fixes are first displayed on screen; B: the routine *Animal Movement* delineates the MCP around the outermost fixes; C: the MCP is manually adjusted to exclude the lake, since the monkey could not have been traversed it in its daily movements.

Table 4.5 Home range area as computed by the MCP method.

Home range type	Home Range Area (km^2)	% of Group Home Range Area
Group home range	2.2	100
Home ranges by sex		
Males	1.9	86
Females	1.4	63
Individual home ranges		
Males		
Archi	1.0	45
Benito	0.5	22
Damian	0.4	18
Licho	0.9	40
Pancho	0.5	22
Average	0.6±0.3	
Females		
Cecilia	0.8	36
China	1.1	50
Claudia	0.9	40
Flor	0.7	32
Pilar	0.4	18
Veronica	0.8	36
Average	0.8±0.2	
All individuals average	0.7±0.2	
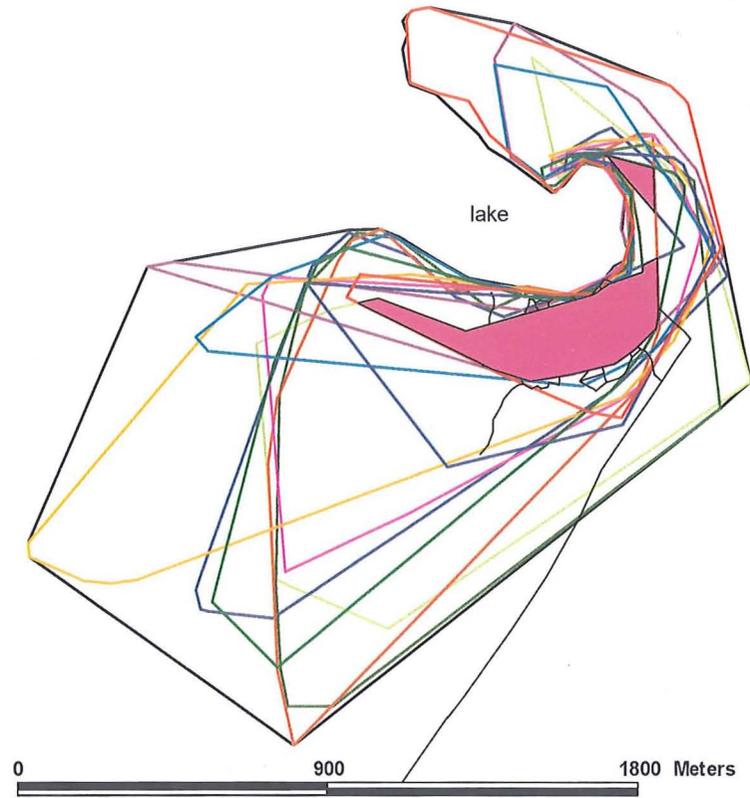
Figure 4.5. Overlap of individual home ranges. The outer polygon represents the group home range. The filled polygon represents the extent of the overlap of all individual home ranges (shown by polygons enclosed within the group home range).
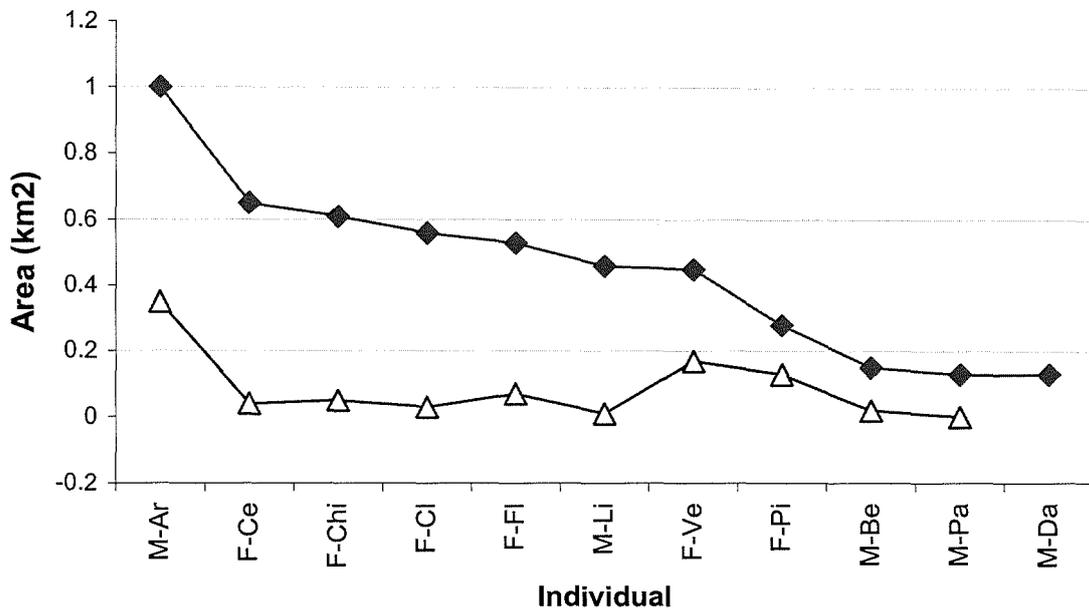
Figure 4.6. The decrease of home range area as each individual home range is added to the computation of shared home range (closed symbols). The M and F letters at the beginning of each individuals' name indicates the gender of the animal. Open symbols: absolute difference between current home range and the subsequent one.

4.5.5 *Summary*

Two non-statistic methods were used to calculate the home range area of the spider monkey group at the Punta Laguna site. The grid-cell count reported a home range area that was consistent with that measured in other studies of spider monkeys. The home range area calculated with the MCP method was larger than that reported for the same study group back in 1999, and this may be due to the increase in group size observed from 1999 to 2002.

Individual home ranges and home ranges by sex were also computed through use of the MCP method. Individual ranges were smaller than the group home range area and the degree of overlap of individual ranges was very low, suggesting that individuals range in different areas.

Differences in ranging behaviour within individuals of the same group may be a result of their social cohesiveness, and ultimately may provide insight into the nature of their social organisation. Thus, measurement of home range area of animals that live in groups should take into consideration the extent of group cohesiveness, and the methods used for analyses should be carefully chosen in accord with the aims of the study. Studies aimed at linking observations of social behaviour with ranging measures are needed in order to gain insights into the dynamics behind the social organisation of spider monkeys and other so-called fission-fusion societies.

Some authors have proposed that spider monkeys live in a highly-segregated social system of female subgroups and male-male alliances with uncommonly low levels of interactions between the sexes (Eisenberg & Kuehn 1968, Fedigan & Baxter 1984). This is somewhat in contrast to the predominant view that they live in typical fission-fusion societies where the group is not a cohesive social unit, yet males and females come into contact periodically (Symington 1988a, 1990). The results of my analysis of home range areas suggest that the spider monkey group at the Punta Laguna site was less cohesive than would be expected under the assumption of group ranging, and point to a possible gender-oriented segregation in ranging behaviour.

CHAPTER 5

MOVEMENT BETWEEN FOOD SOURCES I.

SEASONAL VARIATIONS IN RANGING BEHAVIOUR

5.1 Introduction

Biological environments, like the organisms that inhabit them, are dynamic entities: they undergo periodic transformations in size, species composition, or biomass content. Ecological factors like rainfall or temperature might play a role in determining some of these changes since they trigger or stop the production of leaves, flowers and fruit that different consumers use and that in turn affect the dynamics of food chains.

In order to meet dietary and shelter requirements most primates adjust their ranging and/or feeding behaviour to variations in their environments (i.e. annual rainfall, *Papio anubis*, Barton *et al.* 1992; *Ateles belzebuth belzebuth,* Nunes 1995), but mostly to changes in food availability (*Cercopithecus cephus, C. pogonias, and C. nictitans*, Gautier-Hion *et al.* 1983; *Saimiri oerstedi*, Boinski 1987; *Cebus apella nigritus*, Di Bitetti 2001). Some authors have specifically suggested that the production cycles of certain food plants might play a more direct role (*Ateles geoffroyi, Alouatta palliata, Cebus capucinus*, Chapman 1988), while others have argued that primates make a compromise between variations in food availability, motivation to explore non-visited areas of the habitat, and availability of water holes and/or sleeping sites (*Papio hamadryas*, Sigg & Stolba 1981). Yet others have proposed that a compromise lies between the avoidance of inter-group encounters and the availability of food (*Colobus badius tephrosceles,* Struhsaker 1974). Environmental diversity of primate habitats is large, as is the diversity of primate feeding and ranging strategies. Elucidating general environmental or social determinants of ranging behaviour requires many species/populations/environments to be sampled and documented.

Variations in rainfall are relatively consistent throughout some environments: in temperate, highly-seasonal systems, the dry season is more prolonged than the wet

season; in tropical, wetter seasonal systems, the opposite is closer to the reality. Unless meteorological disasters (i.e. tropical storms or hurricanes, El Niño or La Niña phenomena, etc.) occur, parameters like rainfall and temperature remain reasonably predictable for many environments. When food availability is considered, predictability is more limited, mainly because plants can be quite flexible in how they adjust their reproductive strategies to environmental conditions, thereby adding uncertainty to their own patterns of flowering and fruiting. Variations in food production are thought to be more influential in determining the ranging patterns of primary and secondary consumers than variations in meteorological conditions (i.e."... food availability is likely to have a stronger effect on feeding behaviour than climatic variation *per se* ..." p. 552, Clutton-Brock 1977)

My observations of the study group during a 3-month pilot study at the Otochma'ax Yetel Kooh reserve in the spring of 2001 suggested that spider monkey ranging patterns might be influenced in part by the proliferation of fruits on certain trees, which the monkeys visited on a string of days until the sources were depleted. These events also pointed to the possibility that the monkeys were somehow able to track food abundance in their habitat and perhaps use spatial memory of some fruit-laden locations in their ranging decisions. The spider monkeys in the study group live in a highly-seasonal environment where the species they feed on show variable production cycles (personal observation). As a first step into the investigation of spatial cognitive abilities, I investigated whether seasonal variations in climatic conditions influence spider monkey ranging patterns or whether they were determined by factors other than these. In this chapter there are attempts to clarify the role of ecological variables in determining the ranging behaviour of spider monkeys when they move between food sources. The issue of the use of spatial memory by spider monkeys in their foraging activities will be dealt with in the next chapter.

5.2 Aims

i) To characterise the travel movements made by the monkeys in the study group between important targets.

ii) To determine whether and how ecological variables influenced these movements.

5.3 Methods

I used the travel paths re-constructed from GPS records and feeding duration at feeding sites throughout a travelled route to determine **stop sites**. A stop site was defined as the location at which the focal animal remained stationary for a total of or more than 4 minutes. I regard these sites as potential targets that the animals may have planned to visit in advance or where movement decisions may have been made.

Each day's behavioural records and the matched GPS readings were screened to identify the stop sites in the route. Each day's travel path, a string of GPS co-ordinates, was then split at the stop sites and the resulting **route segments** were used as data points for the analyses. Thus, each route segment had a start, a string of intermediate points, and a stop site.

The usefulness of this approach is that it allowed me to examine how the monkeys moved between locations that were apparently relevant to them. For the analyses, several calculations were computed on the route segments:

a) Length of route segment: this was computed by adding up the scalar distances between each of the GPS readings in a given route segment.

b) Direct distance (or the scalar distance between start point and stop site): this was computed by calculating trigonometrically the distance between the start and the stop site of the route segment.

c) Linearity ratio: computed by dividing direct distance (b) by length of route segment (a)

d) Feeding time at the stop site: computed by adding up the duration of all feeding events that occurred while the focal animal was stationed at the stop site. This includes feeding events on trees that were contiguous (<10m) to the stop site, even if the focal animal moved a short distance to get in touch with it.

e) Total time at the stop site: computed by adding up the total time that the focal animal was stationed at the stop site. This includes non-feeding behaviours.

f) Food identity: this is the species name of the plant on which the focal animal fed while it was stationed at the stop site.

On a few occasions GPS readings could not be produced, probably due to lack of enough satellite inputs to achieve a precise triangulation. If all points in a route segment except the start point and the stop site lacked GPS readings, or if a few of them were grossly inaccurate, that route segment was not included in the analysis.

To determine the duration of the wet and the dry seasons I used the annual precipitation chart that was obtained from the Valladolid meteorological station (see chapter 4 for a graph). The maximum and minimum temperatures remained fairly stable throughout the year, but the rainfall increased steadily from May to June. Thus, between October 2001 and September 2002 the dry season began apparently in late October and extended until May, while the wet season began in June and lasted until my field season was over in late September.

5.4   Statistical analyses

In order to investigate the possibility that individual variation had an effect on ranging patterns, repeated measures one-way ANOVA analyses were performed on linearity ratios, length of segment, and time spent feeding with individual as the factor. The data

used in the test were averages of linearity ratios, length of segment and time spent feeding for each individual in each month. The within-subjects comparison was carried out between the first and the last six months of the year (first six months: October to March, last six months: April to September).

To determine the effect of month of the year and of species consumed on ranging patterns, one-way ANOVA analyses were performed, with month or species eaten as the factor. To account for instances of pseudo-replication, the data entered in these analyses were averages of the median linearity ratios, length of segment, and feeding time of each individual in each month.

Post-hoc comparisons (Tukey's test) were performed to determine which months and/or species of food consumed showed significant differences. For all ANOVA analyses performed, $\alpha = 0.01$, due to the multiple testing involved. For the analyses of linearity ratios and direct distances, I included all route segments, except those where the GPS records were not reliable. For the analysis of time spent feeding, I included all route segments at which time spent feeding was at least 60 seconds. Unreliable GPS data were not a concern in this case, given that the dependent variable (time feeding) could not have been affected by the reliability of the GPS readings.

5.5 Results

5.5.1 *Is there individual variation in spider monkey ranging patterns?*

Linearity ratios

A repeated measures ANOVA was conducted to compare mean linearity ratios during the first six months of the year to those during the last six months of the year. There was a significant effect of time of the year, Wilks' Lambda = 0.77, $F_{(1, 55)} = 15.75$, $p<0.0005$, multivariate eta-squared = 0.22. The effect of individual on linearity was not significant, however, $F_{(10, 55)} = 1.12$, $p = 0.35$, eta-squared = 0.17 (fig. 5.1).
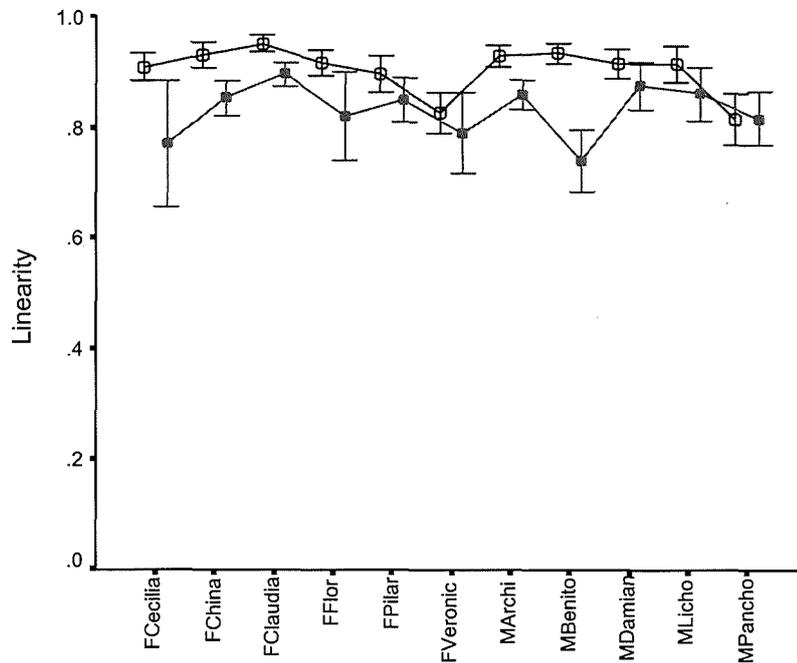
Figure 5.1 Mean linearity ratios of individuals during the first (open symbols) and the last (closed symbols) six months of the study. The error bars are one standard error of the mean.

Segment length

A repeated measures ANOVA was conducted to compare mean segment length during the first six months of the year to that during the last six months of the year. There was a significant effect of time of the year, Wilks' Lambda = 0.9, $F_{(1, 55)}$ = 0.05, p = 0.82, multivariate eta-squared = 0.001. The effect of individual on segment length was significant, $F_{(10, 55)}$ = 7.04, p<0.005, eta-squared = 0.56 (fig. 5.2). *Post-hoc* tests revealed that this effect was due to the high mean segment length of the adult male MPancho, as the significant differences in all cases were related to this individual. Only one of those differences was not significant under the strictly-conservative level chosen (Mpancho v. Mbenito, p = 0.03), thus, it is safe to conclude that in most instances the rest of the study group moved to stop sites that were at distances between 90 and 200m from the start point.
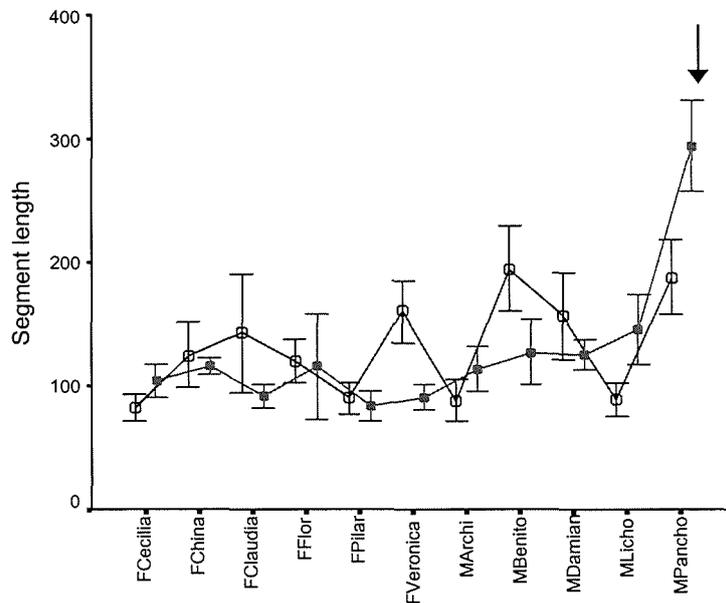
Figure 5.2 Mean segment length (in metres) of individuals during the first (open symbols) and the last (closed symbols) six months of the study. The error bars are one standard error of the mean. Mean segment lengths of all individuals were significantly different from the mean of Mpancho (indicated by the arrow).

Time spent feeding at the stop site

A repeated measures ANOVA was conducted to compare mean time spent feeding during the first six months of the year to that during the last six months of the year. There was no significant effect of time of the year, Wilks' Lambda = 0.97, $F_{(1, 55)}$ = 1.53, p = 0.22, eta-squared = 0.02. The effect of individual on time spent feeding was not significant either $F_{(10, 55)}$ = 1.84, p = 0.07, eta-squared = 0.25 (fig. 5.3).
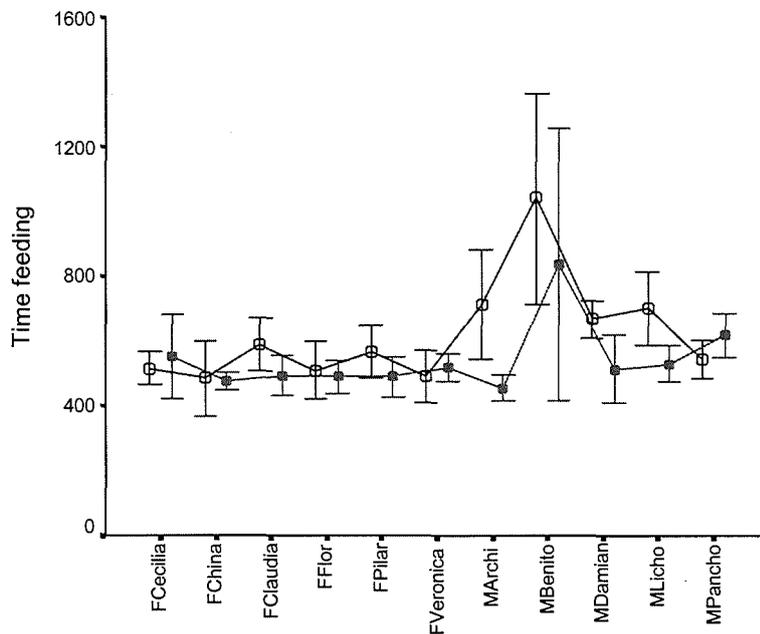
Figure 5.3 Mean time spent feeding (sec/bout) at the stop site during the first (open symbols) and the last (closed symbols) six months of the study. The error bars are one standard error of the mean.

The results so far are consistent with the assertion that there is no individual variation in spider monkey ranging patterns, except for the single case of the unusually long segments of an adult male. I did not follow this individual as intensively throughout the year as I did with others (see chapter 3), however and its sample size of route segments was small relative to other individuals. I thus assume that including data of this individual in subsequent statistical tests will not contribute a considerable effect to the results of the month-by-month analysis. This individual was the oldest male in the group, and informal observations of his behaviour indicate he was no different from the rest of the group, except for the number of days/week that he ranged along with the group (i.e. a rough average of two days every week). Thus, the ranging patterns of this individual would have to be unusually different from the rest of the group in order for it to have an effect in the month-by-month analysis. With this in mind, I combine data for all individuals in the following analyses.

5.5.2   Is there monthly variation in spider monkey ranging patterns?

Linearity ratios

I hypothesised that the monkeys would move over straighter paths (i.e. higher linearity ratios, closer to 1.0) in the dry months than in the wet months. This hypothesis is based on assuming that food availability in the dry months was low and in the wet months was high. Although I did not perform any surveys of food availability at the field site I was aware of periods – mostly in the dry season- when some fruits were absent from the core area. My assumptions are based on this informal observation.

A one-way ANOVA of linearity with month as the factor revealed an effect of month on linearity ($F_{(11, 96)}$ = 2.3   p=0.01, see fig. 5.4). *Post-hoc* comparisons revealed that there were significant differences only between the months of October and June in the direction of my prediction, but not for the rest of the months compared. This analysis also showed that virtually all route segments were close to beeline distances in length (77% of routes had scores above 0.8, and 22% above 0.6), in other words, spider monkeys moved over rather linear paths to reach stop sites throughout the whole year.
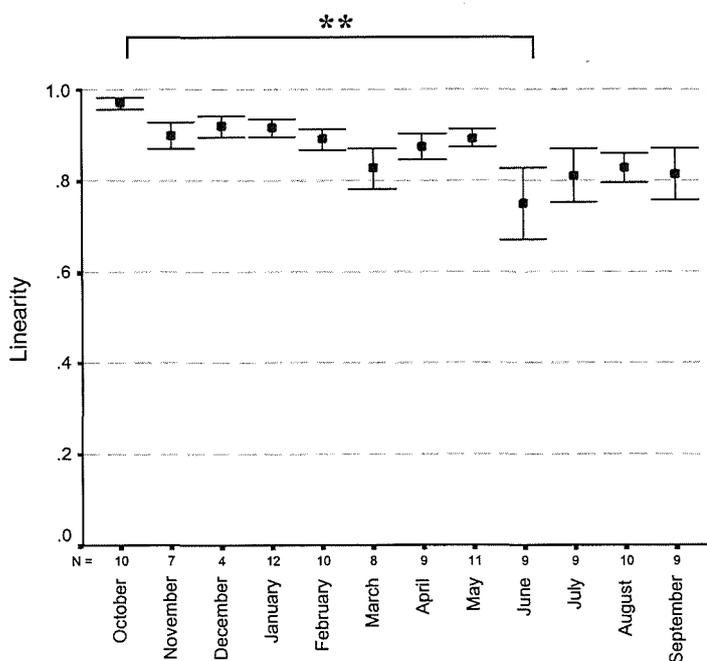
Figure 5.4. Mean linearity ratio (vertical axis) of route segments analysed per month of the year (horizontal axis). Error bars are 1 standard error of the mean. Only significant differences are shown; **: p<0.01.

The route linearity analysis in itself however, is not sufficient to investigate whether these movements took place within sight of the stop sites. It may be that the high linearity ratios observed were a result of movements made within sight of the stop sites. If this was the case, I would expect to observe longer route segments in wet months when food was readily available and probably more easily detected than in the dry months when food was scarce. The next analysis shows the effect of month of the year on route segment length.

Lengths of route segments to stop sites

For this analysis I used all route segments, except those where GPS data were unreliable. A one-way ANOVA of beeline distance with month of the year as the factor did not reveal a significant effect of month on beeline distance ($F_{(11,96)}$ = 1.5 p=0.1, see fig. 5.5).
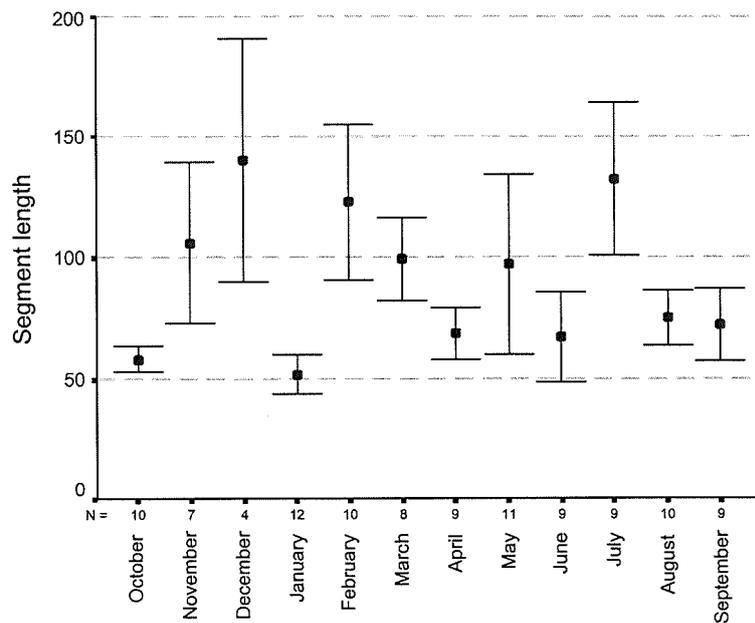
Figure 5.5. Mean segment lengths in meters (vertical axis) of route segments analysed per month of the year (horizontal axis). Error bars are 1 standard error of the mean.

Time spent feeding at stop site

In terms of the time spent feeding at a stop site I did not have a specific hypothesis. Spider monkeys might be relatively flexible in how much time they spent feeding on food sources at different times of the year and I would expect variation in this parameter. For this analysis I included all route segments, irrespective of reliability of GPS data, given that the dependent variable (time feeding) should not have been affected by the reliability of the GPS readings. A one-way ANOVA of feeding bout length with month as the factor did not reveal a significant effect of month on time spent feeding ($F_{(11, 93)}$ = 1.4 p=0.2, see fig. 5.6).
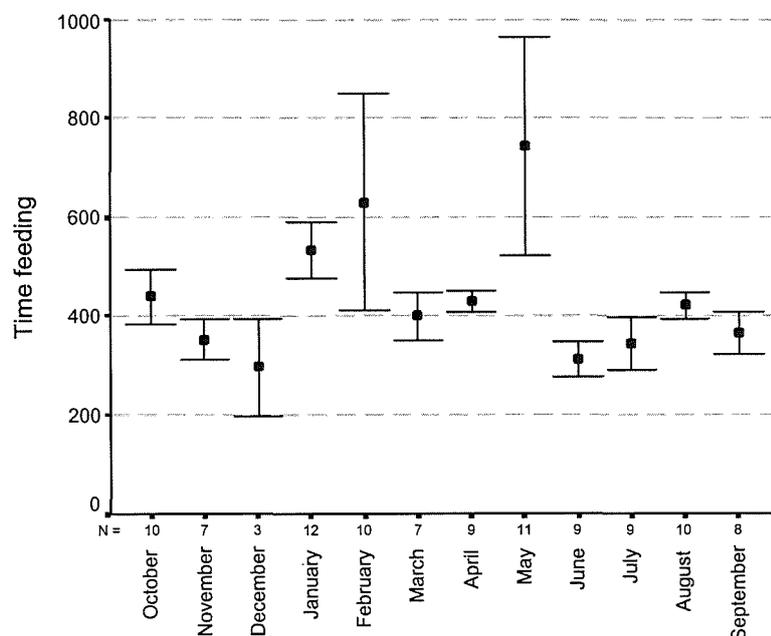
Figure 5.6. Mean time spent feeding (sec/bout) at the stop site, for route segments analysed per month of the year (horizontal axis). Error bars are 1 standard error of the mean.

5.6   Summary of results

i)   Individual differences in ranging did not have a significant effect on linearity ratios, distance to the stop site or time feeding at the stop site.

ii)   Notably, spider monkeys moved over very straight paths to get to food sources. This was evidenced by the fact that all linearity ratios for the year fell between 0.7

and 0.9. The variation in route linearity observed suggests that the ranging behaviour of the spider monkeys at the study site was only slightly affected by the transition from the dry into the wet season, but dry/wet season differences were not consistent, as linearity ratios remained high across the year.

iii)   The monkeys moved over distances of 90 to 200 m to get to the food sources they exploited. The direct distances to stop sites varied within the dry and wet seasons and there were no clear differences between the dry and the wet months.

iv)   The monkeys fed at stop sites for variable amounts of time throughout the year, so that each month of the year was slightly different to the next. This pattern suggests that variations from month to month (i.e. changes in the production cycles of species consumed), instead of from season to season, may be responsible for the variation observed in these characteristics of feeding behaviour.

Although variations in food availability due to variations in the productive cycles of plants in seasonal environments may be closely related to meteorological conditions (Barton *et al.* 1992), the link between these non-biological factors and the monkeys' ranging patterns does not necessarily need to be as direct. In fact, the monkeys in the study group did not adjust features of their ranging patterns (distance to stop site or time feeding at stop site) to the rainfall or temperature patterns observed.

Different plant species show different responses to changes in the physical characteristics of their environment (nutrients in the soil, rainfall, temperature, and climatic disasters). The variable environmental conditions under which many forest species grow have produced different adaptations to the problem of absorbing water and nutrients from the soil. While many plants produce flower and fruits every year, others can delay fruit production until the optimal environmental conditions arise, thus their production cycles are not consistent but rather would appear to be asynchronous.

It might be possible then that the monkeys were adjusting their ranging to the specific fruiting patterns of only one or two of their preferred types of food, regardless of

the availability of other species. Thus, I decided to look more closely at the foods that the monkeys consumed throughout the year. The aim of this approach was to have a better idea of how the spider monkeys move between specific types of resources. This alternative approach takes the natural variation in fruiting cycles of each species into account instead of the variation in temperature or rainfall.

5.7 Diet of the spider monkeys

For these analyses I used the same database of route segments that was used in the procedures described above. As expected, there was an effect of type of food (or water) on time spent feeding/drinking (One-way ANOVA with type of food and water as the factor: $F_{(2,29)}$ = 10.16, p<0.0005, fig. 5.7). *Post-hoc* tests indicated that spider monkeys spent more time feeding on fruits (X = 416.8, SD = 58.4) than feeding on leaves (X = 265.6, SD = 97.5) or drinking water (X = 188.1, SD = 203.4).
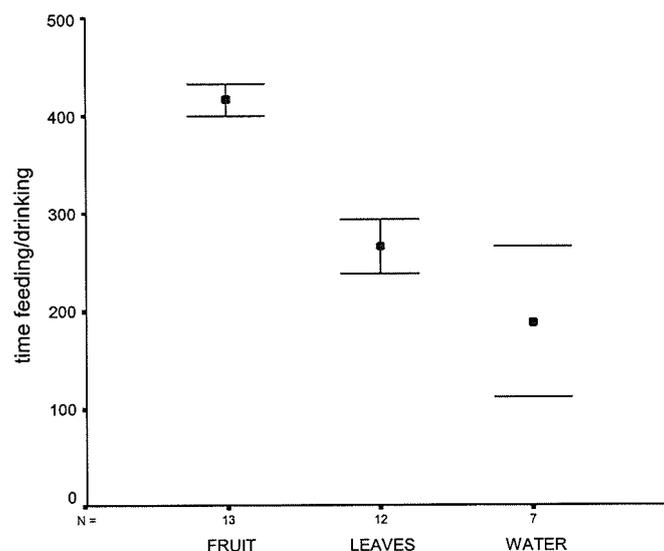
Figure 5.7. Mean feeding/drinking time in s/bout for different resources throughout the year. The spider monkeys also consumed flowers at a stop site, but once only.

Spider monkeys consumed 31 species of fruits at stop sites but only 13 of them made up 1% or more of the diet, by time feeding. Together with leaves and unidentified trees these 13 species make up 95% of the total time spent feeding, (Table 5.1). Spider monkeys fed on the majority of the species listed on Table 5.1 at limited times of the

year. The proportion of time feeding that was spent on each type of fruit species on each month in listed in Table 5.2. The monkeys fed only on three species consistently throughout the year (i.e. *B. alicastrum*, *Ficus* sp. and *F. cotinifolia*) suggesting these were available throughout that period of time. This cannot be confirmed in species that were not consumed on a given month, since it is not possible to know whether the monkeys did not consume them as a result of their ranging decisions (i.e. moving into areas where that particular type of food does not occur) or because they were simply not available.

For the following analyses I include the 13 species on which the monkeys fed at least 1% of the time spent eating plus the rest of the species clumped under the category 'other', NI trees and Leaves.

Table 5.1. Proportions of the annual time spent feeding accounted for by each species consumed at stop sites. Species in bold make up 95% of the total time spent feeding.

Common name	Species	%
Ramon	***Brosimum alicastrum***	22
Alamo	***Ficus* sp.**	16
NI	***Unidentified trees***	13
Copo	***Ficus cotinifolia***	8
LEAVES	***LEAVES***	5
Cheche	***Metopium brownei***	5
Zapote	***Manilkara zapota***	5
Pixoy	***Guazuma ulmifolia***	4
Pich	***Enterolobium cyclocarpum***	3
Kilim	***Spondias lutea***	3
Jujub	***Spondias mombin***	2
Huaya	***Talisia olivaeformis***	2
Sayaak	***NI***	2
Tsilil	***Diospyros cuneata***	1
Yaxnik	***Vitex gaumeri***	1

Table 5.1 (cont.)

Common name	Species	%
Caracolilllo	*Sideroxylon capiri*	0.6
Morax	*NI*	0.4
Copal	*Bursera bipinnata*	0.2
Jirinich	*NI*	0.1
Ceiba	*Ceiba pentandra*	0.1
Ciruela	*Ziziphus jujuba*	0.1
FLOWERS	*FLOWERS*	0.1
Botox	*NI*	0.1
Tsitsmuk	*Dalbergia glabra*	0.1
Xuul	*Lonchocarpus yucatanensis Pittier*	0.1
Guarumbo	*Cecropia peltata*	0.1
Tatzi	*Hippocratea celastroides*	0.1
Pasache	*Simarouba glauca*	0.1
Toxtab	*Guettarda combsii*	0.1
Tohiu	*Coccoloba acapulcensis*	0.1
Cinche	*Caesaria nitida*	0.05
Isaki	*NI*	0.04
Kanaste	*Sideroxylon foetidissimum*	0.03
Anona	*Annona cherimola*	0.02

NI: Unidentified trees

Table 5.2. Percentage of time spent feeding on different species per month. The 13 species in the left column are arranged as in table 1.Cells with >40% are highlighted.

Species	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Brosimum alicastrum	11.1	41.0	--	37.3	18.8	13.9	26.3	3.9	13.3	33.5	28.5	38.3
Ficus sp	15.9	4.6	2.3	11.9	32.3	7.8	5.4	46.7	2.7	--	6.0	3.3
Ficus cotinifolia	24.2	--	--	16.7	8.0	--	6.4	1.0	3.7	0.3	--	--
Metopium brownei	0.1	--	--	--	--	--	3.3	4.7	0.3	31.0	38.4	2.8
Manilkara zapota	0.1	13.7	--	1.8	8.6	19.4	18.6	2.4	1.4	--	--	--
Guazuma ulmifolia	--	3.5	--	12.4	12.4	17.9	--	--	--	--	--	--
Enterolobyium cyclocarpum	--	--	--	--	--	6.4	17.0	8.0	--	--	--	--
Spondias lutea	4.1	--	--	--	--	--	--	--	--	--	--	36.7
Spondias mombin	12.0	10.6	--	--	--	--	--	--	--	--	--	1.5
Talisia olivaeformis	--	--	--	--	--	--	--	--	42.8	9.6	--	--
Sayaak	11.2	--	--	--	--	--	--	--	--	--	6.0	--
Diospyros cuneata	--	6.1	71.6	2.4	2.1	--	--	--	--	--	--	1.3
Vitex gaumeri	--	--	--	--	--	--	--	--	--	--	5.6	9.2
Other*	0.6	1.1	9.5	0.4	5.6	3.6	1.7	1.0	5.8	3.2	4.3	1.2
Total % fruit	**79.3**	**80.6**	**83.4**	**82.9**	**87.8**	**69**	**78.7**	**67.7**	**70**	**77.6**	**88.8**	**94.3**
Total #spp eaten	10	7	3	8	12	7	8	8	10	6	8	8
Leaves	3.15	10.5	--	2.15	4.0	5.6	6.4	9.2	25.3	3.9	2.7	3.8

* refers to species that were not in the top 13 list

5.7.1 *Is there variation due to species consumed in spider monkey ranging patterns?*

Linearity ratios

There was an effect of species on the linearity of the route segments analysed ($F_{(15, 141)} = 4.1$, $p < 0.001$; fig. 5.8). *Post-hoc* tests revealed that this effect was due to the route segments leading to *T. olivaeformis* trees, since these were significantly less linear than those of some of the other species. The same analysis indicated that there were no significant differences in linearity among the route segments that led to other species.

This analysis also showed that virtually all route segments were close to beeline distances in length (82% of routes had scores above 0.8, and 18% between 0.6 and 0.8), in other words, spider monkeys moved over linear paths towards the majority of species in their diet. The next analysis shows the effect of species consumed on the length of segments to stop sites.
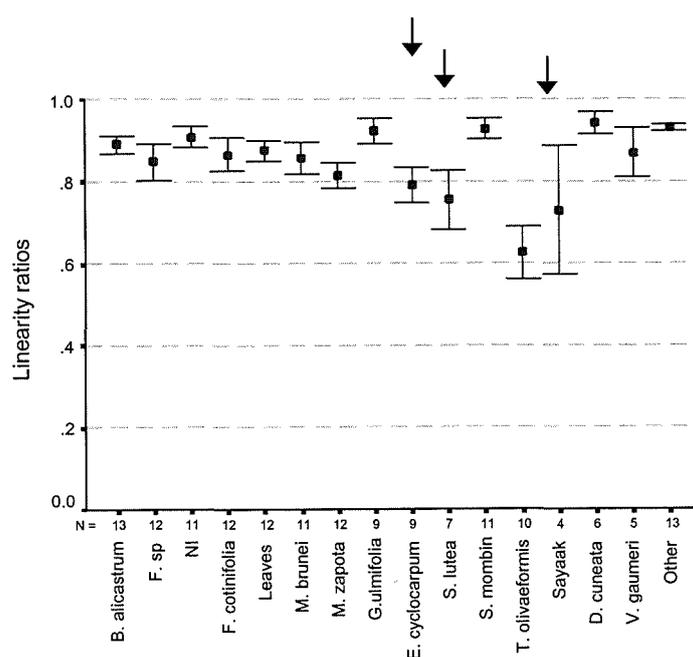
Figure 5.8. Mean linearity ratios (vertical axis) for the 16 species consumed (horizontal axis) by monkeys in the study group. The species are plotted in the same order as in Table 5.1. The bars are 1 standard error of the mean. T. olivaeformis was significantly different (p<0.01) to all species except to the ones indicated by the arrows.

Segment length

There was an effect, albeit weakly significant, of species consumed on the length of segments to stop sites ($F_{(15, 141)}$ = 1.9, p<0.05; fig. 5.9).

Post-hoc comparisons revealed that route segments ending at *B. alicastrum* trees were significantly shorter than those leading to *D. cuneata* trees were. For the rest of the species analysed, there were no significant differences. In the next analysis I investigate variation in time spent feeding on the species consumed.
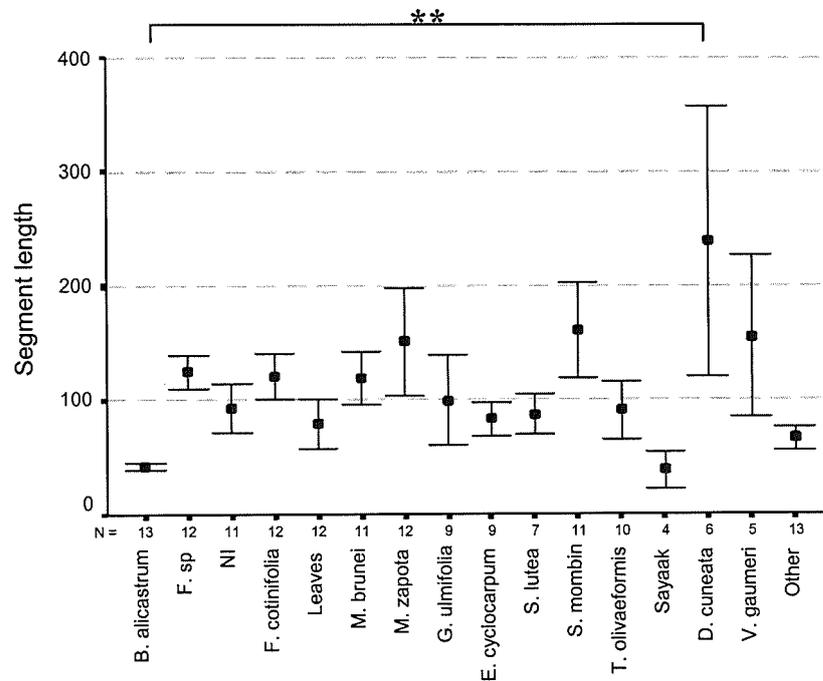
Figure 5.9. Mean segment length (in meters, vertical axis) to stop sites of each of the 16 species consumed (horizontal axis) by the monkeys in the study group. The species are plotted in the same order as in Table 5.1. The bars are 1 standard error of the mean. **: p<0.01

Time feeding

There was an effect of species consumed on time feeding (F $_{(15,148)}$ = 5.9, p<0.001; fig. 5.10). *Post-hoc* comparisons revealed high variation in time spent feeding on certain species. Spider monkeys spent more time feeding on *F. cotinifolia* and on *F. spp.* than on several of the other species that form part of their diet (Table 5.3).
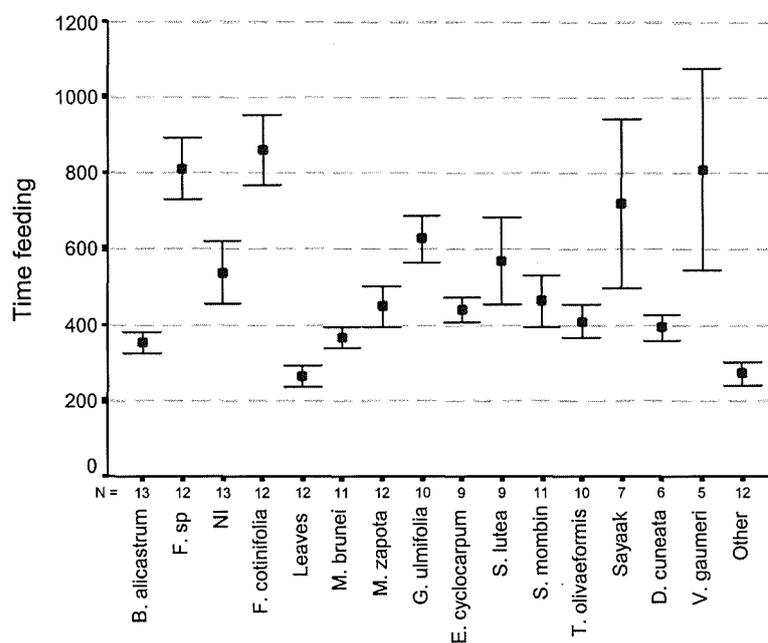
Figure 5.10. Mean feeding time (in seconds, vertical axis) at stop sites for the 16 species (on the horizontal axis) the monkeys in the study group fed on. The species are plotted in the same order as in Table 5.1. The bars are 1 standard error of the mean. Significant differences are displayed in Table 5.3.

Table 5.3 Significant differences in time spent feeding at stop sites of 16 foods consumed by monkeys in the study group.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
X	***		***											***		1 B. alicastrum
	X			***	***	*					*			***		2 F. sp
		X														3 NI
			X	***	***	***		**		**	***		**	***		4 F. cotinifolia
				X								**		***		5 LEAVES
					X											6 M. brunei
						X										7 M. zapota
							X									8 G. ulmifolia
								X								9 E. cyclocarpum
									X							10 S. lutea
										X						11 S. mombin
											X					12 T. olivaeformis
												X		**		13 Sayaak
													X			14 D. cuneata
													X	**		15 V. gaumeri
															X	16 Other

* Significantly different to the shaded rows.

** Significantly different to species with underlined names.

5.8 Summary of results

1) Spider monkey movements to 16 different species of food were highly linear across the year. Moreover, they did not appear to restrict their straight-line movements to certain species (except for the case of movements ending at *T. olivaeformis* trees).

2) The monkeys in the study group were able to move up to 250 m in a near-linear manner (see mean direct distance and linearity to *D. cuneata* fruits, Table 5.4). This is not an isolated observation; in fact, for the rest of the species analysed the mean distance to the stop site was close to this value (ranging from 76 to 197m). This is the first report of the length of free-ranging spider monkey's straight-line movements to feeding sites.

3) The three species that had the highest proportions of the annual time spent feeding were *B. alicastrum*, *Ficus spp.* and *F. cotinifolia*. The longest feeding times were spent on *Ficus spp* and *F. cotinifolia* fruits, but not on *B. alicastrum* fruits. Although feeding time may be related to prey handling time (or "pursuit time", MacArthur & Pianka 1966), I did not see obvious differences in the way the monkeys processed *B. alicastrum* and *Ficus* fruits before ingesting them. Thus the observed differences in feeding times between these species could be related to differences in feeding preferences.

Table 5.4. Summary of route segments towards 13 top fruit species. The species are arranged as in table 5.1.Data in the last three columns are means.

Species	Months eaten	t Feeding (s)	Distance (m)	Linearity
B. alicastrum	11 (Jan-Oct, Dec)	491.2	76.5	0.8
F. sp	11 (Jan-Apr, Jun-Dec)	951.8	151.3	0.8
F. cotinifolia	7 (Jan-Feb, Apr-Jul, Oct)	1024.7	156.1	0.8
M. brownei	7 (Apr-Oct)	451.1	146.9	0.8
M. zapota	8 (Jan-Jun, Oct-Nov)	499.7	126.5	0.8
G. ulmifolia	4 (Jan-Feb, May, Nov)	633.2	101.1	0.8
E. cyclocarpum	3 (Mar-May)	531.2	84.8	0.7
S. lutea	2 (Oct-Sep)	491.1	93.4	0.7
S. mombin	3 (Sep-Nov)	446.4	150.5	0.9
T. olivaeformis	2 (Jun-Jul)	466.5	107.3	0.6
Sayaak	2 (Aug, Oct)	724.7	197.2	0.8
D. cuneata	5 (Jan-Feb, Sep, Nov-Dec)	524.0	230.6	0.9
V. gaumeri	2 (Aug-Sep)	805.5	140.5	0.8

5.9 Discussion

The ranging patterns of a group of wild spider monkeys were influenced, but not entirely determined, by weather conditions when they moved between food sources. Although month of the year had a significant effect on the distance that the monkeys travelled to food sources, this was not as predicted by simple seasonality effects. Moreover, long distances to food sources were observed in only two of the dry months of the year, despite the prediction that long distances would be more likely to be covered during all of the dry season. Month of the year apparently also had a significant effect on the time spent feeding at stop sites, but again this was variable throughout the year. In particular, there was variation within the dry months, revealed by the fact that feeding stops averaged short and long periods in contiguous months (Oct-Nov, Dec-Jan, and Apr-May). Feeding times remained relatively more stable during the wet months than in the dry months.

5.9.1 *Seasonal variations in ranging patterns*

Estimates of food availability were not taken into account in this study so conclusions cannot be made that relate the monkeys' behaviour to periods of high or low food availability. The results indicate that spider monkey ranging patterns were not closely associated to rainfall pattern. This might be due to the fact that the monkeys were tracking other variations in the environment that were not directly related to weather conditions. For example it could be possible that the presence and distribution of preferred or very seasonal, but important, fruit species played a role in determining the ranging patterns. Other factors not taken into account in this study could have been responsible for the ranging patterns observed, i.e. spatial distribution of preferred foods, or asynchronous production cycles of preferred foods. An ecological study of productive cycles of the plant species of the study site would give insight into this matter.

5.9.2 *Relevance of specific food items consumed.*

It was revealed that spider monkeys ate 5 species of fruit during most months of the year (i.e. *B. alicastrum, F. spp, F. cotinifolia, M. brownei,* and *M. zapota*). There was no significant variation in the distance that the monkeys moved to get to these species

despite the fact that it would have been unlikely that the monkeys visited always the same trees of these species in different months of the year. Moreover, these movements were near linear in most cases, with linearity ratios above 0.8. Thus, the monkeys must have relied strongly on the availability of these 5 key species for their diet, and since they could be found in the study site at different times of the year their ranging did not reflect the variation in rainfall patterns.

The monkeys ate the rest of their 'top 13' fruit species only in certain months (range 2-4 months). Informal observations of the availability of these species at different times of the year suggest that they were highly seasonal (e.g. *E. cyclocarpum*, *S. lutea*, *T. olivaeformis*, sayaak and *V. gaumeri* were not visible on trees outside the months when the monkeys ate them). There was no significant variation in the distance that the monkeys moved to get to these species, except for sayaak and *D. cuneata* fruits where the distance was on average, longer than for other species. Nevertheless movements to all of these were also near-linear in most cases, exhibiting linearity ratios above 0.65. Movements made to *T. olivaeformis* trees were not as linear as those made to other species but this might have been due to the spatial arrangement of *T. olivaeformis* trees in the field site. All the fruit-bearing trees of this species that the monkeys visited were near each other. This made them look like an oversized single patch, unlike most other species eaten (personal observation). The few highly linear movements to *T. olivaeformis* trees observed (i.e.linearity scores >0.7) could have been made to reach the patch of *T. olivaeformis* trees, but within this patch the linearity of the movements decreased, probably as a consequence of movements with high turning rates made as the animals were depleting the patch.

5.9.3 *Diet of the spider monkeys at the 4-min stops.*

Ideally, studies of the diet of wild primates should take into account some measure of the nutrient content in the food consumed by the study animals. This was beyond the scope of this study, but the data I collected might provide some preliminary insights into the diet of spider monkeys at the study site, in so far as it relates to the stops made at food sources that were consumed intensively (>4 minutes). Although it was not possible to

determine the times of low and high food availability in the year, the fact that the proportion of fruit in the annual diet of the monkeys remained stable throughout suggests that, even if there were periods of food shortage, the monkeys were able to cope with the task of finding fruits. This also suggests the monkeys might have been maximising their intake of energy in the form of fruit.

Leaves were consumed in different proportions each month, but the highest proportion was consumed in June, which coincided with the start of the rains. At other study sites, the start of the rain brings about an increased production of new leaves, which are a rich source of protein (Hladik 1977). The fact that the monkeys consumed leaves intensively in June suggests they must have been an important source of food. Flowers and stems were also consumed on a regular basis, but never at the stop sites.

Spider monkeys hardly ever consumed animal protein. The only time I observed them eating animals was in July, when they consumed bright green caterpillars that they found on the leaves of trees that were far away from their core area. Feeding on insects or other small animals might be costly in terms of their anti-predator defences, yet many primates include them in their diet, even spider monkeys (Richard 1970). Moreover, the forest in the study site contains a considerable variety of insects and small lizards; thus, it is somewhat striking to note that spider monkeys did not appear to include animal protein in their diet. Spider monkeys may thus be highly specialised to a foli-frugivore regime and the protein requirements might be easily met by feeding sporadically on leaves and flowers and maximising the amount of fruit in the diet. They may have indirectly included animal protein in their diet by feeding intensively on insect-laden food like figs, which in most cases harbour Hymenoptera larvae. This could have been the case in spider monkeys since the longest feeding bouts were observed when they ate two species of figs (*Ficus* sp and *F. cotinifolia*).

5.10 Conclusions

The role of weather factors in determining ranging movements to and between food sources is not evident in the case of spider monkeys at the study site. Although some primates adjust their ranging to the availability of food, which is in turn determined by climatic variables (Barton *et al.* 1992), in other species this response is not as obvious (Chapman 1988). In this study, the main factor influencing spider monkey ranging patterns was the availability of at least 5 key species of fruits.

Other factors that could also have been responsible for the movements observed were the proximity of neighbouring groups of spider monkeys (although inter-group encounters did not occur often during the year), or the need to meet social requirements (i.e. grooming). These were beyond the scope of the present study and no conclusions regarding them can be made.

Importantly, spider monkeys were shown to make near-linear movements of up to 200 m to these key species and to others that form an integral part of their diet. The ranging behaviour of spider monkeys has been described elsewhere (Strier 1987, Chapman 1988, Norconk & Kinzey 1994, Nunes 1995), but this is the first systematic study of the movements of spider monkeys between feeding sites. I am confident that it will provide insights into their spatial cognitive abilities, by combining information on food availability and distribution with observations of ranging behaviour.

CHAPTER 6

MOVEMENT BETWEEN FOOD SOURCES II.

MECHANISMS

Results from the previous chapter showed that spider monkey movements between food sources are highly linear, regardless of month of the year or food species exploited. In some instances, spider monkeys reached food sources that were at distances that must have been outside their field of view. This observation offered a valuable opportunity to investigate the spatial abilities of wild spider monkeys, when they move between food sources, as it suggests they are able to find their way around by mechanisms additional to visual navigation. This forms the topic of this chapter.

6.1   Introduction

The study of animal navigation has focused on large-scale migratory movements by attempting to determine the mechanisms underpinning this behaviour (bird migration Berthold 1991, elephant-seals, Brillinger 1998; sea turtles, Luschi 2001). On the other hand, the study of small-scale navigation and/or food-finding behaviours has been restricted to controlled experiments taking place in captivity (in chimpanzees, Menzel 1973; in hummingbirds, Brown & Gass 1993). The results of these studies confirm that animals have remarkable abilities at finding their way at both large and small-scales, but studies of non-migratory spatial abilities of animals in their natural environments have been neglected, due to the fact that observational studies of behaviour do not allow the same level of control that experimental studies provide, and to the difficulty involved in accurate monitoring of wild animal movements for long periods of time.

Interest in the scientific study of the spatial abilities of animals saw a considerable increase after the publication of "Cognitive maps in rats and men" by E.C. Tolman in 1948. After over 55 years of active research on almost all aspects of spatial cognition in

animals and humans, at least one crucial mechanism of animal navigation that lends partial credibility to Tolman's ideas has received widespread acceptance, i.e. dead-reckoning or path integration. Dead-reckoning is the process whereby an organism is able to compute its current position with reference to a point of departure, by means of continuously recording, storing and updating information on changes of orientation along the route without the help of landmarks (Etienne et al 1998). The ability to return directly to a nest or other 'home' place after being displaced from it, has been reported consistently from experimental studies of animal navigation (ants, Muller & Wehner 1988; hamsters, Seguinot et al. 1993; and humans, Sauve 1989 cited in Etienne et al. 1998). In the absence of visual or chemical cues to guide the way, the homing behaviour of these animals is the "safest operational criterion for dead reckoning" (Etienne et al. 1998, p.56).

Path integration provides a mechanistic explanation for homing behaviour at a small scale, which can be applied to most vertebrates that use one (Andersson 1981) or several (Chapman et al. 1989) central places to return to at the end of a day's ranging. Path integration can also explain movements that project outward from a familiar route, but that lead back to it, as in the movements of wild female wood mice, *Apodemus sylvaticus* (Jamon 1994). On any given day, a female wood mouse would walk along familiar trails that have been previously marked by her or by conspecifics, but she can also walk novel routes that project outwards from the trail, to which she accurately returns later, apparently through dead reckoning. In their foraging trips, however, most vertebrates will have to make decisions based at least on location (where to find food?), and on timing and renewal rates (when does food become available and when is it feasible to go back to previously visited resources?) of food sources. In this case, alternative mechanisms to path integration could be used profitably, not only to return to a desired location after a foraging trip, but also to increase the efficiency of foraging movements. These mechanisms have been categorised into (1) those that require spatial knowledge of food locations and (2) those that do not. Belonging to the former category is spatial memory of food locations over a considerable area (i.e. the home range): its

efficiency is probably increased by an additional ability to manage and update existing databases of representations of landmarks that are input during exploratory trips.

Mechanisms that do not necessarily involve spatial knowledge include, among others (reviewed by Janson 2000), moving short distances in different directions when resources are abundant (Stillman & Sutherland 1990), moving predominantly in straight lines away from a food source that has just been used (Pyke 1983, cited in Janson 2000), or moving continuously in a forward direction to avoid encountering used sources previously (Cody 1971).

Tests that compare these models to observed movements of wild animals have yielded mixed results. Garber and Hannon (1993) compared four foraging models (e.g. random foraging, two different models of olfactory navigation, and one based on the assumption of spatial memory) to wild moustached tamarin (*Saguinus mystax)* foraging patterns and found that random foraging could not account for them. In an experiment where capuchin monkeys were allowed to learn the spatial arrangement of feeding platforms, Janson (1998) compared the group's movements to those predicted by a null model similar to Garber and Hannon's random foraging, but he introduced the visual detection field of the animal as an additional factor. His results confirmed that the model of random movements did not account for the capuchin monkeys performance at finding feeding platforms: under a random foraging assumption, the group's movements would have been less direct and not always towards closer platforms. Conversely, Jamon (1994) concluded that spatial cognition could not be inferred from the observed movement paths of a group of female wood mice. He used a model, termed the random walk (described by Bovet and Benhamou, 1988), but found that the rodents used familiar routes in their daily movements, which do not require spatial knowledge of locations, but cannot be considered as random movements either.

Modelling animal movements, and comparing them to observed movements of wild animals, seems to be a relatively simple yet robust method to assess alternative

explanations for observed foraging patterns in the wild. Its strength lies in the ability to vary the desired parameters without affecting others, thereby allowing for hypotheses testing. Perhaps the only drawback to modelling is that it provides a way of eliminating alternative explanations, without really pointing to a definite answer regarding which strategy(ies) an animal favours in its movements.

The results of my observations of spider monkey movements between feeding sites (Chapter 5) indicated that the monkeys travelled in predominantly straight lines to reach the majority of food resources throughout the year. I decided to extend this investigation to assess the organisation of day routes, in order to determine to what extent segments of straight-line movement are independent from each other, but straight-line movements *per se* are not evidence of the use of spatial abilities in navigation (Janson 2000); they might instead reflect a simple heuristic that tends to avoid re-sampling. If so, the direction of their movements would not tend to maximise food yield: other directions of travel would meet food equally often. Thus I decided to simulate movements based on a relatively simple strategy, similar to Janson's (1998) geometric model, to determine whether the potential for the use of spatial memory in spider monkey movements could be established.

6.2   Aims

i)   To assess the degree of back-tracking *versus* goal-orientation of spider monkey foraging routes.

ii)   To determine the relation between distance to, and quality of, feeding stop sites.

iii)   To simulate foraging routes observed according to a model based on straight-line movements in random directions and to compare the efficiency of the model to matched data on foraging routes in terms of number of feeding sites visited.

6.3 Are spider monkey movements to feeding sites goal-oriented?

If a given day's travel route was goal-oriented, its route segments would be aligned to each other, i.e. the magnitude of the rotation needed to align successive segments would be close to zero/360 degrees. If, on the contrary, a day's travel route was not goal-oriented, its route segments would not necessarily be aligned, but would adopt any possible direction.

I tested the null hypothesis that the route-segment orientations would be uniformly distributed around the circle (e.g. not concentrated around a specific value), by performing the Rayleigh test (Batschelet 1981).

I also tested the null hypothesis that the distribution of the route-segment orientations would be clustered around zero/360degrees, by performing the V test (Batschelet 1981). In other words, the null hypothesis states that in a goal-oriented movement, its route segments will show more forward than backtracking movements.

6.3.1 *Data used*

For the analysis, I included all route segments that ended at stop sites. A route segment can be considered as a vector, and as such, it has two properties: scalar distance, and bearing. Prior to performing the tests, the magnitude of the clockwise rotation needed to align subsequent route segment bearings was computed. In other words, the angle computed for each pair of bearings, was the clockwise rotation that would be needed to turn the first so that it aligned with the second.

Consider the following list of route segments directions:

<div align="center">

Route segment 1: 90 degrees

Route segment 2: 180 degrees

Route segment 3: 145 degrees

</div>

The algebraic differences between route segment numbers 1 and 2, and between route segments numbers 2 and 3 is -90 and 35 degrees, respectively, but the rotation (clockwise) needed to align route segment 1 with route segment 2 is equivalent to computing the positive angle of route segment 1, i.e. 360-90 = 270 degrees. Because the bearing of route segment 2 is numerically higher than that of route segment 3, the clockwise rotation needed to align route segment 2 with route segment 3 is simply the algebraic difference between the two, i.e. 35 degrees.

6.3.2 Statistical procedures

I used circular statistics procedures as outlined in Batschelet (1981), because the bearing of a route segment is a circular variable. The Rayleigh test was used to test for uniformity/randomness of the distribution, and the V test to test for aggregation of the sample around the specified bearing of zero/360°. Each monthly sample was entered in the software package Oriana 2, which performed the Rayleigh and V tests and produced graphical illustrations of the distribution of the variable for each month.

The magnitude of the clockwise rotation described above for pairs of successive route segments, not their crude bearings, was entered in the analyses. I divided the data into twelve groups corresponding to each month of the year when data were collected. Thus, each sample of monthly route segments included data collected from observations of several different focal individuals. To determine whether this combination of data from different focal individuals had an effect on the goal-orientation of the routes, I later divided the data in two groups according to the dry (October2001-April2002) and the wet (May-September2002) season. For each season I used the data of each focal individual observed and performed the tests again. Due to the multiple testing involved in these procedures, I used a significance level of 0.01.

6.3.3 Results

The null hypothesis of randomness was rejected for all months in the dry season, but was not rejected for most months of the wet season (fig. 6.1).
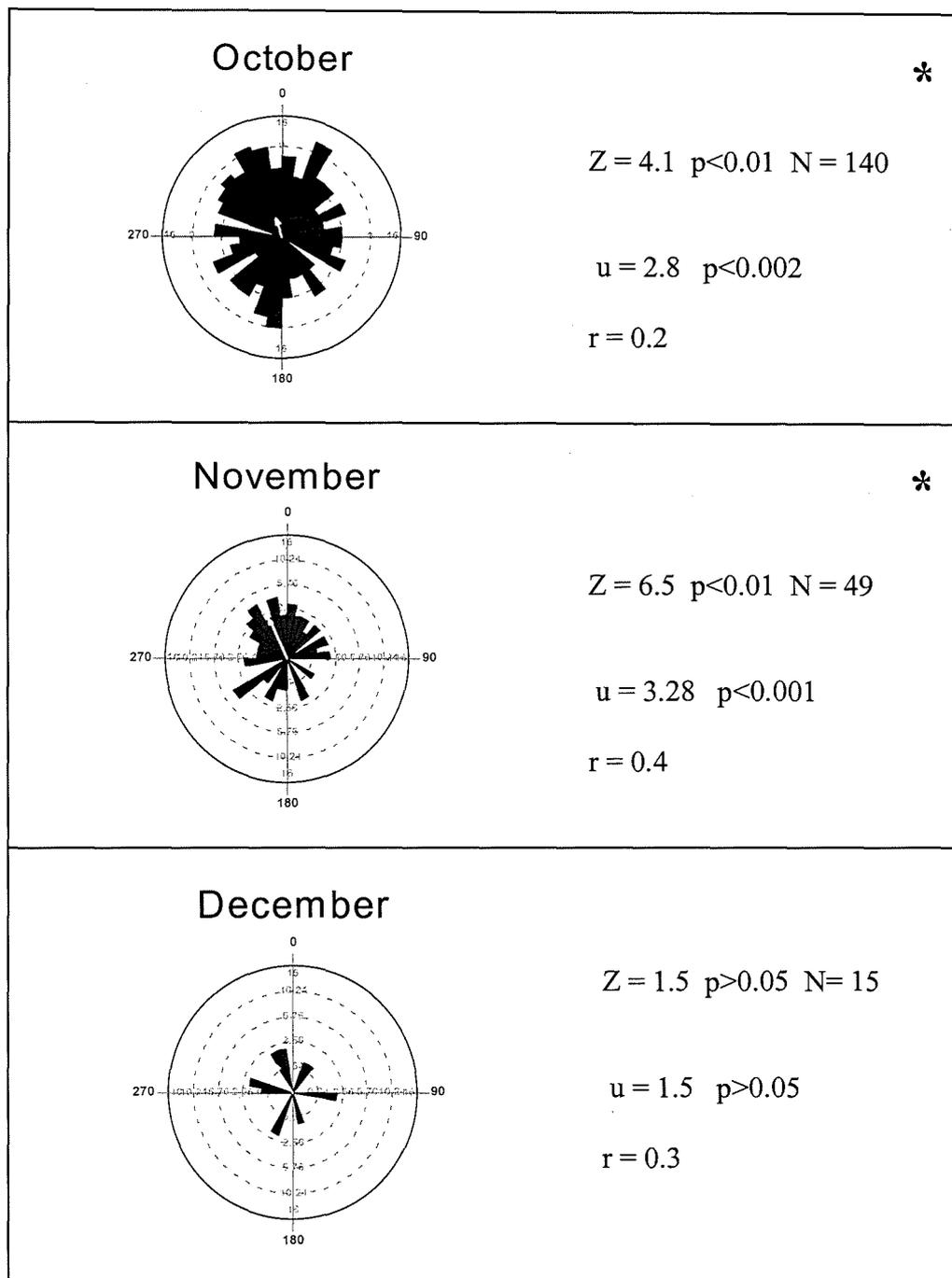
Figure 6.1. Distribution of the magnitude of the clockwise rotation needed to align successive route segments for 12 monthly samples. The light-coloured arrow represents the mean vector (r). An asterisk (*) on the top right corner indicates the distribution was significantly different from random, thus movements were significantly oriented in the forward direction (α=0.01).

January

Z = 4.9 p<0.01 N = 118

u = 3.0 p<0.001

r = 0.2

February

Z = 6.7 p<0.001 N =111

u = 3.6 p<0.0001

r = 0.2

March

Z = 3.3 p=0.03 N = 93

u = 2.6 p<0.01

r = 0.2

Figure 6.1. (Cont.)

April

$Z = 4.6$ $p<0.01$ $N = 135$

$u = 2.9$ $p<0.001$

$r = 0.2$

May

$Z = 2.2$ $p>0.05$ $N = 127$

$u = 1.7$ $p=0.03$

$r = 0.1$

June

$Z = 1.1$ $p>0.05$ $N = 89$

$u = -0.5$ $p>0.05$

$r = 0.1$

Figure 6.1. (Cont.)

July

Z = 4.8 p<0.01 N = 80

u = 2.7 p<0.01

r = 0.2

August

Z = 2.3 p>0.05 N = 105

u = 1.5 p=0.05

r = 0.1

September

Z = 1.6 p>0.05 N = 92

u = 1.7 p=0.03

r = 0.1
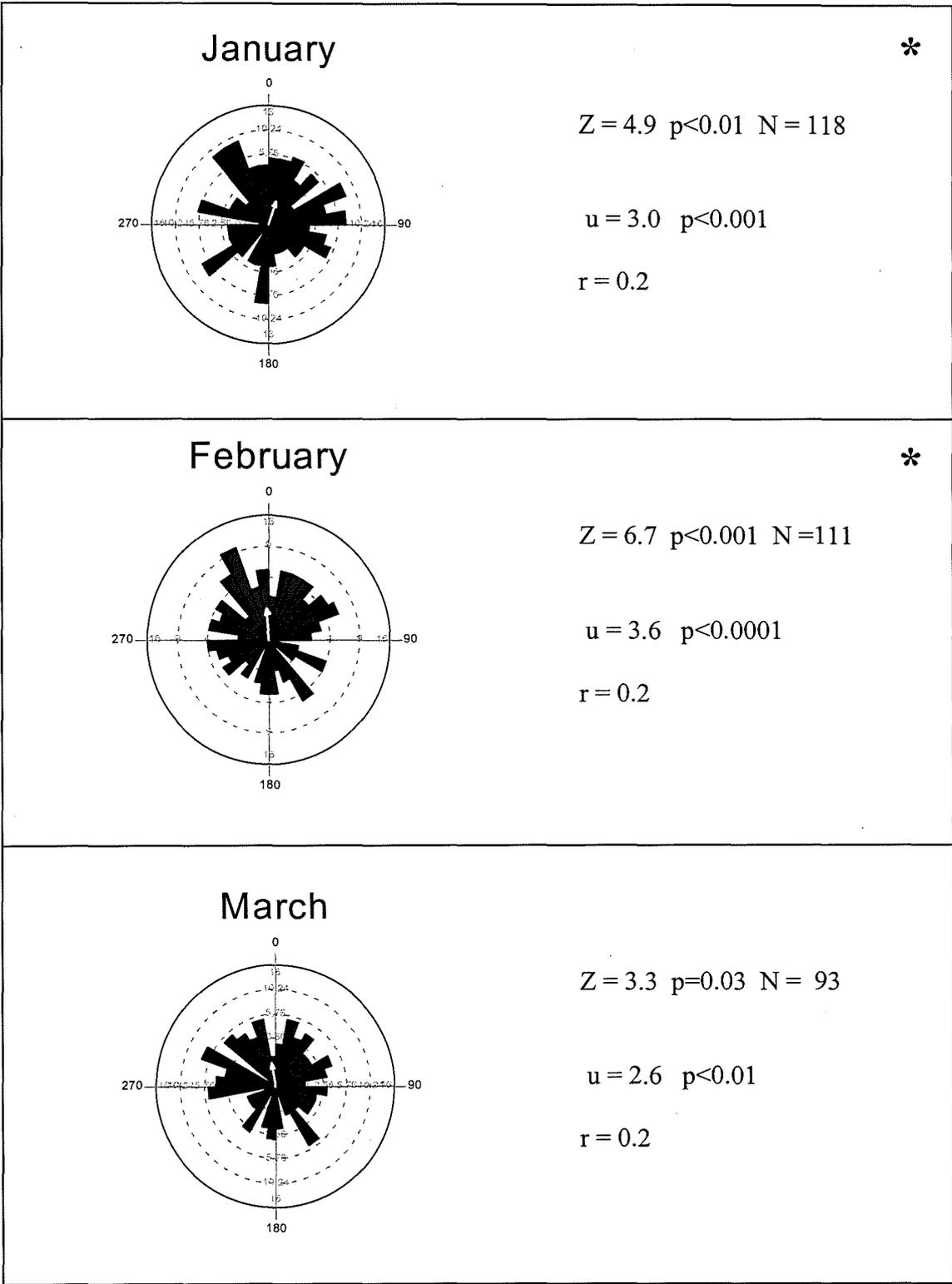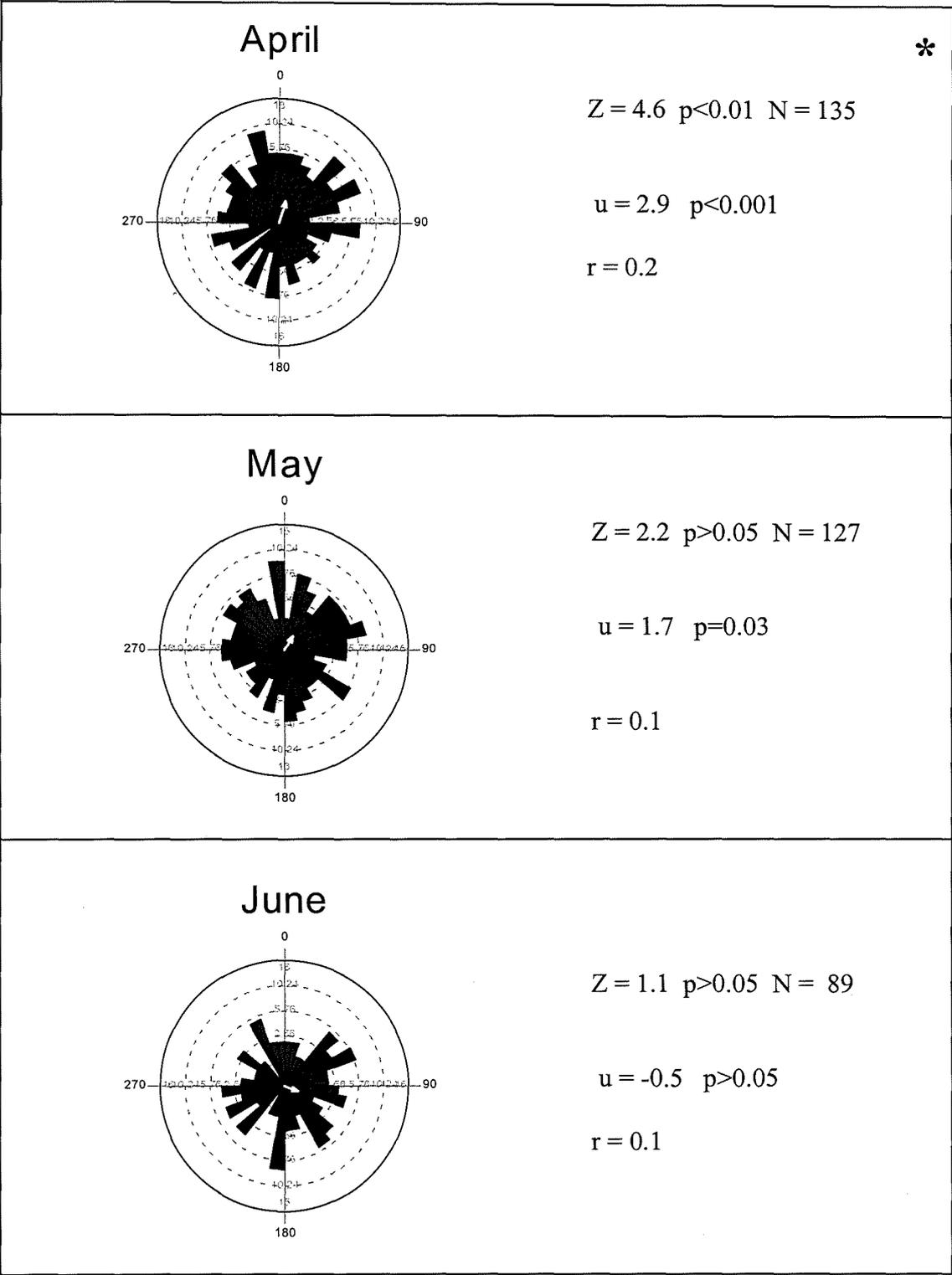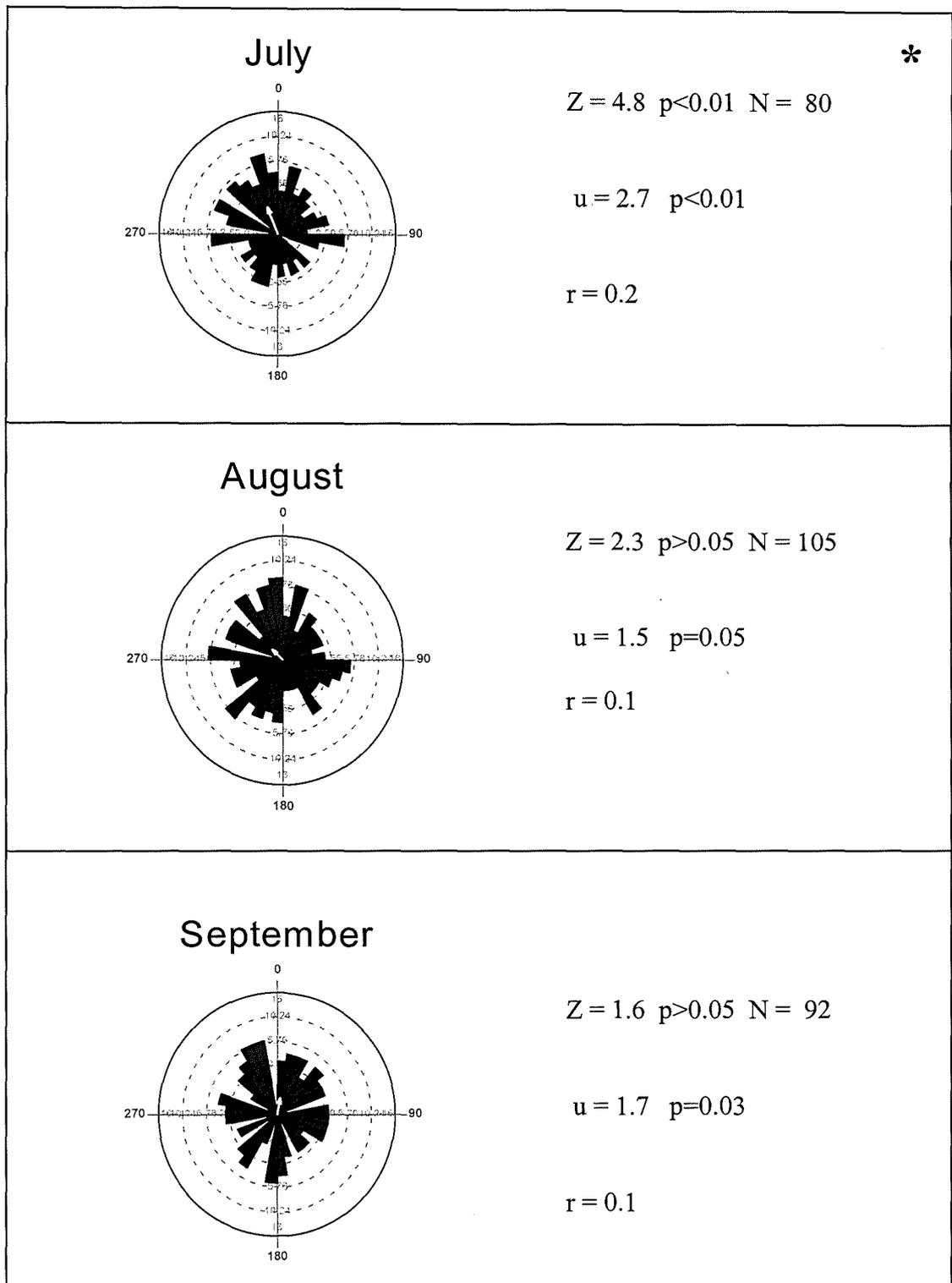
Figure 6.1. (Cont.)

When the same analysis was performed at the level of focal individuals/season the routes of some individuals were oriented forwardly in the dry season, but not in the wet season (Table 6.1), but this effect was not consistent across all individuals. Moreover, the few significant results may reflect the decreased power of the test, as for those individuals, but also others, sample size was rather low. There were no differences in the length of the mean vector between sexes (dry season: Mann-Whitney $U = 20$, $p>0.05$; wet season, $U = 17$ $p>0.05$, $N_1=5$, $N_2=6$ in both seasons).

6.3.4 *Discussion*

The results of this analysis show that, in the dry months (Oct-Apr), the majority of spider monkey movements towards stop sites were in the forward direction. In their movements to stop sites, spider monkeys maintained the same direction (i.e. not making sharp turns along the route), as evidenced by the fact that in many months of the dry season the orientation between subsequent segments was correlated to zero/360°. The month of December was an exception to this pattern, but the sample size for that month was much smaller than in any other month.

In most wet months (Jun-Sept) the pattern of spider monkey movements was the reverse of the dry months: movements were made equally likely in any direction and the monkeys did not tend to maintain the same bearing (i.e. they made sharp turns along the route). This was evidenced by the fact that the distribution of orientations between subsequent route segments was not different from random, and departed significantly from zero/360°.

That travel routes were sometimes organised in this way suggests that spider monkeys may be able to plan further ahead than the next resource visited, but it could also be due to a strategy of avoiding back-tracking movements. Such a strategy need not be inconsistent with some degree of spatial knowledge, since it could involve spatial memory in order to continually monitor the length and direction of current displacements from the last site visited, thus effectively avoiding backtracking.

Table 6.1. Results of the tests performed at the level of individuals per season. Dry season: October-April; Wet season: May-September. **r**: mean vector length **Z**: Rayleigh test; **u**: V test. Numbers in parentheses are sample sizes per season. **: p<0.01

Males (Ndry, Nwet)	Dry			Wet			Females (Ndry, Nwet)	Dry			Wet		
	r	Z	u	r	Z	u		r	Z	u	r	Z	u
Archi (90, 42)	0.2	4.5**	2.9**	0.1	0.2	-0.1	Cecilia (47, 75)	0.1	0.8	1.3	0.1	0.4	0.9
Benito (56, 20)	0.2	2.3	2.0	0.05	0.05	-0.3	China (84, 62)	0.1	0.8	1.2	0.1	0.2	0.4
Damian (24, 33)	0.2	1.1	1.5	0.06	0.1	0.4	Claudia (94, 55)	0.1	1.0	1.3	0.2	1.8	1.3
Licho (59, 38)	0.1	0.4	-0.3	0.3	3.2	1.7	Flor (116, 76)	0.2	3.1	0.9	0.2	3.4	2.6**
Pancho (36, 9)	0.4	4.9**	3.1**	0.5	2.0	0.1	Pilar (73, 41)	0.1	1.3	1.5	0.1	0.5	1.0
							Veronica (77, 66)	0.5	18.1**	4.8**	0.1	0.6	1.1

In the following studies I examine other features of route segments ending at stop sites, in order to evaluate the contention that spider monkeys use spatial memory in their foraging trips.

6.4 Can spider monkeys move in straight lines between stop sites they cannot see?

Animals rely on vision to perceive the world around them. Spider monkeys, like many other primates may rely on their visual perception of targets in order to reach them in the most direct way possible. Thus, the high linearity ratios in spider monkey movements may only reflect the extent of the monkeys' visual acuity.

Here I examine the lengths of highly-linear movements, in order to evaluate the distribution of route lengths. This would allow me to determine the proportion of linear movements made between stop sites that were within sight. This analysis would also establish whether spider monkeys were able to move directly to targets that were not within sight, a central piece of evidence to establish higher-level spatial abilities.

6.4.1 *Data used*

I included all route segments that ended at feeding stop sites, restricting attention to route segments with linearity above 0.7. This value was chosen because it was considered sufficiently stringent that it would restrict the sample to the most linear paths, without being unrealistic in insistence on perfect linearity, given that a complex environment like a sub-tropical forest probably does not offer a system of straight, un-obstructed highways like a system of streets.

Route segments with linearity ratios above 0.7 were close to beeline distances in length, thus their beeline distance is a good approximation to the real length travelled by the monkeys. I entered these segment lengths in the analyses.

6.4.2 Statistical procedure

The statistical package SPSS v.10 was used to display the distribution of lengths of route segments. Statistical parameters of the distribution were derived also with the help of this software.

6.4.3 Results

Spider monkeys moved in linear segments of up to 1300m to reach feeding sites, according to the distribution of the lengths of route segments (see table 6.2 and fig. 6.2). Of 607 highly linear route segments, 336 of them (55%) were potentially within sight (i.e. below 80 m), while 269 of them, (44%) were out of sight, according to my estimate of visibility in the canopy (see chapter 3).

Table 6.2. Statistics for route segments to feeding sites for paths with linearity above 0.7

N	607
Mean length	122.9
S.E.	5.9
S.D.	146.4
Median length	65.3
Min – Max lengths	2.2 – 1363.5
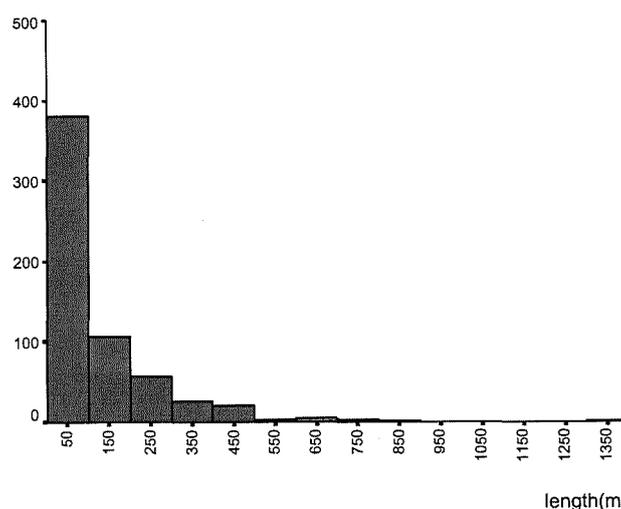
length(m)

Figure 6.2. Distribution of lengths of route segments with linearity >0.7. Number of segments is shown on the vertical axis. Intervals on the horizontal axis are 100m in size, but only the midpoints are shown.

6.4.4 *Discussion*

These results indicate that approximately one out of two highly linear movements that spider monkeys made to feeding sites are unlikely to have been within sight when movement started. Other studies of primate foraging behaviour have also reported straight-line movements to important out-of-view targets (Boesch 1984, Garber 1989, Menzel 1991). However, straight-line movements are not enough evidence of higher-level spatial abilities in foraging movements (Janson 2000). Additional predictions from the spatial memory hypothesis must be generated and tested before a strong argument can be made. In the next two studies I investigate two of these predictions.

6.5 Relationship between distance travelled and resource abundance.

A central issue raised in studies of spatial cognition is whether animals know the location of food resources in their habitat, predict their quality even before they visit them, and plan the order of visits to them, like travelling salesmen. It is possible that some animals would be prepared to travel long distances when they predict or are certain that resource quality at the end of a trip is substantial. In this study I will look at the yields obtained at the end of route segments and how they relate to the distance travelled.

If a relationship were confirmed, this would indicate that spider monkeys were also able to predict the size of future yields, suggesting they hold representations of the state of feeding sites in mind.

6.5.1 *Data used*

I included all route segments that ended at feeding stop sites, except those for which the GPS readings were not reliable.

6.5.2 *Statistical procedures*

I divided the route segments into categories of route segment length (short, medium, long) and resource quality (low, medium, and high). Distance to the stop site was

considered as the beeline distance between start point and stop site for each route segment. Resource quality was considered as the time spent feeding at the stop site, in seconds. I tested the null hypothesis of no association between the variables route segment length and resource quality through a chi-square test.

Given that there was a trend towards increased linearity (Chapter 5), and an apparent trend for goal-orientation of the routes in the dry season, I also decided to explore whether a seasonal difference would be observed in the association between route length and resource quality. To do this I divided the data into dry and wet season and performed a chi-square test on each sample.

It is known that the reliability of chi-square tests can be greatly affected by the sample size used (Zar 1996). Thus I did not perform these tests at the level of individuals, because of the reduced sample size resulting from already subdividing the data into two seasons and into the necessary categories of route length and resource quality. Since I included data from several focal individuals in the statistical tests that I did perform, I increased the level at which results would be considered significant (alpha=0.01).

6.5.3 Results

Length of route segment was not related to the quality of the resource at that stop site. A chi-square test did not reject the null hypothesis of independence between resource quality and distance to the stop site, when data from all months was included in the analysis ($X^2 = 2.69$, $df = 4$, p = 0.75, see Table 6.3).

For the two samples of dry and wet season, length of route segment was not related to the quality of the resource at that stop site. A chi-square test did not reject the null hypothesis of independence between resource quality and distance to the stop site in these cases (dry season: $X^2 = 2.13$, $df = 4$, $0.75 < p < 0.5$; wet season: $X^2 = 2.72$, $df = 4$, $0.75 < p < 0.5$, fig. 6.3).

Table 6.3. Distributions of route segments among three categories of resource quality (seconds) and distance to the stop site. Expected frequencies are shown in bold.

Length of route segment	Resource quality			
	Low (0-240s)	Medium (240-500s)	High (>500s)	Total
Short (0-80m)	104	224	185	513
	106.1	**217**	**188.7**	
Medium (80-200m)	46	83	88	217
	44.8	**92.2**	**79.8**	
Long (>200m)	31	65	49	145
	29.8	**61.3**	**53.1**	
Total	181	372	322	875

6.5.4 *Discussion*

The lack of an association between length of route segment and resource quality implies that spider monkeys may not have been aware of the yield they would obtain in advance of visiting a feeding stop site. This does not mean they are incapable of holding mental representations of the quality of feeding sites, but it does suggest that the cost of travelling over long distances may have been equal to or smaller than that of not consuming resources if they had avoided these journeys. On the other hand, certainty of likely yields could not always be the best strategy to adopt, especially if other groups of spider monkeys know about the location of the same food source.
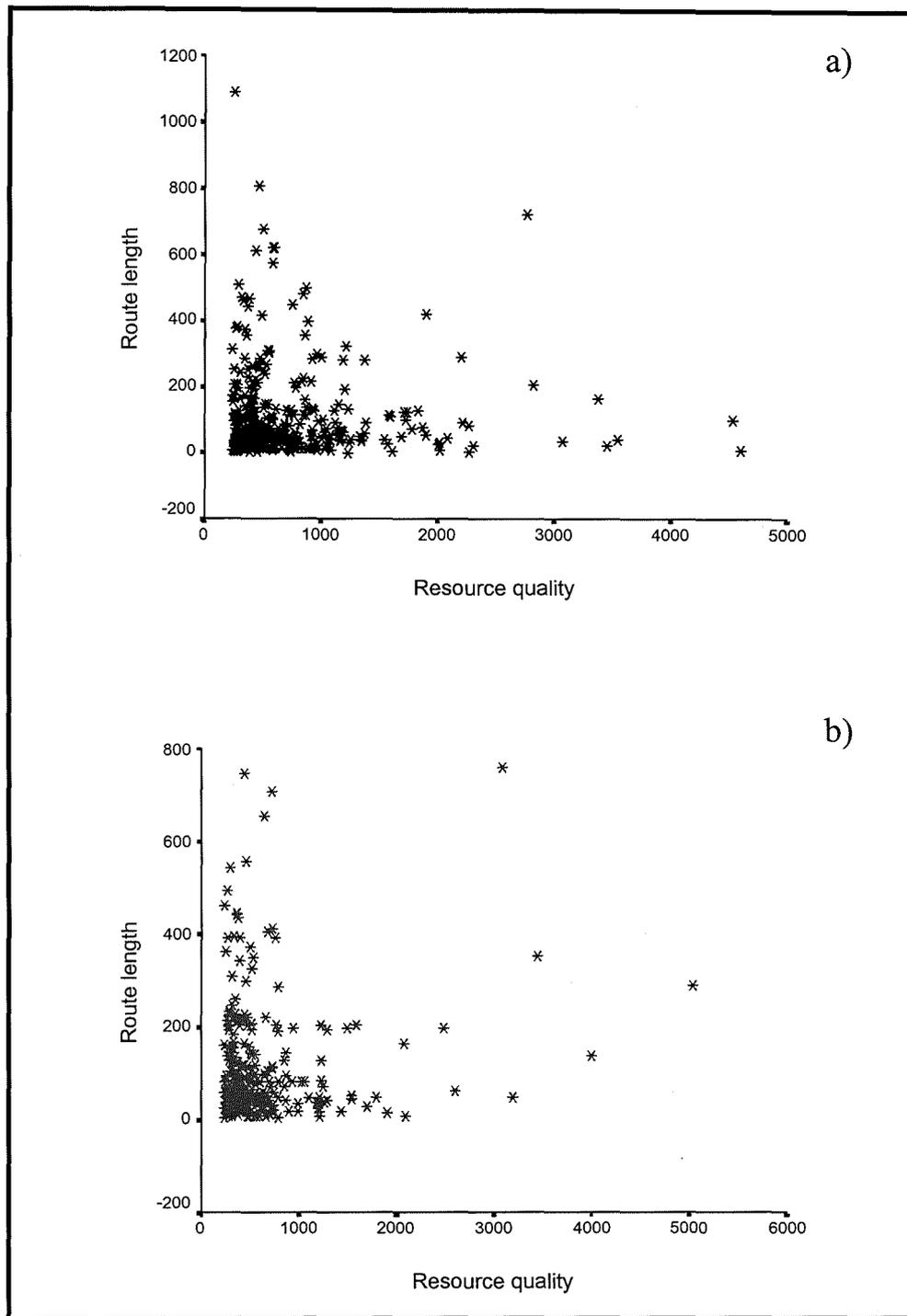
Figure 6.3. The relationship between route length (on the vertical axis, in m) and resource quality (on the horizontal axis, in seconds) for a) the dry season (Oct-Apr) and b) the wet season (May-Sept).

This would be particularly true at sites where overlap of different spider monkey group home ranges is high, or where different monkey groups exploit the same food sources. Thus, for animals with high spatial abilities, the relationship between route length and resource quality does not need to be strong and positive at all times. The degree of overlap with other spider monkey groups in the monkeys of Punta Laguna has not been determined, although the field assistants have reported a few instances of inter-group encounters over the last six years. Comprehensive studies of inter-group interactions in Punta Laguna are needed in order to know whether the spider monkey groups that live around the lake exploit the same set of feeding sites and modify their travel decisions according to the possibility of such inter-specific encounters.

Finally, it is not known whether straight-line movements minimise time and energy invested in otherwise circuitous exploratory movements, but it remains an open possibility that should be further explored in studies of animal movement. Janson (2000) suggested that this strategy could be favoured under some circumstances, i.e. if no spatial knowledge was assumed and if an issue at stake was "to maximise (...) return times to a given location", for example, to sleeping grounds at the end of the day. Janson's hypothesis suggests that walking in straight lines could be conducive to 'running into' desired target sites when there is uncertainty about their location in space. In study 4 I will thus test whether a model of straight-line movements in random directions is efficient at providing frequent encounters with the stop sites that the monkeys in the study group visited.

6.6 Modelling spider monkey movements between feeding sites

Following Garber and Hannon's experiments simulating the movements of South American tamarins (1993) in the forest, I ran a similar simulation of foraging movements, and compared its efficiency in terms of finding feeding sites to the number and type of feeding sites found by the spider monkeys in their foraging movements. Preliminary results of a simple random foraging model led Garber and Hannon to the conclusion that

an animal foraging randomly "was more likely to encounter a feeding site by taking longer step lengths (...)" (p.833). The model I used in the simulations incorporates this caution, but it was mainly inspired by the geometric model of Janson (1998, p. 1234).

6.6.1 Data used

The aim in this study was to compare spider monkey movements during the months of November 2001 and June 2002 to model movements of each of those months. I chose those months instead of others because each belonged to an ecologically-distinct season (November, dry; June, wet), and the analysis presented in section 6.3 confirmed that the movements of spider monkeys were different on each of these month. In addition, the monkeys in the study group travelled frequently to far-off feeding sites in November, while they did not do so at all during June, when different species of trees in their core area bore fruits and new leaves. This led me to believe that food was scarcer in November than in June and thus at that time of year there would be an increased pressure for the use of spatial memory or other food-finding strategies.

I used the area delineated by the polygon enclosing the outer GPS fixes of the monkeys' positions obtained during the course of the study as the simulation arena (see fig.6.4). The feeding sites that the simulated procedure would 'run into' were the feeding stop sites that the monkeys exploited during the month of November 2001 and June 2002.

6.6.2 Characteristics of the model

I performed one simulation for each day of the selected months for which I had collected data of any animal. Simulation bearings were generated as a list of random numbers from 0 to 359 in Excel. In each simulation, the 'monkey' started off in a random direction, but from the same point where the real monkey had started on the corresponding day. Zero degrees were considered on the East of the starting point, 90 degrees on the North, 180 degrees on the West, and 270 degrees on the South. Unlike Garber and Hannon's (1993) experiment, the 'simulation monkey' was allowed to head off in a straight line without step-length restrictions, until it hit either an available feeding site or the edge of the MCP

(i.e. the edge of its home range, fig. 6.4). After this, the 'monkey' would move in a new random direction in a straight line, until it ran into a feeding site or the edge of the home range. In addition, no feeding site would be visited twice in the same day, and the simulation would stop when the 'monkey' had reached the same day range length as the real monkey had on the corresponding day.

I originally assumed an extremely generous detection field of 30m on either side of the simulated monkey's travel path, according to the estimate computed in a study of capuchin monkey's abilities for detecting feeding platforms (Janson 1997). It seemed reasonable to use this detection field, since both capuchin monkeys and spider monkeys live in tropical environments where visibility conditions up in the canopy are similar. Thus, for the simulated monkey to reach a tree, it did not have to be located exactly on the path, but at a maximum distance of 30 m on either side of it. I decided to reduce this distance to 15 m on either side of the travel path, however, after a preliminary examination of the results suggested that the simulated monkeys in the wet month were 'out-performing' the real monkeys on the same month. It is important to note that fruit detection is largely dependent upon the species used; thus, assuming a detection field of 30 m for all species exploited is likely to be extremely generous since many fruits eaten by spider monkeys are small and green, thus possibly inconspicuous to them.
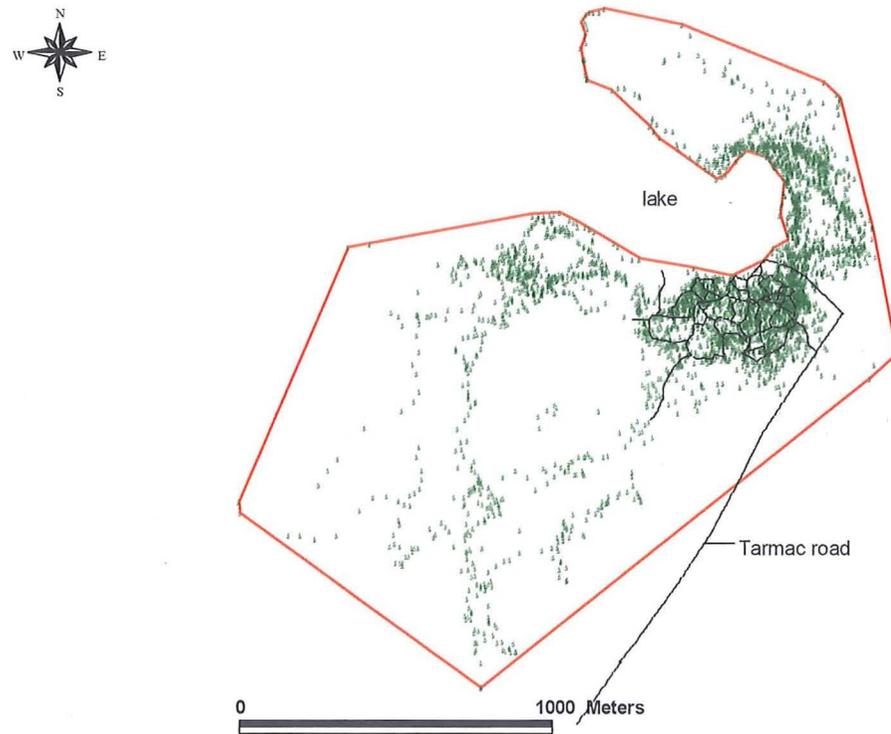
Figure 6.4. Home range of the spider monkey group, delineated by a convex polygon (excluding the lake). This was used as the arena for the simulations (see text). The dots represent the GPS fixes recorded throughout the study.

6.6.3 Statistical Procedures

I compared the number of feeding sites visited by the real monkeys to the number of feeding sites visited by the 'monkey' according to what the model would predict, through a Wilcoxon paired-sample test. I used the same procedure to compare the number of times the real monkey and the 'simulated' monkey would hit the boundaries of the home range.

The test of variance outlined in Zar (1996) was also used to explore further the differences in number of feeding sites visited by the real monkeys and those predicted by the model.

Diversity indices were computed for each season as well as type of route (real monkey or 'simulated monkey'), and were compared within each season through the t test outlined in Zar (1996).

6.6.4 Results

In the 'wet' month, June, the strategy simulated in the previous exercise, i.e. walking in random directions over straight lines until a feeding site is found, yielded the same rewards as the strategy that real monkeys adopted. There was no difference between them (Wilcoxon rank signed test: W = 16, N = 11, p>0.05), but the same strategy yielded far less rewards during the dry month, November, as reflected by the higher number of feeding sites visited by the real monkey than by the simulated monkey during that month (Wilcoxon rank signed test: W = 5, N = 11, p = 0.01; fig. 6.5).

Although the number of feeding sites visited in the wet month by the monkeys and that predicted by the model was similar, the variance was significantly higher for the number of feeding sites predicted by the model ($F_{(10, 10)}$ = 4.79, p<0.05). By contrast, in the dry month, the variance was smaller for the number of feeding sites predicted by the model than for those visited by the monkeys, but the difference was not significant ($F_{(10, 10)}$ = 3.6, p=0.1).
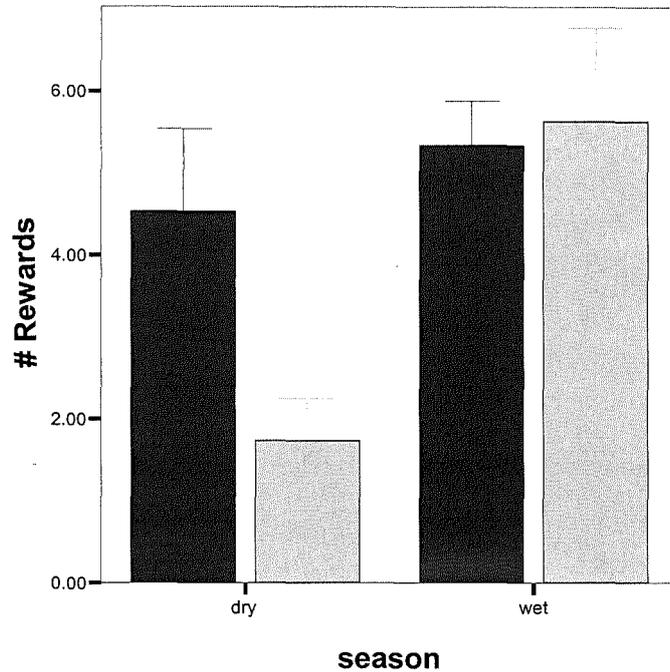
Figure 6.5. Number of feeding sites visited during a dry and a wet month by monkeys in the study group (dark coloured bars) and those predicted by the model (light-coloured bars) when the visual detection field was 15m.

In addition to the differences in number of feeding sites visited, the null model of straight-line movements in random directions also predicted that the monkeys would hit the boundary of the home range more frequently. In the dry month, the monkeys in reality hit the boundary a total of 9 times ($X\pm SD = 0.81\pm1.32$, $N=11$), whereas under the model, they did so a total of 33 times ($X\pm SD = 3.0\pm2.0$, $N=11$). In the wet month, the monkeys hit the boundary a total of 7 times ($X\pm SD = 0.63\pm0.67$, $N=11$), but under the model they did so a total of 22 times ($X\pm SD = 2.0\pm1.0$, $N=11$). Thus, under a model of straight-line movements in random directions the monkeys reached the boundary of the home range significantly more frequently than what was actually observed, in both months (Wilcoxon signed-rank test: November, $W=0$, $N=11$, $p<005$; June, $W=0$, $N=11$, $p<0.005$).

Under the model of straight-line movements in random directions, for the wet month the monkeys omitted visits to 4 species of fruit trees that the real monkeys consumed (Table 6.3) and to 3 species of trees from which only the leaves were eaten. The diversity of food items consumed by real monkeys was significantly higher than by the 'simulated' monkey during the wet season (t = 2.7, df = 48, p<0.02). By contrast, in the dry month, the monkeys omitted 2 species of fruits and also flowers (Table 6.3). The diversity indices of food items consumed by real and simulated monkeys in the dry season were not significantly different (t = 1.9, df = 20, p<0.05).

Table 6.3. Types of food eaten at the stop sites that the real and the simulated monkeys visited. Number of trees visited per each species are shown.

November			June		
Species	Real	Simulation	Species	Real	Simulation
Ficus spp	2	0	*Ficus spp*	2	1
Spondias mombin	6	2	Epiphytes*	1	1
Morax	1	1	*Cinche*	1	0
Brosimum alicastrum	14	7	*Ceiba pentandra*	1	0
FLOWERS	1	0	*Bursera simaruba**	1	0
Dyospyros cuneata	4	0	*Metopium brownei*	1	0
Manilkara zapota	3	1	*Ziziphus jujuba*	1	0
			Ficus cotinifolia	2	2
			*Ducktail**	1	1
			Talisia olivaeformis	6	5
			Jirinich	2	1
			*Kitanche**	1	0
			*Morax**	1	1
			B. alicastrum	9	10
			B. alicastrum *	3	1
			*Saclob**	1	0
			M. zapota	1	1
Total number of species	7	4		17	10
Total number of trees	31	11		35	24

*Tree species of which only the leaves were consumed.

6.6.5 *Discussion*

The differences in the number of feeding sites visited, between the spider monkeys and the simulated animal were more pronounced in the dry season, when the number of food sources visited was in any case smaller than in the wet season. This pattern is probably due to the way the resources were spaced in each season: in November (dry) the resources seemed to be dispersed, while in June (wet) they appeared to be more abundant. By these circumstances alone, the likelihood of encountering a feeding site in the dry month must have been much smaller than in the wet month. Nevertheless, the seasonal difference between model and reality cannot be explained this way.

Moreover, In reality monkeys may be able to detect proximity to the boundaries of the home range and may react in advance by turning back, although of course the 'boundary' was itself defined by the monkeys' previous behaviour. The monkeys in the study group were not noted to make abrupt backtracking movements near the boundaries of their home range, however, and when they approached them it was to consume food sources that were there (personal observation). Thus, spider monkeys may be using an alternative strategy to that of the simulation tested here, in order to minimise unproductive approaches to the boundaries of the home range and thus to maximise encounters with feeding sites.

The model's assumption, that there were no food sources in the home range except for the feeding sites visited by the spider monkeys, might also have been a big departure from reality. However, the model provided a clear picture of what could happen when an animal without any notion of the location of feeding sites sets off in a direction where there are little or no rewards to be retrieved. The model predicted that, in the wet season, although an animal moving over straight lines in random directions could find equal numbers of feeding sites as a spider monkey, it would be exposed to a higher degree of uncertainty (higher variance). On the other hand, in the dry season this variance was small, i.e. spider monkeys consistently visited many feeding sites, unlike the simulated animal. This suggests that, in the dry month and possibly in the wet month,

spider monkey foraging routes were more efficient than the simulated animal routes at maximising encounters with feeding sites and minimising the variance in the number of feeding sites visited, respectively.

When resources were abundant, then, the likelihood of encountering a feeding site must have increased, and one could expect that any strategy that promoted continuous straight-line movement in any direction would be as efficient in finding feeding sites as using spatial knowledge. Although such a strategy had this effect in the simulated movements during the wet season, it did not solve the problem of ensuring a diverse diet as evidenced by the higher diversity of food items consumed by real monkeys. In contrast, in the dry season, the simulated strategy apparently had no effect on the diversity of food items consumed. Thus spider monkey foraging routes were also more efficient than simulated animal routes at maximising the diversity of species sampled.

6.7　Summary of Results

i)　In dry months spider monkey routes were characterised by many forward movements, while in the wet months they showed more backtracking movements. Thus, at times when resources were scarce, spider monkeys apparently planned farther ahead than the next stop site visited.

ii)　Spider monkeys usually moved over near-straight lines of 25-125 m, but they also made near-straight movements over much longer distances, to a maximum of 1300 m. These longer distances are highly unlikely ever to be in spider monkeys' visual range.

iii)　Although spider monkeys were prepared to travel over long distances to reach a feeding site, they were not able to predict the amount of rewards obtainable at that site. They were equally likely to move over short, medium or long distances towards feeding sites on which they fed for long, medium or short periods of time.

iv) The foraging routes of spider monkeys in the dry season provided more rewards than predicted by a model of straight-line movements in random directions. In the wet season there were no differences in the number of rewards encountered by monkeys and those predicted by the model, but the diet diversity was higher for real monkeys than for 'simulated' animals in the wet season. Whatever strategy the monkeys used, it was also efficient at minimising unproductive approaches towards the boundaries.

6.8 Conclusions

The results presented here indicated that spider monkeys were doing more than just moving over straight lines and in random directions to ensure visits to feeding sites. They could have been either planning their foraging routes in advance and/or avoiding backtracking movements, which is a plausible explanation given the forward orientation of their travel routes in November and in other months of the dry season. Avoiding backtracking movements may seem a relatively simple rule that could be added to the model. However, to keep in mind all the locations that had been visited already, effectively avoiding to go back to them, would probably involve a good deal of visual and spatial memory, which would conflict with the original purpose of the modelling analysis (i.e. to produce a model of foraging rules based on the assumption of no knowledge of the environment and/or no cognitive abilities like spatial memory).

A strategy of moving in straight lines in random directions could account for the high linearity of route segment distances, but the simulated routes suggest that such a strategy was not conducive to maximising the amount of rewards obtained. This was best exemplified by the high frequency of encounters with the boundaries: the fact that the simulated foraging paths frequently ended at the edges of the home range suggests that it must pay to know the location of at least a few food sources, when the risk of not finding any is greatest. Selection must have favoured behaviours that increased the probability of finding food when resources were either difficult to find or widely dispersed. Under this

assumption it would not seem surprising that some animals evolved spatial memory of food locations to cope with food scarcity, and that this capacity would have served a purpose too for the alternative condition when food sources were widely abundant. The fact that when resources were abundant (wet season) the diet of real monkeys was significantly more diverse than that of simulated animals, attests to that assertion.

Exactly what sort of mechanism(s) could be governing the movements of spider monkeys between food sources is a question that will only be solved as more experimental evidence on the foraging behaviour of wild primates emerges. Nevertheless, spider monkeys appear to use spatial memory of feeding sites to make foraging trips efficient: straight-line movements to valued sources, coupled with higher yields than models of random movements would predict, and some degree of route-orientation. I believe these results constitute a first step into the elucidation of the types of information that spider monkey cognitive maps encode. Hopefully they will provide a basis for designing future experiments aimed at investigating the extent of their spatial skills in the wild.

CHAPTER 7

JUPP'S TEST: A NOVEL WAY TO STUDY TRAVEL PATTERNS OF PRIMATES.

7.1 Introduction

In studies of primate foraging behaviour attempts have been made to determine whether primates navigate, in search of food or other resources through their habitat, by means of a mental representation of their environment (the so-called "mental map" or "cognitive map", Tolman 1948). An alternative is that they are capable of storing a mental record (but not a map in the strict sense of the word) of the direction and distance of displacement from a base, to which they will return in the near future. That is to say, they are capable of finding their way back to a known location by a process of dead reckoning similar to that exhibited by ants (Wehner et al. 1996) and other animals (reviewed in Chapter 6). A third alternative is the 'local place navigation' idea originally proposed by Cartwright and Collett (1987), and then elegantly tested by Benhamou (1996), where an animal uses 'snapshots' stored in memory, of views near a target, to find its way until it reaches the location where the match between the mental snapshot and the current view is perfect

Observations of primate behaviour in large-scale space allow us to test hypotheses derived from these ideas. In the field of spatial cognition of primates, experimental studies in the wild and in captivity (reviewed in Chapters 1 and 6) have been designed in order to infer spatial memory skills, but fewer studies have used observational data of primate movements between feeding sites to draw conclusions about their spatial abilities (in the wild: Garber 1989; Garber and Hannon 1993 in captivity: MacDonald and Wilkie 1990, reviewed in Chapters 1 and 6).

With the advent of GIS (Geographic Information Systems) and tracking systems (e.g. GPS receivers) a new world of opportunities has been opened for the study of the

spatial abilities of animals, based in their movements in natural conditions. GPS devices can track the positions of animals with precision for long periods of time, and a whole suite of software packages are now able to take up information generated by virtually any GPS receiver and visualise it on-screen. By performing automated geometrical calculations on vast amounts of detailed geographical information, inferences about the spatial abilities of animals can be made reliably and quickly in a way that was not possible a few years ago.

Why involve the potentially problematic study of natural animal movements in investigation of cognitive abilities? The answer is that the study of natural movements is complementary to the experimental study of spatial cognition. Experimentation in the wild allows an experimenter to manipulate variables like the visual or olfactory cues used, and/or the renewal rate of a food source, but cannot fully imitate the natural variation in food availability provided by the environment. Experimental studies in captive conditions give even greater control, but greatly simplify the complex natural scenario on which mental abilities normally operate, i.e. large-scale space. The natural environment poses more stringent constraints on animals' energetic expenditure than the limited space of any captive enclosure (e.g. food abundance depending on time of year, presence of competitors and/or neighbouring conspecifics, predator avoidance, etc. Garber and Paciuli 1997). In order to complement results obtained from experimental work, studies in the wild are called for that look at not only the behaviour, but also the information that animal movements can provide about their mental representations, if conclusive statements are to be inferred about the spatial abilities of animals. In this study I describe a statistical procedure that was devised for this aim, and use it to analyse the movements of my study group of spider monkeys in their natural environment.

7.2 Jupp's Unit-vector test.

Jupp's unit-vector test was designed to determine the location of a significant change in direction in an animal's travel route, referred to as a *change point* from here on. Such changes in direction may be particularly informative if movement after the change point ends at an important target for the animal. This in turn would enable a human observer to

make inferences about primates' travel decisions and possibly about the cognitive mechanisms on which they are based.

Jupp's unit-vector test is a series of mathematical and trigonometric procedures performed on a given travel route. A travel route in my study is made up of the geographical co-ordinates that I collected with the GPS receiver (the numbered dots in fig. 7.1), and joining these with lines produces a series of vectors, like the ones represented in figure 7.1, denoted by letters.

One assumption of the test is that all vectors in a route have the same length, i.e. that they are *unit vectors* (hence the specific name for the test). The test treats vectors before and after a potential change point as samples of vectors and compares the two samples for their directional similarity. Thus, the null hypothesis is that any two samples of vectors in a travel route are collinear:

$$H_0 : \text{sample 1 and sample 2 are collinear}$$

When the two samples of vectors are found not to be collinear, the point where they intersect represents a directional change from one vector to the other (for example, point 3 lying between vectors *r* and *s*, fig. 7.1). Such test of collinearity between any two samples of vectors can be performed at each point along the travel route in order to determine which (if any) points constitute a directional change.

Animal movement data are explored in a number of ways by using this test. Here, my interest is in detecting the point at which a spider monkey's movements first became directed towards an important resource that it reached by travel. Thus, the first 'change point' (i.e. point at which a clear change of direction occurred) in the route before the target is sought. Hence, I applied Jupp's test to the route from any point identified as such a potential target, back towards the start of its day's ranging.
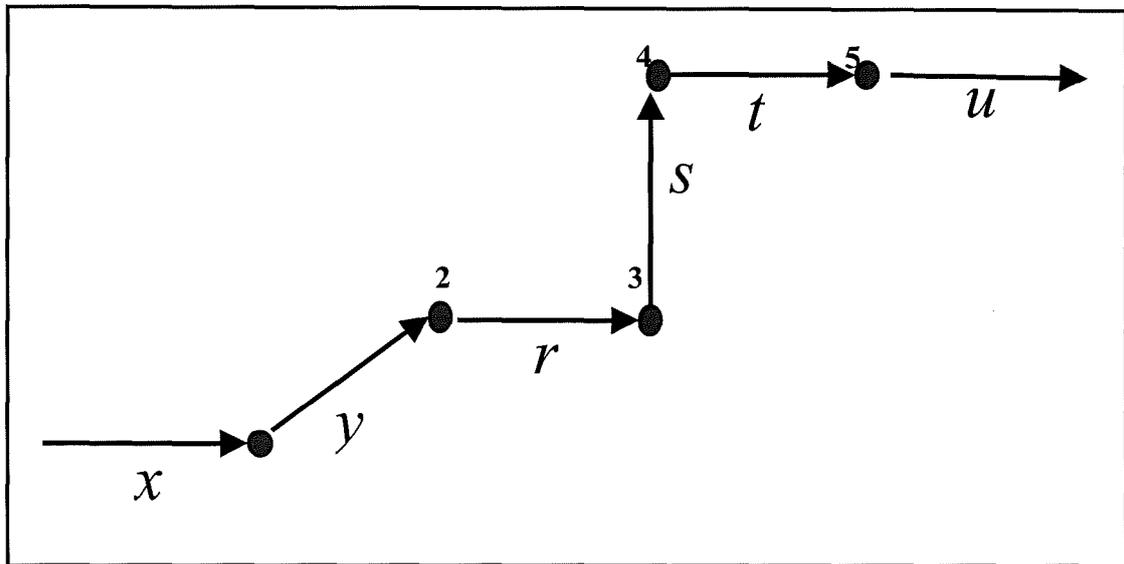
Figure 7.1 The concept of vector colinearity illustrated. The spatial arrangement of points 1-5 influences the distance and bearing properties of vectors x, y, r, s, t, and u. Vectors t and u are collinear, while vectors x and y and y and r are less collinear, and vectors r and s and s and t are the least collinear in this sample.

It is important to clarify the meaning of the words "before" and "after" a given change point that I will use in the rest of this chapter. Because I applied Jupp's test in the opposite direction of the monkey's movements (i.e. from a potential goal towards the point where movement originated), my use of the term "before the change point" refers to the route from the potential target towards the change point. Thus, the term "after the change point" refers to the route from the change point towards the point where movement originated in the first instance.

As with many statistical tests, in Jupp's test two data samples are compared in order to decide whether both of them come from the same population or not. In our case, each sample is composed of one or a series of vectors of unit length. Figure 7.2 shows an example of an imaginary route travelled by an animal. In figure 7.2b, Jupp's test is applied to the point labelled "k1", which is one vector away from the location labelled "target".
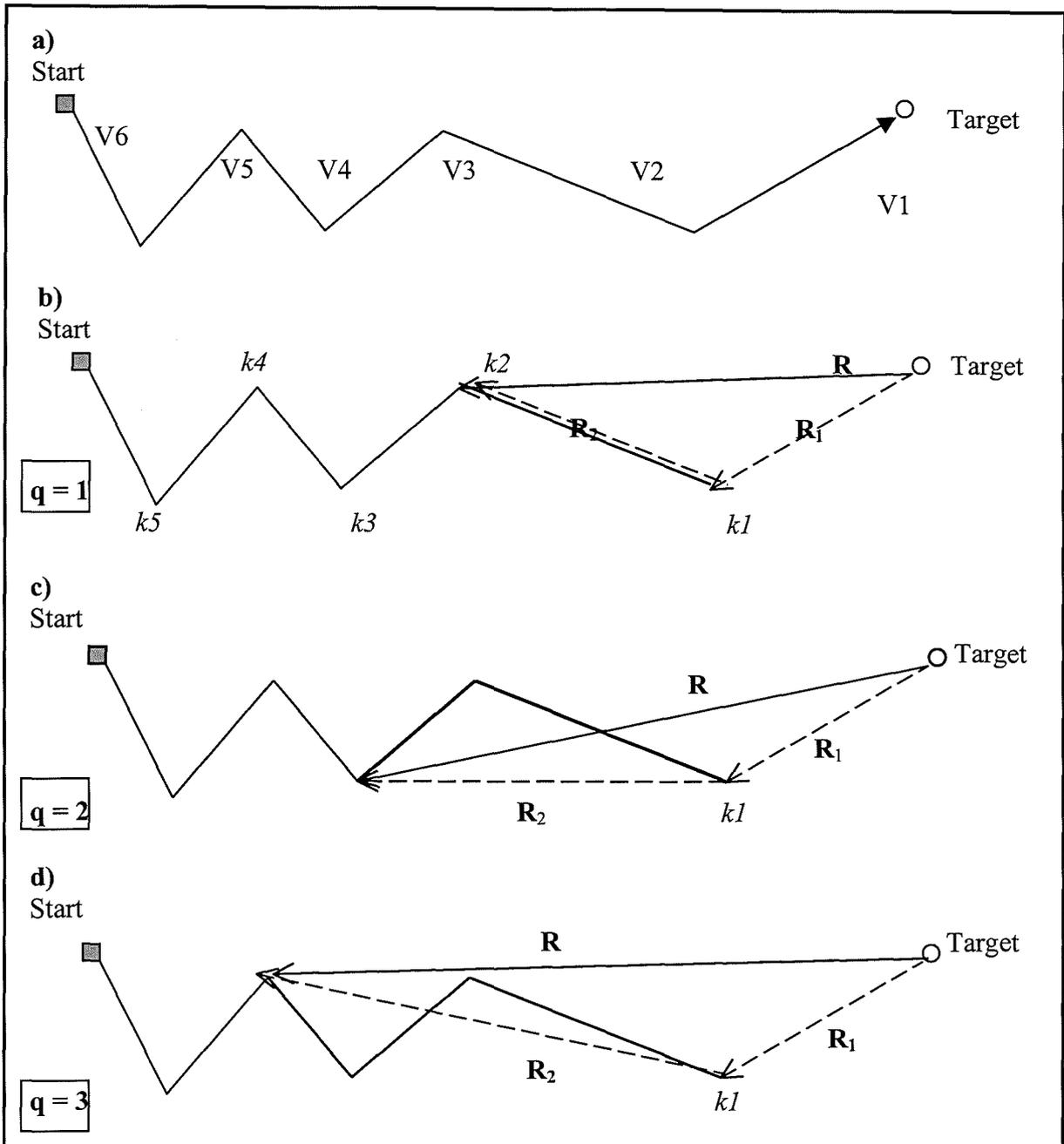
Figure 7.2. a): An imaginary travel route composed of vectors V1-V6 and b)-d): how the same point (namely k1) is tested with three different values of q; the number of vectors considered in each case is highlighted in bold. Refer to text for a detailed explanation of the parameters shown here.

In the simplest version of the test, one vector from the target to point k=1 (represented by R1 in Fig. 7.2b), comprises one of the samples that will enter the statistical comparison and the other sample consists of one vector after that point along the route. Of course, in reality, no statistical test is possible with only 2 data points, but hopefully this example

will make the description of the test easier to assimilate. With Jupp's test the magnitudes of vectors R1, R2 and the resultant R will be computed repeatedly for k_i points along the route (k1, k2...k5 in fig. 7.2b). Note that k=1 comprises one vector, but as one moves towards the point where movement originated, more vectors are added to the sample. If the scalar length of R is significantly smaller than the length of R1 + R2 for a given k_i, a change point will be declared.

It may be misleading, however, to use only one vector after a potential change point in the test, especially when measures of behaviour are involved. To work round this, more vectors can be considered, depending on the specific aims established by the researcher. The number of vectors thus included after the change point will be denoted by the letter q. For example, for q=2, two vectors after the change point, represented by R2 in Fig. 7.2c are included; for q=3 it is three vectors, represented by R2 in Fig.7.2d, and so on. Thus, for the test at k=1 with q=2, one sample comprises one vector before k1 and two vectors after k1. For the test at k=2 with q=3, one sample comprises two vectors before k2 and three vectors after k2 and so on.

7.2.1 *Notation.*

Jupp's test is applied to each point along a given route until H0 is rejected or until there are no more vectors after the k point to enter the test. For example, if a route is composed of 6 points, and one of them is the target, a maximum of four tests will be carried out at q=1:

<div align="center">

k=1 q=1, *

k=2 q=1,

k=3 q=1,

k=4 q=1

</div>

*In practice this test is meaningless, due to low sample size.

At k=5 the test cannot be performed because there are no more vectors after that point. At q=2 the tests are:

$$k=1 \ q=2,$$
$$k=2 \ q=2,$$
$$k=3 \ q=2$$

At k=4 the test cannot be performed because there are not enough vectors after that point to enter the test (see Table 7.1 for a detailed account of the formulas used in each case).

Table 7.1 Formulas of Jupp's test.

q =1	q = 2	q =3
$W = (R_1 + 1 - R) \dfrac{k_n - 1}{k_n - R_1}$	$W = \dfrac{k_n (R_1 + R_2 - R)}{k_n + 2 - R_1 - R_2}$	$W = \dfrac{k_n + 1 (R_1 + R_2 - R)}{k_n + 3 - R_1 - R_2}$

7.2.2 *On the significance level to be used*

Because the above procedure involves multiple statistical testing within the same data sample (a given route), and because the assumption of a von Mises distribution (Batschelet 1981) may not be precisely met, it is necessary to assume a conservative approach in the analysis, and thus it is safer to use a high significance level. I will therefore consider significant results only at $p<0.01$, but will also report results at $p<0.05$ in order to examine the congruence of results at different significance levels.

7.2.3 *On using different values of k*

Inevitably, the variance on the segment from *k* to target increases as *k* increases, regardless of the method applied. This means that a false negative result ("miss") is more and more likely as the value of k decreases (the problem is most acute if q is also low). That is, change points close to the target are liable to be missed. Consequently, a false positive change point becomes liable to be identified, *further* from the target than the real (missed) one. There is thus a danger of attributing greater 'foresight' to the monkey than

positive change point becomes liable to be identified, *further* from the target than the real (missed) one. There is thus a danger of attributing greater 'foresight' to the monkey than was in fact the case, simply as a result of the statistical machinery (and use of a high criterion for statistical significance makes this more likely).

One approach to this problem is to evaluate the linearity ratio (Chapter 5) of the route before the detected change point. The lower the linearity, the more likely the alleged change point was a false positive.

7.2.4 *On using different values of q*

With $q=1$ the sample size *after* each k point that is being tested is only one and thereby the only variance contributed to the test is on the route from k point to target (provided that k is different from 1). With larger values of q, variance is contributed to the test from both samples (i.e. vectors lying before and after k). In practice, one could use as many values of q as desired, but as with any other statistical procedures, it is convenient to have specific aims and predictions in mind before performing a test.

In my analysis of spider monkey routes I was interested in detecting the point at which a spider monkey's movements first became directed towards an important resource that it reached by travel. Thus, I was more interested in examining the route before the potential change point than the route after it, and so I used q values from 1 to 3 exclusively. In this way I was also able to evaluate the movement patterns as they occurred immediately after the change point; for example, if change points were detected more frequently at $q=1$, this would indicate that the route after the change point was either irregular or the vector immediately after the change point was in a different direction than the route after the change point. If, on the other hand, change points were detected more frequently at $q=2$ or $q=3$, this would indicate that the route after the change point was not irregular but linear, since in order to obtain a significant result at those q values, the two or three vectors analysed would have to be aligned with each other in a different direction than the route before the change point (see fig. 7.3).
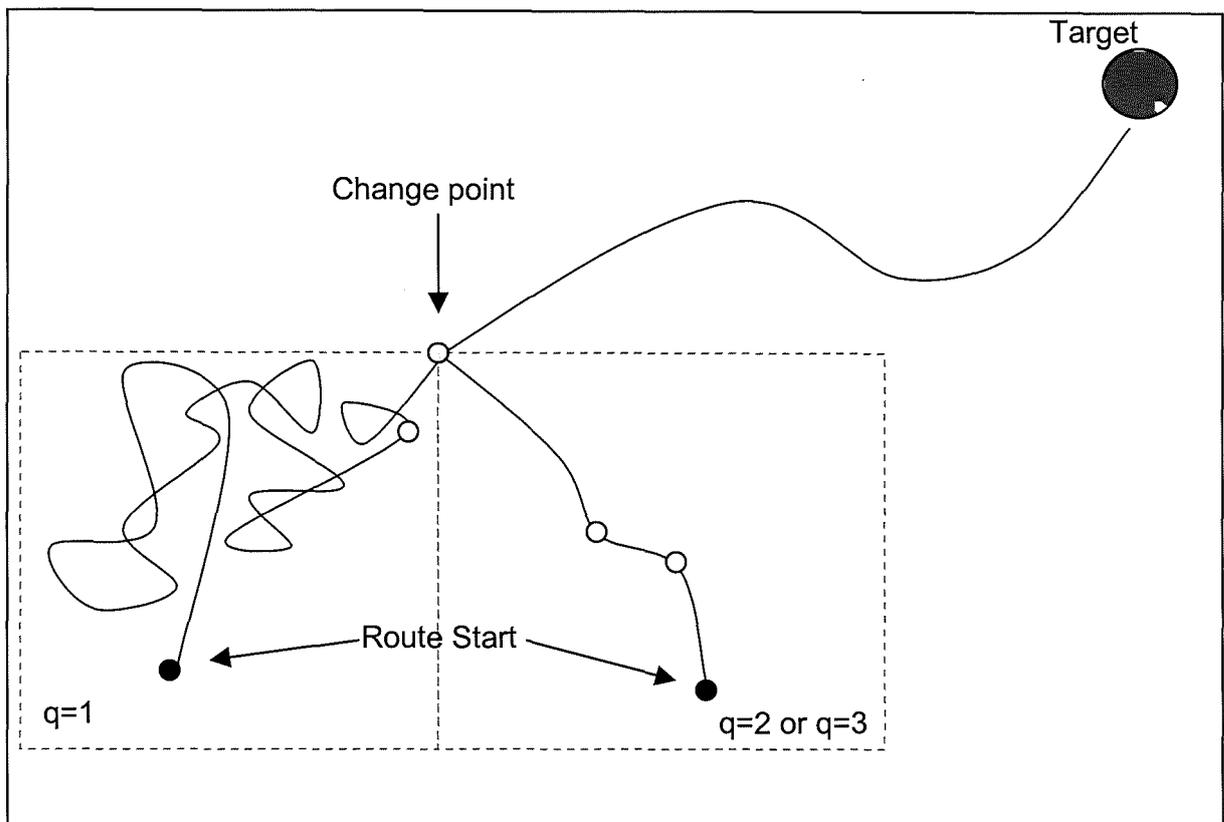
Figure 7.3. A graphical representation of a route and the different types of information that can be deduced from change points detected at q=1 and at q=2 or q=3 (see text). The vector(s) after the change point that were included in each of the tests at q=1, q=2 and q=3 extend from the change point to either of the light coloured circles.

The use of higher values of q would be justified in other cases, e.g. if a researcher wanted to study the route patterns after the change point, that is to say, the route from the point where movement originated to the point where a direction in the movement (a change point) occurred. This would be useful for example to determine how animals move before making a decision to change direction.

In the study described below I present the results of exploratory tests applying Jupp's unit-vector procedure to artificial routes that I created. I did this in order to test the behaviour of Jupp's unit-vector procedure as used in detecting change points, before applying it to real spider monkey routes.

7.3 Aims

i)   To test the power of Jupp's statistical procedure for detecting an evident change point in an artificially-created route.

ii)   To assess the effect that modified versions of such a route may have on the detection of the same change point through Jupp's test.

7.4 Methods

I artificially created routes that contained one potential change point and applied the Jupp test on each of them with different values of q. The routes were designed to simulate the movements of a spider monkey towards a food resource.

Route A (Fig 7.4a) was the simplest. It consisted of two long, straight segments and a potential change point between them. Since animals move in straight lines only to the extent that their environments allow, a simple route like route A does not simulate real animal movements. Nevertheless, it was useful as a control to evaluate the behaviour of Jupp's test in the simplest conditions.

Route B (Fig. 7.4b) was designed to simulate irregularities in the trajectory after the change point, while the route before the change point remained directed towards the target. This would have been equivalent to the erratic movement of an animal who at some point in the route makes a decision to head off determinedly until it reaches the target.

Route C (Fig. 7.4c) was used to evaluate the effect of a small deviation from a straight movement in the detection of change points. Thus I only modified the straight segment before the change point of route A. Finally, route D (Fig. 7.4d) was also used to evaluate the effect of a small deviation from a straight line in a route like route B. Thus I again only modified the straight segment before the change point of route B.
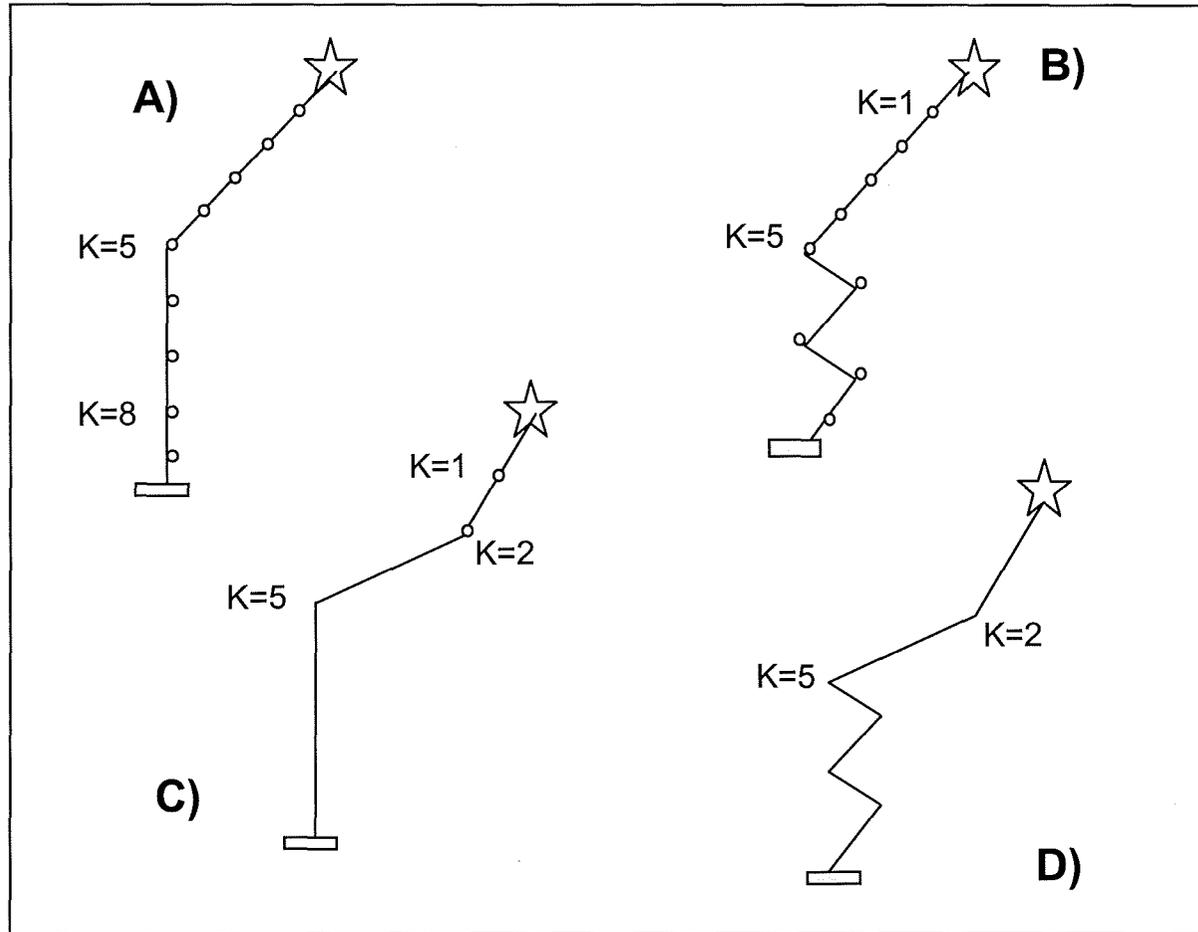
Fig. 7.4. Graphic representation of the artificial routes created for this study. The rectangular bar is the starting point of the route, while the star represents the target reached at the end of it. The dots in A and B indicate successive hypothetical steps taken but in C and D some of these were omitted for clarity. K=2 and K=5 are the change points detected in the analysis, see text

I applied Jupp's unit-vector test to each route, for q=1, q=2 and q=3. To examine the possibility that some change points might also arise at low significance levels, I report results both at p = 0.05 and p = 0.01. The results are summarised in the graphs and tables below.

7.5 Results

Only for route A was the change point detected for all values of q at high and low significance levels (Table 7.2). Moreover, a spurious 'change point' arose in two routes (in routes C and D Fig 7.4c-d.) and this was closer to the target than k=5 detected originally for route A.

Table 7.2. Change points detected at p=0.05 (*) and at p=0.01 (**). The number in a cell refers to the k that was detected as change point (fig. 7.4). NC:no change point was detected for that value of q.

	Route A		Route B		Route C		Route D	
	*	**	*	**	*	**	*	**
q=1	5	5	NC	5	5	NC	NC	5
q=2	5	5	NC	NC	2	5	2	NC
q=3	5	5	5	NC	NC	5	5	NC

When higher levels of q were used, a new and spurious change point (k=2) emerged at low significance levels. This change point was closer to the target than k=5 in routes A and B. Using q=2, change point k=5 on these routes was again detected (fig. 7.4c) at a high significance level when the segment after the potential change point was straight (i.e. route C), but it was not detected when the segment after the potential change point was irregular, as was the case for routes B and D.

When q=3 was used, one change point was detected at high significance levels (k=5 in Routes A and C, Table 7.2), when the route after it was straight. The same change point was detected on route B and D, but only at low significance levels. These routes were highly similar, because the segment after the change point was highly irregular. Thus from results of routes A and C it is safe to conclude that hits at q=3 emerged as

easily as hits at q=2, when the segment after the potential change point was close to a straight line.

7.6 Discussion

The basic procedure of Jupp's unit-vector test, namely finding the first point at which a route to a target became closer to a straight line, was effective when nearly straight lines could be assumed to extend on both sides of a change point. An artificially-created turning point that stands between two straight, but not collinear, segments of a travel route (Route A, Fig 7.4a) consistently emerged as a change point for all values of q at a high significance level. However, as soon as slight deviations from a straight line were introduced to the simple design of the route, different - albeit predictable - results began to emerge.

Hits at q=1 emerged easily when the 5 vectors before the change points lie in a clearly straight line – Route A and B - as long as the vector after it lies in a different direction. The irregularity of the route *after* the point tested (route B) did not affect the results, provided only one vector *after* the change point was considered in the procedure. This is reflected by the persistence of results at q=1 p<0.01 observed when the route after the change point was irregular (see fig. 7.4b, d), but a significant change point was detected at q=1 only when the segment before it was straight (route A), and not when it was slightly irregular (route C).

Raising the value of q to q=2 and q=3 proved to be more effective at detecting change points, provided the route after it was straight (route C), but not when it was irregular (Route D). Higher q values mean that more vectors after the point tested are entered in the statistical procedure. If these lie in variable directions (as are observed on an irregular segment of a route, e.g. B or D), they probably contribute some degree of noise to the calculations, thus preventing the test from reaching significance (as evidenced by results at q=3 p<0.05 for routes B and D). That weakly-significant results emerged when the route before the change point was closer to a straight line (results at

q=2 p<0.05 for routes C and D), confirms that a slight deviation from a straight line, although detected, was not big enough to produce a "false positive".

So, which is the most appropriate level of q to use for analysing travel routes? The answer is not simple. The results of this experiment do not lend strong support in favour of one particular value of q over another. Instead it seems that different values of q provide different types of information about the movement patterns, and thus the 'best' value to use will vary with the monkeys' characteristic patterns of movement. So far, results at high values of q (q=2 or q=3) may be taken as indication that the route after the change point was closer to a straight line; whilst persistent, highly-significant results at q=1 indicate that it was irregular. Weak significant results at high values of q combined with strongly significant results at q=1 also indicate that the route after the change point was irregular. Thus, for an animal which characteristically moves in direct, goal-oriented paths from one resource to another, high values of q can be employed, with the advantage of the greater sensitivity to points of changing direction. However, for any animal which sometimes moves in wandering, undirected paths, using a low value of q may be critical for detection of points at which haphazard wandering is succeeded by a period of goal-directed travel.

The travel routes analysed here were created artificially but Jupp's test was designed to study real animal movements. In the next chapter I analyse a small sample of spider monkey travel routes through Jupp's statistical procedure, in order to determine the location of change points along their routes, and to assess the directedness of their movements from these change points to the targets.

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CHAPTER 8

AN ANALYSIS OF SPIDER MONKEY MOVEMENTS BETWEEN IMPORTANT SOURCES THROUGH JUPP'S TEST

8.1 Background

In Chapter 6 I showed that spider monkeys used straight-line movements to move between food sources all year round, and in the dry season they were able to find more resources than a null model of straight-line movements in random directions would predict. Moreover, spider monkey movements in the dry season were goal-oriented on a larger scale than individual segments between resources, as evidenced by the fact that the orientation of subsequent segments on a travel path tended towards the forward direction (i.e. zero/360°).

Goal-orientation of movements that lead to food sites suggests a preference for the use of least-distance travel to reach specific locations, and could indicate that the animals had planned to reach them even when they were out of view. This in turn would provide additional support for the hypothesis that spider monkeys use mental representations of the location of different resources in their foraging.

To find out how far away routes become oriented I used Jupp's test to determine, within a given route, when the monkeys' direction of movement first became oriented toward an important feeding site. I used Jupp's test for this analysis because it was effective at detecting changes in direction in linear routes, as shown with arbitrarily generated routes in a preliminary test of the procedure (see chapter 7).

8.2 Aims

i) To apply Jupp's test to real spider monkey routes in order to determine the location of change points

ii) To determine the distances at which spider monkey movements became oriented towards an important target

8.3 Study 1. How far in advance do spider monkeys plan their foraging trips to feeding sites?

Presumably, the pressure to plan movements towards rare, highly-seasonal foods is stronger than for staple foods consumed in most months of the year. Thus, I analysed routes that ended with consumption of seasonal fruits and that fitted the definition of stop sites, i.e. stopping for more than 4 minutes. If there was an effect of fruit seasonality on the location of the change points on a path, however, this could be revealed by comparing paths leading to rare fruits with paths leading to staple fruits. Thus, I also chose paths that ended at staple fruits, and matched them to paths ending at rare fruits on the distance travelled from start point to stop site.

8.3.1 *Data used*

For this analysis I used only the movements observed in the dry-season months from October through to March. I did this because the analysis of goal-orientation of the routes presented in Chapter 6 showed a stronger effect in those months, thereby reducing the likelihood of confounding results from low orientation of wet season routes. A total of 22 routes were analysed: 11 of them ended at rare fruit species, and the other 11 ended at staple fruit species.

8.3.2 *Methods*

Lists of waypoint co-ordinates for both types of paths were obtained from files that contained behavioural and geographical data and copied and pasted onto Excel spreadsheets to analyse them. I combined co-ordinates of waypoints that were separated from each other by a distance of less than 25 m. To do this I computed the average of the

eastings and northings UTM co-ordinates of the points that were at distances <25 m apart. If the visual detection field of spider monkeys was similar to that of a related species (capuchin monkeys, Janson and Di Bitetti 1997) this procedure would also have ensured that the majority of the waypoints entered in the analysis indicated movements made between out of sight locations and, in any case, the residual error in GPS would risk spurious 'movements' with locations separated by less than that distance.

8.3.3 *Analyses*

Following results from the preliminary analyses of travel routes outlined in Chapter 7, I applied the Jupp statistical procedure on all paths for q=1, q=2, and q=3 with $\alpha = 0.01$. If there were two or more points on a route at which the statistic was significant, I chose as the change point and for subsequent analyses the point where the k value had the highest observed value of the statistic.

For each travel route I computed the true distance from the detected change point to the stop site and classified them into short or long; thus the distances from change point to stop site were classified in one of the following categories:

i)   Short/Rare: Distances of 1-700m leading to highly-seasonal (rare) resources
ii) Long/Rare: Distances >700m leading to highly-seasonal (rare) resources
iii) Short/Staple: Distances of 1-700m leading to foods eaten trough the year (staple)
iv) Long/Staple: Distances >700m leading to foods eaten through the year (staple)

I also computed the linearity ratios (Chapter 5) of the route segment between the change point and the stop site, in order to confirm that the change points would not constitute false positives.

The counts for each category were entered in a chi-square analysis and the formula indicated in Zar (1996) for 2 x 2 contingency tables was used. For this analysis, $\alpha = 0.05$.

8.3.4 *Results*

The distance from the change point to the corresponding target site ranged between 85 and 1560 m for routes ending at rare species, and between 116 and 764 m for routes ending at staple species (Table 8.1); there were no significant differences between rare and staple species (Mann-Whitney U = 89, p>0.05, N_1=11, N_2=11). The distance from change point to stop site was not dependent upon the type of species consumed at the stop site (short distances to rare species, 6, long distances, 5; short distances to staple species 10, long distances, 1; X^2 = 3.0, p>0.05). However, the variance in distance from change point to stop site was higher for routes ending at rare fruits than for routes ending at staple fruits (Rare fruits X ± SD = 690.98 ± 496.62, Staple fruits X ± SD = 308.09 ± 211.67; Test of Variance: F= 5.50, p<0.02, fig. 8.1).

Table 8.1. Distance (in meters) from the change point to a stop site for the routes analysed.

Rare Species	Distance to stop site	Staple Species	Distance to stop site
D. cuneata	85	*G. ulmifolia*	116
B. bipinnata	131	*Ficus spp*	130
D. cuneata	200	*B. alicastrum*	162
S. capiri	441	*Ficus spp*	162
Sayaak	559	*G. ulmifolia*	188
S. lutea	581	*B. alicastrum*	247
D. cuneata	826	*Ficus spp*	291
D. cuneata	866	*Brosimum*	310
S. lutea	868	*B. alicastrum*	382
S. lutea	1477	*B. alicastrum*	632
S. lutea	1560	*G. ulmifolia*	764

This suggests that, in the case of rare fruits, the point at which the route changed direction and became oriented to a stop site might be far or near to the resource, but in routes ending at staple fruits this took place consistently rather near to the stop site.
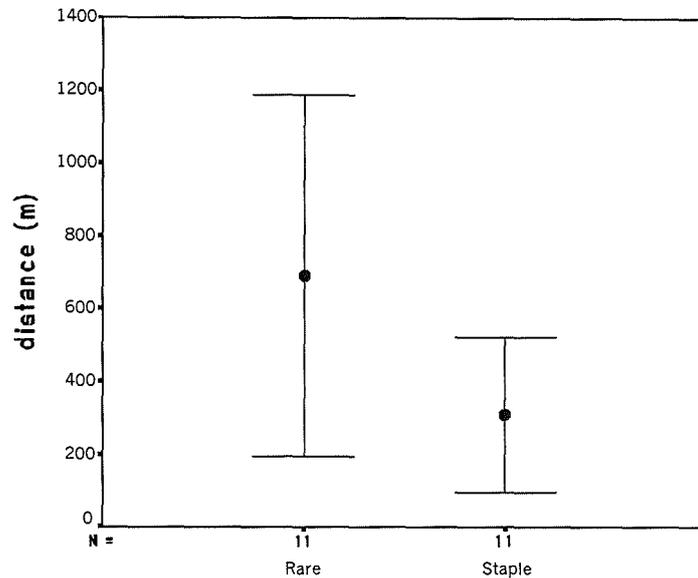
Figure 8.1. Mean distance from the change point to a stop site for routes ending at rare and staple fruits. The bars indicate one standard deviation from the mean.

In all routes analysed, the route from change point to stop site was highly linear (Rare fruits X±SD = 0.817±0.13, Staple fruits X±SD = 0.864±0.1, fig. 8.2), suggesting that the course of the route after the change point was maintained until the stop site was reached, thus the change points detected were not false positives.

8.3.5 *Discussion*

In all routes analysed, the distance from change point to stop site was far above the assumed visual detection field of 80 m. The use of visual cues in finding the stop site from the change point must then be ruled out. From other evidence, this therefore points to the use of least-distance, goal-oriented movements to a stop site. Thus it is plausible to say that in the dry season spider monkeys were able to plan foraging trips to rare fruits up to 1560 m in advance, and even for staple fruits they sometimes planned up to 764 m in advance.

What mechanisms may guide spider monkeys to orient their movements to a specific feeding site? The distances from change point to target sites would suggest that

cognitive mapping is a plausible explanation, and certainly use of visual cues as guides to reach target sites can be ruled out.
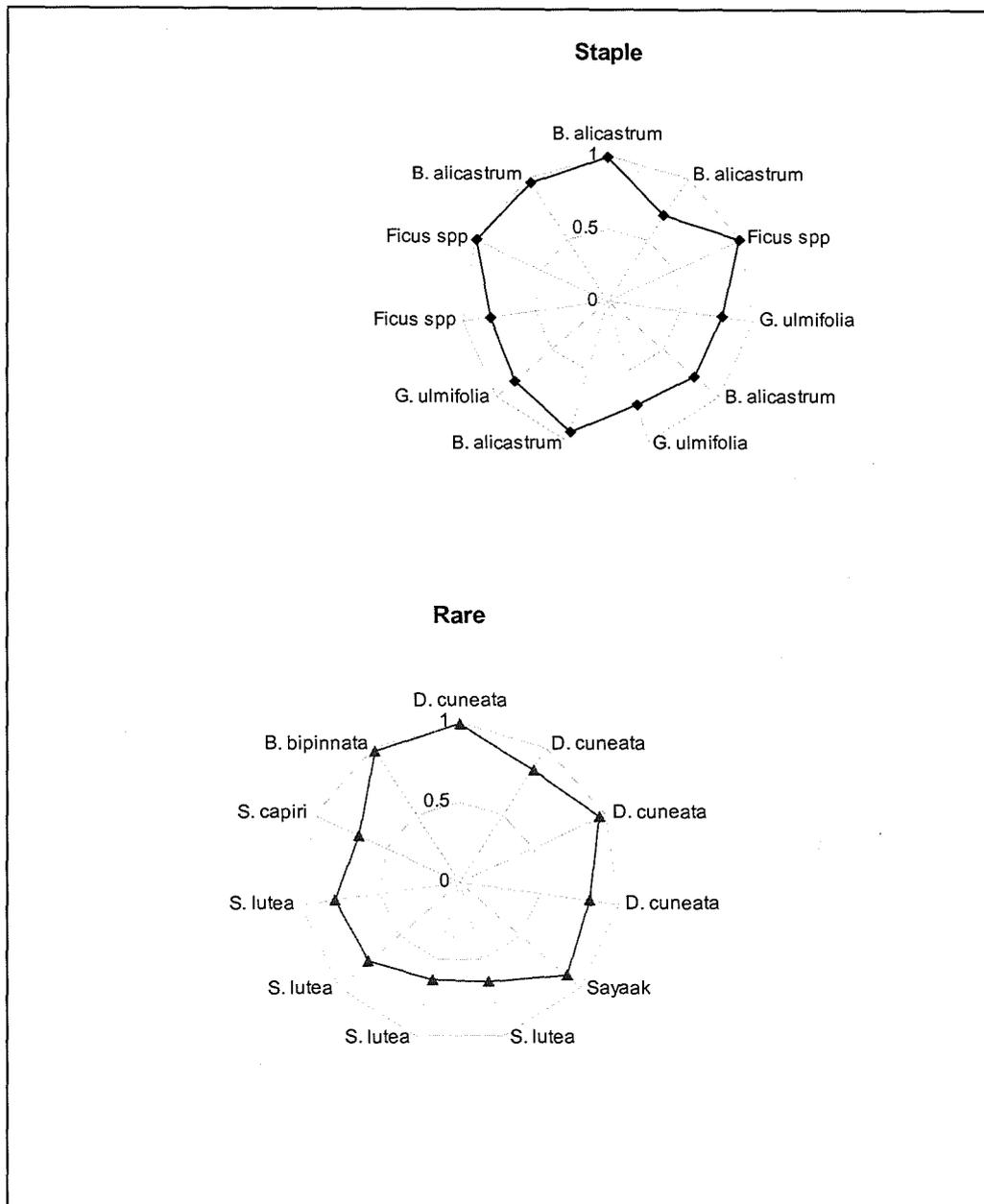
Figure 8.2. Radar graph of linearity of routes from the change point to the stop site for staple (diamond symbols) and rare (triangle symbols) fruits. The closer the graph to the perimeter of the polygon, the more linear was the route.

However, casual observations made while I followed the monkeys to some of these feeding sites suggested they might have used habitual routes to get to them. It has been shown that moustached and saddle-back tamarins can reach important feeding sites from different locations in their environment (Garber 1989), rather than re-using arboreal pathways over and over, which would suggest the use of spatial memory, but that may be an exceptional case. Thus in the next study I examined whether spider monkeys use familiar routes to reach important food sites in their environment or whether they, like the tamarins, are able to reach feeding sites from many different locations in their habitat.

8.4   Study 2. Do spider monkeys use habitual routes to find their way?

8.4.1   *Data used.*

I used all the paths that led to rare species of fruits in the dry season where the rare species had been consumed for more than 4min at the stop site.

8.4.2   *Methods*

I entered the co-ordinates of routes that ended at rare species of fruits in ArcView 3.2 to display them on-screen. I then superimposed all the routes that ended at same species of rare fruits on top of the map of the study site, in order to appreciate them visually.

8.4.3   *Results*

A total of 18 routes to 7 different species of rare fruits were examined in this analysis. Routes ending at rare fruits always started in the MX area, but led to various stop sites, through many different directions.

Superimposing all 18 routes revealed a series of long routes leading to some locations outwith the core area. Three groups of routes were clearly distinguished on the basis of the location of the stop sites visited at the end of these routes: south west routes, north east routes, and north west routes.

Four of the 18 routes analysed (22%) led to *D. cuneata* trees located on the southwest of the core area (fig. 8.3). The monkeys did not travel exactly on the same path to reach these sites, but they maintained the direction of movement (about 225° from their core area) on each of the four routes analysed.

Three of the 18 routes analysed (16%) ended at food sites located to the north-east of the study group's core area (fig. 8.4). At the end of these routes the monkeys ate fruits of *S. lutea, D. cuneata,* and on *B. bipinnata.*

Four of the 18 routes analysed (22%) ended at food sites of different species at different locations, but in all four cases the first half of the route was oriented to the north-west of the study group's core area (fig. 8.5), suggesting habitual route use at least for that part of the route.

The rest of the paths analysed (seven, 38%, fig. 8.6), which were recorded in October 2001, February, March and September 2002, ended at food sites of five different species within the study group's core area.
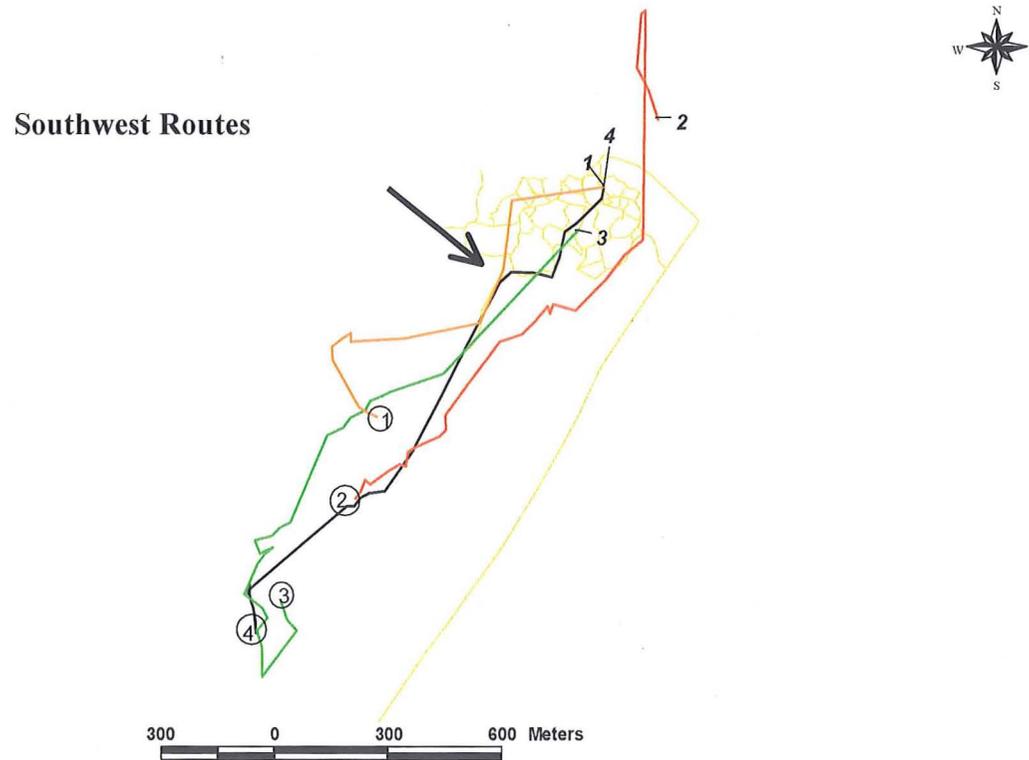
Figure 8.3. Routes to *D. cuneata* trees on four days between November and December 2001. The arrow points to the beginning of the route travelled (see text for an explanation). The open circles indicate the location of the trees visited, numbered 1 to 4. The same, uncircled numbers indicate the start point of each route. The dotted lines are the trail system in the MX area. Routes 1, 3, and 4 originated in the core area of the study group and route 2 in the GUAT area.
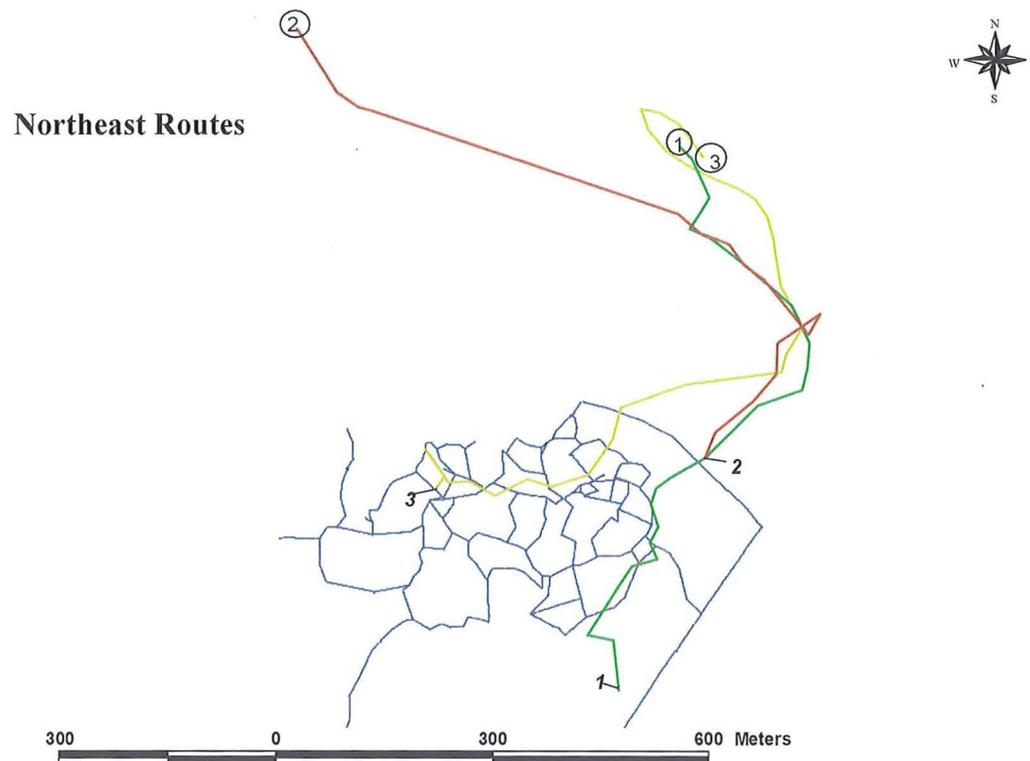
Figure 8.4. Routes to trees located on the north-northeast of the study group's core area. The open circles indicate the location of the trees visited: 1, *S. lutea*; 2, *D. cuneata*; 3, *B.bipinnata*. The start of each route is indicated by the same, uncircled numbers. The dotted lines represent the trail system in the MX area.
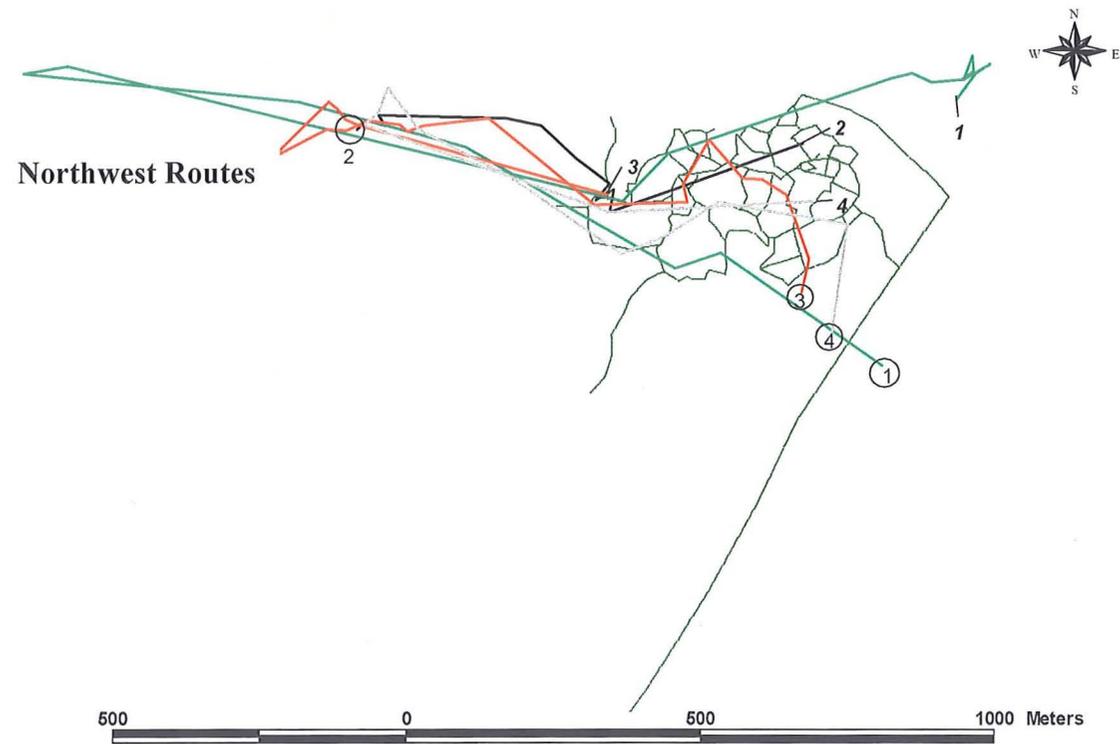
Figure 8.5. Routes that led to the northwest of the study group's core area. The circles with numbers indicate the location of the trees visited: 1 and 2, Sayaak trees; 3 and 4, *S. lutea* trees. The start of each route is indicated by the same, uncircled numbers. The dotted lines represent the trail system in the MX area.
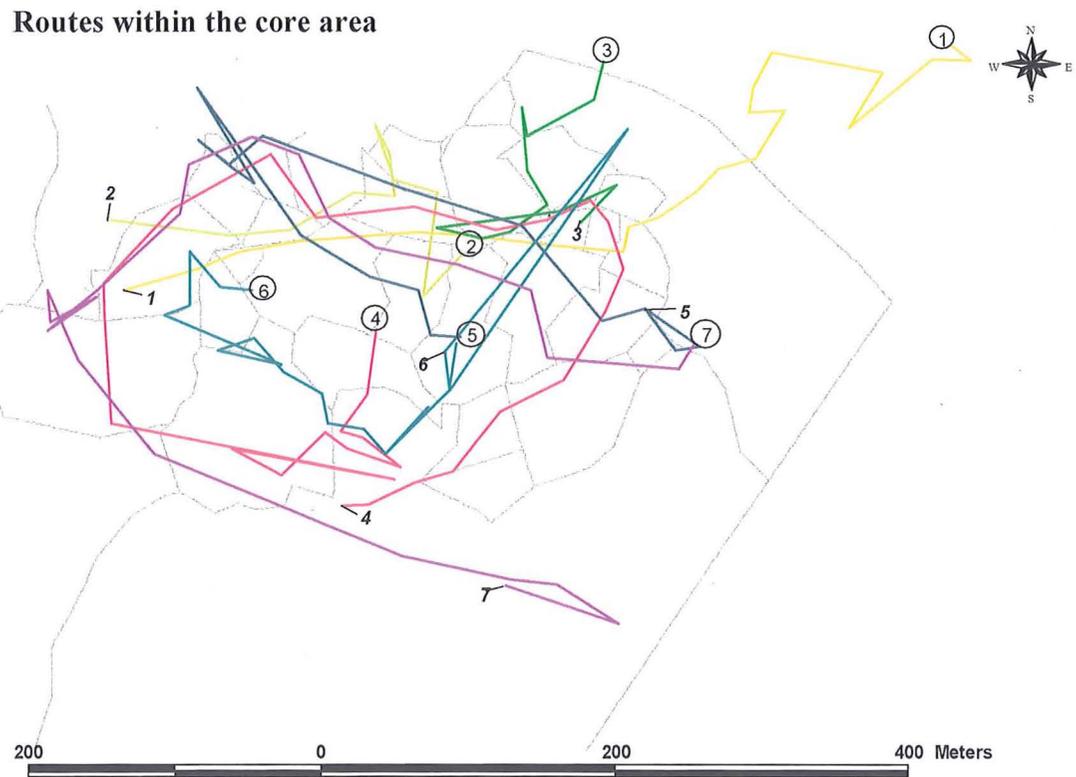
Figure 8.6. Routes that ended at food sites within the study group's core area. The circles with numbers indicate the location of the trees visited: 1, Morax trees; 2, xuul trees; 3 and 4, *S. capiri* trees; 5 and 6, *T. olivaeformis* trees; 7, *S. lutea* trees. The start of each route is indicated by the same number in ***bold italics***. The dotted lines represent the trail system in the MX area.

8.4.4 *Discussion*

Visits to the *D. cuneata* trees of the south-west took place continuously on 16 out of 25 days of follows between November and December 2001, with almost the whole group moving faster than usual from the moment they left the core area. Thus it was difficult to maintain a focal individual on sight for continuous periods of time and a reliable GPS record of the routes travelled was possible on only 4 of the 16 days when the monkeys visited the *D. cuneata* trees on the south-west. The super-imposition analysis performed on these 4 routes did not show habitual use of a single route, but on most of those 16 days I observed the monkeys moving towards the same point at the beginning of the route from different locations within the core area. This suggests that, like the tamarins reaching important feeding sites from a variety of locations (Garber 1989), spider monkeys may have used spatial memory at least to locate the start point of the familiar route. The spider monkeys did not travel these routes in the previous month or even the month before that (according to the accounts of the long-term field assistants), therefore the use of spatial memory to locate the beginning of the route is plausible, but past familiarity can not be ruled out.

A similar explanation may be used for the routes that ended in the north-east. On these routes, spider monkeys maintained a course of movement (about 45° from their core area) on the three routes until they reached the target sites, but super-imposition of the routes also failed to show a single familiar route. This result is thus more consistent with the idea that spider monkeys have some spatial knowledge to visit a few locations that lie outside their core area. The temporal spacing of the visits to these food sites (one in October, one in November and one in February) supports this contention as it suggests that the monkeys had to remember how to get onto the correct route to reach the desired feeding sites each time. However, the monkeys in the study group visited the north-west area on several occasions in these months to feed on fruits that were not classified as rare, thus familiarity cannot be ruled out in this case either. This argument also applies to the routes that ended at sites in the north-west of the area (see below).

The most plausible reason for the trips to the north-west must have been the sayaak fruits in that area, as evidenced by the fact that on these portions of the four routes the monkeys ate that rare fruit. All four cases were recorded at the start of the study, over four days in October 2001, and the long-term field assistants did not report having seen the spider monkeys travelling these routes in the previous month. As in the case of visits to the *D. cuneata* trees on the south-west, and to the north-east area of the forest, the monkeys maintained a course of movement (about 150° from their core area) for some time. On one of the routes examined (route 2, fig. 8.5) I lost sight of the focal animal, thus the route ended midway into the north-west area. On the other three routes (routes 1, 3 and 4, fig. 8.5) the monkeys returned to the core area after some time, by back-tracking on the same path.

For the rest of the routes analysed, none of the stop sites or the routes travelled followed similar directions. There was not a pattern consistent with habitual use of routes in these routes; moreover, all of them except for one (number 1, linearity: 0.72, fig. 8.6) were circuitous (median linearity 0.58, range: 0.06 - 0.72).

8.5   General Discussion and Conclusions

Spider monkeys foraging for fruits were able to orient their movement towards feeding targets at a maximum distance of 1500 m for rare fruits and 760 m for staple fruits, and the path between the orientation change and the resource was highly linear in all cases. Thus, the distances at which spider monkeys routes became oriented towards distant resources was way above the visual detection field calculated for a related species (Janson 1998), and the directness of their movements to them suggests that their visits to these sites were planned in advance. Straight movements also took place when the monkeys oriented toward sources of staple fruits, but apparent 'planning' in these cases took place at shorter distances from the site. The results in Chapter 6 rejected the null hypothesis that spider monkeys were able to find food sources by moving in straight-lines in random directions, and suggested that their movements towards important food sources in the dry season were goal-oriented. The results presented here lend additional support to

the goal-orientation of movements, suggesting that spatial memory may be involved in the straight-line movements that took place from the change point towards the target.

It is unclear whether spider monkeys travelled on habitual routes to reach some of the rare fruits they consumed, particularly outside of their core area. Use of habitual or stereotyped routes (cf. Collett *et al.* 2002) to travel from a central place to a habitual foraging site is common in insects (Collett *et al.* 1992, Wehner *et al.* 1996, Schatz *et al.* 1999), birds (Davoren *et al.* 2003), and to a certain extent in wood mice (Jamon 1994). In some of these species, stereotyped routes may arise as a consequence of trail following behaviours. Trail following is the process whereby an animal moves along a trail of chemical (Banks & Srygley 2003) or other types (see Dehnhardt *et al.* 2001) of cues left by itself or by a conspecific in order to reach a destination. In the case of chemicals, however, efficient trail-following would require an ability to detect minute concentrations of the cue and to discriminate among a myriad of other cues already present in the environment and it may thus be exclusive to species with higher than average olfaction or chemo-reception skills. Species with good chemo-reception abilities favour alternative mechanisms of navigation over trail-following of chemical cues to reach desired locations (spatial memory in kangaroo rats, Timberlake & Hoffmann 2002; sun-guided orientation and memory of junctions in crabs, Cannicci *et al.* 1997, spatial memory in night monkeys and Emperor tamarins, Bicca-Marques & Garber 2004). Spider monkeys could be added to this list, if experimental studies provide convincing evidence that they favour the use of spatial information over other information types in their foraging decisions.

I propose that spider monkeys use spatial memory of the location of highly-distant food sources. This conclusion is based on observations of spider monkeys moving towards the starting point of the routes to the *D. cuneata* trees, and on the fact that they did not habitually use a single route to reach these or other important feeding sites. Moreover, spider monkeys were able to start travel on these routes from different locations in their core area, in the same way as moustached and saddle-back tamarins do to reach important feeding sites in their environment (Garber 1989). It is impossible to

determine precisely what mechanism allows spider monkeys to find food along these habitual routes unless experimental data is gathered from studies in the wild.

Spider monkeys showed a remarkable ability to orient their movements to a desired stop site in anticipation of it, and this only marginally depended on the type of fruit consumed at the stop site (rare v. staple). This suggests they may be able to track temporal variations in the food availability and to modify their travel patterns accordingly. Results from previous chapters indicated that this is a plausible explanation, because the movements of spider monkeys in the dry season were more linear and more goal-oriented than in the wet season. In addition, the large distances at which orientation changes took place from the stop sites, and the variety of directions used to reach the starting point of some routes, suggest that spatial memory may have been responsible for the apparent efficiency of the foraging patterns observed.

CHAPTER 9

GENERAL DISCUSSION

9.1 Summary

Frugivorous primates exploit food sources that tend to occur in spatially-discrete patches in the environment. Compared to leafy foods, the availability of fruit sources varies greatly in time. Preferred food sources for spider monkeys at the study site of Punta Laguna underwent changes in the course of the year: hard, inedible fruits ripened, trees lost their leaves, but replaced them with nutritious fresh young ones, and flowers blossomed, but later died to give way to new fruits. Thus spider monkeys in the Punta Laguna study group exploited food sources by harvesting them from a continuously changing-matrix, which may not be a trivial task. What enables spider monkeys to work round the variability, unpredictability and overall complexity inherent in their environment in order to satisfy their basic feeding requirements?

For an animal living in an environment where no single food source provides food at all times, it would be reasonable to expect variation in the lengths and directions of daily movements in response to changing food availability. The ranging patterns of spider monkeys in their foraging journeys indeed did not remain constant throughout the year. Monthly variations in ranging behaviour were found in the length of travelled routes, relative linearity, and direction of travel. That spider monkeys may have modified their ranging patterns in response to food availability and distribution was suggested by the finding that the month-by-month proportion of fruit in the monkeys' diet remained at the same level throughout the year, even when it was clear that ripe fruit were very hard to find in their core area during November, December and part of January. However, the effect of a fruit diet was most clearly seen when spider monkeys adjusted their ranging to the availability of a few key species of fruit (e.g. *Diospyros*, Sayaak, *S. capiri*) occurring outside their core area, by travelling longer distances than their usual day range lengths to far-off locations. All these variations might be seen simply as a reflection of variation in the availability of the key species exploited, in animals that foraged haphazardly each day

until sufficient food had been acquired. However, my investigation into spider monkeys' movements between food sources suggested that the variation in their ranging patterns was not in fact haphazard: spider monkeys used spatial memory of key locations to move efficiently towards most food sources consumed. Navigation mediated by spatial memory during the dry season, when resources were sparse, was evidenced by route segments during the dry months of the year that 1) were longest, 2) had the highest linearity ratios 3) were forwardly-oriented, but that also 4) yielded more rewards than a null model of direct movements.

Spider monkeys travelled directly (i.e. in near straight lines) to targets that may not have been within their visual reach when the movement started: at least one out of two of the feeding targets they visited was located at a distance that surpassed other primates' abilities to detect stationary targets (Chivers pers. comm; Garber and Hannon 1993; Janson 1997). That spider monkeys are able to move determinedly to targets they cannot perceive at the start of a bout of movement is consistent with goal-directed travel; moreover, their route segments in the dry season were organised in an apparently efficient, forward oriented fashion, suggesting that the monkeys planned their routes for several steps ahead. It might be argued that the monkeys foraged according to simple rules that included a tendency to travel linearly, but simulation of such a simple foraging model showed that the Punta Laguna monkeys were significantly more successful than it would imply. Spider monkeys' use of spatial information was further supported by the finding that they were capable of orienting their movements and moving directly towards a desirable target sometimes at distances that were 1/3 of the total day range length, and that they did not typically travel on familiar routes to reach important but very distant targets outside their core area. These findings are in contrast to those of experiments with capuchin monkeys foraging for bananas throughout an array of feeding platforms (Janson 1998). Janson observed that these monkeys moved directly and in straight lines to feeding platforms, but in most trials they visited the nearest-available feeding platform, thus not showing clear evidence of contemplating future visits to other platforms.

Such clear evidence of the use of spatial knowledge was exclusive to spider monkey movements made in the dry season. In contrast, in the wet season, a simple foraging model of straight-line movements in random directions was equally effective as spatial memory at explaining the spider monkeys' rate of encounters with feeding sites. If food resources were abundant everywhere in the monkeys' home range, the probability of encountering a feeding site by walking directly would be much the same for any direction chosen, thus, initiating movement in a random direction would yield reward. However, this picture of apprent haphazard foraging in the wet season may be simplistic.

Although numerous feeding resources become available in the wet season, thus providing increased chances of encounter, their diversity may not be uniform in space. Such variability is probably due to inter-specific competition among trees for sunlight, or for space and nutrients in the forest floor, which means that some species will predominate throughout space while others will be confined to small, inconspicuous areas. Under these circumstances, walking in straight lines in any direction might no longer be an appropriate strategy to obtain a representative sample of the diversity of food species in the forest, despite its effectiveness at getting rewards. Notably, spider monkeys did in fact sample a more varied set of food sources than would be predicted by the null model of direct movements in random directions. Thus, ensuring a varied diet in the wet season may be a similar problem to that of encountering food sources of any type when food is sparse (in the dry season), because the diversity of plant species is unequal throughout the forest.

In conclusion, it would be unwise to assume that in reality spider monkeys do not rely on memory throughout the year, given that they probably did so in order to move efficiently to approximately half of the important feeding targets they visited. Spatial memory may thus be equally necessary to meet different requirements e.g. finding food sources when they are scarce, and/or finding the food sources that will contribute to a varied diet when these are abundant in the environment.

9.2 Future Work

Spatial memory in animals has traditionally been studied in captive environments, where landmarks and/or the extent of the environment can be relatively easily assessed visually by the subjects (Janson 2000). Moreover, experiments in captive environments seldom include the unpredictability given by the seasonality of some food sources or the complexity of cues that the natural environment provides (but see Menzel 1991; Hemmi and Menzel 1995; Menzel 1996). Thus an attempt must be made to replicate the characteristics of the natural environment as much as possible in a comprehensive study into the spatial abilities of primates, or it must use the natural environment as a background to the study. Experimental studies in natural conditions are particularly well suited to the study of spatial cognition, because they allow the experimenter to manipulate variables such as the location and amount of food, the difficulty of extracting it, or the distance that must be travelled to get to a given resource.

Experimental studies in natural conditions have shown that, when presented with visual and olfactory cues, either in an alternated way or simultaneously associated to feeding sites, Neotropical primates use these as an aid in their foraging trips (Bicca-Marques & Garber 2004). However, they readily switch to use spatial memory of the location of feeding sites when conflicting visual and olfactory cues are presented (Garber & Paciulli 1997). In addition, even night monkeys, *Aotus nigriceps,* a species that routinely uses olfactory cues to find food, rely on spatial information in their foraging trips (Bicca-Marques & Garber 2004), while diurnal capuchin monkeys seem unable to rely solely on visual cues to find food sources, if they move rapidly through the forest (Janson & Di Bitetti 1997). Moreover, capuchin monkeys encountered food sources at rates higher than predicted by 'random' foraging models that take into account their visual detection field, suggesting their straight-line movements towards food sources are guided predominantly by spatial memory (Janson 1998). Spider monkeys also encountered more food sources than predicted by a similar model of 'random' foraging and, contrary to the findings in capuchin monkeys, the organisation of spider monkey routes suggests they were capable of planning ahead farther than the next site visited (this study).

Nevertheless, the picture is not completely clear, and the role of other sensory systems in monkey navigation, e.g. olfaction, and/or hearing studies has yet to be determined. Focusing on these issues through studies of large-scale navigation in natural environments will pave the way to establish which factors influence, as well as which constrain navigation, and characterise the cognitive maps of primates. I offer here a few suggestions for future work in primate navigation mechanisms.

9.2.1 *Olfaction*

Theoretical models of foraging patterns reveal that navigation aided by olfaction may not be as useful as spatial memory in finding feeding sites efficiently (Garber & Hannon 1993). In addition, experimental studies of food-finding behaviours with wild primates have confirmed that some Neotropical monkeys rely on memory of the location of feeding sites when olfactory information conflicts with visual information (Garber & Paciulli 1997). Moreover, it has been hypothesised that non-olfactory cues (e.g. textural and/or taste) might be used preferentially over olfactory ones in feeding decisions (Dominy et al. unpublished data). Although olfaction plays a crucial role in the social interactions of many species of Cebids (Zeller 1988), its potential use as a cue detector and an aid in finding food sources has not yet been clearly established.

Future research must determine experimentally the extent of olfactory capabilities in primates, e.g. the relationship between intensity of the stimulus and the ability to detect it from different distances, and at different intensities of propagation, and/or when it is combined with other odours. In natural conditions, experiments could be carried out on which preferred food odours are emitted mechanically from different directions, at different intensities, and a real or a sham reward is placed at the source of the odour trail. By looking at which routes the subjects use to get to the sites baited with real rewards, it could be determined whether use of spatial information prevailed over use of olfactory information.

9.2.2 *Hearing*

It has been hypothesised that vocal communication should be favoured when visual signals cannot be perceived (Boinski 1993), a common scenario in arboreal environments where visibility is constrained by abundant foliage. Thus, arboreal primates would be expected to emit calls that are associated with, for example, situations where members of a social group are not within visual contact. Under such circumstances, vocal signals could be functioning as auditory landmarks or beacons guiding one or a group of animals towards, or away from, a target. Little is known about the role of calls as aids to navigation, although work on Guinea baboons in Senegal suggests that some calls elicit regrouping after troops have been foraging in smaller isolated parties (Byrne 1981). In spider monkeys, 'whinny' calls have been hypothesised to function in establishing contact with the group after a brief period of isolation (Teixidor & Byrne 1999), with the 'whinnies' given in response probably guiding the 'lost' individual to rejoin the group.

The real potential of contact calls as an auditory beacon, however, has not been explored. Playback experiments with spider monkeys could provide insights into these issues, by broadcasting sequentially, and from different directions familiar and unfamiliar, 'whinny' calls emitted in food or moving contexts, in response to contact 'whinnies' emitted by small parties (or single individuals) of foraging monkeys. By blocking access to familiar routes or landmarks, thereby forcing the animal to make a choice based solely on the auditory information received, it would be possible to establish which type of call, if any, is more likely to elicit a response. Perhaps this type of experiment would be relatively unfeasible to perform in a natural environment with arboreal monkeys, but it could be conducted in a captive enclosure provided that the distances to feeding sites were large enough to prevent visual cues from interfering with the monkeys' behaviour.

9.2.3 *Exploration*

An aspect of primate navigation that has been neglected in field studies of behaviour is how spatial information may be gained for future use in foraging excursions. Virtually nothing is known about this, but in Guyana, Marc van Roosmalen (cited in Byrne 1995,

p. 181) observed certain spider monkeys that appeared to be exploring their habitat, apparently in search of potential feeding targets that were visited on the day after the prospective trips. The main difficulty of approaching this issue in the field is that the arena in which navigational processes take place is not new to the primates studied; thus the researcher is unable to determine whether the routes taken by the study subjects have been used before the study began. Long-term field studies, if they manage to be systematic enough, should be able to shed some light on this issue. The main difficulty of studying exploratory behaviour is to be aware and ready to identify such behaviours when they occur. Exploratory behaviours of other animals have been described from experimental situations, in which a study subject is introduced into a completely new environment (Birke & Archer 1983), but nothing is known about the exploratory behaviour of primates. Thus, one of the principal aims in a study would have to be to achieve a description of the exploratory behaviour of a species. Once the behaviour(s) can be readily identified, an investigation of the determinants of, and the sensorial mechanisms underpinning, these behaviours must be carried out.

It would be no less important to determine which mechanisms are involved in transmission - vertical and horizontal - of information used in navigation to other members of the group. No evidence yet exists to support a role of social learning in these processes, but given the relevance of mother-infant bonds in spider monkey societies, it is highly likely that vertical transmission is a plausible candidate. In addition, given the social dynamics among adult spider monkey males, a significant component of horizontal transmission must also be present.

9.2.4 *Experimental paradigms*

As was mentioned above, experimental studies of foraging decisions in natural conditions have provided insights into how primates use available information in the environment to find and exploit feeding platforms baited with food. This type of paradigm could be used also to study spider monkey feeding decisions. Experiments with feeding platforms could be used, for example, to determine the visual detection field of spider monkeys in natural conditions. Such information would be useful in designing experiments to evaluate

whether landmark-guided navigation is predominantly used in long-scale movements, or if more complex cognitive mapping abilities are present in this species. As was mentioned before, spider monkey routes were organised in a way that suggests planning beyond the next feeding site (this study). Capuchin monkeys foraging for food at baited platforms (Janson 1998) do not seem to plan their visits in such a way, despite sharing similar habitats and dietary habits with spider monkeys. Experiments with spider monkeys on feeding platforms will undoubtedly provide insights to explain this apparent discrepancy in the foraging behaviour of these two ecologically-similar species.

I believe one of the greatest challenges in the study of animal spatial cognition will be to elucidate the neural mechanisms associated with navigation in space. Specifically, there is no information on whether route-based or geometric maps can be or are encoded by any structure of the primate brain. In addition, the energetic or computational costs incurred by using either of these mental representations of space are unknown. Perhaps the first step in this enterprise would be to characterise structures in the primate brain that may be involved in spatial processes, and by doing comparative studies with other species sharing similar cognitive demands (e.g. food-caching birds). Although the task of reducing a high-level cognitive function to neurobiological terms may seem painstaking, pointless and impossible, the information gathered from these studies would undoubtedly prompt new approaches and ultimately advances in the study of spatial cognition.

Finally, experiments in the field of animal spatial cognition should be aimed at discerning between at least two types of cognitive maps: route-based representations of landmarks and targets in space, or spatial representations of the geometrical relationships (distances, bearings) between locations in the habitat and desired targets.

9.3   Epilogue

Primates are not behavioural ecologists, therefore it is difficult to contemplate the possibility of them calculating the costs and benefits of travelling over different alternative routes. Primates also are not mathematicians or economists and it is similarly challenging to imagine them evaluating which is the most beneficial route to follow in terms of the energy spent in moving over given distances compared to the potential gains obtained at the end of foraging trips. Finally, primates do not have access to chemistry laboratories to evaluate the nutritional value of different foods available to them, but spider monkeys possess similar brains to ours, functioning physiologically in apparently similar ways to ours, and we share with them a similar repertoire of sensory systems to interact with the environment. Thus, to understand the sensory and cognitive mechanisms underlying their navigational abilities, and the influence these have in making foraging journeys efficient - with the consequent characterisation of these mechanisms - is bound to provide helpful insights into the evolution of the primate brain. Likewise, a productive approach to studying the evolution of other primate cognitive abilities must take into account the similarities of brain/body function as well as form between primates and hominids, instead of promoting recurrent attempts to widen the gap between them.

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APPENDIX 1

Programmed routines ('scripts') used.

The scripts listed below were used in preparing data collected with the GPS receiver and with the Psion hand-held computer for analyses.

Script 1.

This script was used to divide a list of GPS records that contained data for different days, into separate files, each with GPS data of a single day.

```
#
# Este script "limpia" y separa un archivo en "UTMs".  Estos archivos empiezan
# con el encabezado "Datum,WGS 84".  El nombre del archivo es la fecha que
# se va a procesar.
#
# El archivo separado y limpiado se deja en "D:\separados\FECHA.txt"
#
# Quitamos columnas que no son útiles
#
# Uso: perl limpiautm.pl archivo.txt
#
if ($#ARGC == 2){
    print "Uso correcto: perl limpiautm.pl archivo.txt\n\n";
    print "      Donde archivo.txt es un archivo del UPS que tiene como\n";
    print "      primera linea: Datum,WGS 84 y su nombre codifica una fecha:\n";
    print "   (ejemplo: 010402.txt es el 1ero de abril de 2002)\n";
    die;
}

if ($ENV{"OSTYPE"} =~ /linux/){
    $dir = "/tmp/separa";
    $indir = "/a/UTMs";
} else {
    $dir = "d:/separados";
    $indir = "d:/UTMs";
}
```

```perl
if ($ARGV[0] eq $ARGV[1]){
    print "Error: El archivo de entrada no puede ser el mismo que el archivo de salida\n";
    die;
}

$arch = $ARGV [0];
open ENTRADA, "$indir/$arch";

@meses = ("JAN", "FEB", "MAR", "APR", "MAY", "JUN", "JUL", "AUG", "SEP", "OCT",
"NOV", "DEC");

$dia_numero = substr ($arch, 0, 2);
$mes_numero = substr ($arch, 2, 2);
$ano_numero = substr ($arch, 4, 2);

$mes = $meses [$mes_numero-1];
$fecha = "$dia_numero-$mes-$ano_numero";

$salida = "$dir/$fecha";
print "Extrayendo los datos de: $fecha\n";
print "Enviándolos a: $salida\n";


$firma = <ENTRADA>;
if (!($firma =~ /^Datum,WGS 84/)){
    print "Error: El archivo de entrada no empieza con `Datum,WGS 84'\n";
    die;
}
open SALIDA, ">$salida";
print SALIDA $firma;

while (<ENTRADA>){
    ($wp,$utm,$cod,$dcq,$n1,$n2,$f1,$f2,$fecha_archivo,$ca,$cb) = split (/,/);
    if ($fecha_archivo =~ /$fecha/){
        ($ff, $hh) = split (/ /, $fecha_archivo);
        ($hora,$min) = split (/:/, $hh);

        # horas restadas: 6
        $hora = $hora - 6;
        print SALIDA "$wp,$utm,$cod,$n2,$n1,$ff,$hora:$min\n";
    }
}
close ENTRADA;
close SALIDA;
```

Script 2.

This script was used to join a file with GPS data for a given day, to a file with observational data (created in The Observer 3.0 software package by uploading data from the Psion hand-held computer) for the same day.

```perl
#
# Combina: Nuevo nombre para `njunta'.
#
# Usa archivos en:
#       d:\separados\XXXX
#         d:\txtobserv\YYYY
#
# Y se llama asi:
#    perl combina XXXX YYYY
#
# La salida combinada la deja en:
#       d:\combinado\YYYY
#
# Este script fue actualizado en Abril, 2002
#

if ($#ARGV != 1){
        print "Uso correcto: junta ARCHIVO_GPS ARCHIVO_PSION\n";
}


#
# Esto calcula el directorio "base" para que funcione en Linux o Windows
#
if ($ENV{"OSTYPE"} =~ /linux/){
    $top = "/a";
} else {
    $top = "d:";
}


#
# Estas variables calculan los directorios de datos de entrada y salida
#
$file_gps = "$top/separados/$ARGV[0]";
$file_psion = "$top/txtobserv/$ARGV[1]";
$file_out = "$top/combinado/$ARGV[1]";

print "Leyendo:   $file_gps y $file_psion\n";
print "Generando: $file_out\n";

open GPS, "$file_gps" || die "No puedo abrir el archivo de GPS: $file_gps";
open PSION, "$file_psion" || die "No puedo abrir el archivo de PSION:
$file_psion";
open SALIDA, ">$file_out" || die "No puedo crear el archivo combinado:
$file_out";

$firma = <GPS>;
if (!($firma =~ /^Datum,WGS 84/)){
    print "Error: El archivo GPS no empieza con `Datum,WGS 84'\n";
```

```perl
    die;
}

while (<GPS>){
        $_ =~ s/(\n|\r)*//g;
          ($wp,$utm,$cod,$n1,$n2,$fecha,$tiempo) = split (/,/);
          ($hora,$min) = split (/:/, $tiempo);
          $segundos = (($hora * 60) + $min) * 60;

        # Quitarle las 5 horas de diferencia
          #$segundos -= 5 * 3600;

          $d = "$wp,$utm,$cod,$n2,$n1";
          $datos_gps [$segundos] = $d;
          $fecha_gps = substr ($fecha, 0, 9);
          $momentos .= " " . $segundos;
}

#
# La base es el numero de segundos "base" que se le suman a todas las horas
#
$base = 0;
$basura = <PSION>;
$decoracion = <PSION>;
while (<PSION>){
        if (/^date/){
                $fecha_psion = $_;
        } else {
           print SALIDA;
        }
        if (/^hour/){
                ($a, $b, $hora) = split;
                $h = substr ($hora, 0, 2);
                $m = substr ($hora, 2, 2);
                $base= (($h * 60) + $m) * 60;
        }
        if (/^-----/){
                while (<PSION>){
                        if (/^[0-9]/){
                                ($segs, @resto) = split;
                                $segs = $segs + $base;
                                $datos_d [$segs] = join (" ", @resto);
                                $momentos.= " " . $segs;
                        } elsif (/From/){
                                while (<PSION>){
                                        if (/----------/){
                                                while ($linea = <PSION>){
                                                        chop $linea;
                                                        if ($linea =~ /end/){
                                                                &vacia;
                                                                exit;
                                                        }
                                          $seg = substr ($linea, 0,11);
                                                        $seg =~ s/ //g;
                                                        $seg = $seg + $base;
                                          $cola = substr ($linea, 11,26);
                                                        $cola =~ s/ //g;
```

```perl
                                        $colb = substr ($linea, 38,26);
                                               $colb =~ s/ //g;
                                     $colc = substr ($linea, 65,26);
                                               $colc =~ s/ //g;
                                               $datos_a [$seg] = $cola;
                                               $datos_b [$seg] = $colb;
                                               $datos_c [$seg] = $colc;

                                               $momentos .= " " . $seg;
                                     }
                               }
                         }
                      }
                   }
               }
        }

sub vacia {
format SALIDA =
@>>>>>>>>> @<<<<<<<<<<<<<  @<<<<<<<<<<<<<  @<<<<<<<<<<<<<  @<<<<<<<<<<<<<
@<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<
@<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<<
<<<<<<
$hora        $segs               $cola                $colb                $colc
$cold                                      $colg
.

        $momentos =~ s/^ *//;
        @momentos2 = split (/ /,$momentos);
        print SALIDA <<EOF;

Fecha PSION: $fecha_psion
Fecha GPS:   $fecha_gps

Time ACTI      SEGUNDOS          VOC          TRAV          NOTA              GPS

EOF

        select (SALIDA);
        foreach $i (sort {$a <=> $b} @momentos2){
                $segs = $i;
                $h = $segs / 3600;
                $sr = $segs % 3600;
                $m = $sr / 60;
                $s = $sr % 60;
                $hora = sprintf "%02d:%02d:%02d", $h, $m, $s;
                $cola = $datos_a [$i];
                $colb = $datos_b [$i];
                $colc = $datos_c [$i];
                $cold = $datos_d [$i];
                $colg = $datos_gps [$i];
                write;
        }
}
```