

**COGNITIVE ASPECTS OF TRAVEL AND FOOD LOCATION BY
CHIMPAZEES (*PAN TROGLODYTES SCHWEINFURTHII*) OF THE
BUDONGO FOREST RESERVE, UGANDA**

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**Cognitive aspects of travel and food location by
chimpanzees (*Pan troglodytes schweinfurthii*) of the
Budongo Forest Reserve, Uganda**

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PhD thesis

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May 2005



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Abstract

Finding food in tropical forests poses a potentially major problem for chimpanzees, whose ranging is thought primarily to be directed at locating suitable food resources: (1) chimpanzees are frugivorous, large bodied and live in large home ranges; (2) they lack specialised sensory or locomotor abilities, and terrestrial travel is known to be costly; but (3) fruits are randomly distributed in space and time. Evidence from studies of captive individuals suggests chimpanzees are capable of remembering the locations of out of sight resources and can compute least distance routes to these resources, but whether this ability translates to the natural foraging behaviour of wild chimpanzees has never been investigated. My observational study was designed to assess how the chimpanzees (*Pan troglodytes schweinfurthii*) of Budongo Forest, Uganda, locate these patchy resources.

I mapped the routes of 14 focal individuals over a 12-month period. I considered how these foraging routes were structured by breaking the path into segments of travel between resources. Consecutive segments of travel between resources were found not to be independent, but assembled into “super-segments” that take in a number of resources along one trajectory. These super-segments are not necessarily directed towards feeding resources, however: travel is *not* always food directed. Comparisons of actual chimpanzee routes with randomly generated simulations suggest most individuals do not attempt to minimise their travel distances. There is evidence to suggest energetically stressed individuals can remember the locations of recently visited food resources and return to these patches in order to minimise travel distances when necessary, but overall, food is not difficult to find for this community of chimpanzees. I propose this is because males defend a territory with super-abundant food resources, meaning availability is not a limiting factor of foraging. Male chimpanzees can be characterised as convenience feeders, taking food whilst satisfying other, social needs.



*"I'm afraid you misunderstood.
... I said I'd like a mango."*

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Overview of Study

The cartoon at the beginning of this thesis is, I think, interesting as well as amusing. Without wishing to kill the joke, these extremely accomplished, bipedally dancing apes raise an intriguing point with their request for mangos. Are chimpanzees really capable of formulating intentions in this way, or is this simply as fantastic as them dancing the tango? If chimpanzees do decide in advance what food they would like to eat, would they then know where to find it - how would these animals locate the desired mangos? Locating food items within an irregular forest environment is generally believed to be a significant cognitive challenge, especially for large-bodied, fruit-eating primates, but virtually nothing is known of how wild chimpanzees solve this problem.

In this thesis I will consider the implicit assumptions of this cartoon, and investigate, via a retrospective analysis of real chimpanzee foraging routes, the strategies available for locating food. I will investigate how travel routes are organised. Do chimpanzees base their route choices on rules and heuristics, or do they have accurate spatial representations that they use to plan efficient, novel routes across their range?

This thesis can be divided into two parts. In part one I will define the context of the study, beginning in chapter 1 with an introduction to the questions that will be asked. I will outline the theoretical debates that have acted as the impetus for this study and thus describe the wider scientific picture into which my aims fit. Chapters two and three describe the study site and methods used to collect data respectively, and chapter four presents information detailing the specific ecological environment experienced by the study community during the period of data collection.

Continuing from this description, in part two I will consider the ranging behaviour of a subset of the Sonso chimpanzee community, and present the analyses and results of this investigation into the utility of cognition when foraging. In chapter five I consider how direct are chimpanzee travel paths. Chapter six explores whether routes are comprised of independent, unrelated segments or long, associated periods of travel and in chapter seven I ask how these travel sections are organised, paying particular attention to evidence of

planning. In chapter eight I use model simulations to ask if knowledge and planning really are necessary to locate food items, then in chapter nine I discuss my results and draw conclusions in order to answer the question: do chimpanzees use advanced cognitive abilities to find food?

Part 1

Background Information:

Chimpanzees, food and travel

Chapter 1

Introduction

For all animals, finding enough food is crucial for survival and reproduction. The need to ingest sufficient quantities of food to maintain normal daily activities poses many problems. Decisions must be solved such as *what to eat; where to forage; when to move to the next patch; and where and/or what is the next patch*. Determining how animals resolve such issues in order to maximise fitness has long been of interest to behavioural biologists, but there is a discrepancy between two explanations of how these foraging problems are solved.

Behavioural ecologists have assumed that animals can calculate and remember differing rates of gain provided by different foods at different potential patches, and that animals use this information to compute nutritionally optimal foraging paths through their environment (Charnov, 1976; Giraldeau, 1997). That is, animals can appreciate and mentally represent all aspects of the spatial and temporal distribution of food sources within their environment: they can remember what is located where, when they last went there, and how to get there efficiently.

Learning theorists, on the other hand - whose ideas originate with the school of behaviourist psychology predominant in the first half of the 20th century and, later, Lorenzian ethology - would argue that most animal behaviour, including foraging, can be explained with just “a few simple principles of learning” (Pearce, 1997). They would argue that mental representations - of what, where, when and how - are not necessarily implied by an ability to monitor differing rates of food gain and to formulate efficient routes between patches, nor, indeed, are such mental representations plausible (MacPhail, 1998).

These differing viewpoints were summarised by Krebs and Davies (1997):

“A caricature of behaviour studies in the 1930’s is one where researchers imagined their animals as little machines, blindly following fixed action patterns in responses to external stimuli. A caricature from the early days

of behavioural ecology and sociobiology in the 1970's is the opposite extreme of regarding animals as scheming tacticians, weighing up the costs and benefits of every conceivable course of action and always choosing the best one." (Krebs and Davies, 1997; pp 4.)

The answer probably lies between these caricatures, and we can imagine the tactics adopted by different species as different points on a scale, from animals as "machines" with no mental activity to animals as "scheming tacticians" planning behaviours in advance. Where a species falls is likely to depend upon a combination of pressures, such as complexity of the external environment; quality, diversity and type of diet; and brain capacity of the species.

Where animals fall on this scale is pertinent to questions of human uniqueness. Historically, humans have been argued to be the only species capable of representing information in a flexible way that allows for insight and inferences about the world. However, research increasingly suggests other animals might also be equipped with similar representational abilities, or so-called "cognitive tool kits" (e.g. non-human primates, Byrne, 1995; Call, 2000; domestic dogs, Miklosi *et al*, 2004; corvids, Emery and Clayton, 2004). Any ability of animals to plan efficient foraging routes many steps in advance - the "scheming tacticians" of Krebs and Davies' caricature - must be based on quite sophisticated mental representations whereby the best course of action from a host of possible alternatives is "imagined". Predicting future outcomes from past experiences is not trivial, requiring the integration of many representations of the environment that are not necessarily being currently experienced. Therefore, only animals with *flexible* mental abilities can plan foraging routes many steps in advance, and not be constrained by learning.

What mental abilities do animals need to find food?

Anderson (1983) showed with computer simulations that planning of foraging routes many steps in advance is not always necessary in environments where resources are randomly distributed. "Nearest neighbour" foraging strategies, looking only one step ahead, worked well, and "global" strategies looking more than one step did not necessarily perform better. Furthermore, recent optimal-foraging models suggest that any habitat assessment may not be necessary for animals with low travel costs, even when feeding on patchy resources:

strategies other than “random foraging” are not necessary (Richards and de Roos, 2001). According to this model, using representations of the environment to plan routes is only necessary when the quality of patches varies greatly over space and time.

The models of Anderson (1983) and Richards and de Roos (2001) coincide with a huge body of evidence suggesting that many animals do rely on rules or mechanisms and/or habitual responses when foraging, but do not use mental representations of the environment to plan routes (e.g. see Benhamou, 1996; Dyer, 1991; Esber, 2005; Gallistel, 1990; Giurfa and Capaldi, 1999; Healy, 1998; Kirchner and Braun, 1994; Manser and Bell, 2004; Thiele and Winter, 2005). That is, many animals have elaborate and sophisticated mechanisms allowing them to deal with spatial problems once they are directly faced with them, but there is no evidence that they need to or do plan their behaviours in advance of the situation.

It has been argued frugivores might rely on flexible representations of space to direct foraging paths (Garber, 2000; Milton, 2000). Fruit is rare, patchily distributed in space and time, and of variable quality so it could be advantageous for fruit-eating animals to remember the locations and phenology of food trees and plan routes to these resources in advance (Milton, 1981). The difficulties of frugivory are multiplied in primates, compared with many other animals. Primates have relatively large body sizes and social group sizes compared to other fruit eaters (Janson, 2000) and, therefore, need to find food in patches large enough to support the social group - but such large patches are presumably even rarer. Primates also lack the locomotor adaptations found in many other frugivores, for example, birds and bats, which enable low-cost searching (Janson, 2000); terrestrial locomotion is three or four times more costly per unit distance than flying (Schmidt-Nielson, 1972, in Janson, 2000). Thus some form of habitat assessment and planning of efficient foraging routes is presumed to be particularly beneficial for primates; furthermore, their relatively large brains and recent common ancestry with humans makes monkeys and apes contenders for exhibiting flexible mental representational abilities.

How do monkeys find food?

Despite the extensive theoretical interest in the abilities of primates to locate food, there are surprisingly few studies that investigate how they do so (C. Menzel, 1997). MacDonald and Wilkie (1990) and MacDonald *et al* (1994) concluded captive yellow nosed monkeys

(*Cercopithecus ascanius whitesidei*) and common marmosets (*Callithrix jacchus jacchus*) were able to remember the locations of food sites in large enclosures. These animals switched between win-stay (where food was always placed in the same locations) versus win-shift (when food was initially found in four locations, and subsequently shifted to a different four locations) strategies. This suggests their learning ability was flexible and can be used to inform travel decisions in experiments but does not necessarily tell us anything about the learning, storage and *use* of information for finding food in natural foraging environments.

Charles Menzel (1991) baited well-used trails of Japanese macaques (*Macaca fuscata*) with either ripe *Akebia* fruits, a food that was not in season at the time, or chocolate. Upon finding the fruits, the macaques searched for more fruit, moving to and inspecting locations where the *Akebia* vines grew over distances of up to 80m, for up to ten minutes after initially finding the bait. When chocolate was encountered, they simply looked around the location where it had been placed. Menzel suggested this difference in behaviour was indicative of “detailed knowledge of the feeding environment” and suggested “considerable flexibility in organising an effective search routine”. It is unclear if the *Akebia* vines moved to after finding fruit bait could be seen from the baited location, however. Thus, while this correct *classification* of food types is impressive, it does not tell us anything about the spatial memory of these monkeys, or their planning abilities. Hemmi and Menzel (1995) and Menzel (1996) showed long-tailed macaques could infer the location of hidden food items based on prior learning of successful foraging trajectories. However, this rule-guided foraging again does not illustrate any spatial memory or an ability to plan routes in advance. Menzel (1997) demonstrated that long-tailed macaques (*Macaca fascicularis*) used nearest-neighbour rules to guide movements between up to 21 food items placed in an 880m² field; foraging routes were not planned more than one step in advance.

Observations of wild-living species also support the notion that primates possess an ability to learn and remember spatial information, and that they can use this information to direct efficient, least-distance foraging routes. Garber (1988; 1989) observed the foraging behaviour of two species of wild tamarins; saddle-backed (*Saguinus fuscicollis*) and moustached (*Saguinus mystax*). He stated the tamarins foraged with goal-directed movements, frequently moving from one tree to the next closest example of the same species - as though “traplining”. He suggested the movements were most likely based on

memories of the locations of trees and expectations of the food reward to be gained: trees with limited food rewards were bypassed. Garber and Hannon (1993) compared the travel patterns of these tamarins with computer simulations of “random” (un-informed) foraging, foraging based on following olfactory cues, and foraging guided by spatial knowledge that resulted in least-distance movements to the nearest available food patch. The spatial knowledge model was the best approximation of the actual foraging behaviour of the tamarins. Garber and Hannon suggested the animals simultaneously knew the locations of hundreds of feeding trees, and could remember which trees had fruit and which had been depleted for periods of several weeks, but planning more than one step ahead was not necessary. Bicca-Marques and Garber (2004) showed free ranging night monkeys (*Aotus nigriceps*) and titi monkeys (*Callicebus cupreus*) are also capable of locating food rewards using spatial memory, without the need to plan movements in advance.

Wild-living brown capuchin monkeys (*Cebus apella*) learnt the location of 15 artificial feeding sites within their home range and quickly understood that platforms where the provisioned fruit had been depleted would not provide food again until the following day, e.g. that it was not worth re-visiting a platform twice within a 24-hour period (Janson, 1998). Janson used comparisons with statistical models of “random” (un-knowledgeable) foraging to show the capuchin monkeys used spatial knowledge and an understanding of the rules of replenishment to guide where to move, heading to closer platforms more often than the model, and in straighter lines. But again it was not evident that the monkeys looked any more than one-step ahead when “deciding” where to forage: no advance planning was evident.

Although studies have shown some monkey species are capable of rapid learning of foraging rules that can be used to direct search strategies, and can remember the locations of multiple food resources in their environments, there is no experimental evidence suggesting that the searches are planned more than one step in advance. Moreover, studies of some species of monkey reveal less advanced spatial memory abilities. Andrews (1988) tested the proficiency of titi monkeys (*Callicebus moloch*) and squirrel monkeys (*Saimiri sciureus*) on an eight-arm radial maze. The monkeys frequently revisited sites they had previously depleted. In a further study of squirrel monkeys they again failed to learn which feeding holes were *always* baited in a foraging experiment (Roberts *et al*, 1993). Spatial

learning and memory abilities are apparently not ubiquitous among all monkey species, and even those with spatial memory abilities conform to the expectations of Anderson (1983).

There is, however, one intriguing example of advance planning among monkey species. Kummer (1971) suggested wild-living hamadryas baboons (*Papio hamadryas*) were able to travel to distant resources by direct, efficient routes, implying they can accurately remember the locations of these resources. Most interestingly, hamadryas baboons have also been observed dispersing from the cliff-sleeping site, dividing into smaller foraging groups, and subsequently reconvening at a distant water hole (Sigg and Stolba, 1981; Sigg, 1986) – the direction of which had been indicated in the morning from the initial trajectory taken by the whole band as they left the sleeping site, before dispersing. Apparently, the baboons were able to decide in advance which water hole to head for, and used the memory of the first travel direction of the morning to reach this destination. The researchers interpret the “milling” behaviour of baboons at the sleeping site, prior to departure, as negotiation about places that were distant in space and time, in *anticipation* of the future event of reconvening (see Byrne, 2000).

How do chimpanzees find food?

Despite reports of representational abilities in other, non-spatial, realms (Kohler, 1925; Call, 2000; Hare *et al*, 2000; Tomasello *et al*, 2003; Call, 2004), there are currently no detailed analyses of how wild chimpanzees solve the problem of finding food. There are many descriptions of *what* chimpanzees eat (Ghiglieri, 1985; Wrangham *et al*, 1996), *where* within the territory they spend most of their time (Chapman and Wrangham, 1993; Herbinger *et al*, 2001; Lehmann and Boesch, 2003) and *who* they spend time with (Goodall, 1986; Nishida, 1989), but no empirical understanding of *how* they forage.

It is often argued that all chimpanzee travel is food directed, as the quotes below suggest;

“Within their territory the members of the community are constantly on the move, searching for fruit bearing trees and other sources of food.”
(Ghigliheri, 1985; pp. 84);

“The chimpanzees’ way of life is based on finding a rare and quickly vanishing food”. (Ghigliheri, 1985; pp. 87).

Chimpanzees obviously do locate food effectively, as evidenced by this description of an adult male chimpanzee, followed for 50 consecutive days, at Gombe, Tanzania:

“Figan had no apparent difficulty finding foods...At no time did Figan appear to be searching for food” (Riss and Busse, 1977; pp. 287).

But it is often just *assumed* that wild chimpanzees must be using complex mental representations when foraging: if baboons can, so must chimpanzees!

“Chimpanzees have excellent mental maps of their home range and know the locations of many of the food resources in it.” (Goodall, 1986; pp. 237).

This assumption is based partly on the reasoning that the problem of finding food is even harder for chimpanzees than monkeys. When food is scarce, monkeys switch to other food sources (Wrangham *et al*, 1998) but chimpanzees continue to feed primarily from fruit, thus maintaining higher quality diets (Conklin-Brittain *et al*, 1998). Chimpanzees live in large territories with relatively low population density, which might aid the maintenance of this high quality diet (Leonard and Robertson, 1997). The larger range area suggests there would be more potential food locations to learn and monitor, however, adding to the difficulty of finding fruit. Furthermore, terrestrial travel is costly for chimpanzees (Pontzer and Wrangham, 2004).

Chimpanzees are not central-place foragers, or even multiple-central-place foragers - an adaptation that presumably allows animals to forage efficiently over large spaces, without being constrained by how far they can move from a nest site (Chapman *et al*, 1989). They do not return to one, or one of several, nest sites each night as other primates do. Chimpanzees simply nest close to wherever they have last been feeding. The need for chimpanzees to travel and forage efficiently is imperative, but to maximise energy intake through a diet of fruit that is rare and spread over a large area does appear very challenging (Ghigliheri, 1985) and merits testing.

A number of studies of spatial memory have been conducted on *captive* chimpanzees. Tinklepaugh (1932) showed that two common chimpanzees (*Pan troglodytes*) were able learn which one of pairs of containers held food, and they could retain this information for up to one week. The most important cue for the chimpanzees was the position of the container in the room; containers that had to be identified by their colour or shape as

opposed to location were not remembered as easily. Chimpanzees preferentially remembered and used spatial information to guide their foraging in this small-scale task.

E. Menzel (1973, 1978) hid food in 18 locations around a one-acre outdoor enclosure used by six captive-held but wild-born chimpanzees. Menzel showed one individual where the food was hidden while the other five individuals were held in an indoor enclosure. The individual shown the food items varied across trials. After a delay of at least two minutes all the chimpanzees were released into the outdoor enclosure. On average, the observer individual found 13 pieces of food, and the five-naïve individuals found only one piece. The observer chimpanzee seemed to forage differently to the naïve individuals, moving deliberately between locations in a nearest-neighbour, least-distance path, rather than randomly searching as the naïve chimpanzees did. When half of the 18 food items hidden were preferred foods (fruit), and half were less preferred (vegetables), the observer chimpanzee used a nearest-neighbour foraging strategy between the nine preferred foods first then collected the less preferred items, again with a nearest-neighbour strategy. This suggests the chimpanzees not only knew *where* food was, but they also remembered *what* food was located in each place. Like studies of monkeys, though, the efficient, knowledge-based foraging strategy was only planned one step ahead at a time.

A language-trained chimpanzee - Panzee - was able to remember for up to 16 hours the locations of objects hidden in her outdoor enclosure by experimenters, and could instruct a naïve keeper to go to the location and collect the object. The keeper did not know what had been hidden, nor where it was, and was thus entirely dependent on the information provided by Panzee to retrieve the item and bring it to her (C. Menzel, 1999). Panzee herself determined the delays in this experiment, between watching an experimenter hide the object and her prompting the keeper to retrieve it, and she did not always recruit the keeper at the first possible opportunity. Again, this is a demonstration of remembering location and food-type information, but it also suggests Panzee could anticipate rewards and refer to them to instruct her naïve keeper. Perhaps, like the hamadryas baboons, Panzee is able to anticipate future events and could plan efficient routes to the relevant locations, but this has not yet been tested.

Wrangham (1977) stated that it is *probable* that wild chimpanzees use similar abilities to remember the locations of food patches within their territories and plan efficient routes to

them, but there remains to date no detailed study of this supposition. The performance of captive animals within the limited spaces of their enclosures, remembering and identifying a small number of objects ($n < 28$), does not even begin to match the complexity of the natural forest environment. Chimpanzees range over areas of many square kilometres and have diverse diets (Wrangham *et al*, 1996), with potentially hundreds of plant species consumed (Nishida and Uehara, 1983; Reynolds, in press). There are numerous individual trees of each species exploited within the territory of one community, as well as hundreds or thousands of other trees that are not food species. Remembering the locations of particular trees within a forest is computationally a much harder task. It cannot just be assumed that because chimpanzees show proficiency at spatial-memory tasks in small-scale spaces that these abilities serve to locate food efficiently in their natural environment.

Boesch and Boesch (1984) did present a study of spatial memory in wild chimpanzees, but the analysis was limited to consideration of the location of only one type of object. The chimpanzees of the Tai forest, Cote d'Ivoire, select and transport stone hammers an average distance of 120m to nut-cracking sites, when visibility in this forest is typically restricted to only 20m. In 48 of the 76-recorded cases, chimpanzees picked the hammer that was the shortest distance from the cracking site. Boesch and Boesch suggested this was evidence of the chimpanzees' ability to use a Euclidian representation of space to direct their travel routes, but in fact the paths actually taken to find the hammers were not recorded so there is no evidence that they were least-effort routes; perhaps the chimpanzees searched without knowledge until they found a hammer, and then returned to the nut-cracking site with it. Indeed, even in humans the use of Euclidian representations - where 2-d vector information is preserved - is often restricted to navigation through only the most familiar and limited home environment (Byrne, 1979; 1982; 1983; Wang and Spelke, 2000), at least in humans living in Western cultures.

This thesis forms the first study of how chimpanzees locate food resources in their natural forest environment. Chimpanzees are large-brained frugivores, with diverse diets, living in an unpredictable environment. Terrestrial travel is costly, and their sensory abilities are not specialised for detecting out-of-sight food locations (Prestrude, 1970). Given that they show some, albeit limited, spatial memory abilities in captive experiments, and some other primates show evidence of flexible spatial representations, it is probable that wild

chimpanzees *will* use spatial knowledge to guide their daily foraging activities, but the nature and extent of this knowledge is not known.

Thus, the aim of this thesis is to determine *how chimpanzees find food*. Specifically, I aim to consider:

- to what extent wild chimpanzees (*Pan troglodytes schweinfurthii*) use spatial knowledge to plan efficient foraging routes and locate food patches;
- if routes planned more than one step in advance are utilised; and
- if planned routes are more efficient than unplanned routes.

I will consider the influences of many aspects of chimpanzee socio-ecology on the foraging behaviour of individuals, such as demographic and life history status, party associates, aggressive and affiliative social interactions, vocal interactions, territorial behaviour and feeding ecology, as each of these factors may be significant to travel behaviour. By considering the nature of foraging routes taken by individuals in different situations, I hope to be able to infer something about the mental representations that underlie chimpanzee travel behaviour.

Chapter 2

Study Site and Population

Budongo Forest Reserve

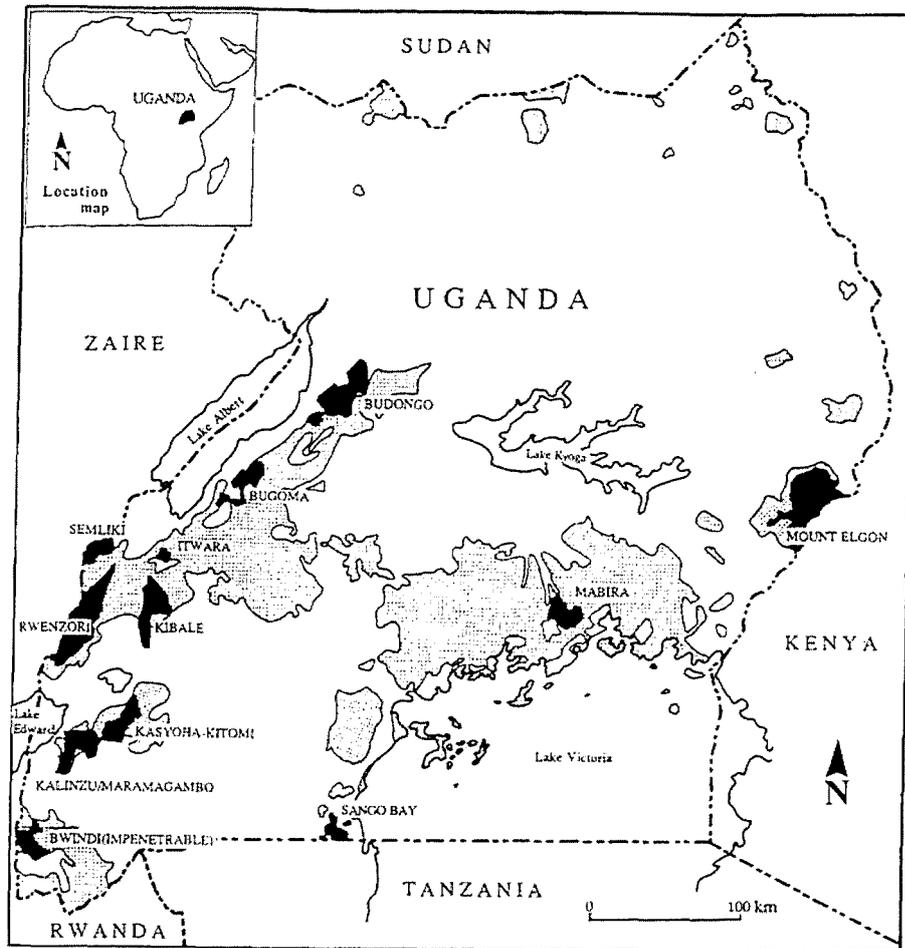
The research presented in this thesis was carried out on a community of chimpanzees residing in the Budongo Forest Reserve, Uganda. In this chapter I will describe the study population and their forest habitat so that the work may be put into context.

Budongo is a moist, medium altitude, tropical forest located in the Masindi and Hoima districts of north-western Uganda. The forest is an isolated fragment of the expansive Ituri Forest which lies to the west of Lake Albert in the Democratic Republic of Congo. Budongo is one of the largest remaining forests in Uganda and with its great bio-diversity is critically important for conservation. As a forest reserve, Budongo comes under the management of the Uganda Forest Authority. Many aspects of forest ecology have been studied in Budongo, and it is often thought to be one of the best-documented forests in Africa: a large literature is available to provide additional information. Here, I will only describe the aspects salient to this study of chimpanzee foraging.

Location

Budongo Forest Reserve is situated in western Uganda [latitude 1°37' – 2°00' N; longitude 31°22' – 31°46' E (Plumptre, 1996)], just to the east of Lake Albert and the western Rift Valley escarpment, as illustrated in figure 2a. The reserve covers 793km² of land, 428km² (53%) of which is forested; the remainder being grassland (Howard, 1991). It is, in its northernmost parts, contiguous with the bush and grassland of Murchison Falls National Park, Bugungu wildlife reserve to the west and Karuma wildlife reserve to the north-east. The forest lies at an average altitude of 1100m (range from 750m to 1250m) above sea level (Egging, 1947), with a gentle slope north-northwest towards the Albertine Rift escarpment. Generally, the terrain is gently undulating.

Figure 2a: The location of the Budongo Forest Reserve in Uganda, showing forests (black) and areas of relic forests (shaded). Adapted from Howard (1991).



Climate

Budongo has a mean annual rainfall of 1620mm (range over 10 years; 1241 to 2187mm) (see Figure 2b) and is characterised as moist, medium altitude tropical forest (Langdale Brown *et al*, 1964).

The forest has a fairly predictable bimodal distribution of annual rainfall, with the wettest periods usually occurring from April to May and September to November, as displayed in figures 2c and 2d - collated from ten years of continuously recorded rainfall data. A dry season is normally evident from December to February. The uncharacteristically high rainfall of November 1997 to February 1998, apparent in figure 2c, is thought to be due to the effects of the El Nino phenomenon when 1253mm of rain fell between October and December 1997. Figures 2c and d illustrate a second, shorter period of reduced rainfall

occurring sometime between June and August, between the two wet seasons. This dryer season varies in its precise timing and is not observed every year.

Figure 2b: Total yearly rainfall (mm) in Budongo from 1993 to 2003

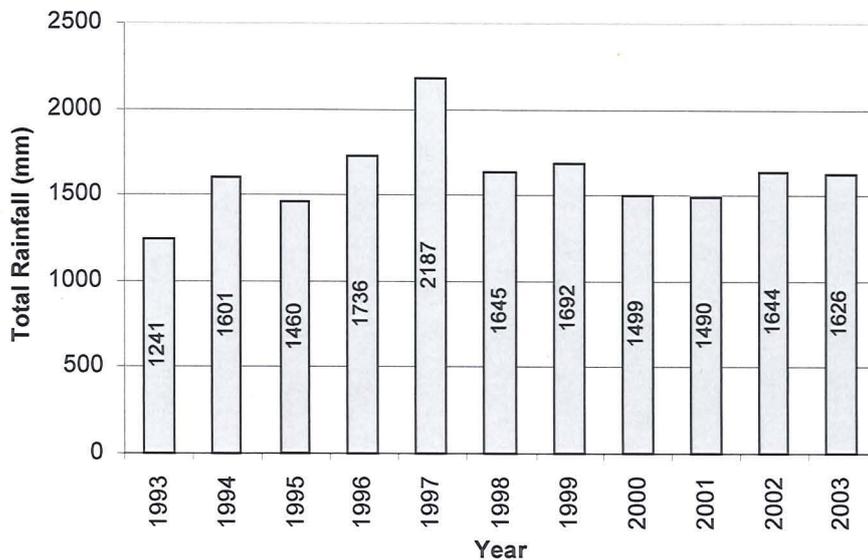


Figure 2c: Mean daily rainfall (mm) per month, from 1993 to 2003

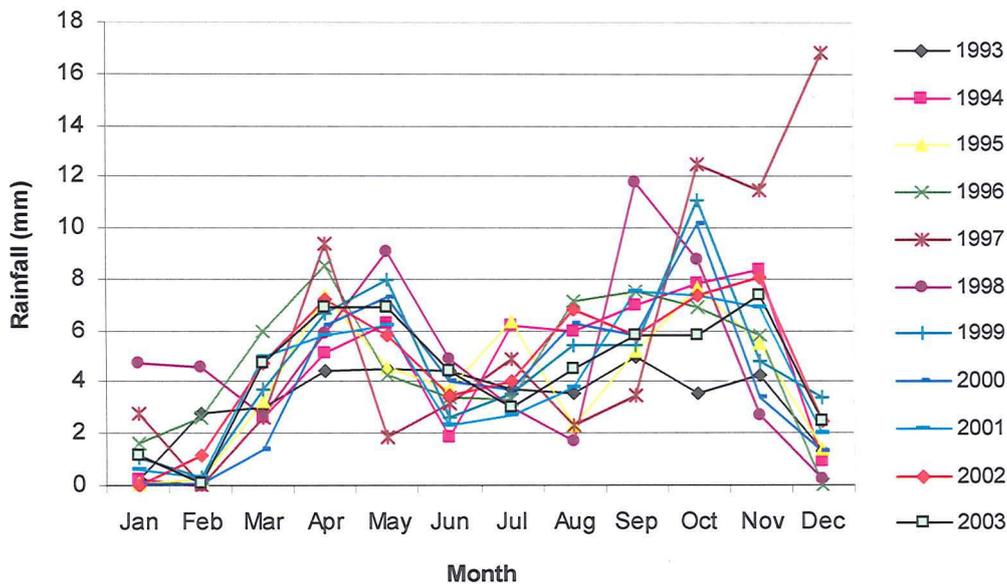


Figure 2d: Total monthly rainfall.
Quantity shown is mean monthly total calculated from 1993 to 2003.

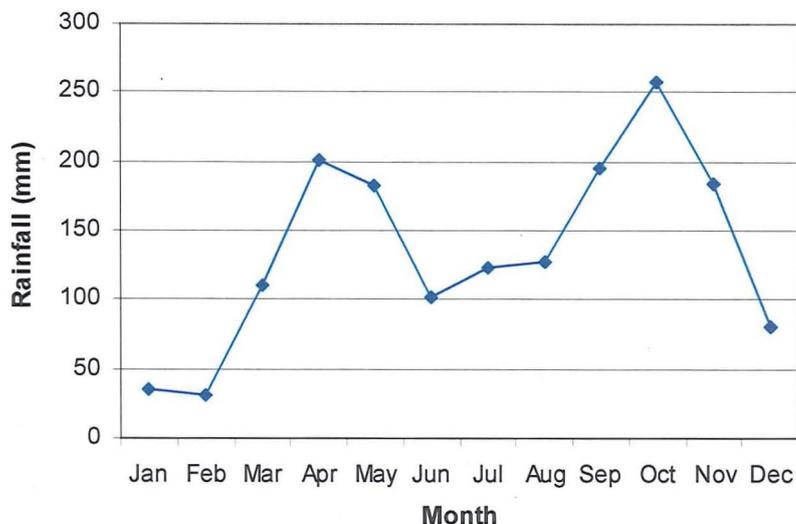
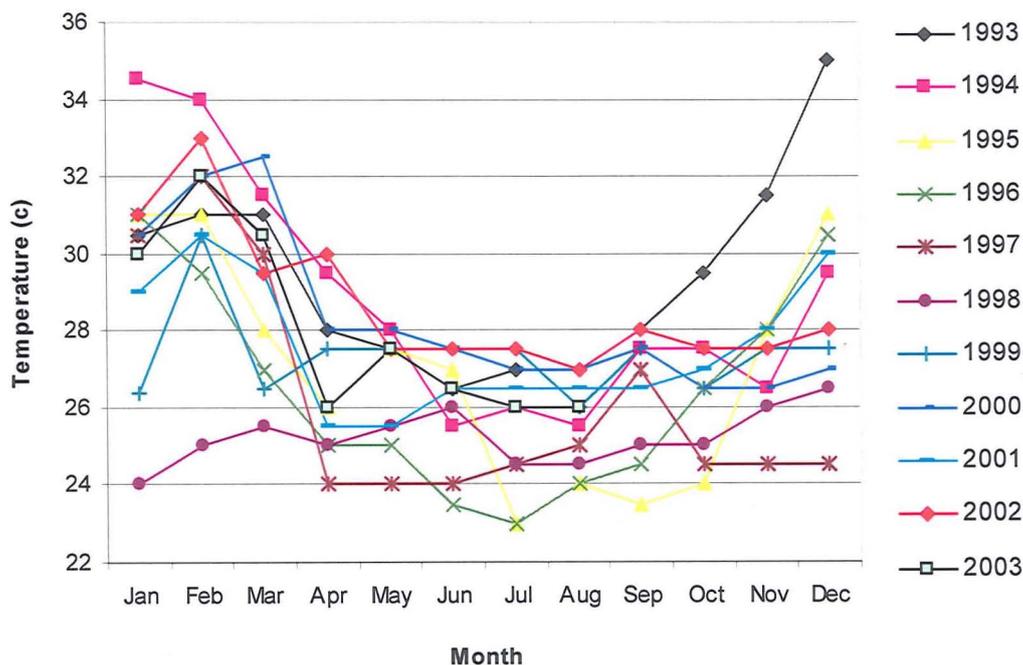


Figure 2e shows the average maximum daily temperature across months for all years between 1993 and 2003. Temperature is almost uniform throughout the year, with a modal maximum daily temperature of 28°C and minimum of 17°C. This alters only during the dry season of December to February, when temperatures often reach a maximum of 35°C, with a mean and mode of 31°C and a minimum modal temperature of 15°C. Thus, temperatures vary more between the minimum and maximum values in the dry season of December to February.

Figure 2e: Mean maximum daily temperature per month, from 1993 to 2003.



The rainfall and temperature variables for the duration of this study have been plotted on a single graph to produce a climate diagram (as according to Richards, 1996). Climate diagrams are used to distinguish three types of month; *wet*: where rainfall exceeds 100mm; *drought*: where rainfall falls below the maximum temperature plot; and *dry* or *intermediate*: where rainfall lies below 100mm but above the maximum temperature. The temperature scale (0-50°C) is twice that of rainfall (0-100mm). Above 100mm, the rainfall scale is reduced by a factor of ten. Mean data from the last ten years (excluding the El Nino period of October 1997 – February 1998) were used to illustrate the general monthly patterns of the Budongo climate, shown in figure 2f. Three drought months are apparent from December to February, confirming this period as a dry season. Eight wet months are also apparent but the dry season does sometimes extend into March, hence the mean lower rainfall of this to other wet months. June falls just within the “dry or intermediate” boundary in this diagram and is evidently dryer than other months, according to figures 2c and 2d. The period from June to August is not a drought like the December to February dry season however, and so these months, which *can* fall in the dry or intermediate boundary, are best thought of as an inter-rains period rather than a second dry season.

Figure 2f: Climate diagram based on mean total rainfall (mm) per month and mean maximum daily temperature per month from 1993 to 2003

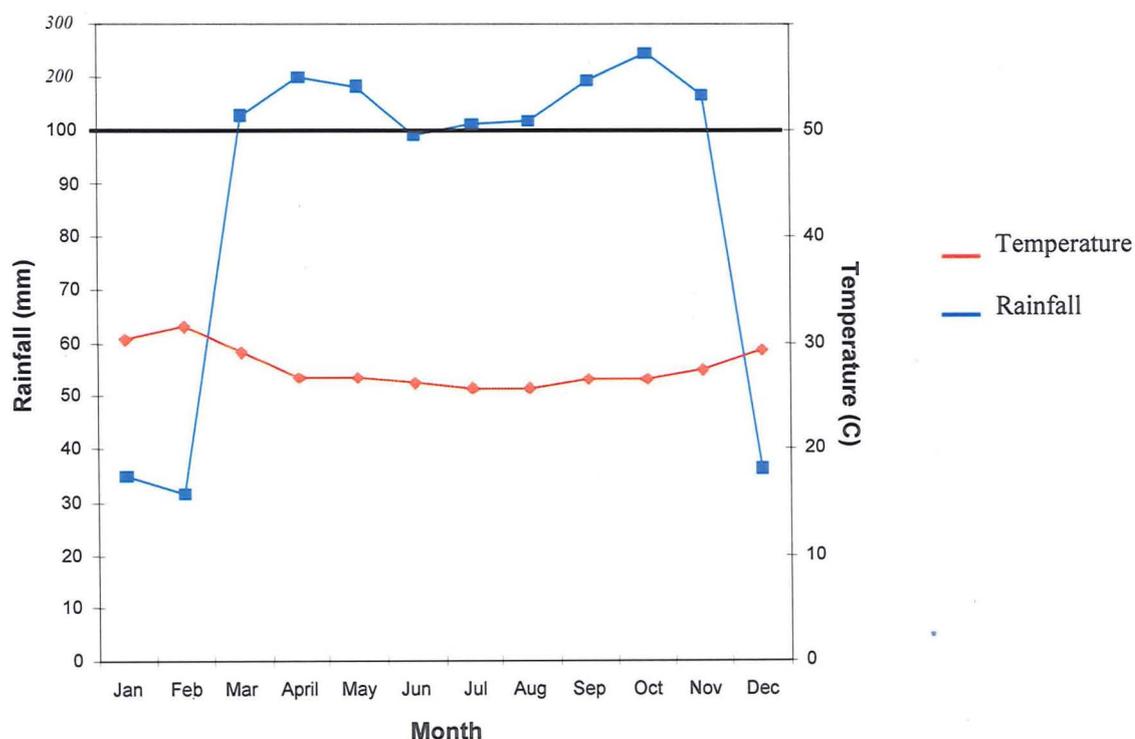
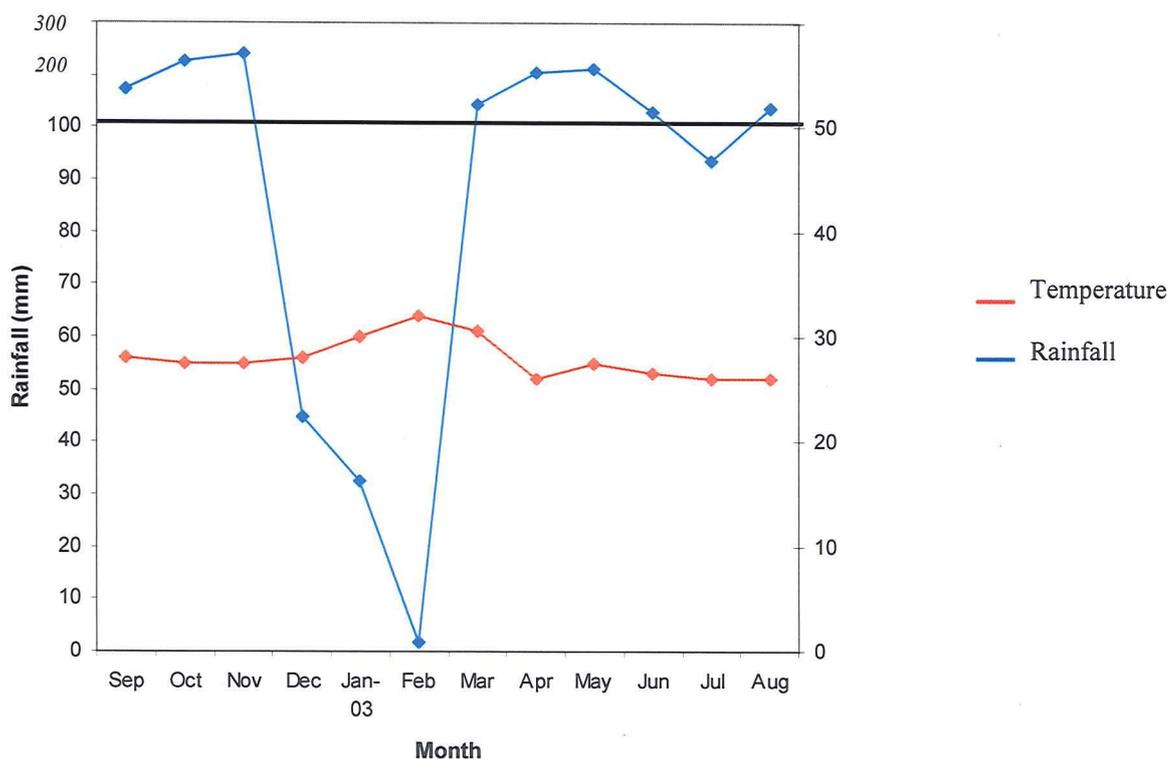


Figure 2g illustrates the specific climatic variables experienced during the year of this study, from September 2002 to September 2003. During this year, the drought months of December to February are again clearly marked, with an intermediate inter-rains period occurring in July 2003. All other months over the course of this study can be described as wet.

Figure 2g: Climate diagram for the study period of September 2002 to 2003. Showing total rainfall (mm) per month and mean maximum daily temperature per month



Dry season: Usually occurring between December and February, this season is characterised by having very low rainfall. The forest dries noticeably and many of the trees drop their leaves. Flooded swamp areas dry up as river levels fall and maximum daily temperatures rise. The relative humidity is lowest in this season, there is the least amount of cloud cover, and more hours of sunshine compared with the rest of the year.

Wet seasons: Occurring between March and May and September to November, these periods are obviously the wettest of the year, with reduced maximum temperatures, increased humidity and much greater cloud cover (Fawcett, 2000).

Inter-rains period: Occurring between June and August, this period has reduced rainfall compared with the wet seasons, but this is not as pronounced as in the dry season. Maximum daily temperatures at this time are the lowest of the year, and noticeably cooler than in any other season. This period receives the least amount of sunshine (Fawcett, 2000) compared with any other time throughout the year. Although it cannot be thought of as a dry season in the same sense as the December to February period, this inter-rains period is perhaps worth treating as a distinct season.

Forest structure and vegetation types

The vegetation of Budongo has been studied extensively by Egging (1947) and Synnott (1985), among others. Egging characterised the main types of forest found within Budongo, and Synnott (1985) published a checklist of all species of vascular plant he observed during a three-year study of seedling regeneration. In this checklist, he recorded over 700 species of trees, shrubs, climbers and herbs in Budongo, including over 200 tree species, nearly 200 terrestrial herbs, 100 shrubs and 100 epiphytes, with the remainder being various types of climber. As he says “this is probably the most complete list of plants published for any large forest in tropical Africa”.

Egging (1947) described Budongo as being composed of a mosaic of four vegetation types, each comprised of a particular mix of species. The four forest types he noted are colonising, mixed, cynometra, and swamp forest. He deliberately excluded secondary forest. I will now summarise the characteristics of these forest types.

- Swamp forest: Lying along permanent and seasonal streams, swamp forest is the least common forest type found in Budongo. The dominant species include *Raphia farinifera* and *Pseudospondias microcarpa*, which are confined to these wet areas (Synnott, 1985). Woody lianas are also common. Swamp forest merges on slightly higher ground with cynometra or mixed forest.
- Colonising forest: This is found in large areas at the forest edges and is dominated by *Maesopsis eminii* and *Cordia milleni*. Small patches of *Maesopsis* or *Cordia* dominated forest can also be found deep within the forest, following the historic patterns of forest succession. The older patches of colonising forest include many other

species such as *Cola gigantea*. Colonising forest is associated with lots of small herbaceous climbers and tall non-woody climbers, but woody climbers are rare. This forest type develops, over time, into mixed forest.

- Mixed forest: This is the most common forest type in Budongo, and has a diverse species composition. There is no single canopy-dominant species, but the commonest are *Celtis mildbraedii*, *Celtis zenkeri*, *Khaya anthotheca*, *Chrysophyllum albidium*, *Ficus* species and *Funtumia elastica*. Woody lianas are common whilst other climbers are less so.
- *Cynometra* forest: This is the climax forest. In *Cynometra* forest areas, 75% of canopy will be dominated by this one species; *Cynometra alexandri*. *Lasiodiscus mildbraedii* is the dominant under-storey tree. Fewer species are found in this type of forest, with less abundant climbers.

Budongo Forest was traditionally surrounded by woodland and grassland (Synnott, 1985). Some of this has now been replaced by villages and cultivated crops.

In 1947, when Egging published his results, about 30% of Budongo was *Cynometra* forest. As described below, the reserve has been extensively exploited for logging, with mainly mahogany (*Khaya* and *Entandrophragma* species) and a few other tree species being utilised (Reynolds, 1992b). This, in addition to exploitation of forest products by local peoples for personal use, naturally occurring tree falls and the presence of elephants in the forest until the mid 1970's, means the reserve today consists of large areas of what can best be described as secondary forest.

This loss of primary forest is not as detrimental to primate species as might at first be anticipated (see Plumptre and Reynolds, 1994). Alder (1991, in Reynolds, 1992b) showed that fig species occur at greater densities in logged (secondary) mixed forest (3.44 fig trees per ha) than in un-logged areas of mixed forest (0.68 trees/ha), or across the forest as a whole (2.16 trees/ha). Thus, a greater number of *Ficus* species are now seen than Egging would have likely observed, and these are important food species for frugivorous primates.

Logging and forest management

Budongo Forest Reserve is the primary timber-production forest in Uganda (Egging, 1947; Howard, 1991; Plumptre *et al*, 1997). It was gazetted between 1932 and 1939 by the British colonial administration and has produced timber on sustainable basis from the 1920's to 1980's (Patterson, 1991).

Up to four sawmills were operating out of Budongo in the past 60 years, the largest of which was Budongo Sawmills Ltd (Reynolds, 1992b). This is now defunct, as are the other sawmills in the area, but illegal timber extraction is commonplace (pers. obs.). Some legal logging concessions are still granted by the Forest Authority, which mainly occur in the form of pit sawing.

Timber extraction has historically focused on mahogany species, *Entandophragma angolense*, *E. cylindricum*, *E. utile* and *Khaya anthotheca*, as well as *Milicia excelsa* in the Biiso, Siba and Nyakafunjo blocks of the forest (Howard, 1991; Patterson, 1991; Plumptre, 1996). The Forest Department divided the forest into 57 compartments, as shown in figure 2h, most of which have been logged at least once. Selective logging occurred on a compartment-by-compartment basis, giving each a unique logging history. Only Kaniyo Pabidi compartments, lying within Murchison Falls National Park, have never been commercially logged. Two designated nature reserves - N15 and W30 - have only had the most valuable timbers removed.

It was initially the intention to remove the valuable trees, re-harvesting them after 80 years, and then every 40 years subsequently (Plumptre, 1996). Due to the re-growth rates versus the damage caused by logging, however, this plan was determined impractical in the 1950's, so modifications were introduced (Patterson, 1991). A plan to replant mahoganies was abandoned in the 1950's as it became apparent that this costly enterprise was no more successful than the natural regeneration process. It was thought that prevalence of the valuable timber trees was reduced by the presence of *Cynometra* trees, so it became Forest Department (as it was then known) policy to reduce the numbers of *Cynometra* and other potentially competing tree species, in order to encourage growth of the commercially valuable species, which could then be sustainably logged. Thus, for a number of years *Cynometra* and other weed species such as *Ficus* species were treated with arboricide

Figure 2i: A Forest Authority pit sawing concession in compartment N2, taken May 2003.



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There is still much illegal pit sawing activity, however, as it is very difficult to police and enforce the Forest Authority regulations. Illegal pit sawyers do not have permission to be in the forest, nor licences to remove timber. The major ecological problem of this illegal logging is that the quantity and specific trees removed are not controlled; for example, important seed trees that the Forest Authority and the forest itself rely on can be felled.

With the logging practices of the past 70 years, there has been a significant increase in the area of mixed forest (Plumptre, 1996). The changes in species composition have not been predictable or uniform, though. The overall structure of forest has changed with logging practices; the un-logged areas have larger trees and a more continuous canopy. Logged compartments differ due to different initial species; being logged at different times; and varying quantities of timber being extracted. This has resulted today in a very complicated mosaic of forest types. Thus, Budongo is basically now a forest “which could be called secondary, with a mixture of older trees from the pre-existing forest and younger trees which have regenerated or grown to tree size since logging and treatment”. (Synnott, 1985). This is true for all of the main Budongo blocks, which are now mostly occupied by species typical of colonising and young mixed forest. The outlying forest block of Kaniyo Pabidi is still more or less primary forest.

Fauna

Budongo has a varied fauna. Much probably remains un-described, and I will only refer to the main species here. All species names are given as they appear in Jonathan Kingdon's *Field guide to African mammals* (1997). Five primate species are found within Budongo in addition to chimpanzees (*Pan troglodytes schweinfurthii*). These other primates are: olive baboons (*Papio anubis*); black and white colobus (*Colobus guereza occidentalis*); red tailed guenons (*Cercopithecus ascanius schmidtii*); blue monkeys (*Cercopithecus mitis stuhlmanni*); and pottos (*Perodicticus potto ibeanus*). Other nocturnal strepsirhines may also be present in the forest but have not yet been identified.

A large-mammal survey conducted in 2001 by the Wildlife Conservation Society confirmed that Budongo is also inhabited by bushbuck (*Tragelaphus scriptus*), red and blue duiker (*Cephalophus callipygus* and *Cephalophus monticola*), bushpigs (*Potamochoerus larvatus*) and possibly also red river hogs (*Potamochoerus porcus*) (Plumptre *et al*, 2001). Other mammal sightings include genets (*Genetta genetta*) and civets (*Civettictis civetta*), tree pangolins (*Phataginus tricuspis*), honey badgers (*Mellivora capensis*), tree hyraxes (*Dendrohyrax arboreus*), giant chequered elephant shrews (*Rhynchocyon cirnei*) and mongoose species. Numerous bat, shrew, squirrel and rodent species are also present.

Until the mid 1970's, Budongo was home to a large elephant population (Patterson, 1991). This had been declining from approximately 5000 in the 1920's to less than 1000 in the 1960's. A specific "control" policy, coupled with civil unrest, eradicated elephants from the Forest by the beginning of the 1970's, although a growing population still exists in the northern sector of Murchison Falls National Park. Buffalo (*Synceros caffer*) are occasionally sighted in the forest, although they are thought to be only transient visitors wandering south from the National Park and the surrounding wildlife reserves. During the period of this research at least two buffalo were seen in the study area during January 2003, coinciding with the annual burning of the grasslands in Murchison Falls National Park.

The main forest block of Budongo is not permanently inhabited by any large carnivores. However, leopards (*Panthera pardus*) are seen in the northernmost compartments of the forest at Kaniyo Pabidi. Lions (*Panthera leo*) have been seen in the study area on two occasions, the last being in February 2002, when I was conducting the pilot study for this

research. An old male lion was seen moving through the camp area on two consecutive nights, before disappearing. Leopards and lions are not generally thought to be a major predation risk to the Budongo chimpanzees, with no evidence of attacks ever occurring.

Budongo is home to over 350 bird species, including long-crested and Cassin's hawk eagles, African crowned eagles, seven species of hornbills and four species of turaco (Rossouw and Sacchi, 1998). There are a multitude of reptiles, including; lizards, skinks, geckos, snakes (such as the Gaboon viper, puff adder, rhinoceros viper, Jameson's mamba and pythons) and many invertebrates, which remain largely un-catalogued.

Budongo Forest Project

The Budongo Forest Project (BFP) was initiated in 1990 by Professor Vernon Reynolds with the aim of studying and conserving chimpanzees and their forest habitat. The project has a practical orientation (Reynolds, 1992a; 1992b), with many studies concentrating on seed dispersal and the effects of logging on the forest structure and diversity, as well as the effects on primates. Funding was initially provided by the Jane Goodall Institute (JGI) and Conservation International (CI), with the Overseas Development Administration (ODA) taking on the role of funder from 1991 onwards, with additional contributions from the National Geographic Society. In 1997 funding of the project was taken over by NORAD, the Norwegian development agency.

The project employs many local Ugandans, and all field assistants have to be educated to at least O level standard, ensuring a high quality of staff. All staff are trained on numerous skills including tree identification and observation techniques for collecting behavioural data on forest primates. The project has provided employment, education, training, and research experience for a great number of Ugandan and international students. Details of the research and conservation activities the Project is involved with can be found on the project website at <http://www.budongo.org>.

History of chimpanzee research in Budongo Forest

Vernon Reynolds first studied the chimpanzees of Budongo in 1962 (Reynolds, 1965). He and his wife, Frankie, set up a research camp near Busingiro Hill, just two years after Jane

Goodall began her seminal study of the chimpanzees of Gombe Stream. Reynolds and Reynolds remained in Budongo for only eight months in this initial study. Further studies were pursued by Sugiyama (1968, 1969) and Suzuki (1971), but during the periods of civil unrest and war of the 1970's and 1980's no further research was possible. Apart from a brief report published in 1976 (Albrecht, in Reynolds, 1992a), no studies of the Budongo chimpanzees were conducted again until the Budongo Forest Project was initiated.

Sonso region

The BFP has habituated and studied the Sonso community of chimpanzees continuously since 1991. The community takes its name from the river running through the centre of the study area, shown in figure 2j. The Sonso community's home range covers compartments N1, N2, N3, N4 and N15 of the Forest Reserve, and borders the village of Nyakafunjo at the southern boundary of the forest (see figure 2j). Selective logging has occurred in each of these compartments except for N15, which is designated a special nature reserve and primarily consists of *Cynometra* forest. Table 2.1 details the forest types and logging history of each of these compartments. Compartment N3 was designated an SSSI (Site of Special Scientific Interest) in the 1990's, following a close partnership of BFP with the Forest Authority. No further logging will now occur in this compartment.

Table 2.1: Logging history and forest type of the Sonso region compartments

	Compartment				
	N1	N2	N3	N4	N15
Forest type	Mixed swamp	Mixed swamp	Mixed colonising	Mixed swamp	<i>Cynometra</i>
Logging years	1945	1945/7 2003	1947/52	1952/54	Unlogged

The Project research station is situated in the north-west corner of a large clearing that previously constituted the Budongo sawmill. This sawmill is now defunct, with much of the clearing now being overgrown with bushes and regenerating forest. The Project was able to procure several of the former sawmill buildings which now house researchers and field staff.

One introduced species now dominates areas of the forest around the sawmill clearing. This species, *Broussonetia papyrifera*, was introduced by Budongo Sawmill Ltd as a potential source of paper fibre in the 1950's. It has now naturalised in areas of the forest edge at the sawmill clearing (Synnott, 1985). Inhabitants of the sawmill have also planted crops in this area, including mango and paw-paw.

The Sonso region borders the southern boundary of the forest. This area is now the site of several villages, the nearest of which is Nyakafunjo which lies at the edge of the forest. The villagers have planted many crops close to the forest boundary, including sugar cane within ten metres of the boundary, and mangos and paw-paw a few hundred metres further south.

Habituation

One of the initial tasks of the Budongo Forest Project was habituating the community of chimpanzees. This endeavour was conducted by the project field assistants, beginning in 1991. By 1993 more than 30 individual chimpanzees had been identified and named. In 1995-6, when the first long-term student - Nick Newton-Fisher - arrived to study the Sonso chimpanzees, this number rose to 46. The persistence of field assistants and researchers meant that by the end of 1995 males could be followed comfortably on the ground and their behaviour observed at distances of less than ten metres. The females remained more reticent, however, until the first intensive study of female socio-ecology was conducted by Katie Fawcett in 1997-8.

As I conducted this study, the vast majority of members of the Sonso community were well habituated, allowing us to follow them on the ground and observe behaviour from just five metres away. Only the newly named females initially ran away as we approached them, but by the end of this study they tolerated our presence. Some of the females, especially the younger adults, remained wary of us when not in large parties and did not like to be followed on the ground. No physical contact has ever occurred between human and chimpanzee at this site, and the project stringently maintains a five-metre rule, whereby no human is allowed closer than five metres to any of the chimpanzees. So far, there have been none of the problems at Budongo occasionally observed at other chimpanzee research sites, with chimpanzees attempting to incorporate humans into their aggressive displays

(Boesch, pers. comm. Wallis, pers. comm.), and it is hoped that the five metre rule will preclude these problems.

Trail system

There is a trail system throughout the main study area of the Budongo Forest Project to aid observation of the chimpanzees, as shown in figures 2j and 2k. The framework for this trail system came from transects cut for census work (Plumptre *et al*, 1994). Trails are approximately 0.5m wide and 100m apart, running from north to south, and east to west. The trails are all labelled, forming approximately 100m² blocks that each have a unique coordinate - illustrated in appendix C. 'Block labels' can thus be used to denote the position of chimpanzees within the trail system. As is evident from figures 2j and appendix C, there is wide variation in the true size of blocks, arising from difficulties in cutting trails through certain areas and sketchy compass use by the trail cutters.

The Project camp is reached along the road that was previously used to enter the sawmill. The first part of this road, stretching from the southern forest boundary at Nyakafunjo village to where it meets the Sonso river, is known as the Royal Mile. The north east of the trail system incorporates the Waibira road, a logging trail running from the sawmill clearing to the northern edge of the forest. There are other trails in the forest, shown in figure 2j, which are only maintained by use. The Forest Authority partially maintains some transects along which it monitors forest regeneration and logging practices. These are spaced approximately 200m apart in the active logging compartments. Pit sawyers often create temporary trails through the forest, in order to remove the planks cut.

The maps shown in figures 2j and appendix C were generated from measurements taken by hand with a compass and tape measure by David Bowes-Lyon, an early visitor to the Project. These paper maps of the trail system were transferred to a GIS map by Vernon Reynolds, using MapInfo software. New trails were subsequently added to the system, and were mapped by Glen Bush in 1998. Six tic points were used for the initial GIS work, and the latitudes and longitudes for these points were obtained from the 1956 Ugandan Forestry Department maps of Budongo (Reynolds, pers. comm.).

Figure 2j: Map of Budongo showing forest edge and compartment boundaries, river, roads and BFP grid system. Enlargement shows the location of the Budongo Forest Project within the Nyabyeya (N) compartments, and the proximity of Nyakafunjo village at the forest edge.

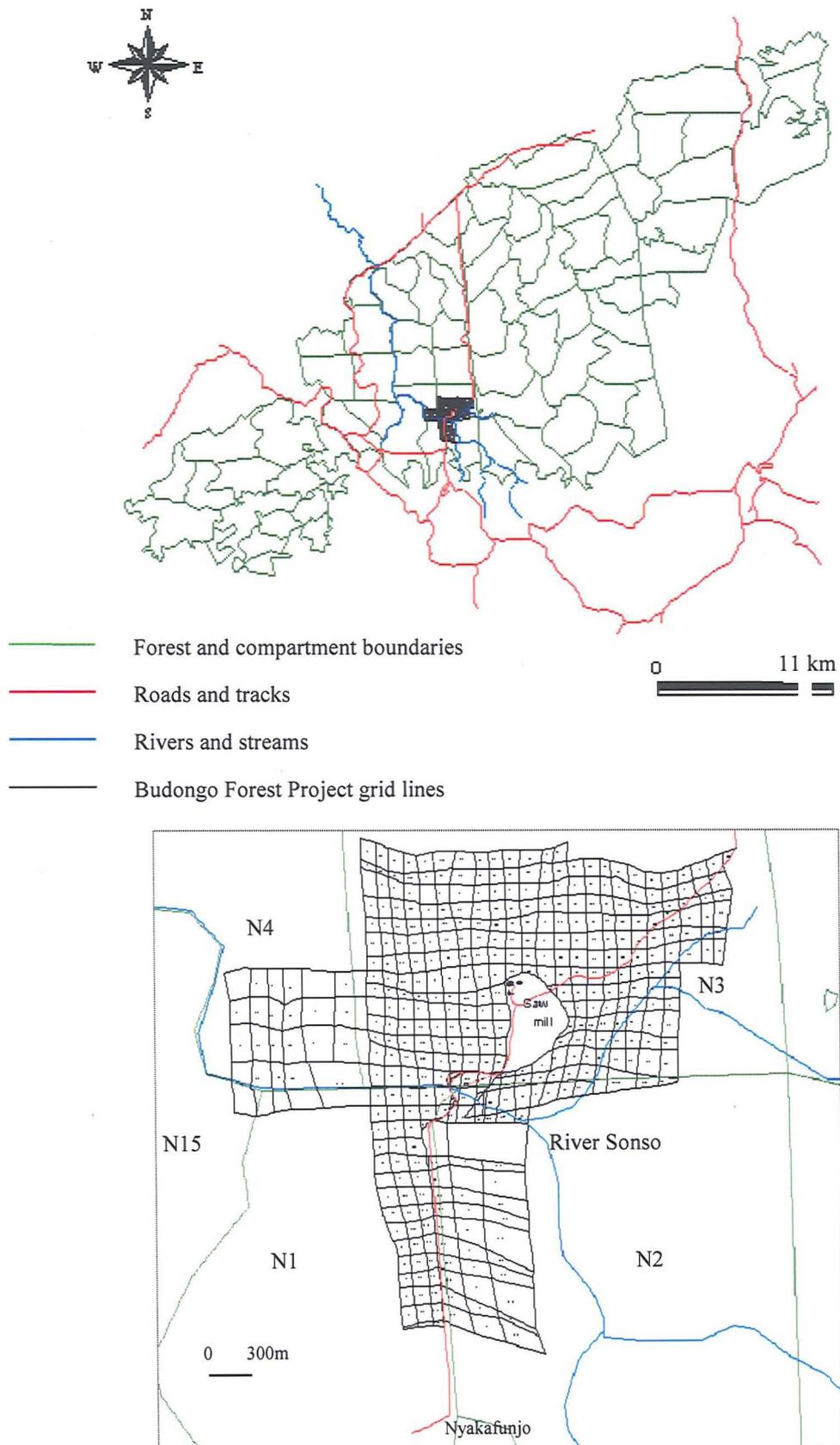
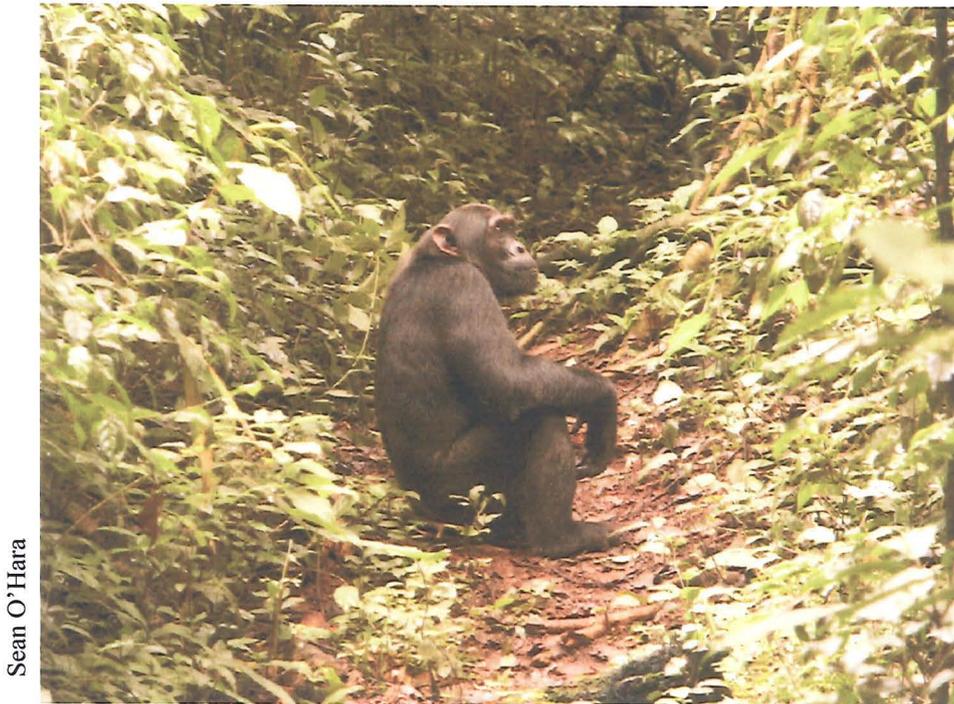


Figure 2k: Chimpanzee (NK) sitting on a trail



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Visibility

As can be seen in figure 2k above, the visibility within the forest is very poor, due to the thick under-storey vegetation. This was quantified using a 1m² board, painted with black and white squares, as described in appendix A. A large painted checker-board is obviously more conspicuous than a black chimpanzee in a dark forest, and so the estimates of the board at 50% obscurity were obtained, as the best approximation of how far into the forest it is possible to see and recognise objects. Taking measurements from 35 separate locations in the forest, the average visibility range before the board was 50% obscured was determined to be only 11m within forest blocks, and 16m when taking trails into account.

Levels of disturbance

Unfortunately, Budongo – like most forests in East Africa - is heavily disturbed. A recent Wildlife Conservation Society report cited many factors contributing to the disturbance of the Budongo chimpanzees, with one of the major aspects being research activities. This thesis is not the appropriate forum to discuss the positive and negative impacts of research conducted in natural habitats; suffice to say BFP is acutely aware of the dangers of over exploitation of the forest and the chimpanzees and has stringent guidelines in place to

minimise its negative consequences, such as limiting the number of researchers allowed at the site at any one time. I will, however, describe the major problems to the Forest that the report noted, as well as my own observations of the problems the Forest and the chimpanzees face.

Plumptre *et al* (2003) identified five major categories of threats to the forests and chimpanzees of Uganda, in addition to the impact of research activities. These fall under the headings of:

- Increased access to the forest
- Local community use of forest products
- Bushmeat hunting and animal collection
- Crop raiding
- Encroachment and forest loss.

I will discuss how each of these threats impact on Budongo and the study community of Sonso chimpanzees in particular.

The defunct sawmill site is still home to some of the former employees of the mill, and as a result there are, at certain times of the year, quite a number of people living within the Sonso region of the forest. When it was an active production zone, the sawmill employees started a school for their children. This school still exists today, with approximately 100 pupils. The vast majority of these children live in Nyakafunjo and other surrounding villages and so walk to and from school every day along the Royal Mile. The consequences for the forest and Royal Mile area are great, including litter and disturbance to primate species. On a number of occasions I and/or other researchers were watching chimpanzees on the Royal Mile that moved away at the approach of large groups of high-spirited children. This problem is slowly decreasing, however, as more and more children opt to attend the better equipped Nyabyeya school, about 3km south of the forest boundary.

Both legal and illegal pit sawing are common in the forest. The advantage to the forest is that pit sawing does not require the construction of logging roads, unlike other logging practices, as planks are removed on foot via smaller trails through the forest. It does, however, require many people to be present in the forest as it is very labour intensive work. The Forest Authority issues licenses and monitors which trees can be felled from any one active logging compartment, but illegal pit sawing is still rife, particularly in the nature

reserve of compartment N15, where a few large mahogany trees can still be found. During the course of this study, compartment N2 was an active logging site, so much pit sawing occurred within the south-east area of the Sonso community range. This meant that we, and the chimpanzees, frequently encountered the loggers and/or Forest Authority officials monitoring the activity. This did not usually seem to disturb the chimpanzees greatly, probably because the noise of the pit sawing would have alerted them to the location of the loggers, but it is impossible to judge fully the impact such extensive logging has on the ranging of the chimpanzees.

Encounters with other people accessing the forest were quite common, particularly when the holiday periods of Christmas and Easter were approaching. The areas surrounding the sawmill clearing and at the southern edge of the Sonso region close to Nyakafunjo village are used by people collecting firewood. Occasionally villagers were encountered further in the forest, collecting rattan cane and raffia strips for furniture and baskets, poles for building houses, and medicinal plants. Generally, though, only students and staff of the Project, loggers, poachers and Forest Authority officials, tend to go deep into the forest.

Poachers enter the forest to set wire snares for catching duiker and bush pig. This practice is not legal but is extensive. The Project employs four full-time snare removers, all of whom used to be hunters, to destroy the snares they find, but the disturbance caused by hunting is still great. During my 12-month study period, the snare removers retrieved over 500 snares from the Nyakafunjo compartments alone. I saw two dead duikers trapped by snares, one that was still alive (that we managed to release), and one trapped blue monkey. Furthermore, four chimpanzees from the Sonso community received limb injuries from snares in just this 12-month period – see below.

Thus, the combined threats to the forest of increased access, logging and the use of forest products, and poaching all have an impact on the chimpanzees, but the magnitude of the effect is hard to judge. Although Sonso is obviously a disturbed community in many respects, a certain level of security seems to be afforded to the chimpanzees by the permanent presence of researchers in the forest; fewer snares are set and retrieved from the central study areas, less illegal pit sawing occurs in these areas (pers. obs.), and compartment N1 has been made a site of special scientific interest, based on the activities of the Project.

Budongo suffers little from encroachment, due largely to the efforts of the Forest Authority to maintain the forest boundaries (Plumptre *et al*, 2003). The Budongo chimpanzees do face one further threat, however, resulting from the planting of crops too close to the forest edge. As mentioned, bordering the Sonso region, villagers from Nyakafunjo have planted sugar cane, mangos and paw-paw very close to the forest edge. All of these crops are attractive to chimpanzees as well as many other frugivorous forest mammals. Although chimpanzees are, overall, responsible for very little crop raiding compared with bush pigs and baboons (Plumptre *et al*, 2003), the Sonso community was observed to raid these crops on many occasions over the course of this study. Mangos and paw-paw are not considered important crops, being rather more food for children, so the occasional pilfering of these fruits by chimpanzees is largely tolerated (Plumptre *et al*, 2003). It is the stealing of large amounts of sugar cane that is not tolerated, as this is an important cash crop for many local farmers. During the course of this study, one adult male chimpanzee was killed by a spear wound to the chest whilst raiding the sugar cane field just south of the forest boundary. In order to prevent this happening again, the sugar works, which buys all the sugar cane grown in the Masindi and Hoima districts, decided to harvest the crop early and make it clear that they would not purchase any more sugar cane grown on this area of land. This decision by the sugar works was mainly an economic one, as the area was actually smaller than their normal criteria of a viable sugar cane plot, but it is still good news for the remaining members of the Sonso community. Although the sugar cane stems are re-growing, nobody currently cares if the chimpanzees consume it as it cannot be sold commercially anyway. This decision sadly comes too late for the male killed in the plantation, but is encouraging for the future of the rest of the community. Furthermore, due to the efforts of BFP and Uganda branch of the Jane Goodall Institute, the sugar works have agreed to re-assess their policy of buying any sugar cane grown too close to the boundaries of the forest around the entire perimeter of Budongo. This should reduce the negative consequences of crop raiding, if alternative, less palatable crops are planted in between the forest and the sugar cane.

Budongo chimpanzee communities

Plumptre *et al* (2003) showed that Budongo has a chimpanzee density of 1.36 individuals per km² and estimated there to be approximately 640 individuals in total. This is the

second largest population in Uganda, after that of Kibale Forest National Park (NP), and Budongo has the fourth highest density after Wambaya Forest Reserve (FR), Kibale NP, Bugoma FR and Kalinzu FR. About 12% of Uganda's total chimp population is thought to live in Budongo.

Sonso community

The BFP concentrates its research efforts on one community of Budongo's chimpanzees, the Sonso community, and has identified and named all chimpanzees observed since 1991. All individuals are named and given a two-letter code derived from letters of their name, once they have been seen frequently enough to be sure they are members of the community and can be recognised as distinct from any other individual. Since 1995 it has been the policy of the Project to name infants with the same starting letter as their mother's name. BFP has established criteria for classifying individuals as adult, sub-adult, juvenile or infant, as described in Appendix B, comparable with the demographic criteria used at other long-term chimpanzee research sites (Boesch and Boesch-Achermann, 2000; Goodall, 1986; Wrangham, pers. comm.).

At the start of this study there were 53 identified individuals within the Sonso community (as listed below in table 2.2), two of which (EM and SB) were seen only very rarely. Over the course of the study, two additional adult females (FL and PL) and their dependent offspring were named¹, one adult male (JM) was killed, six infants were born and named, and one infant died. Thus at the end of the study the community consisted of 62 named individuals. Appendix B describes the composition of the Sonso community as at the end of the study period (September 2003) and details the ages and identifying features of each individual.

Many of the Sonso community have been afflicted by snare injuries. Although snares are not set with the intention of capturing chimpanzees, chimpanzees get caught in the wire contraptions alarmingly often. In 1996 28.9% of the Sonso community had injuries resulting from getting limbs or digits caught in snares (Reynolds, 1997). During the course

¹ Immigration of adult females with offspring is rare among chimpanzees, and is known to occur only after the apparent breakdown of a neighbouring community (Nishida *et al*, 1990) – I will not discuss the potential reasons as to why these females were not known in the community before this study.

of this study, this figure rose to 20 current members (32%) of the community being at least permanently scarred by snare injuries, as detailed in appendix B. The severity of these injuries range from scars and loss of digits to the total loss of utility of hands due to wrist injuries, and even complete amputation of hands or feet in the case of four adult and sub-adult females. Six juvenile and sub-adult chimpanzees still have the snare wires attached to them, so as they grow and the snares tighten they are all at risk of losing their affected hands or feet.

Other Budongo communities

Given the population estimates of Plumptre *et al* (2003), and assuming an average community size of 50-60 individuals, approximately ten distinct chimpanzee communities can be expected to inhabit Budongo. At least two other communities are thought to border the Sonso community, to the west (Nyakafunjo/nature reserve community) and north (Waibira community). Although sightings have been made and calls heard from stranger chimpanzees in these areas, no systematic studies of these chimpanzees have been carried out. A third community potentially borders Sonso to the east, with strangers' calls being heard from this direction regularly. The status of this neighbouring community is also unknown, although a fellow student at BFP saw stranger chimpanzees involved in an aggressive encounter with the males from the Sonso community to the south-east, beyond the normal extremes of the Sonso range (O'Hara, pers. comm.)

Two other communities of chimpanzees have been partially habituated within the Budongo Forest Reserve for the purposes of eco-tourism. These are situated in the west of the forest, at Busingiro (B compartments) and in the north-eastern outlier of the forest at Kaniyo Pabidi (KP compartments). The Kaniyo Pabidi area is un-logged, and as such is a rather different habitat to the main forest block. The suggestion of making Kaniyo Pabidi an eco-tourism site was first voiced when it became apparent in the early 1990's that this area of forest was due to be logged. Eco-tourism was judged to be a sustainable economic alternative, through which the only remaining area of virgin forest in Budongo was protected. Neither of these communities was habituated sufficiently for comparisons with the Sonso community during this study, but the prospects remain exciting for future research.

Table 2.2: Sonso community chimpanzees, as at September 2002 (start of study)
 Names in brackets appear fully elsewhere in the table.
 A – Adult; SA – Sub adult; J – Juvenile; F – Female; M – Male.

Name	Code	Status	Surviving offspring of females			
			Adults	Sub-adults	Juveniles	Infants
Banura	BN	AF	(Zefa)	(Shida)	Beti [BT] F	
Clea	CL	AF				Clint [CT] M
Harriet	HT	AF			Hawa [HW] M	Hellen [HL] F
Janie	JN	AF				Janet [JT] F
Kalema	KL	AF			Bahati [BH] F	Kumi [KM] F
Kewayya	KY	AF				Katia [KA] F
Kigere	KG	AF				Keti [KE] F
Kutu	KU	AF			Kato [KT] M	Kana [KN] F
Kwera	KW	AF			Kwezi [KZ] M	Karo [KR] F
Melissa	ML	AF			Mark [MR] M	
Mukwano	MK	AF				
Nambi	NB	AF		(Musa)	Nora [NO] F	
Ruhara	RH	AF	(Nick)		Rose [RS] F	Ramula [RM] F
Sabrina	SB	AF			Sally [SA] F	
Wilma	WL	AF				
Zana	ZN	AF			Zalu [ZL] M	Zed [ZD] M
Zimba	ZM	AF	(Kewayya)		Zig [ZG] M	
Juliet	JL	SAF				
Recho	RE	JF				
Shida	SH	SAF				
Black	BK	AM				
Duane	DN	AM				
Jambo	JM	AM				
Maani	MA	AM				
Nick	NK	AM				
Nkojo	NJ	AM				
Tinka	TK	AM				
Zefa	ZF	AM				
Bob	BO	SAM				
Bwoba	BB	SAM				
Gashom	GS	SAM				
Musa	MS	SAM				

Chapter 3

General Methodology

Overview

Observational studies assess “real-life”, natural situations, and as such have high external validity (Altmann 1974). That is, the conclusions drawn from observational studies should generally be applicable to the whole population. However, to be sure of the appropriateness of the conclusions, it is necessary to maximise the internal validity of the study. This means that all samples must be treated in the same way so that alternative, artefactual explanations for the results are excluded. With observational studies, treating all samples in the same way requires carefully standardised and controlled data collection methods, which, whilst remaining sensitive to the idiosyncratic behaviours of the animal, limit the possibility that differences in the observed behaviour can be explained by variable behaviour of the observer. In this chapter I will describe the methods I employed to collect data relating to chimpanzee range use and travel behaviour.

I used a combination of sampling techniques, each of which entailed different recording rules. Focal animal sampling was used to collect data relating to one individual’s travel route and associated behaviour and, within the same observation period, I also employed scan sampling and occasionally *ad libitum* sampling to record social and contextual information.

All the data of this thesis were collected over 230 days between September 2002 and September 2003. Within this time I recorded 50 focal animal samples with a mean duration of 14 hours per focal sample (range 2 hours to 34 hours), totalling 647 hours of observation upon which this thesis will be based. The data-collection methods employed in this study were devised and refined in a pilot study conducted in Budongo between February and April 2002. Those data will not be presented here due to the procedural differences.

Observing and collecting chimpanzee behavioural data

A field assistant, James Kakura, who has been employed by BFP since the start of the project, almost always accompanied me into the forest and assisted me with chimpanzee data collection. I also employed other field assistants, Geresomu Muhumuza, Joshua Nkosi and Emmanuel Orijabo, to collect supplementary ecological data. All the chimpanzee data were collected using a Sanyo voice activated dictaphone, paper check-sheets and maps, and a handheld global positioning system (GPS). I used Zeiss 10 x 40 binoculars and a Casio digital wristwatch to aid my observations.

Locating chimpanzees

The most reliable way of locating chimpanzees was to return before dawn to an area where individuals were known to have nested the previous night. Thus, the day before an intended period of data collection commenced I would attempt to locate an appropriate party and follow one chimpanzee to its nest site. James and I would then return the next day, arriving at the nest site before 6.30am, and track that chimpanzee for the subsequent data collection period.

James and I used a number of methods to locate chimpanzees before data collection commenced: visiting known fruiting trees or food patches, and sometimes waiting there for suitable individuals to arrive; following the direction of vocalisations; or, occasionally, chance encounters with chimpanzees when walking through the forest. The method we employed varied daily according to the behaviour of the chimpanzees and the time at which we entered the forest; often, more than one method was used. For example, we would set off towards the previous night's nest site or a known fruiting tree, but if calls were heard on the way we might change direction to intercept the vocalising individuals.

Based on many years' experience, the field assistants believe that following vocalisations is the most reliable method of locating chimpanzees when one is not in the forest at an appropriate time to find them in a nest. Indeed, random searching for chimpanzees within the forest was largely unproductive, and only very rarely did opportunistic encounters with a suitable animal occur. If, even after searching all known fruiting trees, no chimpanzees had been located, we would stop and wait in any small clearing to listen for vocalisations. It was much easier to determine the source direction of calls when we were not moving.

Once a party was located, a suitable study animal was identified and data recording commenced.

Focal animal sampling

I employed focal animal sampling to record the travel route and behaviour of the target chimpanzees. Focal animal sampling, as defined by Altmann (1974) and Martin and Bateson (1995), directs attention to one target individual at a time, which is useful for behavioural data collection as it allows all instances of specified behaviours exhibited by that individual to be recorded. Theoretically, the identity of the target individual and the duration of the sample period should be determined in advance, and all pertinent behaviour occurring within that period should be noted. I used time sampling to note locations, coupled with continuous recording of activity in order to document accurately the travel route and associated behaviour of the target animal. Continuous recording provides an exact record of behaviour, giving actual durations and frequencies of behaviours, as well as the times and, therefore, the order in which each behaviour occurred (Martin and Bateson, 1995). Time sampling, whereby behaviours are noted only at pre-defined time intervals, such as every five minutes, doesn't preserve an *exact* record, but by abbreviating the travel path taken I was able to record accurately the concurrent behaviours.

I defined the maximum sample period for this study as three days of continuously following a target animal: from when it emerged from its nest on day one, throughout the second day, to when it nested (constructed a bed, as defined by Nishida *et. al.*, 1999) at night on day three. I chose this time period as a trade-off between the more intimate picture of an individual's ranging that a longer period could give, and the inaccuracy of data recording that can result from fatigue of the observers. In practice, however, focal sample periods did not always last three full days if the target animal was lost before nesting on the third day or if it was not followed immediately upon leaving its nest on the first day. Furthermore, it was not possible in this study to decide in advance which animal was to be the target in any given focal sample period. I could never be sure which of the potential target animals would be encountered, if any, so the ordering of focal samples was opportunistic.

I selected the target animals for focal samples from a pre-determined list of 15 individuals; seven adult females and eight adult males¹. Most individuals of the Sonso community allow close observation of their behaviour whilst they are on the ground (to within five metres²) but some appear not to like being followed if they are travelling alone or in small parties. This is presumably due to differing levels of habituation to human observers. The 15 potential focal animals, listed in table 3.1, were chosen based on expectations of which chimpanzees were most likely to allow us to follow them for prolonged periods at fairly close distances, even when not in large parties.

If none of the potential targets for focal samples were present in the party initially encountered, I had to decide whether to leave and search for an alternative party or to wait with the initial party until suitable individuals could be located. This decision was based on the perceived likelihood of finding an alternative party, taking account of how vocal the chimpanzees were at the time.

Table 3.1: Focal sample target animals.

Males	No. of samples	Total sample time	Females	No. of samples	Total sample time
Black	3	23.5	Banura	2	30
Bwoba	4	72	Kalema	3	60
Duane	4	74	Kewayaya	1	19.5
Jambo	5	22	Kwera	4	62.5
Maani	4	53.5	Melissa	2	31.5
Nick	4	48	Nambi	4	44.5
Tinka	2	36.5	Zimba	2	17.5
Zefa	6	52			
<i>Total</i>	<i>32</i>	<i>381.5</i>	<i>Total</i>	<i>18</i>	<i>265.5</i>

¹ One adult male, Jambo, died six months into the study, leaving fourteen target animals.

² BFP has implemented a “five metre rule” whereby no-one is permitted to be closer than five metres to any chimpanzee, in order to reduce the risk of cross-species disease transmission.

Selecting a focal animal

The first individual encountered from the list of potential targets was taken to be the focal animal for the duration of the follow. When possible, I alternated the sex of the focal animal from week to week in order to balance the observations, but as stated above, the ordering of focal samples was largely opportunistic.

If a party containing more than one potential focal animal of the right sex was located, I decided who to sample based on the number of previous samples available for each individual; the animal with the least number of prior observations was chosen. Some of the target animals were more elusive than others, and all were not equally comfortable with being followed when travelling alone, hence the variation in times that each were sampled for that is evident in table 3.1.

Following the target animal

Chimpanzees were followed using the trail system wherever possible over the three-day focal sample period, as they often also use the trails. However, it was frequently necessary to leave the trails and enter the blocks in order to keep the target individual in sight.

I always attempted to continue following the target individual even if it moved beyond the boundaries of the trail system, but it was sometimes impossible to do so. Some areas to the south and east of the grid, where the river Sonso flows, were frequently flooded, even during much of the dry season. The lack of trails and bridges in these areas meant we were often unable to move swiftly enough to keep the chimpanzees in view.

If we totally lost track of the target animal even after extensive searching, we attempted to locate another suitable individual using the methods described above. Sometimes the target individual was not visible to James or myself and we did not know its precise location, but it was *not* deemed to be lost, so I did not seek an alternative target. This generally occurred when the animal was moving off the grid system in areas of the forest too dense or wet for us to penetrate but, along with its accompanying party, did remain within our auditory range. This allowed us to re-join the party as it moved back towards the grid system and recommence data recording. Although no data was recorded when the animals were not in view other than to note the timing and direction of vocalisations, I

believe this tactic usually resulted in a longer sample period with more data collected for one individual than if a switch to a different target was made.

Location data collection

The location of the target animal was recorded every five minutes as it moved, so that its daily travel route - its path through the forest - could be accurately plotted. Location information was recorded using either a hand held Garmin 12XL GPS device or on a paper map of the BFP trail system as shown in Appendix C. The GPS device was set to the UTM position format (an alternative co-ordinate system to longitude and latitude, which uses metres as the unit of measurement rather than degrees and minutes) and used the WGS 84 (Zone 36 North) map datum. Published maps of Uganda more typically use the Arc 1960 map datum, but I chose to use WGS 84 so the co-ordinates collected would correspond with the digital maps of the trail system available to me from BFP.

Due to thick forest cover the GPS device was often unable to locate overhead satellites quickly enough to be of use when I was following a moving party of chimpanzees. For this reason I more often recorded the position of the target animal by plotting its location, as estimated by James and myself, on the paper map of the grid system whilst concurrently recording the information verbally on the dictaphone. When not using the GPS device I recorded the position relative to the trail lines and blocks, for example: "In block 4.1, 20 metres east of line 4, 40 metres north of line 1." I tested the accuracy of James' distance estimation when in forest blocks and the error of the GPS device and I deemed the two methods to be similar enough to be comparable. The results of these reliability tests are shown in Appendix D.

When the chimpanzees were travelling off the grid system it was obviously harder to plot accurately the location without the use of the trail lines as a reference. The intermittent Forest Department lines, described in chapter two, were useful when we were moving south or east of the grid, as we knew these were spaced 200m apart and which trail lines they connected to. However, when we were off grid I would use the GPS wherever possible to obtain more accurate location information.

After deciding on the identity of the target animal for the focal sample period, I recorded the start location and all subsequent locations of the target at five-minute intervals. The

start location was defined as the place where the target animal was identified and focal sample recording commenced. All location information was recorded using either the waypoint function on the GPS device, with the corresponding waypoint number noted on the dictaphone, or by plotting a point on the paper map and describing it verbally on the dictaphone. From this point onwards I will use the word “waypoint” to refer to a location that was marked either on the GPS device or the paper map, as well as the dictaphone.

Although I had to keep a continuous mental note of where the target animal was, I only recorded the location on the GPS and dictaphone at these five-minute intervals, rather than continuously, as this allowed me to keep a truthful record of the route taken through the forest whilst still enabling me to monitor and log the behaviour of the animal. Recording location more frequently than this would have interfered with the continuous behavioural recording.

As well as recording the start location and the five-minute location waypoints, I also noted the locations of all the places where the target animal stopped to feed, drink, rest or socialise. Feeding and drinking, as defined by Nishida *et al.* (1999) (see below), were clearly identifiable activities. Socialising (grooming and playing) and resting, again as identified by Nishida *et al.* (1999), were just as apparent, although perhaps harder to imagine. I labelled the waypoints where the target animal stopped to engage in these activities as “stop sites”. When the focal animal stopped travelling I did not record its position again until it had moved away from the stop site. I differentiated these stops from mere pauses in travel, based on the behaviour of the animal. Pauses - where the target animal simply stopped travelling and stood motionless for a period of less than one minute without engaging in any feeding, drinking or social behaviour, and did not sit down or climb a tree – were not recorded.

A new five-minute period began as the target animal moved away from a previous stop-site. Chimpanzees are not always stationary when feeding or socialising and they may change positions when resting, but I was careful not to start counting the five minutes until I was certain the target animal was leaving the immediate area of the stop-site and commencing travel to a new area. This avoided recording trivial local movements within the stop-site. I then recorded the location of the subsequent stop-site irrespective of the time elapsed since the last waypoint: stop sites reset the five-minute time period.

For the purposes of location data, I altered the definition of the size of a stop-site according to the other animals (if any) in the subgroup and the nature of the food patch. The *minimum* size for a stop-site was the area within a ten-metre radius of the initial stopping point of the target animal, as any point within this circle may not have been accurately differentiated by the GPS or by James and myself (see Appendix D). This means that any stop-site was a circle of at least 20 metres in diameter, as estimated by James, centred on the initial stopping point of the target animal. Any movements the target animal made within this circle were not recorded as separate waypoints. Subsequent five-minute or stop-site waypoints were only recorded when the animal moved outside this 20-metre circle.

I increased this minimum diameter of the stop-site if the target animal was associating with other individuals or was feeding, however. When the target animal was in a party with other independent individuals, I defined the size of the stop site by the limits of the party³. When feeding, even if the target animal was alone, the minimum stop-site size was increased to the size of the food patch, if larger than 20m in diameter: when feeding, the stop-site size was dictated by the boundary of feeding patch⁴. Thus, the area of a stop-site is defined either by the spread of the target animals' party or the patch size of its food

³ Newton-Fisher (1997) and Fawcett (2000), in previous studies of the Sonso community, defined a party as all individuals present within a 35 metre radius of a focal individual, as beyond this distance visibility was too poor to be sure of the continued presence of individuals. I also employed 35 metres as the boundary for party membership in this study, so that data is comparable with previous studies of the Sonso community. I decided, however, the 35-metre radius around the target animal could be increased if a number of chimpanzees were feeding on one food patch (as defined below) with an area greater than the 70-metre diameter about the target animal. In practice this was observed only rarely, but I found it useful to maintain this definition so that party sizes were not recorded as being artificially small on the few occasions when the target animal and its associates were feeding in a single large patch.

⁴ Following Chapman *et al.*(1994) and White and Wrangham (1988), a food patch was defined as any discrete area where an individual could feed continuously without having to interrupt its food gathering even when moving within the area. A food patch thus translates as either a food tree isolated at its crown from any others, or adjacent food trees with inter-connecting crowns: I identified the patch as the area covered by the crowns of all the inter-connecting potential food trees.

source, but always with a minimum diameter of 20 metres, as dictated by the error margin of the location estimation.

Whenever I recorded a location waypoint on the GPS device or the paper map, I also recorded the details on the dictaphone. I noted the time of recording the waypoint (using the 24-hour clock), the location with respect to the grid system, and the activity of the target at the waypoint (as defined in the behavioural data recording section, below). This allowed me to match the location data with behavioural data.

Behavioural data collection

I recorded all behavioural data relating to the target animal in parallel with the location data using the dictaphone. Behavioural data was recorded in order to put the travel route information into context. At the start of each focal sample I noted on the dictaphone the date, time of commencement of the focal sample, and the identity and location of the target animal. For the duration of the data-collection period I then recorded the behavioural states and events of the target animal, supplemented with details such as food items, social companions, the actor or recipient of any behaviour, and the time of occurrence of every behaviour, as detailed in table 3.2.

I have defined as *states* those behaviours whose duration was significant to the aims of this study. State behaviours are elements for which the duration of the behaviour is of interest and are, therefore, mutually exclusive of each other. Every time the target animal switched to a different state behaviour, I recorded the time and the details of the new behaviour on the dictaphone. The occurrence of a new state behaviour was a signal that the previous state behaviour had been terminated, so I could accurately calculate the duration of each state observed during a focal sample.

Events are behaviours that may occur concurrently with other behaviours, and usually describe transient acts or those for which duration is not relevant: the *frequency*, as opposed to duration, of events is significant (Martin and Bateson 1995). Again, every time the target animal was observed performing a behaviour I had designated as a significant event, this was noted on the dictaphone with the time of occurrence and other pertinent information.

Table 3.2: State and event behaviours recorded in the focal samples, based on Nishida *et al.* (1999).

Behavioural State	Modifying information recorded	Behavioural Event	Modifying information recorded
Drinking Drinking water in any fashion	Location Start time Party composition	Aggression Any attack or fight directed at or emitted by target	Location Time Actor Recipient
Feeding Ingestion of any food stuffs	Location Start time Party composition Food species Food type	Chasing Pursuing another animal, usually running after it	Location Time Actor Recipient
Grooming Grooming of self or with another	Location Start time Party composition Who is involved in grooming	Copulating Actual or attempted intromission	Location Time Actor Recipient Successful or not
Hunting All attempts to capture another animal	Location Start time Conspecifics involved Species hunted	Displaying Any type of display exhibition from a repertoire of aggressive actions	Location Time Actor Recipient Type of display
Nesting Constructing a platform for sleeping or resting, above or on the ground	Location Start time Tree or ground Tree species Day or night bed	Fission Individuals leaving a party	Location Time Identity of who left
Resting Sitting or lying immobile, on ground or in tree: Inactive	Location Start time Party composition Tree or ground	Fusion Individuals joining a party	Location Time Identity of who joined
Playing Any kind of lone or social play	Location Start time Party composition Type of play Who playing with	Inspection Investigate an object in environment, usually by touching or smelling it	Location Time Actor Recipient/object inspected
Travelling Movement via any means between stop sites	Start time Initiated by who Mode of travel Party composition Where is target in procession	Hear Vocalising All chimpanzee vocalisations I could hear from individuals not in party being followed	Location Time Type of vocalisation Direction of vocalisation
		Vocalising All calls emitted from the target animals' party	Location Time Actor Type of vocalisation

Table 3.2 describes the behavioural states and events I recorded throughout every focal sample, with details of the additional modifying information recorded about each. Each of the states and events recorded was based on the descriptions and definitions of behaviours found in the ethogram of Mahale chimpanzees (Nishida *et al*, 1999). As this is not a behavioural study *per se*, I have lumped into one category many of the behaviours that Nishida *et al*. describe separately. As detailed below, the modifying information I recorded about each category of behaviour often differentiated the activity according to Nishida's description, where this was appropriate to the aims of this study.

Scan sampling

After locating a party of chimpanzees, all the individuals present were identified by James and myself before data collection commenced. James then censused the party every 15 minutes to record the party composition and activity of all individuals present throughout the sample period (which is equivalent to the focal animal sample period). James was aware of the definitions of what constituted a party in this study, and complied with them when recording party composition during the scan samples. This scan sampling was performed concurrently with the continuous focal animal sampling so that the composition and behaviour of the whole party associated with the focal animal was known.

Scan sampling requires rapid scanning of the whole group at regular time intervals, with data recorded at the instant of observing each animal. Scan sampling does not preserve an exact record of behaviour in the way that focal animal sampling does, but it does make it possible to record the presence and activity of a larger group of individuals (Martin and Bateson 1995). The sample point was the 'instant' of time at the end of each of the regular time intervals (clearly, finite time is required to scan a party of chimpanzees for their identity and activities, but crucially the time of recording each individual is independent of its activity). As scan sampling is normally used for time-budget measurement, the duration of the sample interval is important. The interval needs to be brief enough not to frequently miss occurrences of pertinent behaviour, which will happen if an animal changes its state twice within one time interval, but it cannot be so brief as to overload the observer. I employed a 15-minute sample interval as this was a reasonable time for James to locate individuals within the party, allowing him to record accurately their presence and activity at the appropriate point, whilst being brief enough to avoid missing behavioural states. I

did not attempt to calculate the optimal time interval for this study but previous studies of both the Sonso community (Newton-Fisher 1997; Stokes 1999) and other chimpanzee communities (Chapman *et al*, 1994; Wrangham *et al*, 1996) have shown 15 minutes to be a suitable interval time for recording party composition and gross behavioural states. Thus, if chimpanzees were located and identified at 7.00am, for example, the first scan recording would occur at 7.15am, the second at 7.30am and so on at all 15-minute intervals.

A problem with scan sampling is that some individuals and behaviours will be more conspicuous, potentially biasing the data collected; there is a danger that conspicuous or significant behaviours might be recorded even if they occur slightly outside of the sample point, rendering the sampling non-independent. I emphasised to James how important it was that he avoided doing this and that he should keep the scan times as brief as possible. In addition, behaviour should ideally be recorded at the same point in time for all the members of the party to ensure they are all subject to the same external environment. I have not calculated an average time that it took to scan the party; it could take anything from a few seconds to several minutes depending on the size, activities and visibility of the party. However, comparisons of the scan samples and the focal animal samples indicate that James' recording of the time spent engaged in the defined behavioural activities was highly similar to mine, with a significant positive correlation between the time proportions obtained by each data collection method (see Appendix D).

The scans were recorded on a check-sheet like the one in Appendix C, which also details the codes used to denote activity. James recorded the same behavioural categories in the scans as I used in the focal animal samples as these are sufficiently distinguishable to allow rapid decisions about the behaviour of an individual. The only additional behaviour that he recorded was "moving". If, at the time of a scan, an animal was travelling *within* a stop site, this was recorded as moving – the "travelling" code was reserved for movements *between* stop sites. If an individual could be seen but its activity could not be easily determined, the presence of the animal was noted with a tick instead of a behavioural code. James noted individuals that could not be seen but who were not known to have left the party with a question mark. The use of these two codes allowed him to pass quickly through the scan, recording data as accurately as possible without compromising the 'instantaneous' nature of the sampling. As well as recording party composition and

activity on the scan data sheets, James also noted the reproductive state of all the females present in the party, using a four-point scale implemented by BFP (Reynolds, 2005).

Ad-lib. data collection

I recorded *ad-libitum* any additional pertinent behaviour that was not necessarily included or fully described as an event or state. With “*ad-lib.*” data collection there are no constraints on what can be recorded or when; the observer simply records “as much as he can” (Altmann 1974). Salient, visible occurrences were noted on the dictaphone as and when they happened, in addition to the focal sample data. Any *ad-lib.* behavioural recordings were accompanied with details of the individuals involved, the time of occurrence, and the location in the forest. This allowed the *ad-lib.* recordings to be related to the other data collected. *Ad lib.* data collection is biased towards conspicuous behaviours or individuals (Martin and Bateson 1995) but it is useful for recording rare or difficult-to-characterise events. As such, I usually recorded information about hunts (presumed or successful) and aggressive interactions *ad libitum*. Although both these categories were included in the focal behavioural data collected, according to the definition of focal-animal sampling, they would only have been recorded if the target animal was directly involved. I chose to note all such hunts or aggressive behaviours that I observed, even if the target animal was not directly involved, because these could potentially have a significant impact on the party composition, behaviour or movement patterns of individuals in the party, including the target animal.

Supplementary data collection

As well as collecting behavioural and location data for the target animal and its associates, I required additional information about the forest environment and Sonso community in order to put the travel behaviour of the target animals into a socio-ecological context. The following data were collected by myself, James and other BFP employees. Details as to how this information was used can be found in the relevant subsequent chapters.

Rainfall and temperature

Rainfall and temperature data were collected every morning at 7am by a BFP field assistant, either Joseph Karamagi or Geresomu Muhumuza. Average minimum and maximum temperatures (in °C), recorded across two thermometers, and total rainfall (in mm) for the previous 24-hour period were noted down and subsequently added to an Excel database of daily weather recordings for the site from 1993 to the present.

Phenology

Phenology (plant food availability) data assess fluctuations in food supply, and have been collected by BFP field assistants since 1993. BFP currently collects two phenology data sets: a bi-monthly analysis of fig phenology and a monthly assessment of a wide variety of chimpanzee food trees, which gives a more general picture of the food available from many forest tree species. I did not attempt to collect any of this data myself but relied on the information collected by the trained staff members. I believe this allows for a more reliable comparison of food availability within and between seasons over a number of years.

Tree distribution

I employed two field assistants, Joshua Nkosi and Emmanuel Oijabo, to record and plot the distribution of all chimpanzee food-trees found within the grid system. James and I also collected this information when we were not collecting chimpanzee observational data. The positions of all known Sonso chimpanzee food trees of over ten centimetres DBH (diameter at breast height) were recorded on a block-by-block basis. I subsequently entered this information into an Excel file and converted it to ArcView distribution maps, which illustrate the distribution and density of all the Sonso food-trees.

Community information

All six field assistants employed by the BFP to observe the Sonso community collect social data on the chimpanzee parties they encounter each day. They record all social interactions, including grooming sequences, copulations and other pertinent affiliative or aggressive acts, with respect to the approacher, initiator, actor, terminator and timing of each event. They also record the reproductive state of every adult or sub-adult female seen.

Data are recorded either in notebooks or directly onto a purpose-designed checksheet, and are later transferred from the checksheets to an Excel database by a BFP employee. This Sonso community database extends back to 1992 and forms the basis of knowledge of the social status of individuals. From January 2003 onwards the field assistants also used scan sampling methods to record the composition and location of the party every five minutes, and activity of the individuals present every ten minutes.

Analysis

At the end of each focal sample, the dictaphone tapes recording the target animal's behaviour were transcribed and saved as Word .doc files and the UTM co-ordinates of all the waypoints recorded for the target animal's route were entered into an Excel file, obviously preserving the order of occurrence. Waypoints recorded on the GPS device were copied straight into the file, but to determine co-ordinates for the waypoints recorded on the paper maps I had to first plot the points on a digital map of the trail system, using MapInfo Professional (version 6.5). I could then extract the UTM co-ordinates and add them to the appropriate Excel file. The co-ordinates obtained from the MapInfo digital map were rounded to the nearest ten metres, for example, actual co-ordinates of 338458 East and 191293 North would be shown on MapInfo as 338460 and 191290, because James and I had only estimated these distances to the nearest five metres.

Once saved in Excel files, the co-ordinates of each travel route were also converted into ".apr" ArcView GIS project files in order to construct visual maps representing the paths the target animal took through the forest over the course of the focal sample. These Word, Excel and ArcView files form the basis of all subsequent route-based analysis presented in this thesis.

All data presented in this thesis were analysed using Microsoft Excel 97, SPSS version 10 and ArcView GIS version 3.2. Details pertaining to each analysis performed can be found in the subsequent data chapters. Parametric statistics were used, unless otherwise stated, with the confidence interval set at $\alpha=0.05$.

Chapter 4

Territory use and foraging behaviour

In this chapter I will describe the ecology of the Sonso community in order to place the chimpanzees' foraging behaviour in context. It is important when investigating cognitive aspects of range use to know over what area the chimpanzees search for food, what they eat, and when they eat it. I will describe the average distance covered by the Sonso chimpanzees in their daily range, their activity patterns, and details of the diet and availability of food items. The possibility of changes in the pattern of ranging behaviour and diet across the seasons will also be considered. The ideas presented here could and, indeed, have constituted several theses in themselves; hence I only provide a rather brief overview. Further information relating both specifically to the Sonso community and chimpanzees in general can be found in the literature cited.

Territory use of chimpanzees

Chimpanzee territory¹ size and even location can vary within and across years (Goodall, 1986; Boesch and Boesch-Achermann, 2000) as the community demographics, resource availability and behaviour of neighbouring communities change. There is also much variation in the size of the territory of different chimpanzee communities between years. For example, Williams *et al* (2004) report a mean territory size of 9km² for the years 1975 to 1992 for the Kasakela community of Gombe Stream National Park, Tanzania, but varying between ~5km² to ~13km². In the Kibale forest of Uganda, lying to the south of Budongo, territory size of the Kanyawara community is approximately 14km² (Chapman and Wrangham, 1993). Within the Tai forest, Cote d'Ivoire, territories are larger, with a

¹ Although I only witnessed one border patrol and one vocal inter-community interaction during this study period, I argue that the term territory is the most appropriate when discussing the ranging area of chimpanzee communities, as male chimpanzees of all sub-species are known to defend aggressively and cooperatively an area in which females range, to the exclusion of extra-community individuals (Goodall, 1986; Boesch and Boesch-Achermann, 2000; Newton-Fisher, 1999b). Using the term "home range" – meaning the undefended area in which animals normally function (Burt, 1943 in Herbinger *et al*, 2001) - implies only part of the picture: chimpanzees *do* engage in defensive behaviours and aggressive interactions with external conspecifics (Boesch and Boesch-Achermann, 2000).

range of $\sim 16\text{km}^2$ to $\sim 27\text{km}^2$ between 1982 and 1995 (Boesch and Boesch-Achermann, 2000).

Fawcett (2000) estimated the territory size of the Sonso community to be approximately 9km^2 . Newton Fisher (1997; 2002) recorded a slightly smaller range size three years earlier of approximately 7km^2 . It is apparent that the Sonso area is considerably smaller than territory sizes reported at various times for other chimpanzee communities. These variations in size across communities are most likely based on different habitat qualities, varying population and community structure and size, and food availability (Boesch and Boesch-Achermann, 2000; Chapman and Chapman, 2000; Goodall, 1986; Herbinger et al, 2001; Lehmann and Boesch, 2003). The relative importance of each of these factors in dictating the territory size probably varies with time, within and between communities, and as the habitat changes.

As well as variation in size between and within territories, chimpanzees are known to use their territories in a non-uniform way, with animals spending lots of time in a relatively small percentage of the total territory area. For example, at Tai, Boesch and Boesch-Achermann (2000) state that chimpanzees spend 75% of their time in only 35% of the territory and only spend 5% of their time in the outermost quarter. Furthermore, this irregular use is different between the sexes. Females are known to spend most of their time in small core areas, the size and positioning of which are influenced by both feeding competition and male territorial behaviour (Williams *et al*, 2002; Doran, 1997; Nishida *et al*, 1985; Chapman and Wrangham, 1993). A core area is defined as an area within territory that is used preferentially or more frequently than other areas. Males, on the other hand, have been shown to be four times more likely to visit the boundary areas of the territory than females (Chapman and Wrangham, 1993).

The ranging patterns and habitat use of females can vary dramatically with their reproductive state (Goodall, 1986). Swollen (sexually receptive) females travel much further compared to sexually non-receptive (e.g. pregnant or lactating) females. This change in ranging behaviour arises from cycling females associating more frequently with males (Goodall, 1986). Male chimpanzees at other study sites are known to travel further per day than females (Chapman and Wrangham, 1993), and it is thought this increased

distance allows males to search for mates and defend the borders of their territory (Lehmann and Boesch, 2001).

Diet

Chimpanzee diets are dominated by fruit (Wrangham *et al*, 1998). As a result, individuals are found at the highest densities in areas of high fruit abundance (Furuichi *et al*, 2001; Balcomb *et al*, 2000). The chimpanzees of Budongo are known to prefer foods with high sugar levels (Reynolds *et al*, 1998), which is befitting of a diet composed in large part of ripe fruit. Although the vast majority of feeding time is often focussed on only a few species, chimpanzees across Africa are known to have a very broad diet, with many species eaten (Wrangham, 1977; Nishida *et al*, 1983; Tutin and Fernandez, 1985; Tutin *et al*, 1991; Wrangham *et al*, 1996; Newton-Fisher, 1999a). As well as fruit, chimpanzees are known to consume a lot of leaves and terrestrial herb vegetation (THV) (Wrangham *et al*, 1998).

Figs are known to be very significant to birds and primates of tropical forests (Terbough, 1986), possibly because of their high calcium content compared with other fruits (O'Brien *et al*, 1998). Figs bearing wasp larvae are also a rich source of protein (Vellayon, 1981; Kalina, 1988 in Shanahan *et al*, 2001). Within Kibale Forest, Uganda, Wrangham (1991) and Wrangham *et al* (1993, 1996) showed figs to be important "fallback" foods: fallback foods are defined as foods that provide nutrition during periods of general scarcity. Newton-Fisher (1999a) suggests, however, that because in Budongo figs are eaten in large quantities throughout year, they may be better thought of as a staple rather than a fallback food for the Sonso chimpanzees.

Low-quality THV is also a common fallback food in Kibale (Wrangham, 1991; Wrangham *et al* 1996), although its importance as such at other sites is equivocal. Tutin *et al* (1997) showed that chimpanzees of the Lopé Reserve, Gabon, did not always depend on THV during periods of fruit scarcity. Its significance to Budongo chimpanzees also seems to be low: at Sonso THV is only a minor component of diet (Newton Fisher, 1999a). Instead, Fawcett (2000, unpublished data) identified *Broussonetia papyrifera*, *Chrysophyllum albidum*, *Cordia millenii* and *Mildbraediodendron excelsum* as important fallback foods for the Sonso community, as well as confirming the significance of the fig species *Ficus sur*.

Chimpanzees across Africa are known to supplement their fruit-based diets by hunting mammals and even birds, but the capture of animals by chimpanzees occurs at different rates in different communities. For example at Tai, Cote d'Ivoire, Boesch and Boesch-Achermann (2000) report 267 successful captures of prey from 413 attempted hunts over an 11-year period. Riss and Busse (1977) observed five successful hunts in just fifty consecutive days of observation at Gombe. Conversely, Bossou chimpanzees were seen eating meat only five times in eight years of observation (Sugiyama and Koman, 1987). The Sonso community is also rarely seen to hunt. In just under 18 months at the field site I observed members of the Sonso community eating meat on only four occasions (one monkey and three forest antelope). Other observers who concentrated observations on males of the community have witnessed more hunts (Newton-Fisher, pers. comm.), but at nothing like the frequency of occurrence at other research sites. As Boesch and Boesch-Achermann (2000) suggest, differences in hunting would imply that hunting and eating meat is not a critical component of a chimpanzees' diet.

Food availability

Tropical forests are known to exhibit periods of fruit, flower and young leaf abundance and scarcity (White, 1998). Patterns of food availability change seasonally - within years - and even annually, based on rainfall and sunlight patterns (Tutin and Fernandez, 1993; van Schaik et al, 1993; Wright and van Schaik, 1994; Chapman *et al*, 1999). Even within a forest, different areas may exhibit different phenological patterns (Chapman *et al*, 1999), and chimpanzees are known to inhabit ranges that include a number of vegetation types (Plumptre and Reynolds, 1994; Furuichi *et al*, 2001). As the availability of food items changes constantly, so the diet of consumers must be able to cope with these changes. The presence of staple foods (those available consistently throughout the year) and fallback foods (those available during the regular seasons of food scarcity) may accommodate changes in food availability. Of the five fallback foods identified by Fawcett (2000) (see above) for Sonso, no one was available throughout the whole period of lowest food abundance, but across the five species, food was available consistently.

Budongo has not been recorded to experience a period of *extreme* scarcity of fruit, flowers and young leaves, although certain months are associated with lower levels of fruit production than other months (Newton Fisher, 1999a; Plumptre *et al*, 1994, 1997; Newton-Fisher, Reynolds and Plumptre, 2000; Reynolds, 1992; Reynolds and Reynolds, 1965).

Thus, seasonal food shortages may not be a huge problem for this population of chimpanzees.

Behavioural responses to fluctuations in food availability

White (1998) summarised the immense importance of seasonal changes in phenology to primates, which impacts “not only on...diets but also on ranging, habitat use, and ultimately reproduction”. This suggests that the diet, patterns of habitat use and ranging behaviour of chimpanzees could all vary with changes in food availability.

As foods eaten must change to some extent with the seasons depending on what is available, spatial shifts can be expected. Chimpanzees will use different areas of their territory at different times of the year, according to the distribution of forest/tree types. Furuichi *et al* (2001) showed that seasonal changes in range use of the Kalinzu forest, Uganda, coincided with fluctuations in fruit availability. The number of chimpanzees using an area was best predicted by the tree composition of the area. Certain forest types included trees that fruit at different times of the year, and these areas were used preferentially when they offered the most fruiting trees. Range-use shifts may be subtle however, as chimpanzees can cover large distances every day, throughout the year (Boesch and Boesch-Achermann, 2000). Consequently, Herbinger *et al* (2001) found only a weak correlation within the Tai forest between the area of territory use and the season, although the chimpanzees did range more in peripheral areas during times of fruit scarcity, presumably in order to utilise alternative food sources.

As well as shifting the areas of main use, daily range length may increase in times of food scarcity. It is axiomatic that larger groups of animals tend to have larger home ranges (Clutton-Brock and Harvey, 1977; Isbell, 1991) because animals living in larger groups require - and deplete - more food patches. Within the primate order, frugivorous species also show longer daily range length when in larger groups (Clutton-Brock and Harvey, 1977). This finding, the cornerstone of the so-called *ecological constraints model* (Chapman, 1990), is taken to suggest that daily travel distance is more dependent than total range size on food distribution (Isbell, 1991): folivorous species are assumed to feed on much more uniformly abundant food sources than the distinct and patchy resources of frugivores. The ecological-constraints model predicts that group size is directly linked to food availability - larger groups will suffer greater within-group feeding competition if

food is not super-abundant, and so group size is constrained. Increases in within-group feeding competition can lead to increases in the daily range length as patches are depleted more rapidly, requiring animals to travel further in order that they visit more patches to maintain the required level of food intake. If frugivorous primates respond to the increased feeding competition inherent in larger groups by travelling further per day, it follows that they may also respond to seasonal reductions in food availability by travelling further.

The ecological constraints model has been shown to apply to both permanent group living primates (Gillespie and Chapman, 2001) and those living in fluid, fission-fusion societies where group size changes rapidly and frequently (Ghiglieri, 1984; Chapman *et al*, 1995). Chimpanzees should, therefore, increase their daily range length in times of food scarcity even though travelling further obviously expends more energy, so long as the energy expenditure is repaid by the resources subsequently visited (Chapman and Chapman, 2000). Chimpanzee terrestrial travel is known to be energetically demanding, however, with a greater percentage of the daily energy budget spent on terrestrial travel than on any other activity (Pontzer and Wrangham, 2004). Despite these energy costs chimpanzees do travel long distances. They have the longest daily range lengths of any ape except humans (Chapman and Chapman, 2000) and also one of the longest for all primates, after species of *Papio* and Patas monkeys. At Gombe, the average day length of one adult male over 50 consecutive days was 4.5km (Riss and Busse, 1977).

Doran (1997) showed day range length of Tai chimpanzees *decreased* in times of food scarcity, with more time spent feeding and more time feeding on lower quality items. Herbiniger *et al* (2001) also found that Tai chimpanzees don't travel as far in the season associated with reduced fruit availability: the move to more peripheral areas is associated with reduced range lengths. Boesch and Boesch-Achermann (2000) concur that the months of highest fruit production are when the longest daily range lengths are observed. However, in some years the shortest daily ranges coincided with another month of high food availability in the form of nuts. Nuts are a tightly clumped resource, but the overall territory size did not decrease similarly in these months: the short monthly daily ranges did not correlate with territory size. Thus, although food availability does have some influence over territory utilisation and ranging behaviour, Boesch and Boesch-Achermann concluded neither the pattern of food abundance nor distribution can completely explain territory use and daily range length.

During times of fruit scarcity travel costs are even greater compared with times of food abundance (Gillespie and Chapman, 2001). An alternative strategy to increasing the already costly daily range lengths is to alter daily activity budgets. Spending more time resting and less travelling when food is scarce would ensure less energy is expended. Consideration of chimpanzee activity time budgets has illustrated general patterns in the organisation of the day, with individuals feeding predominantly on fruit in the morning, and leaves in the afternoon (Wrangham, 1977; Newton-Fisher, 1999a) with a general decline in feeding behaviour over late morning and early afternoon (Tweheyo and Obua, 2001). Furthermore, Riss and Busse (1977) showed feeding and resting times within a day are inversely related; when more time is spent feeding, resting time is sacrificed. Seasonal impacts on time budgets are not so apparent, however. Wrangham (1975, in Riss and Busse, 1977) found no significant seasonal variations, despite considerable variation in the daily patterns of time use, but Janson (1988) showed the activity budgets of brown capuchins altered with altering feeding stress. Reductions in the time spent resting, allowing greater feeding time, were observed as feeding competition increased.

It is now apparent that food availability is not necessarily a critical factor in chimpanzee social interactions – other variables (such as community demographics) affect party size more. Although food availability may constrain the overall number of individuals that can live in an area, it is not necessarily the factor dictating everyday behaviour. Isabyre-Basuta (1988) showed that, when multiple important foods are available, party size is not related to food. Boesch and Boesch-Achermann (2000) reported similar levels of fruit production across seasons, but one season was associated with large parties and the other not. Similarly, in Kalinzu, Hashimoto *et al* (2001) found no relationship between party size and fruit abundance or distribution, and in Budongo only a weak relationship between food abundance/dispersion and party size was evident (Newton-Fisher *et al*, 2000). At various study sites, food is apparently often abundant enough not to be too consequential to chimpanzee behaviour. This reduction in the significance conferred to food availability merits further investigation.

In this chapter I will attempt to describe the ecological environment of the target animals during the period of my data collection. I aim to ascertain the breadth and composition of the Sonso chimpanzees' diet within this study period, to elucidate what they fed on when,

and I shall attempt to extend the findings of previous studies of Sonso chimpanzee ecology, and confirm:

- The status of figs of staple foods.
- Whether the Sonso chimpanzees are subject to periods of food scarcity, by determining any seasonal patterns in food availability.
- What fallback foods, if any, are consumed during times of food shortage.
- Whether feeding is more likely to occur at particular times of the day.
- The daily range length and activity budgets of target animals, so that any sex differences and responses to seasonal changes in food availability can be determined.

Methods

Daily range length

Daily range lengths of the target individuals are available from the Excel files detailing the routes travelled by each.

Diet

All food species eaten were noted during the periods of systematic data collection by myself and the BFP field assistants. I used observations recorded during both my focal samples and the BFP scan samples to compose a list of all the plant species and parts consumed during this 12-month period of data collection.

In order to determine which foods were important, I used the BFP scan data collected during my study period at five-minute intervals by the Project field assistants. Out of the total number of scans that recorded feeding activity per month, I calculated the proportion of time spent feeding on each species and each food type. The overall importance of a species to the diet was therefore measured in terms of time seen feeding.

Food availability

Phenology data – measuring the temporal patterns in availability of leaves, flowers and fruits of the forest trees – has been collected by the BFP since 1993. However, for the period from 2002 to the end of this study, data was not available due to staffing problems.

Thus, previous years' (1996-98) data were collated and averaged to give a general picture of food availability.

BFP staff collected phenology data on a monthly basis using ten transects within and around the Sonso region of the forest (five in compartment N15 and five in compartment N3). The transects were established in a stratified random manner (Plumptre *et al*, 1997). At 100m intervals along these 2km transects, all tree species were identified in circular plots of seven metre radius, and scores were assigned for the abundance of each phenophase (buds; young leaves; mature leaves; flowers and fruit – ripe, half ripe and unripe) to all trees over 10cm DBH (diameter at breast height). DBH was recorded at 1.3m above the ground. In total, up to 1520 trees were scored each month, covering 101 species. Phenophase-abundance scores are converted into a monthly index of food availability by summing the scores of each phenophase for each example of every tree species. The mean score for each species is calculated and multiplied by the average patch size - measured by the DBH (in cm). This is then presented as an index out of 100, where the highest food availability (maximum phenophase abundance scores) equals 100.

Descriptions of food availability patterns across the seasons were obtained from Fawcett's (2000) detailed study of the phenological patterns in chimpanzee food species.

Activity patterns

All data pertaining to activity time budgets were obtained from the focal sample data I collected. From the 50 focal samples, I selected out the days with eight hours or more of direct observation time of the focal animal, and used only these days to ascertain time budgets.

From this data set I calculated the average length of the daily range of the focal animals, the mean number of times an individual stopped to feed per day and the average time spent feeding, both as a total figure for the whole day, and per stop site. I also determined more general activity budgets, detailing the proportion of the day for which the targets were observed feeding, resting, socialising or travelling.

Analysis

All data were analysed using ArcView GIS 3.2 software, Excel 97 and SPSS version 10. Statistical tests, where used, were applied to independent groups and hypotheses were two-tailed with $\alpha=0.05$.

Daily range length

Using the Excel files of all the waypoints recorded along the travel routes of each target animal, I can apply Pythagoras' theorem to calculate the distance travelled between each waypoint, and then sum these distances to give the total length of travel per day.

Diet

Foods were identified that cumulatively contributed 50% of total feeding time, and those comprising up to 80% of the total feeding time across the year were also noted, by arranging them in order of contribution size, starting with the biggest, following Newton-Fisher (1999a). The major fruit species - those accounting for over 75% of time spent eating fruit, as according to Wrangham *et al* (1996) - were similarly calculated from the scan data.

Food availability

From the extensive list of tree species monitored by the BFP phenology samples, I selected out the ones identified as important food species for chimpanzees of the Sonso community, and present the average level of food available from these trees over the course of a year.

Activity patterns

When comparing activity budgets across seasons, I defined the seasons as according to the BFP weather data presented in chapter two. This shows that the year can be divided into four distinct seasons. The dry season was taken to occur between December and February, the first wet season from March to May, an inter-rains period occurred between June and August and the second wet season was observed from September to November. Some individuals appeared in more than one season comparison group and some did not. I chose to use independent measures as the majority of individuals could *not* be paired across the seasons in a repeated measures design. To avoid pseudo-replication, each individual should contribute only one data point per season, with multiple days from one individual in

one season being averaged. However, this would have resulted in some groups containing only one data point, rendering much of the desired statistical analysis impossible. Therefore, to allow analysis to proceed, I chose to include data points from each day for each individual as an independent point.

All social interactions - affiliative and aggressive - such as grooming, copulating and displaying, were grouped together in the broad state category of socialising so as to simplify the resulting time budget. I also used the focal sample time budget data to determine the likelihood with which each behavioural state would occur throughout the day.

In order to confirm whether feeding is concentrated on fruit in the morning and leaves in the afternoon, I used the BFP scan data set rather than the focal data set because it records the feeding behaviour of many more individuals. I calculated the proportion of feeding scans recording fruit verses leaves for each hour of daylight.

Results

Daily range length

In accordance with other east African chimpanzees, the average daily range lengths for males of the Sonso community were longer than those of females, as shown in table 4.1.

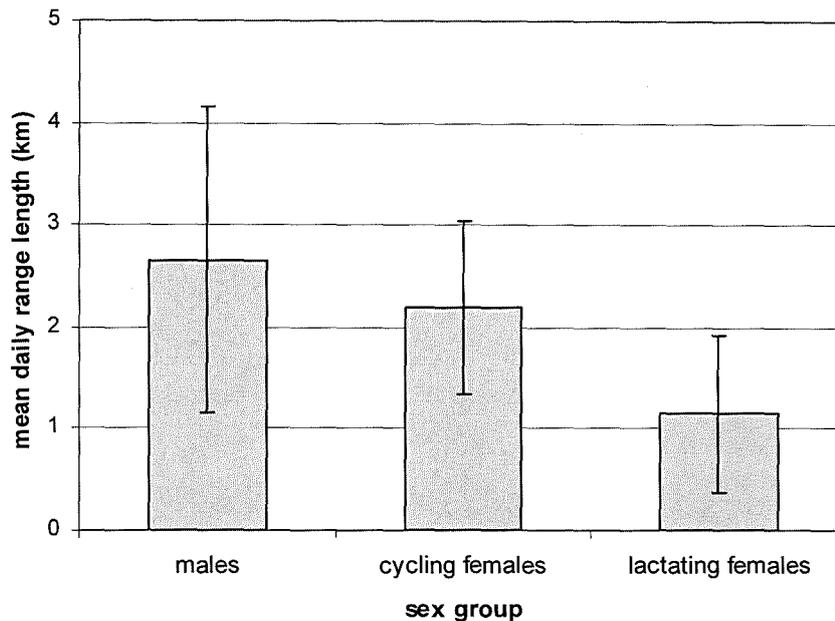
Table 4.1: Average daily range lengths of target animals

	Males	Cycling females	Lactating females
Mean (km)	2.65	2.19	1.15
SD (+/- km)	1.502	0.859	0.775
Median (km)	2.77	2.01	1.13
Minimum (km)	0.68	1.43	0.08
Maximum (km)	6.27	3.12	2.94

Lactating females travelled the least distance per day, but each sex group exhibits quite high standard deviations. The differences in daily range lengths across the sex groups are statistically significant when tested using a one-way, between-subjects ANOVA ($F=5.894$,

df=2,42, $p=0.006$), as illustrated in figure 4a. Tukeys HSD post hoc tests reveal the significant differences to lie between males and lactating females. The range lengths of cycling females appear to resemble those of males more than other females, but this difference is not significant presumably due to the small number of observations of cycling females.

Figure 4a: Mean daily range lengths and standard deviations of males, cycling females and lactating females



Sonso chimpanzee diet

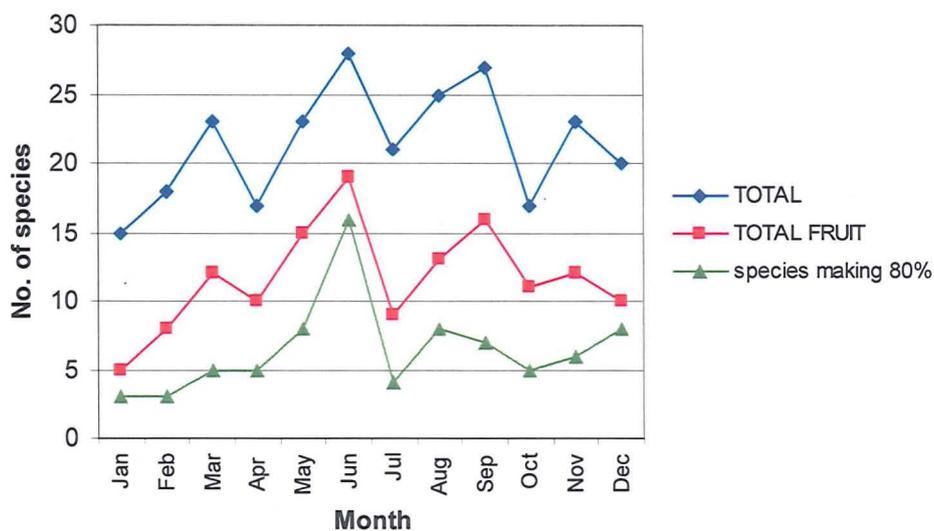
2319 hours of feeding behaviour were recorded by BFP field assistants between September 2002 and September 2003, equivalent to 27,828 five-minute scans. The Sonso community was observed to feed on 63 known plant species during this time (82 items), as listed in Appendix E. The chimpanzees were also seen to eat soil, termites, honeycomb and black and white colobus monkey; these rare items are not included in any subsequent analysis.

An average of 21 plant species were eaten per month, but only four different species were consumed per day on average. The mean number of fruit species eaten was 12 per month, but this varies from as few as five to as many as 18 different fruits in a month, as shown in figure 4b.

Figure 4b shows that the number of species eaten, the number of fruit species eaten, and the number of species comprising 80% of the diet, peaked in June - during the inter-rains

period when rainfall and temperatures are low. The number of species eaten was also high during the months of March, September and November, the start of the first and second wet seasons, and towards the end of the second wet season. The total number of fruit species eaten was also high at the start of the second wet season.

Figure 4b: Number of species contributing to the diet per month; showing the total number of species eaten, the total number of fruit species eaten, and the number of species that contribute to over 80% of the monthly food intake, measured as time spent feeding.



The number of species comprising 80% or more of the total time spent feeding – the “important” food species according to Newton-Fisher (1999a) – was substantially lower than the total number of species or total fruit species eaten. Only in June did the number of important species rise above 50% of the total number consumed: in all other months considerably fewer than half of the total number of species eaten could be thought of as important. The majority of species eaten per month contributed less than 20% to the total time spent feeding.

This observation is confirmed in table 4.2, taken from the data presented in Appendix E2. This shows the majority of feeding time across the whole year of observation was concentrated on only four species: 50% of the total feeding time was spent consuming just 6% of the total number of species eaten, with the alien species *Broussonetia papyrifera* as the biggest single contributor. The last 12 species listed in table 4.2 each contributed about 2% or less to the yearly food intake, with quite a jump in percentage contribution between the sixth most important food (*Ficus mucuso*) at 7.3% and the seventh (*Ficus natalensis*) at

2.1%. If important species are taken to be those that contribute to 80% of the feeding time, only ten species could be considered to be important across the year, confirming the findings of Newton-Fisher (1999a). Even when considering monthly totals, the only additional species that were important in certain months but did not register in the yearly totals were *Lannea welwitschii* and *Syzygium guinense*. Thus, at most, only 12 of the 63 species (19%) were eaten in any substantial quantity across the year. Indeed, only 18 species, or 29%, of the total number of food species eaten, accounted for over 90% of the diet across the year: many foods were eaten only in very small quantities.

Table 4.2: Percentage contribution (measured by time spent feeding) of species over the year long study period (September 2002-September 2003).

Species	% contribution to yearly food intake	Cumulative %
<i>Broussonnetia papyrifera</i>	17.7	17.7
<i>Ficus sur</i>	15.5	33.2
<i>Cordia millenii</i>	12.2	45.4
<i>Ficus exasperata</i>	11.7	57.1
<i>Cynometra alexandri</i>	8.6	65.7
<i>Ficus mucoso</i>	7.3	73.0
<i>Ficus natalensis</i>	2.1	75.1
<i>Mildbraediendron excelsum</i>	1.9	77.0
<i>Celtis mildbraedii</i>	1.7	78.7
<i>Millettia excelsa</i>	1.6	80.3
<i>Chrysophyllum albidum</i>	1.5	81.8
<i>Saccharum spp.</i>	1.5	83.3
<i>Celtis durandii</i>	1.4	84.7
<i>Celtis wightii</i>	1.4	86.1
<i>Ficus varifolia</i>	1.2	87.3
<i>Morus lacteal</i>	1.2	88.5
<i>Uvariopsis congensis</i>	1.1	89.6
<i>Desplatsia dewevrei</i>	0.9	90.5

Of the 18 species listed in table 4.2, only five were not associated with fruit at any point during the year. The Sonso community ate the seeds of *C. alexandri*, the leaves and flowers of *U. congensis*, the pith of *Saccharum* (sugar cane) and the leaves of *C. wightii*

and *C. mildbraedii*. Other leaves and flowers were also eaten from other species listed, but so were the fruits. Fruit accounted for 64% of the total yearly feeding time, as shown in table 4.3, with leaves being the next most important food type.

Table 4.3: Proportion of total monthly feeding time spent on each type of plant part over the study period

	Part of plant eaten						
	Fruit	Leaves	Seeds	Flowers	Rotten wood	Pith	Bark
Jan	0.457	0.024	0.408	0.111			
Feb	0.453	0.029	0.495	0.022	0.001		
Mar	0.901	0.059	0.024	0.006	0.023		
Apr	0.833	0.135			0.002	0.027	
May	0.569	0.357	0.025	0.013		0.036	
Jun	0.684	0.293	0.008	0.015			
Jul	0.733	0.264				0.003	0.001
Aug	0.710	0.252		0.018	0.017	0.004	0.005
Sep	0.505	0.292	0.005	0.178	0.003	0.016	0.002
Oct	0.285	0.336		0.357	0.021		
Nov	0.364	0.324		0.247	0.012	0.053	0.001
Dec	0.545	0.294	0.053	0.027	0.027	0.053	
Average	0.639	0.203	0.090	0.053	0.007	0.009	0.001

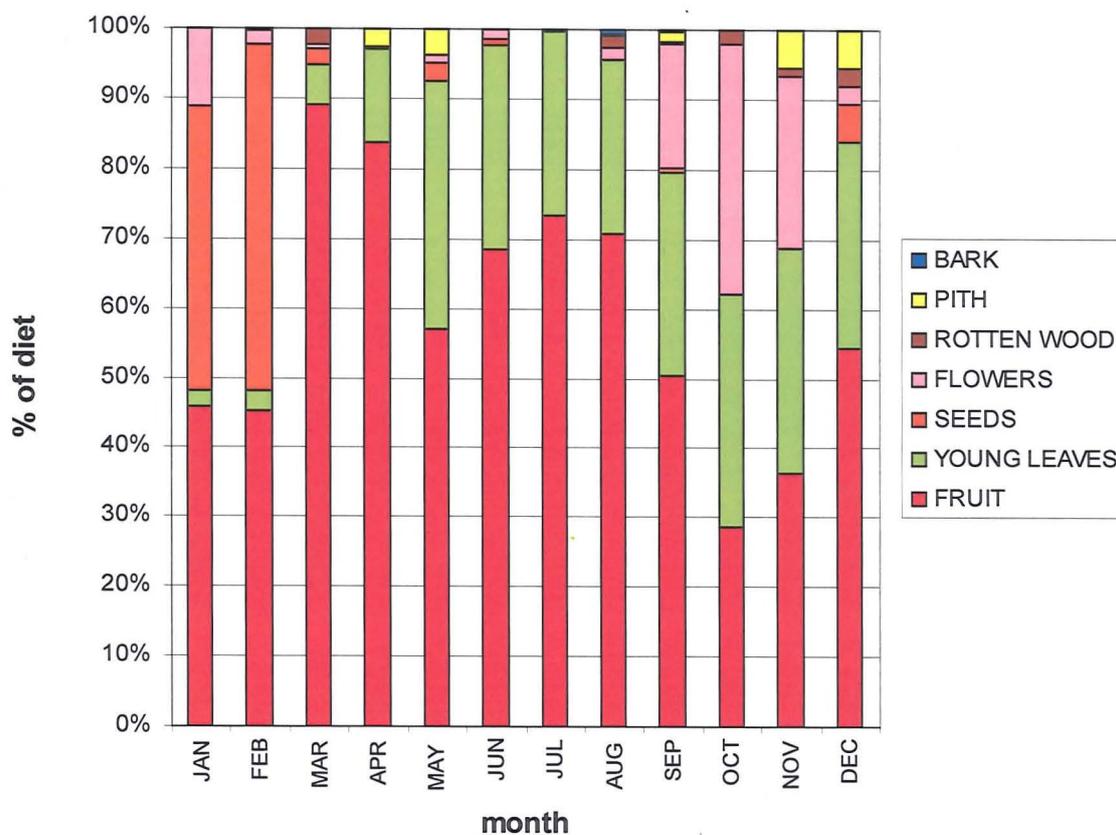
Figure 4c depicts the percentage of time spent feeding on different plant parts across the year. It is apparent from this and table 4.3 that fruit comprised over 50% of the diet in eight out of 12 months of the year, excluding January, February, October and November. In January and February a large proportion of time was spent feeding on the seeds of *C. alexandri*, and in October and November, young leaves and flowers of *B. papyrifera* were consumed. In March and April, over 80% of the time spent feeding was focused on fruits. In March this mostly comprised fruits of the fig *F. exasperata*, and in April, fruits of *F. exasperata*, *F. mucoso* and *F. sur* combined.

The fruit eaten was mostly ripe, with the exception of *F. exasperata*, where unripe fruits were preferred. *F. sur*, *C. mildbraedii* and *B. papyrifera* were eaten throughout the year, although the part of *B. papyrifera* eaten varied. *F. exasperata*, *F. mucoso* and *F. varifolia* were also eaten in 11 months, making *Ficus* the most important genera, with 38% of total

feeding time directed towards fig species. *Broussonetia*, the single most important species, is therefore the second biggest contributor to the diet when considering all the *Ficus* species together.

Terrestrial herb vegetation (*Afromomum* species and unidentified herbs) was eaten only rarely, as shown in appendix E2, and contributed to less than 1% of the total time spent feeding.

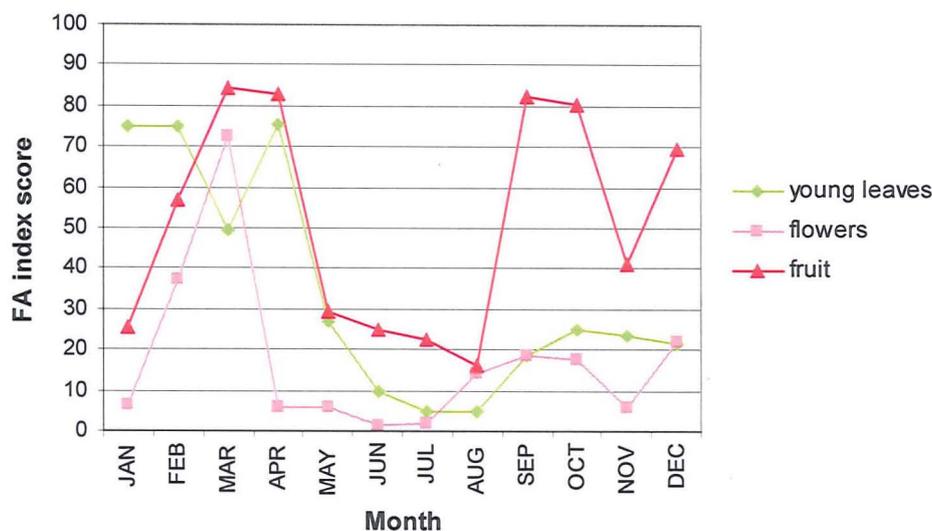
Figure 4c: Percentage of time spent feeding on different plant parts per month during the study period



Food availability

Figure 4d plots the average food availability scores for fruit, flower and young leaf availability per month taken from the BFP phenology data. Buds and mature leaves are also monitored by BFP, but I have not included them in these descriptions as they were not noted as being consumed by the Sonso community in any great quantity during this year of study.

Figure 4d: Food availability, showing the mean fruit, flower and young leaf availability index per month, from the years 1996-1998.



Fawcett (2000) made the following observations regarding the availability of chimpanzee foods in the Sonso area:

Young leaves – produced throughout the year, but with seasonal differences. There was a bimodal peak in abundance during the dry season and the first wet season, which reduced again during the inter-rains period.

Flowers – available in all months. Availability fell during the beginning of the first wet season and towards the end of the second wet season. Availability peaked in the middle of the second wet season.

Unripe fruit – available throughout the year. Availability peaked in the second wet season and continued into the dry season. Abundance fell in August, when ripe fruit was also not available. There were significant seasonal differences in the availability of unripe fruit.

Half-ripe fruit – available every month. Peak abundance also fell in the second wet season and continued into the dry season. Again, significant seasonal differences in half-ripe fruit availability were evident.

Ripe fruit – general period of high abundance at end of dry season/beginning of first wet season and also during second wet season. The number of species producing ripe fruit varied significantly with seasons, but there were not significant differences in the overall availability of ripe fruits.

In summary, the availability of fruit peaked at the beginning of the second wet season and the end of dry season/start of first wet season, as is evident in figure 4d. Fruit was at the lowest abundance during the inter-rains period. Figs were most abundant at the end of the dry season/start of the first wet season. During the inter-rains period, when fruit availability was generally low, *B. papyrifera* had young leaves available, and *C. millenii*, *F. sur* and *M. excelsum* all produced some fruit.

Fawcett (2000) concluded patterns of food availability were seasonal and strongly influenced by rainfall: all phenological states showed an increase in production coinciding with the onset of one of the wet seasons. The dry season had a major impact on food production, with flowers peaking in the middle and fruits at the end, with young leaves also increasing over time. The inter-rains period was associated with periods of reduced production across all phenophases, which is clearly evident in figure 4d.

Daily activity patterns and responses to seasonal fluctuations

During focal follows of eight hours or more, the average time per day spent feeding was 176 minutes. Target individuals made an average of five feeding stops per day, each with a mean duration of 40 minutes. There was no significant difference in the number of feeding stops made by males, cycling females or lactating females, as tested with a one-way ANOVA ($F=1.692$, $df=2,32$, ns). One-way ANOVAs of total time spent feeding per day and per stop did reveal significant differences between the sexes, however (total feeding time: $F=6.007$, $df=2,32$, $p=0.006$; average time per stop: $F=3.605$, $df=2,32$, $p=0.04$), with Bonferroni post hoc tests revealing lactating females feed for significantly longer than cycling females per day, and significantly longer than males per stop, as the boxplots in figure 4e and 4f illustrate.

Figure 4e: Box plot of mean total time spent feeding per day. Data from 5-95% range is shown.

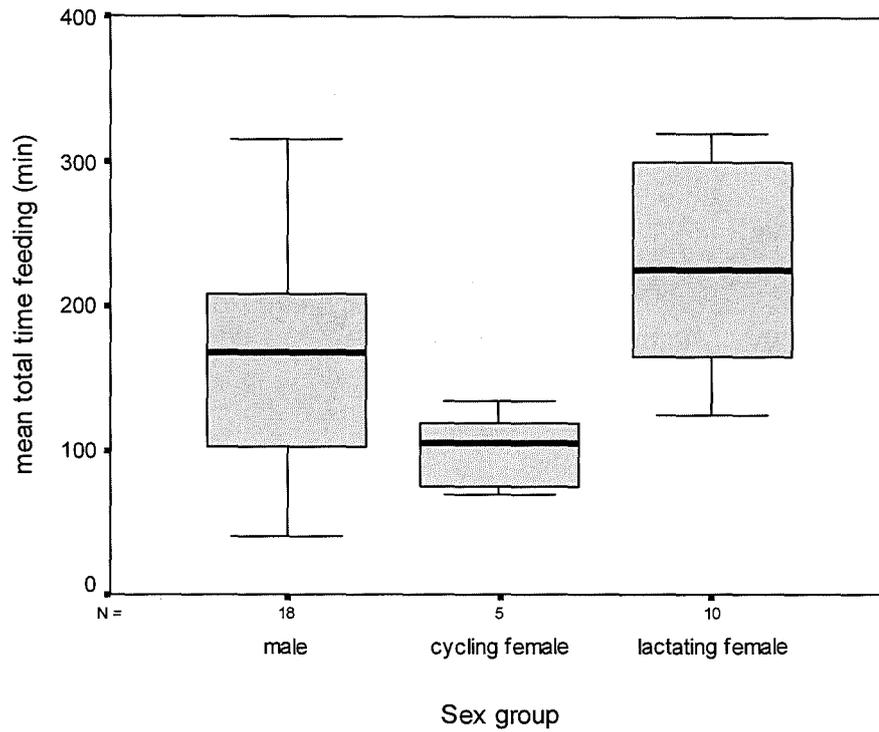


Figure 4f: Boxplot of mean total time spent feeding per day. Data from 5-95% range is shown

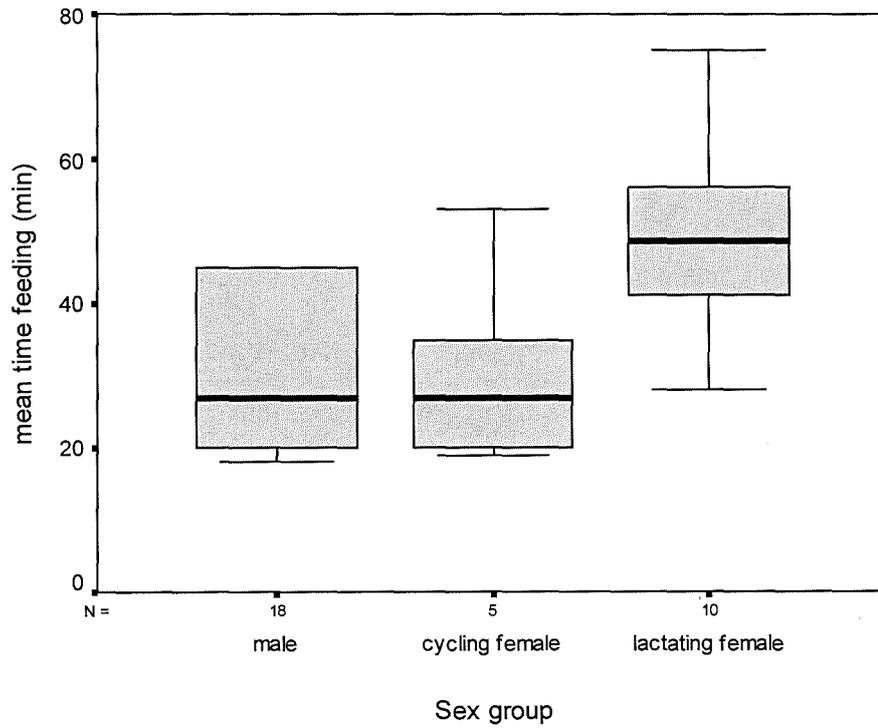
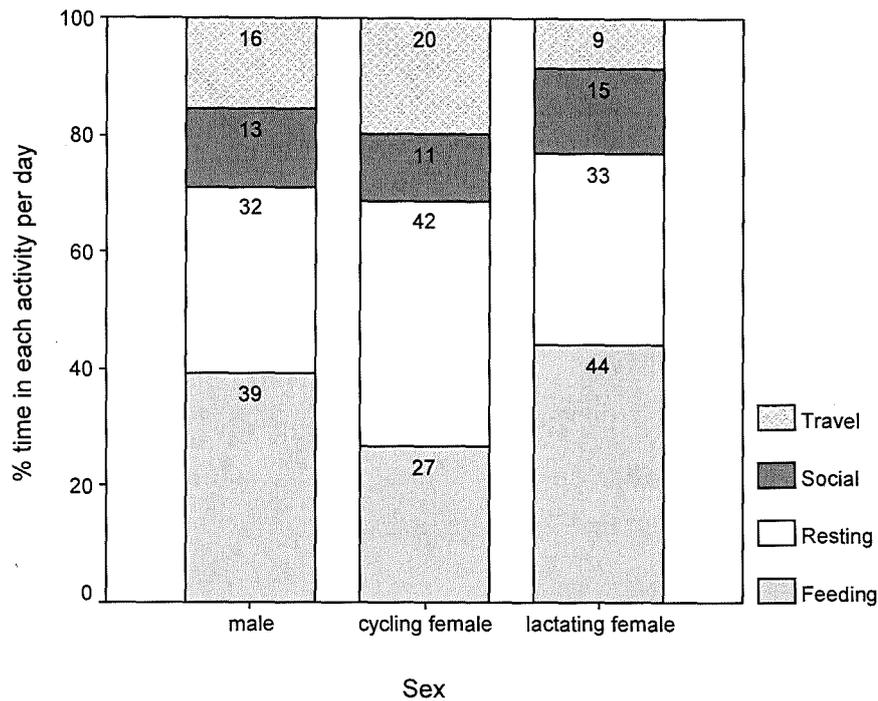


Figure 4g shows the mean percentages of the day (daylight hours from approximately 6.30am to 7.00pm) for which each sex class of individual was engaged in each activity.

Figure 4g: Percentage of the day engaged in each activity, as recorded from BFP scan data



Multivariate ANOVA between the three sex groups and four activity classes showed only one statistically significant effect: time spent travelling altered with sex group ($F=4.041$, $df=2,32$, $p=0.028$), with Bonferroni post hoc tests showing lactating females spend significantly less time travelling than cycling females. Lactating females are known to travel shorter distances per day. Time spent engaged in any of the other activity type did not vary significantly with sex class.

Sonso chimpanzees were observed feeding in all daylight hours, peaking at 4.30pm with slight declines in the late morning and early afternoon, and a small rise in the occurrence of feeding around midday, as illustrated in figure 4h. The diurnal pattern of feeding does not seem to be as pronounced in this data set as has been reported by others (Wrangham, 1977; Newton-Fisher, 1999a; Tweheyo and Obua, 2001).

Figure 4i shows the proportion of fruit and leaves consumed throughout the day. Fruit consumption peaked between 8am and 9am but declined into the middle of the afternoon, when leaf-eating reached its peak. Fruit eating increased again after 5pm.

Figure 4h: Percentage of focal samples exhibiting each activity category throughout daylight hours

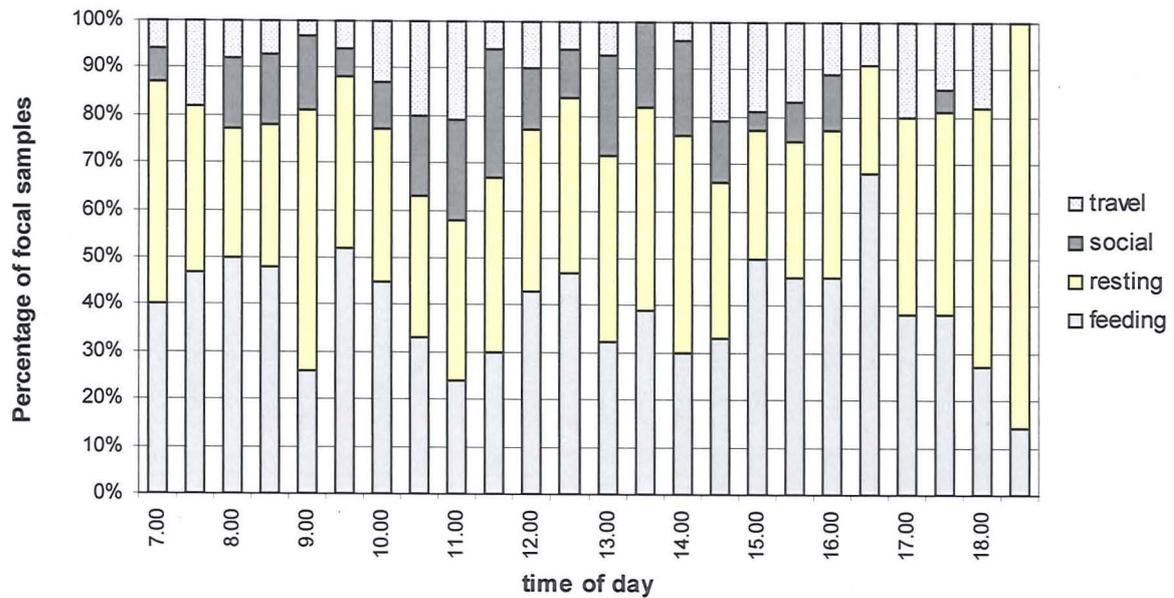
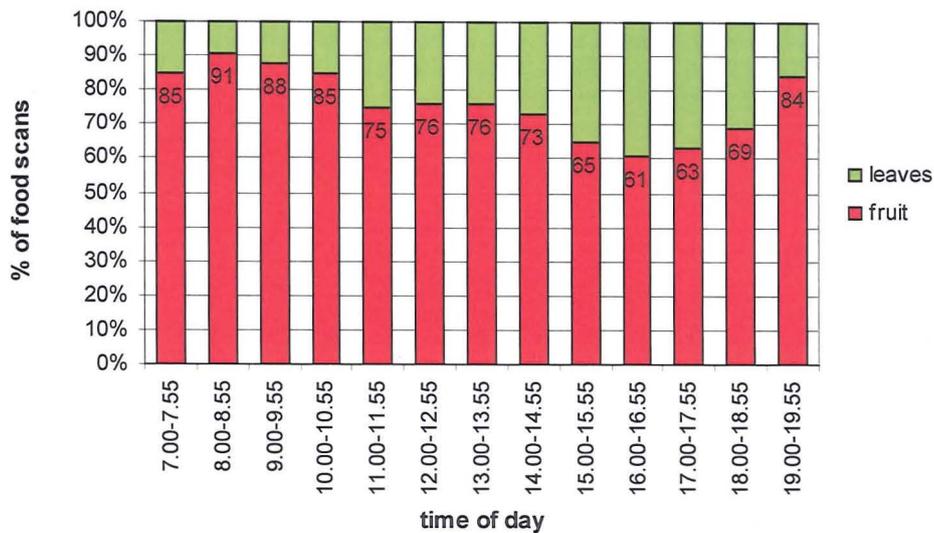


Figure 4i: Percentage of feeding scans devoted to fruit versus leaves throughout daylight hours



Seasonal trends

Food availability has been shown to vary with seasons, thus the four quarters of the year will be used to divide data into periods of differing food abundance.

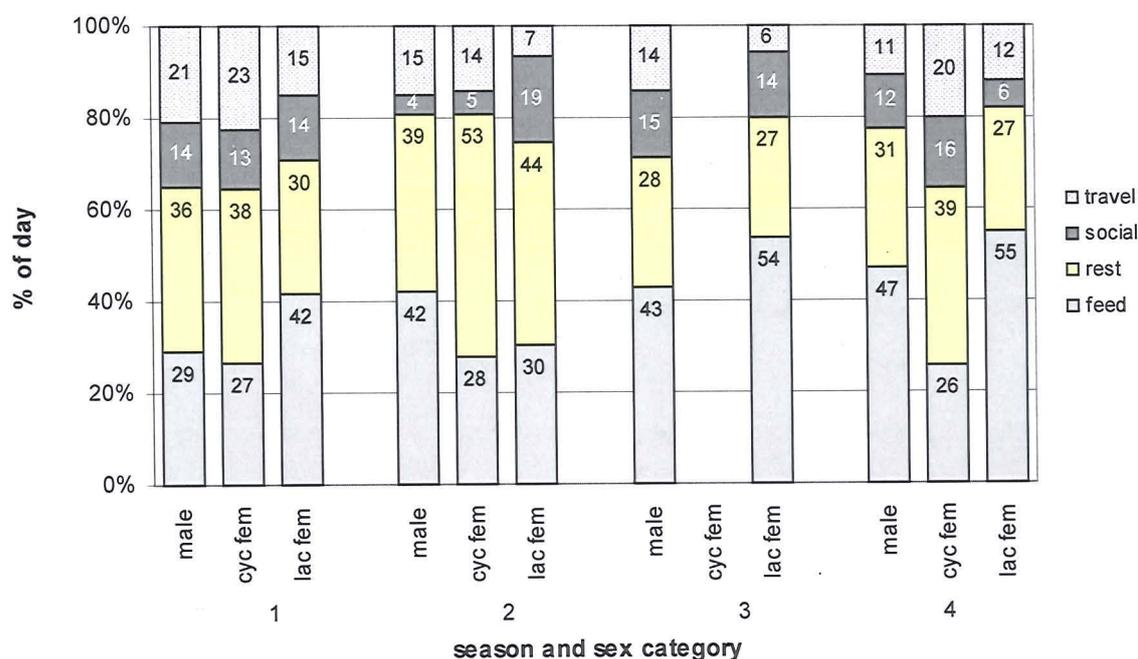
A 4*3 between-subjects ANOVA comparing the effect of season (dry; wet 1; intermediate; wet 2) on daily range length of the sex groups (male; cycling female; lactating female) did not reveal a significant main effect of season - and therefore food availability ($F=0.502$, $df=3,42$, ns), or a significant interaction between sex and season ($F=0.971$, $df=5,42$, ns).

Although daily range length has been shown to vary with sex category, seasonal changes in food availability do not appear to have any effect on the mean distance travelled.

I used a multivariate ANOVA to compare the mean number of food stops made per day, the total time spent feeding per day, and the average time spent feeding per stop across the four seasons. None of these variables changed predictably with the season (number of stops: $F=1.071$, $df=3,32$, ns; total feeding time: $F=2.184$, $df=3,32$, ns; average feeding time per stop: $F=1.918$, $df=3,32$, ns), so fluctuations in food availability do not affect the numbers or times of feeding stops.

Figure 4j deconstructs the mean activity time-budgets of each sex class shown in figure 4g by season. The time spent travelling and socialising was largely constant across each of the four seasons, and feeding time also did not vary in an obvious manner. Multivariate 3*4 ANOVA comparing the effects of sex class and season on activity budgets showed no main effect of sex or season on any of the behavioural categories (Sex: feeding: $F_{(2,32)}=1.958$, ns; resting: $F_{(2,32)}=0.778$, ns; socialising: $F_{(2,32)}=0.144$, ns; travelling: $F_{(2,32)}=1.573$, ns) (Season: feeding: $F_{(3,32)}=1.375$, ns; resting: $F_{(3,32)}=1.124$, ns; socialising: $F_{(3,32)}=0.461$, ns; travelling: $F_{(3,32)}=1.507$) and also no interaction between sex and season (feeding: $F_{(5,32)}=0.711$, ns; resting: $F_{(5,32)}=0.111$, ns; socialising: $F_{(5,32)}=0.796$; travelling: $F_{(5,32)}=0.270$). The loss of effect of sex on activity patterns is probably due to the low power of this analysis.

Figure 4j: Percentage of the day engaged in each behavioural category for each sex class across each season



Discussion

As described in chapter two, the Sonso region of Budongo is dominated by mixed forest, which includes a multitude of *Celtis mildbraedii*, *Chrysophyllum albidum* and *Ficus* tree species. It is evident that the Sonso community, even across its comparatively small territory, maintains a very diverse diet from the forest types it encompasses. Within this broad diet, however, only a few species can be considered important in terms of the time spent feeding on them.

The patterns in the diet observed during this study vary slightly from previously published data. For example, in 1995 (as reported by Newton-Fisher, 1999a) only three species comprised 50% of the diet and seven totalled 80% of the feeding time, as opposed to the four and ten species respectively in this study. During 1995, the diet was dominated by *Broussonetia papyrifera*, *Ficus sur*, *Ficus mucuso*, *Ficus exasperata*, *Celtis mildbraedii*, *Maesopsis eminii* and *Celtis durandii*. *M. eminii* did not even figure in the feeding lists for this study, and *C. durandii* was not one of the most important species. Such variations in the diet are to be expected as patterns of availability of food species change across years (Chapman *et al.*, 1999), with consumers taking the best of what is most abundant in any given year.

The recent planting and maturation of the sugar cane crop at the southern forest boundary may also have exerted an influence over diet composition in the last few years. Although sugar cane contributed only 1.5% to the total feeding time of the combined community data, it may be more significant to certain individuals; not every member of the community was seen to travel out of the forest into the crop plantation, reducing the average impact it had on the community. Chimpanzees are known to prefer foods with high sugar content (Reynolds *et al.*, 1998), and this crop certainly appeared to be highly favoured by the individuals who did feed on it. Its continued presence for the first nine months of this study may have negated the need to feed on alternative, previously important food sources.

The diet of the Sonso chimpanzees is composed of similar proportions of plant parts to that of the Kasekela community of Gombe (Wrangham, 1977), with fruit comprising over 60% of the total yearly intake, and leaves around 20%. Considerably less THV was eaten in Budongo than in the nearby Kibale forest (Wrangham *et al.*, 1996). Figs were eaten in large

proportions throughout the year in Budongo, with *Ficus* species contributing over 50% of total feeding time in March, April and July, and over 40% in January and December. Thus, figs can indeed be viewed as a staple food in Budongo, as Newton-Fisher (1999a) suggested.

The presence of a large number of *Ficus* species, and the introduced *B. papyrifera* seemed to reduce the potential impact of the relatively food scarce inter-rains period. *F. sur*, *F. mucoso*, *B. papyrifera* and *C. millenii* contributed much to the diet across this season, with *C. millenii* being a fall-back food. The phenology data confirmed the inter-rains period was indeed associated with reduced absolute levels of food availability, but this did not influence the daily range lengths or activity budgets in any predictable way. Lactating females consistently display the shortest daily range lengths, with cycling females behaving, as is expected, more like males, with longer daily path lengths, irrespective of season and food availability. As Reynolds (1992a) stated, the inter-rains period was the poorest for food production, but there was no month when fruit was not available. It must be noted that throughout the inter-rains period, when fruit production *is* greatly reduced compared to the rest of the year, fruit remained the largest component of the diet with over 50% of feeding time devoted to it. Indeed, the months when fruit consumption fell below 50% of the diet actually coincided with the periods of greatest fruit production, not the least, at the start of the second wet season.

The number of species contributing to the diet was highest in June, when food production is generally lowest, but the number of species eaten also peaked in March and September - months associated with the greatest food availability. Therefore the number of species eaten cannot necessarily be thought of as indicative of food stress. That more species must be eaten when tree productivity is lowest makes sense, but similarly, when lots of food is available, many species are sampled.

The significance to the Sonso community of the reduction in food availability in general, and fruit in particular, has to be questioned. The reduction did not require the chimpanzees to travel shorter distances and spend more time feeding or resting as has been observed at other study sites (Doran *et al*, 1997; Herbinger *et al*, 2001). Nor did it result in increased daily travel and reduced resting time, as predicted by the ecological constraints model

(Gillespie and Chapman, 2004): food availability evidently remained at a level that allowed the chimpanzees to maintain their “normal” daily activity patterns throughout the year.

The Sonso chimpanzees evidently remain able to find sufficient food in the inter-rains period, with relatively no impact on their daily behavioural patterns despite a 75% reduction in fruit availability compared with the periods of highest productivity. Thus the question remains: how do chimpanzees find their food? Do they utilise advanced cognitive abilities that serve to make the task “easier” for them, or are other strategies employed? I shall address these questions directly in part II.

Part 2

Travel behaviour of Sonso chimpanzees: How travel routes are organised

Chapter 5

The nature of travel segments

In order to determine how chimpanzee travel behaviour is organised, and to establish to what degree - if any - it is based on mental spatial representations, I intend to consider how chimpanzees move between valued resources. Breaking the travel route into a series of segments between important resources will allow me to consider what factors determine where a chimpanzee travels.

In Appendix F I used the behaviour of the chimpanzees' to define what resources are potentially valuable. Using time as a *post hoc* measure of the chimpanzee's appreciation of a resource, I assumed that resources at which the chimpanzee invests a large amount of time are valuable or important in some way (see White and Wrangham, 1988, for an introduction to this approach). Following the analysis of time spent at stop-site waypoints, as presented in Appendix F, I have defined stop-sites of 20-minutes or more as important to the chimpanzee: for the purpose of this thesis potentially valuable resources are those where the chimpanzee stopped for 20 minutes or more. Stops of less than 20 minutes were deemed not important and were ignored in the subsequent analyses of this chapter.

The analyses of this chapter start from the null assumption that all travel segments are independent of each other: that upon satiating the need (be it social, nutritional or physiological) met at one 20-minute stop-site, the period of travel to the next 20-minute stop-site is entirely separate and not related to what occurred previously. This assumption is unlikely to be characteristic of the true state of chimpanzee ranging; at least when foraging, as it pays to not return to a recently visited and exhausted food patch. It is, however, a useful starting point when attempting to determine *how* daily travel routes are constructed. Analyses in subsequent chapters will assess how valid this assumption of independence of travel segments is for chimpanzees, but within this chapter at least, all travel segments are treated as independent.

Having broken down the travel route into segments from one valuable resource to the next, we can ask what are the common features of these segments. Do the segments vary

systematically in any dimension with any particular social or ecological variables? I will consider three aspects of the travel segments in this chapter: length, speed and linearity. Thus, I will ask how far chimpanzees travel between valuable resources stops, how quickly they travel, and how straight (linear) are the paths, in order to begin to answer how they travel between resource sites.

Milton (2000) notes that many primates are reported to move directly to food sources over long distances using straight-line travel. The straightness of the travel segments is relevant because travel in very straight, direct lines between stop-sites could be a first indication that chimpanzees (a) know where they want to go, and (b) can determine how to head directly to it. That is, linearity could be a first indication that chimpanzees might have accurate spatial representations. The length of travel segments is cognitively relevant because chimpanzees may, if they have accurate spatial representations, travel further for certain types of resource than others. This is also true of speed: the desire to reach certain valuable resources may increase the speed of travel to some stop sites, if they are anticipated. Therefore, if chimpanzees do travel further or faster to particular resources, it might be an indication of knowledge and anticipation of expected rewards.

Of course, this chapter is only supposed to be a preliminary analysis and so any patterns observed will not be presumed to provide conclusive evidence for or against chimpanzee mental representations. Straight line travel between valuable resources could result from a default strategy of just walking forwards until a resource is located, rather than from any kind of mental map, and this possibility will be scrutinised further in subsequent chapters. Similarly, if no systematic differences are evident in the length or speed of approach to resources, it may or may not be because the chimpanzees do not know, represent or anticipate the expected reward at a given stop site, and this will also require further consideration in subsequent chapters.

The aim of this chapter then, is to determine how long, how fast and how straight travel segments are, and what factors influence these variables. This is only the first stage in answering the question of whether chimpanzees can remember the location of resources within their territory, and whether they use this information to plan travel routes.

Factors that influence travel

Much work has been published discussing what factors influence the overall length of animal, and specifically primate daily ranges (Chapman, 1990; Isbell, 1991; Janson and Goldsmith, 1995;). I will assess which of these factors also influence the length of individual travel segments, and which, if any, also influence the speed and linearity of travel segments. It is interesting to look at the effects such factors have on individual travel segments, as by elucidating the relationship between daily range and its constituent segments, we begin to close on more cognitive questions, as distinct from the traditional socio-ecological questions asked about range length.

The day journey length of chimpanzees, as well as that of other primate species, is known to vary with ecological variables, such as food availability (Chapman *et al*, 1994; Gillespie and Chapman, 2001; Janson and Goldsmith, 1995), and with social variables, such as sex (Goodall, 1986; Wrangham, 1977; Boesch, 2000) and party size (Chapman *et al*, 1995; Janson, 1988). Furthermore, it has been shown that the energetic costs of travel for an individual vary with life history variables, such as reproductive status (Hunt, 1989) and disability. Because these ecological, social and life history factors are known to influence the overall daily ranging behaviour of individuals, I predict that they will also have an effect on the travel segments comprising a days range.

Specifically, I predict that the length, speed and linearity of travel segments will vary with:

- season (food availability);
- sex;
- female reproductive status;
- male rank;
- disability status;
- party size;
- party type.

If chimpanzees do possess spatial representations, the activity at the stop-site could also affect the travel segment variables. Certain activities, namely resting, socialising and nesting, can theoretically be performed at any location in the forest, but the locality of feeding is obviously dictated by the position of feeding trees. Thus “fixed location”

activities such as feeding may affect travel segments differently than more moveable activities.

It is reasonable to assume that chimpanzees will spend longer at highly desirable resources compared with less desirable resources, and if they have knowledge of the location of such desirable resources they might move to them more directly. By extension, the most desirable food patches might result in very distinct travel segments. If chimpanzees do not have any knowledge of the location or value of various resources, however, none of these factors will influence travel segments. Thus I predict that segment length, travel speed and linearity may vary with:

- the time spent at the end stop site;
- the activity at the end stop site;
- the food species consumed;
- the value of the food patch.

Methods

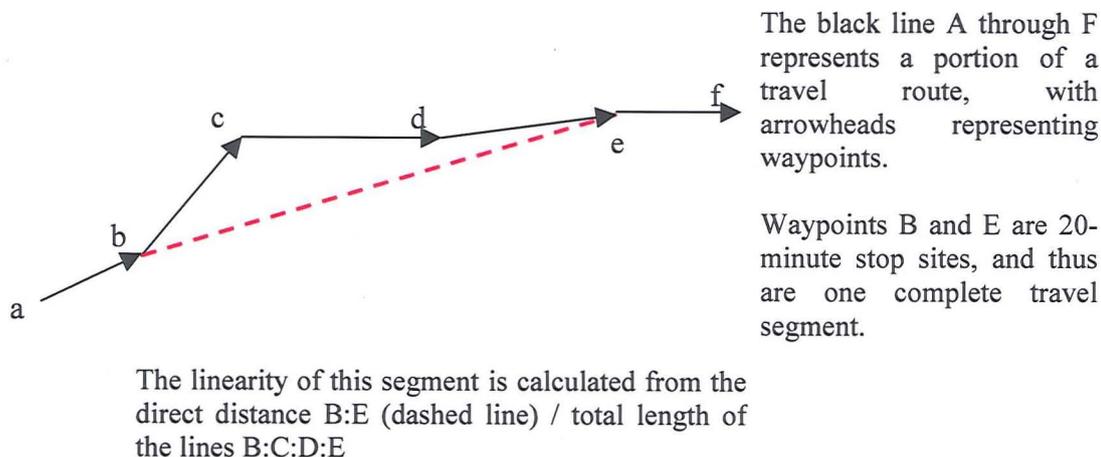
Data Handling

Travel route and behavioural data were collected as described in chapter 3. Using the route maps, waypoint co-ordinate lists and continuously recorded behavioural transcripts generated from the 50 focal samples, daily travel routes were each broken into segments by cleaving them at the 20-minute stop-sites; that is, each focal animal route was broken into sections of travel occurring between stops of 20 minutes or longer.

The co-ordinates detailing each segment were then entered into an Excel spreadsheet. Direct, “crow flies”, distance between the start and end points of the segment, and the actual distance moved by the focal animal (as described by the intervening waypoints), were calculated. A linearity score for the segment was then derived by dividing the direct distance by the actual segment length, as indicated in figure 5a. All pertinent social and ecological data about that segment were extracted from the scan data and continuous behavioural record, and entered into the appropriate column of the spreadsheet. Additional data such as rank or season were subsequently added, using the BFP supplementary data

records where necessary. Table 5.1 lists the data entered into this travel segment spreadsheet.

Figure 5a: Calculating the linearity value of a travel segment.



It is important to note that although there is a column in the spreadsheet (see table 5.1) entitled “travel time”, this does not necessarily mean that all the time was spent travelling; some of the time intervening between leaving one 20-minute stop-site and reaching the next could have included stationary periods of less than 20 minutes, i.e., stops that are not deemed valuable. Thus, the travel speed is an averaged figure that hides what proportion of the time between 20-minute stop-sites was spent actually travelling. It accurately reflects the time taken to get from one stop site to another, however, which is the variable that is important here.

Party size was recorded as the size of the party as it reached a 20-minute stop-site, counting all members that had travelled with the focal animal but not those with whom the focal fused at the 20-minute stop-site. All male parties are those where only adult or sub-adult males are present, with no adult or sub-adult females. All female parties are those with females and their dependent offspring only. Family parties are those where only members of one family are present, but when some members of the family are independent of the female. Mixed parties are those containing adult males and females from different families, but with no sexually receptive (swollen) females; sexual parties are mixed parties with sexually receptive females.

Table 5.1: Data entered into the travel segment spreadsheet, as extracted from the behavioural and scan records.

Data entered	Details
○ Focal sample reference number	
○ Focal animal identity	
○ Direct, crow flies length of segment (m)	
○ Actual distance moved by focal animal (m)	
○ Linearity of segment	
○ Travel time (minutes)	
○ Travel speed (km/hr)	
○ Season	1 (Dec-Feb), 2 (Mar-May), 3 (Jun-Aug), 4 (Sep-Nov)
○ Sex of focal	Male or Female
○ Rank of focal if male	High, Mid, Low (as defined by BFP field assistants)
○ Reproductive status of focal if female	Pregnant, Lactating or Cycling
○ Disability status	Disabled or able-bodied
○ Party size	
○ Party type	All male, All female, Mixed, Sexual or Family
○ Presence of alpha male, other high ranking males, any other males, pregnant females, lactating females, cycling females	
○ Time remained at end stop site (minutes)	
○ Activity at end stop site	Feeding, Resting, Socialising, Drinking, Nesting
○ Tree species/food item if feeding	
○ Patch value if feeding (chimp minutes)	
○ Vocalisations heard up to one hour before travel segment started	Time before travel was initiated Direction vocalisation was heard from
○ Did vocalisation heard match direction of subsequent travel?	

The ‘stop-site activity’ recorded in the spreadsheet was defined as the modal activity recorded on the scan data sheets across all members of the party for the duration of the stop. Hence, if, for a party of five adults remaining at the stop for approximately one hour (four scan periods), seven resting scans, eight feeding scans, one nesting scan and four grooming scans were recorded, the activity would be recorded as feeding. When two or more activities were observed equally often at a 20-minute stop-site, precedence was always given to feeding as I viewed this as the most significant activity: resting and/or grooming can occur anywhere, but feeding has to occur at a particular location.

The 'patch value' of a given food patch, as defined by White and Wrangham (1988), is measured in units of "chimp minutes", i.e. the number of chimpanzees N feeding for X minutes, giving NX chimp minutes. I counted the number of scans that indicated feeding and multiplied this by 15 to determine the total number of minutes spent feeding; only scans where the full 15-minute period before the scan was spent at the stop-site were counted, so to reduce overestimation and maintain accuracy. As per the information recorded on the scan sheets, all adults and sub-adults present who were feeding contributed to the patch value estimate, but juveniles did not. Thus, if anything, the patch value is an underestimation for parties where juveniles were present. As juveniles were not recorded on the scan sheets, this underestimation is unavoidable because I cannot reliably determine for how long each juvenile was feeding.

I only recorded vocalisations heard up to one hour before the party left a site and initiated a travel segment. It is possible that chimpanzees could remember the direction of vocalisations made further back in time than this, but Goodall (1986) states chimpanzees respond quickly to distant pant hoots and Mitani and Nishida (1993) therefore classed behaviour up to one minute after hearing a call as a response – one hour is therefore very generous! I attempted to estimate the direction of all vocalisations that I (and therefore also the chimpanzees, presumably) heard (Kojima (1990) in Mitani and Nishida, 1993, state hearing capabilities of chimpanzees and humans are similar at 1kHz), on an eight-point compass. The subsequent travel direction of the focal animal was recorded as 'matching' in the spreadsheet if the eventual 20-minute stop site fell within ± 45 degrees of the original vocalisation. For example, if a vocalisation was recorded as being heard from the north east, and the 20-minute stop site of the focal animal was anywhere from due north to due east of its starting location (when the vocalisations were heard), it would be recorded as matching the direction. I felt this wide degree of overlap was necessary as it was not possible to reliably test the accuracy of my direction estimation.

Data Analysis

All analyses of segment length, speed and linearity were performed using Microsoft Excel and SPSS, version 10. Data are presented as boxplots, showing inter-quartiles and 5%-95% of data. All data were analysed with parametric statistics unless otherwise stated, and the hypotheses tested are all two tailed with $\alpha=0.05$. The statistical tests applied to the data

were for independent groups: independent samples t-tests and between subjects multivariate ANOVA. I had to use independent groups statistics as the majority of individuals were different, so within-subjects tests would have been inappropriate. Although some focal individuals appear in two or more conditions in some of these tests, many factors (such as season, party size or activity etc.) associated with the two travel segments of the one individual varied. Thus, it would have been impossible to arrange paired or matched-samples tests that were equivalent in all respects aside from the independent variable being considered in that test.

As stated in the introduction to this chapter, I am assuming that all the segments analysed are independent of each other, even though this may not be entirely true in reality. The inclusion of each travel segment as a separate data point, as recorded from the 50 travel routes of 14 focal individuals, may be seen as conflating the n value, but I believe this is acceptable in the initial stages of this analysis. Each individual on each day's follow was subject to different conditions and environmental pressures, and therefore may have responded differently with its travel behaviour. It would be unwise to assume that within each day's ranging the individual segments are dependent, i.e. that they are strictly repeated measurements of the same subject under the same conditions, when factors such as the party size and composition, proximity to food sources and the subsequent activity following a period of travel do not remain constant throughout the day. To group data by any one factor would result in the loss of information relating to other potentially important variables. Thus, travel segments will be treated independently in this chapter in order to identify which factors are relevant to travel behaviour, and then amended accordingly in subsequent chapters. I am aware that treating all segments as separate data points can lead to type I errors (Martin and Bateson, 1995) (falsely rejecting a null hypothesis), and I will consider this when interpreting the results obtained.

Results

A total of 360 travel segments, each of which ended with the focal chimpanzee stopping for 20-minutes or more, were generated from the 50 focal sample travel routes. I shall consider the ecological, individual, social and physical factors that influenced the length, speed and straightness of these travel segments in turn.

As detailed in table 5.2, the mean distance travelled by the focal chimpanzees between 20-minute stop sites was 329m. The mean travel speed of focal chimpanzees across the 356 travel segments where speed could be calculated was 1.9km/hr. The mean linearity figure for all 360 travel segments was 0.946 with an average direct, “crow flies” distance between 20-minute stop sites of 301m. That is, the ratio of the direct, crow flies distance to the actual distance was on average 0.946; overall, the actual path taken by the chimpanzees was only 5.4% longer than the direct, ‘crow flies’ path.

Table 5.2: Descriptive analysis of measures recorded from the travel segments

Descriptive	Travel segment measure			
	Length (m)	Speed (km/hr)	Linearity	Linearity
N	360	356	360	344
Mean	329.4	1.92	0.946	0.943
Standard error of mean	18.1	0.08	0.006	0.006
Median	210.1	1.52	0.994	0.993
Mode	63.3	2.47	1.000	1.000
Standard deviation	343.1	1.57	0.113	0.115
Variance	117740.0	2.48	0.013	0.013
Minimum	22.4	0.19	0.058	0.059
Maximum	2205.9	14.27	1.000	1.000
Percentiles: 25	96.4	1.01	0.946	0.942
50	210.1	1.52	0.994	0.993
75	449.0	2.33	1.000	1.000

The average travel time of these segments was 15 minutes. Thus, approximately two waypoints were recorded between each 20-minute stop site, from leaving one 20-minute stop before reaching the next, based on waypoints being recorded every five minutes. 146 of the 360 travel segments had a linearity value of 1.000 – meaning that no waypoints were recorded between leaving one 20-minute stop site and reaching the next. 130 of these travel segments had a travel time of less than 5 minutes, so no intervening waypoints *could* have been recorded and the linearity is therefore not artificially high for these segments compared with the other segments recorded; the focal animal did move directly from one site to the next in under five minutes. The remaining 16 segments were recorded over time spans of 7 to 96 minutes, when no waypoints were recorded due to problems with maintaining a GPS signal. These greater periods of lapsed time between leaving one 20-

minute stop-site and reaching the next mean I cannot be entirely sure that the actual distance travelled truly did match the direct distance so closely. Given that the average linearity was very high for all the other segments, there is no particular reason to believe that these 16 segments might have significantly lower values, but because I cannot be sure of the true straightness of these segments, I have decided to exclude them from the linearity analysis. This then leaves 344 travel segments included in the linearity analysis, as described in table 5.2. The mean linearity of the 344 segments (0.943) is only marginally different from the value for all 360 segments (0.946). Distance, speed and linearity data were available for 340 travel segments in total, on which the following analyses were based.

The actual lengths of travel segments varied from a minimum of 22m to a maximum of 2206m, with almost 75% of the travel segments being over 100m long. None of the distances recorded were less than 20 metres – so all were longer than my visibility estimates suggest it is possible to see in the forest (see Appendix A). 19 of the travel segments were over 1km long. The speed of travel of the segments varied from 0.2km/hr to 14.3km/hr. The majority of travel speeds fell under 2km/hr and only 12 segments displayed speeds of greater than 5km/hr.

The linearity values range from a minimum of 0.058 to a maximum of 1.00 but, as evidenced by the average values and the percentiles, very few of the 344 travel segments had linearity below that of 0.50 (translating to an actual distance twice as long as the direct distance). In fact, only 8% (26 cases) of the travel segments recorded had linearity values below 0.80. The lowest linearity value of 0.058 arose when the focal animal (DN) moved approximately 85m away from the stop site to meet a party of vocalising males, who then all subsequently returned to feed in the same area where DN had started. Of the remaining 25 segments with linearity below 0.80, three were associated with detours around the sawmill clearing, where the direct line would have meant cutting across the school area, past the inhabited buildings. A further 13 cases were due to the focal individual moving to another location but stopping there only briefly - for less than the 20-minute period used here to define an important resource - before then moving on the end point of the segment. If these cases are viewed as ‘exceptions that prove the rule’, this leaves only nine cases out of 344 where the low linearity cannot be explained, but which seem to be, quite simply, inefficient routes.

This initial consideration of these travel segments strongly implies that chimpanzees generally walked for several hundred metres or more between 20-minute stop sites, in very straight lines, at a fairly slow pace of under 2km/hr. I will now investigate the effect of environmental, individual and social variables on the length, speed and linearity of travel segments.

External cues to travel

In order to draw conclusions about the mental representations of space employed by chimpanzees, it is necessary to first identify any external cues that may have directed their travel behaviour.

Olfactory cues

Comparison of the distance, speed and linearity of approach to “smelly” versus non-smelly foods¹ suggest that olfactory signals had no influence on foraging behaviour as measured here. Multivariate ANOVA of the effects of olfactory cues (smelly vs. non-smelly) on travel distance, speed and linearity was not significant ($F_{(1, 241)} = 0.306$; ns; Wilks $\lambda = 0.996$).

Visual cues

Visual cues have been all but eliminated, by not recording as separate waypoints any sites that were closer than the maximum visibility distance in the forest.

Auditory cues

Only 139 (40%) of the 344 travel segments included in the analysis were preceded by audible vocalisations up to one hour before travel commenced. Thus 60% of the travel segments were *not* preceded by vocalisations. Segments not preceded by vocalisations showed a mean linearity of 0.95, a mean distance of 315m, and mean travel speed of 2.1km/hr compared to a mean linearity value of 0.93, mean distance of 365m and mean speed of 1.8km/hr for travel that was prefaced by vocalisations. I applied multivariate ANOVA to compare the effect of hearing vocalisations prior to commencing travel or not

¹ Characterisation of foods as smelly or non-smelly was based on subjective assessment by me of what foods had a distinct smell.

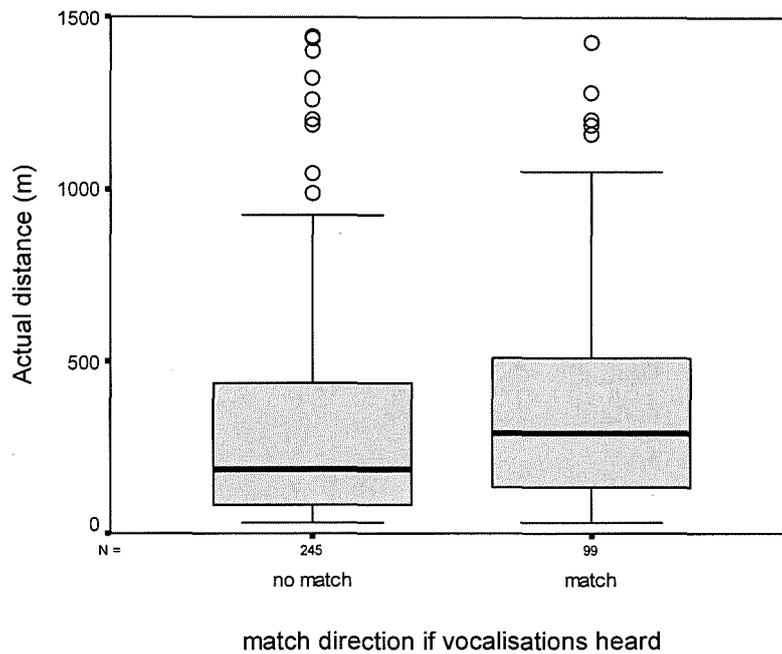
on the three travel variables. No multivariate difference was found on the three travel variables between the hearing-vocalisation and not-hearing-vocalisation conditions ($F_{(1,338)} = 1.750$; ns; Wilks $\lambda = 0.985$).

Whilst overall it seems that vocalisations did not affect the subsequent travel segment, it is possible this lack of difference is due to my lumping different reactions of the receiver upon hearing the call into the same condition. Some vocalisations might have induced the receiver (i.e. the focal animal) to follow them, while others did not. I do not have data on the types of vocalisation made, or the identity, precise location and activity of the caller, so I cannot attempt to determine what makes some vocalisations potentially interesting to the receiver. It is possible, however, for me to consider the response of the focal animal. 99 of the 139 travel segments preceded by vocalisations (28.8% of total travel segments) were heard from a direction matching the eventual direction of travel. Thus, there are 99 cases where the focal animal might have followed the direction of the vocalisation, using it as a cue to where to move.

I applied multivariate ANOVA to compare hearing vocalisations from the subsequent direction of travel with travel that did not match any vocalisations heard. Again there was not a significant multivariate difference between the linearity, distance and travel speed means across these two conditions, ($F_{(1, 338)}=2.037$; ns; Wilks $\lambda=0.982$), but univariate ANOVA revealed a significant difference between the distance travelled when the segment matched the direction of a vocalisation to when it did not ($F_{(1, 338)}= 4.955$; $p=0.027$), as shown in figure 5b. There was no difference in the straightness or speed of chimpanzee travel when the individual was potentially following a vocalisation or not, but this did influence the distance travelled.

When considering the 73 longest travel segments, however (all those over 500m long), only 33 segments were preceded by vocalisations, and in only 25 of these cases did the subsequent direction of travel match the direction of the vocalisation. Although vocalisations can influence the length of the travel segment, auditory cues are not vital for long, straight travel segments. Thus, I will proceed with all further analyses assuming that external cues were not necessary to direct the period of travel.

Figure 5b: Boxplot of length of travel segment when travel was preceded by vocalisations in the same direction and when it was not. Showing 5%-95% range of data and outliers.

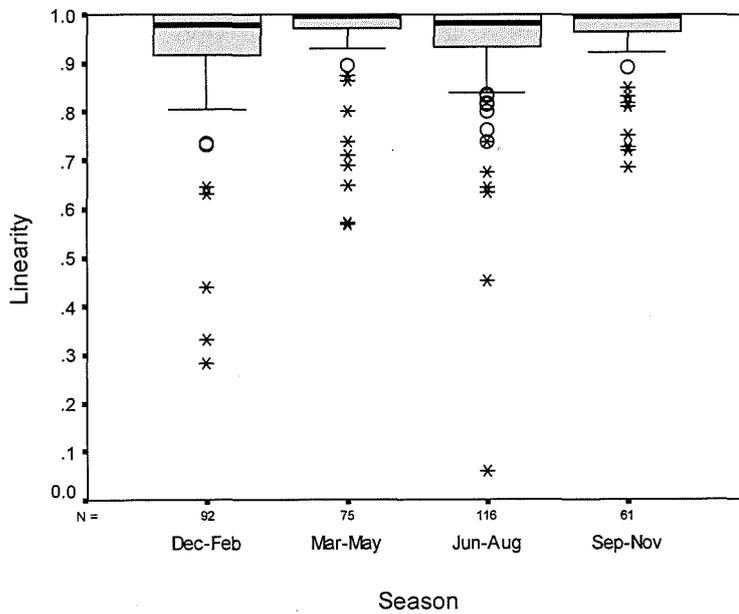
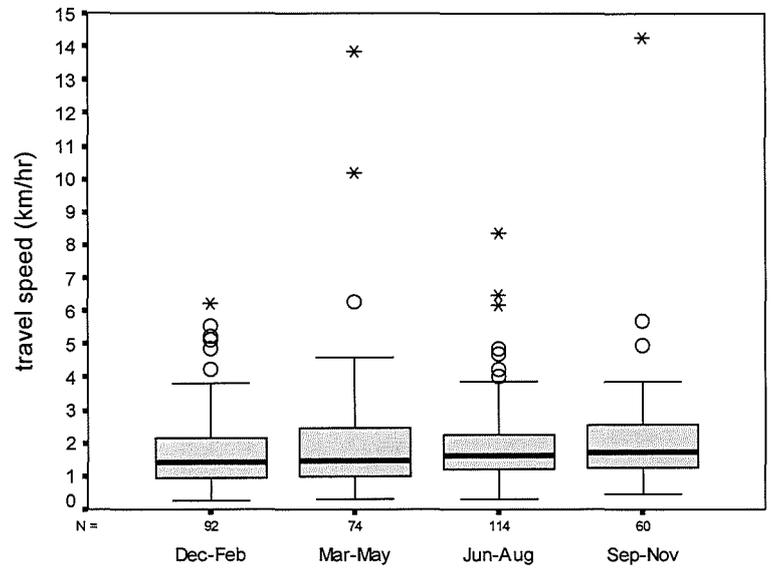
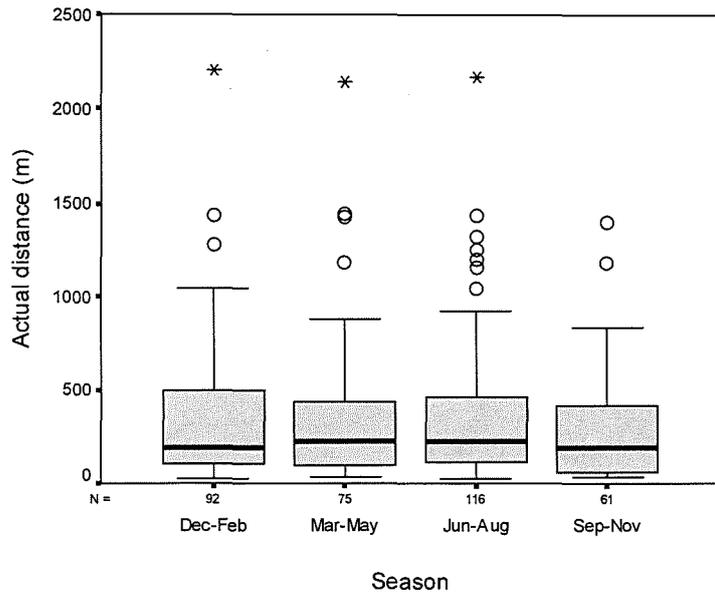


Ecological factors

Seasonality approximates to food availability and so might be expected to exert an influence on travel variables. As shown in chapter 4, desirable foods were most abundant in season 2 (wet), with season 3 (inter-rains period) being the least productive.

To assess whether changes in food availability affected the length, speed or linearity of travel segments, I compared the travel variables of all individuals across the seasons. As shown below in figure 5c, I considered the differences in travel variables across seasons for all individuals together, then also across seasons for males and females separately. Travel variables were compared between the 4 seasons with a multivariate ANOVA. There was no multivariate difference in travel variables across the four seasons ($F_{(3, 336)}=0.927$; ns; Wilks $\lambda=0.975$); the length, speed and straightness of travel segments did not alter across the seasons.

Figure 5c: Boxplot of the differences in travel variables across the seasons.



There is no significant variation across seasons in the travel variables of males ($F_{(3, 220)}=0.782$; ns; Wilks $\lambda=0.979$) or lactating females ($F_{(3, 76)}=1.363$; ns; Wilks $\lambda=0.852$). When considering high-ranked males separately from other males, there was still no significant multivariate effect of season (high-ranked males: $F_{(3, 110)}=0.451$; ns; Wilks $\lambda=0.963$; other males: $F_{(2, 82)}=1.099$; ns; Wilks $\lambda=0.922$). It was necessary to group both mid and low ranking males together in this test, as data for low ranking males was not available across all the seasons.

Thus, it is evident that seasonality, and by extension food availability, did not influence the length, travel speed or straightness of travel segments: chimpanzees travelled in the same highly linear fashion between 20-minute stop sites irrespective of the season and, therefore, amount of food available. Differences in season can thus be ignored in subsequent analyses.

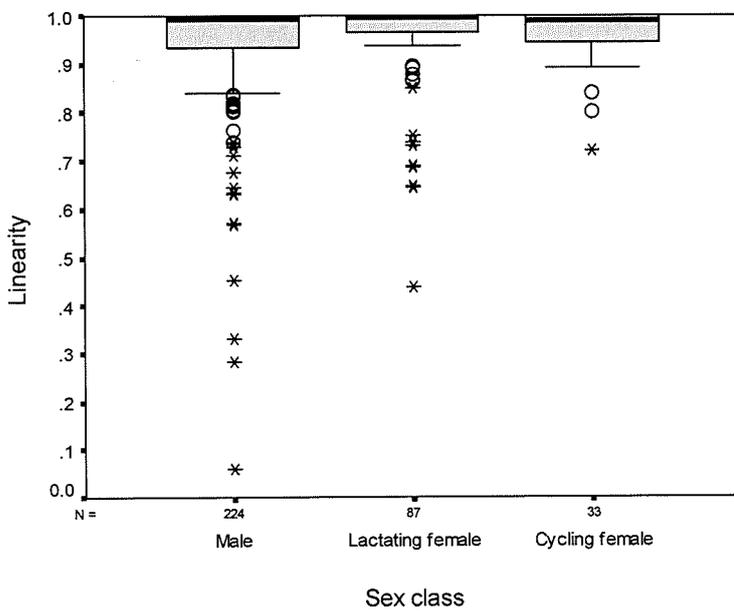
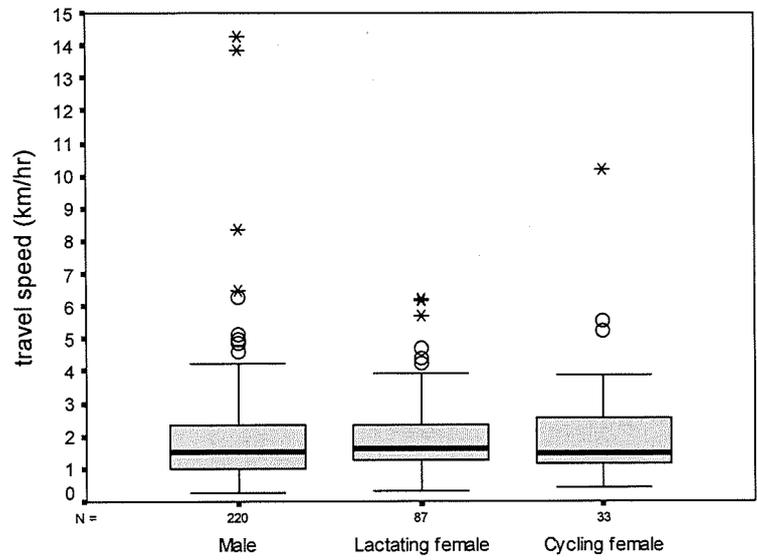
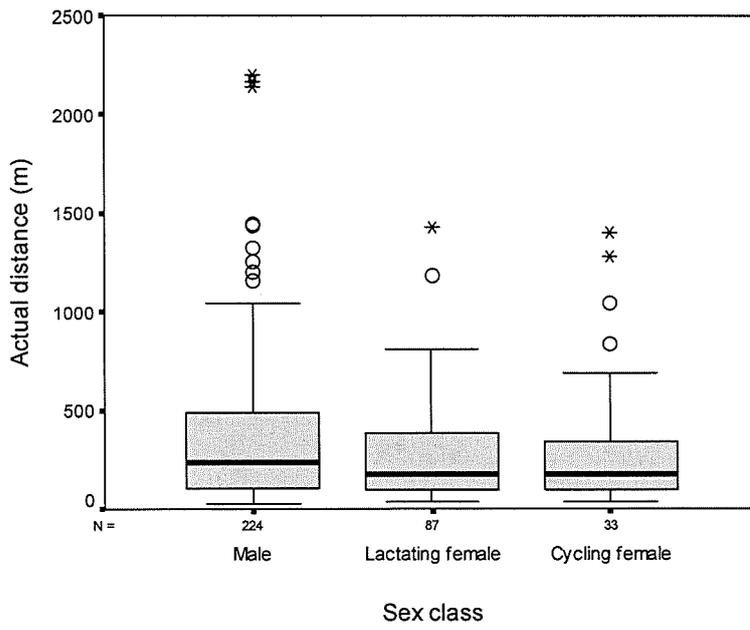
Individual differences in travel segments

The length, speed and linearity of travel segments were compared across sexes, female reproductive status, male dominance rank, and disability status to determine how individual differences influence travel behaviour.

Effect of sex class on travel

Figure 5d illustrates the differences of travel variables between the sex classes; males, lactating and pregnant females, and cycling females. Figure 5e suggests there was a trend for males to travel further than lactating females within an individual travel segment. I used multivariate ANOVA of sex group (3 levels: male; cycling female; lactating and pregnant female) to test this. There was no significant difference between the sex classes on any travel variables ($F_{(2, 337)}=0.875$; ns; Wilks $\lambda=0.985$). Both sexes walked in equally straight lines at similar speeds for similar lengths between 20-minute stop sites.

Figure 5d: Travel segment variables of males, cycling females and other females.



Effect of female reproductive status on travel

To investigate the effects of female reproductive status on travel, I compared the distance, speed and linearity of travel segments of pregnant, lactating and cycling females. Multivariate ANOVA showed reproductive status (pregnant; lactating; cycling) had no effect on the travel variables ($F_{(2, 117)}=0.496$; ns Wilks $\lambda=0.975$). It is evident that females walked travel segments of similar length, at similar speeds, with the same high degree of linearity irrespective of their reproductive status.

Effect of male rank on travel

To investigate the possibility that males of different rank travelled with different characteristics, I compared males of high, mid and low ranks on the distances travelled, speed of travel and linearity of segments using multivariate ANOVA. No significant differences in the travel variables across males of different ranks were evident ($F_{(2, 217)}=0.628$; ns; Wilks $\lambda=0.983$).

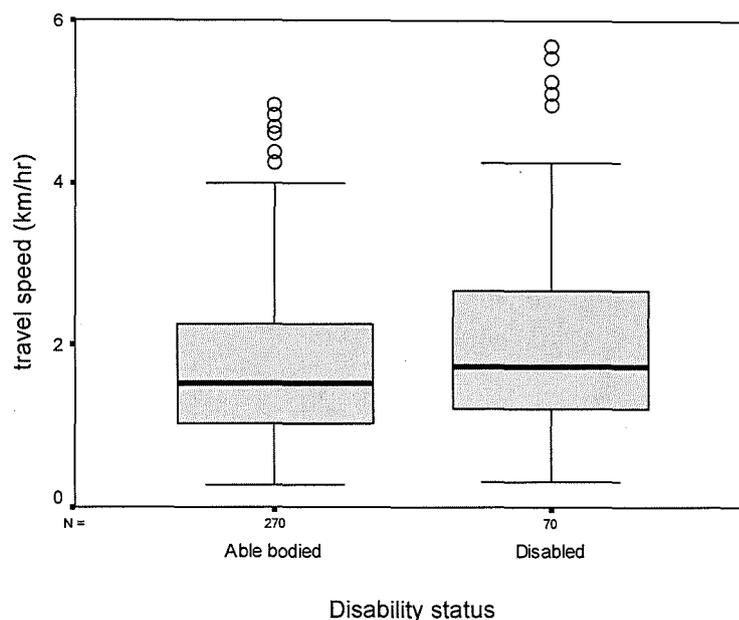
Effects of disability on travel

The effects of a severe, permanent disability on the travel segments were considered using multivariate ANOVA (factors: able bodied verses disabled). There was a significant multivariate difference between the two groups ($F_{(1, 338)}=2.742$; $p=0.043$; Wilks $\lambda=0.976$). An independent samples t-test shows this difference was between the travel speed of able-bodied and disabled individuals ($t=-2.411$; $df=338$; $p=0.016$). As shown in figure 5e, the disabled individuals travelled significantly faster than the able-bodied chimpanzees.

TK, a disabled individual, was the individual who displayed the fastest travel segment of 14km/hr. KL, BN and TK, three of the four disabled individuals sampled in this study, appear 12 times between them in the list of the 30 fastest travel segments. These three disabled individuals produced 40% of the 30 fastest travel segments, although they contributed only 65 segments in total. Thus, 3 out of 4 disabled individuals travel unusually rapidly.

Although disability does appear to be in some way related to travel speed, generally speaking life histories do not seem critically important to travel segments; sex, rank and reproductive status do not dictate how chimpanzees travel between 20-minute stop sites.

Figure 5e: Travel speeds of disabled and able-bodied individuals

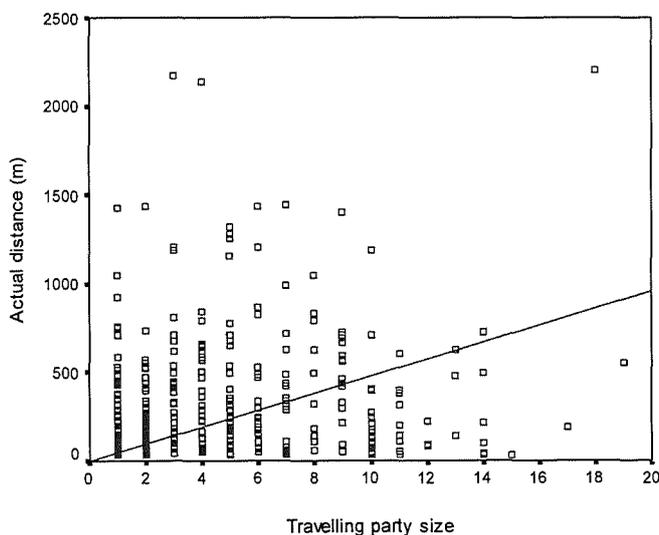


Social factors

Effects of party size on travel

It is generally considered that when in larger parties, individuals will have to travel further to find suitable resources than when in smaller parties (Chapman *et al.*, 1995, Janson, 1988). The effects of party size on the travel variables were analysed with Pearson's product moment correlations. There was a significant weak positive correlation between travelling party size and segment length ($r=0.11$; $n=344$; $p=0.047$) as shown in figure 5f, but no significant correlations between party size and travel speed or linearity (travel speed: $r=0.095$; $n=336$; ns; linearity: $r=-0.03$; $n=336$; ns). All segments were of very high linearity and similar travel speed, irrespective of the associated party size, but party size was weakly correlated with distance travelled.

Figure 5f: Mean travel segment length occurring with different party sizes.



Effects of party type on travel

To investigate the possibility that different party types travelled with different characteristics, I compared male, female, mixed, sexual and family parties on the distances travelled, speed of travel and linearity of segments using multivariate ANOVA. Party type had no effect on the travel segments ($F_{(4, 333)}=0.870$; ns; Wilks $\lambda=0.969$).

Physical factors*Effects of time spent at the stop-site*

Chi-squared tests comparing the time spent at the end stop-site with the linearity ($\chi^2=6.209$; $df=6$; ns), speed of travel ($\chi^2=3.058$; $df=6$; ns) and length of the travel segment ($\chi^2=5.362$; $df=6$; ns) all suggest that the time spent at the stop site is not related to the travel towards it.

Effects of activity on travel segment

If chimpanzees are constantly travelling towards known locations suitable for feeding, drinking, resting and so on, one might expect an effect of the activity at the end on the characteristics of their travel segments. I used multivariate ANOVA to analyse the effect of stop-site activity (five factors: feeding, resting, socialising, drinking and nesting) on the travel behaviour. There was no significant effect of the activity of the focal animal at the stop site on the travel variables ($F_{(4, 334)}=0.989$; ns; Wilks $\lambda=0.965$).

Effects of feeding on travel

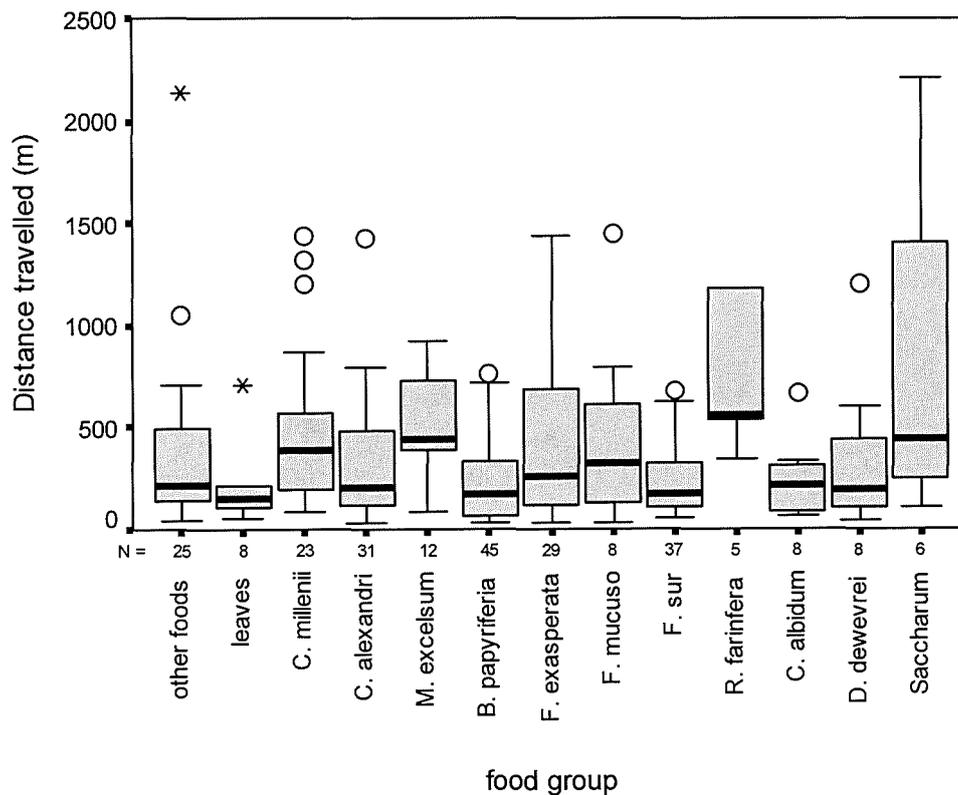
It is important to consider the segments that end in feeding behaviour more closely, as feeding is presented here as the primary motivation behind travel behaviour, and 256 of the 360 travel segments recorded ended with the focal animal and/or its party primarily engaging in feeding behaviour at the stop site. As I have shown in chapter 4, the Sonso chimpanzees eat a large variety of different food species and some of these are seemingly more desirable and/or readily available than others.

In order to assess the influence of different food types on travel behaviour, I used multivariate analysis of food type (13 food categories). Foods that appear only rarely in the travel segment matrix (less than five times) and thus are not often associated with 20-

minute stops have been grouped as “other foods”². Leaves that are available and may be consumed for more than six months of the year, but which are also rare ($n < 5$) in the travel segment matrix because, again, they are not often associated with 20-minute stop sites, have been grouped as “leaves”³. All other food items have been analysed separately as important species; they are all eaten for more than six months of the year and/or appear frequently in the travel segment matrix (more than five times each).

There was a multivariate difference in travel behaviour between the food groups ($F_{(12, 228)} = 1.91$; $p = 0.001$; Wilks $\lambda = 0.749$) and univariate ANOVA showed length of segment was the variable that altered with food type ($F_{(12, 228)} = 3.345$; $p < 0.001$). Tukeys *post hoc* tests showed the significant differences lay between *B. papyrifera* (BPY) and *Saccharum*; *C. alexandri* (CYA) and *Saccharum*; *F. sur* (FSU) and *Saccharum*; and *B. papyrifera* (BPY) and *R. farinifera* (RF), as shown in figure 5g.

Figure 5g: Distance travelled to different food types



² “Other foods” are: LW, MMF, Pawpaw, ALP, SM, ANT, FN, MEX, MOL, MYH, TRA, SZG, BD, ALD, STD, AFM, Climbers, and black and white colobus monkey meat.

³ “Leaves” food group consists of UC, TRR, FVR, CMI AND CZE.

Effect of patch value on travel

Finally, it is necessary to consider if the patch value has any influence on the travel variables. If chimpanzees not only know the locations of particular food sources, but are also able to predict what sort of reward is associated with each location, associations between the patch value, as measured in chimp-minutes, and any of the travel variables might be expected. There is no significant association between linearity and patch value ($\chi^2=8.795$; $df=9$; ns). Similarly, there is no significant association between travel speed and patch value ($\chi^2=4.151$; $df=9$; ns) or segment length and subsequent patch value ($\chi^2=9.303$; $df=9$; ns).

Summary

The findings can be summarised as displayed in table 5.3.

Discussion

When ranging most Sonso chimpanzees travel at speeds of usually below 2km/hr. They cover distances of between 20 and 2000 metres between potentially valuable resources, travelling in very straight lines. Thus, chimpanzee travel segments between resources are fairly slow but very straight and of variable length.

Travel is not dependent on external cues. Olfactory and visual cues were discounted, and vocalisations seem to exert an influence on only one dimension of travel segments: they increase the length of travel segments, but not the speed of travel or the straightness of the path. However, only 40% of all travel segments recorded were preceded by vocalisations and only 29% matched the direction of the vocalisations. Moreover, 55% of the longest travel segments (over 500m) were not preceded by vocalisations. Thus, the influence of vocalisations is evidently limited, even on the distance parameter. Since all segments were highly linear, equally fast and several hundred metres long, chimpanzees clearly do not *rely* on the external cues of hearing vocalisations in order to walk in straight lines between distant sites.

Table 5.3: Summary of the findings of travel segment analysis

Variable	Travel segment measure			
	Distance	Speed	Linearity	
<i>Ecological</i>	Season	No effect	No effect	No effect
<i>External cues</i>	Olfactory cues	No effect	No effect	No effect
	Vocalisations	Travel further if match direction of vocalisations (trend)	No effect	No effect
<i>Individual differences</i>	Sex	No effect	No effect	No effect
	Female reproduction	No effect	No effect	No effect
	Male rank	No effect	No effect	No effect
	Disability	No effect	Disabled go faster	No effect
<i>Social</i>	Party size	Larger parties travel further	No effect	No effect
	Party type	No effect	No effect	No effect
<i>Activity</i>	Time at end	No effect	No effect	No effect
	Activity at end	No effect	No effect	No effect
	Food species eaten	Longer travel to Saccharum and RF	No effect	No effect
	Patch value	No effect	No effect	No effect

There is a possibility that chimpanzees may attend to other external cues, such as hornbill vocalisations. Hornbills are frugivorous birds that eat the same foods as chimpanzees in certain seasons. However, the chimpanzee travel variables were consistent throughout the seasons, whereas hornbills are only seasonal feeders in the forest. If the chimpanzees were dependent on hornbills to locate food patches, differences in travel when hornbills are and are not present would be expected. This is not evident, however, suggesting hornbill vocalisations are not significant to the chimpanzees.

Season, as a measure of food availability, does not have any influence on the length of travel segments. Chimpanzees seemingly do not have to travel further between resources when food is scarce. This mirrors the observation in chapter 4 that daily range lengths do not vary systematically across the seasons. Changes in food availability do not affect how far the Sonso chimpanzees walk between resources.

Linearity is almost uniformly high, with all individuals travelling in extremely straight lines between stop-sites throughout the year. Travel speed only varies systematically with disability of the focal animal. Travel is likely to be more energetically costly for disabled individuals, and as such, they record faster travel speeds as they cannot afford to “dawdle” on the way to a resource as other individuals can.

Travel segment length does vary with party size, with larger parties on average travelling further. This supports the well-documented arguments that larger parties need to travel further to find adequate resources in order to limit within group competition. However, the theories state that *overall* day length is longer with larger parties, as the individuals have to go to *more patches* overall to get enough food (Janson and Goldsmith, 1995). A high quality patch will be depleted quicker if the group is large so it will have to move on to find something else sooner than if a smaller party was feeding there (Chapman, 1990). In contrast, I have shown here that the length to *any one patch* is longer in larger parties; longer travel between resources, as opposed to travel to more resources may be responsible for the longer range lengths of large parties of chimpanzees.

The distance travelled does not vary significantly with the activity at the stop site but some food types are associated with significantly longer travel distances. This could suggest use of spatial knowledge of food locations to plan travel, but this is not necessarily the case. The food types that were associated with longer average travel distances were those that are only found in very distinct areas of the forest, enticingly suggesting that the animals headed toward them knowing where they were and what reward they could expect there. But until it can be shown that the chimpanzee passed by other, alternative foods, on the route to these food sources, ignoring other items in favour of *Saccharum* or *R. farinifera*, the argument that this pattern did not arise from any cognitive abilities cannot be ruled out: The animals may have simply been on trajectories where this was consistently the first available food source.

The lack of association between the distance or speed travelled and the subsequent value of food patches suggests that individuals may not anticipate where they are heading. Accurate prediction of resource value is very difficult, however, as the influence of (unknown) competitors must be accounted for. Therefore, this lack of association does not necessarily mean the chimpanzees do not have any knowledge as to the *location* of resources.

The ability to walk in long, straight lines between resources does appear impressive, but it is important to remember that this result alone does not require or provide evidence for spatial representations in chimpanzees. Chimpanzees could produce such straight lines entirely by simple heuristics such as “walk in straight line until reach some kind of food or there is a need to stop and rest”.

If that is a strategy - walk in a straight line until hit food or need to rest - then some kind of pattern in the spacing of rest stops might be expected. Maybe rest stops only occur if the animal has already had to travel a fairly long distance without food. Resting does not occur after especially long distances, though, and in fact chimpanzees do travel further to reach food than they do to rest, although not significantly so. This could suggest that heuristics are not being used, and the linear travel segments instead arise from the use of a mental representation of the location of resources in the environment. Only further investigation of these 50 travel routes and 360 travel segments can conclusively distinguish between these possibilities though.

Chapter 6

Are travel segments independent?

In chapter five I treated each segment of travel between salient resources conservatively, as independent of all others, and showed that chimpanzees almost invariably move in straight lines between these salient resources. It remains uncertain, however, whether chimpanzees are in fact only able to consider one resource at a time, or if they can compute routes that take account of multiple resources. I will now examine travel paths more closely to determine if each inter-resource segment is independent from those preceding and/or subsequent to it.

In this chapter I am asking whether the decisions of where to travel next are in any way related to what has occurred previously in the chimpanzee's day, or if each travel segment is isolated in the needs it satisfies. Ranging has to satisfy a number of needs, and 'resources' can be anything from food patches to social interactions. The decision processes directing choices of whether to eat or socialise, rest or patrol borders are not of central relevance here. My primary focus is *how* chimpanzees move from one resource to the next; the "why" question of travel is another study in itself. As such, I will not explore any relationship between consecutive activities at the salient stop sites but instead will investigate patterns in the movement between these resources. I will consider if there is any evidence that chimpanzees plan travel routes more than one step in advance, or alternatively whether the conservative assumption of independent segments of travel was correct.

Anderson (1983) argues, following comprehensive computer modelling, that animals do not need to consider resources more than one step ahead. He showed that the strategy of always moving to the next closest resource was as successful as looking ahead a number of steps, in terms of procuring food whilst minimising energetic costs. As discussed in chapter one, this implies that animals may not *need* to plan routes far ahead, and that the computationally undemanding strategy of one-step-at-a-time works well, as is evident in many primate species (Garber, 1988; 1989; Garber and Hannon, 1993; Hemmi and Menzel, 1995; Janson, 1998; C. Menzel, 1996; 1997).

It is known, however, that for some species, foraging segments are not independent but are contingent on previous foraging sequences. For example, the distance bumble bees (*Bombus impatiens*) travel to the next flower depends on the sequence of the previous flowers visited (Dukas and Real 1993). This does not imply that bumble bees “plan” routes but instead illustrates that previous activities and expenditure can, as might be expected, influence future travel behaviour as well as dictating behavioural decisions at stop sites.

I will explore this question of independence of travel segments by looking at the distribution of angles turned between segments. If, as predicted by Anderson’s travelling salesman model (1983), chimpanzees do “think” just one step ahead without considering resources further away in time and space, there should not be any particular pattern in the distribution of angles turned between 20-minute resource stops. A “random” (i.e. circular normal) distribution of inter-segment angles would be observed in this case. Any departure from the normal distribution of angles implies consecutive travel segments are not independent. The null hypothesis of this chapter predicts a random circular distribution of inter-segment angles.

It is possible that, although no sex differences were observed in the linearity of travel segments between males and females, the sexes may have different overall ranging patterns. Males and females do appear to display different travel segment lengths and are argued to have different needs and priorities (Wrangham 1979), therefore I will consider the possibility of sex as well as status differences in the displayed distributions of inter-segment angles. I predict that the distribution of angles turned between resources may vary with:

- Sex
- Reproductive status in females
- Rank in males
- Party composition.

Although chapter five did not illustrate any effect of food availability - as measured by seasonality - on linearity, speed or distance travelled between valuable resources, there may be an effect on the overall strategy of foraging that was not evident when considering one

segment at a time. Therefore, I also aim to consider if the distribution of angles turned through between segments varies as a function of the season.

It is conceivable that different activities will also be associated with different distributions of angles. If foraging is organised in forward direction, it should follow that angles turned towards food resources will collect around 0° . Similarly, it might be expected that angles turned to resting stop sites would occur whilst *en route* to a resource such as food. As such, angles associated with resting stops should also be clumped in the forward direction. Conversely, nesting and social segments may not show the same distribution as feeding and resting. Chimpanzees move from the last resource site of the day to the nearest suitable nesting tree. This will not necessarily be in the same trajectory as the previous segments, and so a more random distribution might be observed. Similarly, social segments may not stick to the same line as feeding and resting stops as, for example, vocalisations produced by individuals in other locations may re-direct the animal to another area, again producing a more random distribution of inter-segment angles. Thus, I also aim to assess whether different 20-minute stop-site activities are associated with different angle distributions.

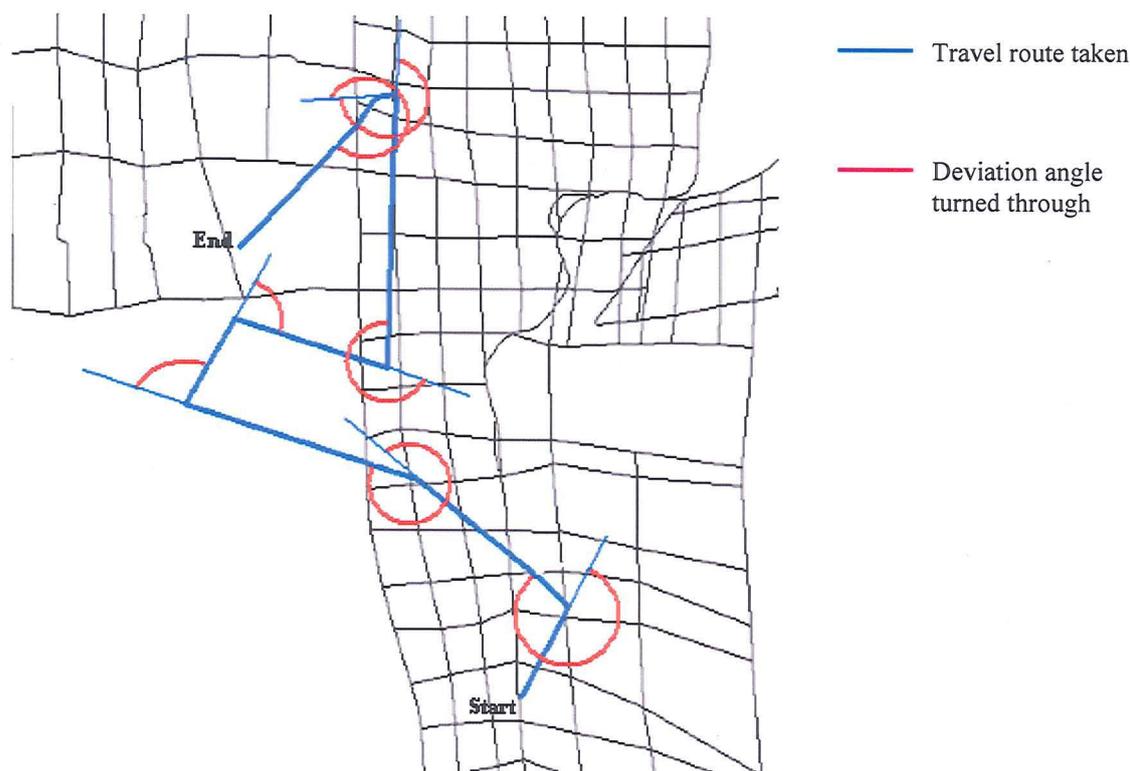
Using the distribution of angles between successive segments is potentially sensitive not only to highly linear day journeys, but also circular routes or “there-and-back” travel, whereby animals return to a previously used resource within one sample period.

Methods

Data handling

The angles turned between each adjacent pair of consecutive travel segments from the 50 focal routes were calculated using ArcView version 6.3. All angles were recorded as the clockwise deviation between the initial course taken and the subsequent path, as illustrated in figure 6a, which shows travel segments recorded between the salient stop sites visited by BK in August 2003. I recorded all angles turned through in a clockwise direction as this potentially provides a full 360° distribution, meaning no further transformations of the angles were required before the circular statistics could be applied.

Figure 6a: Determining angles turned between segments.



Analysis

All the hypotheses considered were two-tailed and tested at the $\alpha=0.05$ significance level. All analyses were carried out using Oriana version 2, available from Kovach computing services. This programme calculated the circular statistics (as described below) that were applied to the angle data. Circular statistics are used to analyse angle and orientation data (Batschelet (1981)). I will briefly describe some of the salient terms and tests that vary from the corresponding linear statistics. Comprehensive descriptions of all of these measures can be found in Batschelet's book.

Centre of mass: If all the angles of a sample are represented as vectors, each vector (data point) has a point mass at its tip. The centre of mass is the point through which all the lines connecting each point mass pass.

Mean vector: Arithmetic means are not suitable for angular data so average directions are calculated using vector algebra or trigonometric functions. The mean vector is the vector that points to the centre of mass of the sample and can be thought of as a weighted mean of all the vectors of the sample.

Mean vector length (r): r = the length of the mean vector, which is calculated from the co-ordinates of the centre of mass of the sample. It is a measure of concentration, showing to what extent angles are clustered about the mean. The closer the r -value is to 1, the more concentrated the points are on the circle. This measure of concentration is influenced by sample size.

Mean angle (μ): The measure of the mean direction of the sample, in degrees, is derived from the tangent of rectangular co-ordinates of the mean vector. The mean angle is most useful as a descriptive statistic if the sample is concentrated, i.e. clumped around the mean.

Median angle: The mid-angle of the data set, whereby half the data points lie on one side of the median line and half on the other side. Median angles are useful if data points are not clustered around the mean angle.

Circular variance (s^2): A measure of dispersion, illustrating what size arc the angles are spread over. Angular Variance = $2(1-r)$.

Circular standard deviation or Mean angular deviation: Another measure of dispersion, measured in degrees. The angular deviation is equal to: $[180^{\circ}/\pi] * [2(1-r)]^{1/2}$.

Confidence interval of the mean: This provides a measure of confidence in the mean angle by showing the range of values that the mean *could* fall between, as dictated by the confidence coefficient, set here at 95%. Thus, as shown in figures 6b to 6i, the confidence intervals represent the range of values between which the mean falls with 95% certainty. The wider the confidence interval, the less sure we can be that the direction of the mean vector has not arisen through chance fluctuations. Confidence intervals are useful for testing mean angles against a known parameter.

Two statistical tests were applied to the inter-segment angle data of the chimpanzee travel routes. The first, the V-test, tests for a directed distribution in the sample as opposed to randomness or uniformity. The second, the Mardia-Watson-Wheeler (M-W-W) test, is a non-parametric test that is the circular equivalent of the Mann-Whitney statistic used for linear variables, which tests whether two or more independent samples are different.

The V-test, as described in Batschelet (1981), tests whether the observed angles are clustered around a given angle θ^0 (here 0°) and are therefore not distributed randomly. V is the projection of the mean vector onto the test direction of θ^0 and can range from -1 to $+1$. If the observed angles are clustered around θ^0 , V is close to 1 and the test value (u) will be

greater than the critical value $u(\alpha)$. In this case, the null hypothesis of a random or uniform distribution of angles can be rejected.

The non-parametric M-W-W test was used to compare samples of angles. Differences in the mean angle or variance can be detected and lead to conclusions of differences between samples. Non-parametric tests were necessary here as the data violated the assumptions relating to the concentration of angles in each sample that are necessary requisites of the parametric Watson-Williams test (Batschelet 1981). The M-W-W test observes the order of the arrangement of the angles of the samples, but changes the spacing between them so that each is equidistant from the next. If the points from one sample are sufficiently separate from the points of the other sample(s), a difference will be detected between them and the null hypothesis of the samples being from identical populations can be rejected.

Both of these tests assume that data is not bimodally or multimodally distributed, and thus are only valid when applied to uniform or unimodal distributions. Rao's spacing test, however, can be applied to bimodal samples and still be expected to reject randomness when appropriate (Batschelet, 1981). Thus, I used this test, which compares the lengths of the arcs between consecutive sample points, to ensure data was uniformly distributed when it appeared from the graphs that it could have been bimodal. A non-significant result in the Rao's spacing test [$U < U(\alpha)$] confirms the null hypothesis of a non-bimodal distribution of angles.

Results

Individual and demographic differences

290 inter-segment angles were calculated and included in this analysis. Table 6.1 shows the descriptive and V test statistics for all focal individuals.

Table 6.1 demonstrates differences in the distribution of inter-segment angles between males and females, with most males showing angles significantly clumped in the forward direction whereas most females did not. These sex differences are evident in figure 6b. The M-W-W test shows that the distributions of angles between males and females were significantly different from each other ($W=9.901$; $n=192, 98$; $p=0.012$). Being a

nonparametric test, the difference could lie in the mean or dispersion of the distributions: looking at figure 6b suggests it is the latter.

Table 6.1: Descriptive and V test statistics for the angles turned by each focal animal. Names in *italics* denote disabled individuals.

Focal Individual		Descriptives					
		N	Mean ^o	Median ^o	Sd ^o	V test (u)	p
High rank males	BK	12	351.5	2.2	67.5	2.4	0.007*
	DN	47	1.5	0.7	65.3	5.1	<0.0001*
	JM	8	4.0	347.1	62.9	2.2	0.013*
	MA	32	33.1	38.3	88.6	2.0	0.021*
Mid rank males	NK	18	5.4	350.6	90.9	1.7	0.045*
	ZF	22	8.9	15.2	94.0	1.7	0.044*
Low rank males	BB	38	31.1	32.3	84.8	2.5	0.006*
	<i>TK</i>	15	49.5	60.3	101.1	0.7	0.229
Cycling females	<i>BN</i>	22	13.1	3.8	69.0	3.1	<0.0001*
	ML ¹	7	1.1	349.0	78.7	1.5	0.074
Lactating females	<i>KL</i>	17	209.9	217.9	87.9	-1.6	0.940
	KW	24	343.6	354.1	129.9	0.6	0.307
	<i>KY</i>	4	154.2	158.1	63.1	-1.4	0.914
	NB ²	16	143.0	136.0	82.3	-1.6	0.946
	ZM	6	354.7	357.1	74.1	1.5	0.069
TOTAL		290	14.8	14.7	94	6.1	<0.0001

As shown in figure 6b.1, the mean angle for females was 29.4^o, with a very large confidence interval (and a standard deviation of 130.6^o). Females did not orient forwards significantly more than other directions (u=0.907; n= 98; ns). Males, on the other hand, did seem to orient forwards, with a mean angle of 13.2^o and standard deviation of 82.3^o. 24 of the angles calculated for males fell close to 0^o (between 345^o and 15^o), whereas only eight fell close to 180^o (between 165^o and 195^o). The V test shows that male angles were not randomly distributed but were clustered around the test value of 0^o (u=6.802; n=192; p<0.001).

¹ ML contributed two angles when she was pregnant. Those detailed here were all observed when she was cycling.

² NB contributed only one angle when she was pregnant, all others were observed when she was lactating.

Figure 6b.1: Angles turned by females

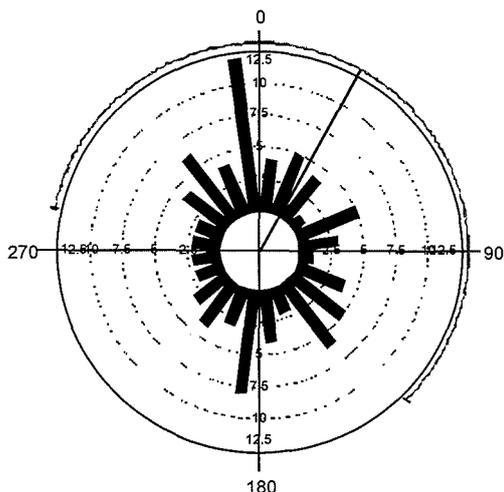


Figure 6b.2: Angles turned by males

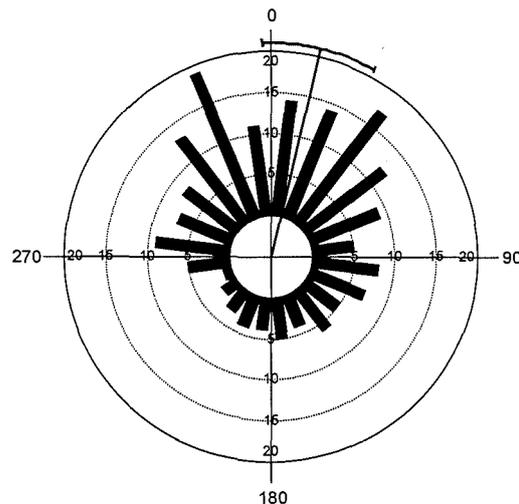


Table 6.1 shows the distribution of angles of lactating females were very different to those of cycling females. Three lactating females (KL, KY and NB) all have mean and median angles far from the forward direction of 0° . KW and ZM both have mean and median angles much closer to the forward direction, but KW displays a very wide dispersal of angles, and ZM has only a very small sample size. None are therefore significantly oriented forward. Tests were not applied to pregnant females as only three angles were computed from pregnant female routes, but figure 6c contrasts the angles observed from lactating and cycling females. The M-W-W test shows that there was a significant difference between the distributions of angles turned between segments of cycling and lactating females ($W=8.283$; $n=27, 66$; $p=0.016$).

Figure 6c.1: Angles of lactating females

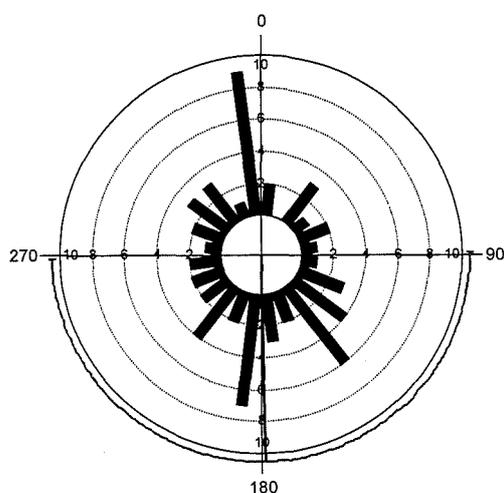
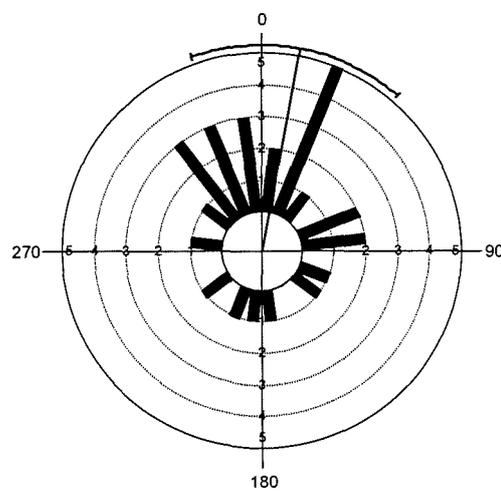


Figure 6c.2: Angles of cycling females



The V test confirms that lactating females made up the subset of females that did not significantly orient their routes forward ($u=-1.246$; $n=66$; ns). There was a visible trend for lactating females to turn back on their routes, with a mean of 179.1° and a standard deviation of 120.8° . 11 of the lactating female angles were close to 0° , but ten were also close to 180° ³, suggesting lactating females were just as likely to turn back on themselves as they were to move forward to the next 20-minute resource.

This suggests lactating females alone were responsible for the differences evident above between males and females. The M-W-W test confirms that lactating females displayed significantly different distributions of angles turned to males ($W=16.223$; $n=192$, 66; $p<0.001$). Cycling females, conversely, behave more like males. The V test confirms that angles of cycling females, when grouped together, were significantly clustered in the forward direction of 0° ($u=3.442$; $n=29$; $p<0.001$) and the M-W-W test does not reveal any significant differences between the angles of males and cycling females ($W=0.832$; $n=192$, 27; ns). The mean inter-segment angle of cycling females was 10.7° (circular standard deviation = 71.4°) and only two angles fell close to 180° . Although the distribution of the cycling female ML's angles was not significantly clumped forward, she did show a trend towards this pattern, albeit with a very small sample size. Given that cycling females associate with males more than lactating females do, it seems intuitive that they should travel in similar ways. If more data were available from ML or other cycling females it would likely follow the same pattern as observed in BN and the males.

Inspection of table 6.1 suggests less distinction between male classes. Figure 6d illustrates the distributions of inter-segment angles of low-, mid- and high-ranking males. With mean values of 34.762° , 7.243° and 7.066° respectively (with circular standard deviations of 89.241° , 92.564° and 73.714°), all male ranks tested oriented travel routes in the forward direction: the angles of males from all three ranks were clustered around 0° . (Low ranking males: $u=2.515$; $n=53$; $p=0.006$; mid-ranking males: $u=2.406$; $n=40$; $p=0.008$; high-ranking males: $u=6.104$; $n=99$; $p<0.001$.) The M-W-W test confirms the distributions of angles of low, mid and high ranking individuals are not significantly different from each other ($W=2.895$; $n=53$, 40, 99; ns).

³ Rao's spacing test shows that lactating females do not have a significant bimodal distribution despite the trend to orient backwards. This validates the application of the V test.

Figure 6d.1: Angles of low-rank males

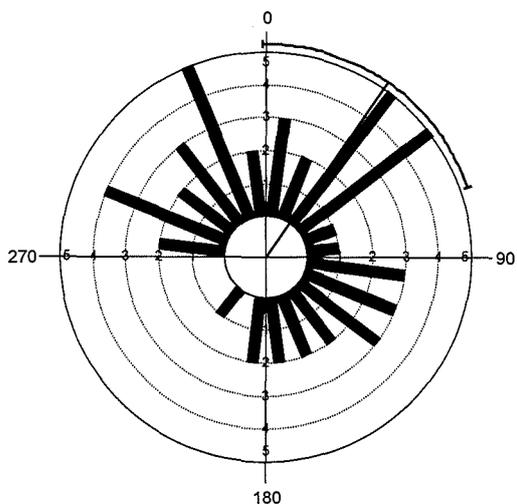


Figure 6d.2: Angles of mid-rank males

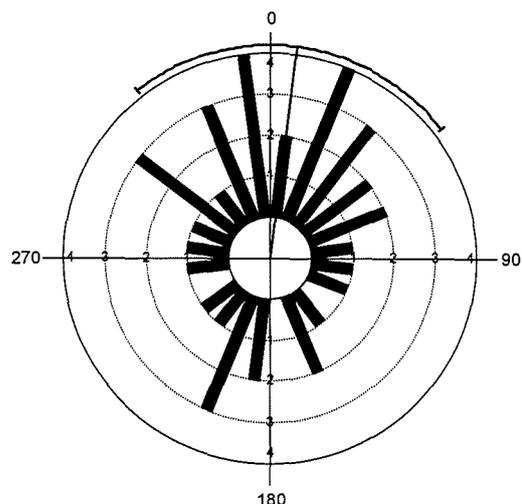
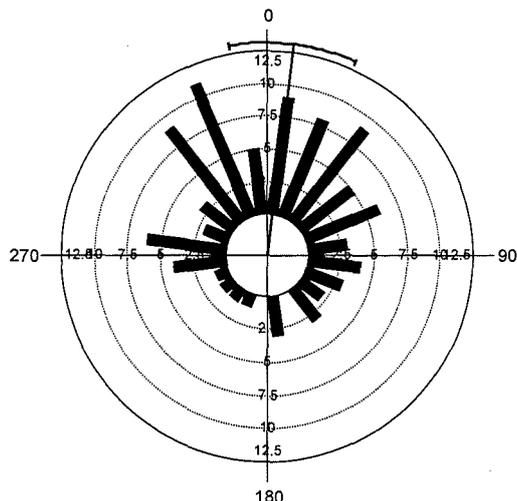


Figure 6d.3: Angles of high-ranking males



The angles of low-rank males seem to be more dispersed than the other male ranks, however, although all had similar standard deviations. The greater spread among low-ranking males is explained when considering individuals. Of the two low-ranked males - BB and TK - BB resembled other males but TK seems to have behaved more like a lactating female. As we saw in the previous chapter, TK, an old and severely disabled individual, exhibits some travel behaviours that are not characteristic of other able-bodied chimpanzees. Although his inclusion in the low-rank male category does not negate the significant result, when considered on his own, TK does not exhibit inter-segment angles that are clustered in the forward direction. As the low-rank male group comprised only two

chimpanzees, it is not possible to state conclusively that low-rank males, like other males, do orient forward significantly more than chance: one did and one did not. With TK being an “atypical” individual though, while BB is younger and not disabled, it seems very likely that if data from more low-ranking males were collected, they would follow the pattern of the other males. Overall, it seems males of all ranks orient their routes forward.

I have not tested the differences between disabled and able-bodied individuals, as the samples are rather messy for this analysis. TK is the only disabled male, and he clearly shows a different pattern to other males. To complicate things further, one of the disabled females was cycling (BN), and the other two were not (KL & KY). The different patterns associated with cycling and lactating seem to override any effects of disability in females, but only longitudinal data of these females as they change reproductive states could decisively confirm this.

Effects of party composition

Given that certain classes of focal animal appear to display different ranging patterns, with cycling females and males mostly heading forward, but lactating females being more likely to turn back on themselves or head in non-forward directions, it is reasonable that different party types will also affect distinct patterns. Parties composed only of lactating females are likely to be very different to all male parties or those of mixed sexes. Figure 6e illustrates the distributions of angles turned between segments by the focal animals when they were in different party types.

Family and female-only parties, which are normally comprised of lactating females, show the distributions expected from the behaviour observed by lactating females. Neither of these distributions varies significantly from a random pattern (family party: $u=-2.622$, $n=23$, $p=0.996$; ns; female only party: $u=-0.11$, $n=20$, $p=0.543$; ns). Conversely, all the parties containing adult males are significantly clumped around 0° (mixed parties: $u=3.71$, $n=67$, $p<0.0001$; sexual parties: $u=5.697$, $n=103$, $p<0.0001$; all male parties: $u=2.801$, $n=74$, $p=0.002$).

Figure 6e.1: Angles turned by family parties

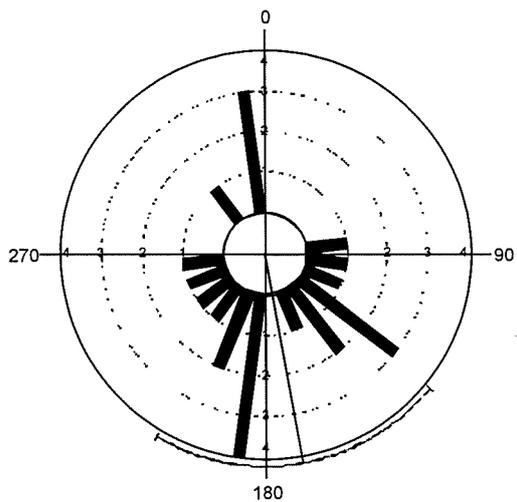


Figure 6e.2: Angles turned by all female parties

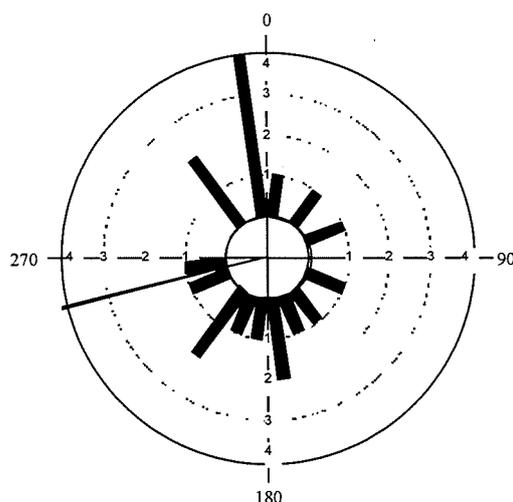


Figure 6e.3: Angles turned by mixed parties

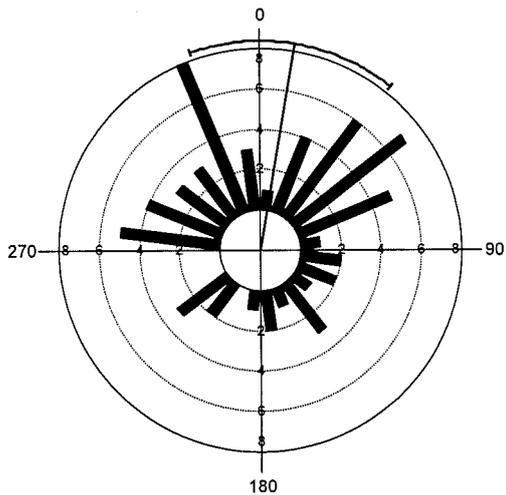


Figure 6e.4: Angles turned by sexual parties

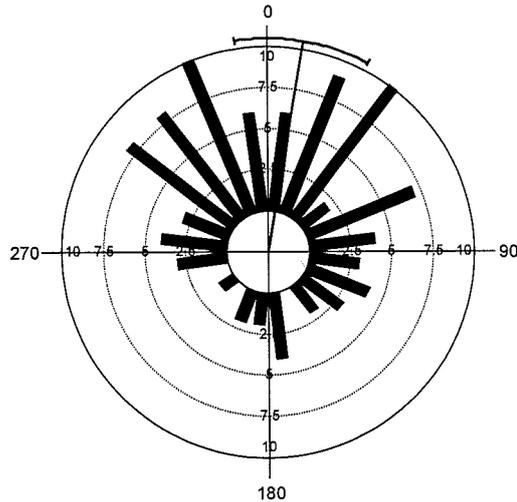
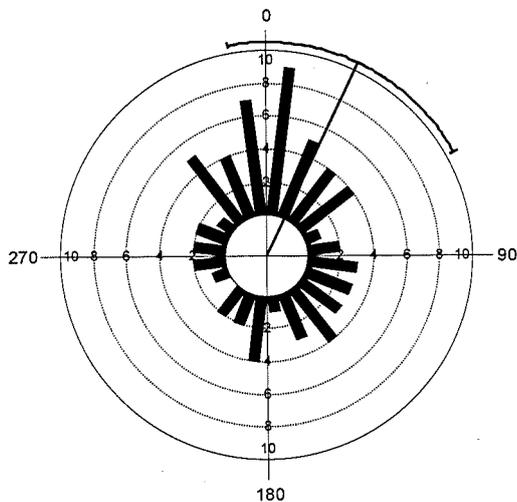


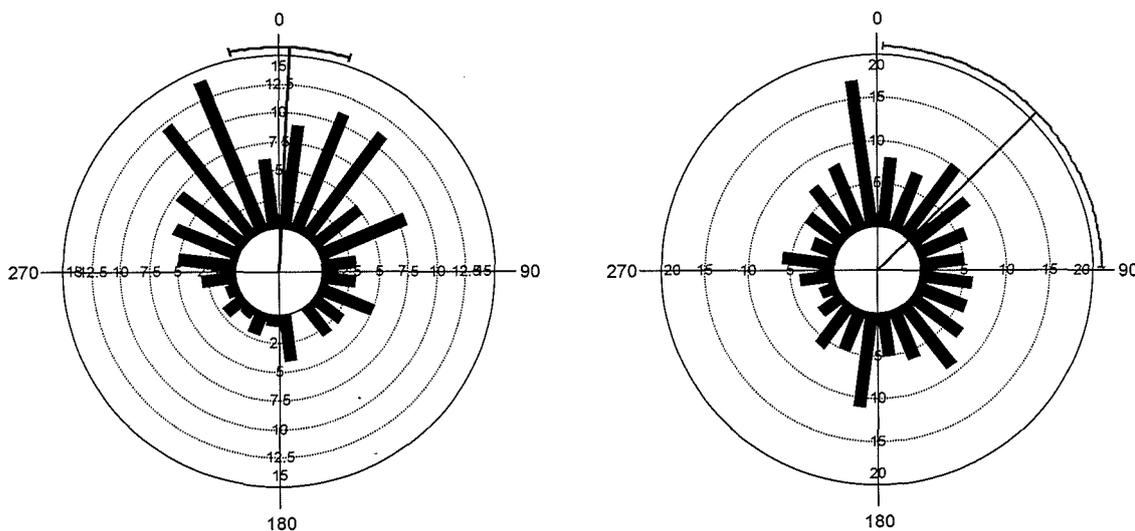
Figure 6e.5: Angles turned by all male parties



The alpha male and his closest associates can be thought of as the “core-male subgroup” (Nishida, 1989). It has been suggested that the presence of this core subgroup has significant implications for the social behaviour and activities of individuals associating with it. Figure 6f shows the distribution of angles observed when the focal animal was and was not associated with the core-male subgroup when travelling to the subsequent 20-minute stop-site. Both of these distributions are significantly oriented forwards despite the greater spread evident when core-males are not present (core subgroup present: $u=6.938$, $n=126$, $p<0.001$; core subgroup not present: $u=1.682$, $n=161$, $p=0.046$). The M-W-W test does show that these two samples, despite both being significantly oriented forwards, do differ from each other ($W=10.981$, $n=160$, 125 , $p=0.004$) but this is probably a function of the dispersion of the angles, rather than a significant difference in the means.

Figure 6f.1: Angles seen when core subgroup present

Figure 6f.2: When core subgroup not present



In order to determine exactly which individuals the core sub-group influence, I have also considered the effects of their presence on males and females separately. For male focal animals, angles turned between travel segments are significantly clumped around 0° , whether the core subgroup was present with the focal animal or not (core sub-group present: $u=6.697$; $n=107$; $p<0.001$; core sub-group not present: $u=2.709$; $n=85$; $p=0.003$), as shown in figure 6g.

The Mardia-Watson-Wheeler test, however, gives a rather ambiguous result as to whether these two samples are distinct from each other: ($W=5.893$; $n=85$, 107 ; $p=0.053$). Strictly

speaking, the two samples should not be considered significantly different from each other as $p > \alpha$, but to claim non-significance on the strength of a 0.003 difference could seem rather “fussy”. Given that, in both conditions, male routes are significantly oriented forwards, these samples might not necessarily differ: males are likely to orient forwards whether they are with the core sub-group or not, but this tendency is increased when they are with the core-sub group.

Figure 6g.1: Angles observed by male focals when core sub-group is present.

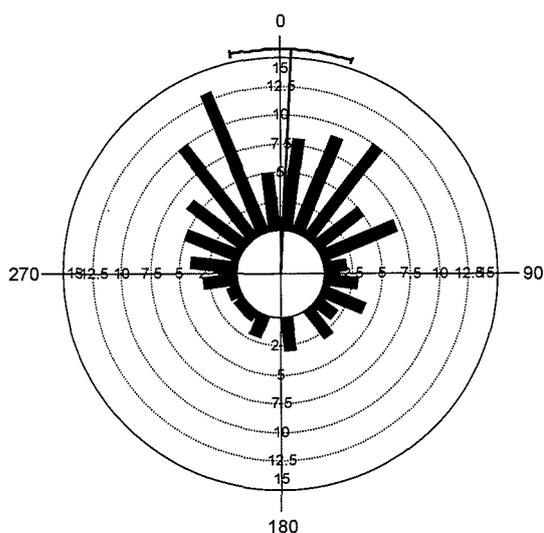


Figure 6g.2: Angles observed by male focals when core sub-group is not present.

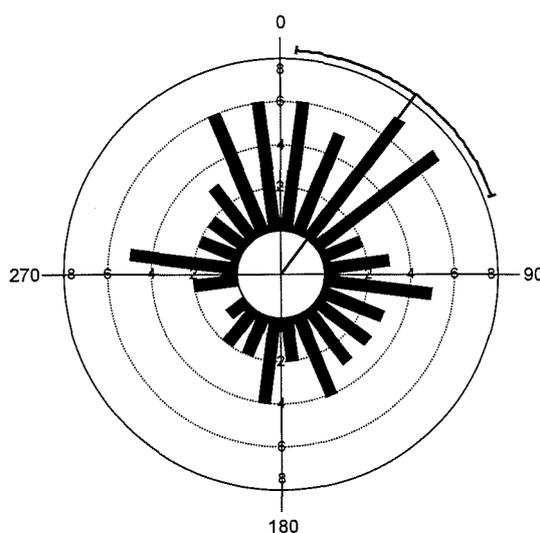


Figure 6h.1: Angles seen in female focals when core male sub-group is present.

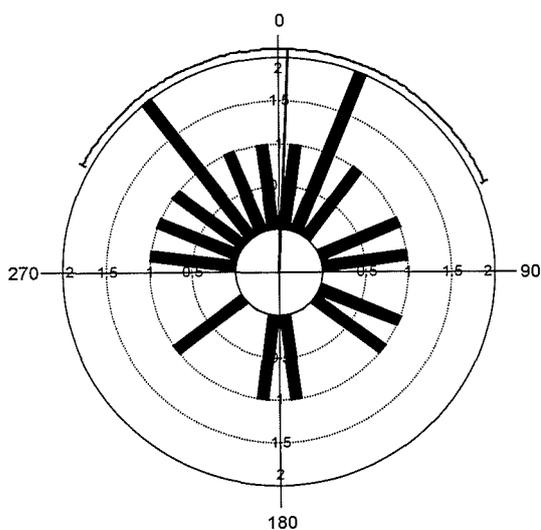
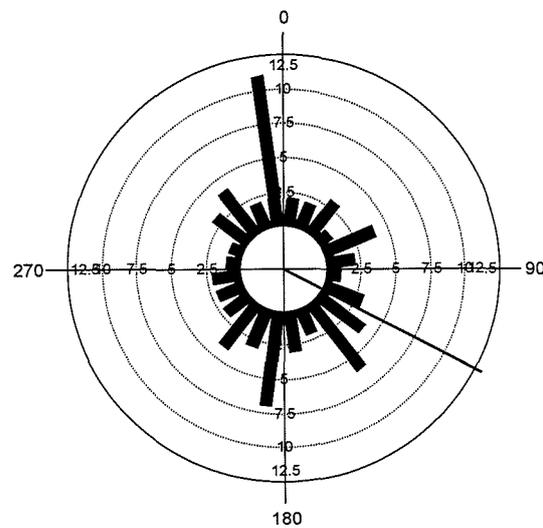


Figure 6h.2: Angles seen in female focals when core male sub-group is not present.



For females a different situation is observed. Females that are not with the core sub-group do not orient their routes forward significantly more than other directions ($u=-0.266$; $n=75$; ns), whereas females that are with the core-male sub-group do show a clumped distribution of angles in the forward direction ($u=1.727$; $n=18$; $p=0.042$). This difference is evident in figure 6h.

Despite one of these distributions being significantly clumped forward whilst the other is not, the M-W-W test does not detect any difference between these two samples ($W=1.77$; $n=18, 75$; ns). This lack of a significant difference, however, between what look like different samples is likely due to the small sample size of focal females present with the core-male sub-group.

17 of the 18 angles observed from females with the core-male sub-group were recorded from cycling females. Cycling females are responsible for the pattern seen in figure 6h.1, with all but one of the lactating-female angles being recorded when the core-male sub-group was not present. Although the M-W-W test suggests that, with these sample sizes, there is no difference between the females that are with the core-male sub-group and females that are not, I have already shown that the distribution of angles observed from cycling females is significantly different from lactating females (see figure 6c), when not considering party composition. When considering only cycling females, divided by being with the core-sub-group or not, the M-W-W test again shows no difference ($W=3.029$, $n=17, 9$, ns). That is, cycling females display similar distributions of angles irrespective of whether they are associating with the core sub-group of males or not. I cannot test the effects of the core-subgroup on lactating females only, as there was only one datum from a lactating female with the core-sub-group. It seems, however, that it is not the presence of the core males that influences the females' angular distribution, but rather the reproductive state of the females *per se*.

Seasonal effects

Chapter five did not demonstrate any effect of season, and thereby gross food availability, on travel segments, and it seems that here also there is no effect of seasonal variation on the distributions of angles seen. The M-W-W test shows that the angles seen in each season, for all individuals, do not differ from each other ($W=4.125$, $n=74, 66, 103, 47$; ns). Season 4 (wet) seems to have an unreliable mean but this is possibly due to a small sample size.

Figure 6i illustrates the distributions of angles turned between travel segments for each of the four seasons.

Figure 6i.1: Angles observed in dry season.

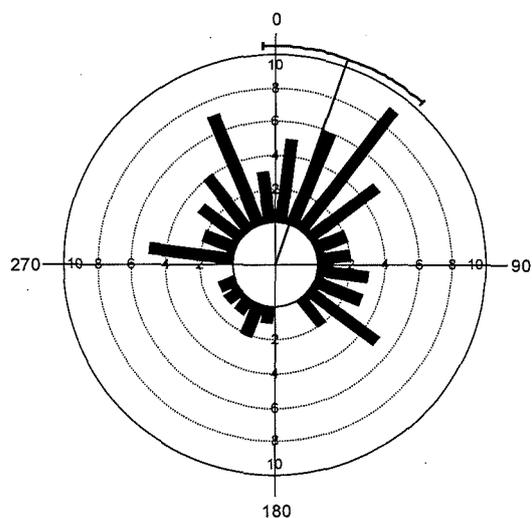


Figure 6i.2: Angles observed in 1st wet season.

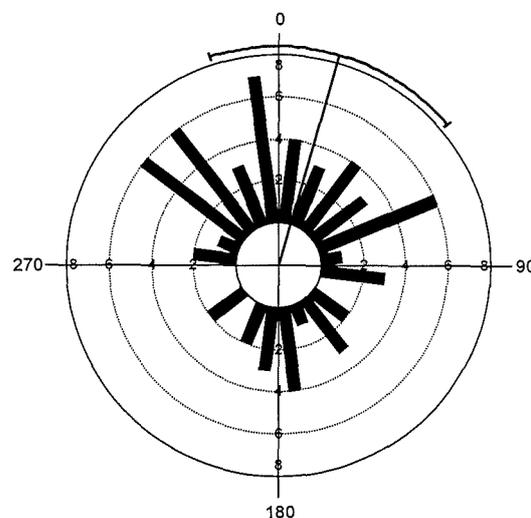


Figure 6i.3: Angles observed in inter-mediate season.

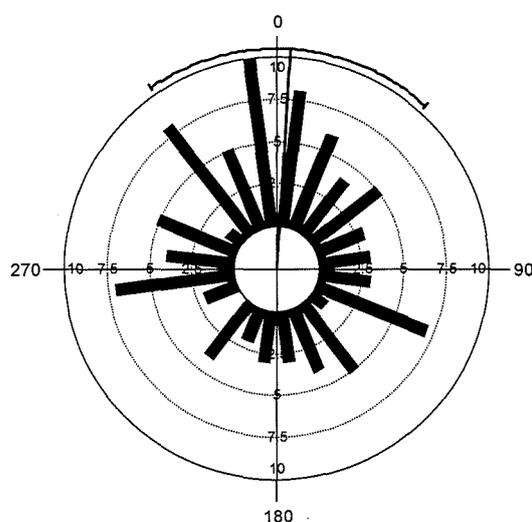
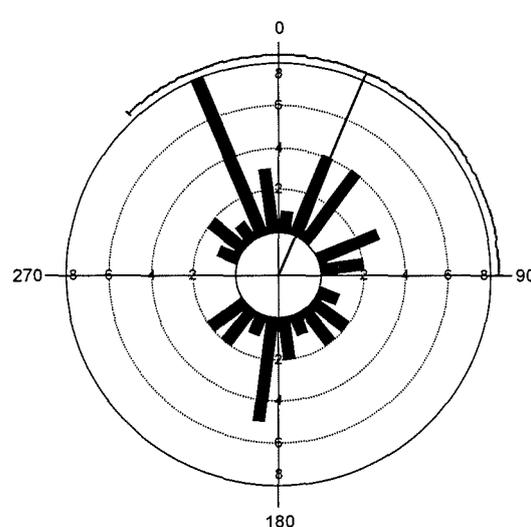


Figure 6i.4: Angles observed in 2nd wet season.



Season (food availability) does not have any differing effects on the different sex groups. When considering season for males and cycling females⁴, the M-W-W multi-sample test again shows there are no differences between the seasons ($W=5.969$; $n=61, 46, 82, 32$; ns).

⁴ I have grouped males and cycling females together for this and subsequent analyses as I have now shown that cycling females behave more like males than lactating females, rendering it more valid to place them with males.

Similarly for lactating females only there was no difference between seasons in the angles turned ($W=2.305$; $n=12, 20, 21, 14$; ns).

Effects of activity

The final variable that might be reasonably expected to result in changes to the distributions of angles is activity. Drinking was not included in this analysis as only two angles were observed between segments that led to a drinking-stop-site. Feeding, resting, socialising and nesting were considered, as displayed in figure 6j, which show the angles observed by all males and females together. Feeding, as expected, shows a clumped distribution of angles in the forward direction ($u=4.361$; $n=198$; $p<0.001$), as does resting ($u=4.958$; $n=43$; $p<0.001$).

Figure 6j.1: Angles associated with feeding segments

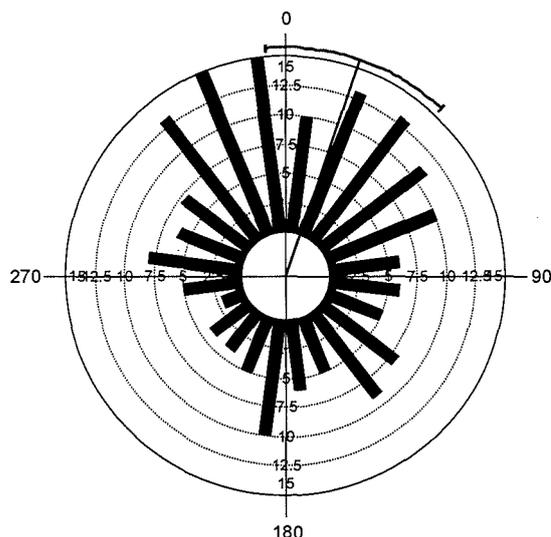
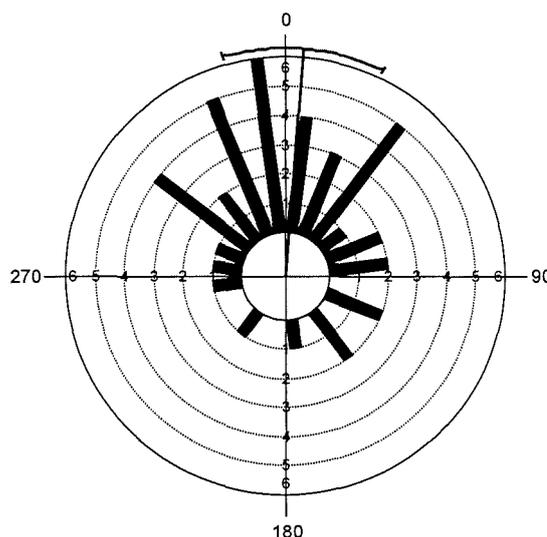


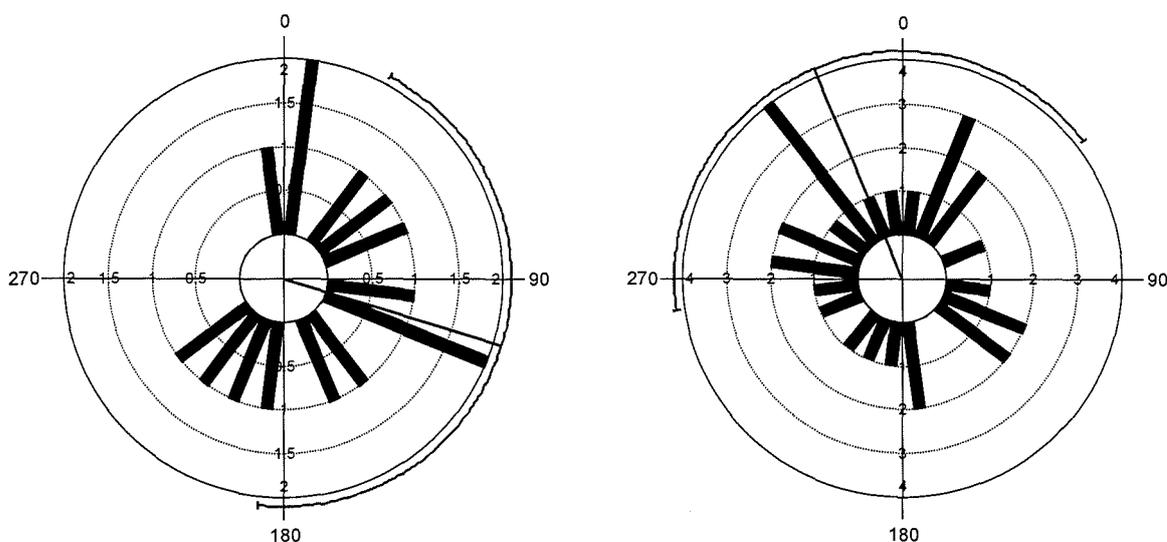
Figure 6j.2: Angles associated with resting



When considering males and females separately, different patterns are observed. Males and cycling females seem to be responsible for the forward-oriented distribution of feeding and resting travel segments (males and cycling females feeding: $u=5.918$ $n=142$; $p<0.001$; males and cycling females resting: $u=5.012$; $n=35$; $p<0.001$). Lactating females do not show distributions clumped around 0° when travelling to feeding or resting resources though (lactating females feeding: $u=-1.238$; $n=54$; ns; lactating females resting: $u=0.604$; $n=7$; ns). Comparing lactating females against males and cycling females for feeding only, there are significant differences in the way the two populations are distributed ($W=18.201$; $n=142, 54$; $p<0.001$).

Nesting and socialising travel segments are not significantly oriented forward compared to other directions when considering all males and females together, as shown in figure 6j.3&4 (nesting: $u=-0.495$; $n=15$; ns; socialising: $u=1.363$; $n=30$; ns). This is also true when considering males and cycling females separately, (males and cycling females nesting: $u=-0.272$; $n=10$; ns; males and cycling females socialising: $u=1.561$; $n=29$; ns). For lactating females, nesting segments were not oriented forwards (nesting: $u=-0.473$; $n=5$; ns) [only one social segment was recorded so no statistics were applied].

Figure 6j.3: Angles associated with nesting segments Figure 6j.4: Angles associated with socialising

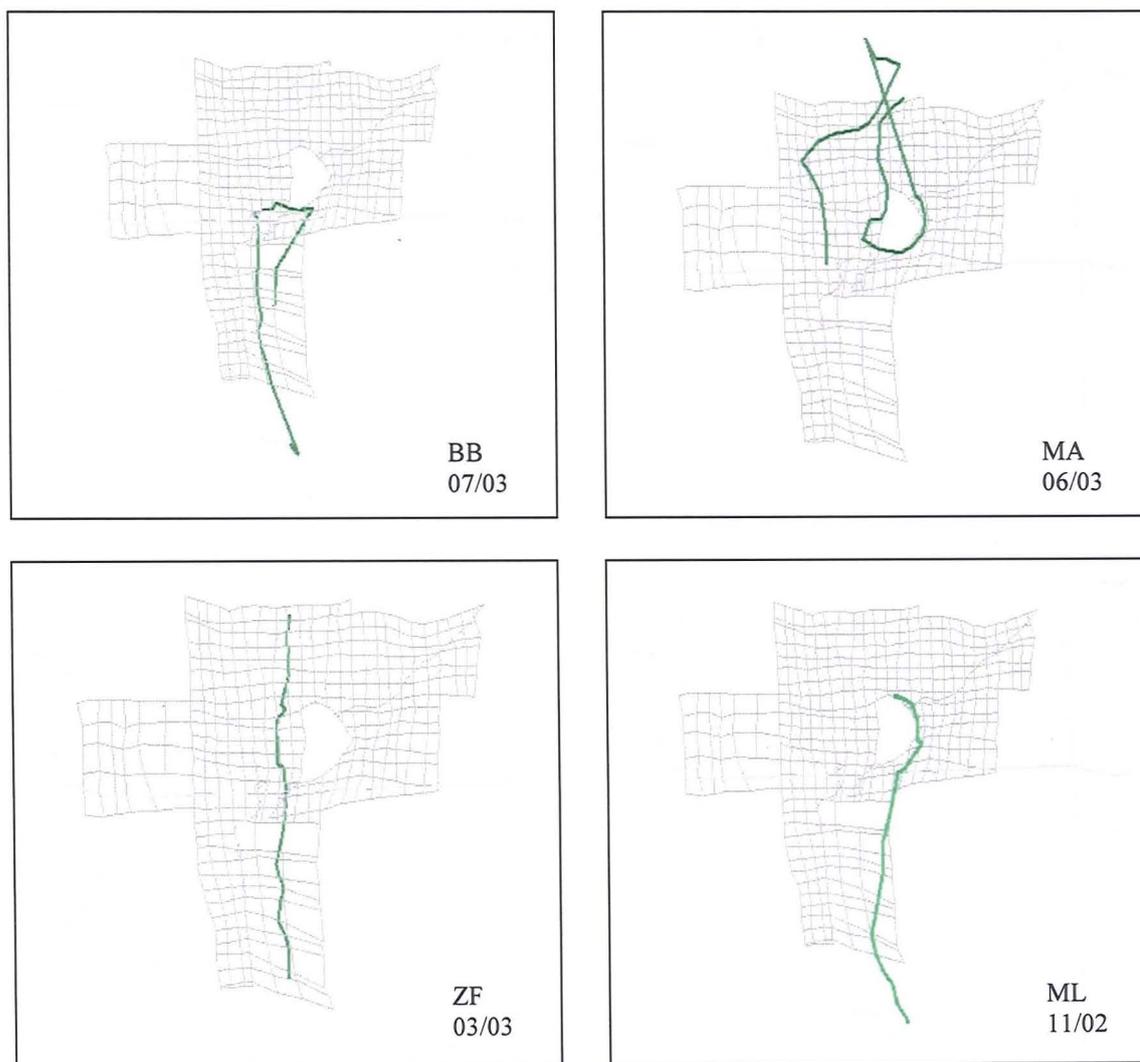


In case social travel segments might be cued by hearing vocalisations, I compared the distributions of the 18 social travel segments that were preceded by vocalisations across males and females, with the 12 that were not. The 18 segments, from both sexes, preceded by vocalisations displayed a random distribution ($u=0.113$; $n=18$; $p=0.456$; ns) of orientations, but the social segments not cued by vocalisations were clustered in the forward direction ($u=2.012$; $n=12$; $p=0.021$). This suggest animals only changed direction of heading to socialise if they were going to “meet” other individuals calling from different areas. The M-W-W test did not detect any differences in these samples at the 2-tailed level, despite one being significantly directed forward and the other not ($W=4.702$; $n=12$, 18 ; $p=0.095$, ns). This may be influenced by the small sample sizes; larger data sets might reveal a distinction between angles of social travel segments that are cued by vocalisations from those that are not.

Discussion

From the analyses presented here it is apparent that male travel-segments were not independent of each other. Males displayed a strategy of walking in straight lines from resource to resource over prolonged periods, as is shown by the fact that very few of their inter-segment angles deviated from the forward direction. Cycling females appeared to move in a very similar way to males, again with non-independent segments arising from long periods of travel on the same trajectory across a number of resources. Given that males and cycling females turned away from the forward direction only infrequently, their routes should be composed of characteristically long, straight lines that pass through many resources. This is confirmed by examining the original travel maps, as displayed in figure 6k. These long periods of straight-line travel can be thought of as “super-segments”.

Figure 6k: Examples of routes composed of long “super-segments” of travel in males (BB, MA, ZF) and cycling females (ML).

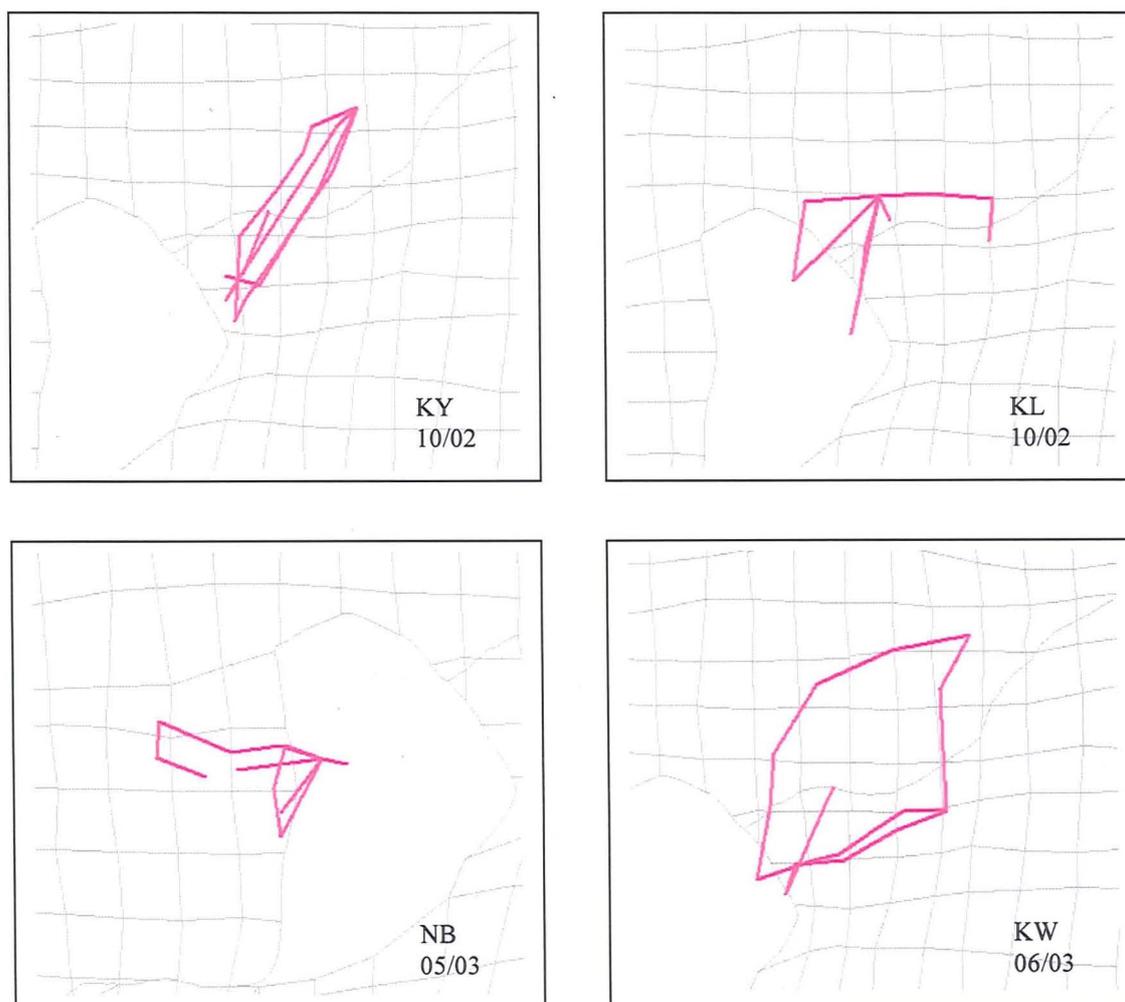


Lactating females show a different pattern to males and cycling females (as shown in figure 6l), and are not so easy to characterise. The travel segments of lactating females are not clumped around 0° . They do not travel long distances in one general direction, taking in a series of resources on the way, as males and cycling females do. When considering the distributions shown in figures 6c.1 and 6e.1&2, there is a large number of backwards-oriented segments: lactating females often seem to turn back on themselves to revisit previously utilised food resources, much more frequently than males and cycling females do. Thus, although the lactating females did display a statistically uniform distribution of inter-segment angles, the frequency with which they turned back on themselves is suggestive of an organised strategy.

Of the ten angles from lactating females that are close to 180° , all were produced when the females left a feeding site, moved to another resource, then moved back to the initial feeding patch. Four of the ten cases occurred overnight, with the female moving away from the feeding patch to nest, then moving straight back to the same resource upon leaving the nest the following morning. The remaining six angles close to 180° all arose within one day's foraging; the females doubled back on themselves from one feeding patch to another already fed from earlier that same day. The times elapsed between these double-backs - i.e. the time spent at the second stop site - range from two hours to eight hours to overnight, and the distances covered between the first and the second site range from 30m to 438m (mean distance = 176m, s.d. = 136m). Three cases involved consuming the same food type at each patch, whereas three comprised different foods at the first (and last) versus second patches. There is no discernible pattern relating to the patch values when females are observed to double back on themselves, with quality estimates ranging from 15 chimp minutes to 270 chimp minutes. In half the cases (five out of ten, or three out of six of the cases when the overnight-nest returns are discounted) the second, middle, patch has a higher value than the patch visited first and then returned to, and in half it didn't. The three cases where the second patch is of better quality than the first do not correlate with the three cases where the same food type was eaten in all patches. Thus, it seems quite random as to when lactating females doubled back on themselves. It can occur within one day's foraging activity or overnight; the distances doubled back vary greatly; and there is no pattern relating to the food type or patch quality.

The two occasions when cycling females were seen to double back on themselves both coincided with nesting. Similarly, of the eight occasions when males were seen to double back on themselves, two were overnight deviations to a nest site and one was observed when the focal male entered into the sugar cane to feed and then returned to rest at the forest edge. A further two cases occurred when the focal male left a patch to head in a direction from which vocalisations were heard, whereupon at the second site they fused with other individuals before returning to the previous patch to continue feeding. This leaves only three instances out of the 192 angles recorded from males when they appear to double back on themselves in consecutive travel segments for no obvious external reason. It seems lactating females return directly to previously visited patches more than other individuals do.

Figure 6l: Examples of the repetitive, circular routes of lactating females (KY, KL, NB and KW). Note; these maps are zoomed in – centring on the sawmill clearing – unlike those of figure 6k.



The strategy of lactating females seems to be to move in more repetitive routes that cover a smaller area of the home range, returning frequently to recently used 20-minute stop-sites. An illustration of this is seen in figure 6i, which shows sample routes from lactating females. In each of these routes, some food patches are returned to frequently, and circularity and doubling-back are clearly evident. This contrasts with figure 6j, showing the long straight “super-segment” routes of males. It would be incorrect to suggest that males or cycling females never re-visit food resources within one focal sample, but these individuals seemingly do not re-visit sites consecutively in the way that is evident in lactating females.

Circular routes, whereby previously utilised food resources are re-visited, could arise coincidentally through a strategy of walking to the nearest available food resource. This is unlikely to be successful with the regularity that is evident in the angle distributions of lactating females, however, without being based on some kind of decision as to whether the resource is worth returning to. For example, if it was entirely random, sometimes segments would return a female to a previously exhausted resource, which was not apparent here. Furthermore, if routes were random, 0° and 180° oriented segments would not be any more likely than segments in any other direction. Although, when all routes were considered together, lactating females’ inter-segment angles were not statistically clumped in a single direction, figure 6c.1 suggests an increased tendency to turn through angles close to 0° and 180° . If analysis of individual routes were possible (which it is not, due to the small number of angles recorded in any one sample), clumped patterns arising from circular or bimodal routes might be apparent. The merging of all the routes into one presentation cannot identify which angles were observed when, which could be responsible for the statistically uniform distribution. Thus, rather than being coincidental, the routes of lactating females might also be following a strategy, using memory of the location of recent food patches: within the circular routes, the orientation of one segment is at least partly based on experiences of earlier travel segments.

It seems that females alter their ranging patterns markedly from when they are lactating to when they are cycling by changing from short, repetitive routes to those that mimic males. It is unclear to what degree cycling females “choose” mates, but from this analysis it seems that long, straight routes are characteristically male, and that cycling females alter their ranging to fit with them.

Sex, and reproductive state within females, seem, therefore, to be the major criteria dictating the arrangements of route segments. Rank of males has little effect beyond increasing the concentration of already forward-directed distributions, and disability and age could not be tested fully here. Party composition and/or the presence of the core-male sub-group also have little effect, again with the different distributions seemingly more dependent on the focal animals' sex and reproductive status. Season also has no effect on the strategies used by males and females, with both sexes showing their same patterns consistently throughout the year. This suggests that food availability is not the limiting factor directing the ranging patterns of these chimpanzees.

The only variable other than sex and reproductive state that seems to affect the distributions of the angles between segments along a chimpanzee's path is the activity at the end point of the segment. Nesting and socialising did, as expected, display random distributions in both sexes. Travel segments to nesting sites and social 20-minute stop sites that are cued by external vocalisations are oriented independently of other segments in all classes of individuals. It makes sense that nesting segments would have a random distribution as chimpanzees, irrespective of sex or reproductive status, stop feeding at the end of the day and normally move a short distance to the nearest suitable nesting tree. There is no reason to assume that this should be in the same orientation as the day's travel up to that point. Similarly, for socialising, a random distribution of angles was anticipated as chimpanzees can potentially travel in any direction in order to fuse with other individuals. It is travel between feeding, resting and non-vocally cued social 20-minute stop sites that create the long, straight routes of males and cycling females: these segments are not independent. Lactating females did not consistently show forward-oriented travel over two or more segments to feeding or resting stops, consistent with these females exhibiting repetitive routes.

For males and cycling females, the *r*-values of the respective feeding and resting angle distributions are interesting. For males, the mean vector length of the feeding distribution is 0.379, but for resting it is 0.608. For cycling females these *r*-values are 0.336 and 0.608 respectively. Although the differences in the distributions of feeding and resting segments are not statistically significant, this does mean the travel segments ending with resting are more concentrated than the feeding segments in these two demographic groups. This

makes sense as resting can be thought of as occurring whilst on the way to more tangible resource sites, thus keeping the resting segment angles very small. Feeding segments, on the other hand, cannot continue indefinitely in one direction as eventually the animal would run out of forest! For this reason, in a number of cases, segments associated with feeding activities will have to include some wider turns that allow foraging to be re-directed toward a new food source.

That consecutive travel segments of males and cycling females are not independent *could* be suggestive of longer-term planning in travel routes. That is, males and cycling females might plan to head to one distant resource, and, in order to limit their travel costs, visit other resources that are approximately on the path to the intended goal. However, the non-independent distribution of angles clumped around the forward direction can be observed without it necessarily implying sophisticated representational abilities. For example, following a simple rule strategy of walking in straight lines until a boundary is reached, taking in all the salient resources passed on the way, would also result in a clumped distribution of angles. Indeed, Janson (1998) showed brown capuchin monkeys (*Cebus apella*) displayed “inertia”, preserving the direction of travel even after stopping to feed, but concluded that this was not necessarily based on more than one-step ahead planning.

This analysis has not *ruled out* the possibility that males and cycling females plan travel routes more than one-step in advance, however, although the cognitive processes underpinning the patterns observed cannot yet be confirmed. I will attempt to differentiate between the possible explanations for these patterns of ranging in the following two chapters.

Chapter 7

Do chimpanzees “aim” for particular resources?

As we saw in the previous chapter, travel segments are not independent for either cycling female or male chimpanzees. Instead of an arbitrary arrangement, the travel segments are organised into successions of long, uni-directional “super-segments” (a series of consecutive single-travel segments that are oriented in the same direction) over the course of which many needs can be met. Meanwhile, lactating females construct their foraging routes rather differently to males and cycling females, with more “backwards” turns between segments (i.e. turns close to 180°) and repeat visits to food patches. I argued that lactating females also show some pattern in the structuring of their travel segments rather than indulging in aimless wandering.

Why do males and cycling females travel in these long, straight super-segments, and what dictates how lactating females organise their routes? The patterns observed so far do not straightforwardly reveal the cognitive processes underlying them. Straight-line travel alone does not imply knowledge (Garber and Hannon, 1993). The co-ordination of successive segments of travel into “super-segments” could be constructed from heuristic rules that do not require any explicit spatial knowledge, or they could be based on computation with some kind of spatial knowledge.

Whether routes result from behavioural rules or use of prior knowledge, it is important to ask what makes the chimpanzee turn around: where and why does one super-segment end and another begin? We can suppose that rule-based travel would entail rules as to when to turn around, such as “turn when have eaten a critical amount of food, when have travelled a certain distance, or when hear vocalisations from conspecifics”. Conversely, if travel is goal-directed and based on spatial knowledge (Garber, 1989; 2000), super-segments would normally be expected to end in some valuable reward. The overall trade-off between consumption of resources and costs of travel must be of the same critical level for survival regardless of which strategy is used, but the pattern of procurement of these resources may be different if travel is rule- or knowledge-based. Thus, by analysing what behaviours are

associated with the ends of super-segments, I may be able to determine if these travel periods are indeed goal-directed, and if so what are the goals or coincidental results of following heuristic rules.

Goal-directed travel can (but does not necessarily) imply advanced mental abilities whereby the chimpanzee plans its route using current spatial knowledge to ensure a valuable resource is reached (Garber, 2000), perhaps whilst concurrently meeting other salient needs. As discussed in chapter one, the ability of animals to plan is a contentious issue, with some psychologists arguing that such forms of “mental time travel” are uniquely human (Suddendorf and Corballis, 1997). There is only sparse evidence of planning in wild primates (Sigg and Stolba, 1981; Boesch and Boesch, 1984) and one experiment on a captive, language-trained bonobo suggesting route-planning (Menzel *et al*, 1999) but these concern planning for events that “correspond to the current motivational state of the animal” (Roberts, 2002). Suddendorf and Corballis (1997) argue that there is no evidence any animals can anticipate future needs they are not currently experiencing. Byrne (1995) describes two scenarios in which wild chimpanzees might actually be anticipating future requirements beyond their current situation: regular border-patrol behaviour and a unique observation of the killing of a leopard cub, neither for consumption nor apparently as a “toy”. Given this fragmentary evidence of planning, any further sign of planning in chimpanzees would be very interesting, particularly if it could be shown that the intended behaviour met needs beyond those currently held by the animal.

In order to consider whether chimpanzees do plan sections of their routes and “aim” for particular resources, I will apply a novel statistical test – the Jupp test – (described in Appendix G) to determine at what point individuals started to head to a resource. Working back from the final “stop site”, the Jupp test aims to identify all the points in the travel route where the target animal significantly changed its general direction of travel. I can then use these “change points” as punctuation marks to delineate the straight, super-segments of travel.

I aim to consider why males and cycling females range along super-segments, and to investigate if lactating females have a similar (or any other) strategy that was hidden from the previous analysis by their frequent backwards turns. I will analyse how long the super

segments are, as a means of exploring how far in advance chimpanzees *potentially* head to a resource, and then examine what lies at the ends of these super-segments: what, if anything, are the chimpanzees heading too? Behavioural differences may be evident whilst travelling along, and when at the ends of, super-segments, according to whether the routes are guided by heuristic behavioural rules or planned using spatial knowledge. I shall investigate the speed of travel along the super-segment as a potential measure of “intention”; chimpanzees may travel faster to a resource they “want” and “expect” to reach. However, a lack of a reward at the end of a super-segment may not always indicate lack of spatial knowledge. For instance, vocal cues could alert an individual travelling towards one resource as to the whereabouts of another, and that might cause deviation from the initial trajectory resulting in a super-segment that ends without an observable reward. Thus, this chapter forms an *initial* attempt to differentiate between rule-based or knowledge-based planned pathways.

In particular, I will examine any potential association between the length and/or speed of these super-segments and the value of the end food-resource. In chapter five a similar analysis did not illustrate any relationship between the length or speed of individual travel segments and the quality of the subsequent food resource, but this does not mean a relationship will not be evident when considering the longer periods of travel composed of numerous individual segments. Visiting less rewarding resources on the way to a very valuable and desirable patch might have masked the effects of the distant, valuable patch. Prediction of reward is very difficult in the forest environment, though, because of the existence of competitors. Therefore, a lack of association between speed or distance travelled and the eventual patch value does not necessarily imply an absence of knowledge about the location of the potential resource: the chimpanzees may just arrive too late sometimes. For this reason, I will also consider the *type* of resource: if fruit is generally of higher value than leaves, and seasonal foods of greater value than constantly available “fallback” foods (Wrangham *et al*, 1996, 1998), travel may be preferentially oriented towards these general species-groupings that are usually known to provide greater rewards.

Thus, in this chapter I aim to explore if there is any evidence that chimpanzees use spatial knowledge to plan foraging routes. If chimpanzee travel is goal-directed and planned more than one step in advance, the following predictions should be upheld:

- Super-segments of travel will normally end in potentially valuable resources.
- There will be an association between the speed and distance of travel along a super-segment and the value or type of the potential reward.

Methods

Data used

Not all of the 50 focal-routes recorded are suitable for analysis with the Jupp test: some are too short and/or have only one salient stop-point recorded while others are too disjointed - due to breaks in the recording when the focal animal was temporarily lost. Thus, from all the routes, I have selected 20 for analysis with the Jupp test; 14 new routes, and six that were analysed in Appendix G. The routes were selected as the longest in both duration and distance covered, with the least number of breaks in recording. Table 7.1 lists all the routes analysed with the Jupp test and details the lengths and duration of each sample.

Data analysis

The co-ordinates recorded at all the stop sites and five-minute waypoints on each of the 20 routes were entered into the Jupp spreadsheet, as described in Appendix G, using the $q=2$ version, and $\alpha=0.05$. The last 20-minute stop-site of the route was taken as the initial end-point. The Jupp algorithm was then applied from the final 20-minute stop-site backwards along the route as in Appendix G. The first change-point identified was then taken as the end-point in the next run of the test, and so on until all the change points within one route had been identified.

The change points identified were recorded in an SPSS spreadsheet with the relevant associated information, as detailed in table 7.2. This spreadsheet allowed me to investigate the nature of the occurrence of change-points and the super-segments of travel. All the hypotheses tested were two-tailed unless otherwise indicated, with $\alpha = 0.05$. Tests applied were for independent groups and, unless otherwise stated, were parametric. I employed log transformations where necessary to ensure data was normally distributed. Data is presented graphically using box plots - showing median values, inter-quartile ranges and 5%-95% of the data range - instead of means plots, to illustrate the spread of the data.

As in previous chapters, there is a problem of pseudo-replication as each consideration of super-segments pools data from the same routes and individuals. However, if we consider the sample as comprised of routes rather than chimpanzees then it is acceptable to treat change points from the same individuals on different routes as independent: each journey was taken at different times, under different conditions, albeit sometimes by the same individual. Within one route super-segments can be thought of as independent as there is no reason to believe that one super-segment is dependent on those preceding it: each super-segment occurs under different conditions, with potentially different party sizes and composition, and ending in potentially different activities. Furthermore, the Jupp test tells us super-segments are statistically independent. Taking route averages for change points would result in the loss of possibly significant information regarding the situation of that particular change point, such as whether it was cued by vocalisations and what the party-composition was.

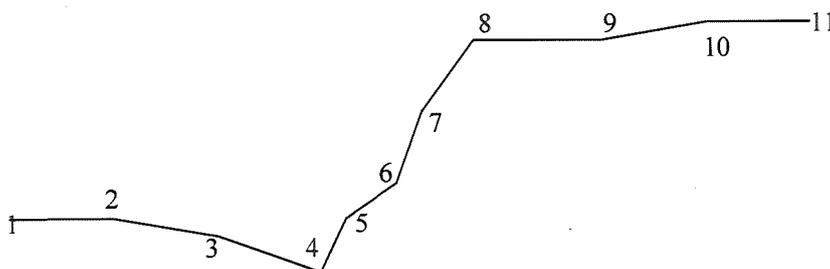
Table 7.1: Routes used in Jupp analysis of route planning
Cycling females are denoted by italics

Season	Focal animal route					
	With duration of sample (hrs) and distance covered (m)					
	Females			Males		
Season 1	KL 20/01/03	24 hrs	3950m	TK 14/01/03	9hrs	4030m
Dec-Feb	<i>BN 24/02/03</i>	<i>20hrs</i>	<i>7730m</i>	DN 03/02/03	29hrs	7780m
				MA 10/02/03	27hrs	10570m
Season 2	ZM 18/03/03	14 hrs	3180m	ZF 03/03/03	11hrs	2840m
Mar-May	<i>BN 08/04/03</i>	<i>10hrs</i>	<i>1430m</i>			
	NB 12/05/03	23hrs	1380m			
Season 3	KW 09/06/03	20.5hrs	2200m	BB 02/06/03	11hrs	4030m
Jun-Aug	KW 30/06/03	28hrs	4610m	MA 04/06/03	9.5hrs	6270m
				BB 07/07/03	34hrs	6220m
				DN 14/07/03	21.5hrs	8890m
				ZF 28/07/03	13hrs	6170m
Season 4	KY 21/10/02	19.5 hrs	2220m	DN 02/09/03	20.5hrs	4410m
Sep-Nov	<i>ML 11/11/02</i>	<i>21 hrs</i>	<i>3150m</i>	TK 30/09/02	27.5 hrs	1880m

Table 7.2: Information entered into SPSS spreadsheet pertaining to each change point identified

Information entered	
Route label	
Waypoint ID of change point	
Length of super-segment (m)	For the first change point of the route: measured from the start of the route. For subsequent change points: measured from the preceding change point.
Number of waypoints recorded along the super-segment	Not including the start and end waypoints of the super-segment.
Number of salient stops recorded along the super-segment	Not including the start and end waypoints of the super-segment.
Mean speed of travel along segment (km/hr)	Mean of the speed of travel between all the waypoints comprising the super segment.
Time spent at change point (minutes)	Time stopped at change point. For travelling change points, duration = 0 minutes
Vocalisations heard before change	Any vocalisations heard from outside the focal's party, whilst the focal animal was at the change point or as it moved away before the next waypoint was recorded (<5min after leaving change point), were noted as potentially cueing the change in direction, starting from the first waypoint of the route ¹ .
Party size as reach change point	Number of adults and sub-adults that reached the change point with the focal individual
Party type	Type of party as measured when the focal animal reached the change point: all male; all female; mixed; sexual; family (as described in chapter five)
Presence of male core subgroup	Were the alpha male and the high ranking males present or absent when the focal animal reached the change point?
Activity at change point	Travelling, feeding, resting, socialising, nesting
If feeding: species eaten	Species code
If feeding: patch value	Chimp minutes – as described in chapter five

¹ If a route consisted of 11 waypoints, with change-points noted at waypoints 4 and 8, any vocalisations occurring before the animal reached waypoint 2 were considered potentially to have cued travel on the first super-segment of waypoints 1-4. For the second super-segment of waypoints 4-8, any vocalisations heard from the direction of waypoint 8 whilst the animal remained at waypoint 4 (the first change-point) or before it reached waypoint 5 were considered potentially to have cued the change in direction, and so on.



Results

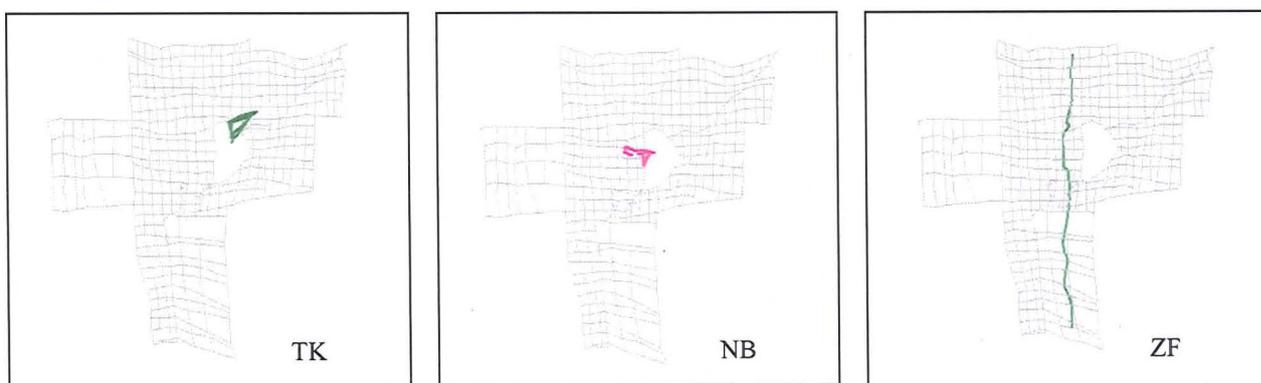
How long are super-segments?

Defining super-segments from the change points identified

The change-points identified by the Jupp test either signal a change of general direction between two straight super-segments, or they denote a change between haphazard wandering and a section of straight, directed travel. In order to separate the sections of haphazard wandering I used the linearity scores of the sections punctuated by change-points to determine which sections should rightly be considered super-segments and which should not. I denoted any section with a linearity score of below 0.65 as not straight and directed, as at scores below 0.65 the chimpanzee travelled 50% further than the direct length between the start and end waypoints of the section.

No change-points were identified on three of the 20 routes. Two of these routes were apparently not composed of any super-segments as the linearity scores from the start to the end of the route were well below 0.65; (TK30/09/02: linearity = 0.132; NB12/05/03: linearity = 0.139). When looking at these routes, as displayed in figure 7a, the lack of super-segments is apparent; they are very repetitive, with many short segments going backwards and forwards between the same trees. The third route (ZF03/03/03) that did not generate any change-points had a linearity score of 0.966, suggesting the entire route was one long super-segment. Therefore this route was included in the analyses.

Figure 7a: Three travel routes where no change points were identified.



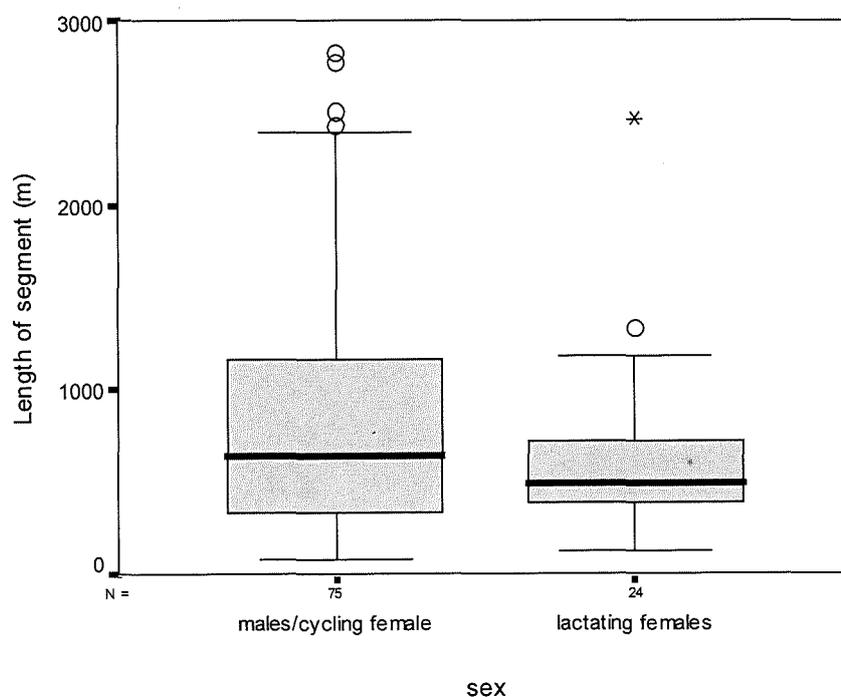
Four sections of travel were excluded from the analyses for having linearity scores of below 0.65, so presumably representing relatively haphazard wandering, giving a data set of 99

straight super-segments all with linearity scores over 0.65 (mean linearity 0.957). Twenty-four of these segments originate from lactating female focal animals, 12 from cycling females and 63 from males. As previous chapters show, the organisation of cycling-female travel-segments closely resembles that of males, and because the size of the cycling-female sample is rather small to consider on its own I will group cycling females with males for all the subsequent analyses.

How far do chimpanzees travel in one direction?

The average length of these 99 super segments was 815m. Male and cycling-female super-segments are approximately 882m long on average, whilst lactating females displayed super-segments with a mean length of 607m. The lengths of both lactating female and male/cycling female super segments have very high standard-deviations and wide ranges. The range of lactating female lengths is not vastly different to that of males and cycling females, but the latter group evidently displays long super-segments more frequently than the former, as is apparent from the median lengths shown in figure 7b.

Figure 7b: Box plot of the lengths of super-segments travelled as observed in males/cycling females and lactating females

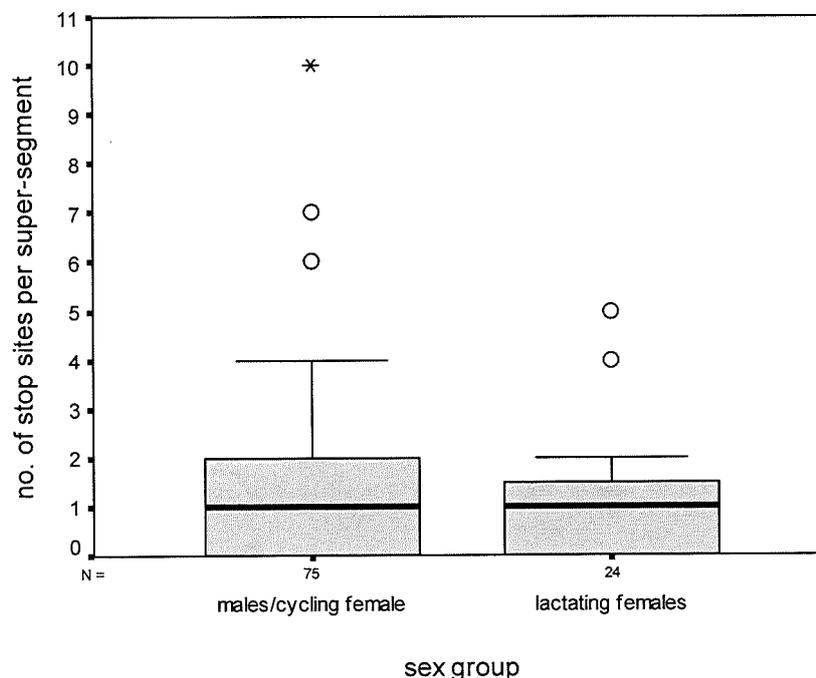


An independent t-test performed on log-transformed data suggests this trend for a difference in super-segment lengths of males/cycling females and lactating females is not

statistically reliable. Males and cycling females display a *trend* to travel further along super-segments than lactating females, but this is not statistically significant ($t=1.505$, $df=49$, $p=0.069$; 1 tailed, not equality of variance). The power of this test is low however, which may be responsible for the lack of a significant effect.

Male and cycling-female super-segments have a mean composition of 6.25 waypoints (5min point samples and/or stops made by the chimpanzees) on average ($sd=4.79$), compared to 5.17 ($sd=4.5$) in lactating females. There is no difference in these means when comparing log-transformed data ($t=1.234$, $df=97$, ns); males and females change direction after a similar number of waypoints. Furthermore, neither sex group seems to stop more often along super-segments than the other (mean number of salient stops for males/cycling females=1.36, $sd=1.75$; for lactating females=1.04, $sd=1.3$), with no significant difference between the log-transformed means ($t=0.606$, $df=60$, ns). Both sexes display a low mean number of stops but with high variation (males/cycling females up to ten salient stops in one super-segment, and lactating females up to five), as shown in figure 7c.

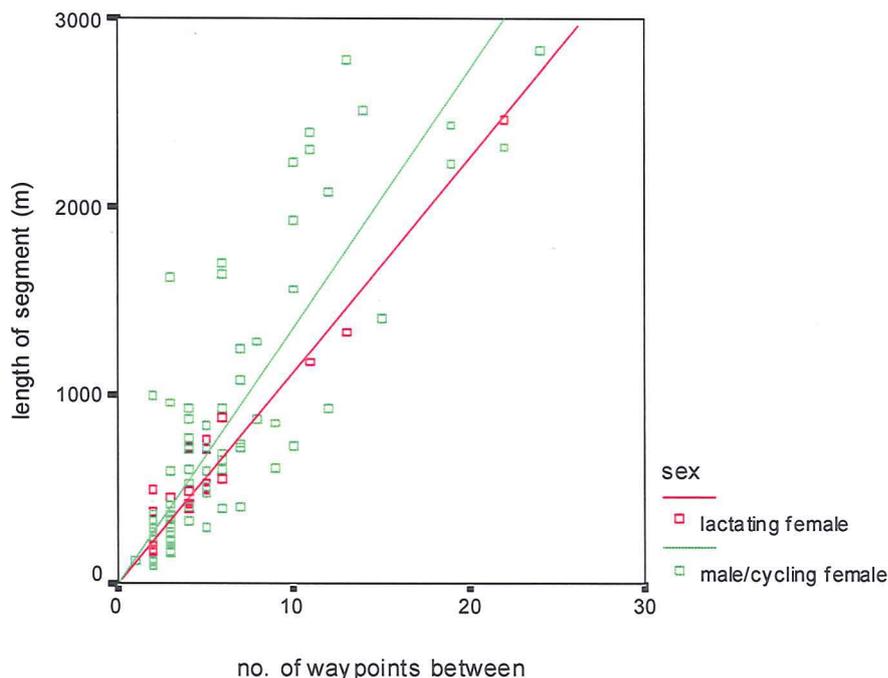
Figure 7c: Number of stops made by males/cycling females and lactating females per super-segment



The number of waypoints recorded increases as a function of the length of the super-segment, as depicted in figure 7d. Although the lengths and number of waypoints recorded

per super-segment have been shown not to vary between the sexes, the trend of males/cycling females to travel slightly further than lactating females, in the same time, is apparent from figure 7d. This suggests that males/cycling females must be travelling faster in each super-segment than lactating females.

Figure 7d: The number of waypoints recorded per super-segment increases significantly as a function of the length of the super-segment for both male/cycling females and lactating females (male/cycling females: $r=0.830$, $n=75$, $p<0.01$; lactating females: $r=0.972$, $n=24$, $p<0.01$).



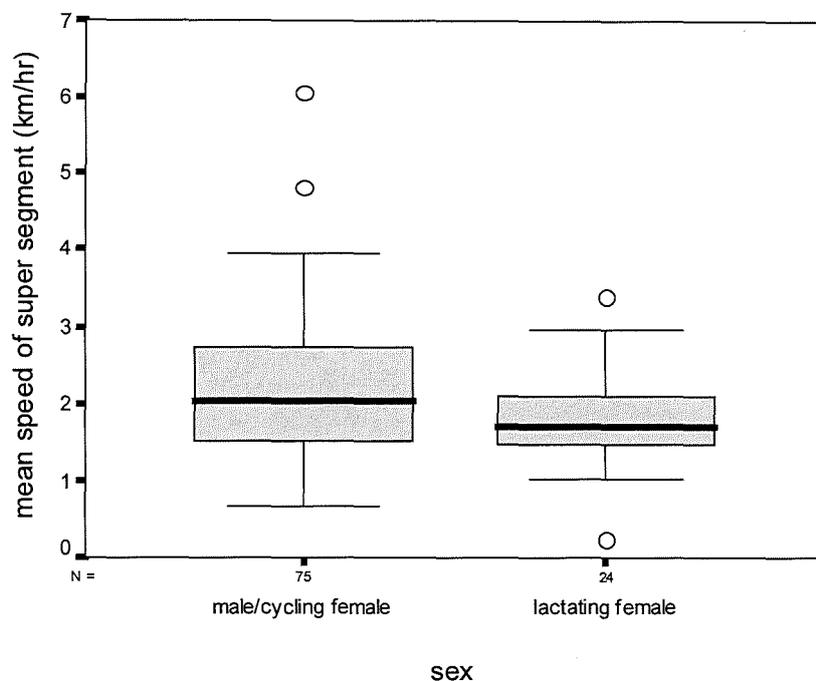
The mean speed per super-segment for males/cycling females is 2.2km/hr ($sd=0.9$) and 1.8km/hr for females ($sd=0.7$). Figure 7e shows the median scores of the average travel speed. A t-test confirms that males/cycling females do generally travel significantly faster than lactating females ($t=2.051$, $df=97$, $p=0.043$), when considering the mean speed across the whole super-segment.

Do lactating females change direction more frequently than males?

I have shown thus far that lactating females construct super-segments despite the greater degree of spread in the distribution of inter-segment angles of lactating females than observed in males and cycling females. Possible explanations for this apparent contradiction include greater variability in the inter-segment angles comprising one super-

segment, or large variation in the angles turned between super-segments combined with a greater number of super-segments per unit distance.

Figure 7e: Box plot of the average speed of travel along a super-segment for each sex group.

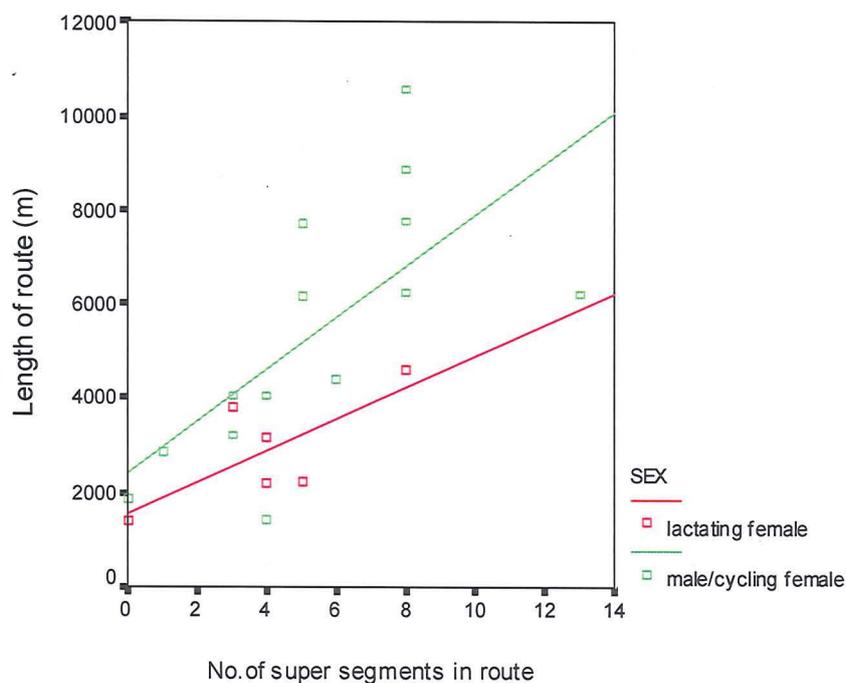


If the super-segments of lactating females were more variable in the directions of their component segments, lactating females would exhibit lower super-segment linearity scores than males/cycling females. This is not the case, however, (mean linearity of lactating females: 0.94, $sd=0.01$; mean linearity of males/cycling females: 0.92, $sd=0.01$) with no differences being found in the mean linearity scores of the sexes ($t=-1.220$, $df=97$, ns). Lactating females do not exhibit less straight super-segments than males, and this cannot account, therefore, for the large variation in inter-segment angles shown in chapter seven.

The pattern must instead arise from lactating females using a greater number of (smaller) super-segments than males/cycling females, giving a more varied spread of angles: i.e. a larger proportion of a lactating females' inter-segment angles will be between super-segments. As shown in figure 7f, this does indeed seem to be the case. Lactating females use more super-segments in the same length of route than males. For example, males/cycling females might construct a route of 4000m from three super-segments but lactating females would be more likely to use eight super-segments in a route of that length.

The use of more super-segments per unit distance is consistent with the suggestion that lactating females use repetitive routes and double back on themselves frequently.

Figure 7f: The total length of the route travelled increases as the number of super-segments identified per route increases. Both males and females exhibit significant positive correlations between the length of the route and the number of super-segments in the route (males/cycling females: $r=0.681$, $n=14$, $p=0.004$, 1 tailed; lactating females: $r=0.733$, $n=6$, $p=0.049$, 1 tailed). Best-fit lines do not pass through zero as it is possible for routes to occur without any super-segments.



What prompts chimpanzees to change direction?

To understand *why* the chimpanzees turn at those specific points, and to explore whether there is any evidence that super-segments are directed towards particular resources, I will examine where and when change points occur, and what behaviours coincide with them, in an attempt to detect underlying patterns that result from the use of heuristic behavioural rules or spatial knowledge.

Boundaries of the territory?

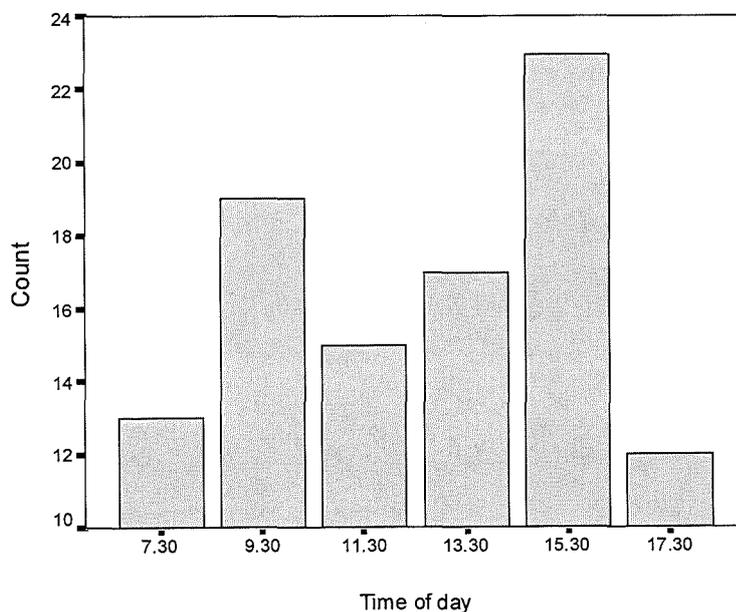
It is possible that change points occur only at the edges of the territory; that the chimpanzees walk in straight lines until they recognise being at a boundary, at which they turn around to head in a different direction within the range. Change points occur only rarely in the outer areas of the range, however. Most of the changes of direction between super-segments actually occur within the central areas of the grid system. What, then,

makes an individual turn around to head in a different direction whilst it is in non-peripheral areas of the range?

Certain times of day?

Changes of direction between super-segments could be dictated by the time of day. Figure 7g shows the time of day, in one-and-a-half-hour long intervals (e.g. 7.30 is equivalent to 7.00-8.30am), for which all the change points between super-segments were seen to occur. Peaks in changes of direction can be seen in the mid morning and mid afternoon, with 19% of the changes in direction occurring between 9.00am-10.30am and 23% occurring between 3.00pm-4.30pm. This coincides with the times when travel is most likely, as shown in chapter four, but these peaks are not dramatic – changes of direction occur with fairly similar frequencies throughout the day. Thus daily cycles cannot be seen to dictate when animals turn from one super-segment to another.

Figure 7g: Frequency of occurrence of change points throughout the day. Each time reference is two hours long e.g. 7.30 extends from 6.45am-8.44am. 9.30 from 8.45am-10.44am etc.



Particular activity types?

Change points coincided with all of the activity states recorded – they do not always coincide with one type of activity such as after feeding or resting. Thus, always turning after engaging in a particular type of activity is not a prompt that chimpanzees can be argued to use. Table 7.3 details the behavioural activities associated with each change point observed for males and females.

Table 7.3: Number of super-segments ending in each behavioural state, for males/cycling females and lactating females.

	Male/Cycling female		Lactating female		Total frequency	
	N	%	N	%	N	%
Travelling	17	23	1	4	18	18.2
Feeding	28	37	19	79	47	47.5
Resting	20	26	4	17	24	24.3
Social	5	7	-	-	5	5
Nesting	5	7	-	-	5	5
<i>Total</i>	75		24		99	

For both males/cycling females and lactating females, the end of a super-segment most often coincides with feeding stops, but the magnitude of this frequency is very different between the sexes: lactating females are much more likely to change direction after feeding than males/cycling females². Lactating females were seen to change direction between super-segments whilst travelling only once, whereas this was seen on nearly a quarter of all male/cycling female change points. The one occasion when a lactating female did change direction whilst travelling was when she (KL20/01/03) had left a feeding stop-site only one waypoint previously. Vocalisations had been heard from the south-east half an hour before she left the stop site, which is the direction in which she initially travelled. Whilst moving south-east, more vocalisations were heard, this time from a north-easterly direction, at which she changed direction to head north, hence the change point. Three minutes after this change point, KL fused with GS, HT, KY and ZM.

Changing direction after a period of resting was also quite common in both sexes, but again more so in males/cycling females. In this sample, lactating females were not observed to change direction at a nest site or after socialising. Instead, females nested either in such close proximity to food sources that separate waypoints were not recorded at all, or they did not significantly alter direction between moving from the nest site to the next resource from

² In all subsequent analyses I have excluded one of the feeding cases, as it ended in MA feeding on a monkey. This hunt could presumably have occurred anywhere so does not have to be associated with any rule or knowledge of the location of the food source. As only one hunting episode was observed, it is necessary to treat this behaviour as an anomaly in this data set and exclude it. Thus, from this point forward, all analyses were conducted on a data set of 98 super-segments.

the previous day's travel. Of the five occasions where males/cycling females did change direction upon leaving a nest site, three were from the same follow (BB07/07/03) where on each occasion the target animal fed on a resource, moved less than 100m away to nest, then returned to the food site first thing in the morning. The fourth example came from a follow of DN (DN14/07/03), when he nested in an adjacent block to where he had been feeding and in the morning bypassed the previous feeding site to fuse with other individuals and eventually head to a different food resource. The final super-segment ending in a nest site was recorded from BN08/04/03 and was actually the end point of the whole route; no more waypoints were recorded after this nest site - the super-segment was directed toward this nest site, and it is not known where BN moved the following morning.

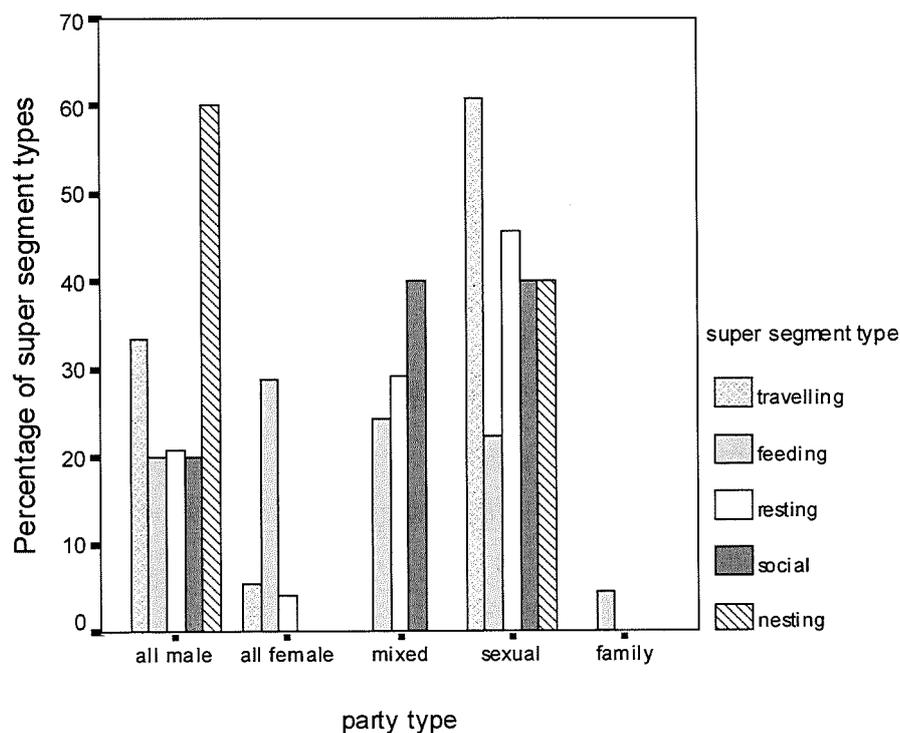
Of the five super-segments ending in social activities, two involved fusion events: one (MA10/02/03) where the target animal moved to fuse with a lactating female who had only shortly before moved away from him, and one (ZF28/07/03) where the target animal and his party had stopped for a few minutes when DN fused with them, subsequently leading them all off on the same trajectory on which he joined them. A third example involved fusion of the target animal (BB07/07/03) with a large party of other males at start of the super-segment, who then all moved together to the change point where they sat and groomed each other for an hour-and-a-half before moving off in a different direction. The last two examples (MA10/02/03 and DN14/07/03) were not associated with any fusion or fission events, but the target animals' party simply stopped to groom each other for some time before moving off in a different direction.

It is evident from this sample that changing direction after social stops is rare, and that there is no obvious pattern allowing us to draw conclusions about how and why individuals change direction after socialising. The only common feature seems to be the presence of high-ranking males – all five cases involved DN or MA in one way, but all five were of different party sizes (2, 3, 7, 7 and 4) and types (all male, mixed and sexual parties). The sample is too small to be sure the presence of high-ranking males has an impact, but this does seem to be a strong possibility. I will therefore now consider the effects of party composition.

Influence of party composition

Super-segments can be grouped according to their terminal activity. Figure 7h shows the frequency of occurrence of each type of super-segment with each type of party. Nesting and social change-points were only observed with parties that involved males – all male, mixed or sexual parties – as lactating females were not recorded using super-segments that end in these activities. Feeding super-segments were likely to be seen across all party types, but – as seen in table 7.3 – travelling super-segments were uncommon in all female parties as female focal animals were only seen to demonstrate a travelling super-segment once. Most travelling and resting super-segments were observed in sexual parties. Overall, party type does not seem to influence the occurrence of activities – change points do not seem to occur when the target animal is associating with a certain type of party.

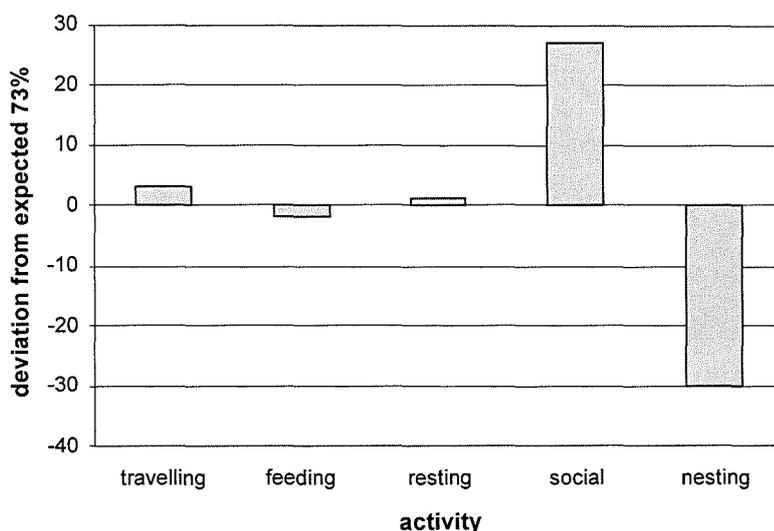
Figure 7h: Percentage of occurrence of each type of activity, separated according to party classification.



Might the presence of core males influence the probability of change points coinciding with certain activities? This is explored in figure 7i. 83% of the total number of super-segments identified involved male-based parties (all male, mixed or sexual), and of these, 73% included the core males (DN plus one or more high ranking individuals). Therefore, each activity can be expected to occur approximately three times as often when the core males are present compared with when they are not (e.g. ~73% of occurrences of a behaviour

should coincide with presence of core males, and ~27% without the core males). Figure 7i shows the deviation from this expected value for the occurrence of each activity when core males were present. It is apparent that travelling, feeding and resting occurred at approximately the expected frequency; the presence of the core males did not increase or decrease the likelihood of these behaviours occurring at the end of a super-segment. As described above, social activities only occurred when the core males were present, but the sample size of five is too small to determine if it was a genuine trend. Similarly, the trend for nesting to be less likely when the core males are present can also not be confirmed due to the small sample-size. Therefore, in subsequent analyses I do not need to treat segments associated with different party types differently.

Figure 7i: Deviation from the expected 73% of activities occurring when the core-male subgroup is present



Because they heard vocalisations?

Changes of direction between super-segments could be cued externally; the animal could abide by a rule of following environmental prompts. Visual and olfactory stimuli are unlikely to act as informative signals dictating the changes of direction: they were shown to be unlikely between single travel segments in chapter five and thus are even more implausible when considering the greater lengths of the super-segments. Hearing and following vocalisations could, however, be a very simple way of “deciding” when to turn around and head in a different direction, i.e., when to end one super-segment and move toward a different area.

In chapter five I showed that although hearing vocalisations sometimes coincided with longer segments of travel, there was no reason to believe that all single-travel segments were directed by and dependent upon hearing vocal cues from conspecifics. This does not mean, however, that they cannot influence changes of direction between the super-segments. I described above the example of a lactating female ending one super-segment whilst travelling and heading in a different direction when apparently prompted by hearing vocalisations. One of the five social change-points was also associated with hearing vocalisations (DN14/07/03). I will now investigate how common this is with other change points.

Of the 98 super segments considered, only 28 (28.6%) were potentially cued by vocalisations. That is, travel was preceded by hearing vocalisations from approximately the same direction as the subsequent path on only 28 of the super-segments. Twenty-three of the 28 super-segments preceded by vocalisations were observed in follows of male animals. Thus, only 21% (5 out of 24) of female super-segments were cued by vocalisations, and 31% (23 out of 74) of male super-segments were cued by vocalisations. From this it seems that vocalisations are not necessary for an animal to change its direction of heading. In the majority of cases super-segments end without being prompted by hearing vocalisations.

Might these vocalisations signal a particular type of resource at the end point of the subsequent super-segment? This does not appear to be the case when considering the coincidence of vocalisations with each potential type of super-segment described in table 7.4.

Table 7.4: Number and percentages of each type of super-segment being preceded by vocalisations, for males/cycling females and lactating females.

	Male/cycling female		Lactating female		Total	
	N	%	N	%	N	%
Travelling	7	41	1	5	8	44
Feeding	6	22	2	10	8	17
Resting	8	40	2	50	10	42
Social	1	20	-	-	1	20
Nesting	1	20	-	-	1	20
Total	23	31	5	20	28	29

Overall, both sexes exhibit super-segments that were preceded by hearing vocalisations, across all behavioural classes, but the majority of segments are *not* associated with hearing vocalisations. When males/cycling females appear to “follow” vocalisations, the super-segments thus begun are more likely to lead to a travelling or resting end point; that is, super-segments ending in travelling or resting waypoints are twice as likely to have started at the same time as hearing vocalisations from the travel direction as are super-segments ending in other behaviours. This probability is even greater in lactating females travelling to resting end points, but the small number of resting super-segments does render this percentage as potentially unreliable. Of particular interest is that most feeding super-segments are *not* cued by vocalisations (78% in males/cycling females, and 90% in lactating females).

Using a multivariate ANOVA, I tested whether travel speed or length of super-segment varied when the super-segments were cued by vocalisations or not. There was no difference in the log-transformed lengths or travel speeds of male/cycling female super segments ending in each behavioural state whether they were or were not preceded by vocalisations (*super-segment length*: main effect of activity: $F_{(4,73)}=1.796$, ns; main effect of vocalisation: $F_{(1,73)}=0.016$, ns; interaction between activity and preceding vocalisations: $F_{(4,73)}=0.732$, ns; *travel speed*: main effect of activity: $F_{(4,73)}=1.071$, ns; main effect of vocalising: $F_{(1,73)}=0.404$, ns; interaction between activity and vocalisations; $F_{(4,73)}=0.465$, ns). Similarly, for lactating females a multivariate ANOVA showed there to be no effect of vocalisations on the lengths or travel speeds of different types of super-segments observed (*super-segment length*: main effect of activity: $F_{(2,19)}=0.467$, ns; main effect of vocalisations: $F_{(1,19)}=1.536$, ns; interaction between activity and preceding vocalisations: $F_{(1,19)}=1.048$, ns; *travel speed*: main effect of activity: $F_{(2,19)}=3.459$, $p=0.052$; main effect of vocalising: $F_{(1,19)}=1.622$, ns; interaction between activity and vocalisations; $F_{(1,19)}=2.318$, ns).

From these analyses it is apparent that vocalisations are not frequently associated with changes of direction between super-segments and cannot be a necessary cue to changing direction. Furthermore, as vocalisations do not have any effect on the length or speed of travel along the super-segment, there is no evidence that the target animals are travelling in

anticipation; incidences of vocalisations occurring at change points between two super-segments may often be simply coincidental with no functional significance.

I will now consider in more detail whether end points of the super-segments share any common features. I will examine how far the chimpanzees travel along each type of super-segment, how many waypoints and stop sites precede each change point, and how fast the animals travel as a means of exploring any potential underlying rules versus the use of spatial knowledge.

Distance travelled to each type of super-segment

So far, the simplest potential rules can be discounted: there are no consistent patterns between when chimpanzees turn around and: a) where they are in their range, b) the time of day, c) the type of behaviour they are engaged in, or d) hearing vocalisations. One further potential rule could be to turn around after a certain distance has been covered. Although, as we have already seen, there was a wide overall variation in the length of super-segments, I will now consider if there was any pattern in the lengths of super-segments associated with different behaviours.

For example, a rule such as “walk up to 500m in one direction” may be utilised, and if no resources are encountered, the individuals turn around, or rest and then turn around. If adequate resources are encountered before the upper limit on distance is reached, they will change direction sooner: hence all the longest super-segments may be “unsuccessful” journeys ending in either resting or immediate continuation into a new super-segment (travelling super-segments). Table 7.5 shows the mean lengths of the super-segments ending in each of the behavioural categories.

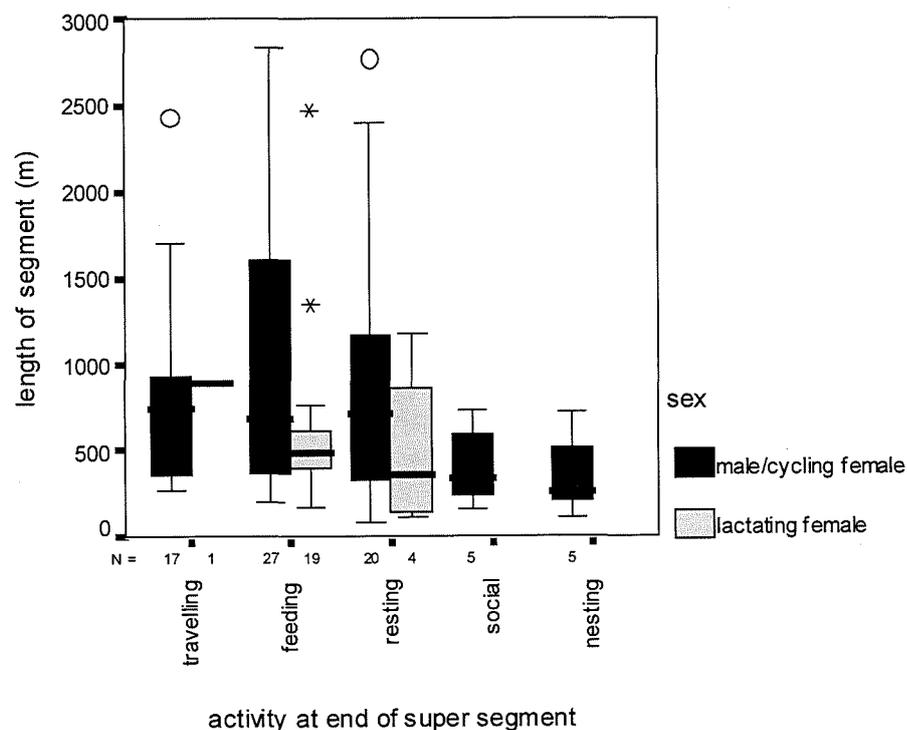
There is evidently variation in the lengths males/cycling females travel to feeding, resting and travelling super-segments, but feeding segments do not generally appear to be shorter than resting or travelling segments, as shown in figure 7j, suggesting these segments cannot be thought of as “unsuccessful” jaunts that were eventually abandoned. The small sample sizes of travel segments ending in nesting and social behaviour make it difficult to conclude if these super-segments really are always shorter in length.

Table 7.5: Mean lengths of super-segments ending in each of the behavioural categories

Activity	Male/Cycling female		Lactating female		Total	
	Mean length (m)	Std. deviation	Mean length (m)	Std. deviation	Mean length (m)	Std. Deviation
Travelling	811.35	570.58	882.00	-	815.28	553.79
Feeding	1040.11	819.61	613.53	515.34	863.89	728.06
Resting	936.05	843.62	506.25	489.41	864.42	803.70
Social	416.40	239.21	-	-	416.40	239.21
Nesting	366.60	251.84	-	-	366.60	251.84
Total	871.78	735.39	606.83	494.14	806.89	691.39

Within the sex groups, one-way ANOVA's comparing the lengths travelled along super-segments that end in different behaviours did not reveal any statistically significant differences in log transformed data (Males/cycling females: $F=1.870$, $df=4,73$, ns; Lactating females: $F=0.958$, $df=2,23$, ns). No one type of super-segment was consistently long and there is no obvious pattern between the distance travelled along the super-segment and the resulting behaviour.

Figure 7j: Box plot showing lengths of super segments ending in each behavioural state for males/cycling females and lactating females

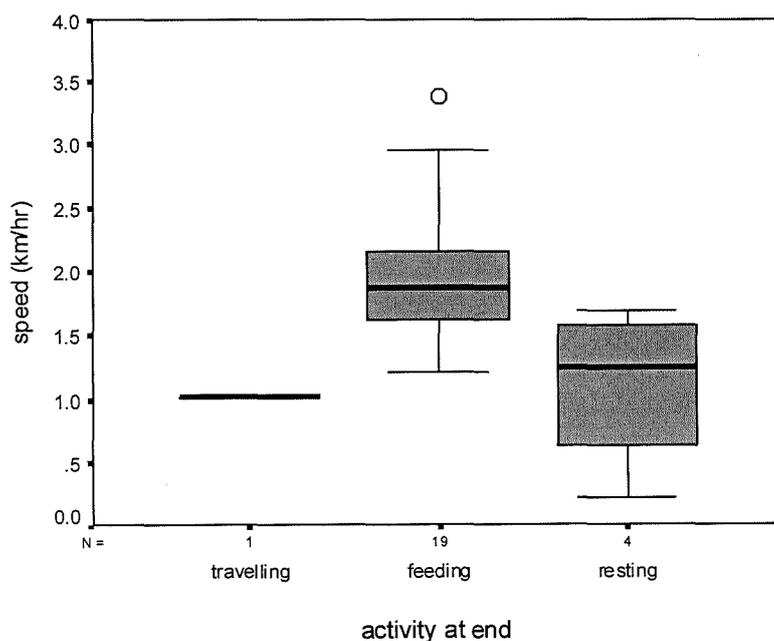


Feeding resources

Several potential rules that *could* dictate when to change direction between super-segments of travel have not satisfactorily explained the patterns observed: super-segments of travel do not seem to be prescribed by heuristics. This does not mean we can simply assume travel is goal-directed and based on spatial knowledge, however. I will now assess the possible use of spatial knowledge by exploring in greater detail super-segments that end in feeding.

Knowledge of the location of a food resource engenders anticipation, which might be detected by changes in the length and speed of travel to a resource; chimpanzees should travel further and/or faster to patches they expect to contain valuable resources. Previous analyses have shown neither males/cycling females nor lactating females travelled *further* along super-segments that end in feeding resources over other super-segments, but there was a suggestion that lactating females travelled *faster* along feeding super-segments. A one-way between-subjects ANOVA comparing the speed of travel of females to feeding and resting stops was performed. This confirmed that females travel significantly faster to feeding resources at the ends of super-segments than to resting stops, as shown in figure 7k ($F=4.715$, $df=2,23$, $p=0.02$).

Figure 7k: Travel speeds of lactating females along super-segments

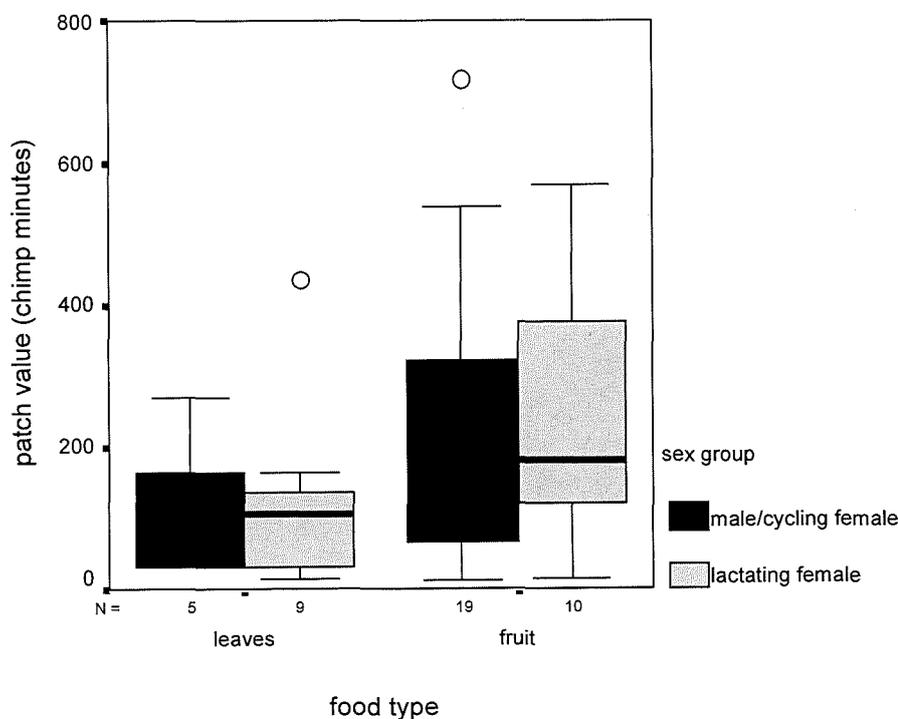


There is no such pattern in the travel speeds of males/cycling females; they travel at similar speeds along all super-segments ($F=0.866$, $df=4,73$, ns). It is not clear, however, if females travel faster along *all* feeding super-segments, or if differences exist between them. It is unlikely all food patches will be of equal worth or significance, and it is possible that those of less value mask the effects on travel of males/cycling females.

Value of feeding resources

Food availability (seasonal or yearly), type (fruit or leaves) and species are variables that may group feeding resources into those that were highly prized and those that were not. Foods were defined as available throughout the year if chimpanzees were seen to feed on them for eight months of the year long study period or more. Foods that were only available for less than eight months were defined as seasonal. The value of a feeding resource was measured in terms of chimp-minutes – the total time a party was observed to feed from one resource.

Figure 71: Box plot of patch values of fruit and leaf patches as consumed by males/cycling females and lactating females

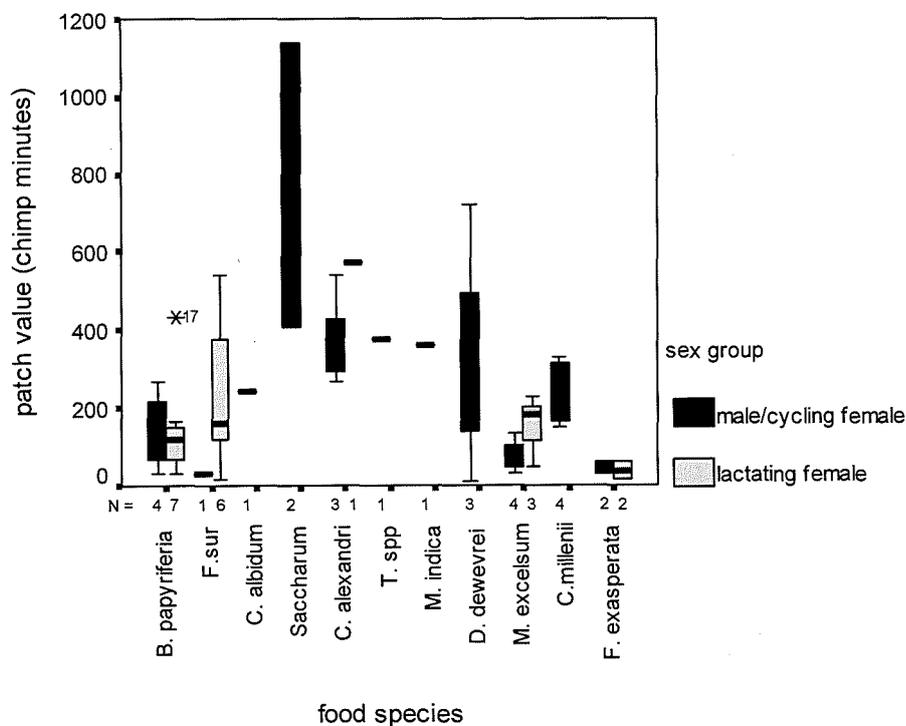


The value of foods did not vary with availability: a 2*2 between-subjects ANOVA of availability type by sex group did not reveal any significant differences in the mean chimp-

minutes associated with seasonal or yearly available foods for males/cycling females or lactating females (main effect of availability: $F_{(1,44)}=0.398$, ns; main effect of sex: $F_{(1,44)}=0.298$, ns; interaction between availability and sex: $F_{(1,44)}=0.278$ ns). Type of food did influence the observed patch value. Excluding sugar cane, fruit patches were of significantly higher value than leaf patches, as shown in figure 7l (main effect of food type: $F_{(1,42)}=4.463$, $p=0.041$; main effect of sex: $F_{(1,42)}=0.003$, ns; interaction between food type and sex: $F_{(1,42)}=0.025$, ns).

Plant species also had an effect on the patch values observed, as shown in figure 7m. An 11*2 between-subjects ANOVA of plant species by sex showed these differences to be significant (main effect of species: $F_{(10,44)}=3.397$, $p=0.005$; main effect of sex: $F_{(1,44)}=1.464$, ns; interaction between species and sex: $F_{(4,44)}=0.327$, ns). Excluding species with only one case, a Bonferonni *post hoc* test revealed the significant differences lay between sugar cane and *B. papyrifera*; sugar cane and *F. sur*; sugar cane and *F. exasperata*; and sugar cane and *M. excelsum*, as illustrated in figure 7m.

Figure 7m: Box plot of patch values of each species consumed by males/cycling females and lactating females



Anticipation of valued resources

I will explore whether the target animals displayed any evidence of anticipating the resources associated with better patch qualities; did they know these “better” resources were there?

A multivariate 2*2 ANOVA of travel speed across sex groups (males/cycling females; lactating females) and food type (fruit; leaves) did not reveal any significant differences in how far or how fast males/cycling females and lactating females travelled to fruit or leaf patches (*length travelled*: main effect of food type: $F_{(1,42)}=0.251$, ns; main effect of sex: $F_{(1,42)}=0.424$, ns; interaction between food type and sex: $F_{(1,42)}=1.770$, ns; *travel speed*: main effect of food type: $F_{(1,42)}=1.044$, ns; main effect of sex: $F_{(1,42)}=1.278$, ns; interaction between food type and sex: $F_{(1,42)}=0.164$, ns). The target individuals did not travel further or faster towards the better-quality fruit patches over leaf patches.

Similar analysis did reveal a significant difference in how *far* individuals travelled to different species, but again no differences in travel speed were apparent (*length travelled*: main effect of species: $F_{(10,44)}=2.159$, $p=0.05$; main effect of sex: $F_{(1,44)}=0.604$, ns; interaction between species and sex: $F_{(4,44)}=0.524$, ns; *travel speed*: main effect of species: $F_{(10,44)}=1.527$, ns; main effect of sex: $F_{(1,44)}=0.007$, ns; interaction between species and sex: $F_{(4,44)}=0.873$, ns). *Post hoc* tests again suggested the differences were between sugar cane and *B. papyrifera*; sugar cane and *F. sur*; and sugar cane and *M. excelsum*. Figure 7n suggests lengths travelled to *C. alexandri* were variable, and *F. exasperata*, a species that did not provide very high-value patches, was eaten after quite long super-segments.

Although the chimpanzees were seen to travel further for certain foods, this does not necessarily imply knowledge of the location of these patches. The longer distance travelled was not always associated with increased patch values, as shown in figure 7o; some high patch-values were observed after only short travel-distances and, more importantly, some of the lowest patch-values were recorded after long periods of travel. A chi-squared test showed there was no association between the length of the super-segment and the patch value ($\chi^2=3.429$, $df=2$, ns).

Similarly, there was also no association between the speed of travel and the resulting value of the patch ($\chi^2=1.921$, $df=2$, ns). As in chapter five, there is no evidence that the chimpanzees predicted better-quality patches, based on measurements of their travel behaviour.

Figure 7n: Box plot of lengths travelled to each food species by males/cycling females and lactating females

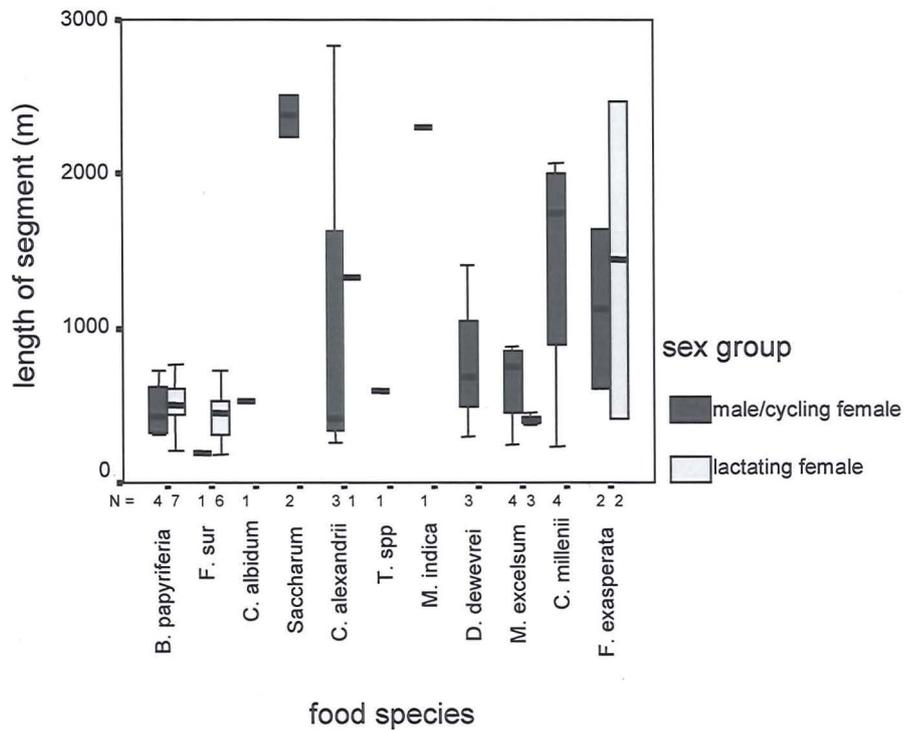
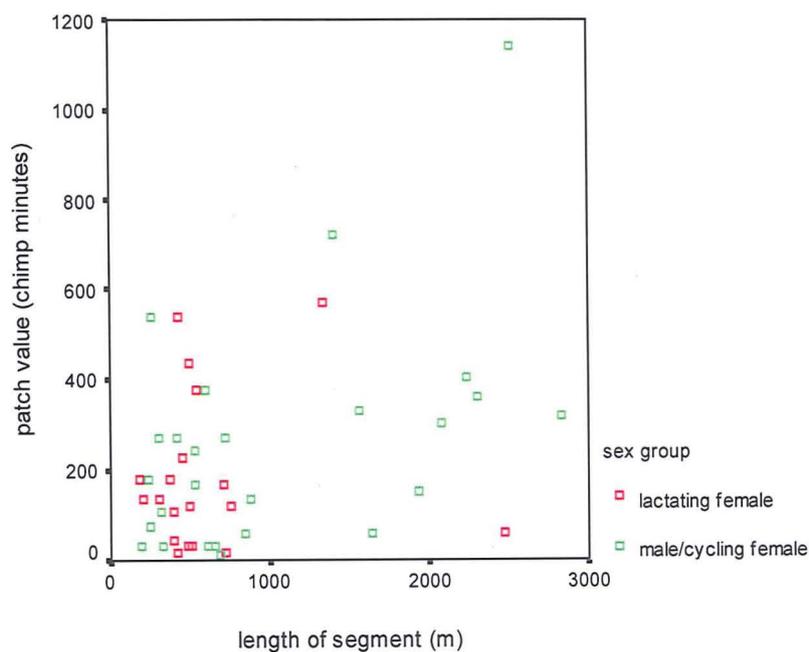


Figure 7o: Variation in patch value as the length of the super-segment increased



Discussion

Both males/cycling females and lactating females organised travel routes into collections of long, straight super-segments, but how these super-segments were put together over the whole route varied. Super-segments were, on average, about 880m long for males/cycling females, and about 600m long for lactating females. The mean linearity of 0.92 confirms these super-segments were very straight and each consisted of five or six waypoints on average, and one or two 20-minute stop-sites. That is, each super-segment was composed of possibly two or three single travel segments, as analysed in chapter five, although the final point of the super-segment did not necessarily coincide with 20-minute stop sites.

Evidently, Sonso chimpanzees walked in straight lines, often to resources that were a long distance ahead in space and time, but this alone cannot imply they knew what lay ahead, or that they “intended” to reach the end-point of the super-segment. Super-segments, although composed of travel segments that are clearly organised in a linear fashion, may not have been the result of prior organisation. They may not have been goal-directed or aimed in any particular direction, but instead could have been based on rules or a more unsystematic strategy.

The use of heuristic behavioural rules producing the pattern of super-segments seems unlikely from the evidence. Change points do not simply occur at certain locations in space and/or time, or when instructed by vocal cues, nor after certain activities have been accomplished or certain distances covered.

If travelling a certain distance were the rule, a relationship would be expected between length and activity, with the longest segments being those that are unsuccessful at finding a resource on the way. On such segments, the animal would reach its ceiling level and literally give up on that path and turn round, so the longest segments should be associated with resting and or travelling as opposed to feeding. This pattern was not evident, but of course for this rule to work as a strategy such unsuccessful jaunts would have to be rare. The animal could not afford to maintain a strategy that did not usually provide it with food and low energetic costs. Therefore, the lack of evidence for this rule does not mean such a rule is definitely *not* being used. However, it does seem extremely unlikely as resting and

travelling were observed at the ends of super-segments of shorter distances than feeding super-segments.

The observation that super-segments could end with the occurrence of any of the behavioural categories, as opposed to just feeding, suggests they may not be goal directed. Chimpanzees oriented long sections of travel in one direction and then sometimes rested or just changed direction at the end of it. This is hard to understand. If all super-segments ended with feeding or engagement in social activity, it would be more immediately obvious that they were goal directed, as tangible goals were being fulfilled. Males are known to be more gregarious than females (Nishida and Hiraiwa-Hasegawa, 1987; Goodall, 1986), and have to maintain social alliances, so it makes sense that they would apparently allow social needs to have dictated direction sometimes, but why resting and travelling should dictate travel segments is less obvious.

One possible reason is that travel was indeed goal directed but occasionally the chimpanzees made mistakes and headed to a patch that no longer contained the food expected. Alternatively, the chimpanzees could have been monitoring potential food resources, as has been suggested for populations of gorillas (Byrne, pers. comm). This would suggest that 56% of the male/cycling female super-segments and 21% of lactating female super-segments were failed attempts at finding food or excursions made entirely to monitor future feeding patches. Given the high costs of terrestrial travel (Pontzer and Wrangham, 2004), this seems like a lot of very expensive mistakes for males/cycling females to make.

The high number of occasions on which males/cycling females rested or immediately headed in a new direction at the end of a super-segment could reflect the border activities of males. Although it seemed overall that there was no pattern in *where* change points of each activity occurred, at least two of the male resting and travelling change points occurred when the focal animal was observed participating in a border patrol (MA04/06/03). Such patrols are characterised by fast walking with frequent stops, and virtually no feeding activity (Boesch and Boesch-Achermann, 2000).

No relationship was observed between the quality of feeding resources (as measured by the value provided to the feeding party in chimp-minutes) and the length or speed of travel along the super-segment leading to the food patch. That is, nothing in the travel behaviour indicated anticipation of good resources. This militates against the possibility that Sonso chimpanzees are using specific spatial knowledge to direct foraging.

Indeed, even if a relationship were found between either length or speed of travel and the resulting patch value, an interpretation invoking knowledge of the resources is not necessary. Longer distances or faster travel could result in larger patch values simply because the animal needs to eat more to recover the energy expended by the travel, without it having any prior knowledge of the location or quality of the patch. This could explain why the patch value of sugar cane was high. Such an explanation seems unlikely, however, because high patch-values were not observed on all long feeding travel segments; long distances were also travelled to *F. exasperata* patches, although this species was associated with low patch values. Thus it remains conceivable that the distance travelled to the sugar cane were consistently long because the chimpanzees knew the location and potential rewards of this patch at least, although they were apparently unable to predict the value of other patches.

The lack of positive effects of food on travel speed and distance could arise because (1) chimpanzees might not alter their travel behaviour even when heading to a valuable resource, i.e. the measures of anticipation were not suitable, or (2) the animals may have knowledge of the location but not the quality of a patch, and so are not able to predict and therefore react to good quality patches, or (3) the animals may simply not know what, if anything, they are heading to. Female chimpanzees were shown to travel faster to feeding resources over other activities, suggesting that travel behaviour can alter when heading to "desired" resources. Females were possibly "excited" by the prospect of feeding, even if they did not know what they were to feed upon.

Thus, the results of this investigation are very ambiguous. Rule-guided foraging based on any one of the simple rules tested here seems unlikely, but the evidence for goal-directed, knowledge-based travel is sketchy at best: super-segments were not always oriented toward apparently valuable resources, and there was no association between the distance or speed

travelled and the resulting value of the patch for most species. Some evidence of knowledge of the location of food resources and an “intention” to feed is conceivable, but this does not fit with all the data. Moreover, the suggested “intention” to feed, arising from the observation that lactating females travel faster along super-segments that end in feeding resources, does not necessarily imply any spatial knowledge. Similarly, sugar cane was the only food for which there is potential evidence of knowledge of location and quality. This is an introduced crop that offered a consistently high-value food and was situated in only one area at the southern border of the Sonso range, with the Royal Mile leading directly to it. To remember the location and value of this patch does not seem to be a particularly demanding task.

Further analysis is therefore required as I am currently unable to determine what mental abilities, if any, the chimpanzees’ ranging is based on. Only by comparing the behaviour of the real chimpanzees with what would be expected from an ape with no knowledge of the location of food resources and no ability to plan goal directed routes will I be able to establish how the chimpanzees of Sonso find food.

Chapter 8

Is cognition necessary?

Does food location entail the complex computational demands it is assumed to (Milton, 1981; Janson, 2000); do chimpanzees actually require mental representations and planning abilities to locate food resources? Although I have found some circumstantial evidence that is not inconsistent with chimpanzees possessing spatial representations, conclusive evidence of the use of spatial knowledge to plan foraging routes is absent so far in this thesis. A radical alternative is that it is equally as productive for chimpanzees to walk without reference to the location of food patches, and simply “stumble” upon resources; knowledge of the spatial location of food resources and planning of foraging routes may not be necessary.

Observational data alone cannot conclusively differentiate between knowledge-based routes that may be planned in advance, and rule-based routes which do not require spatial memory as such. The use of super-segments identified in this study cannot rule out the use of a default strategy of walking in straight lines as opposed to planning routes many steps in advance. Indeed, Janson (2000) states that an animal with no spatial memory of resources “can do no better than to move in a straight line because any turns are likely to bring it back upon previously searched areas”. Therefore, in this chapter I will address the question of what cognitive abilities are *necessary* for chimpanzees to find sufficient food.

Menzel *et al*, (2002) used Monte Carlo randomisation simulations to assess the success of following “road signs” to sites where food was hidden. The location of food items expected by chance (e.g. “random” wanderings) was compared with performance of a language trained, captive ape (Kanzi). Kanzi’s performance was superior to that expected by chance, with the bonobo defeating the Monte Carlo simulation on the majority of trials. That is, Kanzi’s paths were shorter on average than the paths the randomised test took to locate the same places. Kanzi could apparently remember the location of 15 potential feeding places within his 20ha (0.2km²) outdoor enclosure that were not visible at the time and he could use this information to construct travel paths. Kanzi apparently used his knowledge of where the signs were referring to in order to direct efficient searching.

Kanzi was searching for only one food item at a time however, from a possible fifteen locations, and the purpose of his travel was entirely to procure the food. It remains unconfirmed if wild chimpanzees, who forage *and* socialise over a much larger range area with a greater number of potential food patches, also require and use spatial knowledge to plan travel routes.

Following Menzel *et al* (2002), I intend to compare the routes taken by real chimpanzees with a simulated “chimpanzee” lacking all knowledge of the location of potential food, in order to delineate what information is utilised when foraging. Un-knowledgeable individuals - with no information to guide their direction of heading - can only encounter trees by chance along un-planned and un-organised travel routes. The range from which trees can be detected along these routes is constrained by the sensory abilities of the animal and the limits imposed by the environment. Previous analyses in this thesis suggest olfactory and auditory cues to locations of food patches are not important markers for chimpanzees. Appendix A demonstrates the visual detection range in the forest to be 11m when travelling on the forest floor. Thus, the perceptual detection boundary of food trees cannot, presumably, be greater than this distance when travelling on the ground.

Using the tree distribution data and average monthly phenology records, I will compare the length of the foraging routes of real chimpanzees with the minimum distances required by the simulation to locate the same number of food patches. The null prediction must state that the Sonso chimpanzees will perform as well as the simulation in locating food items; there will be no difference between the route lengths of real and simulated animals. If however, the Sonso chimpanzees do use spatial knowledge to plan and execute their daily foraging paths, they should locate food more efficiently than the simulated individual, finding the same number of food rewards whilst expending less energy on travel – as approximated by a shorter range-length.

Methods

The same 20 routes subjected to the Jupp analysis of the previous chapter were used here to compare with simulated foraging paths.

Food-tree locations

Three field assistants and I undertook to map every food tree of potential significance to the Sonso community. Important food trees were defined as those comprising over 80% of the total time spent feeding, as detailed in chapter four. Individual trees of the ten most important food species were recorded. I also recorded the locations of *C. albidum*, *C. durandii*, *C. wightii* and *M. lactea*, which have all been shown to be seasonally important in this year of study or annually important in previous years (Newton-Fisher, 1999). (NB. The locations of *M. excelsum* trees were not recorded.)

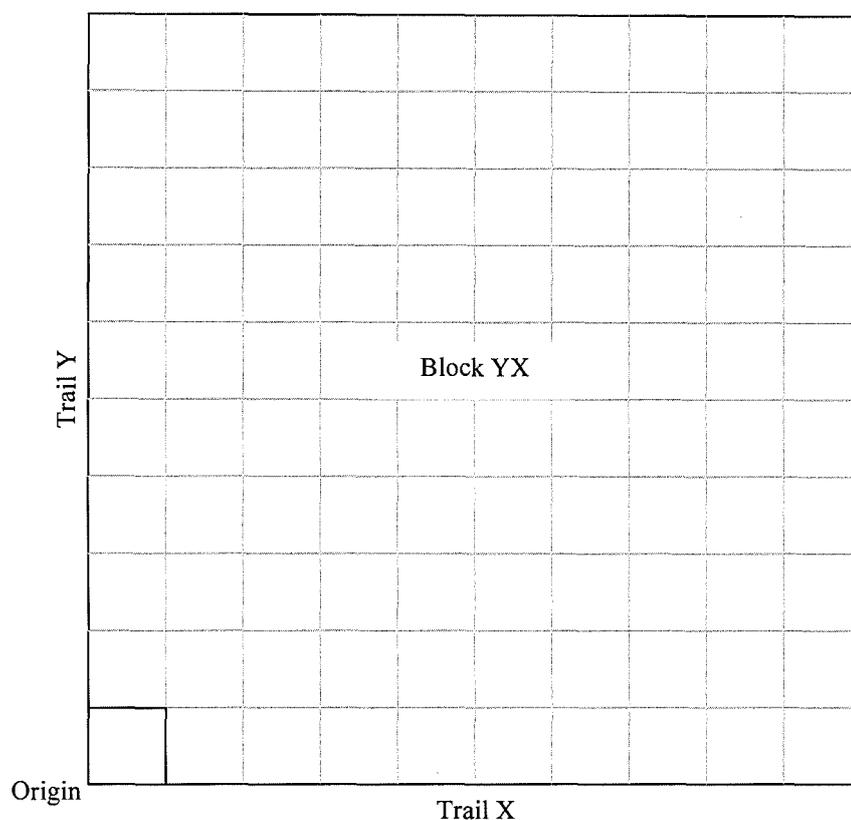
All examples of trees over 10cm diameter at breast height (DBH) from this list of 13 species were recorded on a block-by-block basis, with the location noted within 10m² plots starting from the origin of each block - as illustrated in figure 8a. Trees were listed on checksheets, noting the species, height, crown diameter and DBH to the nearest 10cm. Only trees within the grid system were mapped, reducing the probable size of the range, but it was not possible to assign reliable locations to trees outside of the grid.

From these checksheets, each tree of an appropriate size for feeding chimpanzees was then entered into an ArcView GIS (v.3.2) map of the entire grid system. Suitable examples were defined across all species as those with a minimum DBH of 40cm for trees or height of 20m for epiphytes, except for *B. papyrifera*, for which all trees in a patch over 10cm DBH were recorded. These criteria were chosen based on consideration of height and DBH of feeding trees/epiphytes as recorded at pseudo-random intervals throughout the study period, as described in Appendix H. *B. papyrifera* was included at lower DBH as smaller trees of this species were consistently seen to support feeding chimpanzees.

I calculated the probability that any one tree of each species would provide fruit or leaves in each month, using the BFP phenology data discussed in chapter four. The total number of trees counted that were displaying edible fruits or leaves per month was averaged across the years, and divided by the total number of trees of that species included in the phenology transects. I then rounded this percentage to the nearest ten, with all values between one and five also assigned to the 10% category instead of being designated as corresponding to a 0% chance of providing food. I then generated random binomial sequences with probabilities of positive integers matching each of the phenological percentages (e.g. 1 positive integer in 10, to correspond to 10% probability of having food; 2 in 10 to

correspond with 20% *etc.*). These sequences were used to designate whether each tree encountered would have food available or not.

Figure 8a: Recording tree locations within one block, by dividing each block into 10m² plots



Chimpanzee simulations

I used the same principles to govern the movements of the simulations here as Janson (1988) did in his “geometric model” of capuchin monkeys (*Cebus apella*). Having shown previously that chimpanzees travel in very straight lines until they hit a resource (chapter five), I dictated that the simulation would also travel in a straight line until it detects a resource. This movement rule will show whether the straight-line movements of chimpanzees are based on knowledge (whereby the straight-line movements of the simulation are not as successful at finding food as chimpanzees), or whether no spatial memories are necessary (if the simulation behave like chimpanzees).

For each route, starting from the same point as the real chimpanzee, I advanced the simulated chimpanzee on a trajectory determined by a randomly generated sequence of angles (generated from www.random.org/inform.html). The detection boundary of this naïve simulation was set at 22m – 11m to either side, which is equivalent to the mean 50%

visibility measure when travelling within blocks. Trees outside of this zone were deemed too far away to perceive in enough detail to detect foods. I determined whether food would be provided by any tree that was encountered within the detection zone by cross-referencing the tree species and month of the travel route with the calculated food availability probabilities and used the corresponding binomial sequence to suggest whether the tree was likely to provide food or not. For example, on average one in ten *F. sur* trees provided fruit in June. Therefore, with the randomly generated sequence

[0, 0, 1, 0, 0, 0, 0, 0, 0, 0],

the first *F. sur* tree hit did not provide fruit, nor did the second, but the third did, the fourth did not....the 12th did not, the 13th did, *etc.*

If an encounter with a tree was unsuccessful - no food was provided - the simulation continued along same trajectory until the next tree was encountered, where the above process was repeated. When food was successfully located, the simulated chimpanzee changed direction according to the random-angle generator and the length of the previous segment was recorded. If at any point the simulation's path hit the edge of the grid system, i.e. outside the area of mapped food trees, the path was 'deflected' inwards on the next appropriate bearing, and the segment length was calculated as including both the path sections before and after the deflection.

This process was repeated until the simulated animal had located the same number of 20-minute food patches as the real chimpanzee route. (I assumed that all food patches located on the tree distribution map were capable of providing food to the simulated animal for 20 minutes at least.) Furthermore, the food patches located by the simulation could not include more "leaf" food patches than the real chimpanzee route. So if, for example, the real chimpanzee had fed on three fruit species, one *C. alexandrii* seed patch and one leaf patch, the simulation could not utilise more than one leaf patch along its route: if the first successful encounter provided leaves only, all subsequent leaf-providing trees were ignored and only fruit/seed species attended to. This ensures the composition of the diet of real chimpanzees is maintained in the simulation. If the simulation consumed a larger proportion of leaves, which are abundant in the forest, comparisons with real chimpanzees would be artificial.

When the total number of food patches located by the simulation matched the number of 20-minute food stops made by the real focal animal, I added the lengths of every segment to determine the total length of the foraging route covered by the simulation. This process was repeated five times per focal animal route, giving five simulated travel lengths to compare with one real travel route.

Analysis

I used one-sample t-tests to compare the lengths travelled by the five simulated routes with the one real route, for each of the 20 focal samples, where the length of the actual route was the designated test value in each case. Parametric tests were appropriate despite the small group size as all samples followed a normal distribution and displayed homogeneity of variance. Statistical tests were performed with SPSS (v.10), using two-tailed hypotheses with $\alpha=0.05$.

Results

From the list of 13 species, 4556 trees and epiphytes over 40cm DBH or 20m in height were recorded within the grid system and subsequently mapped. Using this tree location map, and the probabilities of food availability defined by the BFP phenology data, I compared the travel distance required to find the same number of food resources by the real chimpanzee in the 20 focal sample routes selected, and the simulation. Table 8.1 lists the results and Figure 8b illustrates these distances for each focal sample.

Of the lactating females, the routes of three individuals were not significantly different from the lengths of the simulation and three were “better” than the simulated routes, i.e. significantly shorter than the distance required by the randomised simulation to find the same number of food patches. The majority of male routes were significantly *longer* than simulated routes, one (TK30/09/02) was significantly shorter, and three were of equivalent length. For cycling females, two routes were significantly *longer* than the simulated paths, whilst one was shorter.

Table 8.1: Results of five simulated travel routes compared with actual route taken, showing the t values and significance level. Degrees-of-freedom for all tests was four. Italics denote the shorter of significantly different routes.

	ID	Month	Distance travelled (m)	Mean simulated distance (m)	One-sample t-test results	
					t-value	P
Lactating females	KL	January	3954	2831	-2.428	NS
	ZM	March	3176	2543	-1.344	NS
	NB	May	<i>1347</i>	1982	4.620	0.01
	KW	June	2198	2523	1.142	NS
	KW	June	<i>2966</i>	4872	3.845	0.018
	KY	October	<i>2217</i>	3556	6.218	0.003
Cycling females	BN	February	<i>7737</i>	<i>4192</i>	-4.487	0.011
	BN	April	<i>1429</i>	2887	6.272	0.003
	ML	November	3191	<i>1979</i>	-6.123	0.004
Males	TK	January	4025	<i>1619</i>	-11.182	<0.001
	DN	February	<i>7775</i>	<i>3542</i>	-19.597	<0.001
	MA	February	<i>7802</i>	<i>3004</i>	-13.847	<0.001
	ZF	March	2835	2877	0.154	NS
	BB	June	4026	<i>2442</i>	-4.288	0.013
	MA	June	6270	<i>2758</i>	-7.108	0.002
	BB	July	4775	7147	2.257	NS
	DN	July	8887	9043	0.151	NS
	ZF	July	6171	<i>3669</i>	-4.456	0.11
	DN	September	4406	3989	-1.661	NS
TK	September	<i>1877</i>	3110	3.971	0.17	

Figure 8c groups this data according to seasons, as opposed to sex group. From this illustration, no clear seasonal effects are apparent. Four of the five routes that were significantly shorter than distances required by the simulations occurred in seasons two (wet) and four (wet), which are associated with the highest fruit availability. This could be an artefact of fewer males being sampled in these seasons, however, as opposed to a real seasonal difference. One cycling female did travel for significantly longer than was required by the simulation in season four, but all other samples from seasons two and four were of a similar length to that of the simulation.

Figure 8b: Comparison of the actual distance travelled in each focal sample with the mean simulated distance. Stars indicate significant differences. Sex groups are bracketed, with lactating females first, then cycling females, then males.

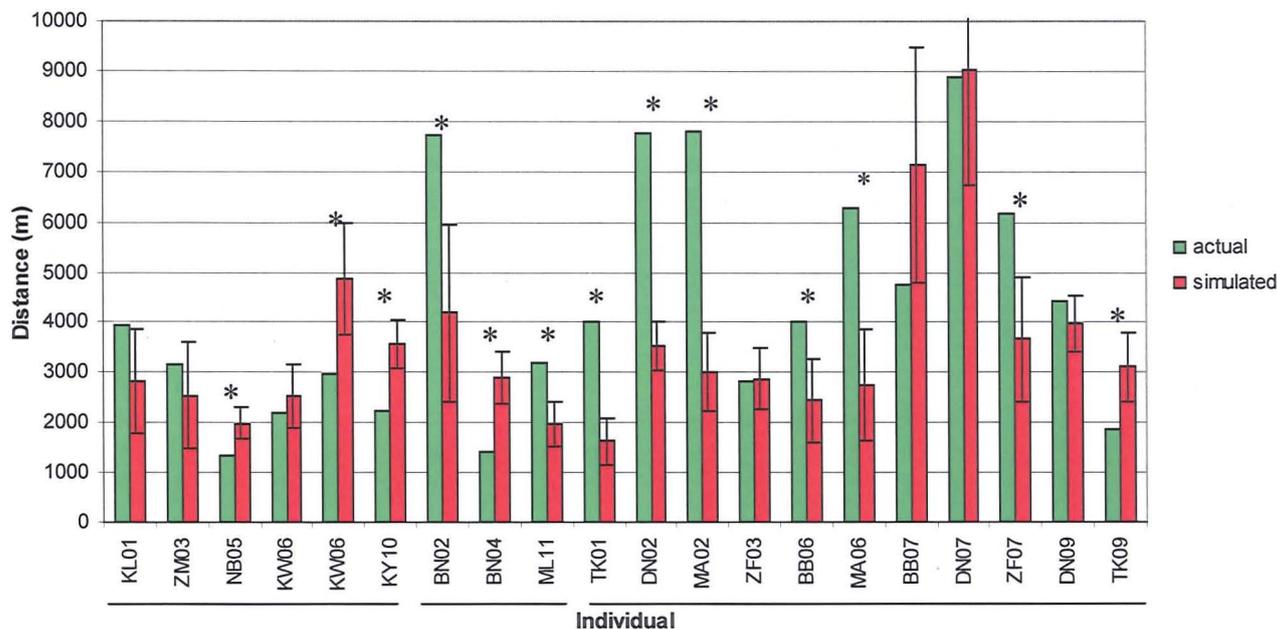
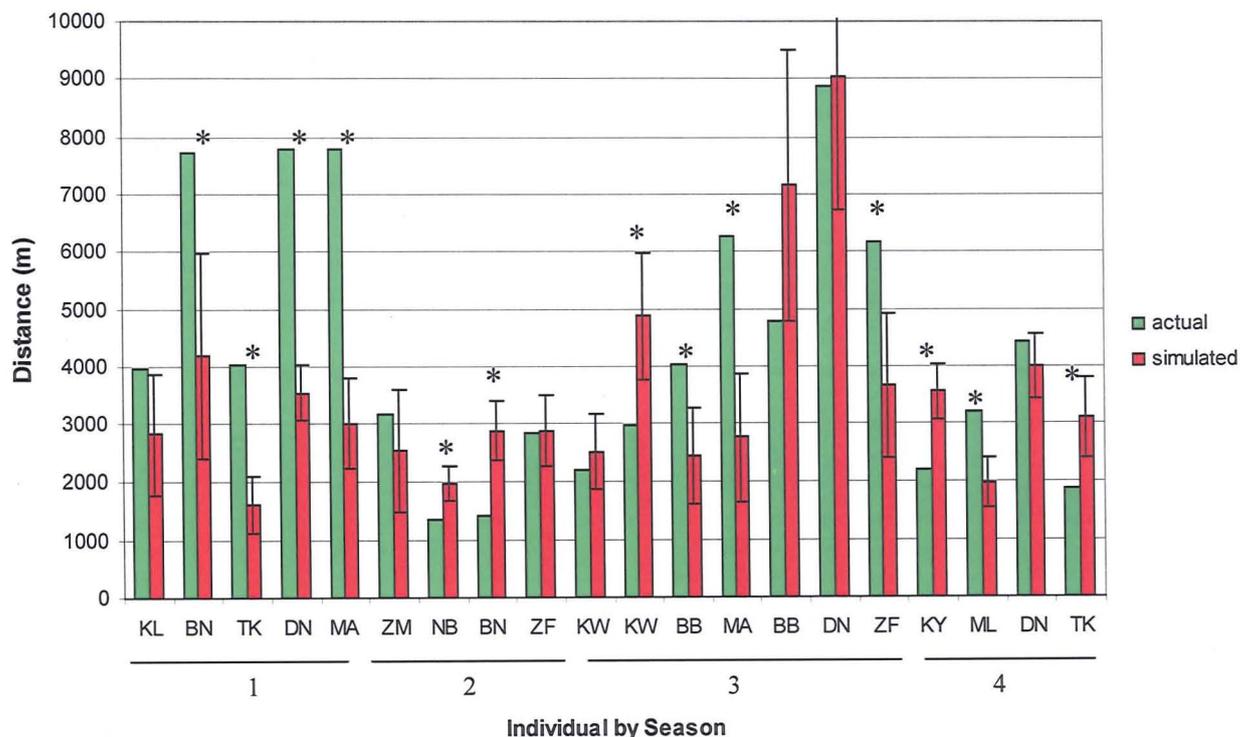


Figure 8c: Comparisons of actual versus simulated distances for each focal sample across the seasons



During season one (dry), when fruit availability is reduced slightly compared with seasons two and four, all routes of males and cycling females were significantly longer than the

simulation, with the one lactating female included in this season travelling a similar distance as the simulation. Season three (inter-rains period), the period recognised as being the most food scarce in Budongo, did not have any obvious effects on the travel behaviour of the individuals sampled over these three months. The lactating female was once seen to walk a similar length to the simulation and once use a significantly shorter path. Male routes were either significantly longer than the distance required by the simulation, or of the same distance.

Discussion

A surprising result is evident from this comparison of the travel distances required by an un-knowledgeable simulation and the travel routes of the real chimpanzees. In contrast to the opinion that chimpanzees must locate food efficiently, they only occasionally appear to limit their travel distances. Only 25% of samples were shorter than the distance required to find food without any *a priori* knowledge of food locations. Seven of the 20 comparisons revealed no significant differences – 35% of focal samples matched a random, un-knowledgeable simulation for foraging efficiency. Most surprising is the observation that eight samples (40%) took significantly longer to find a number of food patches than distances required by simulations with no spatial knowledge, even though the patch definition for the simulations was very conservative.

For seven cases, the null hypothesis cannot be rejected; the real chimpanzee was foraging in such a way that was consistent with the foraging effort of a totally un-knowledgeable individual. This does not necessarily mean these individuals did *not* have any spatial knowledge, rather that they did not need to use it: they would not have expended more energy in travelling had they no knowledge of the location of food resources.

In the majority of cases (13 out of 20), the null hypothesis *can* be rejected – real chimpanzees did not always match the simulation. But of these 13, only five instances were in the direction predicted. Routes taken by real chimpanzees were not shorter than expected by a naïve simulation in eight cases, but were in fact longer than the distance required by an un-knowledgeable animal to find the same number of food patches. These individuals did not display efficient (least-distance) foraging routes.

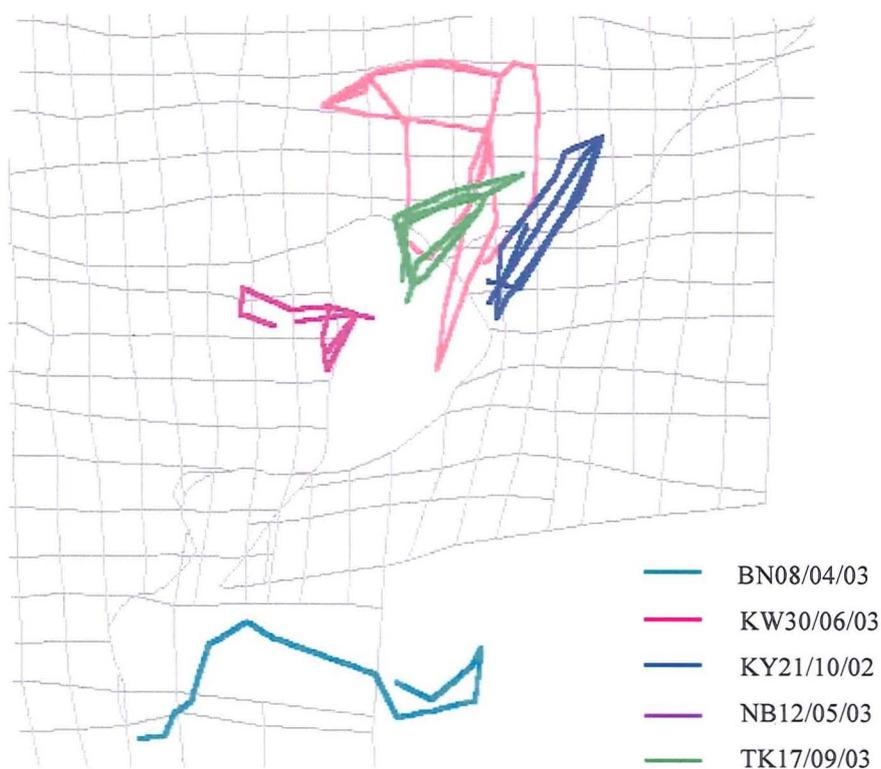
Only cycling females and males displayed routes that were longer than expected. Lactating females matched the simulations or did better (i.e. shorter routes than the simulations). Like all previous analyses, figures 8b and 8c suggest that sexual status had more influence on ranging patterns than season. These observations imply two points: (1) that chimpanzees do have the *ability* to forage efficiently by using spatial memory to find food. And (2) that food - even during the relatively food-scarce months of the inter-rains period - is available in sufficient quantities to have no significant effect on ranging patterns of male and cycling female chimpanzees. Food availability does not seem to be a limiting factor in the daily-range lengths of Sonso chimpanzees. Enough food is available to meet the high energetic costs of terrestrial travel, allowing ranging above and beyond what is the minimum required to find food.

Although spatial knowledge may not be necessary to find sufficient food within the Sonso range in all cases, five individuals *did* display travel routes significantly shorter than the simulations. Three of these individuals (BN, TK, KW; e.g. all those with more than one sample included in this analysis) also displayed, during other focal samples, travel routes that matched or were longer than the mean distance required by the simulation. This suggests the foraging strategy was flexible and dependent on the needs of the individual at the time.

KW showed a change, from a range-length matching that of the simulation at the beginning of June, to a shorter distance than required by the simulation at the end of the same month. June signals the start of the inter-rains period, when food becomes less abundant. Although food apparently remained of a sufficient abundance for males, for KW - a lactating female who is presumably more energetically stressed than males - this reduction may have been of significant magnitude to result in a change of foraging strategy. The change in strategy for BN and TK is less readily explicable; seasonal fluctuations in food availability are less pronounced between seasons one (dry) & two (wet) [BN] and one & four (wet) [TK]. As both are disabled, presumably old individuals, minimising travel distances might be their preferred strategy, with longer-than-necessary routes displayed only when they had particular reasons to travel with other males. Only increased numbers of samples of all individuals across all seasons can determine which are the "normal" foraging patterns for individuals and groups. But the suggestion that energetically stressed individuals have reason, and the ability, to limit their travel routes is upheld by this data set.

NB is an old female who had given birth to what is at least her fifth infant only three months prior to this sample; therefore, her energetic costs might reasonably be assumed to be higher than other individuals. This may require her to reduce her energy budget by minimising travel between food patches. Similarly, KY may need to limit her travel as she is disabled. Her infant (KA) was almost four years old when this sample was recorded but was still being carried by KY almost continually when travelling (pers. obs.), thereby further increasing the cost of travel.

Figure 8d: Routes that were shorter in length than the mean simulated distance required to find comparable food sources.



So yes, chimpanzees that are energetically stressed can reduce travel distances to below the lengths required by the simulation, although this was not observed frequently. But it remains unanswered *how* individuals do this. Figure 8d shows the five routes that were shorter than the simulated comparisons. From this illustration, it is apparent that long super-segments constructed from multiple individual travel segments were not characteristic of these routes. Four of these five routes were very repetitive, with frequent visits back to previously used stop sites. In the randomly generated inter-segment angles of

the simulation, very few turns of close to 180° were made. Although I cannot test this observation statistically, due to the small sample size of angles in each route and simulation, it appears the energetically stressed individuals returned to previously used food patches more often than the simulation. This “return” behaviour is therefore likely based on memories of the location of recently visited patches.

BN’s route is seemingly less repetitive, but she remained within the limited area of the swamp forest throughout the focal sample period. Thus, although these routes are suggestive of the use of spatial memory, the number of food-patch locations that need be remembered and used in travel choices was low, suggesting these foraging paths need not rely on complex computations.

The individuals who displayed the longest super-segments with fewest changes of direction within a route - males and cycling females - walked for as long as or longer than the random simulation. Why did they do so, when other - arguably stressed - individuals could do better than the simulation? For real chimpanzees to use routes that were longer than required by the simulated model they must have been *passing by* trees that had food available; whereas in the simulations, every encounter with a tree that (based on phenological probabilities) had food available was assumed to induce the simulated animal to stop and feed. Why would chimpanzees pass by available food sources, and continue to travel further?

The simplest answer to this question could be that animals did not stop if the patch did not appear to be of sufficient size, whereas the model assumed that all trees with food available were equally attractive. This is unlikely to be the explanation, however, given the parameters I employed in the simulation to denote potential food trees. Sonso chimpanzees only fed from large patches, even when in small parties (see Appendix H), and the tree sizes of these patches were matched in the simulation: only trees of minimum 40cm DBH or 20m height were included. The simulation was not stopping at less attractive patches.

An alternative explanation could be that Sonso chimpanzees do not *attempt* to utilise all the available food patches. They may only feed from a small proportion of “preferred” trees, which they monitor during the appropriate seasons, and only feed from alternatives if they encounter them by accident. Consideration of the number of different trees at which the

Sonso community was recorded eating suggests this may be the case. As shown in Appendix H, the community was recorded feeding from less than 20% on average (range 6% for *C. albidium*, 40% for *F. sur*) of the trees potentially available within the grid system, for six species counted (three seasonally available foods and three fig species eaten throughout the year). Although field assistants could not have recorded every tree that was fed from and not all trees would produce food every year, these percentages are, on average, quite low. That the Sonso community only fed from a certain, limited number of potential food patches, could suggest they remembered the locations of these trees and monitored when food was available on them, and that finding alternative food sources was not a priority.

16 out of 35 resting and travelling super-segments of males and cycling females did end in blocks that correspond with the locations of the six species counted above. Of these 16, 13 of the blocks contained *Ficus* species, which fruit asynchronously and unpredictably. The remaining three super-segments ended in blocks that contained seasonal foods (*C. alexandrii*, *C. millenii* and *C. albidium*), and the super-segment approached these blocks in the season when the trees would be expected to bear fruit. E.g. the apparently non-food-directed super-segment that ended in a block where there was a *C. alexandrii* tree was recorded in January, when *Cynometra* seeds are abundant in the chimpanzee diet. This is suggestive of the possibility that chimpanzees were monitoring trees, using spatial knowledge, but obviously from such a small number of observations no conclusions can be made: more data is required.

Given that Sonso chimpanzees bypass resources, it is apparent that daily range lengths in this community were not *constrained* by finding food. Chimpanzees did not *need* to use knowledge to find feeding patches; un-knowledgeable simulations found as many food patches with significantly shorter path lengths. Only energetically stressed individuals, for whom it was important to limit travel costs, ate from close by resources; a strategy that was likely based on memory of the location and depletion rate of recently visited patches.

Chapter 9

How do chimpanzees find food?

The title of this chapter discloses what I believed I would be discussing at the end of this thesis. When I began, I imagined I would find evidence of chimpanzees employing mental representations of space to plan and direct their daily foraging routes. The task of this discussion would then have been to determine how the chimpanzees formulated plans and evaluate how efficient or effective these plans were, and to attempt to tease out from the data what *type* of representation might be used to support these plans. But, in light of my results, whether or not chimpanzees use mental representations to plan foraging routes may not be the most pertinent question. Aside from a few individual cases, I have found little evidence to suggest that spatial knowledge is used to locate food patches; the data instead suggest that for Sonso chimpanzees, food is abundant enough to render finding it not the primary factor directing daily ranging patterns. This observation entails significant implications for our understanding of chimpanzee socio-ecology and cognition, and raises several questions, including what social or ecological factors do direct travel routes, if not finding food and whether chimpanzees require any spatial knowledge at all. Perhaps the most interesting question is *why* should chimpanzees defend territories that contain super-abundant patches? Following an initial discussion of *how* chimpanzees may find food, I will address these questions in turn in this final chapter.

Do chimpanzees use spatial knowledge to plan foraging routes?

The Sonso chimpanzees move between resources (20-minute stop-sites) using very straight paths and they did not use sensory detection to direct these travel segments (*Chapter 5*). Visual cues could not have been used to orient individual travel segments between 20-minute stop-sites, as all such segments were longer than the distance typically visible in the forest. Olfactory and auditory cues, while they might have been used on occasion, were similarly not *necessary* to direct movements between stop-sites: the majority of movements between 20-minute stop-sites were not guided by vocalisations or strong smelling resources. Some travel segments did coincide with vocal cues from other chimpanzees but this association was not statistically significant.

Furthermore, the travel paths of chimpanzees are organised as opposed to haphazard (*chapters 6 and 7*). Chimpanzee travel routes do not look like the foraging routes of other animals which are known to be perceptually driven, for example desert ants (*Cataglyphis* spp.), whose outbound routes contain thousands of turns where they follow up on every possible hint of food (Wehner and Srinivasan, 1981). Individual travel segments between 20-minute stops sites form structured “super-segments”, whereby the animal travels along the same trajectory across several 20-minute stops, and the variance in inter-segment angles within a super-segment is significantly less than that between super-segments. These facts suggest travel routes are organised according to *something*; chimpanzees do not locate food patches simply by using sensory detection or haphazard wandering. But this “something” does not necessarily have to be planned in advance and based on spatial knowledge – the use of heuristics could also result in structured, organised travel routes.

Super-segments did not appear to be governed by the simple heuristics considered in *chapter 7*, however. None of rules tested (location; time of day; hearing auditory cues; having engaged in certain activities; travelling certain distances) reliably predicted the ending of one super-segment and the start of another. It is possible, however, that some or all of these simple rules interact giving a rather more complicated set of guidelines as to where and when chimpanzees should stop walking in one direction and change to an alternative trajectory. This possibility could not be investigated here, as the sample sizes for each potential combination of rules would have been very small. Therefore, the use of heuristics to direct travel segments and locate food patches cannot be entirely discounted, but there is some evidence to suggest individuals occasionally used spatial knowledge to guide foraging routes.

I presented some evidence suggesting that chimpanzees may be *monitoring* food patches that could be expected to provide food (*chapter 8*). 16 of the resting and travelling super-segments of males and cycling females ended in blocks where potential food trees were located, but this coincidence cannot provide conclusive evidence of knowledge of tree locations. Perhaps the more parsimonious explanation is that this coincidence was entirely accidental, and not based on any knowledge or awareness of the location of food trees at all. If it could be shown that these individuals specifically looked at the trees in question, apparently assessing the food status, a stronger claim of monitoring could be made. Such data are not available from this study, however, and further investigation is required.

Focal animals were more likely to travel further over one segment to *Rafia farinifera* and sugar cane (*Saccharum* spp.) patches than to any other resource (**Chapter 5**). Travelling long distances to particular food species is suggestive of spatial knowledge, and note the observation that the longest super-segments were aimed towards the sugar cane, which provided highly valued food (**chapter 7**). The animals seemingly knew *where* this food patch was and that it offered a high value reward, and thus directed super-segments towards it over long distances. As figure 9a illustrates, the routes to this resource did not all follow one habitual path, but were quite varied. As I discussed, however, sugar cane is only located in one very well defined patch, at the southern boundary of the forest with the Royal Mile road leading directly to it. Thus, directing foraging towards this location may not be computationally demanding – many landmarks and cues point to its location.

Figure 9a: Paths taken to the sugar cane patch south of the forest edge.



I reported there was no overall association between the patch value of places where chimpanzees fed at the ends of super-segments, and the distance or speed travelled to the

patch (*chapter 7*). That is, there was no evidence that the chimpanzees could predict or anticipate the eventual reward of a patch they were heading to, irrespective of whether the route was planned in advance or not. This lack of an association may result simply because it is too hard to predict the size or quality of the patch; certainly predicting the value of a reward is a very difficult problem, as many factors must be accounted for, including the behaviour of other competitors. But there was also no difference in the speed or distance travelled to different *types* of patch. Fruit and leaves, which were consistently associated with different reward values, did not elicit any dissimilar travel behaviour. It should not be very difficult to learn the association that fruit resources generally provide greater reward values. Thus, whilst predicting the absolute reward value of any given patch may be intractable, expecting to observe different travel behaviour between distinct food types is not implausible *if* chimpanzees knew whether they were heading to fruit or leaves. Different rewards should be expected and therefore different travel responses should be evident. The lack of differences in the travel to these patch types therefore suggests that the chimpanzees in fact *did not know* what they were heading to.

Often, super-segments were not even aimed at food sources; only 37% of the super-segments of males and cycling females ended in feeding activity (*chapter 7*). Furthermore, the majority of routes were at least as long as, if not longer than, the distance required by a simulation attempting to find the same number of food resources without benefit of spatial knowledge (*chapter 8*). Finding food within the Sonso area cannot, therefore, be difficult if individuals are able to bypass suitable resources. Janson (1998) suggested brown capuchin monkeys will only bypass resources if there is a large excess of energetic rewards in the environment, i.e. if food is abundant, and this is likely also true of chimpanzees.

Chimpanzees obviously need to find food, but travel was apparently often aimed at other needs, with food being located “casually” on the way and many resources being bypassed: finding food was not the primary factor directing travel. I suggest, therefore, that the male and cycling female chimpanzees of Sonso should be thought of as *convenience feeders*! That is, they feed at some of the resources they happen to pass by when travelling to satisfy other needs. This suggests Sonso chimpanzees do not generally need to use spatial knowledge to find food because of its abundance.

An abundance of food resources could explain why chimpanzees do not travel faster to fruit patches over leaf patches. Rather than the chimpanzees *not knowing* what type of patch they are heading to, they may simply find no patch particularly inspiring as they have an excess of food available: no one type of patch consistently elicits “excitement”, as implied by faster travel.

It is important to note that an abundance of food does not mean that male and female routes should look the same. The routes of lactating females were more often food-directed than those of males and cycling females (*chapter 7*) and therefore they cannot be characterised as convenience feeders. But I argue food is similarly abundant for lactating females as they did not consistently make their travel distances shorter than the un-knowlegeable simulation (*chapter 8*).

Ranging patterns of male and female chimpanzees are expected to be different (Hasegawa, 1990; Chapman and Wrangham, 1993), with female ranging being more closely linked to food distribution patterns (Lehmann and Boesch, 2003). Whilst limiting the distances travelled was evidently not the primary concern of all lactating females, abundance of food alone will not necessarily encourage them to travel as far or for as long as males. There is no need for lactating females to display the same travel patterns as males. Travelling to the same areas or the same extent as males would expose lactating females and their vulnerable offspring to risks (Watts *et al*, 2002) that are simply not necessary if enough food is available for them in smaller areas. The maintenance of sex differences in range lengths and activity budgets (*chapter 4*) and overall travel organisation (*chapters 6 and 7*), at least between males and lactating females, is therefore entirely consistent with the expected behavioural responses to abundant food.

On three occasions lactating females *did* exhibit routes significantly shorter in length than the distance required by the un-knowlegeable simulation, as did one male and one cycling female. Four of these five “efficient” routes were shorter than the simulation because the individuals frequently returned to previously utilised resources (*chapter 8*). The un-knowlegeable simulations did not return to previously used patches with the same frequency as these four real chimpanzee routes did. This provides evidence that chimpanzees are *capable* of remembering the locations of patches over periods of a few

days, and this use of spatial memory is an effective way of reducing overall travel distances.

The individuals that did display efficient travel paths, apparently based on spatial memory, might all have been under unusual energy demands. Three were lactating, which is energetically costly (Altmann and Samuels, 1991), and one of these females was also disabled and another was old. Similarly, the cycling female and male were also old and disabled. Laughlin and Mendl (2004) showed domestic pigs were more likely to remember spatial information if the cost of forgetting was high. The energetic costs of forgetting information were conceivably high for these five old, disabled and lactating individuals, hence the demonstration of spatial memory. That these five energetically compromised - or “stressed” - individuals limited the lengths of their routes does not negate the general claim of food abundance, however. Indeed, that individuals could reduce their travel distances by re-visiting previously used sites indicates the quality and large size of these individual resources, which can only be assumed to be characteristic of food supplies across the whole territory.

Moreover, three of these five individuals (TK, BN and KW) were seen *not* to limit their travel routes on other occasions. Only one of these individuals (KW) displayed the efficient “limited distance” travel route during the less food abundant inter-rains period, so the change in foraging strategy cannot be causally linked to the reduction in overall food availability for two individuals (TK and BN). Instead, it seems individual factors must have caused the change in foraging strategy, as opposed to overall changes in food availability. The remaining two individuals (KY and NB) who displayed distance-minimising routes contributed only one observation each to the analysis of chapter 8, neither of which occurred in the poorest food season. No other samples were available for KY in this study, but the route maps of other samples of NB, although shorter in overall duration, suggest that she used long super-segments at times. Limiting travel distances by frequently returning to previously used resources was not a consistent or unique strategy for her.

I argue no amount of extra food would have allowed these stressed individuals to increase their range lengths at the times when they were seen to minimise the distances travelled. Even with an excess of food *available*, there is still an upper constraint on how much food

one individual can consume based on feeding rates or stomach capacity for example (Chapman *et al.*, 1994). Further investigation of the foraging strategies of lactating females and other energetically stressed individuals is required to gain a better picture of what they do throughout the year, but I predict the strategies employed will not alter the assertion that food availability remains consistently high in Budongo.

That half of the females considered in chapter eight minimised their travel distances at times is perhaps not surprising. Focal individuals were selected on the basis of who could best be followed on the ground, as there was no time available to habituate other individuals to a suitable level (*chapter 3*). The most habituated females were most likely those who ranged around the sawmill area, and did not frequently move large distances away from this area, as those were the individuals field assistants encountered most often. Consideration of all females, with more frequent sampling of each, would likely illustrate that not all lactating females do have to limit travel, but unfortunately such unbiased sampling was not possible in this study due to time constraints.

So in answer to the original questions posed by this study, I conclude that some individuals *can* use spatial memory in certain situations, but generally such spatial knowledge is *not necessary* for the chimpanzees of Sonso as food is abundant enough to render it not difficult to find. It remains uncertain if chimpanzees do plan foraging routes many steps in advance, based on knowledge of the particular locations and reward values of patches, but given the abundant food supply they may not need to. It seems to be almost guaranteed that suitable patches will be found within comfortable distances, in any direction, allowing males and cycling females to feed at their convenience, whilst satisfying other needs.

Throughout this study I have failed to find any effects of season on the travel behaviour of the Sonso community (see *chapters 4, 5, 6, 7 and 8*): changes in food availability associated with the changing seasons did not have any effect on the behaviour of the individuals considered here. Changes in availability could only be insignificant to the Sonso community if food generally remained plentiful - even during the inter-rains period when comparatively less food was actually produced. Even at the poorest food time there were apparently enough resources accessible to ensure individuals did not have to be concerned by falling food production – suggesting that for the rest of the year, food really was super-abundant. This is confirmed by the observation that even during the inter-rains

period, fruit comprised over 50% of the diet, and alternative food sources were not sought (*chapter 4*). Fruit could only continue to make up the majority of the diet if it was plentiful.

Irrespective of what mental processes chimpanzees use to find food, the suggestion that the Sonso community inhabits a territory with super-abundant food resources is interesting in its own right. This finding raises several important questions that I will address below. I can only offer predictions as responses to these questions, as this study was not designed to resolve such issues, but consideration of what is known about both Sonso and other chimpanzee communities does allow for conjecture.

What could direct travel behaviour if not food?

I have illustrated that Sonso travel paths are not “random”, in the sense that they do not look like the simulated routes generated in chapter eight with straight segments occurring at random inter-segment angles, but instead are organised into super-segments (albeit of variable length). But it seems chimpanzees are not primarily searching for food, as their travel routes are longer than necessary for this task alone. Chimpanzees must be travelling for a reason; what then, directs their paths?

As I showed in chapter eight, it is *possible* that some super-segments were aimed at monitoring feeding sites, as the end of some non-feeding super-segments did coincide with the occurrence of potential feeding trees. This is highly speculative, however, and does not account for the occurrence of all super-segments that do not end with food being consumed. Ignoring finding or monitoring food patches, the other factors that could potentially dictate travel behaviour all relate to the social world. That is, social behaviour may direct travel routes.

Chimpanzees are highly gregarious (Goodall, 1986). Travel that allows individuals to remain in contact with many others may be beneficial, in terms of building and maintaining alliances. Whilst this is highly plausible, it should be remembered that relatively few travel segments were cued by hearing vocalisations. Vocal cues are the most obvious guide to the whereabouts of other individuals, but for the majority of segments and super-segments these were not followed. This does not mean that “finding friends” is never a driving force in travel behaviour, but it is unlikely to be the whole answer.

Searching specifically for cycling females, not food or other allies, might explain the travel patterns of males. The long super-segments characteristic of males may be designed to cover large areas of the territory in an attempt to locate swollen females that do not attract attention to themselves with vocalisations. Again this is possible but unlikely. Having shown that females alter their ranging behaviour from when they are pregnant or lactating to when they are cycling, it seems parsimonious that they alter their behaviour to match male ranging as opposed to altering their behaviour to an alternative strategy which males then also adopt. That is, cycling females more likely follow males, rather than males follow cycling females. This is supported by the occurrence of super-segments observed here; males travel in long straight paths whether they are in sexual parties (with cycling females) or not. Cycling females were only rarely seen without males so the same cannot be said of them but it is unlikely that searching for cycling females can explain the travel behaviour of the males in the Sonso community. (Note: This may not apply to other sites. Males in this Budongo community may not need to search for females, as there is such a high ratio of females to males. This suggests it may be in the females' interests to follow males, but not worth the males' while going to look for them. It should not be assumed this is the same across all populations, especially where sex ratios may differ.)

The routes of lower-ranking males are more forward-directed when they are with the core sub-group than when they are not, i.e., they are more likely to change direction more frequently if they are not travelling with high-ranking males (*Chapter 6*). This hints at an alternative explanation of what is directing the travel routes of males. It has been shown at other study sites that high-ranking males are more likely to be involved in territorial defence (Boesch and Boesch-Achermann, 2000; Goodall, 1986; Nunn, 2000). That high-ranking individuals here display the longest super-segments suggests they may be doing so to defend the territory; defence of resources (as opposed to finding them) directs the travel routes.

Defence of the territory is known to be imperative to chimpanzees (Boesch and Boesch-Achermann, 2000; Manson and Wrangham, 1991; Watts and Mitani, 2001; Wrangham and Peterson, 1996), to prevent encroachment by other communities. By covering lots of territory in one day or over a few consecutive days, even without going right to the edges of the territory, males are "defending" their area and preventing others from taking over

their land. Indeed, it may be necessary to travel to the edges of the territory only rarely, as pant hoot vocalisations are thought to be audible over distances of up to 2km (Boesch and Boesch-Achermann, 2000) and so can be used to inform other communities of the presence and locations of individuals without requiring them to meet at borders.

Why defend and maintain a territory with super-abundant food?

A territory with super-abundant food resources has benefits for both males and females in that it reduces within-group scramble competition (WGS) (Wrangham *et al.*, 1996), diminishing the costs of food acquisition. Abundant food also allows all individuals to be more sociable, as enough feeding resources are available to support large parties, whilst reducing the relative costs of additional locomotion (Janson and Goldsmith, 1995). Grouping confers benefits to individuals in the form of predator defence and protection from (van Schaik, 1989; Isbell, 1991).

Surplus food therefore allows individuals to concentrate on other activities. The need for male chimpanzees to form and maintain “friendships” has been well-documented (Goodall, 1986; Wrangham, 1986; 2000; Nishida and Hosaka, 1996) and comparisons of Sonso activity budgets with those of other chimpanzee communities suggests Sonso chimpanzees do have slightly more time available for socialising and resting. At Gombe, between 40% and 60% of the day is spent feeding, and only ~30% is spent resting or socialising (Riss and Busse, 1977); at Tai, 45% of the day is devoted to feeding, 22% to travelling and only 22% to resting and socialising (Boesch and Boesch-Achermann, 2000). In Budongo about 40% of day is spent feeding, in accordance with other sites, but around 40%-50% of the day is spent engaging in resting or social activities, with only 10%-20% of the day spent travelling (*Chapter 4*). More time can be devoted to resting and socialising at Budongo, seemingly because it is not necessary to spend as long feeding and travelling long distances to find large enough resources.

As mentioned in chapter four, terrestrial travel is costly for chimpanzees (Pontzer and Wrangham, 2004) and this cost can be expected to be even higher in pregnant or lactating females who expend more energy suckling and carrying infants (Hunt, 1991; Altmann and Samuels, 1991; Steudel, 2000). Abundant food means females can more easily replace their energetic expenditure, thus reducing the impact of mothering for the Sonso females. (As stated previously, an excess of food does not mean pregnant or lactating females

should be observed behaving as males do, however; travelling as far or being as sociable.) Defending a territory with super-abundant food resources could therefore also attract females to the territory. Williams *et al* (2004) suggest males defend feeding areas, not females *per se*. As food abundance increases, females emigrating from other communities will find the abundant territory more attractive (Wrangham and Smuts, 1980) and therefore be more likely to settle there. Defending super-abundant resources ultimately attracts and holds females to the territory.

But why does population size not increase?

If super-abundant resources do attract many females to a territory, the next question is why population size does not increase to reach the maximum carrying capacity of the range. As any “A-level” biology textbook testifies, it is an axiom of ecology that population size is related to resource availability, as well as other factors such as predation and disease and a relationship between territory quality, food availability and birth-rates has been observed in other primates (Lee, 1987; Cheney *et al*, 1988).

Population size can only increase if enough food is available to support the greater numbers of consumers, and a greater amount of food often, but not always, results in a rise in the population. Many animals may experience periods of food abundance over the course of a year, based on seasonal fluctuations and cycles. But for many species there are also periods of food scarcity which may be regular (seasonal) or unpredictable (caused, for example, by extended climatic changes). It is these periods of reduced food-availability that exert influence over population size (e.g. see Lee and Hauser, 1998). For the Sonso chimpanzees, however, I have shown that even during the period of the severest annual food scarcity, food is still abundant and has no impact on behaviour. If food is plentiful throughout the year, why does the population size in the Sonso area not increase, or – put another way, if the population size is increasing, why is super-abundant food still evident?

I can only speculate on the answer to this question, but I predict it is based on sex ratios. If females are attracted to territories with abundant food (Wrangham and Smuts, 1980; Williams *et al*, 2004), more and more females should enter the community. As more individuals enter, the relative abundance of food per individual decreases, as does the ability of males to defend all the females from infanticide. Thus, the chances of survival of members of the community will decrease, as will the number of new females entering the

community, suggesting the size of any one community will fluctuate over time even if all other variables such as predation rate and absolute food production of the forest remain constant. The Sonso community of Budongo currently has a hugely skewed female: male sex ratio, with 19 parous, adult females present in the community at the time of this study, compared with just eight adult males. The population size of the community has increased over the past ten years (Reynolds, in press) but for how long it continues to do so remains to be seen.

Defending a super-abundant food patch is not unique to chimpanzees. Bell Miner birds of south-eastern Australia exclude other birds and competitors (of other species) from their territories (Loyn *et al*, 1983). This territorial behaviour results in effective defence of food supplies (tree parasites), to the extent where there is an excess of the parasites. The population of Bell Miner birds in one territory cannot eat the parasites at a rate that controls their numbers, meaning the parasites are present at a density whereby they have an adverse effect on the trees. Bell Miners are known to move territories, presumably when the numbers of parasites reach such high levels they impact on the trees. When the Bell Miners were removed from the territory under experimental conditions by Loyn *et al* (1983), other bird species moved in and the numbers of parasites fell – with over 650 psyllids removed per minute by the incoming bird populations, compared to the 280 removed per minute by the Bell Miners. The Bell Miner population did not increase despite there being an excess of food, presumably because factors such as birth rate were already at the maximum. As I have described, birth rate is already high in Sonso, so this may also be the case here.

How might other chimpanzee communities cope?

Having argued that Sonso chimpanzees benefit from inhabiting a territory with super-abundant feeding resources, it is necessary to consider whether other chimpanzee communities inhabit similarly abundant areas as any differences in habitat could result in very interesting differences in behaviour and socio-ecology across communities. Hashimoto *et al* (2003) showed that monthly fruit abundance was high enough for other chimpanzee communities in Uganda, Congo, and Democratic Republic of Congo not to have any impact on party size, stating: “Seasonal changes in fruit abundance did not explain the changes in party size”. Fruit abundance only affected party size for the communities where fruit availability was generally low. This suggests it is possible that

other chimpanzees also inhabit super-abundant areas, but not all communities across Africa necessarily do so.

Food availability does have significant negative effects on some chimpanzee communities. Wrangham *et al* (1996) suggested the annual period of marked fruit scarcity is responsible for the high average inter-birth interval (IBI) exhibited by Kibale chimpanzees. Consideration of mean inter-birth intervals (IBIs) across other long-term chimpanzee study sites suggests that one pattern of food abundance is not common to all communities. As shown in table 10.1, chimpanzees of the Kanyawara community, Kibale Forest, and of the Mahale Mountains, Tanzania, have much higher average IBIs than at other long-term study sites. The study communities at Bossou, Guinea; Tai, Cote d'Ivoire and Gombe, Tanzania, all have comparable IBIs to Budongo, suggesting food at these sites is similarly abundant. Low inter-birth intervals are indicative of reduced food (Williams *et al*, 2002, 2004; Wallis, 1997).

Table 10.1: Inter-birth intervals (months) for six long-term chimpanzee study sites

Chimpanzee site	IBI (months)	Reference
Bossou	~62	Sugiyama (1994)
Budongo	~63	O'Hara (pers. comm.)
Gombe	~62	Wallis (1997)
Kibale	~72	Wrangham (2002)
Mahale	~72	Takahata <i>et al</i> (1996)
Tai	~65	Boesch and Boesch-Achermann (2000)

It is remarkable that the IBIs of the Kanyawara community of Kibale are so much greater than those of Budongo, when the two forests are geographically close and were probably historically linked (Patterson, 1991). Plumptre *et al*, (2003) suggest the density of chimpanzees in Kibale forest is almost twice that of Budongo. It is possible then, that the Kibale population is in a different stage of the fluctuating population cycle, with the rate of population increase now declining having reached the maximum carrying capacity of the forest, whereas Budongo appears to be in an increasing phase. That the Kanyawara community of Kibale forest is known to rely on Terrestrial Herb Vegetation as a fallback food (Wrangham *et al*, 1996) might be symptomatic of a population that is at the carrying capacity.

Consideration of IBIs is only a proximate measure of food abundance, however, and tells us nothing about the *types* of food available in each of these locations. A standardised measure of food availability is required to determine exactly what conditions each community lives in, but this would be very hard to achieve as such a measure must account for the different food species and levels of competition from other animal species at each site.

Assessment of the published records of chimpanzee diet from each of these sites does reveal interesting differences, however, particularly between the study sites with similar IBIs. Considering the diets and behaviours seen in Budongo, Bossou, Gombe and Tai, an intriguing possibility emerges. Chimpanzees at Bossou, Gombe and Tai are known to use a variety of tools to extract food resources not exploited within Budongo (Whiten *et al*, 1999). It seems plausible that these communities maintain low IBIs by using complex cognitive abilities to extract embedded resources (see Call, 2000 for an analysis of the mental representations that could underlie such foraging). That is, chimpanzees in other areas may “cope” with lesser fruit availability by “imaginatively” exploiting other food resources that the Sonso community do need to consume. In fact, Sonso chimpanzees display only one tool-using behaviour out of 27 seen at other long-term study sites that result directly in obtaining food (Whiten *et al*, 1999). This one behaviour, pounding fruit on wood to smash open the hard casing, was observed only once during this study, performed by ZM – a lactating female. I do not mean to suggest that Sonso individuals lack the cognitive abilities to make and use more tools, but rather that, again, they simply do not need to bother as plenty of food is already available. If necessity is the mother of invention, the Sonso chimpanzees simply do not need such innovations.

Across Budongo forest, the un-logged areas of Budongo have a lower density of fig trees and the prevalence of monkey species is different but chimpanzee density remains constant (Plumptre and Reynolds, 1994): the same number of chimpanzees live in the similar-sized logged and un-logged compartments of Budongo. If these un-logged areas do have less abundant food - as would be expected given the lower monkey densities and fewer fig trees, coupled with the absence of sugar cane and introduced *Broussonetia papyrifera* - the chimpanzees must have to “work harder” to find suitable resources. Evidently they do manage to find enough resources as their numbers are not reduced. This must be based on

the use of spatial knowledge or some other adaptation. The differences in behaviour and ecology of Budongo chimpanzees in logged and un-logged areas are thus a very exciting study prospect.

One important implication of this study is that sweeping generalisations about the difficulty or harshness of environments may not be valid; not all tropical forests are going to present the same problems and challenges to chimpanzees, and not all communities will be subject to the same social and ecological constraints. We therefore have to consider each population in its own environment and compare differences in ecology and behaviour more systematically, with standardised sampling techniques.

Do chimpanzees have any spatial knowledge?

I have shown that chimpanzees use spatial memory to remember the locations of suitable food patches over the course of a few days, and orient their travel segments directly to these patches. This kind of spatial memory is not perhaps akin to the precise “where, when and how much” representations of food locations that Optimal Foraging theory predicts and many primatologists assume, however (Todd, 1993; Bateson and Kacelnik, 1995; Giraldeau, 1997). But even though I have not found indisputable evidence of this type of complex representation in chimpanzees, it would be silly of me to claim chimpanzees did not have *any* spatial knowledge.

Every time I mention territorial defence, I am implying spatial knowledge on behalf of the chimpanzees. Chimpanzees must have knowledge of where their borders are, as they cannot defend an area if they do not “know” it is theirs. In some species this knowledge can be based on recognition of scent markings as opposed to long-term memories of spatial locations, but chimpanzees are not scent-orientated animals and do not have the specialist adaptations to use such cues (Prestrude, 1970). Yet other species use vocal cues to determine the edges of their range. For example, Waser (1977) showed grey-cheeked mangabey groups of Kibale forest, Uganda, adopt a spacing system based on site-independent avoidance, as opposed to defending a territory. This system is characterised by loud, frequent vocal exchanges with retreats by one group, resulting in a fluid home range. This type of inter-group spacing does not necessarily require spatial knowledge, just avoidance responses upon hearing long-distance vocalisations of other groups. Chimpanzees are definitely not engaging in such site-independent inter-group avoidance;

they are known actively to *defend* a territory (Boesch and Boesch-Achermann, 2000; Goodall et al, 1979; Watts *et al*, 2002; Wrangham and Peterson, 1996), which is not fluid in this way. Such a territory can only then be maintained through spatial knowledge, by remembering and recognising where the edges of their own territory lie, and where the territory of the next community begins.

Thus, although I cannot determine anything about the type of mental representation chimpanzees use to encode the spatial layout of their environment, or how much detail is remembered within the territory boundaries, I cannot dispute the assumption that chimpanzees do have some spatial knowledge. Whilst the Sonso chimpanzees do not need to store precise information of the locations of all potential food resources, it is beneficial for certain individuals to remember the locations of recently visited patches at times when they may be under energetic or nutritional stress. Whether or not other chimpanzees require or, indeed, have the ability to use more detailed or complex representations of their spatial environment remains to be tested. Based on the evidence of the Sonso community, it is possible that no chimpanzees code more specific information about the location of food patches. This would only be likely if all communities inhabited territories with super-abundant feeding resources, however; when food is plentiful and fairly evenly distributed, spatial representations of locations may not be necessary as food can generally be found within distances that can be supported by energy budgets. But as I discussed above, this super-abundance is probably not the case for all communities (although greater consideration of absolute food supply is required). Therefore, similar studies at other sites across Africa may yet reveal flexible spatial representational abilities in wild individuals that reflect more the capabilities hinted at in studies of captive chimpanzees (Tinklepaugh, 1932; E. Menzel, 1973; C. Menzel, 1999; C. Menzel *et al*, 2002) and other species (Sigg and Stolba, 1981). Such abilities may well be present in Sonso chimpanzees, but they are not evident. To answer questions about the nature of chimpanzees' spatial knowledge, consideration of communities other than Sonso are required.

Conclusions

The aim of thesis was to determine whether chimpanzees use spatial representations to plan foraging routes. I have not been able to answer this question satisfactorily, but I have shown that finding food is *not* very difficult for the chimpanzees of the Sonso area of

Budongo. They can, when necessary, use memories of the locations of recently visited trees to minimise their travel distances. So chimpanzees *can* use spatial knowledge of food-patch locations, but within Sonso the need to do so is uncommon. I cannot, therefore, draw any inferences about the type, complexity, scope and utility of the spatial representations chimpanzees may use, as planning abilities were apparently un-necessary in this study community. This lack of evidence regarding the use of spatial knowledge should not be taken to imply that chimpanzees are not *capable* of using complex representations of space, however. As with any scientific investigation, negative results do not necessarily negate hypotheses. Chimpanzees may well use, or be capable of using, complex cognitive “maps” to plan travel routes, and only further investigation of the spatial knowledge of other communities can show whether this is so.

The general assumption that travel is largely food directed and constrained by the need to minimise distance is not correct: finding food was not a sufficient pressure to explain the patterns of travel observed in the Sonso community. Moreover, the chimpanzees of Sonso defend and utilise a territory that encompasses super-abundant feeding resources, and this allows the males of the community to be “convenience feeders”. Travel was not dictated by the need to locate limited or scarce food resources, but instead food patches were common enough to allow travel frequently to be directed towards satisfying other needs, such as territorial defence, with food taken as it was passed along the way. Many animals may experience periods of food abundance; the difference is that in Sonso this abundance seems to be constant. This is a remarkable finding given the common assumptions that food is very difficult to find for large-bodied, social living, fruit eating animals (Milton, 1981, 1988; Gibson, 1986; Janson, 2000).

This conclusion has important implications on both a practical level, and a theoretical level. Investigating feeding behaviour has direct implications for conservation and management issues (Bakuneeta *et al*, 1995; Plumptre and Reynolds, 1994). A better understanding of chimpanzee (and other animal) socio-ecology is required to predict how changes in forest structure will affect communities, but the importance of maintaining a diverse and abundant food supply is clear. While chimpanzees may have the mental abilities to cope with reduced food availability, such reductions will probably greatly influence their social behaviour and population structure. Loss of naturally occurring food sources will encourage chimpanzee to seek alternatives and this may often mean raiding crops grown in

close proximity to forest areas. Indeed, sugar cane crops were one of the most important food species contributing to the Sonso diet, despite there being plentiful food within the forest. Loss of food trees within the forest would surely only exacerbate the problem of crop raiding. Thus, forest-management policies must pay close attention to the important food species of chimpanzees and other forest animals. The relationship between understanding what animals know and “think”, and how we should act to conserve them, is becoming increasingly important.

Investigations of other primate species are also required to determine the validity of suppositions that food is particularly difficult to find for frugivorous monkeys and apes. Chimpanzees may be the only primates capable of defending super-abundant resources, or it may be evident across many taxa. Furthermore, we may have to rethink what we know about forest-dwelling chimpanzees; the basic assumption of food being difficult to find is apparently not true for all communities. By defending a super-abundant feeding area, chimpanzee socio-ecology - at least of the Sonso community - is not what it was thought to be (for example, see Ghiglieri, 1985). Investigation of other communities is required to determine whether the situation at Sonso is unique. The Sonso ecology may be unusual in permitting this strategy to be used, or this situation may be common to many chimpanzee communities. Until similar studies are performed on other communities, we would be wise not to assume that all chimpanzees are necessarily conforming to the same socio-ecological constraints.

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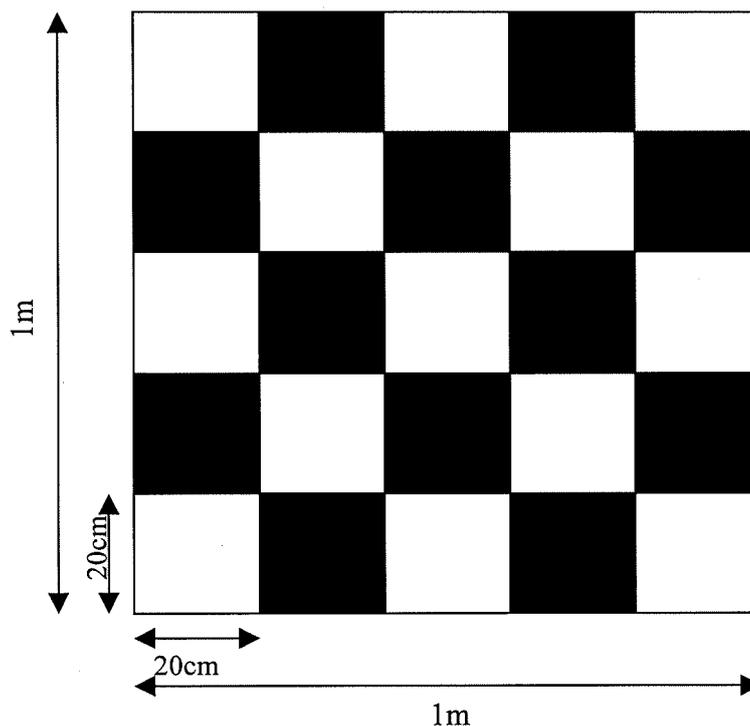
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Appendix A

Visibility calculations within the forest

Visibility was recorded using a 1m^2 board painted with alternating 20cm^2 black and white squares, like a checkerboard (13 white squares and 12 black). This was placed vertically on the ground at a defined location by the field assistant, and one end of a tape measure secured on the ground next to it. I then walked away perpendicular to the painted side of the board. I used the tape measure to determine the distance at which 50%, 75% and 100% of the black and white squares were obscured by the undergrowth, that is, when I could only see approximately 6, 3 or no black squares. This is equivalent to 50%, 25% and $>1\%$ visibility.



I recorded visibility measurements from five randomly chosen blocks, at five locations from the trail into the block or within each of these blocks, and east and north along the trails from the origin of the block. Thus, visibility was recorded to 50%, 25% and $>1\%$ levels at 35 locations within the forest, as shown in the table below.

Block	Visibility level (%)	Measurement (m)									
		Within Block					On Trail		Mean		
		1	2	3	4	5	East	North	Block	Trail	All
<i>G.E</i>	<i>50</i>	8	13	8	15	7	20	29	10	25	14
	<i>25</i>	11	16	11	18	12	29	30	14	30	18
	<i>>1</i>	16	20	13	22	16	31	35	17	33	22
<i>I.E</i>	<i>50</i>	12	12	13	9	11	29	21	11	25	15
	<i>25</i>	16	17	22	10	16	32	26	16	29	20
	<i>>1</i>	21	24	25	14	18	35	28	20	32	24
<i>C.3</i>	<i>50</i>	20	12	11	7	8	44	28	12	36	19
	<i>25</i>	24	15	13	9	11	49	37	14	43	23
	<i>>1</i>	29	21	16	12	16	55	42	19	49	27
<i>G.6</i>	<i>50</i>	7	9	14	7	15	30	31	10	31	16
	<i>25</i>	8	14	16	9	19	35	36	13	36	20
	<i>>1</i>	11	18	19	11	21	40	37	16	39	22
<i>B.C</i>	<i>50</i>	13	12	14	9	15	29	21	13	25	16
	<i>25</i>	14	15	16	13	18	30	21	15	26	18
	<i>>1</i>	17	20	19	16	22	34	26	19	30	22
<i>Forest mean</i>	<i>50</i>								11	28	16
	<i>25</i>								14	33	20
	<i>>1</i>								18	37	23



Appendix B

Classification of Sonso Community

B1: Age group classifications

Classification	Age criteria	Characteristics
Infant 1 (Inf 1)	Birth to 2 years	Moving with mother. Consume some solid foods but not weaned from mother's milk.
Infant 2 (Inf 2)	2 – 4 years	Moving away from mother. Feeding on solids more than Infant 1, becoming weaned. Still carried by mother.
Juvenile (J-)	5 – 9 years	Still close association with mother but now feeds and walks independently. Mother has resumed cycling. Increasing independence from mother. May or may not be in same sub-group as mother.
Sub Adult Male (SAM)	10 – 15 years	Development of testes. Beginning to challenge females for dominance.
Sub Adult Female (SAF)	10 – 14 years	Beginning of sexual swellings, which may be irregular or prolonged. Adult males not very interested when in oestrous. No offspring.
Adult Male (AM)	16 years +	Sexually mature; testicular development complete. Face fully black. When socially adult will dominate females and may challenge other males.
Adult Female (AF)	15 years +	Regular swelling cycles.
Old		Baldness developing around the head and lower back. May be skinny and bony.

B2: Sonso Community as at September 2003

Name (code) Date named	Age/Sex	Characteristics
Black (BK) 9/10/93	Adult Male	Black face. Strong. Very hairy. Very black.
Bwoba (BB) 2/9/92 (coward) e.d.o.b 1988	AM	Flat brown face. Small bald patch. Big testicles. Mother is Zana. <i>Juv : 93-97</i> <i>SAM: 98-03</i> <i>AM: 2003/4</i>
Duane (DN) 1/10/93	AM	Alpha male. Confident. Strong and steady. Dimples on cheeks. Heavy brow ridge. Intense eyes.
Maani (MA) 5/8/92 (strong)	AM	Muscular, some grey hairs on back. Back has defined shape. Second finger on right hand half missing and third swollen. Long face. Two white scars by nipples.
Nick (NK) 3/1/95 e.d.o.b 1985	AM	Son of Ruhara. Round, brown face with dark patches, lighter big round ears. <i>Juv: 90- 94</i> <i>SAM: 95-00</i> <i>AM: 2001</i>
Nkojo (NJ) 4/9/92 (scar)	AM	Slit on lower left ear. Black around bald patch. Oldish looking. White hair around mouth. Nervous around people. Two white scars on top of head.
Tinka (TK) 30/9/92	AM	Both hands deformed. No hair on right hand or wrist of left hand. Scarring on right hand, with permanently bent fingers, can use thumb though. Left hand twisted. Eye problem and possible eczema – scratches a lot. Walks with stoop.
Zefa (ZF) 25/11/93	AM	Brown body. Black spots on face. Dimples. Stocky legs. Middle finger on right hand half missing and third swollen. Mother is Banura.
Banura (BN) 20/10/93	Adult Female	Bald head. Large ears facing forward. Black face with deep sunken eyes. Swollen right club-foot. Mother of Zefa, Shida, Beti (and Ben, died December 2001 (12/01)).

Clea (CL) 27/8/97 e.d.o.b. 1985	AF	Brown face with long hair. Immigrated 1997. Mother of Clint - born 04/02.
Flora (FL) 8/5/03	AF	Right hand is missing from wrist like WL. Has cut in right ear and toes of right foot are splayed. Scar on upper lip.
Harriet (HT) 11/9/96	AF	Small bald patch. Black face. Looks old. Mother of Hawa and Hellen. Immigrated 1996.
Janie (JN) 28/9/95	AF	Long hair around face. Dark thick hair. Stocky legs. Mother of Janet.
Kalema (KL) 28/4/92 (lame)	AF	Right hand twisted – can't move it. No hair on wrist. White beard on muzzle. Mother of Bahati and Kumi.
Kewaya (KY) 28/4/92	AF	Right hand more twisted than Kalema's – hand sticks out away from body – not used. Dimples and dark masculine face. Daughter of Zimba. Mother of Katia.
Kigere (KG) 11/3/92 (foot)	AF	No foot on right leg. Slit on right ear. Mother of Kadogo (dead), Keti and Kuki. Premature infant stillborn, early 09/97.
Kutu (KU) 8/8/92 (ear)	AF	Slit on top of left ear. Edges of face brown. Round muzzle with white hair like Kalema. Mother of Kato, Kana and Kasigwa.
Kwera (KW) 5/8/92 (brown)	AF	Brown face and belly. Belly covered with thin hair. Receding hairline with short spiky hair on top of head. Mother of Kwezi and Karo.
Melissa (ML) 10/01	AF	Wrinkly masculine face like Jambo. Mother of Mark and Monika.
Mukwano (MK) 28/4/92 (friend)	AF	Brown face with black spots. Slim. Right foot lame. Very bald head. Thought to be pregnant 1998. Mother of Monday born 11/02 , disappeared 07/03.

Nambi (NB) 21/6/94	AF	Dominant Female. Bald patch on forehead. Slit on upper part of left ear. Old looking. Confident around people. Mother of Muga (dead), Andy (dead), Musa, Nora and Night.
Polly (PL) 07/03	AF	White scar on back of right hand and extending up arm. Mother of Pascal. First seen 01/03.
Ruhara (RH) 10/4/93 (bald)	AF	Black face with large bald patch. Thin hair on back. Mother of Nick, Rose and Ramula. Looks old.
Sabrina (SB) 04/01	AF	Large bodied with round face. Mother of Sally and Sean. Seen infrequently; only twice between 08/02 and 08/03.
Wilma (WL) 10/01	AF	Right hand missing with wart under right eye. Balding. Black face. Mother of Willis-disappeared 12/01.
Zana (ZN) 2/9/92	AF	No fingers on right hand but thumb present. Left hand twisted and loose. Third finger stiff and straight. No hair on wrist. Mother of Bwoba, Zalu and Zed.
Zimba (ZM) 11/8/93 (swollen)	AF	Back of right hand palm swollen. Broad ears facing forward. Mother of Gonza (disappeared), Zig, Zak and Kewaya.

Non adult members of Sonso Community

Name (code) Date named	Age/Sex	Age group changes	Characteristics
Gashom (GS) 20/7/94 e.d.o.b 1989	Sub Adult Male	JM: 94-98 SAM: 99-04	Gentle. Large emerging testicles. Small black line across nose. Knuckles of index and forefinger swollen on right hand.
Bob (BO) 14/12/92 e.d.o.b 1990	SAM	JM: 95-99 SAM: 00-05	Mother is Ruda (dead). Big ears and very round muzzle.
Musa (MS) 21/6/94 e.d.o.b 1991	SAM	Inf 2: 94 - 95 Juv : 96-00 SAM: 01-06	Mother is Nambi. Darkening face.

Kato (KT) 13/10/93	SAM	Inf 1: 9/93-8/ 95 Inf 2: 9/95-8/98 JM: 9/98-8/03 SAM 9/03-9/08	Mother is Kutu. Has brow ridge too. Fluffy hair sticking out of sides of face.
Shida (SH) 21/10/93 e.d.o.b. 1990	Sub Adult Female	Inf 2: 10/92-09/95 JF: 10/95-09/00 SAF: 10/00-09/04	Mother is Banura. Snared in 06/98 – left hand missing. Right leg snared with nylon still wrapped around.
Juliet (JL) 01/02 e.d.o.b 1990	SAF	SAF: 00-04	Immigrant, first seen sporadically from 01/02. Snared on left hand with wire still present.
Emma (EM) 9/98 e.d.o.b. 1991	SAF	JF: 96-00 SAF: 2001-2005	Immigrant. Brown face. Looks like Bahati (not sisters.)
Fred (FD) 8/5/03 e.d.o.b 1994	Juvenile Male	JM: 99-04 SAM: 2004	Mother is Flora. FL first seen with FD and FK. Has light face and large ears. Age estimate based on being similar size to KT.
Kwezi (KZ) 28/1/95	JM	Inf 1: 1/95-12/96 Inf 2: 1/97-12/99 JM: 1/00-12/04	Mother is Kwera. Small brow ridge. Likes staying with mother. Long thin face. Long hair on side of face. Screams a lot – spoilt!
Zalu (ZL) 12/7/95	JM	Inf 1: 6/95-5/97 Inf 2: 6/97-5/00 JM: 6/00-5/05	Mother is Zana. Has brown face.
Hawa (HW) 11/9/96	JM	Inf 1: 9/95-9/97 Inf 2: 9/97-8/00 JM: 9/00-8/05	Mother is Harriet. HT first seen with HW. Resembles Kwezi with more of a tail tuft.
Zig (ZG) 7/97	JM	Inf 1: 6/97-5/99 Inf 2: 6/99-5/02 JM: 6/02-5/07	Mother is Zimba. Confident. Gangly – long thin arms and legs with human nose.
Mark (MR) 10/01 e.d.o.b 1997	JM	JM: 02-07	Mother is Melissa. ML first seen with MR. Age estimate based on ML cycles.

Pascal (PS) 07/03 e.d.o.b 1998	JM	JM: 03-08	Mother is Polly. Resembles Zig with large ears and light face. First seen with mother 01/03.
Bahati (BH) 16/12/94	Juvenile Female	Inf 1: 12/94-11/96 Inf 2: 12/96-11/99 JF: 12/99-11/04	Mother is Kalema. Looks like Emma. Has brown face, resembles Duane. White beard like mothers.
Sally (SA) 04/01 e.d.o.b 1996	JF	JF: 01-06	Mother is Sabrina. SB first seen with SA. Seen infrequently.
Nora (NO) 9/4/96 e.d.o.b. 2/96	JF	Inf 1: 2/96-01/98 Inf 2: 2/98-01/01 JF: 2/01-01/06	Mother is Nambi. Very bold and fluffy. 02/03 snared on right arm – wire still present.
Beti (BT) 2/10/96	JF	Inf 1: 10/96-09/98 Inf 2: 10/98-09/01 JF: 10/01-09/06	Mother is Banura. Snared on right hand around fingers - 03/02. Wire no longer present but some scaring.
Rachel (RE) 9/7/97	JF	Inf 1: 6/97-5/99 Inf 2: 6/99-5/02 JF: 6/02-5/07	Mother is Ruda – dead. Has brown face and big ears like mother. White beard. Moves with Bob.
Rose (RS) e.d.o.b. 15/11/97	JF	Inf 1: 11/97-10/99 Inf 2: 11/99-10/02 JF: 11/02-11/07	Mother is Ruhara. Has sun-bed tanned face and white mouth.
Keti (KE) 22/9/98 e.d.o.b. 1/9/98	JF	Inf 1: 9/98-8/00 Inf 2: 9/00-8/03 JF: 9/03-8/08	Mother is Kigere.
Kana (KN) 29/10/98	JF	Inf 1: 10/98-09/00 Inf 2: 10/00-09/03 JF: 10/03-09/08	Mother is Kutu. Has black splodge under left eye – looks like she has a black eye. Snared on right foot Feb 03.
Frank (FK) 8/5/03 e.d.o.b 1999	Infant Male	Inf 2: 02-04	Mother is Flora. Has very light plasticine face and very large ears. Mother first seen with FD and FK. Age estimate based on FL cycles.

Zed (ZD) e.d.o.b. 05/01	IM	Inf 1: 05/01-04/03 Inf 2: 05/03-04/06	Mother is Zana.
Clint (CT) 04/02	IM	Inf 1: 04/02-03/04	Mother is Clea. Very agile and playful
Zak (ZK) 12/02	IM	Inf 1: 11/02-10/04	Mother is Zimba. Doesn't move away from mother much.
Kasigwa (KS) 11/03	IM	Inf 1: 08/03-08/05	Mother is Kutu.
Katia (KA) d.o.b. 30/12/98	Infant Female	Inf 1: 12/98-11/00 Inf 2: 12/00-11/03	Mother is Kewayu. Looks like mother. Small brow ridge. Very bold and playful. Birth observed by Zephyr.
Janet (JT) 25/10/99	IF	Inf 1: 10/99-9/01 Inf 2: 10/01-9/04	Mother is Janie. Long skinny limbs. Has dark face. Very bold and confident.
Kumi (KM) 15/9/00	IF	Inf 1: 8/00-7/02 Inf 2: 8/02-7/05	Very small for age, but very playful. Has dark sunken eyes Mother is Kalema.
Helen (HL) 23/02/01	IF	Inf 1: 02/01-01/03 Inf 2: 02/03-01/06	Mother is Harriet.
Karo (KR) 11/01	IF	Inf 1: 11/01-10/03	Mother is Kwera. Becoming very bold, likes copying KZ's displays.
Ramula (RM) 13/09/02	IF	Inf 1: 09/02-08/04	Mother is Ruhara.
Night (NT) d.o.b. 06/2/03	IF	Inf 1: 02/03-01/05	Mother is Nambi. Already very agile, tries to move away from NB a lot.
Monika (MN) 7/03	IF	Inf 1: 06/03-05/05	Mother is Melissa.

Kuki (KI)
11/03

IF

Inf 1: 09/03-08/05

Mother is Kigere.

B3: Dead or Missing Chimpanzees (from 1998 onwards)

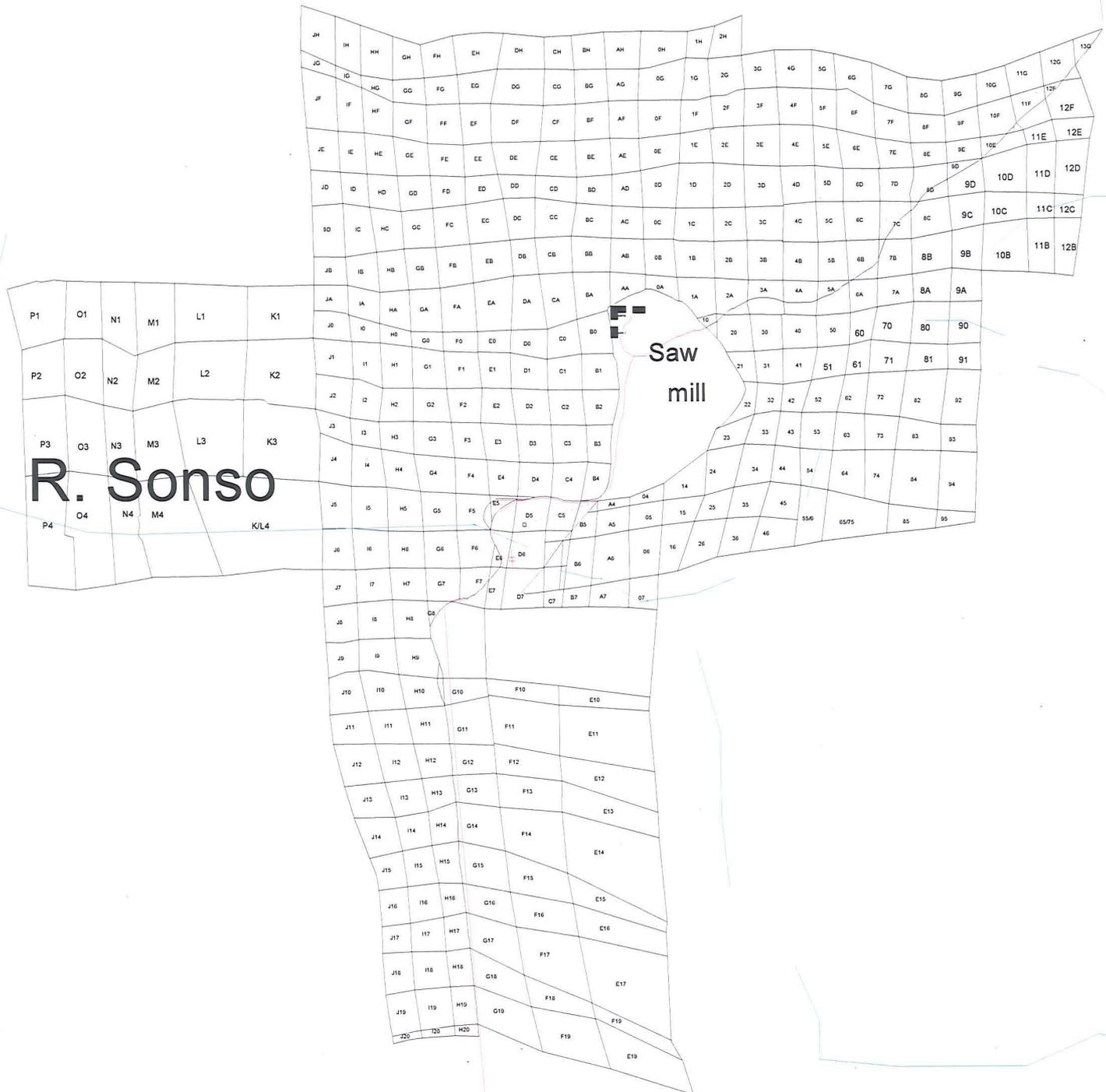
Name (code) Date named	Age/Sex	Characteristics	Date Disappeared
Vita (VT) 9/4/93 (war)	JF	Left hand hooked. No bald patch. May be daughter of Ruda.	Last seen 26/5/98
Kikunku (KK) 30/9/92 (stump)	AM	Left hand missing at wrist. No hair on right wrist.	Last seen 6/7/98
Mama (MM) 17/6/95	AF	Joined Sonso community in 1995. Mother of Muhara.	Last seen 13/8/98
Zesta (ZT) 17/2/93	AM	Young. Brown allover. Scattered hair on chest and legs. Pink face, light hands and feet, floppy ears.	Killed by Black, Duane and other community males on 4/11/98
Grinta (GT) 10/4/93	JF	Mother is Ruhara.	Last seen 9/6/99
Vernon (VN) 26/4/94	AM	First toe on left foot short.	Last seen 28/6/99
Magosi (MG) 5/8/92 (big testicles)	AM	Old. Large with large testicles. Patches of grey hair on back, legs and head.	Died. Body found in forest on 4/7/99
Salama (SL) 20/10/93 (greetings)	AF	Facially resembled Kalema.	
Kadogo (KD) 11/7/92	JM	Mother is Kigere.	Died. Last seen 5/7/99
Sara (SR) 27/1/95	AF	Has small bald patch on forehead, with black face	Last seen 29/2/00
Muga (MU) 8/8/92 (stump)	AM	Right hand missing from wrist. Hair on wrist. Clean cut as break. Brown scar on right cheek below eye.	Last seen 23/3/00
Andy (AY) 21/6/94	SAM	Right foot slightly lame. Very lanky, long thin body. May be son of Nambi.	Found dead in forest 28/7/00 Cause of death unknown

Ruda (RD) 14/11/92 (belly)	AF	Big belly. Big ears. Moves with confidence. Mother of Bob, and Rachel. Brownish. Size of a male.	Found dead in forest 29/10/01. Autopsy available.
Bwoya (BY) 5/8/92 (hairy)	AM	Hilly head (gorilla like). Brownish hair. Thin.	Disappeared 12/01. Body found in forest 01/02, presumed to be Bwoya.
Ben (BE) 10/01	IM	Born September 2001, son of Banura	Disappeared 11/01
Willis (WS) 10/04	JM	Mother is Wilma. WL first seen with WS.	Disappeared 12/01
Muhara (MH) 28/8/95 e.d.o.b. 1990	SAF	Black face with sad eyes. Immigrated with mother – Mama (1995).	Disappeared 01.02. Last seen?
Gonza (GZ) 11/8/93 e.d.o.b. 1992	SAF	Mother is Zimba. Has thin hair on belly.	Disappeared 01/02. Presumed emigrated. <i>Body found in N2 03/02, possibly Gonza – tbc.</i>
Jambo (JM) 20/10/93 (Hello)	AM	Very big. Hairy. Brown feet. Pink lipstick lips. Long hair coming out of ears. Very wrinkly face with squashed nose.	Murdered in Nyakafunjo sugar cane. Body found 6/5/03.
Monday (MD) 11/02	IM	Mother was Mukwano. Very agile and likes pant hooting with the adults.	Mukwano seen 07/03 without Monday. Last seen with him 04/03

Appendix C

Check-sheets used for data collection

C1: Map of forest used to plot routes taken



0 300m

Codes used by field assistant to complete scan check-sheet:

Code	Activity	
✓	Present	but activity not determined
F	Feeding	Ingesting any food item
T	Travelling	Locomotion <i>between</i> stop sites
M	Moving	within stop site Locomotion <i>within</i> a single patch or stop site
R	Resting	Inactivity. On tree, ground or in nest
G	Grooming	Any grooming: to self, or with another.
N	Nesting	Construction of day or night nest
D	Drinking	Ingestion of water
V	Vocalising	Individual emitting calls mouth
S	Displays and other Social Interactions	Includes aggressive and affiliative interactions; attacks, tree drumming, play, etc.
C	Copulation	Actual or attempted intromission
?	Out of Sight	- Unclear if present

Appendix D

Reliability Tests

D1: Distance Estimation

I tested James' distance estimation twice; once in October 2002 and again in August 2003 to ensure he was consistent throughout the study period. I asked him to estimate a series of distances in the forest, some along trails and some within the blocks. He gave his estimate of a category of five metre intervals, and then I measured the actual distance to the nearest 0.5m with a tape measure.

Categories used were 0-4, 5-9 etc through to 55-59, 60+ metres.

Trial	Actual distance (m)	Estimate (m) Oct 2002	Estimate (m) Aug 2003
1	25	25-29	25-29
2	16	15-19	15-19
3	58	50-55	55-60
4	35.5	35-39	35-39
5	14	15-19	15-19
6	34	30-34	30-34
7	22.5	20-24	25-29
8	13	10-14	15-19
9	31	30-34	30-34
10	25.5	20-24	25-29
11	8	5-9	5-9
12	28	25-29	25-29
13	59	55-59	55-59
14	6	5-9	5-9
15	41	40-44	45-49
16	10.5	10-14	10-14
17	4	0-5	0-4
18	3	0-4	0-4
19	16	15-19	15-19
20	19	20-24	15-19

When tested in both October 2002 and August 2003 James was correct on 16/20 trials. That is, he was able to estimate distance accurately to within five metres 80% of the time.

In both tests, the four trials that he judged incorrectly were cases where the actual distance was only 1m or less away from a category boundary, and James always decided upon the category that was within ten metres of the actual answer.

His performance over the two test periods is significantly positively correlated ($r = +0.987$, $n=20$, $p<0.0001$). Thus it can be said that James' distance estimation was accurate to within 10m on 100% of these test trials, in October 2002 and August 2003.

D2: GPS Receiver Reliability

To test the inherent inaccuracy in the receiver, I decided on four points within the Sonso region where a signal could easily be picked up, and then compared the co-ordinates recorded by the GPS device on five separate occasions. All readings were taken in UTM (zone 36N) coordinate system, with the WGS 84 map datum.

Location	Date	Time	Location reading	
			Easting	Northing
1: Within camp clearing	13/08/03	13.25	0338126	0190795
	21/08/03	10.50	0338121	0190798
	29/08/03	12.30	0338127	0190792
	05/08/03	10.30	0338124	0190796
	11/09/03	11.50	0338123	0190798
Variation			6m	6m
2: Edge of forest in sawmill clearing	13/08/03	13.15	0338340	0190515
	21/08/03	10.40	0338341	0190514
	29/08/03	12.20	0338339	0190523
	05/08/03	10.20	0338343	0190517
	11/09/03	11.40	0338437	0190521
Variation			6m	9m
3: Edge of forest at river	13/08/03	13.10	0337714	0190048
	21/08/03	10.35	0337715	0190041
	29/08/03	12.15	0337717	0190055
	05/08/03	10.10	0337711	0190046
	11/09/03	11.30	0337717	0190051
Variation			6m	14m
4: Entrance to forest at top of Royal Mile	13/08/03	12.40	0337464	0188116
	21/08/03	10.25	0337460	0188121
	29/08/03	12.10	0337458	0188120
	05/08/03	10.00	0337463	0188118
	11/09/03	11.20	0337456	0188124
Variation			8m	8m

In all but one case, the variation of the GPS recordings did not exceed 9m. Once it was 14m. It can be said therefore that the GPS device is reliable to within 20m.

D3: Scan sampling accuracy

The activity budgets ascertained from five instantaneous scan samples were compared with those derived from the focal animal samples over the same observation period.

Activity	Percentage of day	
	From focal sample	From scan sample
Feeding	31	28
Resting	39	43
Travelling	15	16
Socialising	15	13
Feeding	30	31
Resting	32	37
Travelling	23	21
Socialising	15	11
Feeding	36	36
Resting	28	31
Travelling	17	14
Socialising	19	19
Feeding	41	45
Resting	28	30
Travelling	17	15
Socialising	14	10
Feeding	45	50
Resting	30	32
Travelling	15	12
Socialising	10	6

Pearson product moment correlation showed the activity budgets derived from the two sampling methods were significantly positively correlated ($r=0.989$; $n=20$; $p<0.0001$).

Appendix E1: Foods consumed by Sonso Community
September 2002- September 2003

Family	Species	Code	Type	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Acanthaceae	Whitfieldia elongata	WHT	Herb							YL						1
Anacardiaceae	Lannea welwitschii	LW	Climber		RF									RF	RF	3
	Mangifera indica (Mango)	MMF	Tree				UF	UF	RF							3
	Pseudospondias microcarpa	PSM	Tree						RF							1
Annonaceae	Asimina spp. (PawPaw)	Paw paw	Tree					RF				UF		UF		3
	Monodora angolensis	MOA	Tree										RF			1
	Monodora myristica	MOM	Tree									RF	RF	RF		3
	Uvariopsis congensis	UC	Tree	FL	FL					YL	FL	FL				6
Apocynaceae	Alaphia lawdolphoides	ALP	Climber		RF					RF				RF	RF	4
	Alstonia boonei	AB	Tree							BK						1
Boraginaceae	Cordia millenii	COM	Tree	UF		UF	RF		RF	RF	RF	RF				8
Euphorbiaceae	Alchornea laxiflora	AL	Tree									YL				1
	Croton sylvaticus	CSY	Tree									SD				1
	Macaranga lancifolia	ML	Tree				UF	UF								2
Flacourtiaceae	Caloncoba schweinfurthii	CLS	Tree	YL												1
Guttiferae	Mammea africana	MA	Tree						RF							1
Hernandiaceae	Illigera pentaphylla	ILP	Climber								YL					1
Leguminosae	Cynometra alexandri	CYA	Tree	SD	SD	SD					FL			BK	SD	6
	Mildbraedi dendron excelsum	MIE	Tree				UF	UF, RF	RF	RF	RF					5
Loganiadeae	Strychnos mitis	SM	Liana			SD										1
Marantaceae	Marantaochloa spp.	MAR	Herb								P					1
Meliaceae	Trichilia spp.	TRR spc	Tree		YL	YL	YL	YL	FL	YL		YL	YL	YL	YL	10
Moraceae	Antiaris toxicaria	ANT	Tree		RF, YL	RF				YL		YL				4
	Broussonetia papyrifera	BPY	Tree	YL	RF	RF, YL	RF, YL	YL, RF	YL, RF, FL	YL, RF	YL, RF	YL, FL, RF, FL	YL, RF	YL, FL	FL, YL	12
	Ficus barteri	FB	Tree						RF				RF	RF	RF	4
	Ficus exasperata	FE	Tree	UF	UF	UF	UF	YL	YL, BK	YL	B, YL, RF	B, YL		YL	UF, YL	11
	Ficus mucoso	FM	Tree	RF, UF		UF, RF	RF	UF, RF	UF	UF, RF	RF	UF	UF	RF	RF	11
	Ficus natalensis	FN	Tree					RF			UF, RF	RF	RF		UF	5
	Ficus polita	FPO	Epiphyte			RF					UF	UF	UF	UF	UF	6
	Ficus pseudomangifera	FPS	Tree								UF					1
	Ficus sansibarica	FSA	Epiphyte					UF								1
	Ficus saussureana	FSS	Epiphyte									RF		RF	RF	3
	Ficus sur	FSU	Tree	RF, UF	RF	UF, RF	RF	RF	RF	RF	UF	UF, RF	RF	RF	RF	12
	Ficus thonningii	FTH	Tree						UF					UF		2
	Ficus vallis-choudae	FVL	Tree						RF							1
	Ficus varifolia	FVR	Tree	YL	YL	YL		LV	YL	YL	B	YL, UF	YL, UF	YL	YL, RF	11
	Milicia excelsa	MEX	Tree			YL, FL, RF	RF	UF, RF	RF	RF						5

Appendix E1: Foods consumed by Sonso Community
September 2002- September 2003

	Morus lactea	MOL	Tree	YL	RF									YL	3	
	Myrianthus holstii	MYH	Tree				UF, RF			RF	YL, RF				3	
	Treculia africana	TRA	Tree	YL						RF					2	
Myrtaceae	Psidium guajava (Guava)	PSG	Tree						RF		UF	UF			3	
	Syzygium guinense	SZG	Tree				UF, RF		RF						2	
Olaceae	Strombosia scheffleri	SS	Tree						RF						1	
Palmae	Raphia farinifera	RF	Tree	RW	RW	RW				RW	RW	RW	RW	RW	8	
Poaceae	Pennisetum purpureum	Elephant grass	Grass					P							1	
Rhamnaceae	Lasiodiscus mildbraedii	LM	Tree	FL		YL, FL							YL	LV	FL	5
	Maesopsis eminii	ME	Tree						RF							1
Rutaceae	Balsamocitrus sawei	BD	Tree					RF		RF	RF					3
Sapindaceae	Crossonophelis africanus	CRA	Tree				RF									1
	Lynchnodiscus cerospermus	LYC	Tree	YL							YL					1
Sapotaceae	Chrysophyllum albidum	CAL	Tree	RF	RF	RF										3
	Chrysophyllum gorungosanum	CGO	Tree							RF						1
Sterculiaceae	Cola gigantea	COG	Tree						SD	SD						2
	Sterculia dawei	STD	Tree							RF		YL	YL			3
Tiliaceae	Desplatsia dewevrei	DD	Tree				RF	UF, RF	RF	UF, RF	RF	RF	RF	RF	RF	9
Ulmaceae	Celtis durandii	CDU	Tree		LV	YL						UF, RF	RF	RF		5
	Celtis mildbraedii	CMI	Tree	YL	YL	YL, UF, RF	YL	YL	YL	YL	YL	YL	YL	YL	YL	12
	Celtis wightii	CWI	Tree				YL	YL	YL, FL	YL	YL	YL	YL	YL	YL	8
	Celtis zenkeri	CZE	Tree				YL	YL		YL	LV	YL	YL	YL	YL	7
	Chaetachme aristata	CHA	Tree		RF	RF										2
Urticaceae	Urera cameroonensis	URC	Climber	FL						YL	YL, FL	YL, FL				3
Zingiberaceae	Afromomum spp.	AFM	Herb					P		P	P	P			P	5
	Saccharum species	Sugar cane	Crop	P	P	P	P	P					P	P	P	9
TOTAL				15	18	23	17	23	28	21	25	27	17	23	20	
TOTAL FRUIT				5	8	12	10	15	19	9	13	16	11	12	10	
species making 80%				3	3	5	5	8	16	4	8	7	5	6	8	

Appendix E2: Foods consumed by Sonso Community
September 2002- September 2003

Family	Species	Code	Type	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Acanthaceae	Whitfieldia elongata	WHT	YL							0.001706						0.000354
Anacardiaceae	Lannea welwitschii	LW	F		0.00576									0.02834	0.085561	0.001827
	Mangifera indica (Mango)	MMF	F				0.005391	0.076157	0.015038							0.009194
	Pseudospondias microcarpa	PSM	F						0.007519							5.89E-05
Annonaceae	Asimina spp. (PawPaw)	Paw paw	F					0.003484				0.004743		0.004049		0.001179
	Monodora angolensis	MOA	F										0.008511			0.000118
	Monodora myristica	MOM	F									0.002372	0.008511	0.004049		0.00053
	Uvariopsis congensis	UC	FL	0.085082	0.00144					0.00199	0.004125	0.005929				0.011669
Apocynaceae	Alaphia lawdolphoides	ALP	F		0.014399						0.002843			0.008097	0.005348	0.001945
	Alstonia boonei	AB	B								0.000569					0.000118
Boraginaceae	Cordia millenii	COM	F	0.002914		0.004171	0.005391		0.045113	0.128766	0.516499	0.181818				0.121578
Euphorbiaceae	Alchornea laxiflora	AL	YL									0.001976				0.000295
	Croton sylvaticus	CSY	S									0.003162				0.000471
	Croton macrostachys	CMC	YL											0.016194		0.000236
	Macaranga lancifolia	ML	F				0.005391	0.002987								0.000413
Flacourtiaceae	Caloncoba schweinfurthii	CLS	YL	0.000583												5.89E-05
Guttiferae	Mammea africana	MA	F						0.015038							0.000118
Hernandiaceae	Illigera pentaphylla	ILP	YL								0.002291					0.000295
Leguminosae	Cynometra alexandri	CYA	S	0.407925	0.4946	0.023132									0.053476	0.085924
			FL								0.00275					0.000354
			B											0.00125		1.77E-05
	Mildbraediendron excelsum	MIE	F				0.086253	0.039323	0.082707	0.044912	0.027956					0.019153
Loganiadeae	Strychnos mitis	SM	S			0.001517										0.000236
Marantaceae	Marantaochloa spp.	MAR	P								0.002291					0.000295
Meliaceae	Trichillia spp.	TRR spc	YL		0.00072	0.006447	0.005391	0.002489		0.003411	0.00275	0.002767	0.012766	0.008097	0.010695	0.0033
			F						0.030075							0.000236
Moraceae	Antiaris toxicaria	ANT	F		0.010799	0.031475										0.005775
			YL		0.0036	0.001138				0.000284	0.00275	0.003557				0.001414
	Broussonetia papyrifera	BPY	YL	0.009324	0.00432	0.002275	0.09434	0.279741	0.12782	0.205514	0.076077	0.149407	0.148936	0.214575	0.139037	0.11819
			F			0.007205	0.110512	0.136884	0.030075	0.013076	0.013291	0.011858	0.008511			0.025076
			FL						0.007519			0.171937	0.297872	0.259109	0.02139	0.033827
	Ficus barteri	FB	F						0.007519				0.012766	0.072874	0.010695	0.001414
	Ficus exasperata	FE	F	0.00641	0.275018	0.452787	0.113208				0.00275				0.058824	0.095766
			YL						0.031359	0.022556	0.021603	0.044455	0.034783		0.052632	0.032086
			B						0.007519			0.000917	0.001976			0.000471
	Ficus mucoso	FM	F	0.114219		0.156617	0.150943	0.01991	0.015038	0.092098	0.054537	0.017787	0.059574	0.076923	0.28877	0.073902
	Ficus natalensis	FN	F						0.054754			0.001375	0.092885	0.008511		0.020685
	Ficus polita	FPO	F			0.002275						0.001833	0.001976	0.017021	0.004049	0.005348
	Ficus pseudomangifera	FPS	F									0.001375				0.000177
	Ficus sansibarica	FSA	F					0.002489								0.000295
	Ficus saussureana	FSS	F									0.013439		0.012146	0.010695	0.002298
	Ficus sur	FSU	F	0.31993	0.092873	0.057641	0.285714	0.030861	0.18797	0.392268	0.027498	0.070751	0.093617	0.032389	0.064171	0.155052

Appendix E2: Foods consumed by Sonso Community
September 2002- September 2003

	Ficus thonningii	FTH	F					0.007519				0.004049		0.000118			
	Ficus vallis-choudae	FVL	F					0.015038						0.000118			
	Ficus variifolia	FVR	YL	0.001166	0.00288	0.001138		0.002987	0.015038	0.006822	0.021998	0.019763	0.017021	0.008097	0.016043	0.008722	
			F					0.022556				0.014229	0.012766	0.101215	0.010695	0.004066	
			B								0.001375					0.000177	
	Milletia excelsa	MEX	YL			0.004551	0.06469	0.022556	0.022166							0.001143	
			F					0.136884								0.016207	
	Morus lactea	MOL	YL		0.00576									0.005348		0.00053	
			F			0.081532										0.012671	
	Myrianthus holstii	MYH	F					0.007466			0.006874	0.014229				0.00389	
	Treculia africana	TRA	F								0.000917					0.000118	
			YL			0.00072										5.89E-05	
Myrtaceae	Psidium guajava (Guava)	PSG	F					0.007519			0.003557	0.021277				0.000884	
	Syzygium guinense	SZG	F					0.02994	0.105263							0.004361	
Olacaceae	Strombosia scheffleri	SS	F					0.015038								0.000118	
Palmae	Raphia farinifera	RF	RW		0.00144	0.022753	0.001617				0.016499	0.003162	0.021277	0.012146	0.026738	0.007031	
Poaceae	Pennisetum purpureum	Elephant grass	P					0.010951								0.001297	
Rhamnaceae	Lasiodiscus mildbreadii	LM	YL			0.005688					0.012832			0.004049		0.002593	
			FL	0.002331		0.00493									0.005348	0.001061	
	Maesopsis eminii	ME	F					0.022556								0.000177	
Rutaceae	Balsamocitrus sawei	BD	F					0.00448		0.003695	0.000917					0.001414	
Sapindaceae	Crossonophelis africanus	CRA	F			0.003792										0.000589	
	Lynchnodiscus cerospermus	LYC	YL	0.002331							0.004548					0.001179	
Sapotaceae	Chrysophyllum albidum	CAL	F	0.013986	0.020158	0.078498										0.015264	
	Chrysophyllum gorungosanum	CGO	F					0.015038								0.000118	
Sterculiaceae	Cola gigantea	COG	S					0.020408	0.007519							0.002475	
	Sterculia dawei	STD	F					0.007519		0.03758	0.018182					0.007602	
Tiliaceae	Desplatsia dewevrei	DD	F				0.010782	0.026381	0.030075	0.021216	0.016499	0.000395	0.004255	0.012146		0.009842	
Ulmaceae	Celtis durandii	CDU	YL		0.00144	0.001517										0.000354	
			F									0.089328	0.046809	0.016194		0.014203	
	Celtis mildbraedii	CMI	YL	0.008159	0.006479	0.021236	0.026954	0.003484	0.06015	0.004264	0.012832	0.018182	0.157447	0.020243	0.085561	0.014497	
			F		0.0036	0.015169										0.002652	
	Celtis wightii	CWI	FL					0.012942								0.001532	
			YL			0.000758	0.002695	0.036834	0.022556	0.010133	0.028414	0.013043		0.016194		0.012405	
	Celtis zenkeri	CZE	YL		0.001138	0.002695			0.022556	0.001137	0.00275	0.003953		0.008097	0.005348	0.001739	
	Chaetachme aristata	CHA	F		0.019438	0.004171										0.002239	
Urticaceae	Urera cameroonensis	URC	FL	0.000583					0.007519	0.002217	0.005958					0.001297	
			YL							0.002533	0.017874					0.00277	
Zingiberaceae	Afromomum spp.	AFM	P					0.001493		0.002558	0.001375	0.004743		0.012146		0.001768	
	Saccharum species	Sugar cane	P	0.025058	0.034557	0.006447	0.03504	0.025386					0.024111	0.042553	0.040486	0.053476	0.015116
	UNIDENTIFIED									0.011939	0.028414					0.006129	

Appendix F

Defining a “valuable” resource

In order to determine how chimpanzee travel behaviour is organised, and to establish to what degree - if any - it is based on mental spatial representations, I intend to consider how chimpanzees move between valued resources. In order to do this, I must first determine what these valued resources are; I need to differentiate the important resource stops from the irrelevant ones. It may seem intuitive to use an independent measure to define resources as “valuable”, but this approach is wrought with problems. Nutritional quality could be used as a measure of food resources, but precise nutritional quality is difficult to determine, and the quality of one fruit or leaf on a tree is not necessarily indicative of the quality of all the other food items on the same tree (Dominy *et al*, in prep); nutritional quality is not uniform across one resource, much less one species. Furthermore, the dietary needs of individual chimpanzees can be expected to alter over time, and, as food availability fluctuates across seasons, the relative importance of different foods will vary for chimpanzees over time. In addition to these problems, measuring nutritional status only tells us about *food* resources; other potentially important resources would be ignored with such an approach. For these two reasons, rather than an independent measure of food quality, I will use the chimpanzees’ own behaviour to define what resources are valuable to them. I make the assumption that resources at which the chimpanzee invests a large amount of time are valuable, or important in some way: I am going to use time as a *post hoc* measure of the chimpanzee’s appreciation of a resource (see White and Wrangham, 1988, for an introduction to this approach).

It is unreasonable to suppose that every brief stop a chimpanzee makes, and every nibble of fruit or leaf, is valued, desired or intended! Indeed, many of the shorter stops that chimpanzees make on their daily travel paths are probably of very little consequence, and as such are best ignored when considering travel between *important* resources. A valued resource, therefore, is most likely one where the chimpanzee spends a long time. But what is a “long time” for a chimpanzee? Is stopping for five minutes a sufficient indication of value, or is one hour necessary? The aim of this appendix is therefore to determine what

constitutes a large time investment for a chimpanzee. I will use this time criterion to define which stop sites were potentially important and which were irrelevant.

I will summarise the attributes of the stop site waypoints recorded across all the routes, and from this I will decide on a minimum time criterion. [As explained in chapter 3, the waypoints recorded are either instantaneous samples of location recorded at five-minute intervals, where the target chimpanzee did not stop, or they can be stop sites. Stop sites are locations where the chimpanzee stopped for one minute or more, and the activity of the target animal at the site was recorded.]

Methods

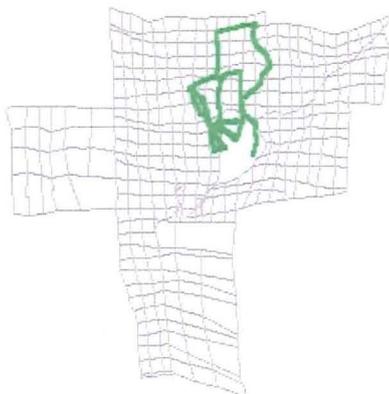
Travel route and behavioural data was collected as described in Chapter 3. From these fifty travel routes I selected a sample of six with the longest duration and distance (three from male chimpanzees and three from females), as long routes incorporate the most waypoints. One of the females (BN) was cycling, two were lactating (KL and KW), and two are disabled (BN and KL). Of the male routes selected, DN is the alpha male, MA is his beta, whilst BB is a young, low ranking male. This selection of routes therefore provides a representative sub-set of the data from which to calculate a suitable time criterion. Figure Fa illustrates each of the routes selected and table F1 gives details of these routes.

Table F.1: The six sample routes used to define a minimum time criterion for a valuable resource.

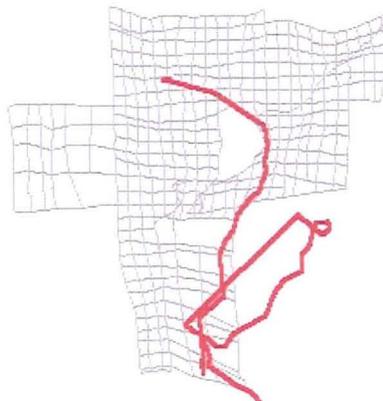
Details of focal animal		Details of travel route			
		Duration (hrs)	Distance (m)	Total no. of waypoints	No. of stop sites
BB07/07/03	Low ranking AM	34	6,273	66	37
DN03/02/03	Alpha AM	29	7,775	59	23
MA10/02/03	Beta AM	27	10,572	77	23
BN24/02/03	Cycling AF	20	7,736	55	13
KL20/01/03	Disabled, lactating AF	24	3,954	35	22
KW30/06/03	Lactating AF	28	4,608	41	34

Figure Fa: Sample travel routes selected for consideration of minimum stop time criteria

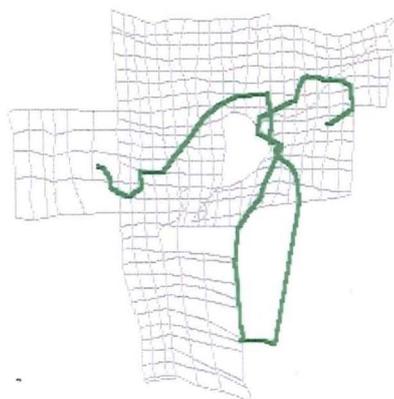
BB07/07/03



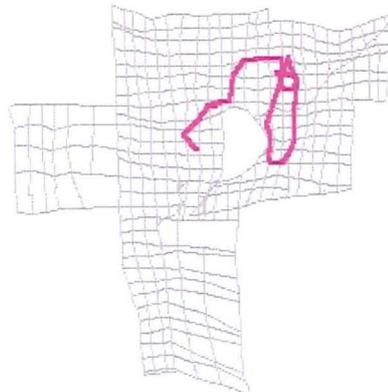
BN24/02/03



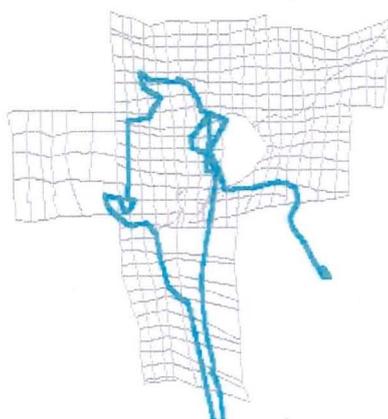
DN03/02/03



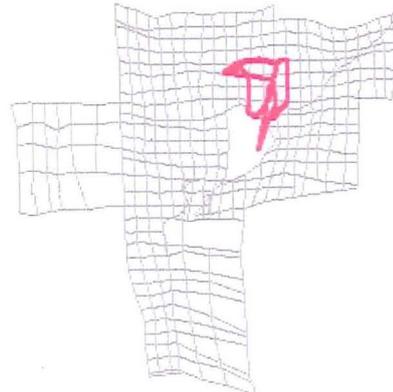
KL20/01/03



MA10/02/03



KW30/06/03



Each of the stop sites recorded from each of the above six routes were entered into an Excel spreadsheet, with information on the duration of the stop (in minutes) and the activity of the focal animal at the stop. “Activity” was determined from the behavioural states recorded at the stop site, as defined in Chapter 3. When more than one behavioural state was recorded for the target animal over the duration of one stop, the behaviour that was observed for the longest time was noted as the main activity. This spreadsheet was used to generate graphs, from which I made the (subjective) choice of the minimum time criterion for an “important” resource. The time criteria should cut out as many rest stops as possible as these are not location driven, but the majority of feeding stops – which are determined by location – should be included.

Results

152 stop sites were considered, ranging from 1 to 946 minutes in duration. Of these, 76 stop sites were primarily associated with feeding, 55 with resting, 12 with social interactions and 9 with nesting. Table F.2 summarises the duration of stop sites for each of the four activities noted.

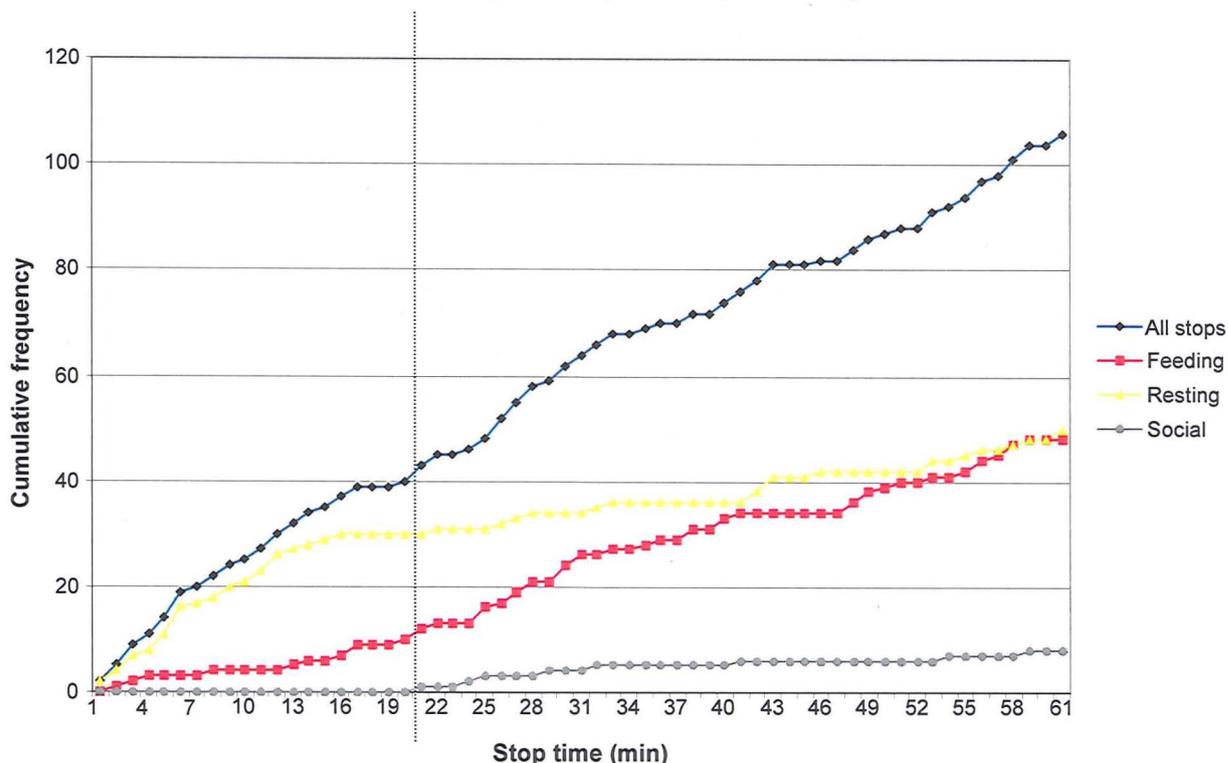
Table F.2: Summary of the time spent at stop sites when each behavioural state was recorded.

Details	Duration (minutes)				
	At all stop sites	At feeding stops	At resting stops	At social stops	At nesting stops
Mean	98	67	29	73	820
Median	42	50	15	61	807
Minimum	1	2	1	21	678
Maximum	946	268	160	157	946
25 th Percentile	17	27	6	28	762

75% of all the stop sites recorded in these six routes were over 17 minutes in duration. As figure Fb shows, the focal chimpanzees were mainly observed resting (inactive) in the 25% of stops that were under seventeen minutes long, with a median duration for resting stops of 15 minutes. No social stops were observed under 20 minutes. The cut off point therefore seems to best lie between seventeen and twenty minutes. Given this, I selected 20 minutes as the minimum time criterion (based on the simplicity of using round

numbers). That is, only stops of twenty minutes or more will be considered as putatively valuable or important; stops under twenty minutes are irrelevant.

Figure Fb: Cumulative frequency of occurrence of time spent at stop sites, for all stop sites and according to each behavioural state recorded. Data is only shown up to 1 hour, for ease of presentation.



Discussion

Overall, consideration of this sample data suggests that 20 minutes is a suitable criterion for defining a putatively valuable stop site for Sonso chimpanzees. Selection of a time criterion is an arbitrary process, but I argue that by using the descriptive statistics and graphical representation of the frequency of occurrence of stop times, I have selected the most obvious minimum time. Thus, I will now consider all stops of 20 minutes or more as potentially valuable to the chimpanzee.

This time criterion is reasonable as chimpanzees are not grazers: they generally stop for long periods of time when they feed. Indeed, only nine feeding stops out of the 76 recorded (<12%) lasted for less than 20 minutes, as illustrated in figure Fb. Furthermore, social interactions were only recorded at stops of longer than twenty minutes. Social interactions, such as grooming, sexual or aggressive acts, and fusions, are all conceivably important to chimpanzees, and thus it is imperative to use a time criterion that includes the majority (if not all) of such interactions in an analysis of what factors influence chimpanzee

travel behaviour. On the other hand, “resting” stop sites, where the chimpanzee is largely inactive, are intuitively less consequential to travel decisions. A time criterion that cuts out just over 50% of these stops is thus attractive.

The time criteria I have identified here is purposefully low, at approximately the 25th percentile, so only 25% of stop sites overall will be ignored – the majority of which are resting stops: most genuinely valuable resources will be accounted for above this cut-off point. Stop sites that are ignored are those that are so brief they are generally going to be of little consequence to the target animal. If however, the time criterion were raised above twenty minutes, many feeding stops would be ignored. It is better to underestimate the critical time length, i.e., to pick a lower time than may really indicate value to chimpanzees, as it is better to include more stop sites than to miss any genuinely valuable resources.

I will use this 20-minute stop site criterion in analysis of how chimpanzees move between important resources.

Appendix G

A novel analysis tool

The Jupp Test

This novel statistic was designed by Peter Jupp with the specific intention of analysing two-dimensional spatial information recorded from primate travel routes. The Jupp test treats a travel route as a connected series of sections and looks for the point at which the path trajectory changes to a period of travel in which successive sections are aligned. The test is applied backwards from the end of path, analysing the sections between waypoints as independent vectors - as shown in figure G1.

The Jupp test is based on the principles of the two-sample Watson-Williams circular statistic, as described in Batschelet (1981). The procedure compares the mean scalar lengths of two samples of vectors and tests whether they differ significantly from each other. If they do differ, then a change point is identified between the two vectors. Resultant vectors (R1 and R2) are derived from the path, and these are tested against the combined sample vector (R), as shown in figure G2. The null hypothesis of the test states that the mean lengths of the two samples do not differ from each other. That is, if the sum of lengths R1 and R2 approximately equal the length of R, the null hypothesis is accepted and a change point is not discernible. In the first instance, R1 and R2 are equal to V1 and V2 respectively, with R, the combined sample vector, being equivalent to V1:V2, as illustrated in figure G2.

If the null hypothesis cannot be rejected, and no change point is found, the procedure is repeated continuing backwards along the travel path. R1 then corresponds to V1 + V2, and R2 to V3, and R becomes V1:V3. If again the null hypothesis is accepted, and no change point is found, then we continue with R1 = V1+V2+V3, R2=V4, and R = V1:V4 (as shown in figure G3) and so on with R1 = V1 + V2 + V3 +...Vi, R2 = Vi+1 and R = V1:Vi+1 until the null hypothesis is rejected. Mathematically, the null hypothesis is rejected when

$$(k-1) * (R1 + R2 - R) / (k-R1) > F_{(1, k-1; \alpha)}$$

where $F_{(1, k-1; \alpha)}$ is the upper α integer of the $F(1, k-1)$ distribution and k is the end point of vector i , equivalent to the number of vectors comprising $R1$ (here, i). (For calculations, $R2$ is replaced by the value 1, as the test uses unit vectors for computational simplicity.)

Figure G1: The Jupp test works backwards from the endpoint (waypoint H) of a travel path, converting the sections into vectors. Thus, the final travel section between waypoints G and H becomes vector 1 ($V1$), the penultimate travel section between waypoints F and G becomes vector 2, and so on.

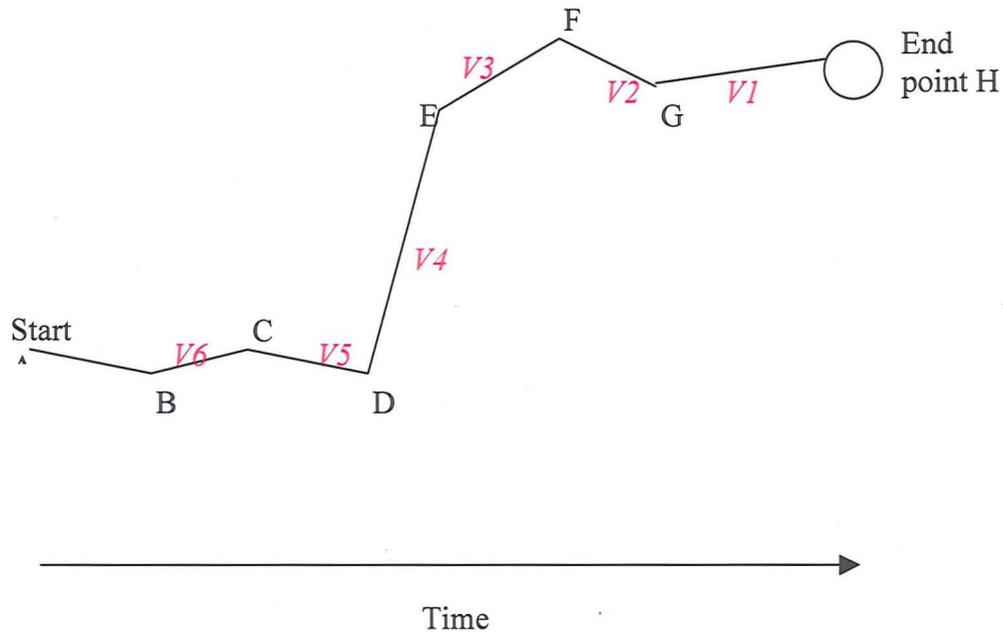
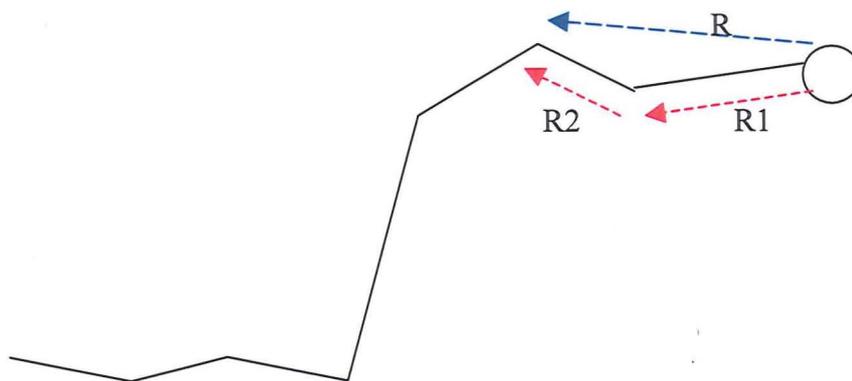


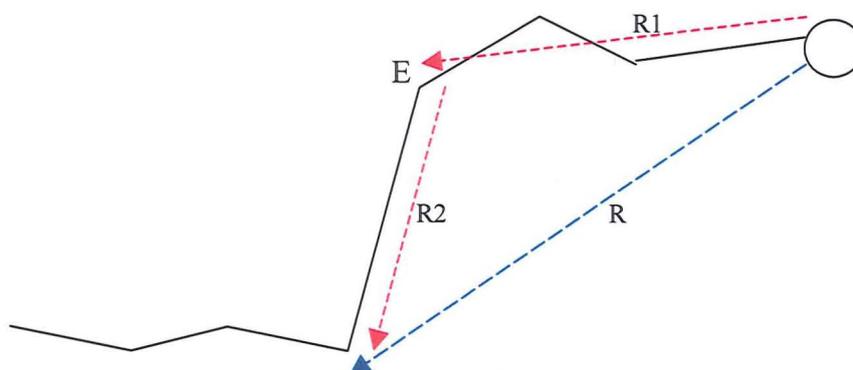
Figure G2: Resultant vectors $R1$ and $R2$ are compared with the combined vector R , derived from the original path vectors. In this example, vectors $R1 + R2$ are approximately collinear, so their scalar values do not differ significantly from that of R and the null hypothesis is accepted: there is not a change point between vectors $V1$ and $V2$.



In the example given in figure G3, the null hypothesis is rejected when $R = V1: V4$ as the endpoints of the vectors $R1$ ($V1 + V2 + V3$) and $R2$ ($V4$) are not collinear; the scalar sum

$R_1 + R_2$ is significantly greater than R (or $R_1 + R_2 - R > 0$). Thus, the test stops here with a change point identified between R_1 and R_2 , that is, at the endpoint of vector 3, equivalent to waypoint E. When a change point is identified, this can be taken as the new endpoint of the route up to that point and the test can be applied again to the data, so that the preceding change point can also be identified. This process can be repeated until all the potential change points in one route have been identified.

Figure G3: The procedure is repeated using vectors $V_1 \dots V_i$ until the null hypothesis is rejected and a change point is identified. Here, the null hypothesis is rejected when $R_1 = V_1 + V_2 + V_3$ and $R_2 = V_4$, as there is a significant difference between $R_1 + R_2$ and R . The change point occurs at the end point of vector $V_1 + V_2 + V_3$, between R_1 and R_2 , equivalent to waypoint E in figure 5a.



In algebraic terms, the null hypothesis states that the mean angular variance (v_2) of two samples, s_2 and t_2 , should be approximately equal to the angular variance of the combined sample (u_2). That is, $u_2 \approx v_2 = (n_1 * s_2 + n_2 * t_2) / n$, where n equals the number of vectors. The test statistic, F , is derived from this equation, as described in Batschelet (1981). If u_2 is larger than v_2 (or $u_2 / v_2 - 1 > 0$), the null hypothesis is rejected and a change point is identified.

The Jupp test can be varied to compare a different number of vectors in R_2 against those comprising R_1 . This then requires not just one V vector to lie in a different direction, as shown in the examples so far, but two or three or whatever is the pre-determined value. Thus, if R_2 is composed of two vectors, it would require two consecutive vectors oriented in a different direction to R_1 for a change point to be identified. We use “ q ” to denote how many vectors before the potential change point define the previous path; that is, q is equal to the number of vectors comprising R_2 . Varying q will give different patterns of results

from the same initial travel path, as each q value will result in a test that is differentially sensitive to “wiggles” in the route. The test formulae when $q=2, 3$ and 4 are as follows:

$$q=2: F = k (R1 + R2 - R) / (k + 2 - R1 - R2)$$

$$q=3: F = (k + 1) * (R1 + R2 - R) / (k + 3 - R1 - R2).$$

$$q=4: F = (k + 2) * (R1 + R2 - R) / (k + 4 - R1 - R2)$$

If the path is composed of large sections of haphazard wandering, with occasional linear sections, $q=1$ will often detect the straight sections when higher values of q cannot, as these require two or more vectors to be aligned *before* a change point to a straight line in a different direction. Thus, change points detected only when $q=1$ are characteristic of a travel path composed of random wandering interspersed with particularly straight ‘bee-lines’. If, however, the travel routes consist of a series of quite straight lines, but which may appear a little wiggly due to obstructions and minor deviations, the Jupp test using $q=1$ may not detect any change points. Higher values of q , however, will detect the change points, as the size of the sample of pre-change point data on the original path is greater. Thus, slightly wobbly but *approximately* straight-line paths are best tested using values of $q=2$ or greater. If values of q become too large, however, a false positive result may occur. In such a case, significance is found, but only because the q vectors ($R2$) *before* the potential change point are straight, whilst the k vectors ($R1$) after it may have been random and not straight at all. Thus, the optimal value of q for studying primate-ranging behaviour probably depends on the species’ typical ranging patterns being tested and is one of the aspects of the Jupp test that must be evaluated.

Applying the Jupp test to chimpanzee travel routes

I applied the Jupp test to a sample of six travel routes representing three male chimpanzees (DN, MA and BB) and three females (BN, KL, KW). One of the females (BN) was cycling, two were lactating, and two (BN and KL) are disabled. Of the males selected, DN is the alpha male and MA his beta, whilst BB is a young, low-ranking male. This selection of routes therefore provides a representative sub-set of the data collected from which to appraise the Jupp test. One travel route was selected from each of these target animals, chosen for being the longest in duration and distance and the most continuous follow of that individual. Table G.a details the routes selected and figure G4 shows maps of each of these routes.

Table G.a: The six sample routes used to evaluate the Jupp test

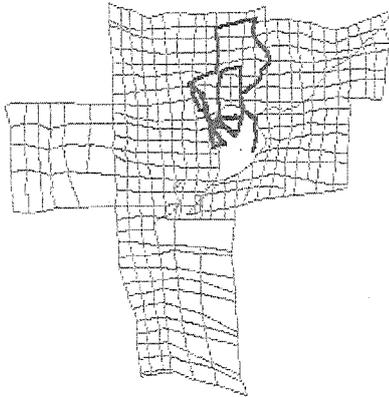
Details of focal animal		Details of travel route		
		Duration (hrs)	Distance (m)	No. of waypoints
BB07/07/03	Low ranking AM	34	6,273	66
BN24/02/03	Cycling AF	20	7,736	55
DN03/02/03	Alpha AM	29	7,775	59
KL20/01/03	Disabled, lactating AF	24	3,954	35
KW30/06/03	Lactating AF	28	4,608	41
MA10/02/03	Beta AM	27	10,572	77

Three variations of the Jupp test were compared, where $q=1, 2$ and 3 . The co-ordinates of the waypoints for each of the above six routes were copied into an Excel spreadsheet and the necessary calculations performed. Initially, all waypoints were entered, up to the waypoint of the last stop site recorded. The waypoint corresponding to the first change point identified (working backwards from the end of the route, i.e. the change point nearest the end of the path) was then used as the end point of the route. Thus, for each of the six routes, the Jupp test was applied repeatedly until all the possible change points for the whole route had been identified. This was done with $q=1, 2$ and 3 .

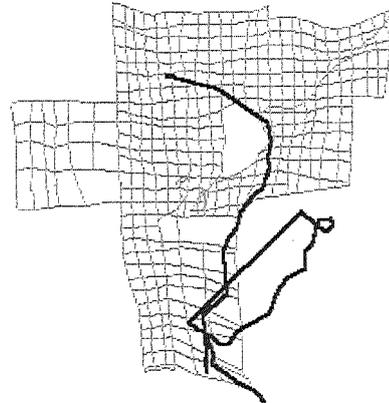
Using the Jupp test to identify all the change points in a route does entail the problem of multiple testing. The significance level should ideally be adjusted by using values of α that depend on k , but this is not easy to incorporate in a practical version of the statistical procedure, and Peter Jupp has not yet been able to do so. Furthermore, the Jupp test approximates real vectors by unit length vectors so that a distribution can be used and significance levels calculated. The actual scalar lengths of the vectors therefore should be similar and normally distributed. The Watson-Williams test upon which this procedure is based assumes data follows a Von Mises distribution – a normal circular distribution. Peter Jupp states that the statistical test is still applicable even with slightly skewed data, however (pers. comm.), as the von Mises distribution is very robust; as long as data is not heavily skewed or bi-modal for example, it is suitable. Because of the multiple testing and potential breaching of the normal assumption, quite strict significance criteria ($\alpha=0.05$) were used for this test.

Figure G4: Travel routes the Jupp test was applied to.

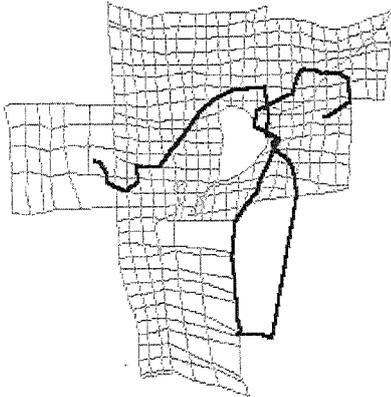
BB07/07/03



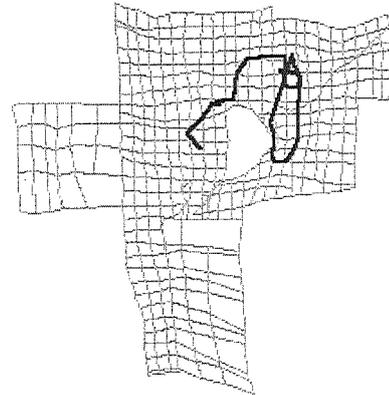
BN24/02/03



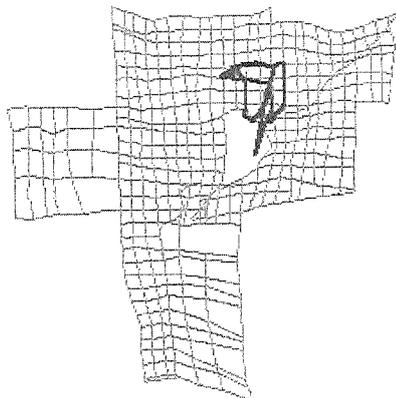
DN03/02/03



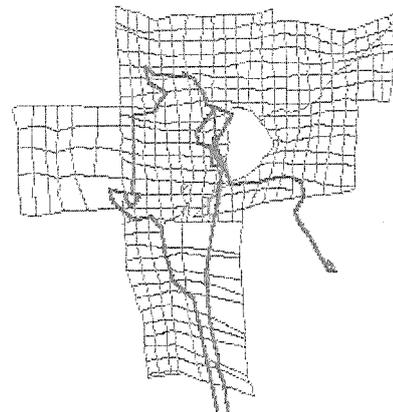
KL20/01/03



KW30/06/03



MA10/02/03



The Jupp statistic may cross the chosen threshold for significance at two or more consecutive change points. For example a change may be identified at $k=4$, $k=5$ and $k=6$ with $p=0.001$. In this situation, taking the first of these points as the change point ($k=4$) may be misleading as it may anticipate the “real” change point in the path. (With $q=1$ this problem does not arise.) For this reason, when consecutive change points were identified, I determined the “real” change point using a plot of the calculated values of F against the critical F values, at the given level of probability. The peak of the difference between F and F_{crit} was taken to be the real change point as this represents the largest vector difference, or the largest change in direction. An example is shown in figure G5, taken from the travel route DN03/02/03.

Figure G5: A section of a histogram plot comparing F with F_{crit} when $q=3$, for the route DN03/02/03. Note the k values go down in descending order, as the Jupp test works backwards from the end of the route: $k=1$ occurs at the end of the sample travel route. It is apparent from this plot that $k=2$, $k=3$ and $k=4$ are all statistically significant. However, $k=3$ represents the greatest vector difference and thus this is likely to be the first “real” change point, when working backwards from the end of the route (equivalent to waypoint 56 in this route).

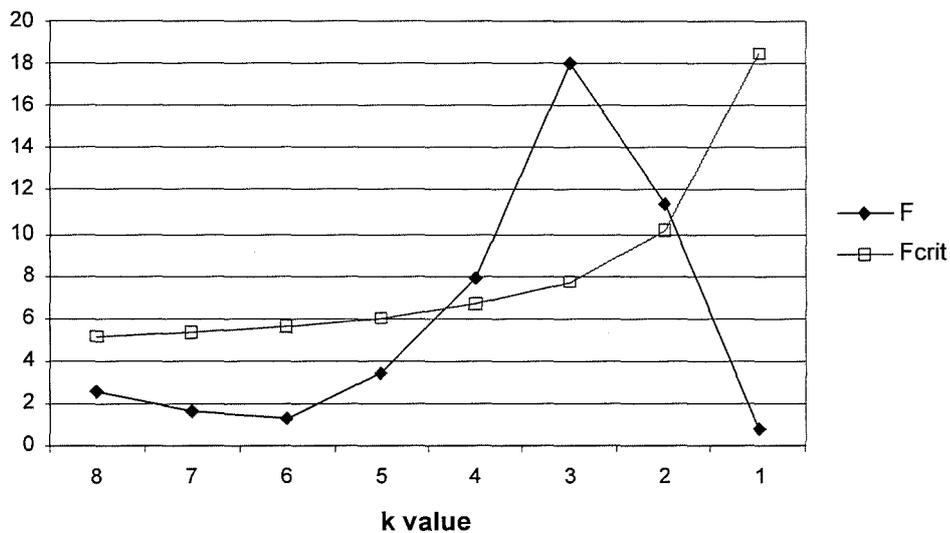


Table G.b shows the change points identified in the six routes at $q=1, 2$ and 3 .

As stated above, the test requires similarity in the inter-waypoint distances (the lengths of the vectors), not a spread over a huge range or multi-modality, but this is not always the case with the data used here. Figure G6 shows histogram plots of the lengths of the vectors for each of these six sample routes.

Table G.b: Change points (cp) identified for each of the six routes, at q=1, 2 and 3, with the time spent at the waypoint (min) and the activity recorded at the waypoint. Waypoints identified as change points by two versions of the Jupp test are indicated in italics, those identified by all three versions are highlighted in bold.

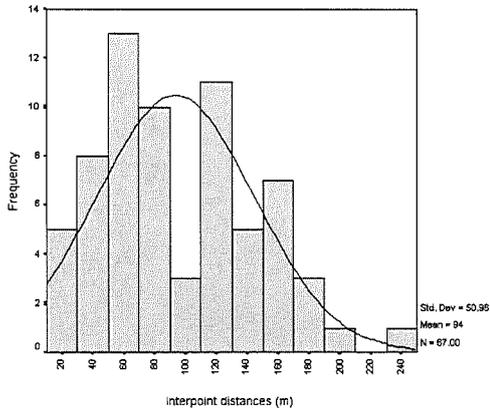
Route	Change points identified with each version of the Jupp test								
	q=1			q=2			q=3		
	CP	Time	Activity	CP	Time	Activity	CP	Time	Activity
BB	24	767	Nesting	<i>4</i>	574	Nesting	<i>4</i>	574	Nesting
	39	110	Feeding	<i>8</i>	48	Feeding	<i>7</i>	14	Feeding
	<i>46</i>	89	Feeding	<i>14</i>	35	Feeding	<i>14</i>	35	Feeding
	51	798	Nesting	<i>22</i>	65	Feeding	24	767	Nesting
	59	93	Social	24	767	Nesting	39	110	Feeding
				39	110	Feeding	51	798	Nesting
				<i>41</i>	0	Travel	<i>56</i>	0	Travel
				<i>44</i>	0	Travel	59	93	Social
				<i>46</i>	89	Feeding			
				51	798	Nesting			
				<i>56</i>	0	Travel			
				59	93	Social			
	BN	<i>51</i>	4	Resting	<i>4</i>	0	Travel	<i>5</i>	28
				<i>23</i>	124	Resting	<i>23</i>	124	Resting
				<i>45</i>	53	Resting	<i>27</i>	0	Travel
				<i>51</i>	4	Resting	<i>41</i>	21	Resting
							<i>46</i>	16	Feeding
DN	<i>57</i>	0	Travel	<i>7</i>	58	Feeding	<i>7</i>	58	Feeding
				<i>15</i>	0	Travel	<i>14</i>	0	Travel
				<i>18</i>	24	Resting	<i>18</i>	24	Resting
				<i>37</i>	0	Travel	<i>27</i>	0	Travel
				<i>43</i>	756	Nesting	<i>31</i>	51	Feeding
				<i>49</i>	61	Resting	<i>34</i>	3	Resting
				<i>56</i>	56	Resting	<i>35</i>	46	Resting
							<i>40</i>	0	Travel
							<i>43</i>	756	Nesting
KL	<i>31</i>	131	Feeding	<i>5</i>	0	Travel	<i>6</i>	70	Feeding
				<i>11</i>	0	Travel	<i>11</i>	0	Travel
				<i>22</i>	1	Resting	<i>18</i>	92	Feeding
KW	30	98	Feeding	<i>3</i>	56	Feeding	<i>7</i>	25	Feeding

36	12	Resting	7	25	Feeding	13	36	Feeding
			15	920	Nesting	18	162	Feeding
			18	162	Feeding	23	157	Feeding
			23	157	Feeding	27	26	Feeding
			27	26	Feeding	30	98	Feeding
			30	98	Feeding	36	12	Resting
			36	12	Resting			
<hr/>								
MA			3	74	Resting	4	98	Feeding
			12	0	Travel	12	0	Travel
			17	0	Travel	17	0	Travel
			24	14	Resting	25	49	Feeding
			48	16	Resting	36	27	Resting
			59	5	Feeding	44	59	Resting
			72	3	Resting	48	16	Resting
			74	2	Resting	59	5	Feeding
						72	3	Resting
<hr/>								

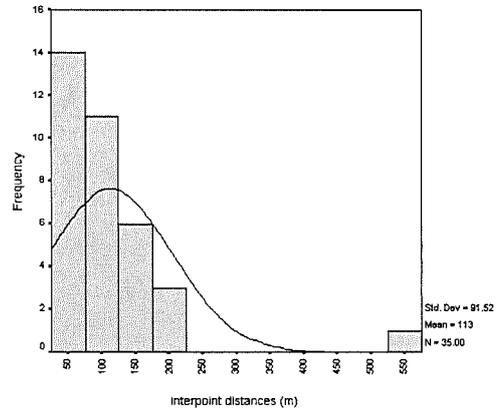
It is apparent from figure G6 that four of the routes (BN, DN, KL and MA) have inter-waypoint distances that are quite skewed to the right, due to one or two very long distances. The longest of these distances arose when the target animal was lost and subsequently found, but with no waypoints being recorded in the interim period. To determine how influential this was on the outcome of the Jupp test, these four routes were divided at the point where the animal was lost and treated as two separate routes. As shown in figure G7, this reduced the spread of the inter-waypoint distances so that all appear to be more normal curves. The Jupp tests performed on these 'cut' routes did not identify any different change points to those noted above in table G.b, however. This confirms that the Jupp test is indeed very robust and able to cope with slight deviations from normal data, as predicted by Peter Jupp, and also corroborates the authenticity of the change points recorded.

Figure G6: Histogram plots of the lengths of vectors (inter-waypoint distances) for each of the focal routes.

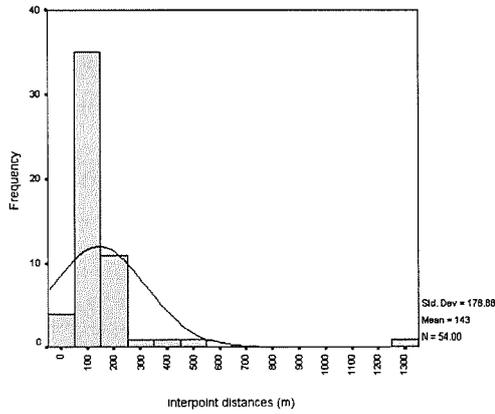
BB07/07/03



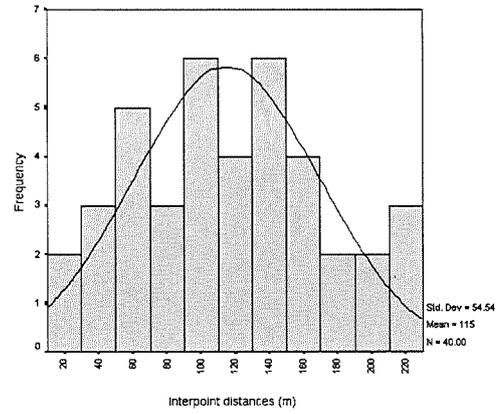
KL20/01/03



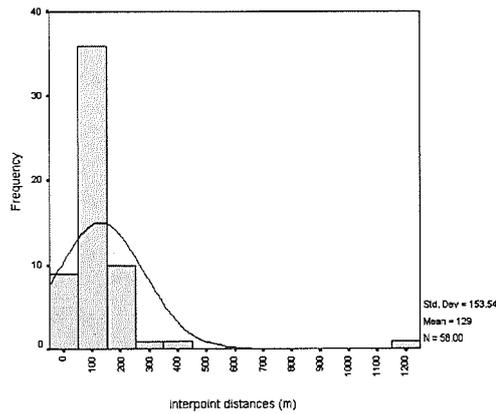
BN24/02/03



KW30/06/03



DN03/02/03



MA10/02/03

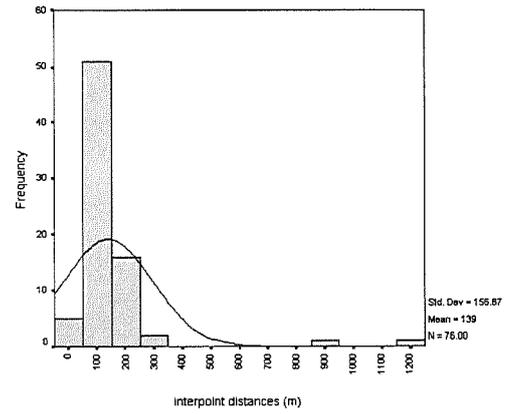
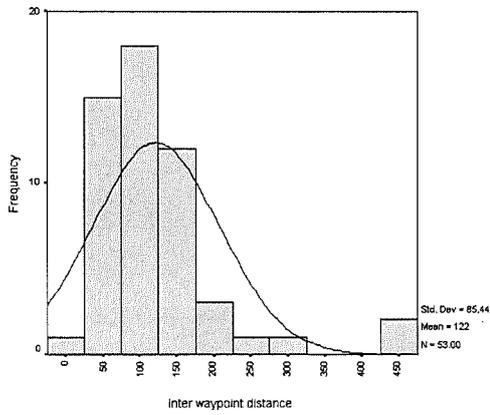
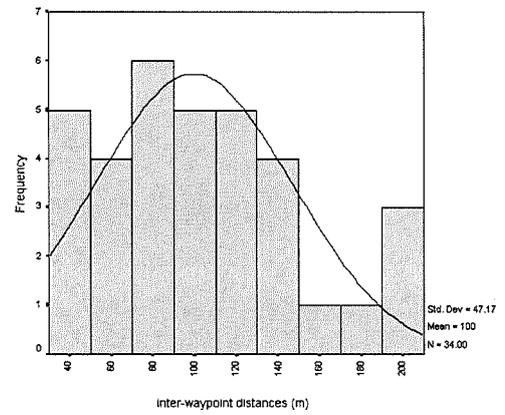


Figure G7: Histogram plots of the lengths of vectors (inter-waypoint distances) after routes had been cut at points where animals were lost.

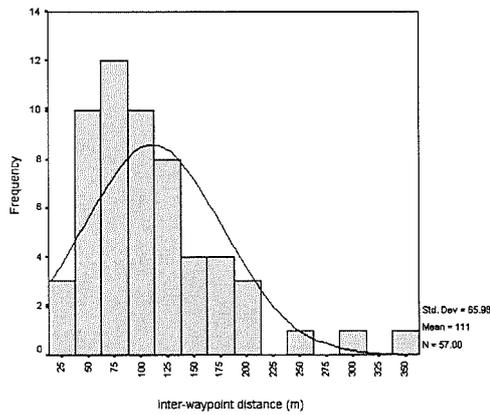
BN24/02/03



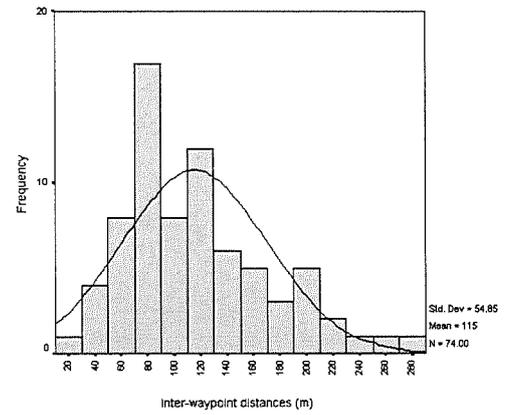
KL20/01/03



DN03/02/03



MA10/02/03



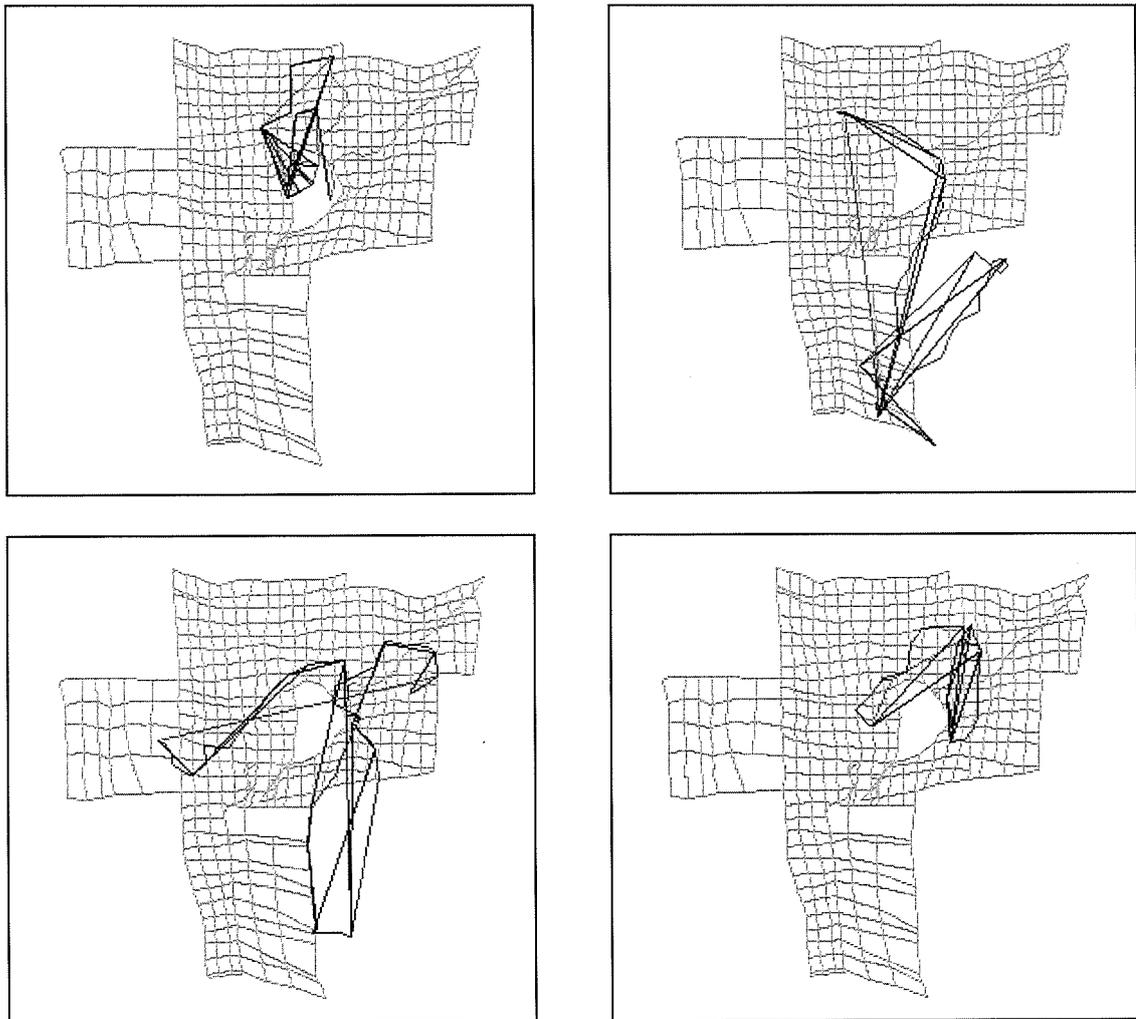
Which Jupp test version is the most appropriate for chimpanzees?

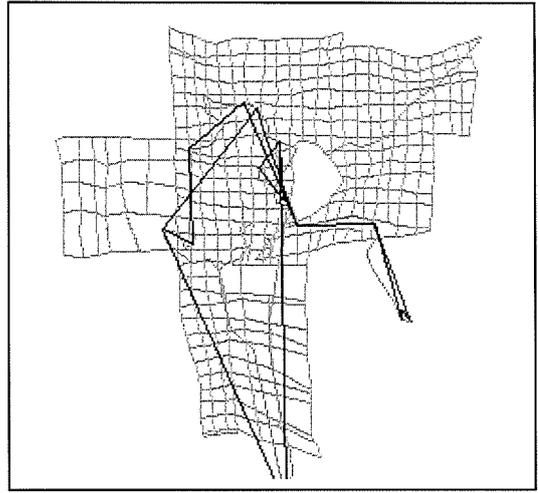
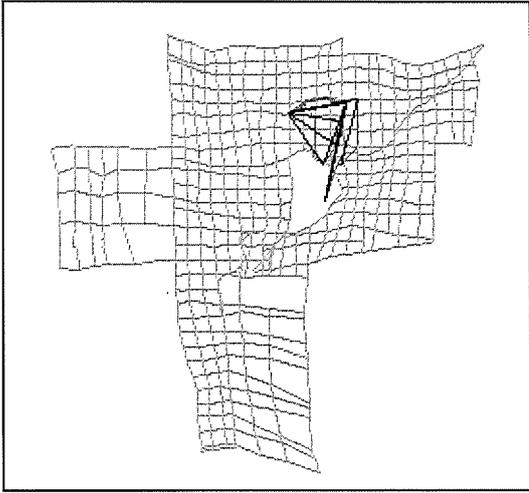
It is apparent from the results presented in table G.b and figure G8 that the q=1 version of the Jupp test is insensitive to change points in chimpanzee ranging, indicating only ten change points in total, compared with the 42 and 43 identified when q=2 and q=3 respectively. Only six locations were identified as change points by all three versions of the test. Two locations across the six routes were identified by versions q=1 and q=2, and 19 locations were jointly identified by versions q=2 and q=3. Two locations were identified by q=1 only, 15 were identified by q=2 only, and 18 were identified by q=3 only.

The large difference in numbers of change points found at $q=2$ and $q=3$ compared with $q=1$ suggest $q=1$ is not suitable for chimpanzee ranging, suggesting that chimpanzee travel routes are not composed of random wiggles followed by dead straight bee-lines. $q=2$ is approaching the asymptote of the number of change points that will be found, consistent with the idea that chimpanzee paths are composed of many consecutive, *quite* straight lines, with deviations occurring due to environmental obstructions or distractions. As higher values of q increase the likelihood of Type 1 errors, as described above, I suggest that $q=2$ is the most suitable version of the Jupp test to apply to chimpanzee ranging data.

Figure G8: The original routes taken – as shown in figure G4 - and the same routes as approximated by the change points found when using the Jupp test with $q=1$, $q=2$ and $q=3$.

Dark grey lines indicate route between change points identified by Jupp test version $q=1$, blue lines denote route between change points identified by $q=2$, and black lines represent the route between change points identified by the $q=3$ version.





Appendix H

Food trees used

H1: Heights/DBH of trees fed from

Food species	Height (m)	Party size	Duration of feeding party (min)	Food species	Height (m)	Party size	Duration of feeding party (min)
TRR	15	4	10	FM	20	16	30
FM	45	6	>20	BPY	20	16	
FSU	35	3	>20	FSU	35	3	
CYA	35	11	25	BPY	15	2	
FE	30	4	10	BPY	20	2	30
FM	45	24	>20	FE	20	6	95
FE	35	24	85	CYA	30	20	20
FM	45	19	>20	FE	20	1	80
FM	45	4	230	BPY	20	1	20
FVR	35	?	>20	CYA	35	5	80
FVR	35	25	>20	ALP	Climber	2	
FM	45	28	>20	BPY	15	8	
CMI	10	2	25	FE	30	7	30
FM	35	12	75	CYA	45	6	
BPY	15	11		BPY	20	11	
BPY	20	9	40	BPY	20	13	
FM	45	13		MOL	30	3	50
FM	45	18	110	BPY	20	19	20
FM	45	9		FE	25	5	70
BPY	20	16	50	CYA	45	19	25
FM	45	25	50	COM	40	14	
COM	35	25	15	ALP	Climber	6	
COM	40	19	110	CYA	45	18	
BPY	20	10		FM	40	7	70
FM	45	14		FSU	30	11	30
FM	45	6	20	CMI	10	2	
FE	35	20		FM	40	8	195
CAL	40	20		FM	40	9	20
COM	40	17	20	FVR	25	1	
DD	10	3		CMI	10	13	30
CAL	35	5	35	ANT	25	4	35
FE	30	3		CMI	20	5	
FM	45	3	15	CYA	45	2	
COM	40	2	20	CYA	50	7	30
COM	40	2		CMI	15	4	50
BPY	10	3		CAL	35	33	20
BPY	15	6	30	RF	Dead	3	
FSU	35	8	80	CP	35	2	
FSU	35	20	15	CMI	15	5	15
BPY	20	7	390	CAL	30	3	155
FSU	35	4		CYA	50	14	
FE	30	10	15	FSU	25	2	25
BPY	30	14	70	BPY	20	6	20
				FSU	35	2	45
				URC	Climber	2	10

CMI	10	2	5	MOL	30	6	100
CMI	10	2	15	URC	Climber	4	25
CMI	15	2		CAL	40	1	15
CYA	45	2	10	CMI	10	1	
CYA	35	2	20	FVR	35	7	30
URC	Climber	2	10	ANT	45	3	10
CYA	35	2	20	FSU	30	8	70
FE	40	2		FSU	35	17	80
FE	40		10	FE	20	23	35
FSU	35	3	45	FSU	35	1	75

Mean height of all feeding trees: 30.7m sd= +/- 11.8

Median height of all feeding trees: 35m Range 10m-50m

Mean tree height excluding *B. papyrifera*: 32.9m sd= +/- 11.4

Median tree height excluding *B. papyrifera*: 35m Range 10-50

H2: Number of trees community seen to feed from:

	F. exasperata	F. mucoso	F. sur	C. albidium	C. millenii	C. alexandri
No. seen feeding from	85	11 ¹	54	8 ²	85	43
No. in grid	351	102	134	139	351	589
% used	24	11	40	6	24	7

¹ Low possibly because only very large FM trees were fed from.

² Low because many of these fruits were eaten from trees outside the grid system.