FRUITS OF ENLIGHTENMENT

FRUIT LOCALISATION STRATEGIES IN WILD MANGABEY MONKEYS

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for the degree of Doctor in Philosophy

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To my mother

Johanna Maria Petronella van Schaik

and

the late mother of Agnes and Rose

Angela Ateenyi

Contents

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ABSTRACT

Using both observational and experimental approaches, I investigated a number of the fruit localisation strategies in two frugivorous rain forest primates: the grey-cheeked mangabey (*Lophocebus albigena johnstonii*) in the Kibale National Park, Uganda and the sooty mangabey (*Cercocebus atys atys*) in the Taï National Park, Ivory Coast. The results of these studies suggest that in order to find fruit mangabeys used a flexible search mechanism, in which search (by use of sensory cues or memory) for particular fruits was activated by the encounter of a certain threshold density of fruit bearing trees of that same species. For species in which fruit does not emerge synchronously among conspecific trees, like some figs, other localisation strategies were investigated. No evidence was found that the mangabeys regularly used auditory cues of sympatric frugivores to discover fig fruits. Observations of visiting patterns and approach speed towards a pre-selected number of fruit trees indicated that the monkeys relied on spatial temporal memories of fruiting states to locate fruits. In fact, mangabeys were less efficient in finding edible fruits from particular fig species in less familiar areas of which they had fewer spatial memories than in more familiar areas. Further analyses suggested that the monkeys were able to anticipate quality changes (the number of edible fruits) of fruit bearing trees between subsequent visits. The probability of a revisit of a fig tree, that was known to previously carry fruit, was best explained by past temperature values and solar radiation values of the morning before the revisit. This suggests that monkeys were able to integrate memories of previous fruiting states with time and weather variables in order to optimise their arrival time at fruit trees. I discuss the implications of these findings for theories of primate cognitive evolution.

* * *

INTRODUCTION

"Most attempts to say when and how human intellectual abilities arose begin with fossil evidence and end up with modern human achievements. In between comes speculation: careful, plausible speculation" (Byrne 1995).

Two evolutionary scenarios for primate cognitive evolution

Our human brain is uniquely large among other primates and remorseless in its energy demand. In adulthood, the brain consumes about 20 percent of our basal metabolic rate, i.e. the rate at which energy is used when we sleep (Aiello & Wheeler 1995). When energy fails to be provided for longer than 4 minutes the brain will be irreparably damaged; a slightly longer period will result in death (Byrne 1995). Primate brains in general differ significantly from those of most other mammals in their large size, particularly their large cortices and the higher proportion of the basal metabolism devoted to brain function (Armstrong 1983; Harvey & Krebs 1990). What explains the evolution of such an energetically costly piece of equipment in humans and other primates? One of the proposed advantages of a large brain is the ability to perform intelligent behaviour that helps primates to solve problems in daily life. For many years, primatologists have sought factors in the lifestyles of particular primate species that might place special demands on information processing capacities and hence that might have selected for the unusual large brain of monkeys, apes and humans (for animals of their size), (e.g. Romanes 1882; Byrne 1995; Dunbar 1998; Barton 2000). As a result, two main evolutionary scenarios have emerged on how primate intelligence may have evolved: the social intelligence hypothesis (Jolly1966; Humphrey 1976; Byrne & Whiten 1988; Brothers, 1990; Dunbar, 1998) and the ecological intelligence hypothesis (Clutton-Brock and Harvey 1980; Milton 1981; 1988).

Social intelligence hypothesis

Most primate social groups have a stable social structure, and some individuals are permanent members. This is not the case for groups in many other animal species, for instance the large herds of antelope. As a result, primate group members know one another individually and establish enduring relationships. By identifying individuals and observing their interactions with other group members primatologists were able to reveal complex social behaviours like keeping allies, making friends, sharing food, knowing about others' social lives, sophisticated communication about predators and food locations and learning to manipulate and deceive (see Byrne & Whiten 1988; Byrne 1995; Whiten & Byrne 1997; Arnold & Zuberbühler 2006; Cheney & Seyfarth 1990). Primate groups are based on a delicate balance between competition and cooperation. The reproductive success in such groups is expected to depend on the cognitive skills with which an individual manages this delicate balance. This realisation resulted in the social intelligent hypothesis (Jolly 1966; Humphrey 1976). The hypothesis claimed that the most cognitively demanding aspect of the lives of many primate species is the behaviour of the other members of their social group. To test this hypothesis primatologists used the comparative approach, which was first used by Darwin's successor Romanes in 1882. They compared 1) measures that are related to intelligence, i.e. several types of brain measurements, such as relative or absolute brain (ratio to that of the rest of the body) or neocortex size (ratio to that of the rest of the brain), with 2) measures of social complexity (group size) and behavioural complexity (deceptive behaviour), for a large number of primate species. The significant correlations found between both type of measures strongly supported the hypothesis that primates evolved relatively larger brains as an adaptation for social interaction (Barton 1996; Byrne 1997; Dunbar 1998).

Ecological intelligence hypothesis

Although the social intelligence hypothesis currently enjoys widespread support, there are reasons to remain sceptical about its power to explain the evolution of primate intelligence in general. For instance, the hypothesis seems plausible for large multi-male groups, where individual variation in reproductive success is large and intra-group competition for resources is strong, but it is less clear how and why individuals need sophisticated social skills when living in small one-male groups or semi-solitarily, as many primate species do (Smuts et al. 1987 and see Byrne 1997 for discussion of other weaknesses).

Hence, primatologists continue to investigate its main alternative, an ecological intelligence hypothesis, first introduced by Clutton-Brock & Harvey (1980) and Milton (1981). This hypothesis claims that the ecological complexity of the environment is cognitively the most demanding aspect of primate lives and that this complexity favoured the evolution of intelligent behaviour in primates. In 1981 Catherine Milton proposed extensive mental mapping skills as the explanation for the large brain of the frugivorous (fruit-eating) spider monkey (*Ateles geoffroyi*) relative to that of the more folivorous (leaf-eating) howler monkey (*Alouatta palliata*). These two species are the same size in body, but in brain the spider monkeys is nearly twice as large. Spider monkeys often split off from the group to forage, and Milton suggested that the search for edible fruit around the range requires each individual to have an efficient cognitive map. She argued that the leaves that howler monkeys are able to feed on are more abundant and much less patchily distributed in the forest than fruit. This would enable them to forage as a cohesive group and manage with far smaller home ranges, so they have little need of efficient cognitive mapping skills. A similar comparison was made by Barton (2000) between two great ape species, gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*). Gorillas are more folivorous, have smaller home ranges, and have smaller brains compared to their body size than do chimpanzees. The hypothesis that a fruit dependent diet placed special demands on the cognitive apparatus was supported by a number of comparative brain studies that revealed a significant correlation between both the relative neocortex size and absolute brain size and the level of frugivory of a large number of primate species (Clutton-Brock and Harvey 1980; Barton 1996; 2000). The results of a comparative study that was free of phylogenetic bias suggested that not only social group size but also the degree of frugivory are important; each being independently correlated with relative neocortex size (Barton 1996).

The challenge of finding fruit

Debate continues on the challenges encountered by fruit eating primates. What exact challenges triggered the evolution of a more costly brain? Is it indeed the spatial and temporal distribution of fruits that requires special foraging skills or should other aspects of fruit be considered? Byrne (1995) suggests that leave eating howler monkeys may confront just as severe spatial memory problems on a more intricate scale. Howlers, unlike colobines, do not have special gut adaptations to neutralize the poisonous secondary compounds of mature leaves and unripe fruit in tropical forest, yet they eat both. Kenneth Glander (1978) has shown that the howlers know exactly which individual trees have the lowest toxin levels and appear to be in need of a detailed and elaborate spatial memory. Glander observed a careless howler drop to the forest floor, poisoned – suggesting that selection pressure to evolve sophisticated memory skills could even be higher for folivores than for frugivores. Milton's focus on mental mapping was also opposed by Barton (2000), who stressed that many animals possess extended spatial memories of food locations and not all of them are noted for their mental abilities. Moreover, Barton argued that the degree of frugivory remains significantly correlated with relative neocortex size even when home range size has been partialled out (Barton 2000). It therefore seems to be frugivory per se, rather than the size of the ranging area that the animal must map, that is associated with relative neocortex size and absolute brain size. Barton proposed visual specialisation as a plausible explanation for the association between frugivory and neo-cortex size (Barton 2000). He argues that variation in neo-cortex size in primates is at least partly a product of selection on specific visual mechanisms, such as colour vision. Fruits often change colour during ripening (Sumner & Mollon 2000). Trichromatic colour vision enables animals to distinguish between ripe and unripe fruit and in addition aids in detection of fruits against the background of leaves (Osorio & Vorobyev 1996). However, Lucas & Dominy (2001) argue that it is folivory and the advantages of detecting young coloured leaves against mature foliage that maintained colour vision instead of detecting ripe fruit.

The ephemeral and inviting nature of rain forest fruit

In this thesis, I focus on another characteristic of fruit that may provide a cognitive challenge to fruit eating primates and that possibly has played an important role in the evolution of primate intelligence: temporal distribution. The timing of fruit emergence can be complex and once the fruits emerge they are only present for short periods in time (Milton 1981; 1988; Chapman 1999; 2004). In addition, most ripe fruits have an *inviting* nature and *want to be eaten* to enable seed dispersal. Consequently, fruits are relatively *attractive* to consume in terms of digestibility levels and toxic compounds, which makes them *desirable* by a large number of animal species (e.g. Waterman 1977; Struhsaker 1997; Houle 2004). As a result, frugivores can face high levels of competition since a large number of animals eat the same food within relatively short time periods (Hauser & Wrangham 1990; Houle 2004). In addition, frugivores may experience higher levels of within group competition, since fruits, large fruits in particular, can be more easily defended than leaves (Dunbar 1987; Sterck 1995). A premium is therefore placed on individuals that are able to arrive first as soon as fruits become edible and those that avoid trees that are depleted. Hence, I argue, that it is not the spatial-temporal distribution as such, that could have triggered the evolution of complex cognitive skills, rather the high level of competition for fruit, due to its inviting and ephemeral nature.

Why are primates more challenged?

Comparative brain studies on other animal species showed that fruit-eating species also have larger brains among bats and rodents (Harvey & Krebs 1990). However, primates have much larger relative brain sizes than these other frugivores (Janson 2000). Janson argues that two factors in particular distinguish primates from nearly all other fruit eating animals: first, primates do not fly, and second, most primates are both large and social. The costs per unit distance for terrestrial locomotion are three or four times greater than for flying animals (Schmidt-Nielsen 1972). This difference is likely to further exaggerate for arboreal primate species, which must climb up and down trees. The fact that primates, especially apes, are large and social means that they need to find relatively large fruit sources to fulfil the group's daily nutritional need (Milton 1981, 1988; Boinski & Garber 2000; Janson 2000). Rain forest primates in particular are thought to be challenged. Tropical rain forests are generally characterized by a high diversity of tree species (e.g. Myers 1980). Most species have very low densities and individual trees of each species tend to be widely dispersed in space (e.g. Milton 1977; 1981; Chapman et al. 1999). Unlike in more temperate regions rain forest fruits do not appear in fixed seasons. Fruiting seasons can be widely and irregularly distributed over a year and some species do not fruit within a season at all. When they do, not all trees carry fruit at any location. Hence, fruit eating rain forest primates could benefit from minimising their foraging route distances (Milton 1981; 1988) by remembering fruiting states of individual trees and anticipating subsequent states.

How to deal with the ephemeral and inviting nature of fruit?

To date, somewhat surprisingly, little attention has been given to the large variation in temporal occurrence of rain forest fruit (van Schaik 1986) and the possible strategies or skills that have evolved to deal with this variation. Many studies have attempted to test whether primates adjust their ranging behaviour to seasonal changes in fruit distribution (e.g. Clutton-Brock 1977; Terborgh 1983; Waser 1975). Sometimes correlations between seasonal changes in ranging behaviour and food distribution are found (e.g. Kinsey 1977; Chivers 1977; Buij et al. 2002.). Often determinants are not clear and factors such as mate-competition seem to complicate analyses (e.g. Clutton-Brock 1977; Steenbeek 1999). Few studies however, have attempted to show evidence of the strategies and skills used to asses fruiting periods – the strategies that enable a group of primates to adjust their ranging behaviour to changes in fruit distribution. Most of these studies are focussed on the use of a spatial memory (e.g. Milton 1981; Garber; 1989; Janson 1998; 2000). In this thesis I therefore focus on the temporal aspects of fruit distribution and the strategies used by foragers to predict the start and ending of fruiting periods in individual trees.

Fruits of enlightenment: Research Questions

The title of this thesis is ambiguous. First I attempt to gain insight in the question whether a dietary dependence of fruit could indeed have triggered the evolution of complex cognitive skills. This was investigated by studying the current habitats or current evolutionary setting of a fruit-eating primate in an African rain forest and the distribution and phenological characteristics of the primate fruit trees within it. I investigated what particular challenges monkeys encounter within their natural environment and what cognitive skills could potentially be helpful. Second, I tried to find out what the “fruits” of the enlarged brain and the proposed higher cognitive abilities of (frugivorous) primates are. What exactly are the fruit-eating primates capable off and what fruit localisation strategies and skills can be discovered by studying their foraging and ranging behaviour? In this thesis I systematically investigated a number of fruit localisation strategies in two species of frugivorous rainforest primates, the grey-cheeked mangabey (*Lophocebus albigena johnstonii*) in the Kanyawara research area, Kibale National Park, Uganda and the sooty mangabey (*Cercocebus atys atys*) in the Taï National Park, Ivory Coast. The main question that I aim to answer within this thesis is: "How efficient are mangabey monkeys in localising fruit bearing trees and what strategies and skills do they use to optimise the timing of arrival at fruit trees?" In other words, do they know where the fruits are and if so, how do they manage to arrive at the right place and at the right time?

Study species and research habitat

Sooty mangabeys in Taï forest

The sooty mangabey is found in the West African rain forest along the equator from Ivory Coast to Senegal (Gust 1995). The species is closely related to mandrills (*Mandrillus sphinx*) (van de Kuyl et al. 1995) and live semi-terrestrial in large groups that can range in size from 30 to 120 individuals (Range & Noë 2005; personal observation). The sooty mangabeys form multi-male groups, perform frequent vocalizations, and advertise estrus with swollen and brightly coloured perineal skin (Gust 1995; Range & Noë 2005). Wild sooty mangabeys seem especially promising for research on complex fruit-search strategies. First of all, a large proportion of the sooty mangabeys' diet consists of fruit (in the period March-August 68% of their diet consists of fruits, Bergmüller 1998). Although, at first sight, the mangabeys' idiosyncratic travel routes seem to indicate a strategy of random search (see fig.1), more detailed analysis suggest the opposite. An increase in daily feeding time on fruit trees of e.g. *Anthonata fragrans* species, significantly increases day journey length (Rutte 1998), suggesting that mangabeys plan travel towards fruit-bearing trees and possibly other parts of their day journey. Second, due to a terrestrial mode of travel in dense vegetation (visual detection field of approximately 15 m (Boesch & Boesch 1984)), the mangabeys' daily visual detection field is limited. Knowing that my study group has an average group spread of 102 m and an average day journey length of 2.2 km (Rutte 1998) I can calculate that the group has a daily search swath of 291,9 m^2.

This indicates that it will take them 23 up to 27 days to cross their home range of 7-8 km^2, making regular check ups of fruit edibility *en route*, as has been suggested in monkeys with smaller home ranges (Milton 2000), unlikely. Instead sooty mangabeys are expected to predict fruit availability by more complex strategies.

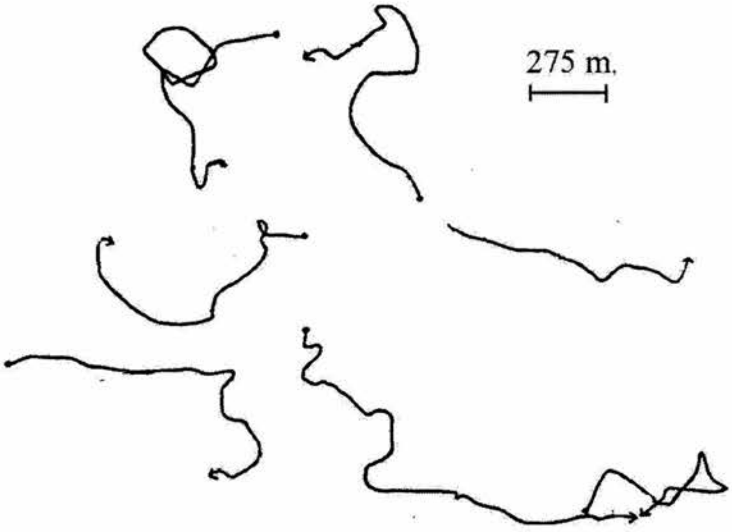

Fig. 1. Example of 7 daily travel routes of a group of sooty mangabeys (Rutte 1998)

Study site

The sooty mangabeys were studied at the research site of the Taï Monkey Project on the western border of the Taï National Park in the Ivory Coast (5° 52‘ N, 7°20’W). The park is the last remaining major block of undisturbed lowland rain forest in West Africa and covers approximately 454,000 ha. The forest is classified as a low-land tropical moist forest (elevation: 120m, topographic relief (highest – lowest point): 40m, mean daily minimum temperature 21.7 °C, mean daily maximum temperature: 30.1 °C, rainfall: 1875 mm/p. year (average of 1991 – 1999; data from the Taï Monkey Project) and has two rainy and two dry seasons each year (see Boesch and Boesch-Achermann 2000 for an extended description of the study area). The study area of about 7 km^2 contains a grid and trail system (fig. 2). Twelve primate species live in the study area, three of which are nocturnal. The main predators of the monkeys are chimpanzee, *Pan troglodytes*, crowned eagles, *Stephaneoaetus coronatus*, leopards, *Panthera pardus*, and human poachers (Zuberbühler et al. 1997).

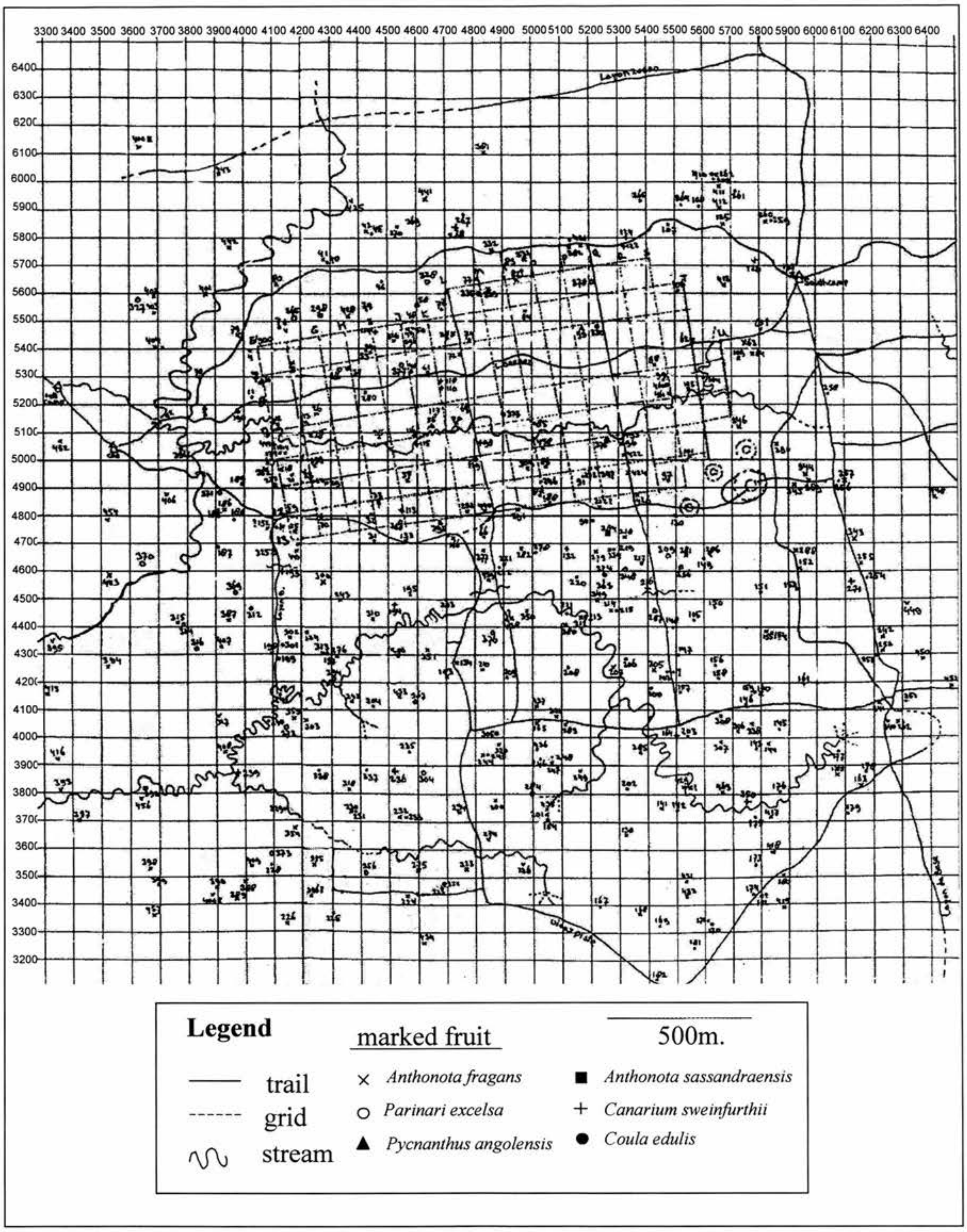

Figure 2. Hand drawn map of the trail system of the Taï research area. Fruit trees are marked within the range of the main study group of sooty mangabeys (pers.com F. Range; this study).

Grey-cheeked mangabeys in Kanyawara forest

Due to political unrest in Ivory Coast I terminated my studies on the sooty mangabeys in October 2002, to continue my investigations on a closely related monkey species, the grey-cheeked mangabey in the rain forest of the Kibale National Park in Uganda in March 2003. Most of the data presented in this thesis was collected on the grey-cheeked mangabeys.

Grey-cheeked mangabeys range from the Central African coast to Central Uganda (Kingdon 1984). They have a different phyletic origin than the sooty mangabeys and are more closely related to the baboons (van de Kuyl et al. 1995). Like the sooty mangabeys they live in multi-male groups, perform frequent vocalizations, and females advertise estrus with swollen and brightly coloured perineal skin (Kingdon 1984). According to the literature the grey-cheeked mangabeys are strictly arboreal, however, the study group was regularly observed on the ground (chapter 4). Group size ranges between 5 and 29 individuals (Freeland 1979; Waser 1974; Olupot et al. 1994; Barrett 1995; this study). Their average home range size is smaller than that of the sooty mangabeys, however, much larger than that of the sympatric living arboreal monkey species in the Kibale forest (Houle 2004; O'Driscoll Worman 2004; Janmaat et al. 2006b; chapter 3). Especially the groups that range in disturbed forest areas (Kanywara research area) are known to have large home ranges of up to 410 ha (Waser 1976). The home ranges of groups that range in undisturbed forest at Ngogo are significantly smaller than the ones in semi-logged areas at Kanyawara. The lower density of food trees in Kanyawara appeared to account for this difference; home ranges at both sites were found to contain a similar number of food trees despite a four-fold difference in size (Barrett 1995). Grey-cheeked mangabeys in Kanyawara seemed promising candidates for research on complex fruit-search strategies. Previous studies show that 59% of all feeding observations concerned feeding on fruits (Waser 1975; Olupot et al. 1997). Day journey length of grey-cheeked mangabey groups seems to be determined by levels of insect foraging, within small groups (Waser 1974; Janson & Goldsmith 1995; Janson pers. comm.), however, ranging patterns also appear to be strongly influenced by fruit availability and the distribution of large fig trees in particular (Waser 1974; Olupot et al. 1997). The number of mangabey groups seen per kilometre walked was also marginally correlated to fruit availability (O'Driscoll Worman 2004).

Grey-cheeked mangabeys are arboreal. As a result visual detection distances vary more than those of terrestrial foragers. Knowing that the average group spread of a grey-cheeked mangabey group is 57 m and the average day journey length is 1127 m, I estimated that the daily search swath is between 176.9 m^2 (for a detection distance of 15 m on either side of the group) and 402.3 m^2 (for a detection distance of 150 m on either side of the group). This indicates that it would take a grey-cheeked mangabey group 41 to respectively 10 days to traverse a home range of 410 ha. These estimations point out that it is difficult to tell whether the mangabeys can make regular check ups of individual trees *en route* by use of visual cues and whether or not they could benefit from more complex localisation strategies to locate fruit. However, Waser (1976) suggests that some food trees within the home ranges were not approached for months at a time, suggesting that the mangabeys may benefit from an ability to predict fruit availability. Grey-cheeked mangabeys (like sooty mangabeys) therefore are thought to be promising candidates for finding evidence of ecologically intelligent behaviour in relation to fruit localisation skills.

Study Site

The Kanyawara study site is located west of the Kibale National Park, Uganda that covers around 76,600 ha. The study area around the site is comprised of mid-altitude moist tropical semi-logged forest (location: (0°34'N, 30°22'E), elevation: 1500 m, topographic relief (highest – lowest point): 200 m, rainfall 1700 mm/year (1984-1996), mean daily minimum temperature 15.5°C, mean daily maximum temperature: 23.7 °C (1990-1996; Chapman & Chapman 1997; 1999) and has two rainy and two dry seasons each year (though the length and severity varies greatly). The fruiting of tree species in Kibale is usually synchronous, though the timing of fruiting can be irregular, sub-annual, annual, or super-annual depending on the species (Chapman et al. 1999b). Eleven primate species live in the study area, three of which are nocturnal. The main predators of the monkeys are the chimpanzees, *Pan troglodytes* and the crowned eagle, *Stephaneoaetus coronatus*. Details of the study area can be found elsewhere (Kingston 1967; Struhsaker 1997). Prior to becoming a national park, the area was a forest reserve with the last logging in the natural forest occurring in 1969. The study area that is comprised of a mosaic of tall primary forest, swamp, grassland, thicket and colonizing forest (fig. 3) is approximately 5 km^2 and contains an extended trail system (fig. 4).

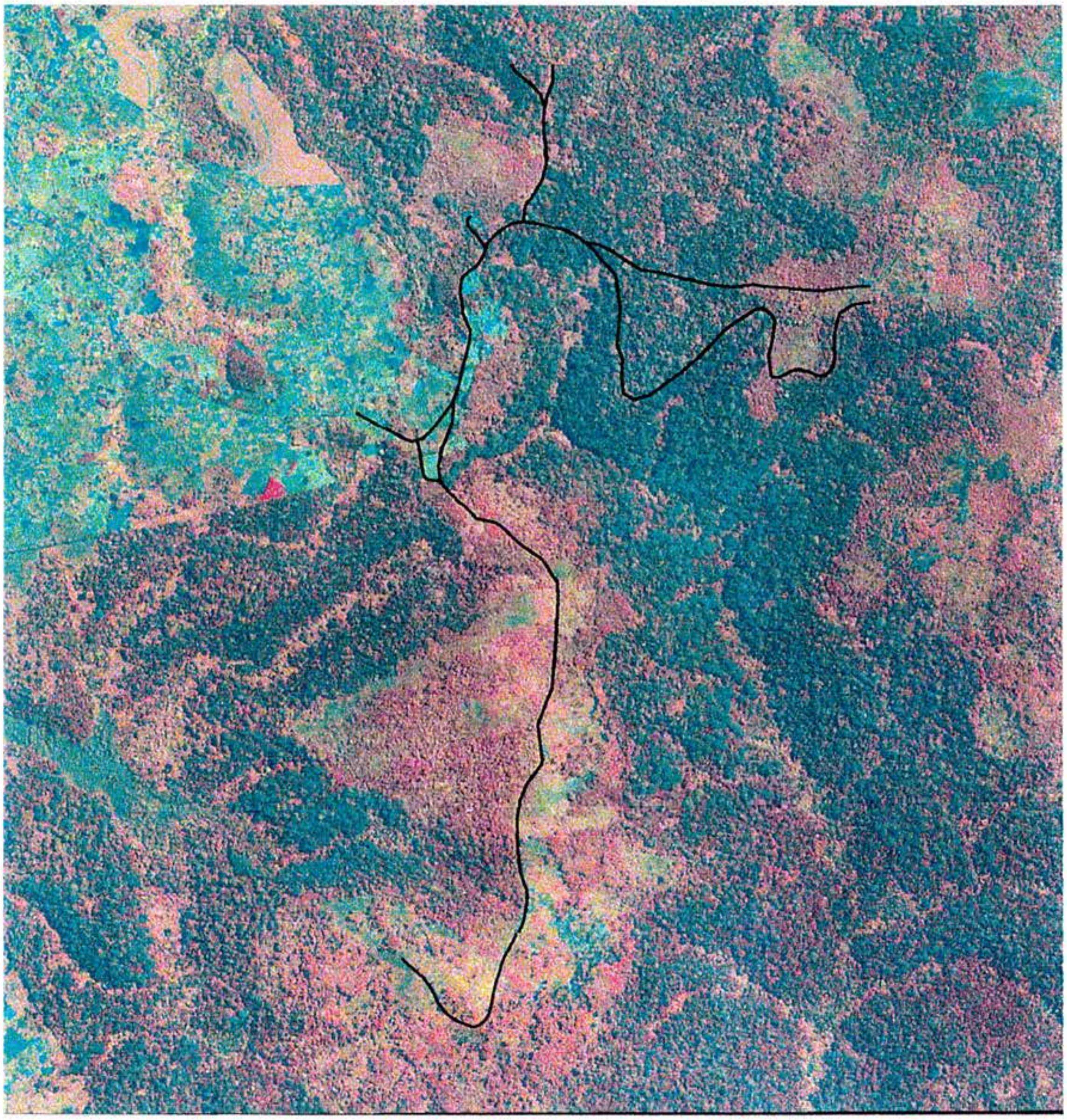

Fig. 3 Aerial picture of the Kanyawara study area. The black lines are logging roads. The satellite image is a Quickbird (high resolution, 2.4 m) from DigitalGlobe, Inc., Longmont, CO, USA.

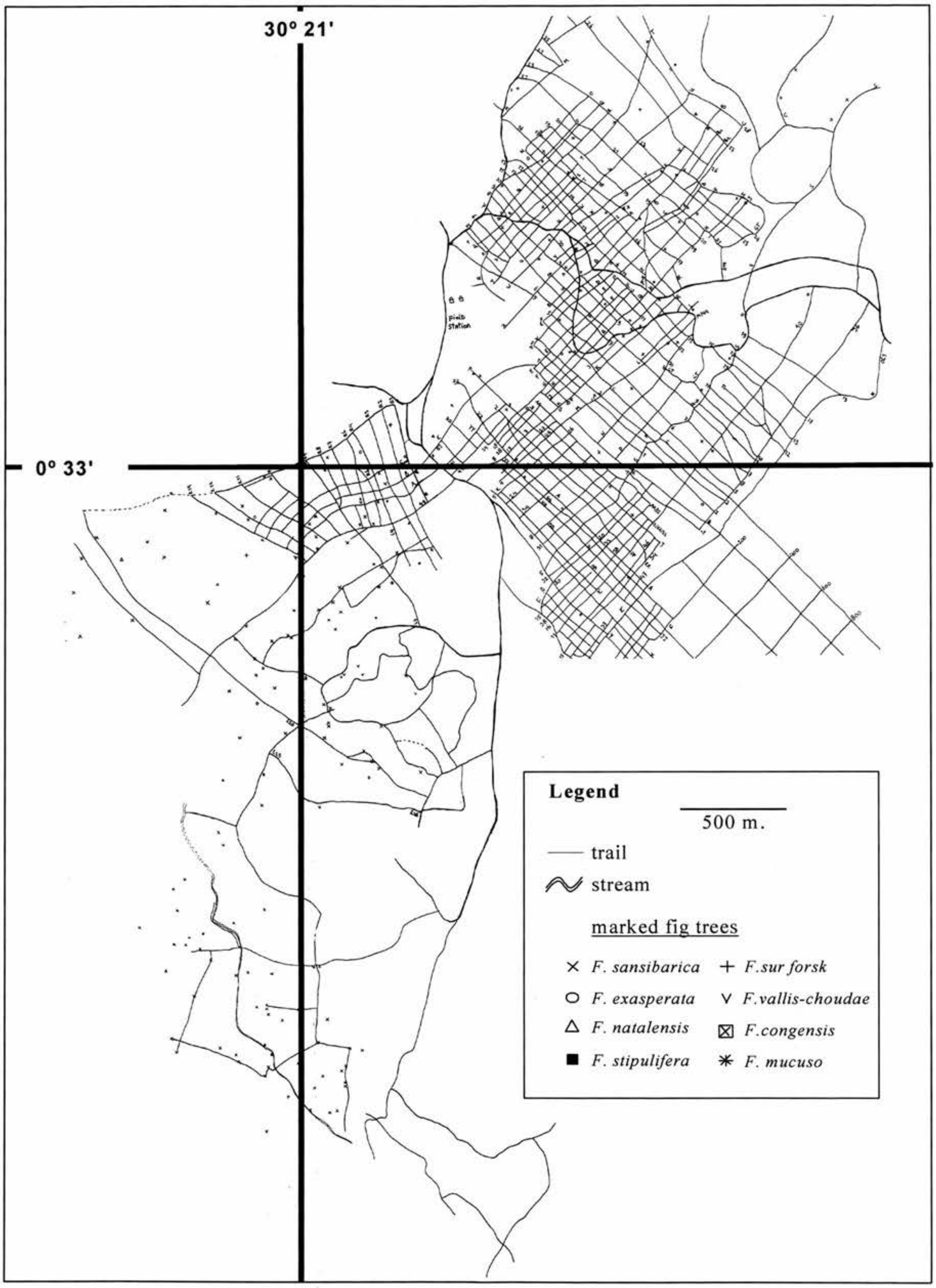

Fig. 4. Hand drawn map of the trail system in the Kanyawara study area. Fig trees were marked within the home range of the main study group of grey-cheeked mangabeys (this study; Olupot thesis)

OVERVIEW THESIS

Fruit- Search Efficiency: Do mangabeys know where fruits are?

The first step in this study was to test the mangabeys' knowledge concerning the location of fruits within their home range. In order to investigate the level of efficiency with which the mangabeys found fruit I first compared the success rate of grey cheeked mangabey individuals in locating trees with edible fruits with the success rate of human observers who walked a random transect within the same area (chapter 1). In addition, I compared the visiting behaviour of two groups of mangabeys (sooty and grey-cheeked) in relation to a number of pre-selected fruit trees that carried either fruit or no fruit (chapter 3).

Fruit localisation strategies: How do mangabeys locate fruit?

Within the remaining part of the thesis I will be focussing on potential strategies that mangabeys could use to localise fruits. Before generating hypotheses on the type of strategies that may be used, it is important to realize the difficulties of predicting the timing and duration of fruiting periods of individual rainforest trees. A number of factors make such predictions especially difficult. First, only a finite number of trees produce palatable fruits and mangabeys need to develop substantial botanical knowledge. Previous research has shown that grey-cheeked mangabeys consume the fruits of at least 54 different species (Waser 1977). Second, between-fruiting intervals may be considerably long (half a year to four years (e.g. Chapman et al. 1999; van Schaik 1986)) and weather conditions cause variation in the starting of a fruiting period, without obvious cues (e.g. Chapman 1999; Anderson et al. 2005). Thirdly, within a tree's lifetime, the beginning and end of fruit production is extremely variable. Local soil and weather conditions determine the starting age, the moment of decay or collapse and the new tree species that can take its place, leading to a constantly changing spatio-temporal distribution of fruit (Milton et al. 1994; Chapman et al. 1997; Olupot 1998; Chapman et al. 1999). Finally, the nutritional quality of emerged fruit can vary substantially between and within species between different periods of the year and between different locations within the forest (Chapman et al. 2004; O' Driscoll Worman & Chapman 2005). Nevertheless, a number of potential strategies can be used to help the monkeys in their anticipations. I investigated the existence of the following fruit-localisation strategies that could be used separately or in combination with each other by the mangabeys within the study areas.

The use of synchronicity (Chapter 1)

In most tree species in the Kibale forest, individual trees fruit synchronically (Chapman et al. 1999). If mangabeys suddenly encounter fruits in a tree of a synchronically fruiting species they could use this cue as an indicator for the emergence of fruit in other members of that species throughout their home range (Milton 1981; Menzel 1991). By using a memory of each fruit species characteristics in combination with a synchronicity cued search mechanism a large number of fruits could be localised in a relatively efficient way. In chapter 1 I investigated the existence of this strategy by comparing the localisation efficiency of nine grey-cheeked mangabey males in relation to fruits species with markedly different levels of synchronicity. Relative localisation efficiency was measured by comparing the density of trees that were close to the males' travel routes with the density of trees within a control strip at 15 m distance from the males' route. Comparisons of localisation efficiency were made between seasons and between different locations in the home range.

The use of auditory cues (Chapter 2)

For species that do not fruit synchronically, such as figs, whose fruit crops appear and disappear in seemingly unpredictable manners, other strategies are expected to be more rewarding (Waser 1974; Milton 1991; chapter 5). The use of auditory cues, produced by other fruit eating foragers, could be a highly efficient mean to keep updated on fruit locations. Especially when visibility is limited or fruits lack to emit visual or olfactory cues, mangabeys could improve localisation efficiency for edible fruit by attending to particular auditory cues. In chapter 2 I investigated the use of this strategy by collecting a combination of observational and experimental data on five different groups of grey cheeked mangabeys. I conducted a follow up on previous play-back experiments (Olupot et al. 1998) and broadcasted loud calls from two sympatric frugivores (yellow casqued hornbills (*Bycanistes subcylindricus*) and chimpanzee) from 12 m. up a fig tree. By focussing on observations of fruit discoveries and by conducting play-backs from fig trees with unripe or no fruits I attempted to exclude the potential use of spatial memory.

The use of spatial temporal memory of fruiting states (Chapter 3)

For trees of highly preferred fruit species with large fruit crops it could also be beneficial to remember their previous fruiting state. This memory could simply involve the presence of edible fruit, however it could also contain information on the number of edible fruits previously encountered and the likelihood of depletion at a future visit or the number of unripe fruits that may become edible in the near future. In addition, the mangabeys are expected to benefit from remembering which trees were depleted recently and are therefore not likely to carry new ripe fruits within the near future. In chapter 3 I investigated the existence of the various types of memories of fruiting states by recording the ranging behaviour of two groups of wild mangabey monkeys (sooty mangabeys, *Cercocebus atys atys,* and grey-cheeked mangabeys, (*Lophocebus albigena johnstoni*) relative to a number of pre-selected target trees within their home range. I observed the groups' visiting patterns and speed, when approaching within a critical distance of a target tree, as a function of the tree's fruiting state. By a careful choice of fruit species and type of fruit trees and the design of a new method of data collection, I attempted to exclude the possible use of sensory cues. In this way I attempted to provide evidence that wild primates have a spatial memory of their natural food sources.

The use of long-term memory (Chapter 4)

Each of the above strategies is expected to help the monkeys most efficiently if it is used in combination with a long-term memory of tree locations. Once a synchronous fruit comes into season, the monkeys are expected to locate fruits of this same species most efficiently by remembering the specific locations of other trees or patches of that same species. Also, since most calls of sympatric frugivores are intermittent, the monkeys cannot always follow the direction of a caller and are expected to benefit from remembering the location of specific fruit trees that is likely to carry fruit in the particular area from which auditory cues were heard. Lastly, a long term memory of fruit tree locations could help the monkeys to find newly emerged fruits by monitoring trees that were known to have carried fruit in the past and that are reproductively active. In this thesis I made use of a unique opportunity to test the importance of long-term memories of relevant locations, e.g. fruit trees, within a primate's home range by observing the consequences of an unexpected range shift. During the study the main study group was observed to move into an area in which they had not been observed for a discontinuous yet regular observation period of six years. In chapter 4 I compared fruit localisation efficiency, day journey length, exploration rate, terrestrial behaviour and sleeping site distribution between the familiar and a new or less familiar area.

Predicting fruit emergence, ripening and depletion (chapter 5 and 6)

Other potential strategies that could be rewarding are the use of knowledge of fruit emergence, ripening and depletion rates. As is suggested by anecdotal observations on chimpanzees (*Pan troglodytis*, Wrangham 1977) and orang-utans (*Pongo pygmaeus*, Galdikas 1997), the reward gained by a revisit to a particular tree can be optimised by remembering the previous fruiting stage and combining it with knowledge of species-typical fruit ripening rates and depletion rates (Olupot et al. 1998). In chapter 5 and 6 it is investigated whether the monkeys are able to take into account tree-typical depletion rates, fruit emergence intervals and the relation between weather and ripening rates. These investigations were done by continuous recordings of the ranging behaviour of one groups of grey-cheeked mangabeys over continuous periods of 50, 60 and 100 days relative to a number of pre-selected target trees within their home range. I observed the groups' visiting patterns and speed, when approaching within a critical distance of a target tree, as a function of 1) the tree's previous and current fruiting state 2) the revisit interval and 3) past and current weather conditions.

It is clear that many more strategies could potentially be used by the monkeys to locate fruits. Especially the use of visual and olfactory cues that are emitted by edible fruit could be highly rewarding (Janson & Di Bitetti 1997; Dominy et al. 2001; Sumner & Mollon 2000). However, considering the time frame of this study, I chose to investigate those strategies that seemed practically most feasible for investigations.

Ecological relevance of proposed strategies

The first aim in this thesis was to search for evidence for the existence of any of the fruit localisation strategies proposed above. Secondly, I investigated whether I was right suggesting that the monkeys would benefit from using these particular strategies and whether these strategies made sense from an ecological perspective. In other words, I investigated how rewarding some hypothetical strategies would be when ecological and environmental factors were considered. For example, how realistic is it to expect a monkey to correctly predict fruit emergence in a-synchronous fig trees? Hence, I investigated 1) how fruit emergence of individual trees was distributed in time (chapter 5), 2) whether fruit bearing trees indeed contained more frugivores that could produce auditory cues, than empty trees (chapter 2) and 3) how percentages of fruit-bearing rain forest trees or synchronicity fluctuated in time and space (chapter 1). In the general discussion I evaluate the results of all the six data chapters and briefly discuss some of the cognitive skills that are required to perform the revealed strategies. Furthermore, I discuss the consequences of my results for theories on the origins of primate intelligence.

* * *

CHAPTER 1

A "SIMPLE" WAY OF DEALING WITH COMPLEX DISTRIBUTIONS OF RAIN FOREST FRUIT: USE OF LOCAL SYNCHRONICITY

Uvariopsis congensis ripe fruit

Field assistant (P. Irumba) collecting ribbons along the male's travel route

Field assistant (J. Rusoke) determining fruiting state of *U. congensis* tree

INTRODUCTION

“In no case is an animal activity to be interpreted as the outcome of the exercise of a higher psychical faculty, if it can be fairly interpreted as the outcome of the exercise of one which stands lower in the psychological scale”. (Morgan 1895).

The challenge of locating fruit

Primates and tropical forest trees share a long history of association. At one time, it was popularly believed that tropical forests were stable and unchanging environments that offered an almost unlimited food to the plant-eating animals inside them. Recent research, however, indicated that this was a wrong assumption. Despite the large number of trees that grow inside a primate’s home range – which can reach for example over 100,000 trees for the rainforest monkey *Lophocebus albigena* - it is only a very small number that represent significant sources of food at any given time (Waser 1974). First of all, not all trees produce items that can be eaten by primates. Second, tropical forests generally show considerable seasonal variability with respect to phenological patterns. At certain times of year, many tree species produce an abundance of new leaves, flowers, or fruit; at other times, however, there are notable and persistent lows in the production of such items and concomitant lows in their availability as foods (e.g. Hladik 1976; Milton 1980; 1981; Chapman et al. 1999a; 2005). For example, the total percentage of trees that carry ripe fruit in the Kibale rain forest in Uganda can vary from 15.98 % down to 0.14 % per month (Chapman et al. 2005). This means that within a home range that contains 100,000 trees, the number of trees of which fruits can be eaten by primates and that indeed carry fruit, can vary between 3307 to only 29 trees[1], at any given time. Hence, a premium is placed on means of acquiring, transmitting and retaining information concerning the location and timing of food concentrations, and on their efficient use. In order to explore the

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[1] In this calculation I used *L. albigena* as an example primate species. This monkey species is known to eat fruit from only 54 out of a total of 260 woody species that grow in the Kibale forest (Waser 1977; Struhsaker 1997). 54/260 * 100,000 results in 20,700 trees that can carry edible fruits within the monkey’s home range. 15.98 % and 0.14 % of 20,700 trees results in 3307 and 29 trees that indeed carry fruit at any given time. Note that this is a very rough estimation; especially since primate food species may have a higher density than the other 206 woody species that grow in the forest. Also Chapman’s estimations are based on a limited number of fruit tree species.

type of strategies that are used by rain forest foragers we first need to understand the nature of the food sources and their strategies of survival and reproduction.

Survival and reproductive strategies of primate food

Rain forest plants do not passively accept the destruction and removal of their leaves, flowers, and unripe fruits by herbivores, but rather have a variety of strategies for counteracting or minimizing such damages. Plants protect their vegative and reproductive parts with a wide variety of toxic or distasteful chemicals as well as mechanical devices such as thorns or stinging hairs (e.g. Hladik 1978; Milton 1979; Chivers 1984; Waterman 1984; Byrne & Byrne 1991; 1993). In addition, tropical plants show a wide variety of temporary patterns in which leaves, flowers and fruits are produced in order to avoid predation, yet also to attract pollinators or seed dispersers. Their phenological behaviour varies from nearly continuous activity to repeated bursts, and from complete intraspecific synchrony to complete asynchrony (e.g. Waser 1974; van Schaik 1993; Chapman et al. 1999a; 2005). Examples of plants that display a continuous activity (so called "key stone species") are figs. Most figs fruit highly asynchronously in time (Waser 1974; Milton et al.1982; Milton 1991; chapter 5). This fruiting pattern has been described as essential to ensure the continued survival of obligate pollinators and or to improve the dispersal of unusually tiny seeds into large light gaps to ensure germination (Ramirez 1970; Rathcke & Lacey 1985; Milton 1991). Most tropical woody plant species however, produce new leaves, flowers and fruits in bursts rather than continuously. In the Kibale rain forest for example, fruiting was synchronous within species for 64% of the studied species (Chapman et al. 1999a). Such phenological clumping in time leads to peaks separated by long periods with little or no activity. The sharpness of these peaks is thought to result from selection to satiate seed/fruit/leave predators, but also to attract pollinators and seed dispersers; while the timing is thought to be related to abiotic factors such as levels of rain fall and solar radiation (van Schaik 1993; Chapman et al. 1999a; Anderson et al. 2005). In the Kibale forest the months of peak fruiting and flowering of some species varied markedly among years within species as well as within the plant community (Chapman et al. 1999a; 2005). Even for species that exhibit a fairly regular pattern of fruiting, like *Uvariopsis congensis*, where approximately 60% of the community fruits synchronically typically at June or July, one year 50 % of the community was found fruiting in December. At one point the entire community stopped fruiting for four years in a row (Chapman et al. 2005). In sum, the combination of both biotic and abiotic factors result in a highly variable and seemingly unpredictable distribution of flowers, leaves, and particularly fruits in space and time.

Fruit localisation strategy: Use of synchronicity

It has been suggested that in order to deal with the large variation in phenological patterns of tropical plants, primates have developed complex cognitive skills, which would enable them to localise food efficiently (e.g. Milton 1981). Tropical rain forests are generally characterized by a high diversity of tree species (e.g. Myers 1980). As many as 40, or even 100, species can be counted on 1 hectare (Walter 1984). As a consequence trees of individual primate fruit species have a low density and tend to be widely dispersed throughout a primate group's home range (Milton 1977; 1981; Chapman et al. 1999a; Vooren 1999). The timing of their fruiting is variable and widely dispersed in time and once fruits emerge, they are edible for a short time period only (e.g. Milton 1981; 1988; Chapman et al. 1999a). Hence, frugivorous primates, and in particular those in highly competitive environments, are expected to have evolved a sophisticated spatial temporal memory and an ability to predict fruit emergence and ripening rates (Milton 1981; Potts 2004; chapter 3, 5 and 6). In this chapter however, I hypothesise that the majority of fruit can be located in a fairly "simple" way, namely by the use of synchronicity in fruiting. If the seasonality is sufficiently clumped, and a high enough number of trees carry fruit within a particular species, a forager can use the observation of fruit in one tree as an indicator for the presence of fruit in other individuals of that same species. By activating search (by use of sensory cues or memory) for trees or patches of trees of this particular species, the forager could localise large numbers of fruit bearing trees in a fairly efficient way.

Use of synchronicity in temperate regions

Indications for the existence of such a particular search strategy were first observed by Menzel (1991). Menzel conducted an experimental field study in which native akebia fruits (*Akebia trifoliata*) and other food items were presented to a group of free-ranging Japanes macaques (*Macaca fuscata*) out of season. He found that before the akebia-feeding season, the proportion of trials in which at least one monkey (of those that came close enough to the test location to have seen the presented fruit) inspected an akebia vine was significantly higher for the akebia condition than for control conditions in which other food items were presented (Menzel 1991). The most intriguing part of the experiment was the finding that the macaques manipulated both *Akebia trifoliata* and *Akebia quinata* vines. Both species fruit simultaneously, yet the two species differed markedly in their leaf configurations and the appearance of the fruits. These observations indicated that the monkeys were not simply searching for the original source (vine) of the presented fruit. Yet, the results strongly suggest that the monkeys possessed a long-term memory of the simultaneous and synchronous fruiting patterns of both species and that visual contact with these fruits activated search for more fruit..

Use of synchronicity in the tropical rain forest

This study is a continuation of the field study conducted by Menzel (1991). I investigated whether the encounter of fruits also activated search routines for rain forest fruits. Seasonality is less profound in a rain forest than in temperate or dry tropical zones (O'Driscoll Worman & Chapman 2005; Walter 1984). There is a large inter and intra species variation in the percentage of trees that actually carry fruit (e.g. Milton 1981; Chapman et al. 1999a; 2005;). Clearly, the discovery of fruits in one tree does not always ensure the presence of fruit in co-specific trees. I therefore, continued to investigate the monkeys' reaction towards different levels of synchronicity between and within fruit species. I investigated this by studying the foraging behaviour of grey cheeked mangabeys in the Kanyawara research area of the Kibale forest in Uganda. The mangabeys in this area are highly dependent on fruits (59% of feeding time; Waser 1977; Olupot 1998) and the distribution patterns of these fruits vary substantially in levels of synchrony within species and between areas (Chapman et al. 1999a).

The localisation of three fruit species

I investigated the movement of nine individual male mangabeys in relation to trees of three different fruit species within two time periods. For the first two species *Uvariopsis congensis* and *Diospyros abyssinica*, the distributions of fruiting events were well investigated and was known to be clumped or synchronous in time (fruiting takes place in one period) (Chapman et al. 1999a). The distribution of *D. abyssinica* however, is less clumped (Chapman et al. 1999a) and a lower percentage of trees are found fruiting within the fruiting period than for *U. congensis* (table 1). The third species (*Ficus sansibarica*) has a much lower density and its fruiting pattern is less well studied, however data of previous research and a pilot study indicated a uniform or highly asynchronous fruiting pattern (Waser 1974; table 1; chapter 5). In order to investigate whether the monkeys were using the proposed *synchronicity strategy* I tested whether the encounter of edible fruits of each of the concerned species activated the monkeys to approach (and presumably inspect) other empty or fruit bearing trees of that same species and whether this approaching behaviour was influenced by the differences in synchronicity levels of the concerned species. Since the proportion of trees that carry fruit is known to vary between different areas in the Kibale forest (Chapman et al. 1999a), I also investigated the monkeys' reaction towards different levels of synchronicity within the most synchronous species (*U. congensis*) within different areas in the monkey's home range. In addition, I tested the hypothesis that high encounter rates of the highly synchronous *U. congensis* fruit triggered the monkeys to inspect trees of *U. congensis* only, and not those of similar looking sympatric tree species, such as *Teclea nobilis*.

Do Kibale monkeys search?

The Kibale forest has some of the highest primate densities ever recorded (Chapman et al. 1999b; Chapman et al. 2000). Many of these primates eat fruits and competition for fruits is consequently thought to be high (Hauser and Wrangham 1990; Houle 2004). I therefore expect that early detection of fruit will pay and that the monkeys will actively try to find fruits in this forest. However, as mentioned earlier, within some time periods the abundance of fruit in a rain forest can be high, which can make active search redundant. In some rain forests this period lasts for complete study periods, which suggests that the availability of fruits was never a limiting factor (Hladik 1976; Bates 2005). Hence, the first step in my investigation is to test the hypothesis that grey-cheeked mangabeys in the Kanyawara study area indeed search for fruits within my study period. *Search* refers to search by use of sensory cues and or memory.

METHODS

Study species

Study group

Within this study I investigated one group of grey-cheeked mangabeys in the Kanyawara study area in the semi-logged moist evergreen forest of the Kibale National Park in Uganda (0°34'N, 30° 21'W) (see Waser & Floody 1974; Chapman et al. 1997 for extended description of the study area). In the beginning of this study period the group consisted of 20-27 independently moving individuals; 8 cycling females, 4-10 adult males, 1 sub adult female, 3 juvenile females, 4 juvenile males, 1 unknown juvenile (that disappeared during the study), (and 0-2 infants). During the study the group split in two subgroups. Subgroup I consisted of 10 independently moving individuals; 4 cycling females, 3 adult males, 1 sub adult female, 1 juvenile male, 1 juvenile female (and 1 infant). Subgroup II consisted of 12 independently moving individuals; 4 cycling females, 3 adult males, 3 juvenile males, 2 juvenile females. All individuals were well habituated to human observers on foot, allowing observation as close as 2 meters.

Fruit species

I investigated the monkeys' behaviour towards trees of two synchronous fruit species with a high and low level of synchrony (*U. congensis*, *D. abyssinica*, respectively) and one a-sychronous fruit species *(F. sansibarica)*. *U. congensis* is a small under story tree with a relatively high and clumped (patchy) distribution (Chapman et al. 1999a; table 1). The fruiting events have a clumped or synchronous temporal distribution and the fruits are ranked 23rd on the mangabeys' preference list (Waser 1977; table 1). *D. abyssinica* is a middle height canopy tree with a relatively high and clumped distribution, yet less high and less clumped than *U. congensis*. Trees are dioecious, meaning that there are male and female trees and only half of the trees can bear fruit (Struhsaker 1997). The fruiting pattern has a clumped or synchronous distribution, yet due to its dioecious way of reproduction *D. abyssinica* is expected to have a lower percentage of fruit bearing trees in season than *U. congensis*. The fruits are ranked 16th on the mangabeys' preference list (Waser 1977; table 1). Mangabeys mainly eat ripe fruits of *U. congensis* and *D. abyssinica*, however, they are also observed to eat fruits of both species when they are unripe (pers. observation). *F. sansibarica* is a strangler fig that emerges from the canopy with a relatively low and uniform distribution (Chapman et al. 1999a; table 1). The fruiting pattern has a random or asynchronous distribution and the fruits are ranked 4th on the mangabeys' preference list (Waser 1977; chapter 5; table 1). The mangabeys eat *F. sansibarica* fruits when ripe, yet they are also observed to eat the unripe seeds or weevil larvae inside unripe fruit (pers. observation; chapter 3; Waser 1977). Unripe *F. sansibarica* fruits are often infested by weevil larvae such as *Omophorus stomachosus* (Waser 1977) (69% of fruit bearing trees visited; chapter 6; Janmaat et al. 2006a).

In order to determine species preference of the fruit species, I used Selection ratio's (Clutton-Brock 1972) as well as Electivity indices (Krebs 1989) (table 1). The selection ratio's were calculated as follows (Waser 1977):

$$SR = \frac{\text{(number of feeding observations in species A / thousand feeding observations)}}{\text{(number of enumerated trees of species A/ ha enumerated)}}$$

Electivity indices are a variant of the more familiar selection ratios, but have the advantage of only varying between –1 (not selected) and +1(highly selected), rather than between zero and infinity. They were calculated as follows:

$$EI = \frac{(r_i - n_i)}{(r_i + n_i)}$$

R_i is the percentage of species i in the diet, and n_i is the relative availability of species i (Barrett 1995). The coefficient of dispersion (CD) was used to represent the synchrony of fruiting events (Sokal & Rohlf 1981; Chapman et al. 1991; table 1). CD values were calculated as follows (chapter 5):

$$CD = \frac{\text{variance}}{\text{mean for the number of trees that were fruiting per month within the monitoring period}}$$

Data collection

Data were collected on fruit localisation behaviour of individual adult males. I chose to work with adult i.e. fully grown males because they were known to be more independent of other group members in the study group than females, sub-adults and juveniles (Waser & Floody 1974.), but also for practical reasons of identification. In the first observation period, before the group split I and my assistants followed seven individually identifiable males between 8 Sept. 2003 and 29 Nov. 2003, while ranging in familiar and less familiar area for a total distance of 18,900 m, respectively. In the second period we followed four males in subgroup I and four males in subgroup II, between 4 May 2004 and 26 June 2004, for a total distance of 8,400m and 9,000 m respectively. (One of these males had shifted from subgroup II to I halfway the observation period). Two of the males that were followed in the first observation period had left the group in the second observation period (Em and Ha; see table 1). For the second period I therefore selected two new males (Pl and Sp).

Observations on the males

Data collection started by identifying and locating one of the randomly selected males. We tried to follow the male for a distance between 300 and 400m, before we continued to follow another randomly selected male. If we lost the male or could not find the particular male in the first place for a period of over one hour we switched to the first other selected male that came in sight. I chose this method because males tended to linger at the periphery or outside the group. Determined search for particular males would have been too time consuming. The activity of the focal male (e.g. travelling, resting and foraging) was recorded for every minute that the individual was visible (one-zero sampling, Martin & Bateson 1986). Foraging was defined as a measure of food consumption and manipulation, including time spent examining mossy branches and epiphytes for insects but not time spent chewing while engaged in activities other than ingestion. We recorded the distance travelled per minute (in steps) and the number and names of mangabey food trees that were entered and fed in. We specified if the male was feeding on fruits of the concerned tree or on other food items within the tree. In order to keep track of the males and their activities we followed the males with two observers. Observations stopped when we collected a minimum of five trajectories per male.

Transects parallel to the male's route

The day after each following day we walked a transect route parallel to and at 15 m distance of the male's route (fig. 1). I chose to directly link the location of the transect and the male's route for the following reason. *U. congensis* trees occur in patches of at least 20 trees with each a crown diameter of around 4 m (Barrett 1995; personal observation). Transects placed at random distance from the male's travel route would therefore automatically have a lower density of *U. congensis* trees, once the male is foraging on *U. congensis* fruit. A transect that is 15 m from the male's travel route is expected to be close enough to expect an equal tree density along the transect and the male's route, if the male would choose a random route. A difference in tree densities would then be an indication that the males are actively inspecting *U.congensis* trees. To minimize the effect of inter-observer variability, transects were walked by the same observers whom had followed the male at the previous day. (The distance towards the male route was estimated by sight, since this route was marked with brightly coloured ribbons). We mapped each tree of the three selected species (*U. congensis, D. abyssinica* and *F. sansibarica*) that had a trunk was within 5 m of the middle of the transect route and determined their fruiting state.

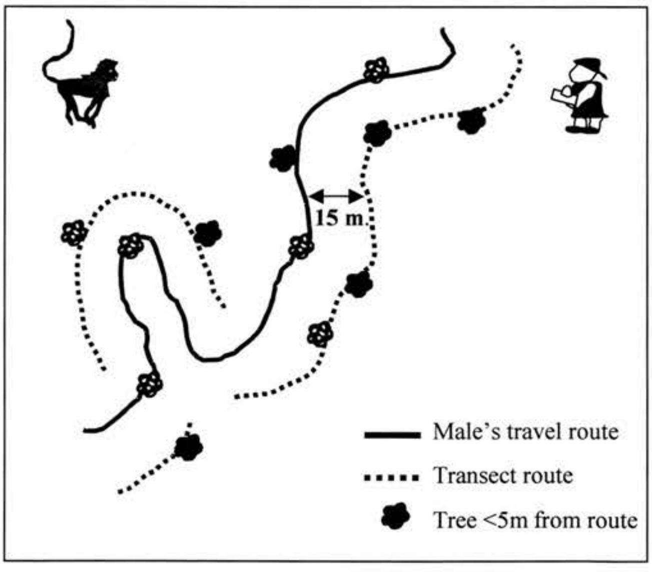


Fig. 1. Measuring searching behaviour. The schematic diagram illustrates part of a mangabey male's travel route (bold line) and the transect route (dotted line), which was walked parallel at 15 m distance from the male's route. We measured the number of tree trunks of *U. congensis*, *D. abyssinica* and *F. sansibarica*, and the fruiting state of the trees within 5 m of each route. Within this example, we recorded four trees that carried fruit and one empty tree within 5m from the male's route and three versus five trees that carried fruit or were empty, respectively, within 5m from the transect route.

In addition, we walked the male's travel route of the previous day and did the same measurements for the area within 5m of the male's travel route. For the second observation period we also determined which tree crowns of the three selected species overlapped with the male's route and the transect route. Within this same time period, measurements were taken on the arrival and departure directions of the *U. congensis* trees. The observer's step lengths were calibrated over a stretch of 500 m within the forest habitat with varying elevation levels. I analysed the number of food trees per 100 m travelling for each route/trajectory of 300-400 m, that were separated in time by one day for each male.

Table 1. Number of observed 300-400m trajectories for each male

	Individuals	Bg	Ma	Sp	Me	Lb	Em	Ha	Pl	Mg
Period I	Before split	12	12	6	7	5	12	9		
Period II	Subgroup I	9				4			7	8
	Subgroup II		9	10	7	4				

Inter observer tests

Data were collected by two teams that consisted of one researcher (K. Janmaat or R. Meijer) and one local field assistant. Tree species determination was done by the local assistants who had been trained and active in species determination within the study area for nine and four years. Inter observer tests between the two local assistants showed an overlap of 83-85% and 85-100% in the determination of fruiting state and the density of trees that belonged to the three selected tree species, within two 5 m wide, 200 m long, transects, respectively, that were walked at the beginning of each observation period. Intra observer tests, which were done by walking similar transects from opposite directions, showed an overlap of 82-85% and 89-98% for determination of fruiting state and the density of the three selected tree species, respectively over two transects of 200 m.

Statistical analyses

Since all our variables were not normally distributed we relied on non-parametric Wilcoxon signed rank test, Mann Whitney U-test, X^2 tests and Spearman correlation analyses (Siegel 1956). All tests were two tailed. In each case I assessed evidence about specific hypotheses, and hence did not adjust critical alpha levels using Bonferroni procedures (Perneger 1998). Some of the males joined the same group, however I assumed that the data collected on the searching behaviour of the nine individual males could be treated as independent data, since mangabeys rarely travel in line, but instead have a relatively wide group spread, also during travel (Waser 1985; Olupot et al. 1997; pers. observation). Furthermore, males are known to range relatively independently from other group members and are regularly found at the periphery of the group or even solitary outside the group (Waser & Floody 1974; Waser 1985; Olupot & Waser 2001). The trajectories for each male were separated by at least one day. Since grey-cheeked mangabeys travel fairly large distances per day (X = 1167m ± 401m before the split, with a maximum of 2501m (chapter 4; Waser 1974; Waser 1975)) and perform low percentages of back tracking (Waser 1974; Barrett 1995), I assumed that each 300-400 m trajectory could be treated as an independent event.

In order to attain a relative value for the monkeys' search efficiency I used the following equation: relative localisation efficiency (RLE):

$$\text{RLE} = \frac{(\text{ \# trees whose crown overlapped with the male's route})}{(\text{ \# trees whose crown overlapped with the transect route} + 1\text{ })}$$

I calculated separate RLE values for trees that carried ripe fruit and for empty trees. In order to be able to use a larger number of trajectories (some transects did not contain any ripe fruits) I added the value 1 to the divider. However, I only analysed trajectories in which at least one tree of each concerned species was observed either on the male's route or in the transect.

RESULTS

Fruiting patterns and characteristics of the fruit species

Figure 2 shows the percentages of trees that were encountered within 5 m of the 300-400m transect route(s) that carried ripe fruit, for each observation day. The figures illustrate clearly that the first observation period (Sept-Nov 2003) coincided with a fruiting season of *D. abyssinica*, while the second period (April-May 2004) coincided with a fruiting season of *U. congensis* and visa versa. As expected, the total percentage of trees that carried ripe fruit (fig 2; table 1) was higher for *U. congensis* than for the diocious *D. abyssinica*. No significant increase in the percentage of ripe fruit-bearing trees was found during the progress/continuation of the fruiting period, for *U. congensis* and *D. abyssinica*, respectively (r_s = -0.192, P = 0.162, N = 54; r_s = -0.146, P = 0.266, N = 60). Yet, a significant difference was found between the percentages of *U. congensis* trees that carried ripe fruit in the transects that were located within each subgroup's range (range I and II) (U = 230.0, P= 0.019, N_I = 25, N_{II} = 29; fig 3, 4). I only included transects that contained at least one *U. congensis* tree.

Table 1. Fruit species characteristics. The density, the coefficient of dispersion (CD), total percentage of ripe fruit bearing trees, selection ratio, rank and electivity indices (EI) of *U. congensis*, *D. abyssinica* and *F. sansibarica* in the study area. See Methods for detailed descriptions of each of the variables. The percentage of ripe fruits were calculated for transects that contained at least one of the concerned species.

Species	Density (individuals ha $^{-1}$) (Chapman et al. 1999a)	Seasonality CD (Chapman et al. 1999a; chapter 5)	Total % trees with ripe fruit in study	Selection ratio (rank) (Waser 1977)	EI (-1,1) (Barrett 1995)
Uvariopsis congensis	60.0	Highly Synchronous CD=1.27	22 In season	0.62 (23th)	- 0.75
Diospyros abyssinica	40.0	Moderately Synchronous CD=1.19	7 In season	5.38 (16th)	0.2
Ficus sansibarica	1.7	Asynchronous CD=1.083	6 Total	46.05 (4th)	0.87

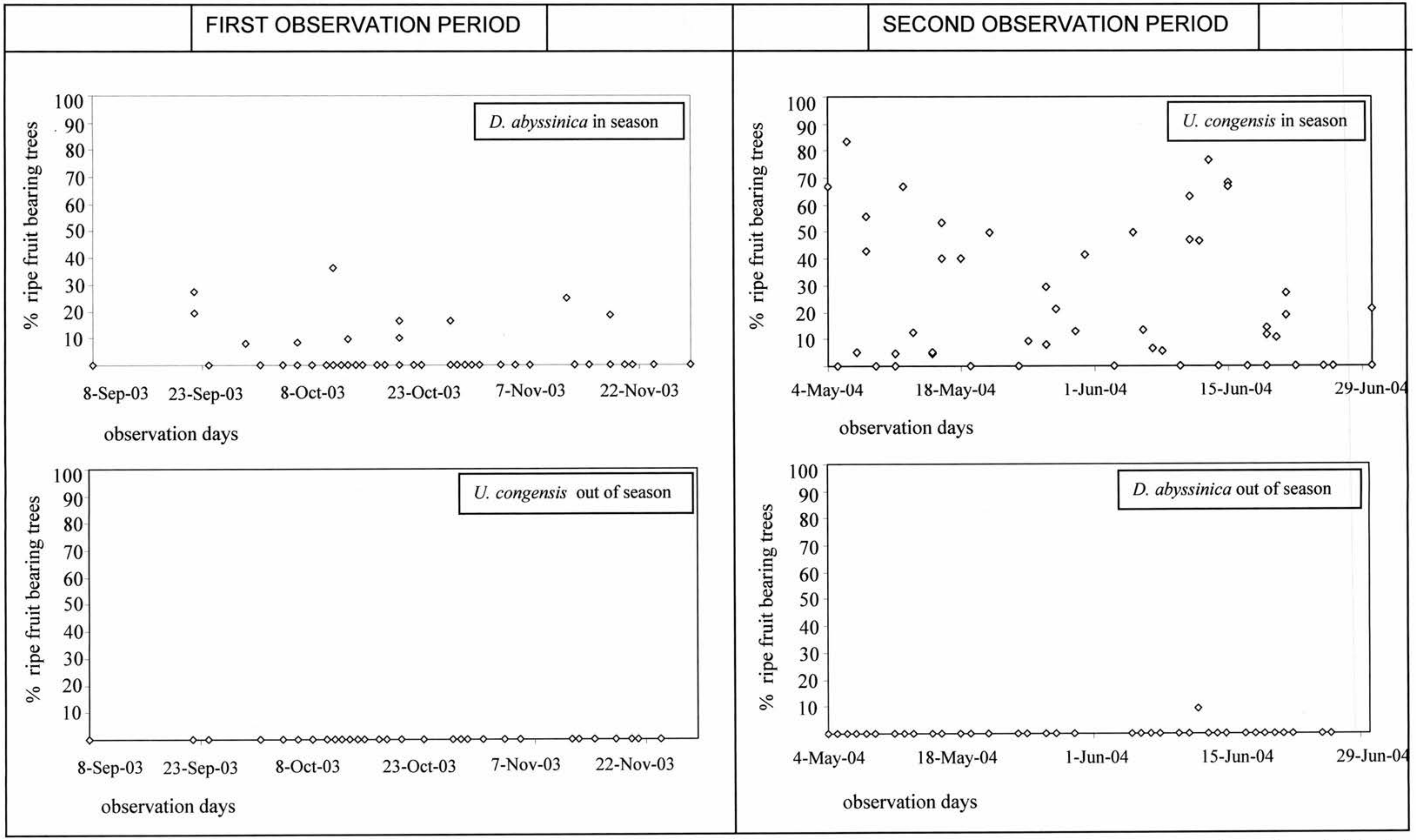


Fig. 2. Percentages of ripe fruit bearing trees of *D. abyssinica* (a) and *U. congensis* (b) within 5 m of the transect route(s) plotted per observation day, within each observation period. I only included transects that contained at least one tree of the concerned species

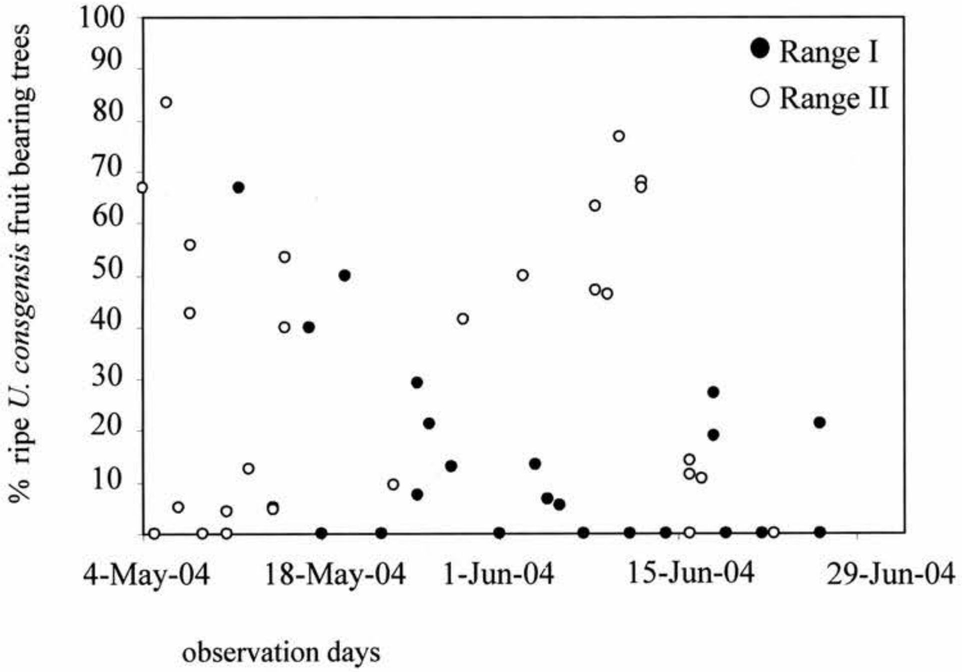


Fig. 3. Figure 2 replotted for *U. congensis*. Percentages of highly synchronous *U. congensis* trees that carried fruit within 5 m of the transect(s) plotted per observation day in the first observation period. Closed circles are transects that were located in range I, open circles are transects that were located in range II.

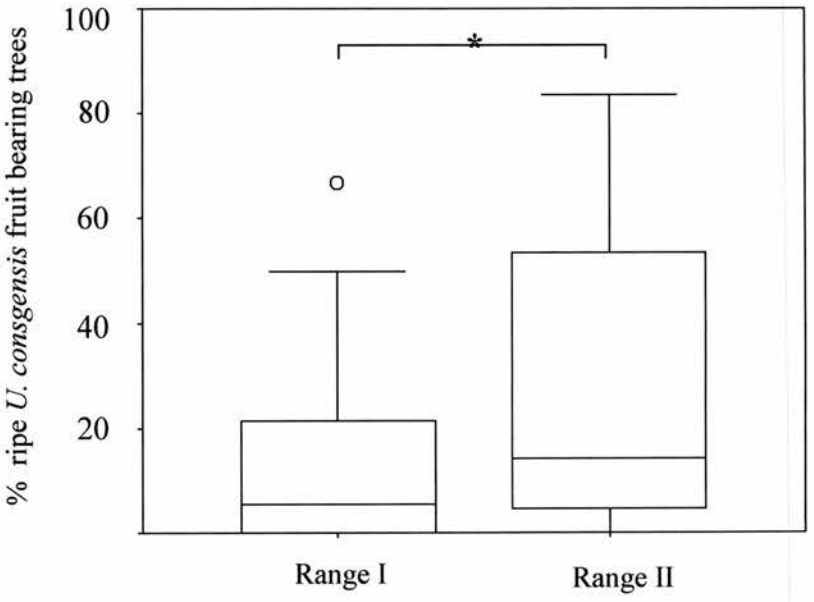


Fig. 4. Figure 3 replotted. Percentage of *U. congensis* trees that carried fruit within 5 m of the transects located in range I and II. Bars represent the median percentages, while the top and bottom of the boxes represent the 75 and 25 percentiles. The highest and lowest whiskers represent the highest and smallest values, which are not outliers. The circle represents an outlier.

Do mangabeys search for fruit?

In order to investigate whether the mangabey males indeed searched for fruits (by either use of sensory cues or memory) I compared the density of trees that carried ripe fruit within near distance (< 5m) of the male's travel route with that of the transect route. The middle of the transect route was located at 15 m distance from the male's route. I pooled all the data from each male

for analyses. I found that in season (second observation period) the density of the highly synchronuous *U. congensis* trees that carried either ripe fruit or fruit in general (ripe + unripe) was significantly higher within 5 m from the males' travel route (# trees p.100m) than within 5 m from the transect route. (ripe fruit: $Z = -2.366$, $P = 0.018$, $N = 7$; fruit (unripe or ripe): $Z = -2.197$, $P = 0.028$ (Wilcoxon signed rank (WSR)); fig 5a). For the less synchronuous *D. abyssinica* I found no significant difference between the densities of trees that carried either ripe fruits or fruits in general between both routes in season (first observation period) (ripe fruits: $Z = -1.014$, $P = 0.310$, $N = 7$ (WSR); fruits (unripe or ripe): $Z = -1.352$, $P = 0.176$ (WSR) fig 5b). When I pooled both observation periods the densities of asynchronous *F.sansibarica* trees that carried either ripe fruit or fruit in general were both significantly higher within 5 m from the males' travel routes than within 5 m from the transect route (ripe fruit: $Z = -2.201$, $P = 0.028$, $N = 9$; fruits (unripe + ripe): $Z = -2.521$, $P = 0.012$, $N = 9$; fig 5c). These results suggest that the monkeys were actively inspecting trees of both *U. congensis* and *F. sansibarica* in search of fruit, but not trees of *D. abyssinica*.

Does a high encounter rate of ripe fruits trigger the search?

Trees with fruit

In order to investigate whether the availability and densities of ripe fruits, in season, influenced the males' searching behaviour I compared the males' encounter rate of the highly synchronous *U. congensis* and the less synchronous *D. abyssinica* trees in season with that of out of season. I found that the males entered significantly more *U. congensis* trees in season (second observation period) than out of season (first observation period) ($U = 28.0$, $N_{\text{in season}} = 7$, $N_{\text{out season}} = 7$, $P = 0.001$). For the less synchronous *D. abyssinica* no difference was found ($U = 22.0$, $N_{\text{in season}} = 7$, $N_{\text{out season}} = 7$, $P = 0.805$). Possibly, the above difference simply resulted from the monkeys

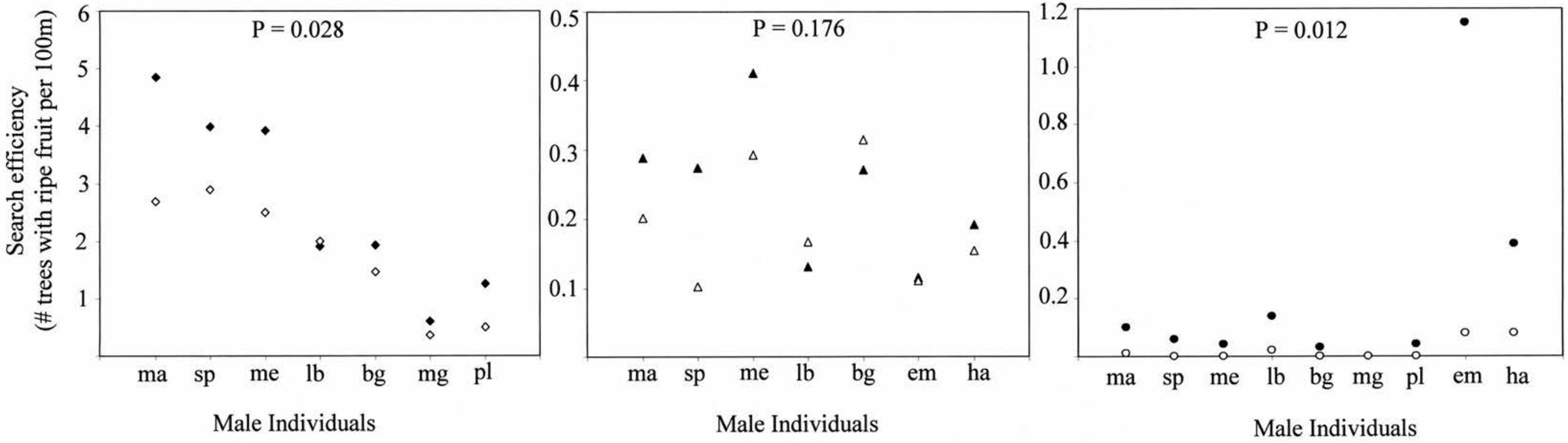


Fig. 5 Search efficiency of 7-9 individual males in finding fruits. Densities of *U. congensis* (diamonds), *D. abyssinica* (triangle) and *F. sansibarica* (circles) trees that carried ripe or unripe fruit within 5 m from the male's travel route (filled) and that within 5 m of the transect (open).

entering more U. congensis trees with ripe fruit in season, because more fruits were spotted on route.

Empty trees

To test whether the monkeys indeed actively searched for trees and fruit of *U. congensis* I did additional analyses for empty trees only. Due to the low visibility at the under story level of *U. congensis* trees in the Kibale forest, the monkeys may fail to spot the fruits while inspecting a tree from far away distances. Moreover, since *U. congensis* trees often carry small numbers of ripe fruit, the monkeys may fail to spot the one or two single ripe fruits in the middle of the tree crown, while checking from the outside only. I therefore expected that the monkeys would need approach and enter the trees to properly assess their fruiting state. I found that the males entered significantly more empty *U. congensis* trees in season than out of season ($U = 5.0$, $N_{\text{in season}} = 7$, $N_{\text{out season}} = 7$, $P = 0.01$). No difference was found between the numbers of empty *D. abyssinica* trees that were entered in and out of season ($U = 12.5$, $N_{\text{in season}} = 7$, $N_{\text{out season}} = 7$, $P = 0.128$). In addition, I found that, in season, the number of empty *U. congensis* trees that were entered by the males tended to be positively correlated with the number of *U. congensis* trees that was fed in ($r_s= 0.755$, $N = 7$, $P = 0.05$). No such tendency was found for *D. abyssinica* ($r_s= -0.143$, $N = 7$, $P = 0.760$,) (in season) or *F. sansibarica* (in both observation periods) ($r_s= 0.385$, $N = 9$, $P = 0.306$). When I investigated the values per 300-400 trajectory separately, I found that the number of empty *U. congensis* trees that were entered by the males (p.100m) significantly increased with the percentage of trees that carried ripe fruit within 5 m of the corresponding transect route ($r_s = 0.280$, $P= 0.005$ $N = 98$). No significant relation was found for *D. abyssinica* or *F. sansibarica*, respectively ($r_s= 0.079$, $N = 116$, $P = 0.399$; $r_s= -0.055$, $N = 26$, $P = 0.791$). (This only included trajectories of which either the travel route or the transect contained at least one tree individual of the concerned species).

Do monkeys know about spatial differences in ripe fruit availability?

Earlier results showed that the density of trees with ripe *U. congensis* fruit differed significantly between the ranging areas of the two subgroups (Fig. 3 and 4). This situation enabled me to investigate whether the monkeys took spatial differences in fruit densities into account and whether they searched more actively for *U. congensis* fruits in areas that contained more trees with ripe fruit than in areas with fewer or no ripe fruits within the season. In order to test the difference in the monkey's response to each fruit density within the two different areas I used the values of the 300-400 m trajectories that were each separated by at least one day per male. Because I was mainly interested in the monkeys' behaviour in areas in which potential feeding trees were known to be present, I again only included trajectories of which either the travel route or the transect contained at least one tree individual of the concerned species. In order to investigate whether the monkeys searching activity was influenced by the ripe fruit density of the area, I first calculated the *relative localisation efficiency* (RLE; see method for formula) which is equal to a ratio of the number of trees whose crown overlapped with the male's route and the number of trees whose crown overlapped with the transect route. I found that the males' relative localisation efficiency of trees with ripe *U. congensis* fruit was significantly higher in the "ripe fruit rich" area (range II) than in the "ripe fruit poor" area (range I) (U= 117.0, P = 0.025, $N_I = 15$, $N_{II} = 27$). (For this analyses I again only included trajectories of which either the travel route or the transect contained at least one tree individual of the concerned species). In addition, the males tended to approach relatively more empty *U. congensis* trees in range II than in range I. The *relative localisation efficiency* (RLE) of empty *U. congensis* trees tended to be higher in the fruit rich area (II) than in the fruit poor area (I) (U = 287, p=0.059, N_I=27, N_{II}= 30).

Even though range I had a much lower overall density of ripe fruits, more detailed analyses suggested that the tree patches in range I that did contain ripe fruits had an equal density of ripe fruit as the ripe fruit containing tree patches in range II. When I analysed a subset of the data that only contained transects located in areas with ripe fruit, i.e. transects that contained at least one tree with ripe fruit, no significant difference in percentages of ripe fruit was found between range I and II (U =116.0, N_I =13, N_{II} =23, P = 0.281). In addition to the rather rough comparison between the two ranging areas, I therefore also conducted a more general analysis in which I investigated the effect of local fruit distributions on the searching behaviour of the monkeys into more detail. I pooled the observations from both ranges and split the data in trajectories in areas that contained ripe fruit and those that did not contain any ripe fruit. I found that in season, the relative localisation efficiently of empty *U. congensis* trees was significantly higher when the transects contained ripe fruits than when the transects did not (U = 207.0 P = 0.032, $N_{\text{no ripe fruit}} = 18$, $N_{\text{ripe fruit}} = 36$; fig. 6). These results suggests that the males more actively inspected the fruiting state of empty *U. congensis* trees in areas with ripe fruits than in areas without ripe fruits within the same time period.

Do the monkeys make detours to inspect empty trees?

The above results suggest that the males actively inspected empty trees of *U. congensis*. In order to investigate whether the monkeys also made deviations from their foraging route in order to inspect these empty trees I measured the number of times that the males made a detour before entering an empty *U. congensis* tree. To do so I first determined the minimum angle between the direction from which the male approached the tree (from the tree's perspective) and the direction in which the male departed (Rutte 1998; but not Janson 1998). A detour was defined as a visit in which this angle was smaller than 90°. I tested whether the males made more detours in order to enter empty *U. congensis* trees in areas with higher percentages of ripe fruit than in areas without ripe fruit.

I found that the availability of ripe fruits (either zero or a higher percentage of ripe fruit bearing trees within 5 m of the transect route) was not significantly associated with the detour behaviour of the males (X_2= 0.204, N = 64, df = 1, P=0.751). This suggest that the males did not more often deviate from their route to inspect empty *U. congensis* trees in areas that contained more ripe fruit bearing trees. In fact, no association was found between the fruiting state of individual *U. congensis* trees and the detour behaviour either. The proportion of times that the males made a detour did not differ between empty or ripe fruit bearing trees (X_2= 2.102, N = 295, df = 1, P = 0.196). This contradicts the finding for the more rare trees that carry the highly preferred fruits of *F. sansibarica* in which a clear association was found between the fruiting state and the angle between arrival and departure direction of the group (chapter 5).

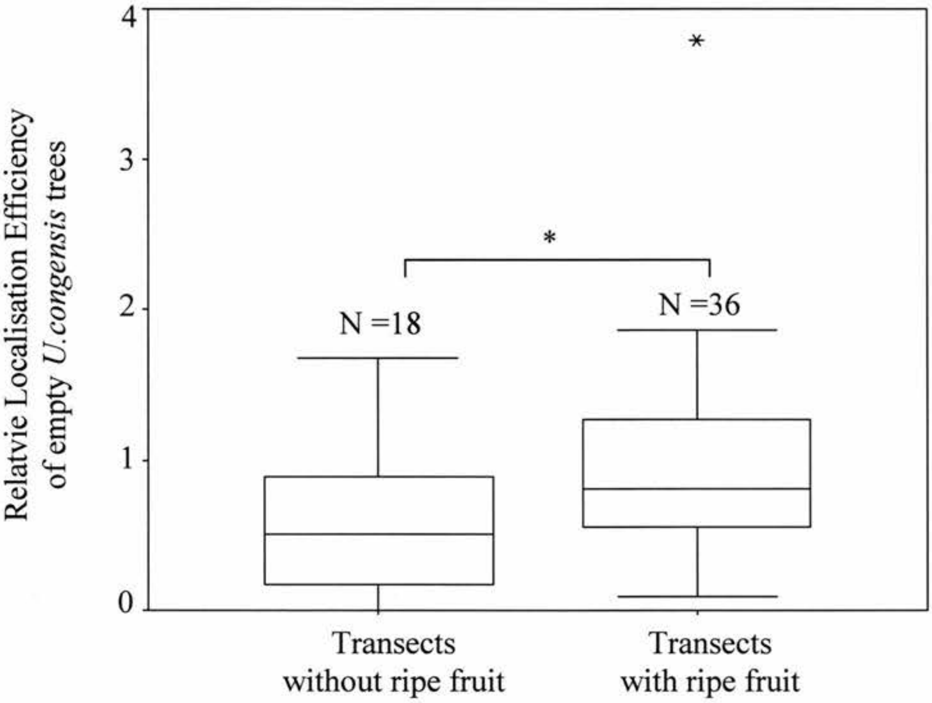


Fig. 6. Inspection of empty *U. congensis* trees in areas with and without ripe fruits. The bars represent the relative localisation efficiency of empty *U. congensis* trees of seven mangabey males, while the top and bottom of the boxes represent the 75 and 25 percentiles. The highest and lowest whiskers represent the highest and smallest values, which are not outliers. The star represents an extreme value.

Tree recognition

Apart from the three selected species the mangabey males entered and fed on a large number of other fruit species (N = 28). One of the tree species that were entered (*Teclea nobilis*) was very similar in appearance to *U. congensis* (Fig 7). Here I investigated whether the mangabeys could distinguish between the empty trees of both species and whether the encounter of ripe *U. congensis* fruits indeed only triggered the entry of empty *U. congensis* trees, and not the entry of trees of *T. nobilis* as well. First, I found that the males did not enter more *T. nobilis* p. 100m travelling in the *U. congensis* season (second observation period) than out of season (first observation period) (U=53.0, P = 0.744, $N_{\text{in season}} = 13$, $N_{\text{out season}} = 9$). Because trees of *T. nobilis* have a patchy distribution, I only included male routes in areas in which at least one *T. nobilis* tree was entered. Second, I found no significant relation between the number of empty *T. nobilis* trees that were entered (#trees p. 100m) and the density (# trees p. 100m) of ripe fruit bearing *U. congensis* trees within 5 m of the male route ($r_s = -0.194$, $P = 0.40$, $N = 21$). Here I only included trajectories in which the male route contained at least one *T. Nobilis* and one *U.congensis* tree.

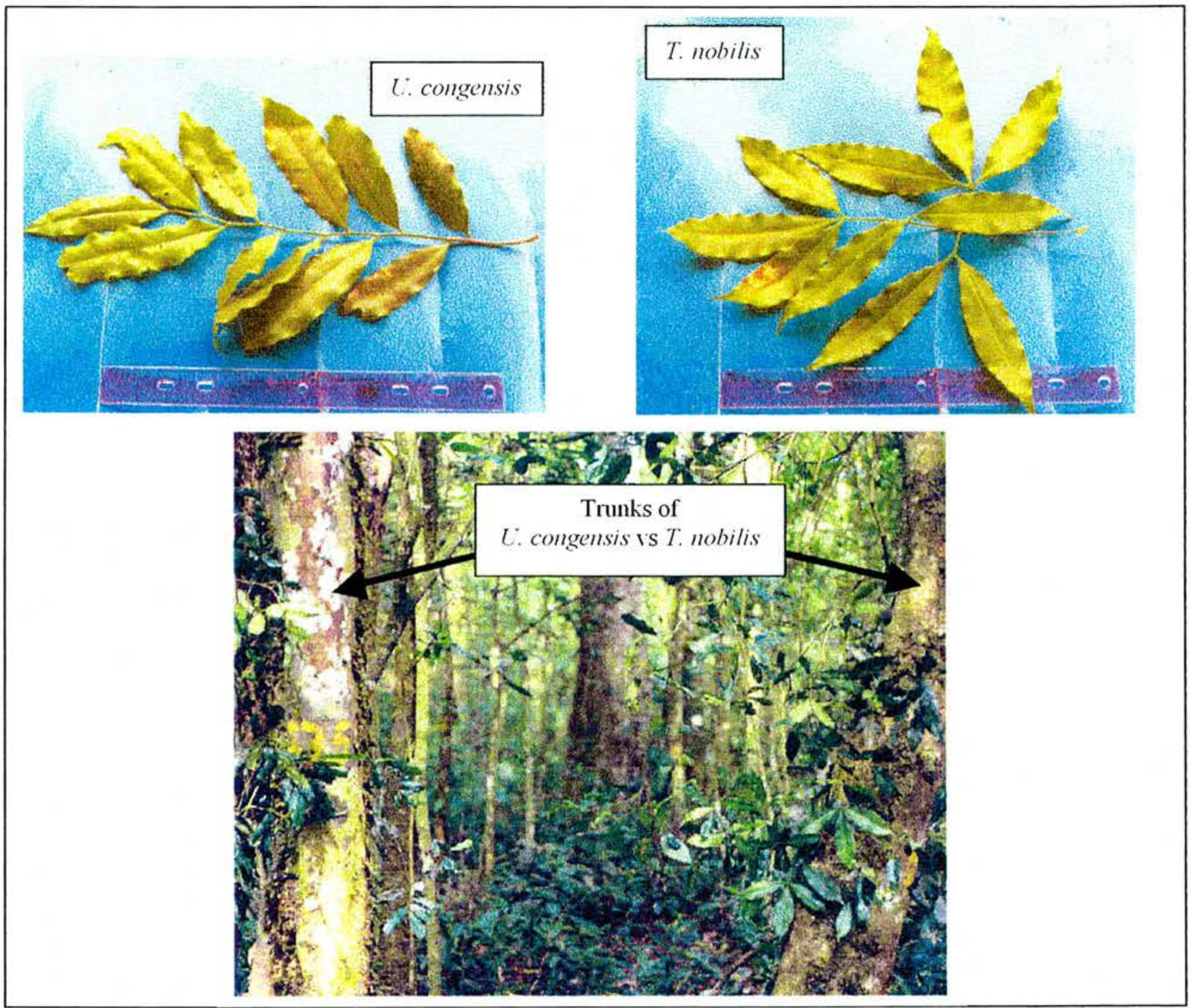


Fig. 7. Illustration of the similarity in appearance of *U. congensis* and *T. nobilis* trees. Leave shape, colour and leaf configuration of *U. congensis* (top left) and *T. nobilis* (top right) and a close up of the (yellow marked) trunks of both tree species (botom).

DISCUSSION

Searching for fruits of different species

Within this chapter I investigated whether grey-cheeked mangabeys used the synchrony in fruit emergence as a conceptual tool to locate fruit. I investigated whether the availability of certain fruits activated search for other fruits of that same species and whether the monkeys adjusted their searching activities (while using either sensory cues and or memory) to the large inter and intra species differences in synchronicity levels of rain forest fruit. I recorded the foraging behaviour of nine individual grey-cheeked mangabey males in relation to fruits of two synchronous species with a high and lower level of synchronicity (*U. congensis*, *D. abyssinica*, respectively) and one a-synchronous species (*F. sansibarica*).

The results of this study showed that the mangabey males approached significantly more *U. congensis* trees that carried ripe fruits, per distance travelling, than human observers did when they walked a transect that ran parallel at 15 m from the male's travel route. This was not true for trees of the fruit species *D. abyssinica*. These results suggest that the monkeys were actively inspecting trees of *U. congensis* in search for fruits, but not trees of the less synchronous species *D. abyssinica*, that had a much lower percentage of ripe fruit bearing trees within season.

Did fruit availability activate search behaviour?

Additional analyses further indicated that the monkeys entered more *U. congensis* trees in season than out of season. This was also true for empty *U. congensis* trees, that were expected to be entered or approached closely to enable the monkeys to inspect the fruiting state. In fact, the number of empty *U. congensis* trees that were entered by the males, per distance travelling, tended to increase with the number of trees that was fed in and significantly increased with the percentage of trees that carried ripe fruit within 5 m of the transect route. These results suggest that the monkeys were not simply spotting more fruits on route when more fruits were available, but that the encounter with and or the feeding on ripe *U. congensis* fruit had triggered them to actively search for and inspect other trees of *U. congensis*, including empty trees. None of the above significant relations were found for empty trees of the a-synchronous fruit species *F. sansibarica* or the less synchronous fruit species *D. abyssinica*. Neither did the males enter more trees of *D. abyssinica* in season than out of season. The finding that none of the above patterns or relationships were present for trees of the less synchronous species *D. abyssinica* cannot be explained by the monkeys' lack of interest in fruits of *D. abyssinica* trees. Previous research has shown that fruits of *D. abyssinica* were more preferred by the grey-cheeked mangabeys and much higher ranked on their preference list than fruits of *U. congensis* (Waser 1977; table 1). The difference in approach behaviour towards the trees of both synchronous species is therefore more likely to be explained by the difference in the percentage of trees that carried ripe fruits. The percentage of *D. abyssinica* trees that carried ripe fruit was much lower than the percentage of ripe fruit bearing *U. congensis* tree.

Spatial variation in fruit availability: Local synchronicity

Phenological recordings of trees along transect routes indicated that the levels of synchronicity of *U. congensis* showed substantial variation between different areas within the habitat. The newly explored area of the home range, which later became the range of subgroup II, contained a significantly higher percentage of ripe fruit-bearing *U. congensis* trees than a more familiar area, that later became the range of subgroup I.

Do monkeys adjust searching activity?

In order to investigate whether the monkeys took this spatial difference in ripe fruit availability into account I first determined a relative measure of searching activity; *the relative localisation efficiency* (RLE). In order to use a relative variable for the monkeys search efficiency I divided the number of trees (that carried either ripe or no fruit) that were *approached* by the male, i.e. whose crown overlapped with the male's travel route, with the number of trees (that carried ripe or no fruit) that were *approached* by me on the transect route. Using this measure I found that the mangabey males approached relatively more trees per distance travelling (100m) that carried ripe fruits (relative to the transect) in "ripe fruit rich" than in "ripe fruit poor" areas (range II and I respectively). Remarkably this was also true for the number of empty trees. In addition, when I pooled the data of both ranges, I found that the monkeys approached a relatively higher number of empty *U. congensis* trees per distance travelling when the parallel transect contained ripe fruits than when the transect contained none. *U. congensis* trees are clumped in space, i.e. have a patchy distribution (Barrett 1995; pers. observation). Hence, the above results, could have been a simple by-product of the monkeys' increased foraging on ripe fruits inside a *U. congensis* tree patch and the increased need to enter suitable substrates, e.g. empty *U. congensis* trees, to cross from one ripe fruit-bearing tree to another. However, if this was true I should have encountered a similar amount of empty trees within the transect which was located at only 15 m distance from the travel route and which was most likely located within the same patch of *U. congensis* trees. Yet, since the monkeys were approaching relatively more empty trees than I did in the transect, in "ripe fruit rich" areas than "ripe fruit poor" areas, I conclude that the monkeys were indeed searching and inspecting empty trees of *U. congensis* and that they did this more actively in fruit rich areas. These results suggest that the activation of searching routines is flexible and that the monkeys do not just act upon some memory of species-specific differences in synchronicity levels. The results strongly suggest that the monkeys' searching activity was triggered only by a particular high frequency of ripe fruit-bearing trees (local synchronicity) that were encountered.

The adaptive value of flexible search behaviour

Considering the large fluctuations in the levels of synchronicity between years and different locations (Chapman et al. 1999a; Chapman et al. 2005) this flexible search strategy could be highly profitable. As mentioned earlier, synchronicity levels of tropical fruits can vary immensely between years. For example, the Kanyawara population of one of the mangabey fruit species *Strombosia scheffleri* was found fruiting only 4 times within 12 years and reached overall percentages of below 5, around 10 and 50% of trees that carried ripe fruit, respectively (Chapman et al. 2005). Synchronicity is also known to vary within species between different locations. For example in May 1996, 60% of the *U. congensis* population in Kanyawara carried fruit while none did at the other three research sites that were all within 12 km distance (Chapman et al. 2005). In addition, recent studies have shown that even when fruiting patterns appear highly synchronous, not all fruits within a species are qualitatively equal. Nutritional values of particular fruit species can vary substantially between different periods of the year and again between different locations within the forest (Chapman et al. 2003; O' Driscoll Worman & Chapman 2005). For example the lipid content of another mangabey fruit species *Celtis durandii* varied from 0.03-30.8% over 6 months, with more fruit being eaten by the mangabeys when it contained more lipids (O' Driscoll Worman & Chapman 2005). In some cases the variation in fruit quality among sites was greater than the differences among species (Chapman et al. 2003). For example, for *Funtumia latifolia*, another fruit species that is eaten by the mangabeys, the protein-to-fiber ratio differed 28% between two locations (Chapman et al. 2003). A flexible search mechanism that is only activated by certain (local) levels of synchrony would enable the monkeys, yet also other fruit eating rain forest foragers, to deal more efficiently with these spatial and temporal fluctuations in quality and would enable them to adjust their searching activities accordingly.

Spatial memory

Despite the fact that the fruits of *F. sansibarica* show such a highly a-synchronous and seemingly unpredictable fruiting pattern, the monkeys were significantly more efficient in finding the fruits than I did when walking the transect (1.8 times). In contrast to the monkeys' apparent temporary disinterest in *D. abyssinica* fruit, the males were clearly searching for fruits of *F. sansibarica*. Most likely, the monkeys used different localisation strategies to locate this highly a-sychronous and preferred fruits, such as the use of long distance sensory cues, spatial temporal memory and predicting strategies (see chapter 2, 3, 5 and 6).

Since, the density of *U. congensis* trees is so high (60 trees per ha. resulting in an estimated amount of 37,380 trees within the total home range); table 1) it is highly unlikely that the monkeys were able to remember the spatial location of individual *U. congensis* trees, and no indication for the existence of such a memory was found. In contrast to the results found for the much more rare *F. sansibarica trees* (chapter 3) the proportion of detours was not higher for trees that carried fruit than for trees that carried none and no indications for goal-directed travel towards individual trees was observed. I think is likely that the monkeys did possess a memory of certain tree patches that contained high densities of *U. congensis* trees and or patches that contain good quality fruits (Chapman et al 2003), however this remains topic for further research.

Memories of visual appearance of trees

If the monkeys were indeed inspecting empty trees of *U. congensis*, it implies that the monkeys must have been able to identify the tree species without the presence of the fruits, suggesting that they used a memory of the visual characteristics of the tree itself. This idea was supported by the finding that the availability of large numbers of fruit bearing *U. congensis* trees only triggered the approach or inspection of empty *U. congensis* trees but not of empty trees of *T. nobilis* that are very similar in appearance (fig.7). Observations of primate's abilities to distinguish between small differences in visual appearances of plant species have been reported in earlier studies (e.g. Byrne 1995). The visual similarity between sympatric fruit species stresses that the apparent simplicity of the use of synchronicity may not be as simple as I initially assumed. The long-term memory of specific visual characteristics of a large number of different fruit species and their edibility states could indeed be a very demanding cognitive trait (Barton 2000) and is a topic for further research.

SUMMARY CHAPTER 1

In this chapter I investigated whether grey-cheeked mangabeys (*Lophocebus albigena johnstonii*), in the Kibale rain forest in Uganda, used the synchrony in fruit emergence as a conceptual tool to find fruit in a similar way as it was observed in monkeys in more temperate habitats (Menzel 1991). I tested whether the availability of certain rain forest fruits activated search (by use of sensory cues or memory) for trees of that same species and whether the monkeys adjusted their searching activities to temporal and spatial differences in synchronicity levels. I recorded the ranging behaviour of nine individual males in relation to trees of two synchronous fruit species with a high and low level of synchronicity (*U. congensis* and *D. abyssinica*, respectively) and one asynchronous species (*F. sansibarica*). I found that the males entered more *U. congensis* trees, yet also more empty trees in season, when ripe fruits were available, than out of season when no ripe fruits were encountered. In fact, the number of empty *U. congensis* trees that were entered by the males, per distance travelling, tended to increase with the number of trees that was fed in, and significantly increased with the percentage of trees that carried ripe fruit within 5 m of the transect route, which was located at 15 m distance from the male's route. None of the above relations were found to be significant for empty trees of the a-synchronous fruit species *F. sansibarica* or the less synchronous fruit species *D. abyssinica*. Neither did the males enter more trees nor empty trees of *D. abyssinica* in general, in season than out of season. In addition, I found that the ratio of the number of ripe fruit-bearing *U. congensis* trees that were approached by the males per distance travelling and the number that I approached within a parallel transect was significantly higher in "ripe fruit rich" than in "ripe fruit poor" areas. This was also true for the number of empty trees. The results of this study strongly suggest that the monkeys' searching behaviour for fruits (the inspection of trees) was activated by particular encounter rates of ripe fruit-bearing trees of that same species within a certain area and not by a general understanding of synchrony. I suggest that this type of flexible searching behaviour and use of *local synchrony* can be highly efficient and enables rain forest monkeys to quickly adapt to the frequent yet irregular fluctuations in synchronicity levels in time and space.

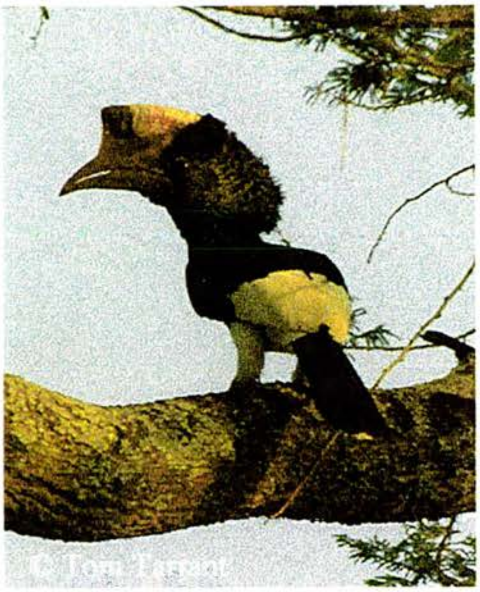
Despite the a-sychronic nature of *F.sansibarica*, the mangabeys were relatively efficient in locating edible fig fruits. In the next chapters I continue to investigate how mangabeys manage to locate these highly preferred fig fruits. I start by testing whether they use auditory cues produced by sympatric frugivores as a cue for fig availability.

* * *

CHAPTER 2

DO GREY-CHEEKED MANGABEYS USE CALLS OF SYMPATRIC FRUGIVORES TO ASSESS THE FRUITING STATE OF FIG TREES?

Chimpanzee eating figs



Black and White casqued hornbill

Yellow rumped tinkerbird

INTRODUCTION

"A solitary orangutan (*pongo pygmaeus*) moves through a Sumatran forest in Indonesia, attracted to a fig tree by the noise of hornbills and fruit doves consuming brilliant red fruits", M. F. Kinnaird & T. C. O'Brien (2000).

Frugivores can shorten daily travel distances by knowing where to find fruit over large distances. Although remembered space is the longest-range food "sense", acting well beyond an individual's immediate sensory environment, it is the least updated. In other words, frugivores may know where exactly fruit was found in the recent past, it is uncertain whether the fruit is still present on subsequent arrival. Especially the emergence of new edible rain forest fruit and their depletion rates can be highly unpredictable and ephemeral in time (Milton 1977; Chapman et al. 1999; R. W. Wrangham, C. A. Chapman; chapter 5). Hence, a more reliable way of locating fruit patches may be to use visual, olfactory or auditory cues. For fruit species that do not emit a strong odour or clear visual cues of their edibility state, such as a particular colour or size, the presence of other frugivores may serve as a reliable indicator of the fruit's edibility. For example, birds (Krebs et al. 1972) and fish (Pitcher et al. 1982) can locate food by watching foraging conspecifics. When visual cues are obstructed by vegetation frugivores can still use auditory cues, such as feeding sounds (falling fruit) or calls. Several species of birds and primates are known to locate food by approaching specific calls from co specifics (e.g. tamarins, *Saguinus labiatus*: Caine et al. 1995; macaques, *Macaca mulatta*: Hauser & Marler 1993, *Macaca sinica*: Dittus 1984; swallows, *Hirundo pyrrhonata*: Brown et al. 1991; ravens, *Corvus corax*: Heinrich 1988; chickens, *Gallus domesticus*: Marler et al. 1986; house sparrows, *Passer domesticus*: Elgar 1986). Apart from using auditory cues elicited by conspecifics, frugivores could also use auditory cues from other species. For example, red tailed monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*) and grey-cheeked mangabeys have been suggested to recognise the food-arrival calls of sympatric frugivores (Hauser & Wrangham 1990). Some primatologists take it as an established fact that primates use auditory cues from sympatric frugivores to locate food: "A solitary orang-utan (*Pongo pygmaeus*) moves through a Sumatran forest in

Indonesia, attracted to a fig tree by the noise of hornbills and fruit doves consuming brilliant red fruits". (Kinnaird & O'Brian 2001). However, little experimental research has been done to verify these assumptions. Also little is known about the frequencies with which auditory cues are used by primates in every day foraging.

The mangabeys in the Kibale forest are omnivores, however the majority of their diet consists of fruit (59% (Waser, 1977, Olupot et al., 1997). The fruits are found in extensive home ranges that can reach exceptional large sizes of 410 ha (Waser 1977). The rain forest of the Kibale National Park has one of the highest primate biomass density known to date (Struhsaker 1972; Chapman et al. 1999, 2000). Many of these primates eat fruits and could potentially provide auditory cues while doing so (Struhsaker 1997). In sum, both study species and site are ideal for investigations on fruit localisation by use of auditory cueing from sympatric frugivores.

Within this study I first investigated whether the use of auditory cues could be a successful fruit-localisation strategy in the Kibale forest. I tested whether there was a relation between the occupancy by frugivores and the fruiting state of a number of randomly encountered fig trees. Secondly, I investigated whether the mangabeys use cues of other large frugivores by use of observational data on fruit discoveries and the use of playback experiments. I conducted a follow up on the study of Olupot et al. (1998). This study suggested that the mangabeys of the Kibale forest use auditory cues produced by the black and white casqued hornbills (*Bycanistes subcylindricus*) (Olupot et al. 1998). The results showed that mangabeys were more likely to travel in the direction of areas where hornbills had been observed to call earlier in the day. Despite the negative results from a small number of play back experiments (N = 11), the results from the much larger observational data set suggested that the mangabeys used the hornbill calls to find fruit (Olupot 1998). However, the results could easily be explained by the fact that the monkeys already knew that the particular areas from which the hornbills were calling contained fruits. In other words, it is difficult to exclude the possibility that the monkeys may have used their memory to relocate fruit bearing trees. To rule out this alternative explanation I first investigated the approach behaviour of newly discovered fruit in a number of pre-selected fig trees, using data that was collected during an earlier study (Janmaat et al. 2006b; chapter 3). Secondly, I conducted a series of playback experiments from fig trees that carried no fruit or unripe (inedible) fruit only. Since the trees did not contain edible fruit or weevil larvae, an approach of the experiment trees could not be explained by a use of memory. I investigated the monkeys' reaction towards playbacks of calls of two large frugivores: the Black and White casqued hornbill and the Chimpanzee (*Pan troglodytes*). Since Olupot et al. had shown that grey-cheeked mangabeys were more likely to move in the direction of areas from which hornbill vocalisations had been heard, I decided to continue investigations on the level of attention that monkeys pay to play backs of hornbill calls. Since little is known about the meaning of hornbill loud calls it is particularly tricky to record the appropriate vocalisation for a playback experiment.The recorded call could have nothing to do with feeding behaviour, in the worst case it could be an alarm call that may scare the monkeys (Rainey et al. 2004). To minimise this risk I recorded calls that were made by the hornbills when feeding inside fig trees. The recordings were made when the hornbills were feeding together with a mangabey group. I made sure that the calls did not elicit alarm calls by the monkeys. I played these sounds from at least 12 m. up a fig tree for continuous periods of either 10 or 30 minutes. In this way, I tested whether a continuous long-lasting presence of hornbills (represented by their calling) inside a fig tree was interpreted and used by the monkeys as an indicator for the presence of fig fruit. I chose to conduct the playback from fig trees because figs are known to have highly irregular fruiting periods (chapter 5). Unlike the more synchronous fruiting species, fig fruits cannot easily be found by the monitoring of random fig trees, once fig fruit are encountered in one particular tree, (chapter 1; Menzel 1991). Tracking auditory cues was thought to be an efficient way to find edible figs. Also figs form the large proportion of the mangabey diet (14.7 % feeding time (Waser, 1977), 16% feeding time (Freeland, 1979)) and are amongst the preferred food species of the mangabeys (Waser 1974, 1977; Barrett 1995; Olupot 1999). For these reasons I expected that calls broadcasted from fig trees would catch the monkeys' interest.

To test the usage of an auditory cue that is even more clearly related to a feeding event I used vocalisations of chimpanzees broadcasted from at least 12 meters up a fig tree. Chimpanzees are terrestrial animals that only climb trees to feed or to sleep (Doran & Hunt 1994; Pontzer & Wrangham 2004). The calling of chimpanzees (a pant hoot followed by a number of feeding grunts) from high up in a fig tree during daytime was therefore thought to be a clear indicator for the presence of edible figs. I conducted two types of experiments. The first type concerned a small number of playbacks (hornbill and chimpanzee) from inside fig trees that were for sure within 50 to 200 m. of a mangabey group at the start of each experiment. The second type of experiments concerned a large number of playbacks (of hornbill calls only) from inside fig trees, at any time (including times in which I was not sure whether any primates or other frugivores were nearby). During the experiments I made recordings of two types of behavioural responses. The first type of response was the observation of whether or not the group approached into sight or continued to enter the play-back tree. The second type of more immediate response was the latency after which and the duration with which the monkeys looked in the direction of the speaker, variables that are considered to be related to their level of attention (Cheney & Seyfarth 1990, Onishi & Baillargeon 2005).

METHODS

Study species

I conducted playback experiments with five neighbouring groups of grey-cheeked mangabeys (Mikana (N = 15), Butanzi (N = 20-29), Lowercamp I (N = 15), Lowercamp II (N = 7) and CC (N = 16-17). During the second experiment session the Butanzi group had split in Butanzi I (N = 11) and Butanzi II (N= 12), (see table 1 for group composition). The groups ranged within a semi-logged moist evergreen forest of the Kibale National Park in Uganda (0°34'N, 30° 21'W, see Waser & Floody 1974 and Chapman et al. 1997 for an extended description of the study area). Grey-cheeked managebeys are considered arboreal (Waser 1974), however the Butanzi and Lowercamp I groups regularly foraged on the ground (Chapter 4; unpublished data). All five groups were habituated to human observers on foot, allowing observation as close as 10 meters. The main study group (Butanzi) allowed observations as close as 2 meters.

Table 1. Group composition of the five study groups. Number of adult females (fully grown), adult males, not fully grown, yet independently moving individuals and infants within each group

	# Adult females	# Adult males	# Not fully grown	# Infants	# Total
Mikana	4	3	5	3	15
Butanzi	7	4-10	9-10	0-2	20-29
Lowercamp I	5	4	6	0	15
Lowercamp II	3	1	3	0	7
CC	5	2	6	3-4	16-17

Some of the study groups had been subject to playback experiments before, yet these were done in 1993 (Olupot et al. 1998). I investigated the monkeys' behaviour towards Ficus trees (*Moraceae*) of the following species: *Ficus sansibarica, F. exasperata, F. natalensis, F. sur norsk, F.trichopoda and F. saussureana.*

Data collection

Occupancy of fruit bearing figs

The study was conducted between 24 February 2003 and 31 July 2004. To determine the occupancy of figs by frugivores in relation to their fruiting state I walked random routes along the trails of the Kanyawara grid system for a total of 12 days. I recorded the content of each *Ficus* tree that came in sight. Any presence of large frugivores and fruit was recorded by use of binoculars from as far away as possible to minimise disturbance. Large frugivores were either: black and white casqued hornbill, great blue turaco (*Corythaeola cristata*), black and white colobus (*Colobus guereza*), red-tailed monkey (*Cercopithecus ascanius*), blue monkey (*Cercopithecus mitis*), l'hoest's monkey (*Cercopithecus lhoesti*), olive baboon (*Papio anubis*), chimpanzee, grey-cheeked mangabey or african civet (*Civettictis civetta*). For each tree, I measured the diameter at breast height (DBH) and the crown diameter. Crown diameter was determined by averaging the N-S and E-W projection on the ground. I only included trees that had a DBH and crown diameter greater than the smallest tree ever observed carrying fruit during the study period (Chapter 3; Janmaat et al. 2006b).

Fruit discovery

To collect data on fruit discoveries I followed the main study group (Butanzi) for a total of 50,60 and 100 consecutive days between 24 February 2003 and 30 April 2004. I recorded their visiting behaviour towards a large number of pre-selected fig trees (see chapter 3 for detailed description of the methodology). Two observers followed the group from the first movement in the morning to final resting-place at dusk. Whenever the group entered a specified critical radius surrounding one of the target trees (100 meter) one of the observers rushed to the target tree to estimate the fruiting state and whether other frugivorous animals were present. When the group continued to approach the observer under the tree then measured whether or not individuals entered and ate the fruits. At the same time, the primary observer stayed with the individual closest to the tree to measure approach speed. Speed was measured in steps per minute in which the group moved in the direction of the tree (the observer's step lengths were calibrated over a stretch of 500 metres within the forest habitat with varying elevation levels). To keep each other informed about the position of the tree in relation to the moving group, the two observers communicated via calling, or used walkie-talkie. (See chapter 3 for an extended description of the methodology). By following the group for such continuous long time I was able to determine when particular fig trees within the home range were visited and when newly emerged fruits were encountered for the first time.

Playback Stimuli

Vocalisations were tape-recorded with a Sony WMD6C Professional Walkman and a Sennheiser K3/MEG7 directional microphone. Hornbill calls were recorded when feeding in the same fig tree as a mangabey group. The recorded calls did not elicit alarm calls by the mangabey group and were assumed to be either food or contact calls. I used vocalisations from the yellow-rumped tinkerbird (*Pogoniulus bilineatus*) as a control call. Tinkerbird recordings were made throughout the study area. The pop vocalisation was heard regularly in the forest and was chosen to be the control call because it was thought to be a territorial call most prominently heard in the breeding season, and never heard during feeding (Fry et al. 1988; personal com. A. Kirschel).

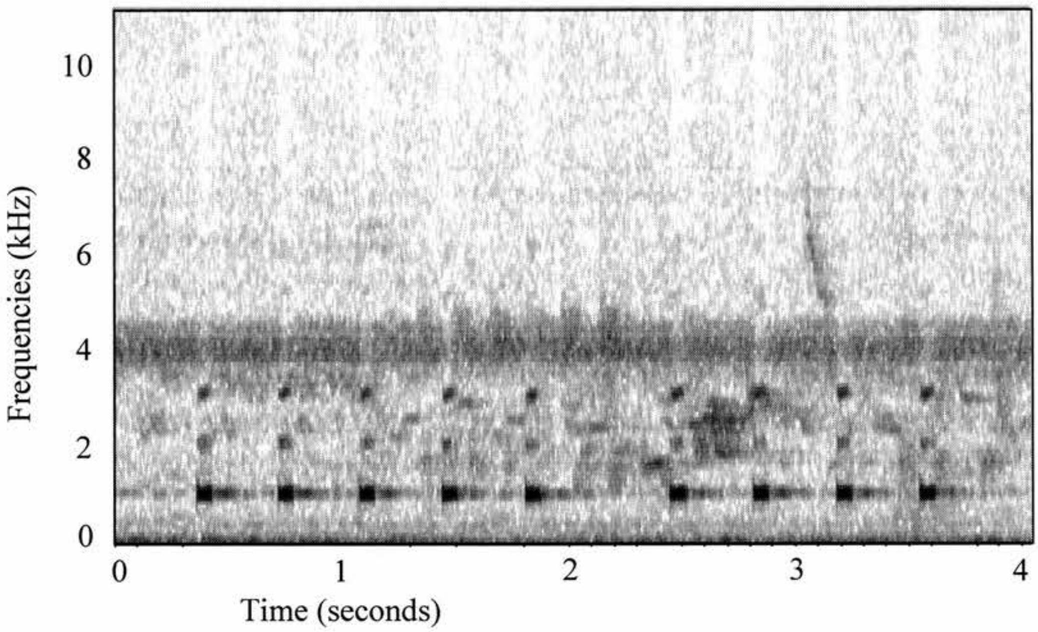


Fig.1. Spectogram of a short bout of the control (tinkerbird) calls. The total stimuli has a duration of either 10 or 30 minutes (T10 or T30). Here I only present 4 seconds of the total stimulus duration. Time is plotted against call frequency (Hz.).

Recordings were digitised and edited with the software program Cool Edit 2000. Both 10 minute call stimuli of tinkerbird and hornbill (T_{10} and H_{10}; fig. 1 and 2) were composed from five different recordings of presumably five different groups of hornbills or tinkerbirds each. Thirty-minute call stimuli (H_{30} and T_{30}) were composed from a random mix of 10 minute call stimuli.

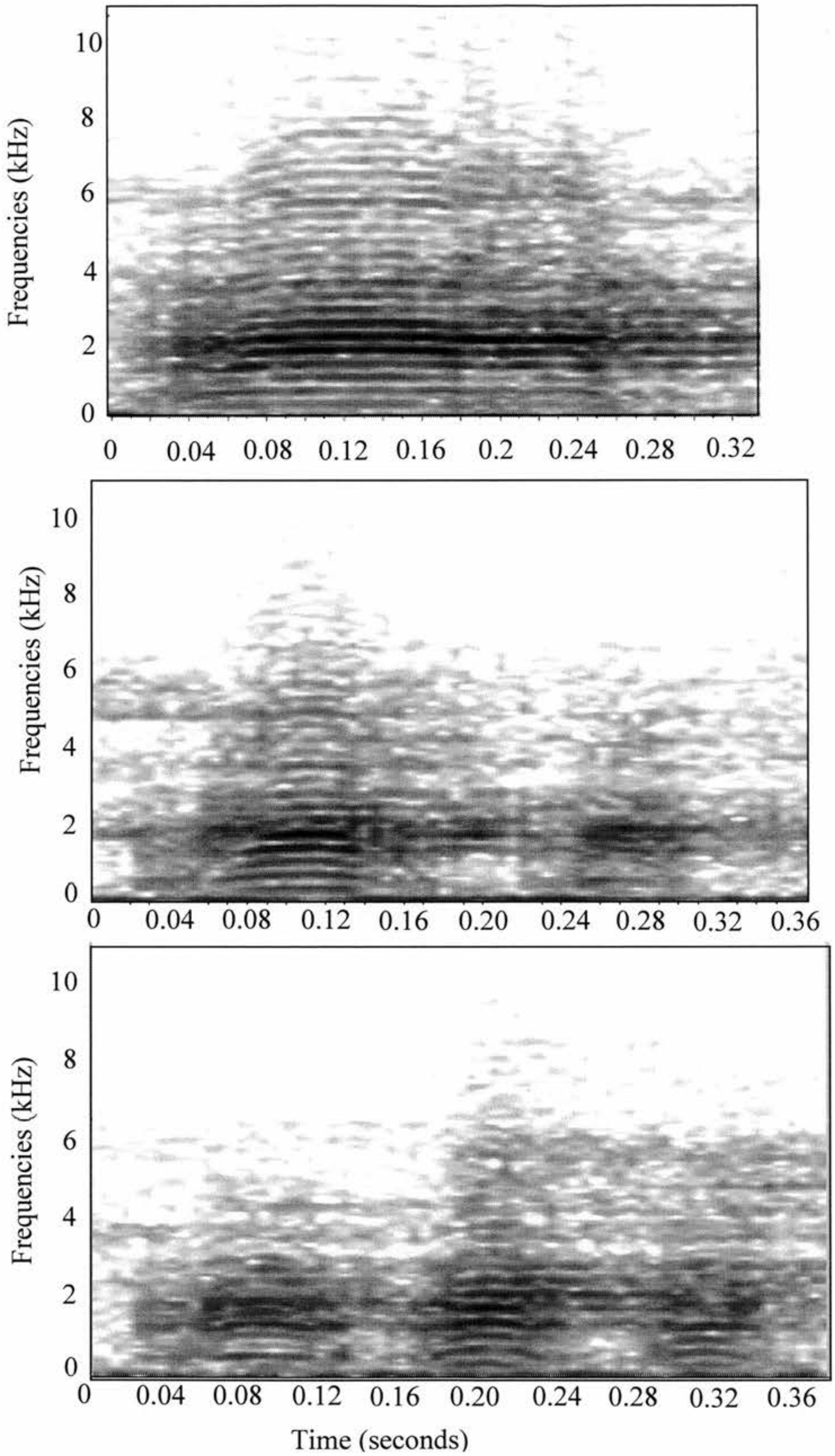


Fig. 2. Spectrograms of three similar types of the hornbill calls (a)1, (b)2 and (c) 3 calls respectively) that were broadcasted within 10 or 30 minutes stimuli sequences (H_{10} or H_{30}). Time is plotted against call frequency (Hz.) for each call.

Vocalisations of chimpanzees were recorded during one long feeding event in a *Ficus natalensis* tree. The mangabey group got chased out of the tree and presumably ate figs of a similar ripeness state as the chimpanzees. The chimpanzee calls did not elicit mangabey alarm calls.

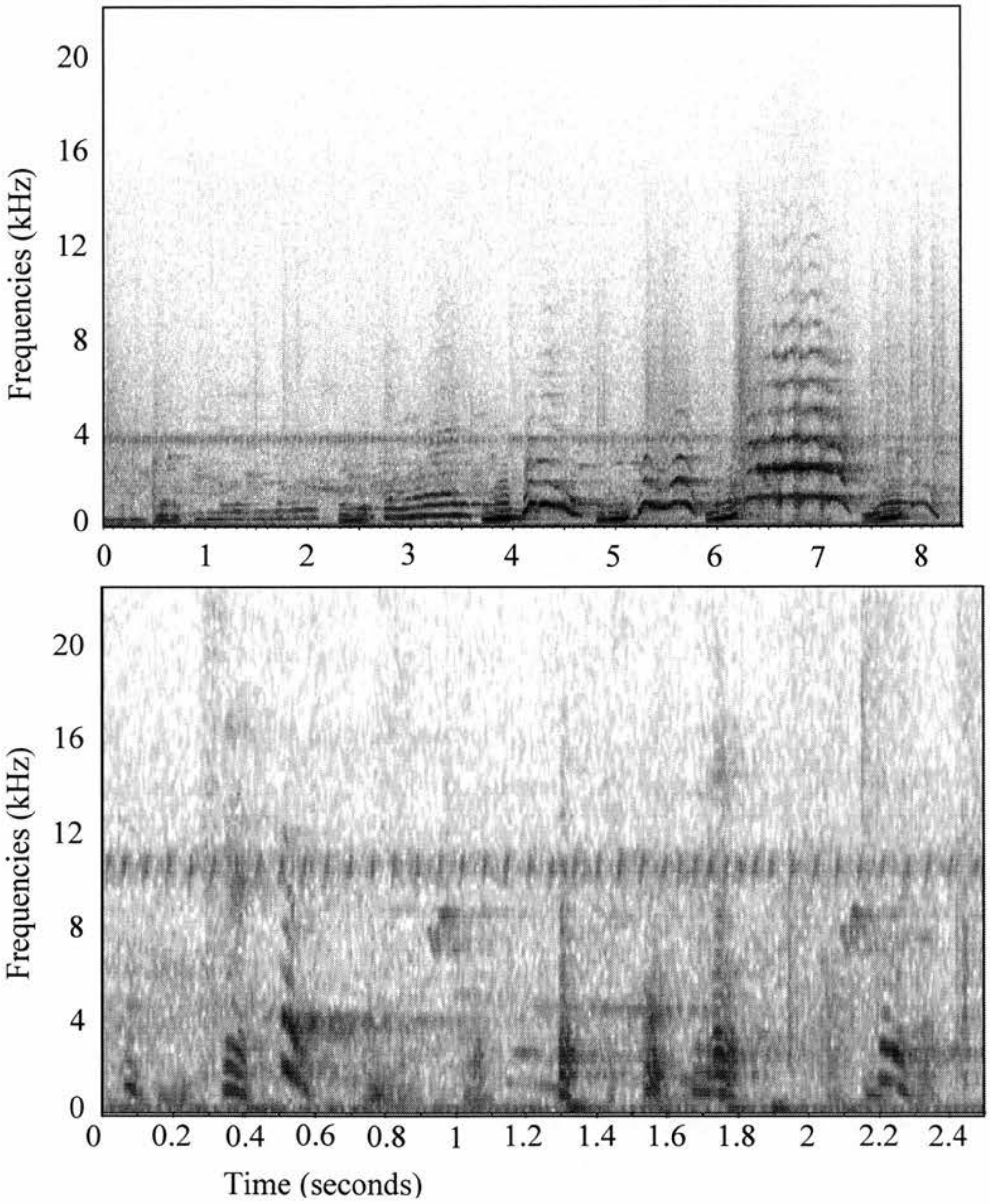


Fig. 3. Spectrograms of two elements from the chimpanzee call stimuli: a) pant hoot (up) and b) feeding grunt chorus (below). The C_1 stimulus is composed of one pant hoot, 5 seconds silence, followed by one feeding grunt session. The C_2 stimulus is composed of one pant hoot, 5 seconds silence, followed by another pant hoot. Time is plotted against call frequency (Hz.).

For the playbacks I used five different call stimuli that were sequences composed of one pant hoot (of ± 10 seconds each), a 5 seconds silence followed by one bout of feeding grunts (of ± 10 seconds each), (C_1 ; fig. 3a). In addition I made five stimuli composed from the same recordings yet the sequence contained two similar pant hoots only (25 seconds in total)(C_2; fig 3b). No editing was done on the calls themselves; I only silenced the space in between calls. For hornbill and tinkerbird calls, sequences were copied and pasted as many times after each other as needed to reach a total duration of 10 (T_{10} or H_{10}) or 30 minutes (T_{30} or H_{30}). Between each call sequence I placed a silence whose duration was equal to the natural intervals that were recorded. The order of each of the call stimuli was mixed randomly per group per experiment, yet each group experienced a play back of at least four different stimuli of chimpanzee (C_1), hornbill (H_{10} and H_{30}) and control calls (T_{10} and T_{30}). Each group experienced a play back of at least one C_2 call from the ground.

Experimental set up

Experiments were conducted between 27 January 2004 and 31 July 2004. Two types of experiments were conducted. The first type of experiment was conducted in proximity of a mangabey group. Once the group had settled down to eat or rest, one of the observers would search for a fig tree. Once a fig was found, the observer determined the fruiting state and contacted the observer who stayed with the group to ask for the group's location via walkie-talkie. When the tree was at the appropriate distance of the group (determined by use of the Kanyawara grid system and Global Positioning System (Garmin 12XL), the speaker would be raised (by use of a slingshot) at a height of at least 12 meters above ground level, inside or within 5 meters of the fig tree. When the distance between the group and the tree was still within a critical radius, and the group was still resting or feeding, the observer under the tree would search for a focal animal to film (using a Sony DCRPRV16E digital video camera recorder). Once the filming had started the observer communicated to the observer at the tree to start the experiment. Once the focal animal went out of sight a new animal was filmed. During filming the observer commented on the direction of head movements in relation to the direction of the speaker. While using the video recordings I determined the latency between the start of the experiment and the first time that the individual looked in the direction (within ±45 degrees) of the speaker. I also determined the duration and frequency with which the focal animal looked in the direction of the speaker. At the end of the experiment the observer under the tree waited under the tree and recorded when mangabey individuals of the experiment groups came into sight or entered the tree. When the playback concerned a hornbill or control call the observer also noted when hornbills entered the tree and the number and type of calls made by hornbills that were within audible reach from under the tree, from the start of the experiment till two hours after. Within the first set of experiments (A) the observer under the tree waited for two hours and the tree was within 100 and 200 m from the group. For the hornbill and control calls, playbacks were conducted from a total of ten fig trees that carried no fruit per call stimuli. For the chimpanzee calls playbacks were conducted from six fig trees with unripe fruit and five trees without fruit (table 2). In the second set of experiments (B) the observer under the tree waited for the remainder of the day (minimum of 6 hours) and the tree was within 50 and 150 m. from the group. The hornbill and control experiments playbacks were conducted from 5 trees that carried unripe fruit and 5 that carried none, for each call stimuli. For the Chimpanzee calls (C_1) playbacks were conducted from seven trees that carried unripe fruit and six trees that carried no fruit. Seven C_2 experiments were done from ground level from a location in which no other fig trees were observed within sight. All group experiments were conducted between 7:30 h and 12:30 h. Each group was tested at least twice per set of experiment (A or B)(but sometimes more if time and conditions allowed it), per call stimuli. Each call stimuli was played to them with an interval of at least three days. For the playbacks of control calls the speaker was placed on the ground in order to save time. These calls were played at a louder volume (see below). The ripeness state of a tree was determined by the assessment of elasticity and colour of fallen fruits and the colour and smell of the fruits inside the tree. Playback experiments were conducted from empty trees of *Ficus sansibarica, F. exasperata, F. natalensis, F. sur norsk, F.trichopoda and F. saussureana.* Fig trees that carried unripe fruits did not concern trees of *F. sansibarica*, because of the high chance that fruits contained weevil larvae (chapter 1 & 3).

The second type of experiments concerned playbacks of 30-minute call sequences of either a hornbill (H_{30}) or control (tinkerbird) calls (T_{30}) inside a total of 35 individual *F. exasperata* trees, that carried unripe fruits within the study area. The trees were located by random search along the Kanyawara trail system. The hornbill stimuli were played at least 12 m above ground level. The control stimuli were played from ground level similar to the group experiments. I conducted one hornbill and one control experiment in each tree under the condition that the experiments were separated by at least one day. To control for time effects playback of hornbill calls preceded that of control calls. Once all large frugivores (see above for definition) had left the tree the experiment was started and the observer recorded whether any large frugivores came into sight of the tree or entered, within 2 hours of the start of the experiments. The observer recorded the species and the number of individuals. Within that same time period the observer noted the number and type of calls made by hornbills that were within audible reach from under the tree.

Table 2. Overview of the total number of experiments conducted for each mangabey group (Mik, LCI....But II), from different type of fig trees with either no fruit (nf) or unripe fruit (fu). Experiments (type A and B) were conducted with calls from black and white casqued hornbills (H), tinkerbirds (control) (T), chimpanzees, broadcasted from either the tree (C1) or from the ground (C2), or without any call (Ts). *no good recordings of head movement.

Type A (100-200m, 2h response time)									**Type B** (50-150m, min 6h response time)									
Exp type	H (10min)		T (10min)		C_1 (25sec)		T_s (no call)			H (30min)		T (30min)		C_1 (25sec)		C_2 (25sec)	T_s (no call)	
Tree type	nf	nf	nf	nf	fu	nf	nf	nf		nf	fu	nf	fu	nf	fu	nofig	nf	fu
Mik	1	1	1	1	1	1	1	1	Mik	1	1	1	1	1	1	2	1	1
LC1	1	1	1	1	1	1	1	1	LC1	1	1	1	1	1	1	1	1	1
LCII	1	1	1	1	1	1	1	1	LCII	1	1	1	1	1	1	1	1	1
CC	1	1	1	1	2	1	1	1	CC	1	1	1	1	1	1	1	1	1
But	1	1	1	1	1	1	1	1	But I	1	1	1	1	1	1	1	1	1
									But II			1	2^*			1		

Playback stimuli were broadcasted with a Panasonic SL-SX315 portable CD player connected to an Interm NO.PS-30 speaker-amplifier. Stimulus intensities were measured with a Radio Shack sound-level meter 33-2050, C-weighted, at 1m distance from the speaker. Vocalisations were played back in the following amplitude range: Chimpanzee pant hoot 92-98 dB; Chimpanzee feeding grunts, 98-102 dB; Hornbill call 90-92 dB; Tinker bird call, 102-105 dB. Since the tinkerbird stimulus was played from ground level the sound was more reflected by vegetation. Hence I chose to play the stimuli at a higher amplitude than the other stimuli, to make sure that a difference in the sound intensity could not explain a potential difference in response between playback and control call. Since, the authors wanted to avoid interference with the research of the Kibale Chimpanzee Project, chimpanzee stimuli were only broadcasted when chimpanzees were away from the experiment area.

RESULTS

How rewarding is the use of auditory cues?

Large frugivores

To investigate whether the tracking of auditory cues is a rewarding fruit localisation strategy within the Kibale forest, I first tested whether fig trees that carried fruit were indeed occupied more frequently by frugivores than trees that carried none. In the transects I encountered a total of 314 fig trees (Fsan: N = 128; Fe: N = 114; Fn: N = 48; Fsu: 10; Fsa: 12; Ftr: N = 2). I found a significant association between the presence of large frugivores and the fruiting state of the encountered trees ($X^2 = 20.23$, $P = 0.000$, $N = 314$, $Phi = -0.254$, $P = 0.000$; fig. 4). The proportion of times that the frugivores were observed inside the encountered fig trees was higher for trees that carried fruits than for trees that carried none. However, when I looked at the absolute frequencies of cases in which frugivores were found in either tree type I found little difference (16 vs. 22 cases), suggesting that the tracking of visual or auditory cues of frugivores, does not necessarily result in the encounter of a fruit-

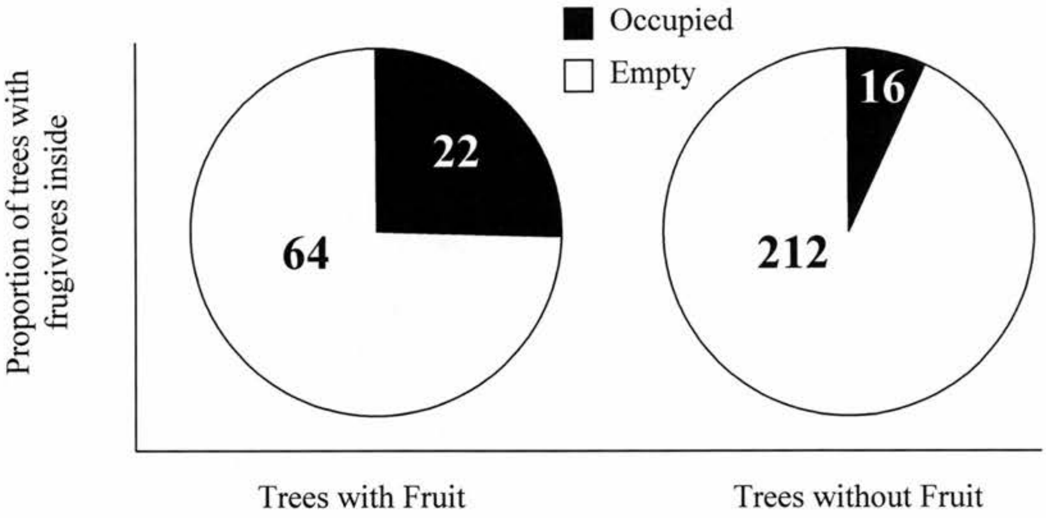


Fig. 4. Occupancy of Ficus trees by large frugivores in relation to the fruiting state of the trees. Black numerals in white segments: number of times that one or more large frugivores were found inside a fig tree. White numerals in black segments: number of times that no large frugivores were spotted inside a fig tree.

bearing tree more often than that of a tree without fruit. Yet, I did find that that the number of animals inside each tree differed significantly between each tree type ($U = 98.5$, $P = 0.010$, $N_1 = 17$, $N_2 = 22$). These results suggest that if a larger number of frugivores are noisier than a small number, search by use of auditory cues could potentially be a rewarding strategy.

Chimpanzees

Since chimpanzees are known to hunt monkeys one expects the mangabeys to be hesitant in approaching trees from which chimpanzee vocalisations have been heard. To investigate whether this is true I followed one group of mangabeys (Butanzi) for three periods of 50,60 and 100 consecutive days and recorded all interactions with chimpanzees in relation to food trees. Seven times I observed that the group was feeding in a fig tree when chimpanzees arrived. Three of these times the mangabeys left the tree after being chased by male chimpanzees (Number of chimpanzees > 4). Four out of seven times they continued feeding together with the chimpanzees. Two times one of the mangabey males chased a female chimpanzee from the tree. Six times chimpanzees were spotted while feeding inside a fig tree within sight of the observer that travelled with the mangabey group. All six times the study group entered the tree; 5 times within 100 minutes while the group was waiting at the same spot and 1 time within 6 hours, after the group had continued travelling. These observations suggest that mangabeys can use the auditory cues produced by chimpanzees within 6 hours after they detect chimpanzees inside a fruit tree.

Do mangabeys use auditory cues?

Observational data

To investigate whether mangabeys use auditory cues to locate fruit bearing trees I first analysed observational data of cases of fruit discovery. By continuous following of the main study group I collected data on rare cases of fig fruit discovery. A discovery was defined as a visit in which the group ate fruit in a particular tree for the first time since the last fruiting period of that same tree. I pooled data of four types of discoveries: type a) a feeding visit that succeeds a visit in which the group entered but did not eat (N = 3), b) a feeding visit in which the tree had grown new fruits during the observation period (N = 2), c) a feeding visit in which the tree had grown new fruits during the observation period and that succeeds a visit in which the group entered but did not eat (N = 1), d) the first time that feeding was observed in a tree after a period of at least 40 days in which the group did not come within 100m of the same tree (N = 3). I analysed the speed of approach for all these "discoveries" (first feeding visit) and the subsequent time that the group entered the tree (second visit). The speed with which the group approached the target tree on the first feeding visit tended to be slower than the speed on the subsequent visit (Z = -1.955, P = 0.051, Wilcoxon signed rank matched pairs test (WSM); fig 5). This suggests that in the majority of cases the monkeys did not anticipate finding fruit at the first feeding visit. Hence, they were unlikely to have used auditory cues to discover the fruit. However, in three particular cases the group did not approach slower the first time, and in two of those cases primates (chimpanzees and mangabeys) had been observed inside the target tree before the group's arrival.

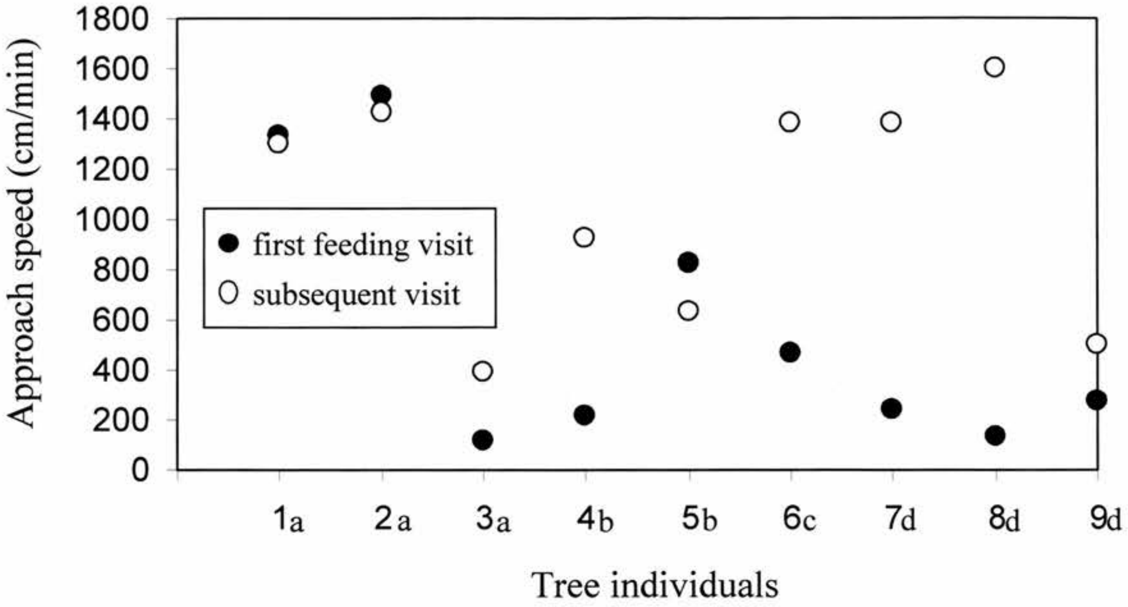


Fig. 5. Speed of approach at discoveries of edible figs. Closed circles represent the speed with which a mangabey group approached a fig tree in which the group was thought to discover edible fruits for the first time. Open circles represent the speed with which the group approached the same tree at the subsequent visit. Tree 1 and 2 were occupied before the group's arrival. A, b, c and d represent the type of discovery visit (see § observational data)

Experimental data

Since observations of first feeding visit are so rare, the best way to investigate the use of auditory cues is by playback experiments.

Reaction to Hornbill calls

Quality of signal

I found that at significantly more experiments one or more black and white casqued hornbills entered the experiment tree within 2 hours of the start of the experiment when hornbill calls were played than when control (tinkerbird) calls were played. This was true for both group and tree experiments (X^2 = 7.05, P = 0.020, N = 40, df = 1; fig. 6; P = 0.008, N = 35 (Wilcoxon signed rank matched pairs (WSM)). The total frequency of calls of surrounding hornbill individuals within 2 hours after the start of an experiment was higher when hornbill calls were played than when control calls were played. I found a significant difference for the group experiments and a trend for the tree experiments (U = 134.0, P = 0.033, N_t = 21, N_h = 20, Z = -0.1889, P = 0.059, N = 35). These results indicate that the signal broadcasted in the playback experiments sounded natural enough for the hornbills to respond, suggesting that the call stimulus was of sufficient quality.

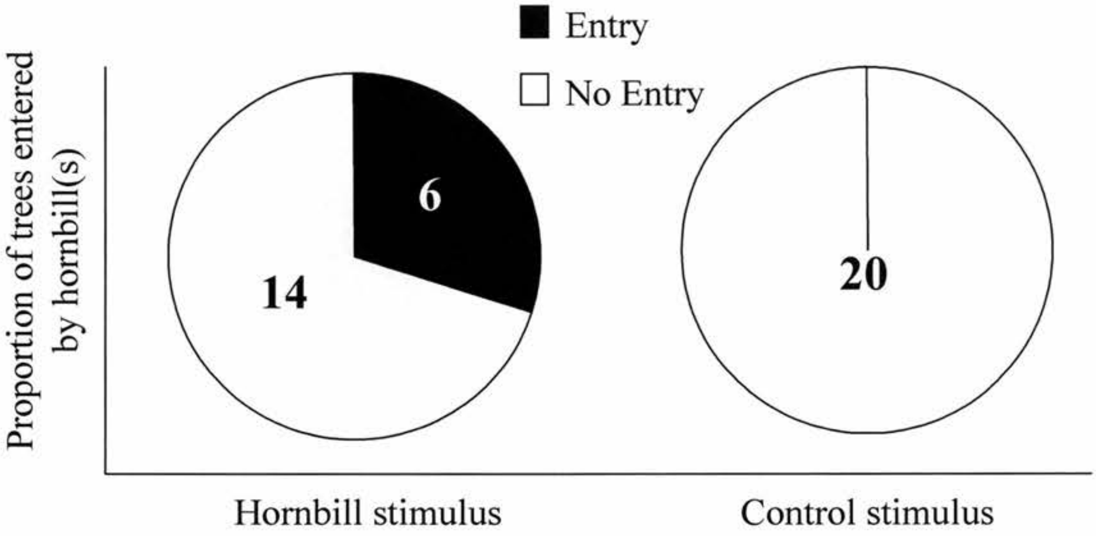


Fig.6. Approach behaviour of hornbills to playbacks of either hornbill (H_{10} and H_{30}) or control calls (T_{10} and T_{30}). Black numerals in white segments: number of times that one or more hornbills entered the experiment tree from which either control or hornbill stimuli were played. White numerals in black segments: number of times that no hornbills had entered the experiment tree.

Group experiments

Approach of Experiment tree

The percentage of experiments in which a group moved into sight of the observer under the experiment tree did not differ between the experiments in which hornbill calls were played and those in which no play-back was done. This was true for both series of experiments; A) 10 minute call session from 100-200m distance and a recording of response of 2 hours: (WSM: $Z = -1.00$, $P = 0.317$, $N_{\text{number of groups}} = 5$), B) 30 minute call session from a 50-150 m. distance and a recording of response of the remaining of the day (WSM: $Z = 0.00$, $P = 1.0$, $N_{\text{number of groups}} = 5$). The same was true for the percentage of experiments in which a group continued to enter the experiment tree (WSM: A: $Z = 0.00$, $P = 1.0$, B: $Z = 0.00$, $P = 1.0$).

Attention towards call

The percentage of time with which the focal animals looked in the direction of the speaker during the playback (10 or 30 min), out of all time in which individuals were observed during the experiment, did not differ between playbacks of hornbill and control calls. This was true for both series of experiments (WSM: A: $Z = -0.405$, $P = 0.686$ $N_{\text{number of groups}} = 5$, B: $Z = -0.135$, $N_{\text{number of groups}} = 5$). The average rate of looking did also not differ between playbacks of hornbill and control calls for neither of the series of experiments (WSM: A: $Z = -0.135$, $P = 0.893$ $N_{\text{number of groups}} = 5$, B: $Z = -1.214$, $N_{\text{number of groups}} = 5$). When I compared the response to hornbill sessions that lasted 10 minutes with sessions that lasted 30 minutes, I also found no difference between the percentage of times and average rate of looking (WSM: $Z = -1.1214$, $P = 0.225$, $N_{\text{number of groups}} = 5$, $Z = -0.135$, $P = 0.893$, $N_{\text{number of groups}} = 5$). These results suggest that the monkeys did not pay more attention towards the play back calls when the duration of calling lengthened.

Tree experiments

Large frugivores did not approach the experiment trees into sight more often (within 2 hours after the experiment started) when the speaker played hornbill calls than when it played control calls ($X^2 = 0.933$, $P = 0.334$, $N_{\text{number of trees}} = 35$, $N_{\text{number of experiments}} = 70$). Neither were they entered more often when hornbill calls were played ($X^2 = 0.233$, $P = 0.629$, $N_{\text{number of trees}} = 35$, $N_{\text{number of experiments}} = 70$). The total number of individuals that entered a tree within two hours of a playback of hornbill calls did also not differ from the number that entered the same tree within two hours of a playback of control calls (WSM: $Z = -0.180$, $P = 0.857$, $N_{\text{number of trees}} = 35$, $N_{\text{number of experiments}} = 70$).

Reaction to Chimpanzee calls

Quality of the signal

The average of latencies between the start of the experiment and the first moment that the focal animal looked in the direction of the speaker differed significantly between playbacks of chimpanzee and control calls ($Z = -2.023$, $P = 0.043$, $N_{\text{number of groups}} = 5$). Figure 7 shows that the averages of response latencies are much shorter for the chimpanzee calls than for the tinkerbird control calls. The average of duration with which the focal animal looked in the direction of the speaker for the first time since the start of the experiment also differed significantly between playbacks of chimpanzee and control calls (WSM: $Z = -2.023$, $P = 0.043$, $N_{\text{number of groups}} = 5$). The median duration of looking was higher after playbacks of chimpanzee calls. These results suggest that the monkeys thought that the playback calls were elicited by real chimpanzees. I believe therefore that the quality of the signal was good. However, it is unclear why the monkeys reacted differently to the chimpanzee calls. Did the monkeys check the direction of the sound of chimpanzees more quickly and longer because they wanted to assess the location of potential predators or did they want to assess the location of indicators for the presence of fruit? To investigate this I conducted the following series of experiments.

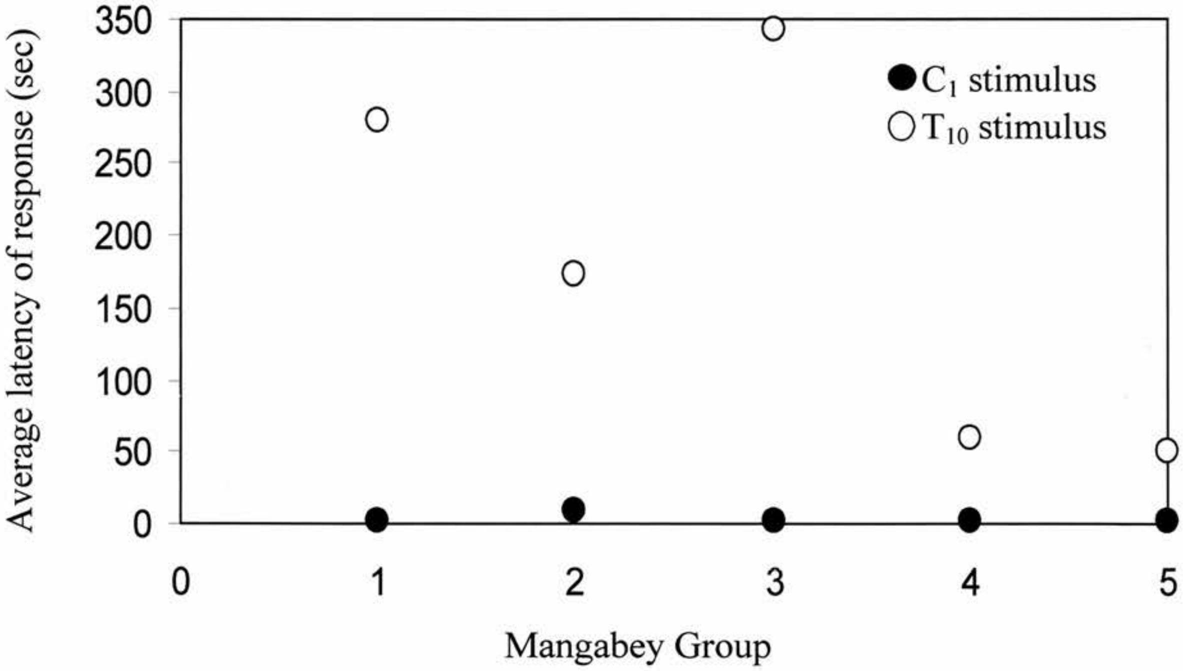


Fig.7. Latency of response of mangabey individuals from five different groups towards chimpanzee (C_1) or control stimuli (T_{10}). Circles represent the number of seconds between the start of the playback and the first time that the focal animal looks in the direction of the speaker. Open circles represent the latency of response when chimpanzee calls are played; closed circles represent the latency of responds when control calls were played.

Group experiments

Approach of experiment tree

The percentage of experiments in which a group moved into sight of the observer under the experiment tree, did not differ between the experiments in which chimpanzee calls (C_1) were played and experiments in which control calls were played. This was true for both series of experiments: A) playbacks at 100-200 m distance and a recording of responses during 2 hours: (WSM: $Z = -1.342$, $P = 0.180$, $N_{\text{number of groups}} = 5$), B) playbacks at 50-150 m distance and a recording of responses during the remaining of the day (minimal 6 hours) (WSM: $Z = -0.577$, $P = 0.564$, $N_{\text{number of groups}} = 5$). The same was true for the percentage of experiments in which a group continued and entered the experiment tree (WSM: A: $Z = 0.00$, $P = 1.0$, $N_{\text{number of groups}} = 5$ B: $Z = -1.0$, $P = 0.317$, $N_{\text{number of groups}} = 5$).

Attention towards calls

Feeding grunts

To investigate whether the monkeys pay special attention to chimpanzee feeding grunts I compared the percentage of experiments in which the group responded to the second call of either the C_1 (Pant hoot + feeding grunts) or C_2 (Pant hoot + Pant hoot) experiments, by looking in the direction of the speaker. I found that the percentage of times in which focal individuals responded (by looking in the direction of the speaker) right after the second part of the experiment call did not differ between the playbacks that contained one pant hoot and one feeding grunt session (C_1) and the playbacks that contained two pant hoots (C_2). ($Z = -0.526$, $P = 0.599$, $N_{\text{number of groups}} = 6$).

Height of broadcasting

The average latency between the start of an experiment and the first time that the focal animal looked in the direction of the speaker did not differ between call stimuli that were broadcasted from the ground (C_2: Pant hoot + Panthoot) and play back calls that were broadcasted from at least 12m up a fig tree (C_1: Pant hoot + Feeding grunts) (WSM: $Z = -0.135$, 0.893, $N_{\text{number of groups}} = 5$). However the averages of the total duration that focal animals looked in the direction of the speaker within one minute after the start of the experiment, tended to be longer when calls were broadcasted from up a fig tree (WSM: Z = –1.782, P = 0.075, $N_{\text{number of groups}}$ = 6. However the difference was not significant. (N is different from above because in one group the focal did not look, so the first measure could not be compared).

Fruiting state experiment tree

The finding that the monkeys tended to look longer in the direction of the speaker that were broadcasted from at least 12 m. up a tree suggest that the monkeys interpreted the chimpanzee calling as an indication for the presence of edible figs. However they may also have been more interested in the call because they thought that the chimpanzees were hunting. To investigate whether the monkeys' attention was related to food search behaviour or predator avoidance behaviour I did the following additional analyses. I tested whether the monkeys responded differently towards chimpanzee playbacks broadcasted from fig trees that carried fruit and fig trees that did not carry fruit. The average latency between the start of an experiment and the first time that the focal animal looked in the direction of the speaker did not differ between playbacks that were broadcasted from fig trees that had unripe fruit and figs tree that did not contain fruit (WSM: Z = -0.135, P = 0.893, $N_{\text{number of groups}}$ = 5). The averages of the total duration that focal animals looked in the direction of the speaker within one minute after the start of the experiment did not differ between play backs broadcasted from fig trees with unripe fruit and without fruit (WSM: Z = –0.135, P 0.893, $N_{\text{number of groups}}$ = 5). The percentage of times in which individual responded to the feeding grunts did also not differ between the playbacks that were broadcasted from trees with unripe fruits and trees without fruit (WSM: Z = -1.131, P = 0.258, $N_{\text{number of groups}}$ = 5).

DISCUSSION

The results of this study indicate that the Kibale forest is an ideal environment to use auditory cues of sympatric foragers to find fruit. The likelihood of spotting large frugivores, such as primates, hornbill and turaco birds, inside a fig tree was significantly associated with the fruiting state of the tree. Also, a larger number of frugivorous individuals were found in figs that carried fruit than in figs that carried none. This suggests that in theory, the tracking of sounds produced by sympatric frugivores, could be a rewarding search strategy in order to find edible fruit in the Kibale forest. However, whether the primates of the Kibale forest use the auditory cues produced by these frugivores, remains unclear. Observational data, collected within a 120 days' continuous following of one mangabey group, showed that during discoveries of newly emerged edible fig fruit, mangabey monkeys do not use auditory cues as regularly as expected. In only 2 out of 10 new fruit discoveries, other frugivores were present before the moment of discovery. For these two cases, speed of approach at the first feeding visit was almost equal to the speed of approach at the subsequent visit. For 7 other visits speed of approach was slower at the first feeding visit than at the subsequent visit, indicating that the monkeys had not expected to find fruit and therefore did not use auditory cues for the majority of their discoveries. Experimental data confirmed these findings. I conducted a series of experiments with five groups of mangabey monkeys, using call stimuli from two sympatric frugivores, the black and white casqued hornbill and the chimpanzee. Playbacks were conducted from at least 12 m height within 5 m. or inside a fig tree that either carried unripe or no fruit. The hornbill stimuli contained calls that were not clearly identified as food calls. Some of the calls had been heard in non-feeding context and were thought to be contact calls. I therefore expected the monkeys to respond to the calls only after hearing the hornbill stimuli for a considerable duration in time. I expected a response not towards the call itself, but towards the long lasting presence of hornbill calls. Hornbill calls were played in sessions that lasted either 10 or 30 minutes. As chimpanzee calls that are broadcasted from a height of 12m, are a more clear indication for the presence of food, the chimpanzee stimuli were broadcasted within only 25 seconds. The chimpanzee stimulus was composed of one pant hoot and one session of feeding grunts. The results of these experiments did not provide any indication that the mangabeys made regular use of calls of the two sympatric frugivores in order to find fruit. The percentage of experiments in which a group moved into sight of the observer under the experiment tree, or continued to enter the tree, did not differ between the conditions in which hornbill calls or chimpanzee calls were broadcasted and each of the control conditions. This was true for two different sets of experiments. It was true for experiments in which calls were broadcasted from fig trees that were located between 100 m and 200 m from the experiment group and in which response was recorded within 2 hours after the start of the experiment. Yet it was also true for experiments in which calls were broadcasted from a closer distance, between 50 and 150 m and when response was measured during the remainder of the day (minimum of 6 hours). Even for the second set of experiments in which I tested the response of all large frugivores to playbacks of hornbill calls from a large number of fig trees (N= 35), I failed to find a difference in the approaching and entering frequencies of either large frugivores or the total number of individual frugivores, of trees from which hornbill or control calls were broadcasted. These findings are consistent with the results from the small number of playback experiments conducted by Olupot et al. (1998). Olupot et al. (1998) found that in cases in which hornbill calls were broadcasted, the mangabeys responded with an immediate approach of the speaker 2 out of 11 times (N = 11). In cases in which chimpanzee calls were broadcasted, the monkeys responded with an immediate advance in 2 out of 5 times (N = 5)).

To investigate whether the monkeys paid attention to the calls at all, I also recorded more immediate behavioural responses, such as whether or not focal individuals looked in the direction of the speaker. I found that the monkeys did not look longer or more frequent into the direction of a speaker that broadcasted hornbill calls than one that broadcasted the control calls, neither for the 10 min nor 30 min sessions. To investigate whether the duration of the presence of hornbill calls influenced the monkeys' interest and attention to the playback calls I compared the reaction to hornbill sessions that lasted 10 minutes with sessions that lasted 30 minutes. The results of this analysis indicated that the monkeys did on average not look longer or more frequently during the 30 than during the 10 min. sessions. The monkeys did look more quickly and longer in the direction of the speaker that played chimpanzee calls than to one that played control calls. However, this does not necessarily imply that the monkeys were interpreting the chimpanzee vocalisations as indicators for the presence of food. I found a slight indication that the monkeys did, since the monkeys tended to look longer at chimpanzee calls that were broadcasted from the tree than calls that were broadcasted from the ground ($P < 0.1$). However, this finding could also be explained in a way that monkeys were wearier of chimpanzee calls heard from high up in trees, since chimpanzees in trees could be hunting. Or it could be explained by the fact that the monkeys perceived the calls that were broadcasted from the ground with a lower volume, due to habitat obstruction. To investigate whether the response was truly related to fruit search behaviour I first compared the monkeys response to chimpanzee stimuli that included feeding grunts and stimuli that did not. I compared the percentage of experiments in which the group responded to the second call of either the C_1 (Pant hoot + feeding grunts) or C_2 (Pant hoot + Pant hoot) experiments, by looking in the direction of the speaker. I found that the percentage of times with which focal individuals responded (by looking in the direction of the speaker) right after the second experiment call did not differ between the two call types. This suggests that the monkeys did not pay more attention to feeding grunts than to pant hoot vocalisations. To further investigate whether the monkeys response was related to fruit search behaviour I analysed the monkeys response to chimpanzee vocalisation broadcasted from trees that carried unripe fruit and trees that carried none. Trees that carried unripe fruit were more likely to contain feeding chimpanzees, especially when trees contained small fig fruits that can ripen in one day (Houle 2004), while calls from empty trees are unlikely to indicate the presence of feeding chimpanzees. Assuming that the mangabeys possibly remembered the fruiting state of the experiment trees, from previous visits, I expected that they would respond differently towards calls from both tree types. However, I found no difference in response, concerning the latency of response and the total duration of looking between the two cases. I also did not find any indication that the monkeys paid more attention to the second part of the call stimuli, the feeding grunts, when the stimuli was played from a tree that carried unripe fruit or a tree that carried no fruit.

One of the most obvious explanations for the lack of locomotive responses to both hornbill and chimpanzee playbacks could be that the quality of the signals was insufficient. To investigate this possibility I recorded the response of the hornbills towards the call stimuli. These data showed that unlike the mangabeys the hornbills themselves did react to the experimental calls. I found that significantly more hornbills approached and entered the experiment tree when hornbill calls were played than when control calls were played. The hornbills also called significantly more frequently in response to hornbill playbacks than to control call playbacks. Since, I attempted to conduct chimpanzee experiments outside the hearing reach of real chimpanzees, I do not have data on the response of the chimpanzees towards the chimpanzee calls. However, the finding that mangabeys responded more quickly to playbacks of chimpanzee calls than to the control calls by looking in the direction of the loudspeaker, suggest that the monkeys were aware of the identity of the caller. In sum, I conclude that the lack of locomotive response to both call stimuli cannot be explained by a deficiency in either the quality of the stimuli or the experimental set up. Nor does a potential lack of habituation of the monkeys to human observers under the experiment tree explain these results, since all groups could be approached within 10 m.

The finding that the group did not approach or enter fig trees from which chimpanzee or hornbill calls were broadcasted more often than in control conditions does not necessarily mean that the monkeys did not use the cues. Possibly, they had planned another route and did not want to travel to the experiment tree on that particular day. However, the results in chapter 5 show that once the group came within 100m of a *F. sansibarica* tree with fruit they entered 64% of the times (chapter 3; Janmaat et al. 2006b). For ripe fruits this was 85% (chapter 5). Because *F. sansibarica's* rank on the mangabey's preference list is similar to that of most other fig species selected for the experiment (Waser 1975), one would expect that if the monkeys understood the relation between chimpanzee's high altitude vocalisations or the long lasting vocalisations of hornbills and the presence of edible figs, they should have visited the experiment trees in at least 64% of the trials. However the group entered the experiment tree in only 25% (6 out of 24) of the times when chimp calls were broadcasted and in only 5% (1 out of 20) of the times when hornbill calls were broadcasted. A possible explanation for the finding that the monkeys did not approach the hornbill stimuli could be that hornbills are unreliable indicators of food. Possibly, the calls did not guide the monkeys to particular trees, but to particular forest areas only. Kalina (1988) records substantial inter monthly variation in the density of hornbills in certain areas of the forest and suggest that high densities are related to the presence of fig fruit. Large flocks not only call from fig trees, yet also from non-feeding locations.

A possible explanation for the finding that the monkeys did not approach the chimpanzee stimuli could be that they were afraid to approach potential predators. However, observational data showed that the main study group did enter trees in which chimpanzees were feeding within 1 hour for 9 and within 6 hours for 1 out of 10 times. I therefore consider it unlikely that the monkeys were avoiding entering trees in which chimpanzees were known to feed in the recent past, to minimize predation risk. Also observations of interactions between chimpanzees and mangabeys inside feeding trees, does not give reason to believe that the mangabeys would in all cases be too afraid to approach.

Apart from the lack in locomotive response, observations of looking behaviour also did not provide in any indication that the monkeys paid more attention to hornbill calls than to control calls. Neither could I confirm that the monkeys paid more attention to chimpanzee calls as an indicator for the presence of fruit.

I conclude therefore that despite the rewarding potential of the use of auditory cueing of sympatric frugivores, the monkeys did not regularly use auditory cues of hornbills and chimpanzees as a sole indicator of newly emerged fruit. I do not exclude the possibility that the monkeys do use auditory cues. Possibly, the monkeys did not pay attention to the calls or were reluctant to approach the experiment trees, because they had recently visited the tree and knew that the chance of finding edible fruit was low. Possibly, the monkeys use auditory cues in combination with a spatial memory of the previously observed fruiting state of trees only.

SUMMARY CHAPTER 2

The use of auditory cues made by sympatric frugivores during feeding could provide individuals with information on the fruiting states of rainforest trees. In this study I investigated whether and with which frequencies five groups of grey-cheeked mangabeys in the Kibale forest in Uganda used such cues in order to find preferred yet irregularly emerging fig fruit. I found that fig trees that carried fruits contained a larger number of frugivores than fig trees that carried none, suggesting that using auditory cues, could potentially be a rewarding strategy. However, in only two out of ten times in which newly emerged fruits were discovered by the main study group, other frugivores were present before the moment of discovery. Speed of approach was significantly slower at the first feeding visit than at the subsequent visit, indicating that the monkeys had not expected to find fruit for the majority of their discoveries. The results of play-back experiments in which loud calls of black and white casqued hornbills (*Bycanistes subcylindricus*) and chimpanzees (*Pan troglodytes*) were broadcasted from at least 12 m. high up a fig tree did not indicate a regular use of auditory cues either. I found a significant difference in the frequencies with which the experiment tree was approached by hornbills, yet no difference was found for either mangabeys or other frugivores, between experiment and control conditions. Neither did I find a difference in the latency and duration with which the monkeys looked in the direction of the speaker. I conclude that grey-cheeked mangabeys did not regularly rely on auditory cues of hornbills and chimpanzees as a sole indicator for the presence of fruit. However, it is possible that auditory cues are used in combination with a spatial memory of the previously observed fruiting states. In the next chapter I will investigate whether the mangabeys use a spatial memory to locate fruit and what aspects of the fruit source they remember.

* * *

CHAPTER 3

EVIDENCE FOR A SPATIAL MEMORY OF FRUITING STATES OF RAIN FOREST TREES IN WILD MANGABEYS

Results of this chapter are accepted in Animal Behaviour (Janmaat et al. 2006b).

Sooty mangabey eating *A. fragans* fruit

Grey-cheeked mangabey checking *F.sansibarica* fruit

Anthonota fragans fruit

Ficus sansibarica fruits

INTRODUCTION

"Primates able to remember the locations and phenological patterns of a wide variety of plant foods could move directly to such foods when and where available without wasting time and energy in random search" Milton (1981)

Rainforest primates with a frugivorous diet are promising candidates for investigations of ecological intelligence. Tropical rainforests are characterized by a high diversity of tree species with low densities and species-specific fruiting patterns (e.g. Myers 1980; Chapman et al. 1999). Individual trees tend to be widely dispersed throughout a group's home range and can fruit at different and irregular times throughout the year, adding further complexity (e.g. Milton 1977; 1981; Chapman et al. 1999;Vooren 1999). At the same time, most primates operate under a variety of constraints that lower foraging success: group living, large body-size, high travel costs, and specialised dietary requirements. One way of increasing foraging success in these circumstances could be to continuously monitor and remember fruiting states of individual trees within the home range and to anticipate subsequent states (Milton 1981; 1988). It has been argued, therefore, that frugivorous rain forest primates have evolved a specialised cognitive apparatus that can trace changes in fruit availability in time and space (Milton 1981, 1988; Boinski & Garber 2000; Janson 2000). Although plausible, little empirical work is currently available in support of these ideas. Evidence for spatial memory mainly comes from experimental studies with captive animals (e.g. rats, *Rattus norvegica*: Tolman 1948; chimpanzees, *Pan troglodytes*: Menzel 1973; sticklebacks, *Gasterosteus aculeatus*: Girvan & Braithwaite 1997; nutcrackers, *Nucifraga columbiana*: Balda & Kamil 1998). Far less is known about how spatial memory is used in the natural habitat, that is, in evolutionarily relevant circumstances. For a number of animal species, there is limited evidence that individuals possess knowledge about the location of food sources in their natural habitat (e.g. sunbirds, *Nectarinia spp.*: Gill & Wolf 1977; nutcrackers, *Nucifraga columbiana*: Van der Wall & Balda 1977; chimpanzees, *Pan troglodytes verus*: Boesch & Boesch 1984; hummingbirds, *Selasphorus rufus*: Armstrong et al. 1987; tamarins, *Saguinus spp.*: Garber 1989; macaques, *Macaca fuscata*: Menzel 1991).

Possibly the best evidence for the use of a spatial memory in the wild comes from experimental field studies on digger wasps (*Ammophila campestris*: Tinbergen 1972) honeybees (*Apis mellifera*: Dyer 1996) and capuchin monkeys (*Cebus apella nigritus*: Janson 1998). For non-human primates, the use of spatial memory may be the dominant strategy used to relocate experimentally introduced food sources (Garber & Paciulli 1997; Janson & Di Bitetti 1997; Bicca-Marques & Garber 2004). However, to our knowledge, there is still no good evidence that primates rely on spatial memory when searching for natural food sources in everyday foraging. In addition, little is known about what aspects of the natural food sources are remembered.

In the first part of this study I investigated whether two species of rain forest primates, sooty and grey-cheeked mangabeys, possess a general knowledge of the location of food sources in their home range. I pre-selected a number of food trees and observed the mangabeys' ranging behaviour in relation to these target trees. I analysed the monkeys' visiting patterns and approach speed to these trees as a function of their current fruiting state. Previous studies have shown that speed is a good measure of individuals' expectations about the resources to be found (Pochron 2001; Janson 1998; Sigg & Stolba 1981).

Our null hypothesis was that monkeys used sensory cues to find natural food sources, rather than relying on spatial memory. This hypothesis is plausible as well as parsimonious: indeed, previous studies have found it difficult to exclude the sensory cue hypothesis completely (e.g. Garber 1989). Visual cues are a particular problem: fruit trees often emerge from the rainforest canopy and become visible over considerable distances, even from the ground. Humans can easily spot fruits in an emergent tree from a distance of 150 meters if the view is unobstructed, suggesting that other primates have comparable abilities (K.R.L. Janmaat, unpublished data; Golla et al. 2004). To minimize the value of sensory cues I selected tree species that did not offer any obvious visual or olfactory signals that might have allowed the monkeys to detect fruiting state over long distances. I investigated when auditory cues were available using post-hoc analyses.

METHODS

Study species

The sooty mangabey group was studied in primary lowland rainforest of the Taï National Park in Ivory Coast (5°52'N, 7° 20'W), and consisted of 5-7 fully-grown males, 35 fully-grown females, and 53-54 not fully-grown, yet independently travelling individuals (F. Range unpublished data). Sooty mangabeys forage in a largely terrestrial way (McGraw 1996). The grey-cheeked mangabeys were studied in semi-logged moist evergreen forest of the Kibale National Park in Uganda (0°34'N, 30° 21'W, see Waser & Floody 1974 and Chapman et al. 1997 for an extended description of the study area). The group consisted of 4-10 fully-grown males, 7 fully-grown females, and 9-10 not fully-grown individuals. Grey-cheeked mangabeys are considered arboreal (Waser 1974); however, our study group regularly foraged on the ground (K.R.L. Janmaat, chapter 4). Both groups were extremely well habituated to human observers on foot, allowing observation as close as 2 m.

For sooty mangabeys, I investigated the study group's ranging behaviour in relation to *Anthonota fragans* trees (*Ceasalpiniaceae*), which accounted for 25.8% of their diet when fruiting (Bergmüller 1998). *Anthonota* fruits are 6-12 cm long capsules, with no smell that can be detected by humans beyond 20 cm. Sooty mangabeys eat the seeds inside the capsules at every stage of ripeness. In the peak of the fruiting season the mangabeys visited up to 20 different trees per day (K.R.L. Janmaat, unpublished data). The fruit was eaten by these monkeys even long after it had fallen to the ground, but the fruit appeared to be ignored by other frugivorous species, possibly because it contains bitter chemicals (Bergmüller 1998; Voorhoeve 1965). Fallen *Anthonota* fruits have a brown coloured velvety skin and are hard to spot in the leafy ground substrate, making them ideal for exploring the use of spatial memory.

For grey-cheeked mangabeys, I focused on the strangler fig *Ficus sansibarica* (*Moraceae*), a highly preferred food of grey-cheeked mangabeys (Waser 1974, 1977; Barrett 1995; Olupot 1999). The ripe fruit ranged in size from 1.4 to 5.1 cm. Individuals mainly ate ripe fruit but sometimes also the seeds of unripe fruit (K.R.L.

Janmaat, unpublished data). Individual trees can show marked differences in the amount of fruit produced during different fruiting periods, suggesting little relation between the size of a tree and its crop (Chapman et al. 1992). The fruit shows no obvious visual signs of ripeness, such as colour or size. Chimpanzees assess edibility by entering trees and squeezing individual fruits (Dominy N.J., Lucas P.W., Wrangham R.W. & Ramsden L. unpublished manuscript). Unripe figs are also attractive to the monkeys because they often contain weevil larvae, such as *Omophorus stomachosus* (Waser 1977). These unripe fruits produce no smell that humans detect from further than 20 cm. Mangabeys identify infested fruits by turning them, presumably to check for the distinctive small black spots made by the weevils. *Ficus sansibarica* trees tend to produce fruit in an asynchronous manner (Waser 1975), so I was able to test for the mangabeys' ability to distinguish two types of trees without fruit: those that had recently been depleted and those that had not yet grown any fruit, as well as to collect data throughout the year. In sum, the strangler fig was an ideal choice because of its complex fruiting pattern and because long-range visual cues (the size of the tree and the characteristics of its crop) were unlikely to allow monkeys to make judgements about the suitability of the tree as a food source.

Data collection

(a) Target trees

Both mangabey groups had a large home range (SM: 700-800 ha over ca. 32 months Fördingen 2001; Bergmüller 1989; F. Range, unpublished data; GCM: 623 ha over ca 38 months: Olupot 1999, G. Arlet, chapter 4), which enabled us to investigate the groups' behaviour towards a relatively large number of target trees. Prior to each observation period I located trees of the chosen tree species and then selected and labelled a number of trees with fruit. These trees were selected in such a way that a maximum number of trees could fit in the study area, under the condition that individual trees were separated by at least 300 m. (*Anthonota fragrans*) or 200 meters (*Ficus sansibarica*) (fig.1). I chose a smaller critical distance for *Ficus sansibarica* because the average group spread of grey-cheeked mangabeys was smaller than that of the sooty mangabeys (GCM: $\overline{X} \pm SD = 57.0m \pm 31.2$, Oluput et al.1997;

SM: $\overline{X}$ ± SD =102m ± 52, K.R.L. Janmaat, unpublished data). In regions without fruiting exemplars of the target species, I identified trees without fruit using the same distance criterion. This resulted in a roughly equal number of target trees with and without fruit. In Taï forest, I selected 33 *Anthonota fragrans* trees, 16 of which carried fruit at the beginning of the study period (natural tree density: 0.5 trees/ha, Bergmüller 1998). In Kibale forest, I selected 56 *Ficus sansibarica* trees, 27 of which carried fruit at the beginning of the study period (natural tree density: 1.7 trees/ha, Chapman et al. 1999).

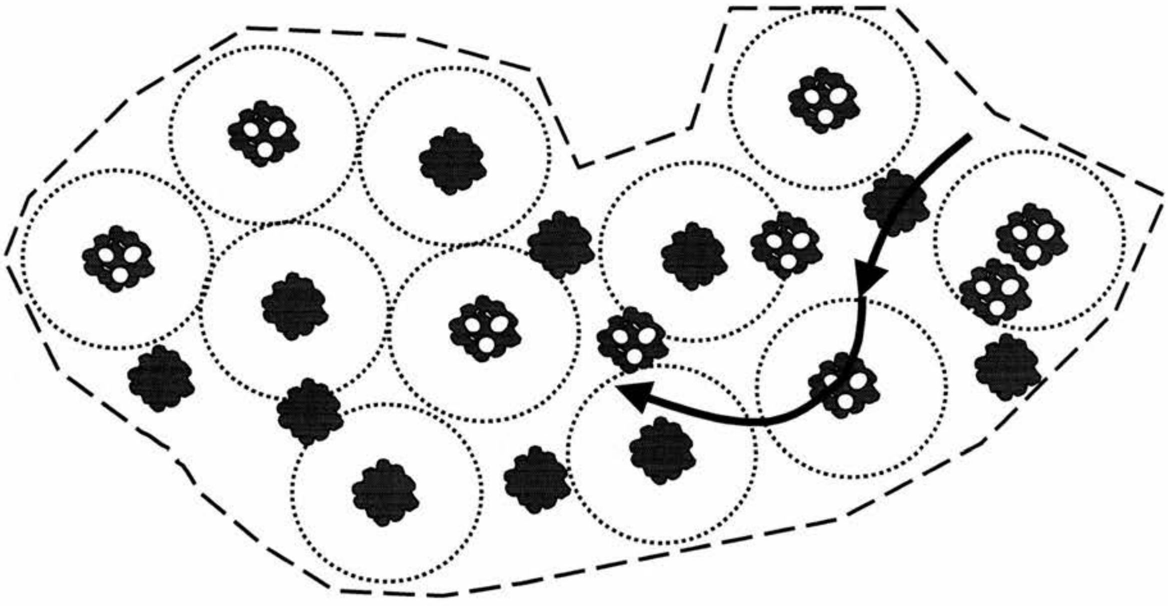


Fig. 1. Measuring visiting behaviour. The diagram illustrates an example of part of the study groups' daily route (arrows) amongst target trees, each surrounded by an imaginary 100/150m-radius circle (dotted line). Once the group entered the circle, one observer rushed to the tree to determine the fruiting state and whether the group came into sight and entered the tree. In this example, the group visited one tree with fruit and bypassed one without fruit.

For each tree, I measured the diameter at breast height (DBH) and the crown diameter, by averaging the N-S and E-W projection on the ground. I only included trees that had a DBH and crown diameter greater than the smallest tree ever observed carrying fruit during the study period. For *Ficus sansibarica* I analysed data only of target trees that had been observed to bear fruit before, during or after the observation period. In addition, I excluded target trees that appeared to have other food items inside, such as fruit from host trees or lianas. Some areas of the group's home range did not contain any *Ficus sansibarica* trees, so I also collected data on two closely related fig species *Ficus exasperata* (N=6) and *Ficus natalensis* (N=6). From the data collected on these trees, I only analysed observations of fruit-handling behaviour.

(b) Foraging behaviour

Each monkey group was followed for continuous periods of several months between 31 January 2002 and 30 April 2004. The sooty mangabey group was followed during two continuous periods of 30 days each. The grey-cheeked mangabey group was followed during three continuous periods of 50, 60 and 100 days. Two observers followed each group from the first movement in the morning to the final resting-place at dusk. Whenever a group entered a specified critical radius surrounding one of the target trees (SM: 150 meter; GCM: 100 meter; fig. 2) the primary observer stayed with the individual closest to the tree to measure approach speed, while the other observer rushed to the target tree to estimate the quantity of fruits and whether other frugivorous animals or group members were present. Fruit quantity was scored (1-4) according to the percentage of branches containing fruit: 0 (no fruit), 1 (1-25%), 2 (26-50%), 3 (51-75%) and 4 (76-100%). Additional notes were made on the presence of young fruit buds in *Ficus sansibarica.* The observer at the tree then measured (1) the time that the first individual came into sight and its age-sex class, (2) the time that the first individual entered the tree (for GCM and SM) or walked underneath it (for SM) and its age-sex class, (3) the number of individuals that entered and left the tree (for GCM and SM) or the area underneath it (for SM) and (4) whether or not individuals ate the fruit.

At the same time, the primary observer measured the speed at which the group moved towards the tree (in steps per minute; Fig. 2; the observer's step lengths were calibrated over a stretch of 500 m within the forest habitat with varying elevation levels). Speed refers to the component of movement towards the tree only (see legend of Fig. 1 for detailed explanation). To keep each other informed about the position of the tree in relation to the moving group, the two observers communicated via calling, producing click sounds or using a walkie-talkie. Data on speed was analysed post-hoc over different

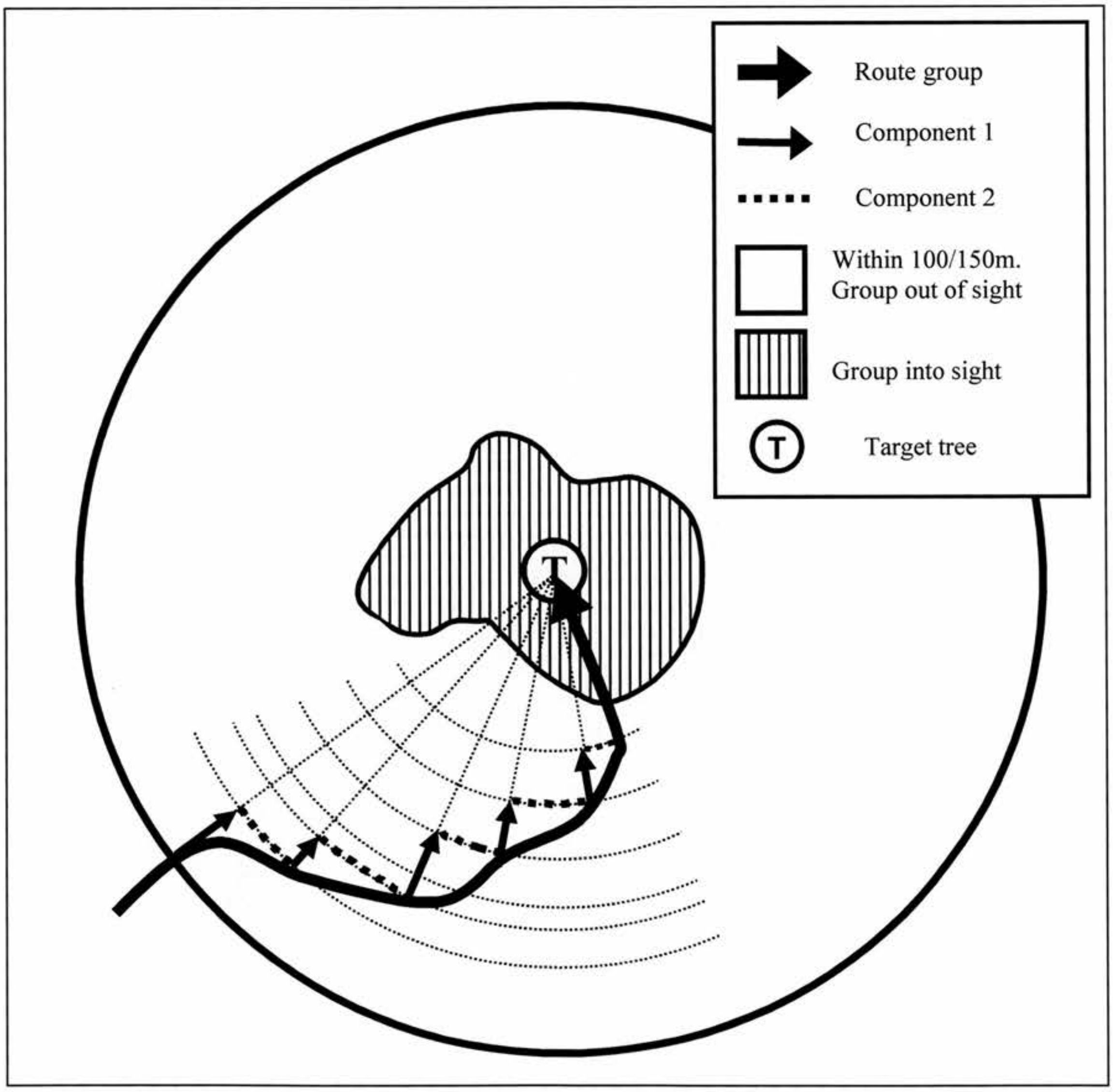


Fig. 2. Illustration of the method used to measure speed towards a target tree. The observer follows the group while staying within 5m distance of the individual that is closest to the target tree. Following took place in two components of direction, either along (a) component 1 (arrow) that is directed towards the tree trunk or (b) component 2 (thick dotted line), that is directed along the imaginary circle around the tree trunk. Speed was determined by counting steps per minute when walking in direction of the tree (component 1) only. The primary observer was updated on the direction of the tree trunk by the calling or clicking sounds produced by the secondary observer who was waiting under the tree trunk. The outer circle has a radius of 100 or 150 meters dependent on the species. The shaded area represents the area in which the group comes into sight of the observer who is waiting under the tree.

stretches, according to the tree species. For both tree species, we began to measure speed from about 150 to 50 m. from the trunk, depending on how quickly the observer was able to reach the front of the group. We stopped before the point where visual access to assessment cues might have been available. *Anthonota fragans* fruit was eaten in any ripening state, so the monkeys could assess a tree's suitability from the moment that it came into their sight. Therefore, we stopped measuring speed 5 m before the tree became visible to the primary observer. For *F. sansibarica* I am confident that the mangabeys could not visually assess the edibility of the fruits from outside the tree (see above), so I analysed speeds measured up until the first individual began to climb the trunk. To exclude the potential use of auditory cues to fruit availability, I only analysed approaches where no other group member or frugivorous species, such as black-and-white casqued hornbills, *Bycanistes subcylindricus*, were present before the arrival of the study group.

Once the group had entered a target tree, the primary observer recorded the total number of fruits eaten or rejected (by touch of hand or nose) by the first mangabey observed in the tree. In addition, the same observer recorded whenever the individual changed its location on fruit-bearing branches. When the view was obstructed observation switched to the next individual that came into sight, until 10 full minutes of data were collected. We determined whether the individuals ate ripe fruits, weevil larvae or seeds of unripe fruits, using direct observations and by inspecting dropped fruits. As soon as the first monkey moved out of sight, the primary observer continued to follow the group. As soon as all individuals had left the tree, and the main part of the group had left the predefined outer circle (fig. 1), the secondary observer returned to the group or moved directly to another target tree.

The ten-minute focal data were collected by two observers who were both experienced in the use of focal animal sampling (Altmann 1974). Interobserver tests were not conducted, because few places allowed two independent observers a similar view of a monkey high up in a fig tree, but I analysed an equal number of 10-minute observations per fig species for each observer.

Because the fruits of *F.sansibarica* can contain weevil larvae, the fruits are considered edible even when the fruits itself are not. Within this manuscript *edible fruits* will therefore refer to fruits that contain nutritious value to the mangabeys either in the form of ripe fruits or as weevil larvae or seeds.

(c) Assessing tree quality

Ideally, the quality of a tree is defined by the number of edible fruits. However, the edibility of *F. sansibarica* fruits cannot be determined by visual cues. Moreover, the density and developmental state of weevil larvae and fruit are likely to vary within the crown (Houle 2004), making assessments of tree quality by sampling fruits impractical. Hence, I instead defined tree quality (Q) as the cumulative number of monkeys inside the tree per minute, provided that at least one individual was feeding on figs (analogous to methods used by White & Wrangham 1988 and Garber 1989; Chapman et al. 1992 showed a similar behavioural variable to be correlated to the visual estimation of fruit quantity, for species with large fruits). Q-values varied between visits, as did the fruit quantity class. These data were collected by different observers (in Taï: N=2, in Kibale: N=5). Inter-observer tests showed a strong correlation for simultaneously collected data on both variables (Q: $0.758 < r_s < 0.964$, $P < 0.001$; fruit quantity: $0.830 < r_s < 0.928$, $P < 0.001$).

Statistical analyses

Ninety-three percent of all repeated approaches to trees were separated by at least one day, suggesting that repeated approaches should be treated as independent events. In some rare cases, the group approached a particular tree two or three times in the same day. I only included these visits in our analyses if the group had moved out of the outer circle between successive visits (see fig. 1). Most data were analysed with non-parametric Spearman correlation analyses and X^2 tests, which are sensitive to proportions and frequencies (Sokal & Rohlf 1995). Data on speed and number of fruits eaten or rejected were transformed into normal distributions using a log10 and square root function, allowing us to use independent sample t-tests and Pearson correlation analyses. All tests were two tailed. In each case I assessed evidence about specific hypotheses, so I did not adjust significance criteria with the Bonferroni method (Perneger 1998).

RESULTS

Can Mangabeys Distinguish between the Fruiting states of Trees?

Sooty mangabeys

During the two observation periods, the group came within the critical distance of 150 m of, 11 and 9 *Anthonota fragans* trees with fruit, and 14 and 14 target trees without fruit, respectively. A total of 184 of such approaches were observed. Both observation periods were pooled for analysis.

I found a significant association between the frequencies with which the group, once they approached within 150 m, continued into sight of a target tree and the probability of this tree carrying fruits ($X^2 = 6.26$, df = 1, $P < 0.05$, Phi = 0.184, $P < 0.05$). The same was true for the frequencies with which the group proceeded underneath or entered the tree ($X^2 = 20.6$, $P < 0.001$, df = 1 Phi = 0.333, $P < 0.001$). The proportion of times that the group came into sight or proceeded in or under the tree was higher for target trees with than for trees without fruits (fig 2). In addition, the group approached target trees with fruit significantly faster than they did trees without fruit (fig. 4: $N_{\text{trees with F}} = 8$, $N_{\text{trees without F}} = 12$, $t = -3.50$, df = 14.54, $P < 0.01$).

Grey-cheeked mangabeys

During the three observation periods, the group came within a the critical distance of 100 m of a total of 11, 20 and 28 *Ficus sansibarica* trees with fruit, and 20, 24 and 31 target trees without fruit, respectively. A total of 577 of such approaches were observed. Data from the three observation periods were pooled for analysis.

I found a significant association between the frequency with which the group, once within 100 meter, continued into sight of a target tree and the probability of this tree carrying fruit ($X^2 = 42.11$, $P < 0.001$, df = 1, Phi = 0.270, $P < 0.001$). The same was true for the frequencies with which the group proceeded and climbed the tree, once they had come into sight of it ($X^2 = 71.10$, $P < 0.001$, df = 1, Phi = 0.351, $P < 0.001$). The proportion of times that the group came into sight or entered the tree is higher for target trees with than for target trees without fruit (fig 3). In addition, the group approached target trees with fruit significantly faster than trees without fruit (fig 4. $N_{\text{trees with F}} = 34$, $N_{\text{trees without F}} = 27$, $t = -3.05$, df = 93.63, $P < 0.01$).

Do Mangabeys rely on Visual Cues or Memory?

The findings presented so far indicate that both groups distinguished between trees that did and did not carry fruit. In order to assess whether this could be a result of mangabeys' relying on visual cues, I conducted the following analyses.

Visiting pattern of trees with empty crown

Sooty mangabeys

During the observation periods, 12 *Anthonota fragans* trees had empty crowns (no fruit or flowers) but a large number of fruits were still available on the ground, thus, no cues were available to distant visual inspection. I used this subset of target trees, to investigate whether the visiting pattern shown above resulted from distant inspection, conducting the same series of analyses. I found a significant association between the frequencies with which the group, once they approached within 150 m, continued into sight of a target tree and the probability of this target tree having fallen fruit ($X^2 = 10.87$, $P < 0.001$, df = 1, Phi = 0.295, $P < 0.01$). The same was true for the frequencies with which the group proceeded underneath or entered the tree ($X^2 = 10.87$, $P < 0.001$, df = 1, Phi = 0.295, $P < 0.01$). The proportion of times that the group came into sight or proceeded in or under the tree was higher for target trees with fruit on the ground than for trees without fruit. (($N_{\text{trees with fruit}} = 4, 9$, $N_{\text{trees without}} = 14,14$: into sight or entered respectively, fig. 5). These results do not differ from those for all *Anthonota* trees, suggesting that distant inspection did not influence the monkeys' behaviour.

Grey-cheeked mangabeys

Unlike *Anthonta* fruits, *Ficus* fruit is consumed only when it is on the tree. Fruits hanging in a tree are much easier to spot than fruits on the ground, especially by the more arboreal grey-cheeked mangabeys. To investigate whether the grey-cheeked

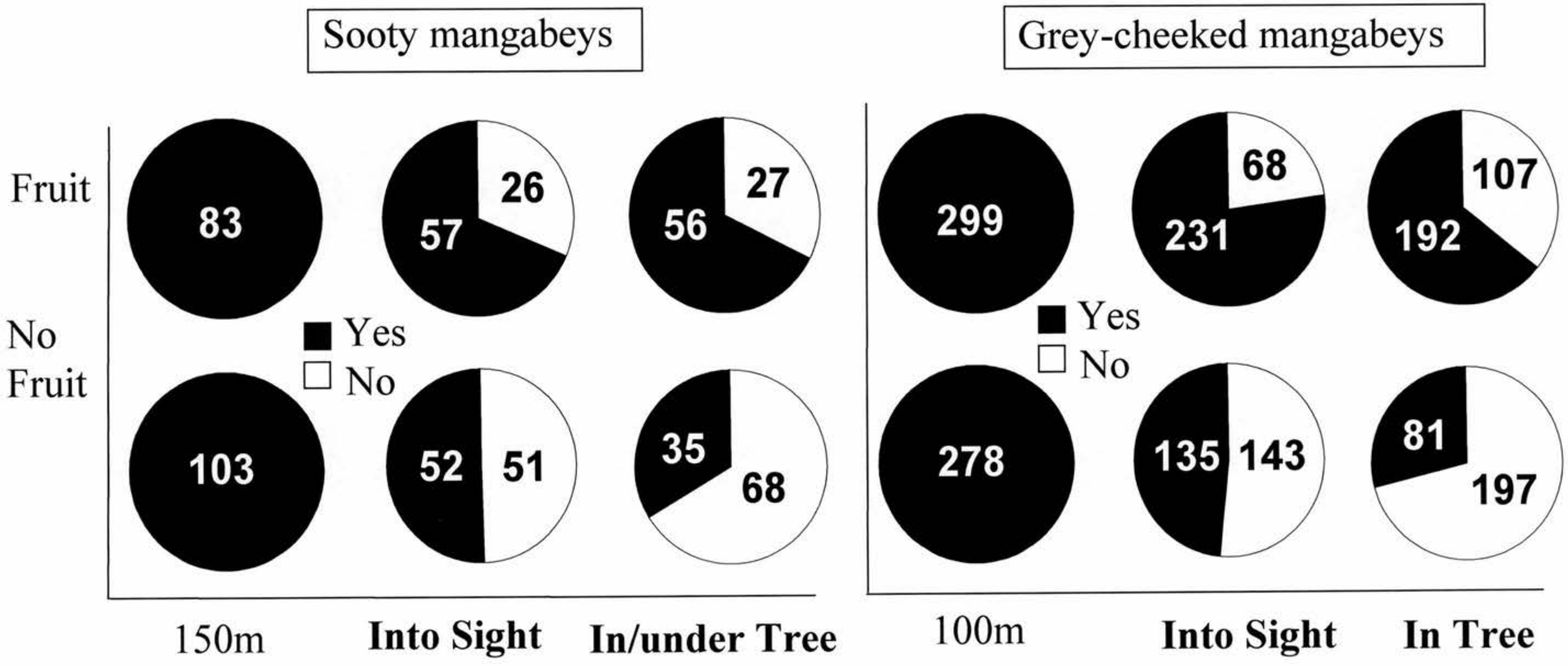


Figure 3. Left: Ranging behaviour of a group of sooty mangabeys towards target trees of Anthonota fragans with and without fruits. Each circle represents the proportion of time that the group 1) approached the trees within 150 m distance (150), 2) was visually detected from under the tree (In Sight) and 3) entered or passed under the crown of the tree (Tree). The white numerals in black segments: the number of times that the group entered the 150 meter circle came in sight and entered or passed under the crown of the tree. The black numerals in white segments: the number of times that the group did not come in sight and entered or passed under the crown of the tree.

Right: Ranging behaviour of a group of grey-cheeked mangabeys towards target trees of *Ficus sansibarica* with and without fruits. Each circle represents the proportion of times that the group 1) approached the trees within 100 m distance (100), 2) was visually detected from under the tree (In Sight) and 3) entered the tree (In Tree). The white numerals in black segments: the number of times that the group entered the 100 meter circle, came in sight and entered the tree. The black numerals in white segments : number of times that the group did not come in sight or entered the tree.

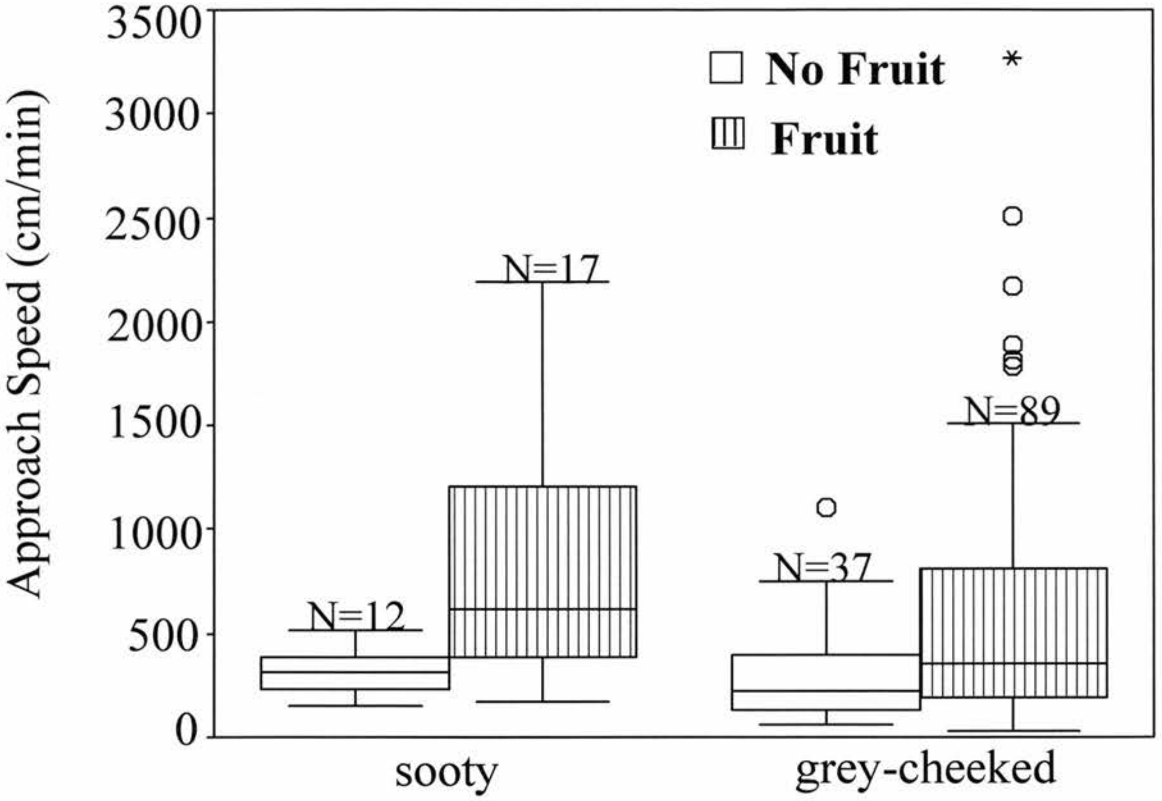


Fig. 4. Speed of approach to trees with and without fruits. For both mangabey groups, bars represent the median speeds, while the top and bottom of the boxes represent the 75 and 25 percentiles. The highest and lowest whiskers represent the highest and smallest values which are not outliers. Circles and stars represent outliers and extreme values.

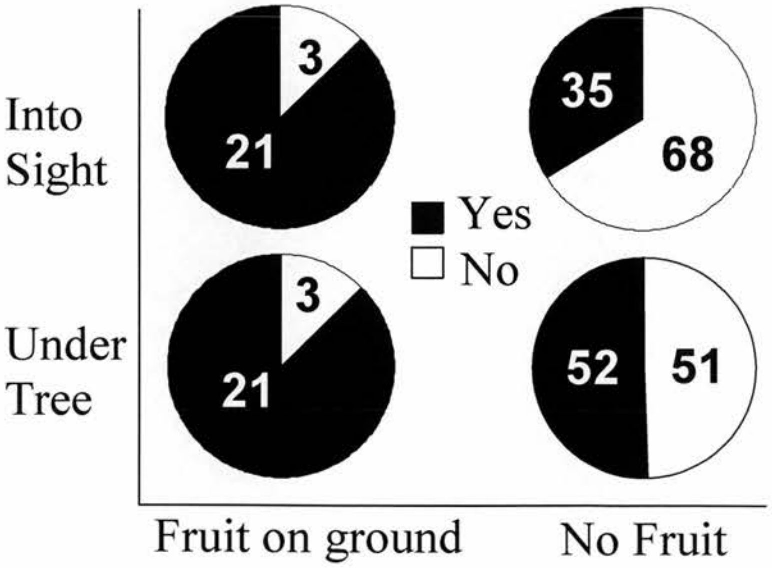


Fig. 5. Ranging behaviour of sooty mangabeys towards target trees with fruits on the ground and trees without fruits. Each circle represents the proportion of times that the group came into sight of, or entered the area under the target trees, once they approached within 150 m of the target tree. White numerals in black segments: number of times the group came in sight or entered the area under the tree. Black numerals in white segments: number of times that the group did not come in sight or under the tree.

mangabeys relied on distant visual cues to distinguish between potential food trees, I analysed their behaviour towards target trees that carried no fruit. I compared the monkey's behaviour towards two types of trees that were alike in not carrying fruit or fruit buds, but were different because of their potential to grow new fruits: depleted trees and trees that had not had fruit within the observation period. I predicted that mangabeys would regularly check empty trees that had had no fruit yet, but to avoid empty trees depleted during the observation period.

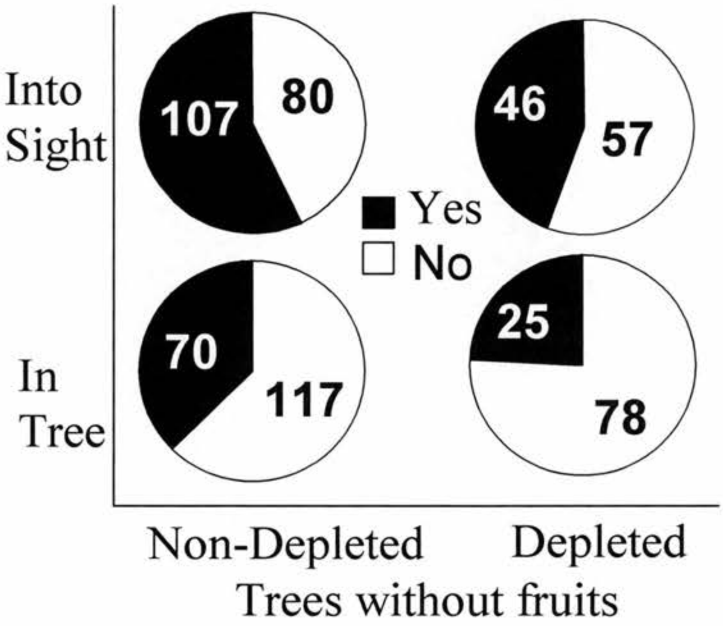


Fig. 6. Ranging behaviour of grey-cheeked mangabeys towards depleted and non-depleted trees. White numerals in black segments: number of times that the group entered trees of each type. Black numerals in white segments: number of times that the group did not enter trees of each type.

I found a significant association between the frequencies with which the group, once they approached within 100 m, continued to approach within sight of a tree and the probability of this tree being depleted ($X^2 = 4.20$, $P < 0.05$, df = 1, Phi = 0.120, P = 0.040). The same was true for the frequencies with which the group proceeded and entered both tree types ($X^2 = 5.22$, $P < 0.05$, df = 1, Phi = 0.135, P = 0.022). The proportion of times that the group came into sight or proceeded to enter the tree was lower for the depleted target trees (N = 25) than for the trees that did not have fruits within the observation period (N = 50, fig. 6). In addition, I found that the interval differed, between the times at which the group came into sight of both tree types, and the times at which they re-approached into sight after leaving the critical radius ($U = 501$, $N1 = 33$, $N2 = 45$, $P < 0.05$). The re-approach interval was longer for depleted target trees ($N = 15$) than for the trees that had not yet had fruit within the observation period yet ($N = 18$). Since the crowns of both tree types were empty the monkeys could not have relied on any visual (olfactory or auditory) cues to assess their difference.

Edibility judgements of figs.

To further investigate whether or not grey-cheeked mangabeys relied on visual or olfactory cues when approaching target trees with fruit I observed their fruit handling behaviour inside target trees of three different fig species. In two species, the figs undergo obvious colour changes during ripening (*F. exasperata* (Fe) and *F. natalensis* (Fn)), while in the third type colour change is unrelated to ripening state (*F. sansibarica*), (Dominy N. J., Lucas P. W., Wrangham R. W. and Ramsden L. unpublished manuscript; Dominy & Lucas 2004; Sumner & Mollon 2000).

In line with these differences fruits of *F. sansibarica* were regularly touched by hand or nose without being eaten or picked from the tree. In contrast, fruits of *F. natalensis* (Fn) and *F. exasperata* (Fe) were hardly ever rejected by touch. For the three species, touching of fruits was significantly related to species ($X^2 = 721.68$, $P < 0.001$, $df = 2$, F_n: $N = 6$; F_e: $N = 6$; and F_s: $N = 15$, fig. 7).

For *F. sansibarica* the number of fruits rejected by touch and the number of fruits eaten were significantly related ($r = 0.664$, $N = 32$, $P < 0.001$; log-transformed), suggesting that monkeys had to rely on tactile information to judge edibility of individual fruit, while visual information was potentially available for the other two fig species. A similar relation was found for *F. sansibarica* trees with only unripe fruits that were attractive because of the chance of finding weevil larvae and edible seeds, ($r = 0.569$, $N = 23$, $P < 0.01$, square root transformed). Since infested fruits can be recognised by small black spots, these results further suggest that close range visual inspection was required to assess the possibility of finding edible weevil larvae inside fruits.

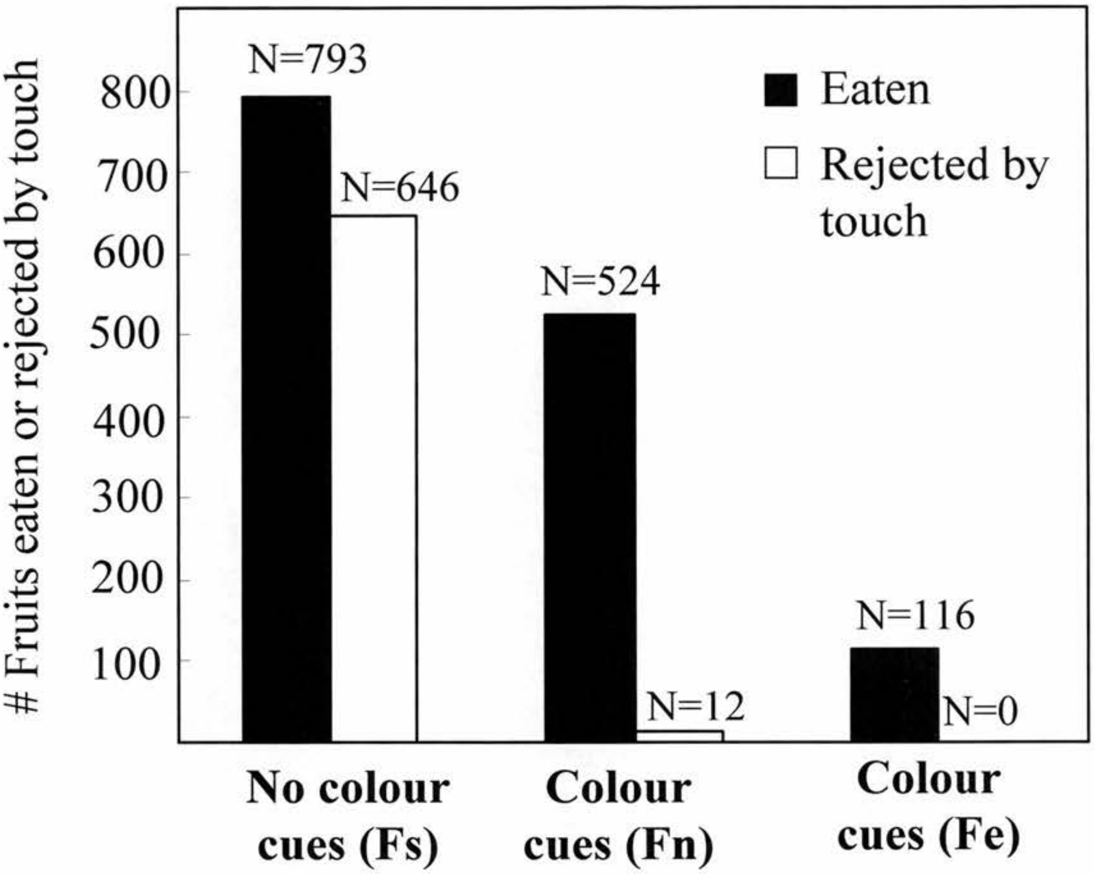


Fig. 7. Rejected and accepted fruits in three different fig species The number of fruits, that are touched and rejected within the first 10 observable minutes after the group entered *Ficus sansibarica* (Fs), *Ficus natalensis* (Fn) and *Ficus exasperata* (Fe) trees, in relation to the number of fruits that are eaten.

Can mangabeys remember previous feeding experiences?

Over one third of the *Ficus sansibarica* trees that carried fruit were not entered (Fig. 3). This result suggests that not all trees that carry fruits were valued similarly. To investigate whether mangabeys remembered differences in quality of trees encountered in the past, I conducted a series of additional analyses. I first examined the groups' revisiting behaviour towards *Ficus sansibarica* trees with fruits. I compared the quality values of current visits with the previous ones and found a number of patterns. First, previous quality values of target trees that were re-entered were significantly different to those not re-entered ($U = 4496$, $N_1 = 89$, $N_2 = 142$, $P <$

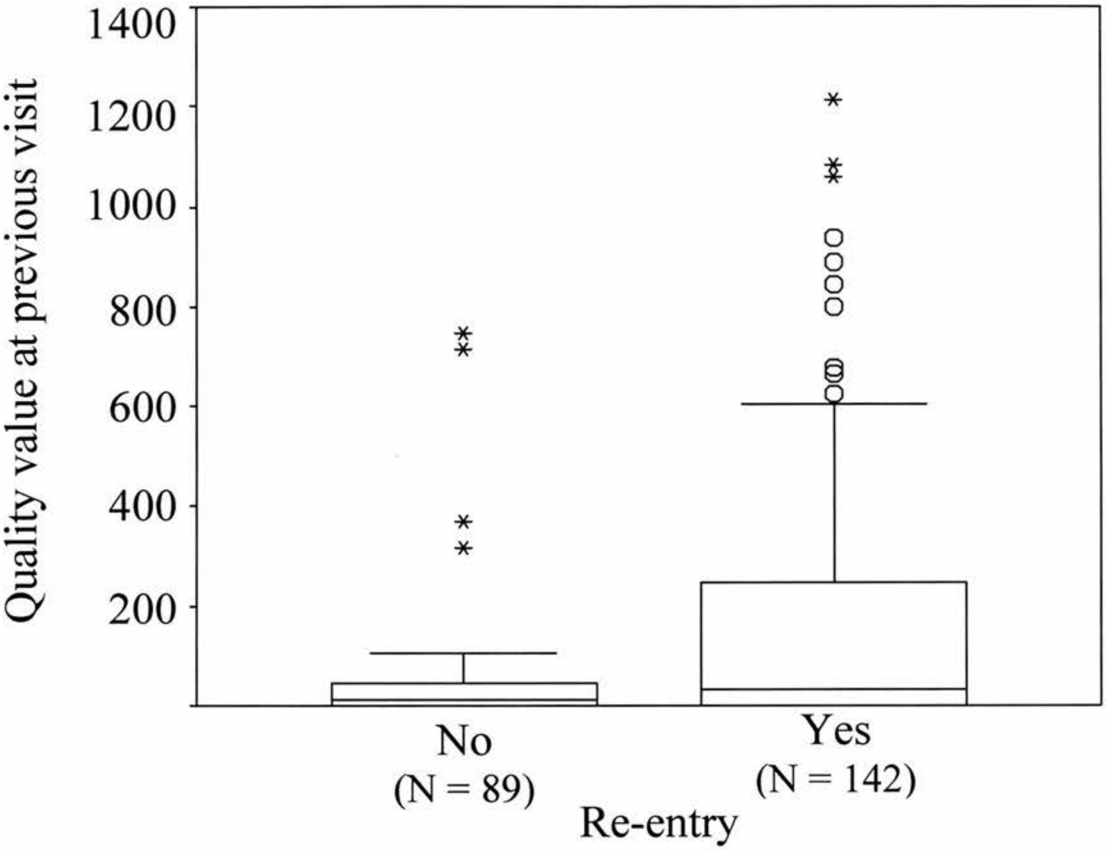


Fig. 8. Revisiting pattern of *Ficus sansibarica* trees with fruit with different past quality values. The right box represents the past quality values of trees that have been re-entered the subsequent time that the group came within 100 m. The left box represents the past quality values of the trees that have not been re-entered the subsequent time that the group came within 100 m. For both mangabey groups, bars represent the median past quality value, while the top and bottom of the boxes represent the 75 and 25 percentiles. The highest and lowest whiskers represent the highest and smallest values, which are not outliers. Circles and stars represent outliers and extreme values.

0.001, $N_{trees} = 32$, fig. 8), suggesting that the previous experience with a particular tree guided the monkeys' foraging behaviour. The same was true for target trees with unripe fruits at the current visit (which were attractive because of the chance of finding weevil larvae or seeds), demonstrating that olfactory cues could not have driven the monkeys' behaviour ($U = 1841$, $N_1 = 83$, $N_2 = 56$, $P < 0.05$, $N_{trees} = 27$).

However, because the quality values at previous and current visits were significantly related ($r = 0.433$, $N = 34$, $P < 0.01$; log-transformed) I used the speed data to determine the origin of this effect - whether the monkeys relied on either a "frozen memory" of the previous quality or a knowledge of the current quality, while approaching a target tree.

I analysed data for trees with unripe fruits (no odour cues) only. Approach speed (S; log-transformed) was significantly positively related to quality of the previous visit (Qp; $r = 0.302$, $N = 43$, $P < 0.05$, $N_{trees} = 17$). If current quality was kept constant (using partial rank correlation), then approach speed and previous quality were no longer significantly related (partial rank correlation coefficient: $r_{Qp\,S\,.\,Qc} = 0.063$, $N = 34$, $P = 0.715$). However, if previous quality was kept constant, approach speed remained significantly related to current quality ($r_{Qc\,S\,.\,Qp} = 0.5203$, $N = 34$, $P < 0.01$). These results suggest that the monkeys' behaviour was driven by knowledge of the current quality state of each target tree. To investigate whether this knowledge was assessed via detection of sensory cues emitted by the fruit-bearing trees, or whether it was computed from the monkeys' ability to combine knowledge of the past fruiting state with that on changes in larvae development or fruit depletion, I conducted the following analyses.

Approach speed was not correlated with the estimated quantity of unripe fruit in target trees ($r_s = 0.168$, $N = 80$, $P = 0.137$, $N_{trees} = 23$) nor was it correlated with the DBH or crown diameter of the target trees with unripe fruit ($r_s = 0.163$, $N = 80$, $P = 0.642$, $r_s = -0.057$, $N = 80$, $P = 0.731$, $N_{trees} = 23$), suggesting that the monkeys did not rely on long-distance visual cues, such as the number of fruits or the size of a target tree. Approach speed was unlikely to be related to differences in hunger level. The monkeys did not approach trees with fruit faster in the morning (7.00h to 10.00h) than during the rest of the day ($U = 847.0$, $N_1 = 28$, $N_2 = 74$, $P = 0.156$, $N_{trees} = 32$). Instead, speed was positively related to the average quality values of the target trees that carried unripe fruit ($r = 0.513$, $N = 23$, $P = 0.012$), suggesting that approach speed was related to the characteristics of the target trees. An analysis of a weighted regression, that takes the size of the sample from which each average value was calculated into account, further ascertains that 33% of the variation in average speed can be explained by average quality for my sample ($R^2 = 0.330$, $F_{(1,23)} = 10{,}349$, $P = 0.0041$).

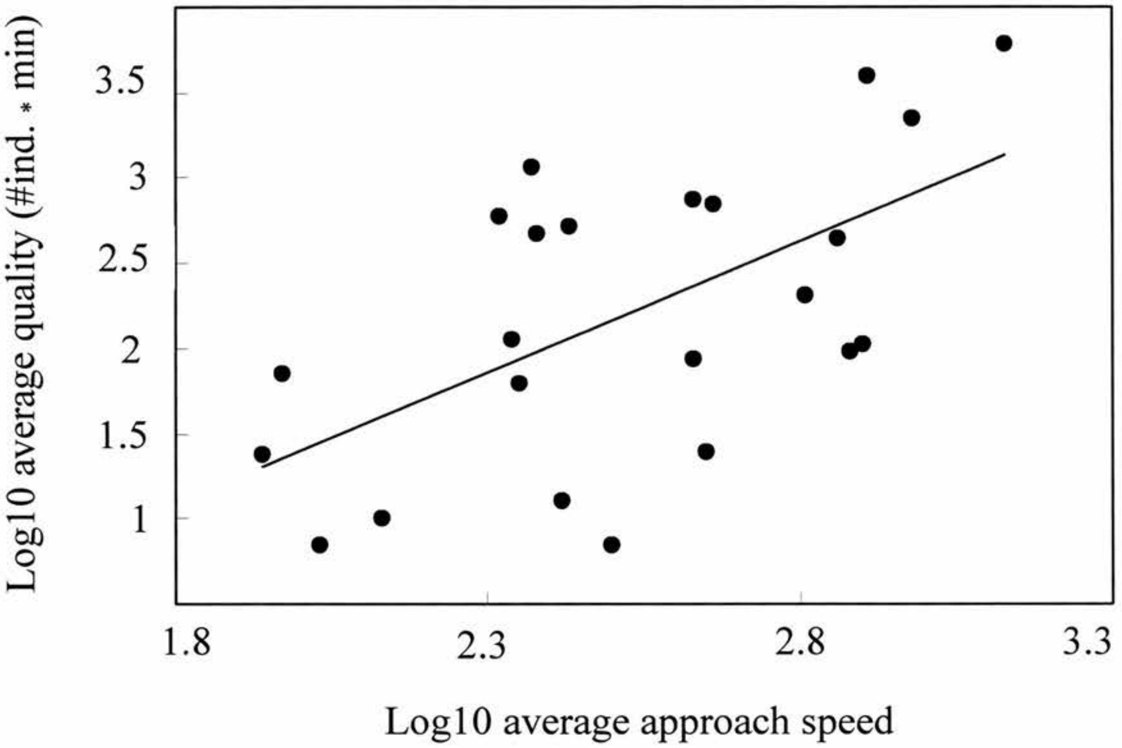


Figure 9. Approach speed to trees of different quality. The sum of quality values per tree is plotted in relation to the average of the total of speeds with which the grey-cheeked group travelled towards that tree (both data log10-transformed). Each dot represents the values of a target tree that carried unripe fruits. Values are based on an average number of three visits ($N_{min} = 1$, $N_{max} = 11$).

Who Knows Best?

To investigate whether group members differ in their ability to distinguish between trees with and without fruit, I recorded, when possible, the sex and age class of the first individual that arrived within sight and proceeded under or in the target trees. I analysed the results for three different age-sex classes (fully-grown males, fully-grown females and not fully-grown, yet independent travelling individuals).

In sooty mangabeys I found that the fully-grown males arrived first into sight and in or under the tree most often (respectively, 67% and 48%). However, there was no relation between the frequencies with which individuals of each age-sex class, once they approached within 150 m, arrived into sight, in or under the target tree and the probability of the target tree carrying fruits ($X^2 = 0.137$, N = 79, df = 2, P = 0.755,; $X^2 = 0.122$, N = 69, df = 2, P = 0.804,).

In grey-cheeked mangabeys, fully-grown males arrived first into sight and in the tree most often (53% and 57%). There was again no relation between the frequencies with which individuals of each age-sex class arrived into sight or in the target tree and the probability of the target tree carrying fruits ($X^2 = 3.801$, $P = 0.149$, $N = 257$, $df = 2$; $X^2 = 0.764$, $P = 0.682$, $N = 200$, $df = 2$).

These results suggest that within both groups neither fully-grown males and females nor fully-grown individuals and those that had not yet reached adult size, differed in their ability to distinguish between trees with and without fruit.

DISCUSSION

Both sooty and grey-cheeked mangabeys appear to possess knowledge about the fruiting state of various trees within their home range. Once the monkeys were within a critical distance from a target tree, beyond the average visual range in the forests, they were more likely to visit and approached faster if the tree carried fruit, suggesting that they knew something about fruiting state. However, in many cases, groups came into clear sight of target trees without fruit but then did not enter them (Fig. 3), indicating that the monkeys were able to spot the presence or absence of fruit from greater distances (e.g. emergent trees, local clearings). To address this concern, I carried out a series of further analyses that clearly showed that foraging patterns in these monkeys could not have been guided by visual assessment alone.

First, I found that sooty mangabeys distinguished between two types of *Anthonota* trees with empty crowns: those with fruit scattered on the ground and those with no fruit at all. It is extremely unlikely that the monkeys were able to discriminate the brown-coloured, inconspicuous fruits among the leafy substrate of the forest floor, from a distance that was further than the point at which the monkeys were visible to a human observer under the tree. However, target trees with fallen fruit were associated with relatively more visits and approaches to within sight. The assumption that the monkeys could not have seen the fruit is supported by a number of comparative studies indicating that visual acuity thresholds for humans are lower than for non-human primates, which have typically smaller eyes and hence smaller retinal image size (e.g. Cavonius & Robbins 1973; Merigan & Katz 1990; Golla et al. 2004). Since I excluded all cases in which other mangabeys, the only animal species that has been observed to eat *Anthonota* fruits (Bergmüller 1998), were present in or under the tree before the arrival of the group, it is also unlikely that the group relied on auditory cues to make the distinction between the two tree types. I cannot exclude the possibility that auditory cues were heard from other mangabey groups before the moment that the group came within 150 m of the target tree. It seems unlikely, however, that the group would be able to locate the target tree among the approximately 502 other trees with a DBH of greater than 30 cm within the 150-m circle (Vooren 1999), just by remembering the direction of an intermittent auditory cue that was heard from a distance of more than 150 m. Moreover, in only 3% of the cases other mangabeys were present under or in the tree when the group had entered the 150-m circle, (these approaches were not analysed), strongly suggesting that the use of auditory cues cannot explain the observed behaviour either. I cannot exclude the possibility that the group used the clicking and calling sounds made by the observers to locate the tree. However, this communication was done at both tree types, so it does not explain why the group went more often to target trees with fallen fruits than towards those without. Since non-human primates and humans are known to fall within the same range of olfactory performance with regard to sensitivity to isoamyl acetate, the major component in a large variety of fruit odours, (Laska & Freyer 1997; Laska et al. 1999; 2000; 2003), I also believe it to be unlikely that the mangabeys were able to smell the fruit. Humans could not detect the fruit's odour from further than 20 cm, so mangabeys were unlikely to have done so from further than the point at which the first individual came into sight of the tree. I conclude that the most likely explanation of the observed behaviour is that the sooty mangabeys remembered the fruiting state of the target trees and used this memory to relocate them.

Second, grey-cheeked mangabeys behaved differently towards trees that had been depleted recently, than to trees that had lacked fruit for longer periods and thus had more potential to carry new fruit. When grey-cheeked mangabeys came within 100 m of a tree without fruit, the proportion of times that they approached into sight and entered a tree was lower for recently depleted target trees than for trees that had not produced fruits within the study period. In addition, I found that the interval between the times that the group came into sight and re-entered into sight was longer for the depleted target trees. Both tree types had an empty crown that showed no obvious differences in appearance. The depleted trees did not contain obvious signs of a fruiting history, such as hanging branches; fruit only grows on the trunk and heavy branches, nor did the trees show early signs of fruiting, such as fruit buds. Therefore, this pattern is best explained by the hypothesis that memories of previous visits guided the monkeys' visiting patterns.

Grey-cheeked mangabeys do use visual cues to assess edibility of fruits if these cues are available. With the two fig species (*F. exasperata* and *F. natalensis*), that show an obvious colour change during ripening, mangabeys seldom touched and discarded fruits. *F. sansibarica* on the other hand offers no colour cues for edibility, and monkeys determined the edibility using tactile cues.

One unexpected finding was that mangabeys did not enter about one third of fruit-bearing target trees. To investigate whether grey-cheeked mangabeys chose not to enter a particular tree because they remembered its low value from a previous visit, I first analysed the monkeys' revisiting behaviour. I found that revisited target trees had been valued higher at the previous visit than trees that were avoided. This was also true for target trees with unripe fruits that were attractive because of the weevil larvae or edible seeds. In addition, I found that the speed with which the group approached target trees with unripe fruits was significantly correlated with the quality values measured at the previous visit. These results initially suggested that the monkeys were able to remember differences in the quality experienced at previous visits. Yet, subsequent analyses showed that past quality and current quality values were related and that the above relationship may have been an effect of current quality values only. Results of partial correlation analyses revealed that this was indeed the case. No difference was found between the speed of approach measured early in the morning and later during the day, suggesting that the relation between speed and current quality value was not a function of differences in hunger. In addition, the relation between average quality values and average speed of approach indicates that speed was related to the value of individual trees and not simply to the level of hunger. The finding that the grey-cheeked mangabeys approached faster towards high-valued *F. sansibarica* trees is best explained by the hypothesis that individuals did not rely on a "frozen memory" of the past fruiting state but that instead they were somehow able to assess knowledge of the current fruiting state and anticipated what they were going to find inside the tree.

Although sensory cues are likely to play an important role in the mangabeys' foraging behaviour, it is unlikely that the mangabeys relied on sensory cues to anticipate the quality of the target trees with unripe fruits; to do so, they would have needed to detect the content of the fruits (hatched larvae or edible seeds) from before the point that the group entered the tree. Even if the characteristics of the black spots could reveal the developmental state of the weevils inside, observations of fruit handling indicated that close-range inspection would be necessary. Furthermore, I found no correlation between the simple quantity of fruits in a tree, or the size of a tree, and the speed with which the group approached it. Finally, it is unlikely that the monkeys could use olfactory cues to detect edible unripe fruits, because the unripe fruits produce almost no smell detectable to humans. I am confident that no obvious sensory cues were available, so I suggest that the monkeys anticipated the quality of a target tree by using their memory of the latest fruiting state in combination with knowledge of the rate of larvae development and/or fruit depletion (chapter 6; Janmaat et al. 2006a).

Even though I followed the groups continuously for long periods, the mangabeys might have used knowledge from visits that were undetected by the observers. In both mangabey species males sometimes leave the group temporarily (Waser & Floody 1974; Olupot 1999; Range 2005) and solitary males have been observed to feed in fig trees up to 500 m from their group (K.R.L. Janmaat, unpublished data). The finding that fully-grown males were often the first to arrive near or at target trees suggests that they might lead the group towards good-quality trees. However, male early arrival was not significantly related to the fruiting state of the tree, suggesting that this was a by-product of males' peripheral foraging behaviour. I found no evidence that the males had foreknowledge about the state or value of target trees gained on one of their solitary exploration trips.

Taken together, these results indicate that both species of mangabeys possess a fairly sophisticated spatial memory of fruit availability, providing the monkeys with information on the present and previous fruiting state and possibly its present quality. This memory seems to contain not only information about the condition of trees with fruit but also about differences between different types of empty trees. In addition, the results of the study suggest that the mangabeys used their memory in combination with visual cues, if these were available.

One particular anecdote further supports the hypothesis that mangabeys use memory to find fruit. After one of the best quality target trees had been depleted, I were surprised to observe that the sooty mangabeys nevertheless approached the tree at high speed. I discovered that the monkeys did not approach the tree itself, but a small pool of water next to it, which formed part of a small river. As the dry season progressed, the water level in the river continued to drop and fruit that had fallen into the pool gradually became accessible to the mangabeys. After arriving at the site, the monkeys immediately began to reach into the pool and retrieve the sunken fruit, suggesting they had remembered the site for a significant time period; comparable to the ability of food caching birds to remember specific locations over long periods of time (e.g. Balda et al. 1987; Clayton et al. 1998).

Several studies have shown that primates will travel to more distant resources if the quality of the distant source is sufficiently high (Garber 1989; Boesch & Boesch 1984; Janson 2000; Cunningham 2003). Our findings raise the possibility that mangabeys may make finer categorizations of fruit trees on the basis of their <u>future</u> potential. First grey-cheeked mangabeys seem to be able to anticipate the quality value of a target tree without the use of obvious sensory cues. Second, they seem to be able to anticipate differences in fruiting potential. That grey-cheeked mangabeys visited depleted target trees less often than non-depleted ones might simply reflect avoidance of depleted trees. The results, however, are also consistent with the possibility that non-depleted trees were avoided less often because the mangabeys knew that these trees had more potential to grow new fruit than were the recently depleted ones. Approach speed may serve as a valuable variable to assess such forms of prospective behaviour. Each study group travelled significantly faster towards target trees with fruit than towards those without; in addition they travelled faster towards trees of higher overall quality. These results suggest that the monkeys approached faster if they expected to find food, and that approach speed was related to the quality of food that they expected to encounter. It will be of interest to further examine approach speeds of successive visits, ideally between the first and second times that the group eats in a particular fruiting tree or when the quality values have changed substantially. Such studies may identify whether monkeys understand the concepts of depletion, renewal and emergence rates of new fruits. Further investigations on the existence of such abilities and their distribution among frugivorous species should improve understanding of relevant selection pressures favouring intelligent behaviour.

SUMMARY CHAPTER 3

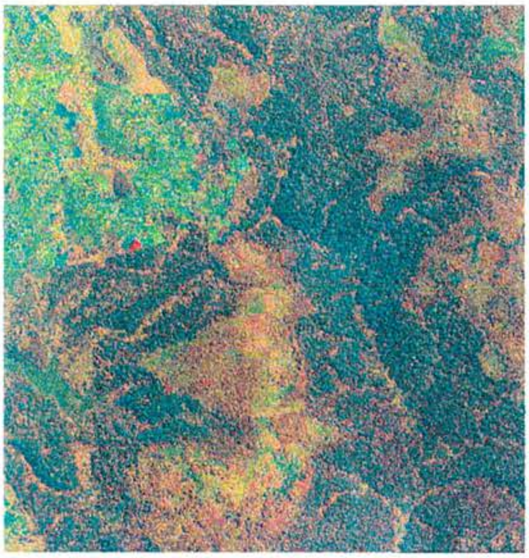
I investigated the ranging behaviour of two groups of wild mangabey monkeys (sooty mangabeys, *Cercocebus atys atys,* and grey-cheeked mangabeys, *Lophocebus albigena johnstoni*) relative to a number of pre-selected target trees within their home range. I observed the groups' visiting patterns and speed, when approaching within a critical distance of a target tree, as a function of the tree's fruiting state. For both groups, the likelihood of coming into sight or actually entering these trees was significantly higher if fruits were available. In addition, target trees with fruit were approached significantly faster than trees without fruits. Additional analyses showed that these behavioural differences were unlikely to be the result of cues available over long distances, auditory, visual or olfactory, suggesting that monkeys relied on spatial memory to (a) relocate fruit trees and (b) distinguish between trees that had and had not carried fruit in the immediate past. The results further indicated that the monkeys made a clear distinction between different types of fruit bearing target trees. To assess each tree's differences, I suggest that the monkeys use memory of previous feeding experience and have an ability to anticipate changes in fruit quality. I found no indication that individuals belonging to a particular age- or sex-class led the group towards trees with fruits more often than others. In the next chapter I investigate the advantages of spatial memories of the locations of fruit trees and other relevant aspects of a monkey's home range and the consequences of being in lack of such memories.

* * *

CHAPTER 4

MOVING INTO LESS FAMILIAR AREAS

ADVANTAGES OF LONG TERM SPATIAL MEMORY IN RELATION TO FORAGING EFFICIENCY AND PREDATION RISK IN WILD GREY-CHEEKED MANGABEYS.



INTRODUCTION

Ranging patterns and home range shift

Lophocebus albigena groups in the Kibale forest, western Uganda, exhibit considerable home range overlap, showing no signs of site-specific or territorial defence (Waser 1974; 1976; 1977). Home range boundaries seem flexible. Intergroup separation is maintained by mutual, vocalisation-mediated avoidance, yet avoidance only occurs at relative short distances (< 200 m) and is no greater near the edge of the home range (Waser 1974). Like in many other primary consumers, food abundance is a major factor influencing the mangabeys' ranging patterns (e.g. Waser 1975; Gautier-Hion 1981; Chapman 1988; Barton et al. 1992; van Schaik et al. 1993; Olupot et al. 1997). However, long term analyses of the mangabeys' ranging locations within the home range suggest little long-term attachment to particular feeding areas. The monkeys are described to reflect a continuous and erratically shifting over several square kilometres of forest, while following evanescent food super abundances. (Waser 1974; 1975; 1977; Barrett 1995). In fact, Waser (1974) suggests that the groups' home range location was mainly limited by the presence of neighbouring groups. In theory, this could mean that groups can shift their home range to any given location within the habitat, as long as they would remain "equidistant" to neighbouring groups. This type of nomadic ranging would be an odd behaviour that loses the cardinal reason claimed to underlie hefted ranging by mammals, the advantage of accumulated local knowledge of the habitat. However, during this study, indications for such nomadic behaviour were observed when our main study group shifted their range to an area in which they had not been located within 6 years of discontinuous, yet regular, observations. The shift to this new area created a unique opportunity to investigate the potential advantages or costs of range shifts in relation to the loss of long term information on potential feeding sites, sleeping sites and efficient travel and foraging routes.

The consequences of lacking spatial memories

Feeding sites

The grey-cheeked mangabeys' food supply is characterised by large, temporary concentrations of food, widely separated, relatively rare trees, highly variable and seemingly unpredictable times of fruiting (Waser 1974). While dealing with these aspects of food supply mangabeys face a continual problem of how to locate food. In models of foraging strategy, an efficient strategy is expected to maximize the net return of energy from time or energy spent in foraging (Schoener 1971). Unlike many secondary consumers, grey-cheeked mangabeys do not have to pursue their food once it is located; on the other hand, they cannot use the "sit and wait" strategy on the chance that edible food will suddenly pass by. Grey-cheeked mangabeys, like all primates, must travel to locate their food. Since travel is energetically costly, they are expected to minimize the energy spent in travel to locate food (Milton 1980; Muruthi et al. 1991; Isbell et al. 1999; Steudel 2000). One strategy to minimise travel distances is to use a long-term spatial memory of the location of potential resources and efficient travel routes between them (e.g. Milton 1980; Garber & Hannon 1993; Barrett 1995). Primates have shown to use such memories of either artificial or natural food sources in a large number of studies (chimpanzees, *Pan troglodytes*: Menzel 1973; *Pan troglodytes verus*: Boesch & Boesch; tamarins, *Saguinus spp.*: Garber 1989; macaques, *Macaca fuscata*: Menzel 1991; capuchin monkeys, *Cebus apella nigritus*: Janson 1998; grey-cheeked mangabeys: Janmaat et al. 2006b; chapter 3). A lack of such memories, while travelling into less familiar areas, is therefore expected to involve costs, i.e. less food may be encountered and or longer distances may need to be travelled.

Sleeping sites

Apart from food there are several other aspects of the habitat that are expected to be important to primates and that are known to affect their ranging behaviour, such as the location of water holes (Sigg & Stolba 1981; Barton et al. 1992; Cunningham 2003) and sleeping sites (Barton et al. 1992; Crook & Aldrich-Blake 1968; Tenaza 1975). The location of good quality sleeping sites that are either save from predators or that have nearby feeding sites that are suitable for early morning foraging, are expected to be of particular importance to the grey-cheeked mangabeys. A lack of memories of such locations is expected to be costly, since it can force the group to travel longer distances in order to find them.

Forest floor locations

The grey-cheeked mangabeys perform a noticeable quieter way of locomotion that involves a higher percentage of quadrupedalism than most other sympatric monkey species, like the black and white colobus (*Colobus guereza*) and red colobus (*Piliocolobus badius*) (Aronsen 2004; Gebo & Chapman 2000). A previous study on the locomotive behaviour of grey-cheeked mangabeys in the Kibale forest showed that, (like in the red colobus monkeys), frequencies of "expensive" locomotion (leaping, bridging and climbing) were much higher than the "cheaper" locomotor mode of quadrupedalism (walking on branches or forest floor) in the primary than in the secondary or semi-logged forest (Gebo & Chapman 2000; Aronsen 2004). While combining this information with published data on lower lean body mass in the semi-logged forest (Olupot 2000), Aronsen suggested that quadrupedalism, which includes terrestrial locomotion, is used as a way to save energy expenditure. A lack of spatial memories of the location of areas or routes that are suitable for terrestrial travel, i.e. open forest floors with little ground vegetation, or terrestrial feeding and drinking sites, is therefore expected to be costly.

Aim of the study

The main aim of this study was to investigate the value of spatial memories of relevant locations within the home range. I used an unexpected shift in home range location into a less familiar area of one group of grey-cheeked mangabeys as a natural experiment to test the consequences of being in lack of such memories. I focussed on memories of the locations of food (in particular fruit), sleeping sites and areas suitable for terrestrial travel, foraging or drinking. I compared day journey lengths and exploration behaviour, distribution of sleeping sites and terrestrial behaviour within familiar and less familiar areas. In addition, I conducted detailed analyses on the fruit localisation success per distance travelling and the percentage of time spent resting and foraging of individual male group members within the respective areas. Mangabeys, though utilizing a wide variety of food types and species, tend to specialise on relatively few (Waser 1974; Barrett 1995). Among the species that account for large percentages of foraging time are several which are represented by small numbers of large, scattered trees, such as fig trees. Figs are highly preferred by the mangabeys and profitable to exploit in terms of energy gain (which is suggested to stem mainly from its larger size rather than any major difference in calorie density) (Barret 1995). They are thought to strongly influence the mangabeys ranging behaviour and possibly increase their day journey lengths (Waser 1974, Barett 1995). Another food item that is thought to influence the mangabeys ranging behaviour is animal matter (an average of 29% of scan feeding records Olupot 1998). Hladik (1975) suggest that for primates with similar diet composition (*Macaca*, *Cebus*, *Cercopithecus*, *Papio*) the availability of animal matter highly affects ranging behaviour. For the mangabeys the importance of insect foraging may be reflected in the low return rate to explored grids/areas (Waser 1974; Olupot et al. 1997) Additional analyses that focus on the foraging on fig fruits and animal matter in particular, will therefore be conducted. At the end of this chapter I briefly address the question why the group shifted their range and split in two and I will speculate about the underlying biological triggers.

METHODS

Study species

The group of grey-cheeked mangabeys was studied in Kanyawara study area in the semi-logged moist evergreen forest of the Kibale National Park in Uganda (0°34'N, 30° 21'W) (see Waser & Floody 1974; Chapman et al. 1997 for extended description of the study area). In the beginning of this study period the group consisted of 20-27 independently moving individuals; 8 cycling females, 4-10 adult males, 1 sub adult female, 3 juvenile females, 4 juvenile males, 1 unknown juvenile (that disappeared) and 0-2 infants. During the study the group split in two subgroups. Subgroup I consisted of 10 independently moving individuals; 4 cycling females, 3 adult males, 1 sub adult female, 1 juvenile male, 1 juvenile female and 1 infant. Subgroup II consisted of 12 independently moving individuals; 4 cycling females, 3 adult males, 3 juvenile males, 2 juvenile females. All individuals were well habituated to human observers on foot, allowing observation as close as 2 meters. All cycling females and a total of 9 males (including two resident males that were radio collared in 1997 (Olupot 1999)) could be identified. Grey-cheeked mangabeys are considered arboreal (Waser 1974); however, our study group(s) regularly foraged on the ground. The diet of the mangabeys within the Kanyawara study area consists of fruits (59% of feeding time), flowers and flower buds (4.2%), leaves and leaf buds (4.6), bark and pith (3.3) and invertebrates (28.9%), (Olupot 1998).

Data collection

The study was conducted from March 2003 until July 2005. The study group was followed for total of 462 days by me and R. Chancellor. On 314 days we collected its geographic location every half an hour for 10.5 hours per day (3,297 contact hours). Fixes of the spatial location were made using a 12XL Garmin G.P.S. in combination with a detailed map of the Kanyawara trail system (fig.1). During the remaining of the observation days, at least two or more group locations were collected per day. In these periods I followed male individuals. So group locations could only be determined when the males were in the centre of the group.

Range shift

Before the start of this study the study group (Butanzi) was studied intensively by an almost continuous follow up of alternating researchers for a total period of 6 years (W.Olupot (July 1997- Jan 2001; G. Arlet (February-June 2001); J. Lambert (June 2001-June 2002); R. Chancellor (July 2002 – September 2002)). Within this time period the group had never been observed south of the 0° 32' 42" (0.54500 decimal degrees) latitude (pers comm and unpublished data W. Olupot, G. Arlet, J. Rusoke (field assistant of Olupot, Arlet and Lambert) and R. Chancellor). Five and a half months after the start of this study (17 September 2003), the group crossed this latitude and continued to travel further south. Based on the observations of previous researchers I assumed that it was the first time that the group moved this far south, suggesting that they moved into unknown area. However, it is unlikely that the area was completely new to all group members. Since the start of my study the group had experienced an in and out-flux of unfamiliar males. These males may have travelled south of the 0° 32' 42" latitude earlier in time. I therefore defined the area south of this latitude as the *less familiar* area and the area north of it as *familiar* to the study group.

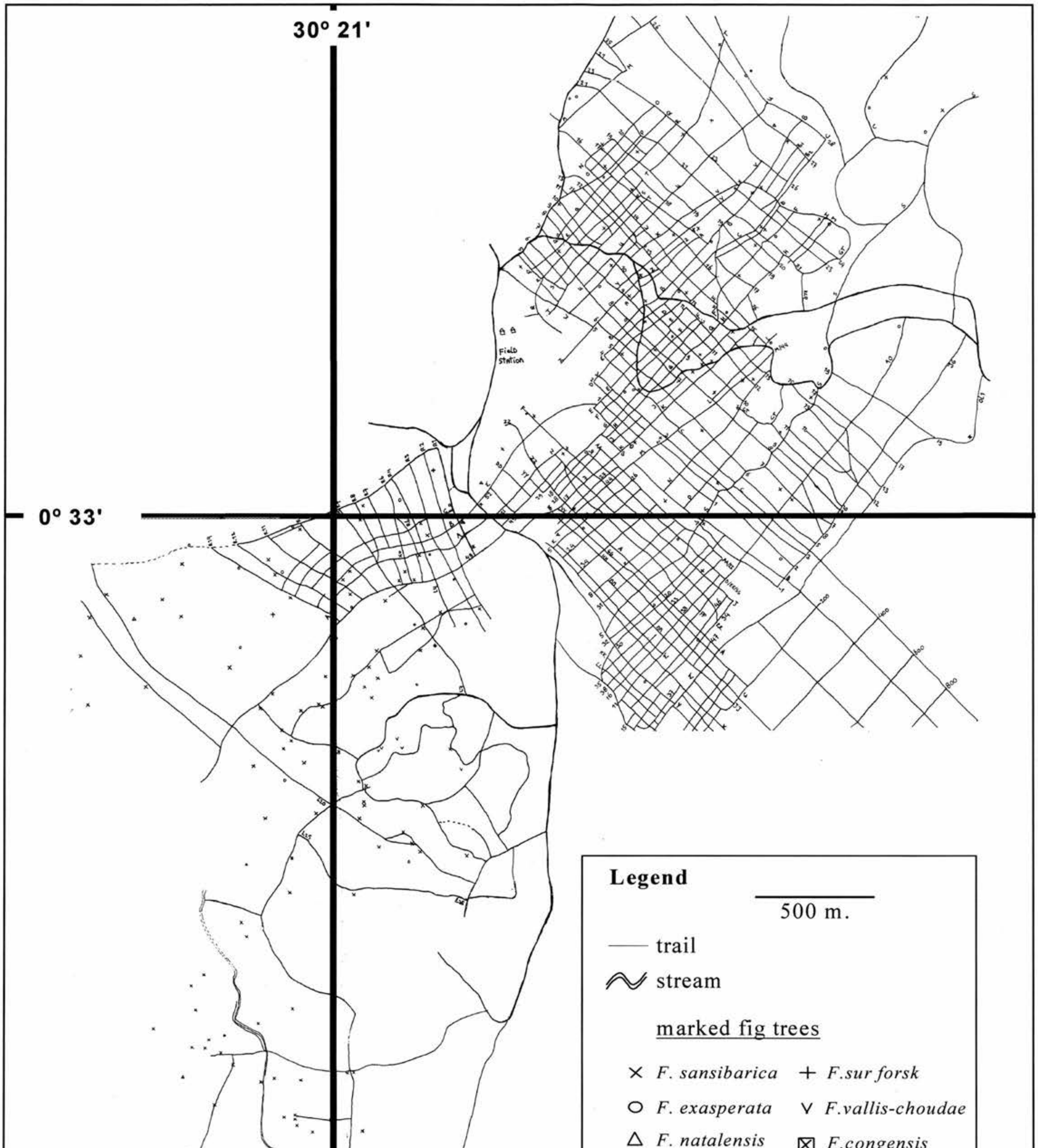


Fig. 1. Kanyawara trail system, Kibale National Park, Uganda

Group split

Seven months after the group had moved into less familiar area the group split in two permanent subgroups. The first split occurred on 15 April 2004, after which the group rejoined. The final split occurred on 23 April 2004, some days after one of the females gave birth and one of the resident males (Ma) fell ill. Both subgroups were not observed to meet until 23 February 2005. At this date both groups had been observed within the old ranging area and were involved in an aggressive fight that included aggressive attacks by the females. One adult male (Ma) and one juvenile male transferred from subgroup II to subgroup I. Both subgroups were never observed to rejoin within the study period.

Observations of the group

Four aspects of ranging behaviour - day journey length (DJL), exploration rates, sleeping site distribution and terrestrial behaviour - were investigated within four different data sets. The first and second data sets contained observations from the group before the split in either familiar or less familiar areas. The third and fourth data set contained observations from the two subgroups after the split, namely subgroup I, while travelling through familiar area, and subgroup II, while travelling through the less familiar area. The first two data sets were collected from 1 April 2003 until 14 April 2004. Data on the subgroups were collected within two different time periods, in which both groups were followed from 23 April until 24 July 2004 and 2 November 2004- 30 July 2005.

Observations of individual males

Data on the group's ranging data were collected almost continuously by each of our two research teams (Janmaat & Chancellor). In addition, within a shorter time period, data were collected on the foraging behaviour of individual males. I chose to work with males because they were known to be most independent to the behaviour of other group members in the study group (Waser & Floody 1974), but also for practical reasons of identification. In the first observation period before the group split I followed seven individually identifiable males between 8 Sept. 2003 and 29 Nov. 2003, while ranging in familiar and less familiar area for a total distance of 12,000 and 6,900 m, respectively. In the second period I followed four males in subgroup I and four males in subgroup II, between 4 May 2004 and 26 June 2004, for a total distance of 8,400m and 9,000 m, respectively. (One of these males had shifted from subgroup II to I halfway the observation period). Two of the males that were followed in the first observation period had left the group in the second observation period (Em and Ha). For the second period I therefore selected two new males (Pl and Sp). Data collection started by identifying and locating one of the selected males randomly. I tried to follow the male for a distance between 300 and 400m, before I continued to follow another randomly selected male. If I lost the male or could not find the particular male in the first place for a period of over one hour I switched to the first other selected male that came in sight. I chose this method because males tended to linger at the periphery or outside the group. Determined search for particular males would have been too time consuming. The activity of the focal male (e.g. travelling, resting and foraging) was recorded for every minute that the individual was visible (one-zero sampling (Martin & Bateson 1986)). Resting was defined as anything but moving, grooming, foraging or copulation. Foraging was defined as a measure of food consumption and manipulation, including time spent examining mossy branches and epiphytes for insects but not time spent chewing while engaged in activities other than ingestion. I recorded the distance travelled per minute (in steps) and the number of mangabey food trees that were entered and fed in. The observer's step lengths were calibrated over a stretch of 500 m within the forest habitat with varying elevation levels. I analysed the number of food trees per 100 m travelling for each trajectory of 300-400 m, that were separated in time by one day for each male (table 1).

Table 1. The total number of 300-400m trajectories for each male

Individuals		Bg	Ma	Sp	Me	Lb	Em	Ha	Pl	Mg
Period I	Familiar area (before split)	10	11	3	3	1	9	3		
	Less Familiar area (before split)	2	1	3	4	4	3	6		
Period II	Familiar area (Subgroup I)	9				4			7	8
	Less familiar area (Subgroup II)		9	10	6	4				

In order to keep track of the males and their activities we followed the males with two observers.

Transects parallel to the male's route

The day after each following day we walked a transect route parallel to and at 15 m distance of the male's route (see chapter 1). To minimize the effect of inter-observer variability, transects were walked by the same observers whom had followed the male at the previous day. (The distance towards the male route was estimated by sight, since this route was marked with brightly coloured ribbons). We mapped each tree of two selected species (*U. congensis* and *F. sansibarica*) whose trunk was within 5 m of the middle of the transect route and determined their fruiting state. In addition, we walked the male's travel route of the previous day and did the same measurements for the area within 5m of the male's travel route. For the second observation period we also determined which tree crowns of the three selected species overlapped with the male's route and the transect route.

Inter observer reliability

Data on the males was collected by two teams that consisted of one researcher and one local assistant each. Tree species determination was done by two local assistants who had been trained and active in the field of tree species determination within the study area for 9 and 4 years. Inter observer tests between the two local field assistants showed an overlap of 80-82% and 83-85% in the determination of fruiting state and the density of trees that belonged to 29 selected mangabey food species, within two 5 m wide and 1000m long transects, respectively. Intra observer tests (2 per assistant) were done by walking similar transects in opposite direction. The tests showed an overlap of 81-83% and 88-95% for determination of fruiting state and the density of 29 selected tree species, respectively over two transects of 1000m.

Data analyses

Day journey length (DJL) and exploration rates were analysed for full observation days only. Before the group split, a full day consisted of continuous half hour locations from 7:00h until 17:30h. After the split the second subgroup had moved that far away from camp that DJL's were calculated for continuous half hour fixes from 8:00h until 17:00h only. Observations of terrestrial behaviour were recorded within similar time periods yet from January 2004 till July 2004 only. DJL was calculated by summing the straight-line distances between the consecutive half-hour locations. Exploration rates were defined as the amount of new area added to the range per full day of observation. The area was defined using the minimum convex polygon technique in the Animal Movement extension in Arc View 3.3 (Altman & Altman 1970; Hooge & Eichenlaub 1997; Newton-Fisher 2003). (A minimum convex polygon is the smallest area polygon to encompass all of an animal's locations).

Statistical analyses

Data on day journey length were analysed using the independent sample t-test and Pearson correlation analyses. Other data were analysed using the non-parametric Mann Whitney U test and X^2 tests (Sokal & Rohlf 1995). All tests were two tailed. In each case I assessed evidence about specific hypotheses, so I did not adjust significance criteria using the Bonferroni method (Perneger 1998).

RESULTS

Overview group locations

Figure 2 shows all half-hour locations and the estimated home range of the study group before the split, before and after the shift to the less familiar area. Figure 3 shows a plot of cumulative home range size based on minimum convex polygons drawn around sightings, for the days before and the first days after the shift to the less familiar area. The cumulative range size seems to level off to approximately 350 ha. The cumulative range size increased again when the group moved into less familiar area, illustrating that the group was exploring a new area. Figure 4 shows all half-hour locations and the estimated home ranges of subgroup I and II for the entire observation period.

Do mangabeys travel further in less familiar areas?

Day journey length (DJL) of the study group in the period before the split, was significantly longer on the days spent in the less familiar area than on the days spent in the familiar area (t = 2.298, df = 195, P = 0.023, N_{old} = 133, N_{new} = 64; fig. 5a). Mean DJL was 1120m (sd = 394) and 1260m (sd = 401) in familiar and less familiar area, respectively. DJL was also significantly longer for subgroup II on the days spent in the less familiar area than for subgroup I on the days spent in the familiar area, (t = -2,566, df = 78, P = 0.012, N_{old} = 45, N_{new} = 35; fig. 5b) Mean DJL was 895 m (sd = 294) and 1088 m (sd = 378) for subgroup I and II, respectively.

Do mangabeys explore faster in less familiar places?

The cumulative home range size of the group calculated from a similar number of full days of observation (N = 64) is higher for days spent in the less familiar area (516 ha) than in the familiar area (313 ha). The cumulative range size of the subgroups calculated from a similar number of days (N = 35) of observation was also higher for subgroup II while travelling through less familiar area (421ha) than for subgroup I, while travelling through familiar area (200 ha.) as well.

When the group moved into areas that had not been explored yet within the previous days, they tended to explore more area per day when being in the less familiar area than in the familiar area (U= 205.0 N_{old} = 27, N_{new} = 22, P = 0.064; fig. 6). No such tendency was found for the exploration rate between subgroup I and II (U= 102.0 N_{old} = 15, N_{new} = 19, P = 0.167; fig. 6).

Do mangabeys use fewer sleeping sites in less familiar areas?

Figure 7a shows the spatial distribution of 64 randomly selected sleeping sites in the familiar and less familiar area before and right after the shift. The location of sleeping sites in less familiar area appears to be more clumped than in familiar area, due to the preference for one particular sleeping area (near a fruit patch of *Celtis durandii*) in the less familiar area, right after the shift. Figure 7b represents the spatial distribution of 54 randomly selected sleeping sites for subgroup I, while travelling in familiar area and subgroup II, while ranging in less familiar areas. The figure does not suggest that the distribution of sleeping sites was more clumped for subgroup II than for subgroup I.

Are mangabeys less terrestrial in less familiar areas?

Grey-cheeked mangabeys are reported as strictly arboreal monkeys that prefer to travel through the higher levels of the forest canopy (70 feet and above), (Chalmers 1968). Yet, in familiar area, our study group was observed on the ground in 72% of all observation days. Out of the total time in which individual males were observed 1.6 % was spent on the ground. This behavioural difference was possibly due to a higher level of habituation to human observers in my study compared to earlier studies (Campbell et al. 2005). The monkeys were seen on the ground while feeding (on fruits of *Blighia unijugata*, *Myrianta cloa*, *Strombosia scheffleri*, seeds of *Diospyros abyssinica*, ants, dirt, animal matter inside logs) or while drinking water or eating algae from ponds or creeks. However, the monkeys were also observed on the ground while travelling. This concerned terrestrial travel by all group members through logged areas as well as secondary or primary forest areas. The latter concerned travel on research trails (40 % of all observations) or through areas with little ground vegetation.

For the period before the split, I found that the number of days in which one or more mangabey individual(s) were observed on the ground was significantly associated with their familiarity to the area. Figure 8 shows that the proportion of days in which individual(s) were observed on the ground was higher in familiar than in less familiar areas ($X^2 = 31.58$, df = 1, $P < 0.001$, Phi = 0.599, $P < 0.001$; fig. 9a). A similar association was found for the days that subgroup I travelled in the familiar area and subgroup II travelled in the less familiar areas. ($X^2 = 3.820$, df = 1, $P = 0.05$, Phi = -0.249, $P = 0.05$; fig. 9b).

When I pooled the observations of individual males that were followed for different trajectories within both areas, I found similar results. In the period before the split, the percentage of time in which individual males were observed on the ground, was significantly higher in familiar than in the less familiar area ($U = 337.0$, $N_{old} = 23$, $N_{new} = 39$, $P = 0.008$). When travelling in the familiar area, the males of subgroup I also tended to spend more time on the ground than the males from subgroup II when travelling in less familiar areas ($U = 343.0$, $N_{old} = 29$, $N_{new} = 30$, $P= 0.061$).

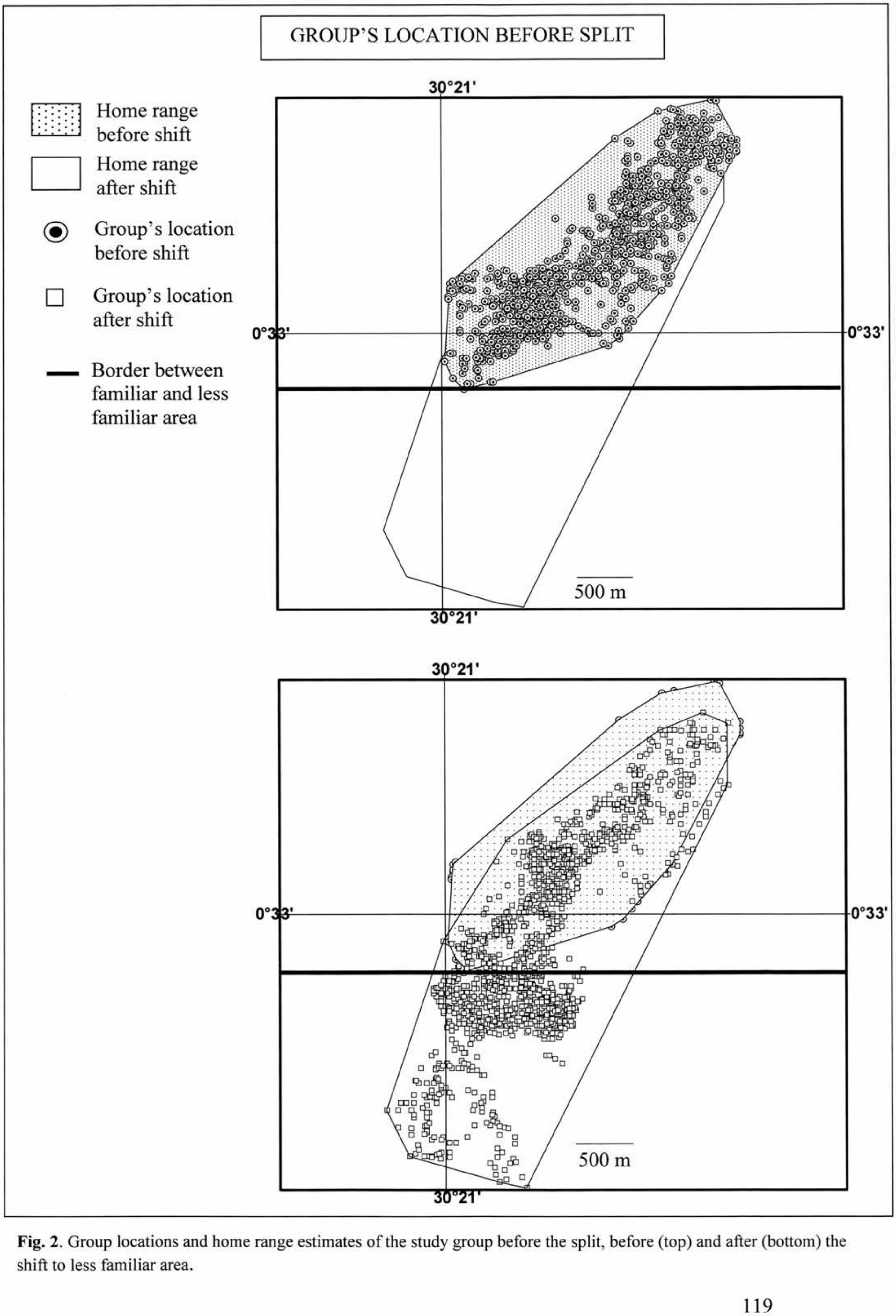


Fig. 2. Group locations and home range estimates of the study group before the split, before (top) and after (bottom) the shift to less familiar area.

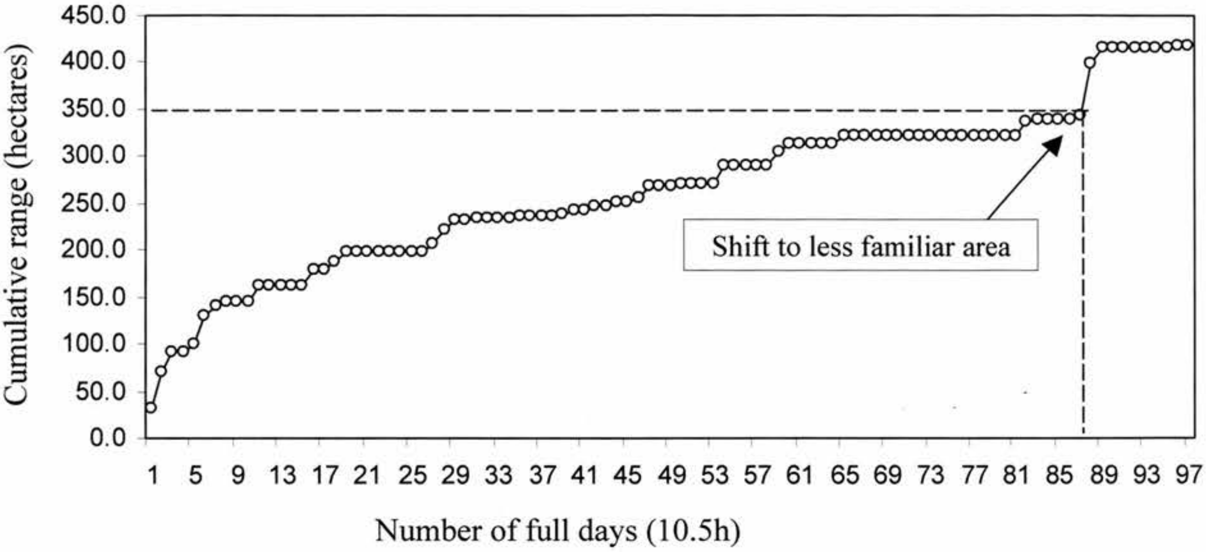


Fig. 3. The cumulative range size before and after the shift to the less familiar area plotted against the number of days of observation.

At the start of the data collection on terrestrial behaviour the group had already been ranging within the new less familiar area for some time, meaning that I was too late to follow the process of familiarisation. However, on the 26th of February the group moved substantially further south and past the latitude 0° 32' 24", which gave us a new opportunity to follow the process of habituation. Within this new area (south of 0° 32' 24") it was only 3.5 months later that the first individual had been observed on the ground. Within 4 months after this new shift southwards one or more individual(s) had been observed on the ground only 2 out of 38 observation days (5%). Between 4 and 11 months after this shift the percentage raised to 54% (7 out of 13 days). These results further indicate that terrestriality is related to the familiarity of the area.

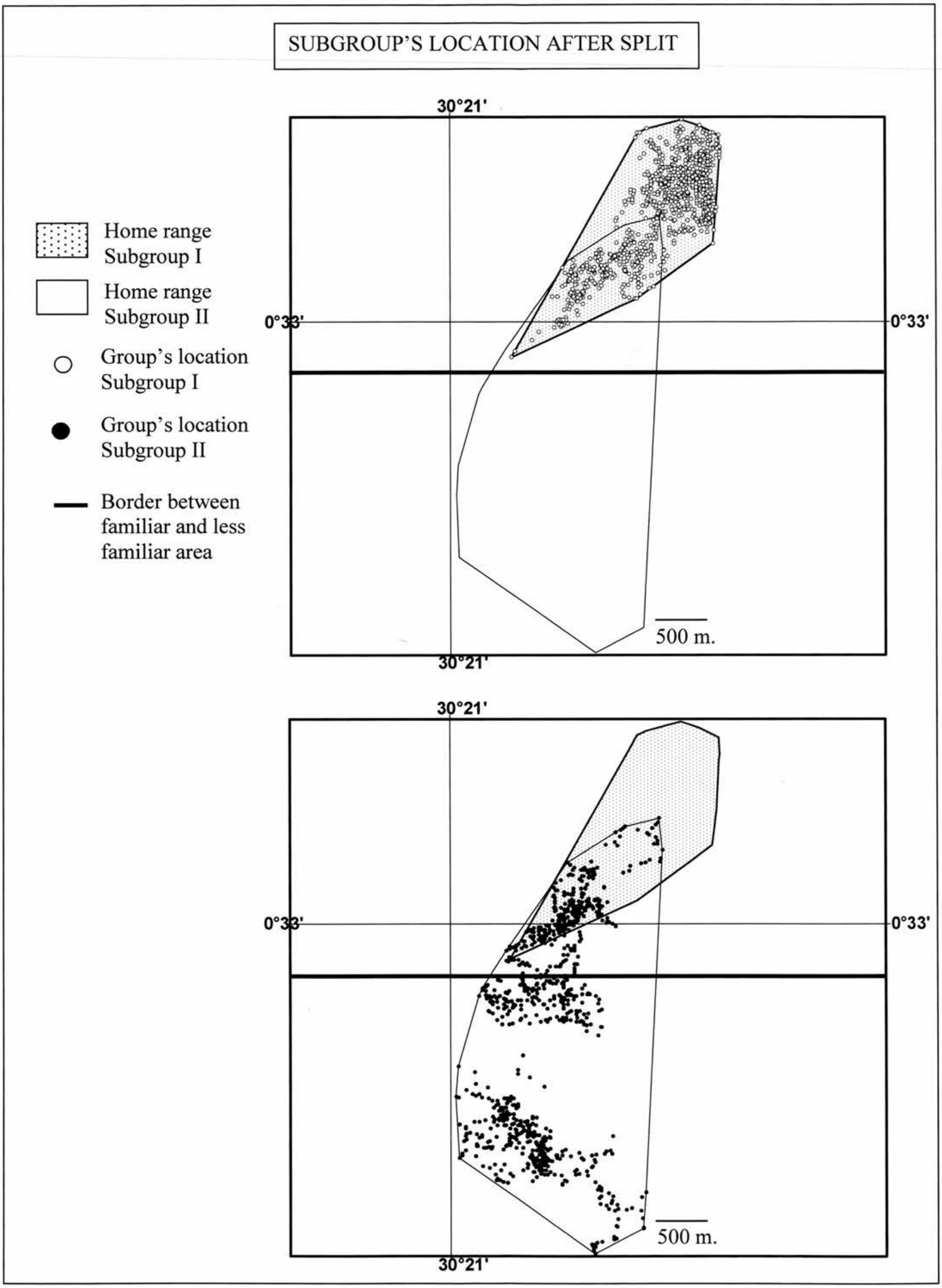


Fig. 4. Group locations and home range estimates of subgroup I (top) and subgroup II (bottom) after split

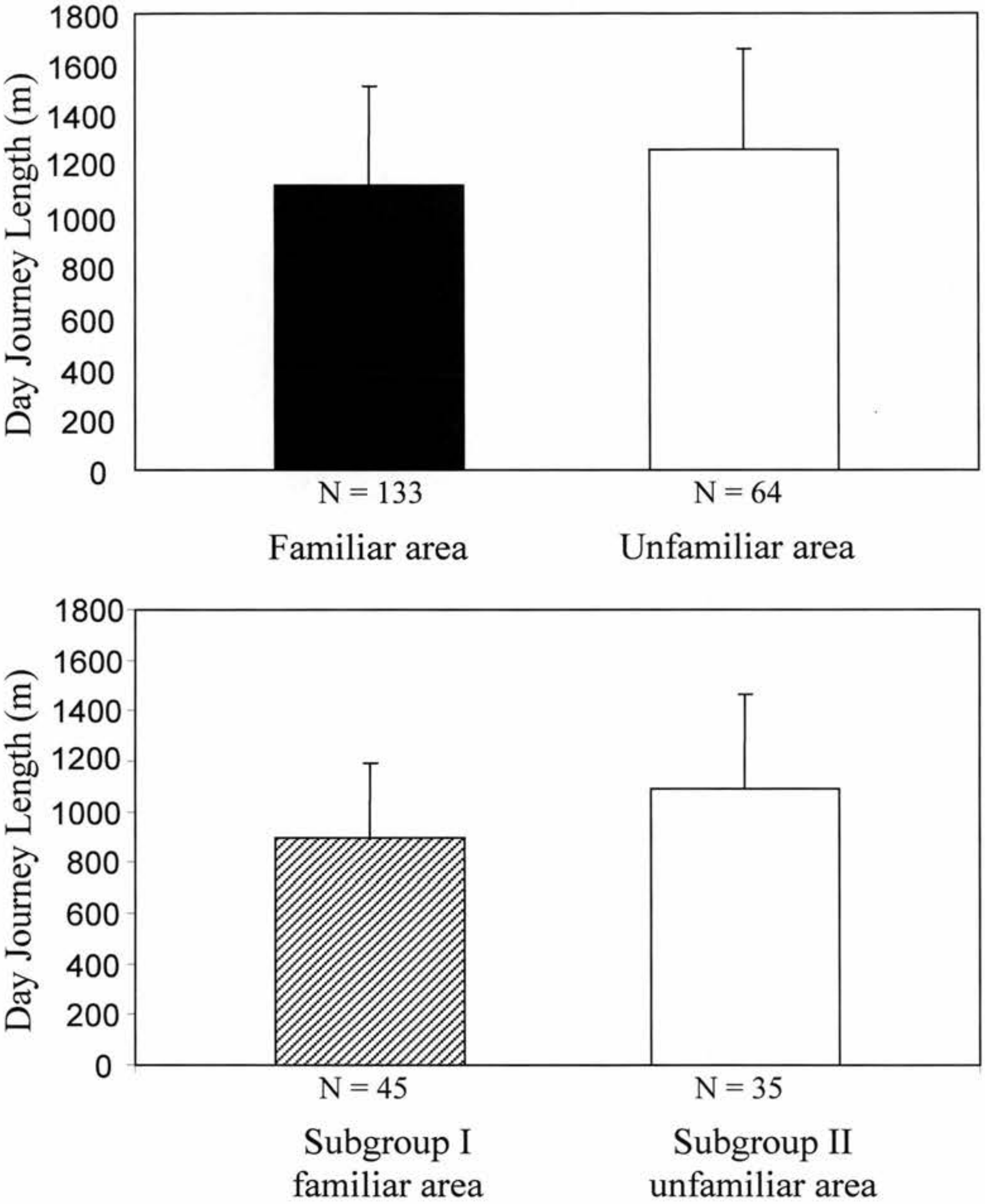


Fig. 5.Bars represent the mean day journey lengths (DJL) within familiar and less familiar areas. Error bars are standard errors. Top: DJL of the group before the split, when traveling in familiar versus less familiar area. Below: DJL of subgroup I, when traveling in familiar area and subgroup II, when traveling in less familiar area.

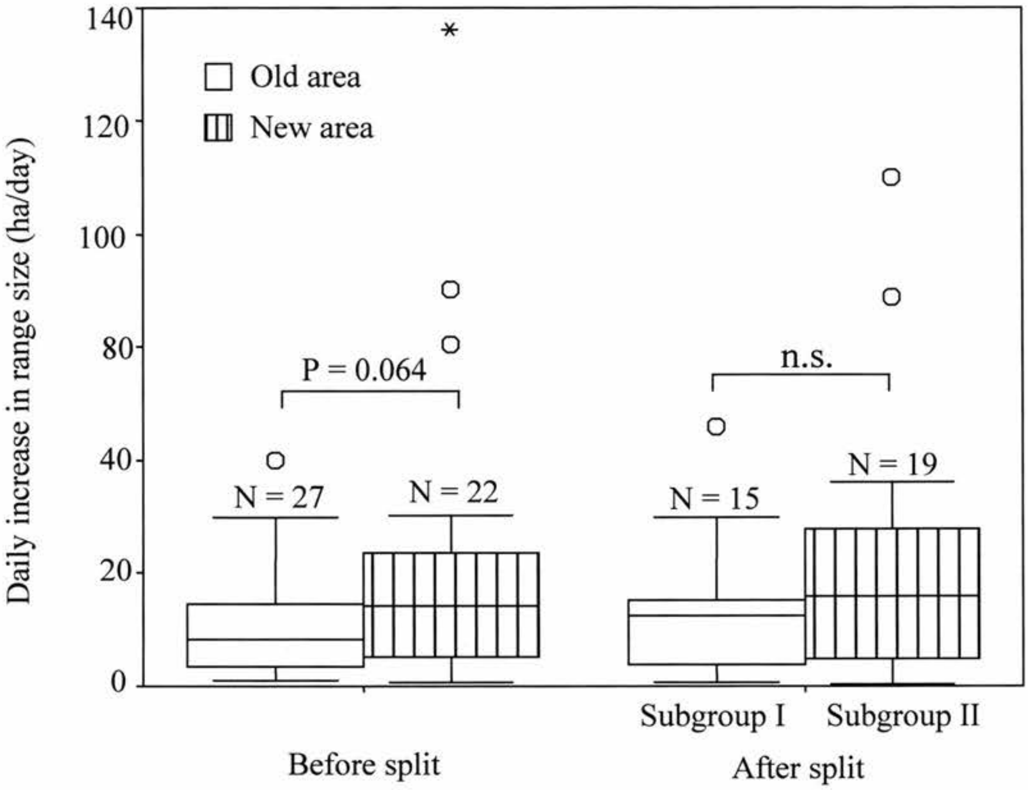


Fig. 6. Daily increase in range size in familiar (old) and less familiar (new) areas for two sets of data. The boxes on the left represent the number of hectares that were newly explored per day by the complete group (before the split) while ranging through either familiar or less familiar areas. The boxes on the right represents the number of hectares that were newly explored per day by 1) subgroup I when ranging through familiar area, or 2) subgroup II when ranging through less familiar areas (same time period). Boxes in white represent familiar (old) areas, shaded boxes represent less familiar (new) areas. For both type of datasets, bars represent the median daily increase in range size, while the top and bottom of the boxes represent the 75 and 25 percentiles. The highest and lowest whiskers represent the highest and smallest values, which are not outliers. Circles and stars represent outliers and extreme values. The increase in range size only includes exploration days, i.e. when the monkeys entered an area in which they had not been observed yet, according to the previous ranging data.

Fig. 7a

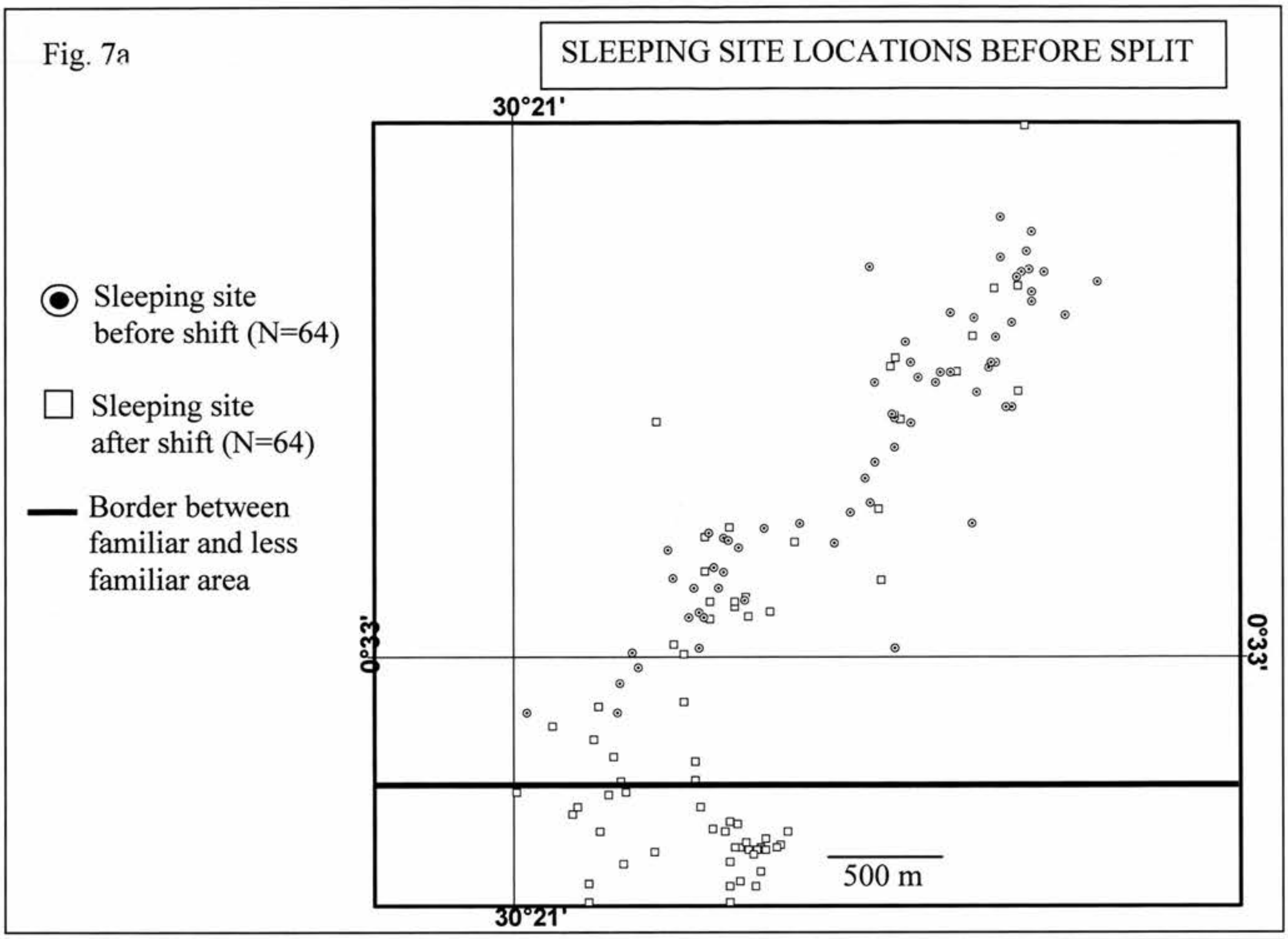


Fig. 7b

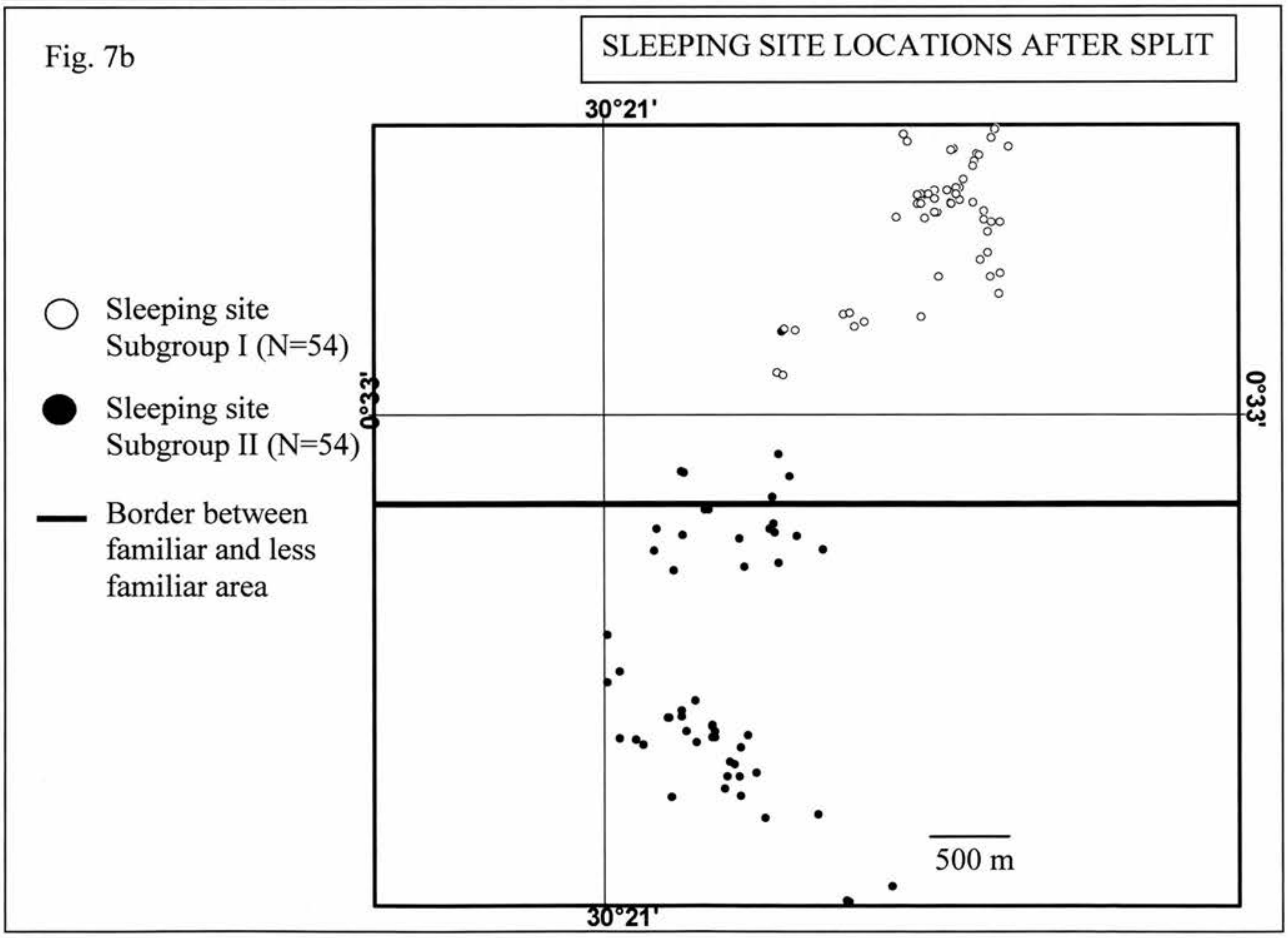


Fig. 7. Locations of an equal number of sleeping sites in the familiar and less familiar area before split (a) and after split (b).

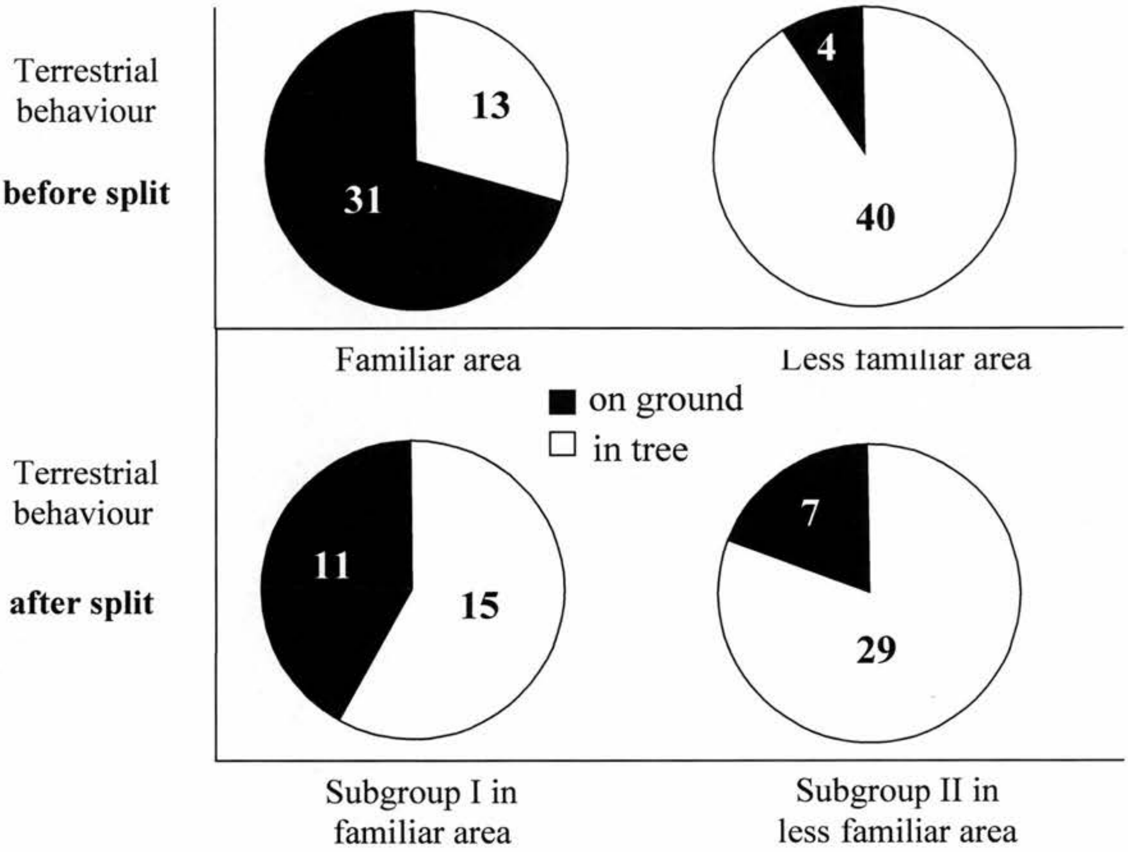


Figure 8. Terrestrial behaviour in the familiar and less familiar area. Each circle represents the proportion of days that at least one individual 1) before the split and 2) after the split, was observed on the ground in the familiar or the less familiar area. White numerals in black segments: number of days that individual(s) had been observed on the ground. Black numerals in white segments: number of days in which none of the individuals were observed on the ground.

Fig. 9a

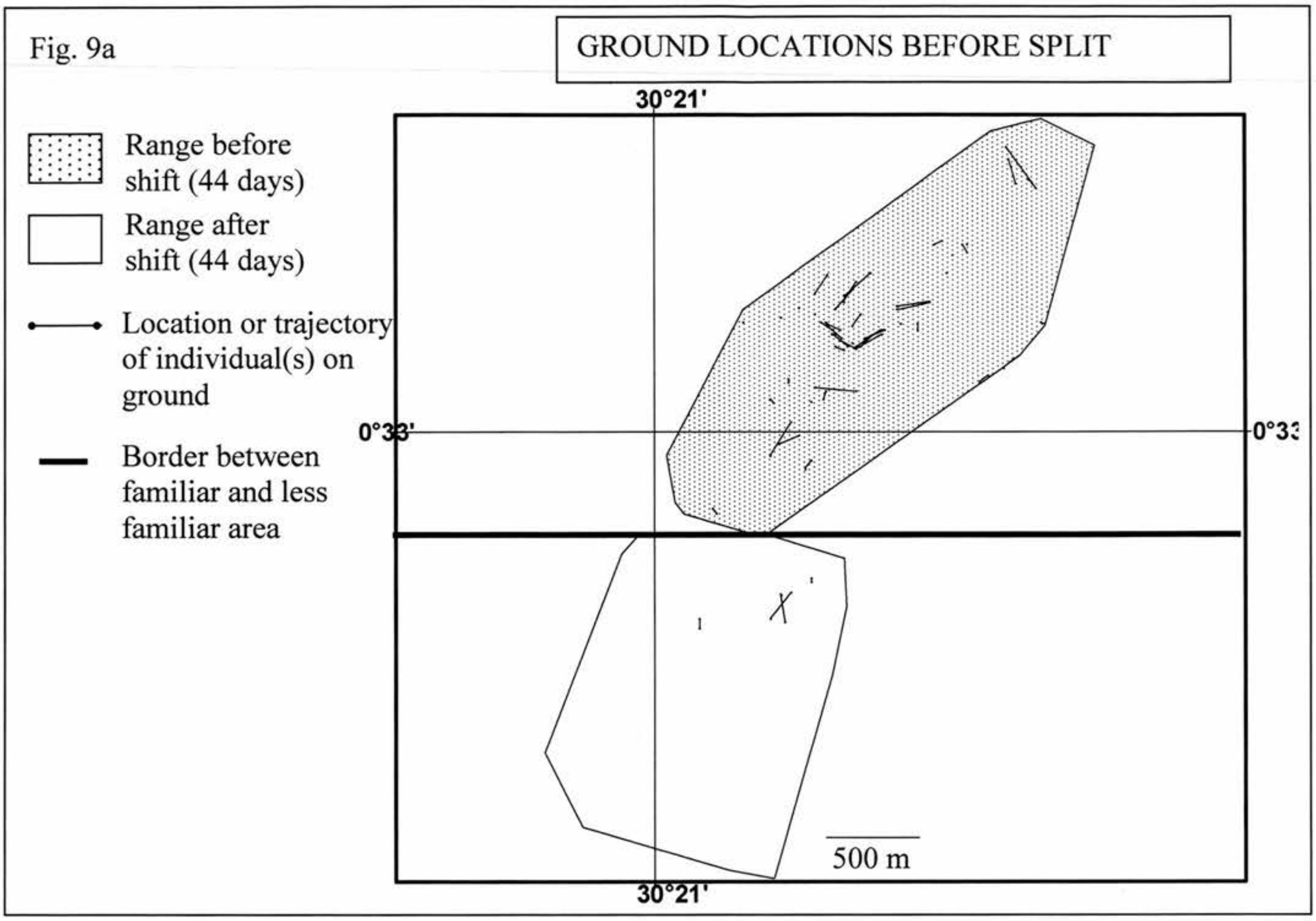


Fig. 9b

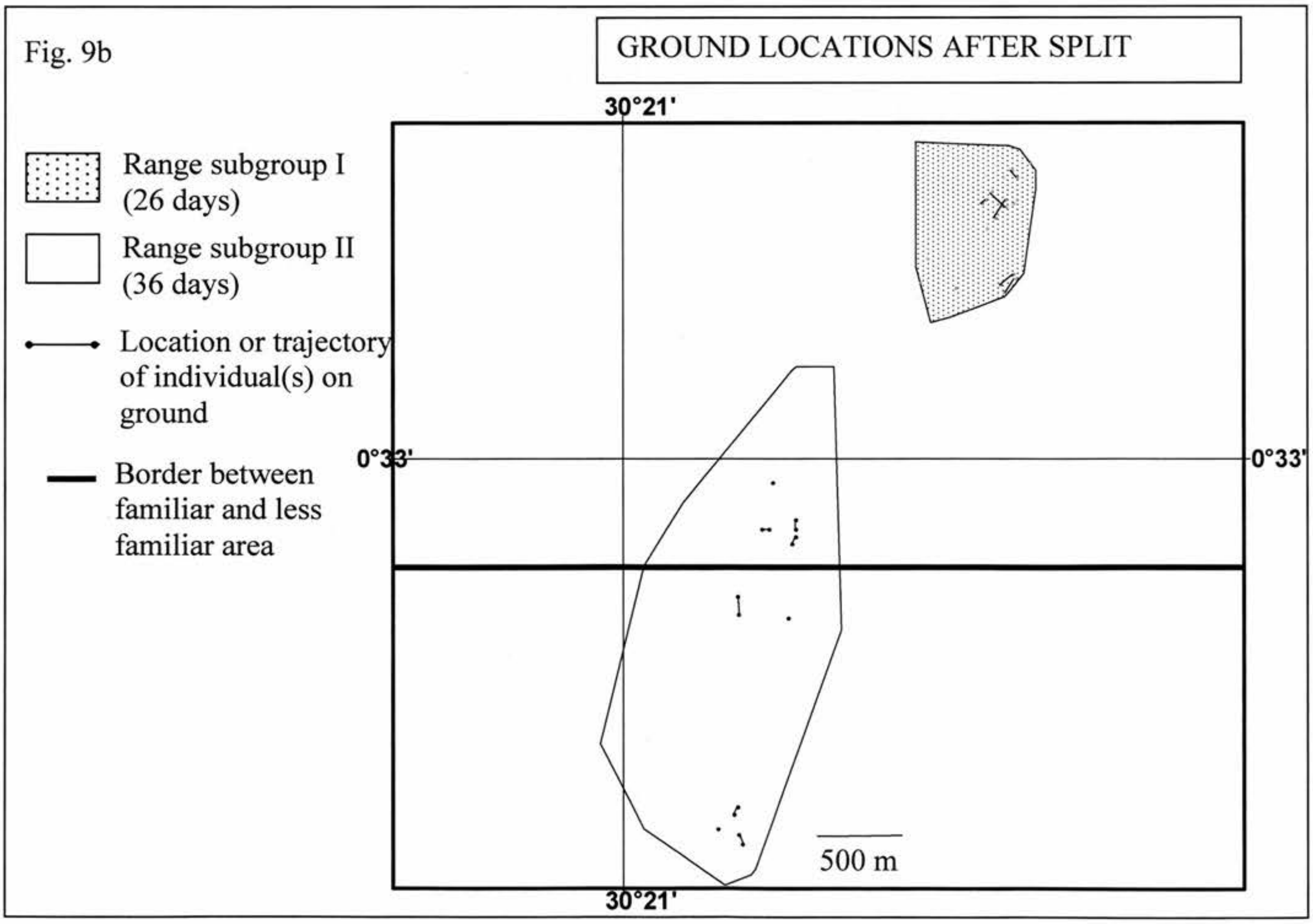


Fig. 9 Locations and trajectories in which at least one group member was observed on the ground to either forage, drink or travel before (a) and after (b) the split. The polygons represent the area surrounding all sightings in either the familiar or less familiar area, within the period of data collection (of terrestrial behaviour).

Are mangabeys less efficient in locating food in less familiar areas?

Food in general

To investigate whether familiarity influenced the monkeys' foraging success I first compared the percentage of resting and foraging time of individual males within the different areas. The nutritious value of different food trees is not only known to vary greatly between species, but also between individual trees that grow in different areas, which is thought to be related to differences in soil conditions and micro climates (e.g. Waterman 1974; Chapman et al. 2003; O'Driscoll Worman & Chapman 2005). Instead of analysing feeding time and fruit intake rates, I therefore chose to analyse the time spent on resting and foraging, since it was thought to give a more honest representation of the actual amount of nutrients that was consumed in both areas (see to Bronikowski & Altmann 1996). For the period before the group split, no difference was found between the percentage of time males spent resting and foraging in the familiar area than in the less familiar area ($U = 437.5$, $N_{old} = 23$, $N_{new} = 39$, $P = 0.873$; $U = 400.0$, $N_{old} = 23$, $N_{new} = 39$, $P = 0.787$). For the period after the split, the males in subgroup I (that were travelling in the familiar area) spent a significantly higher percentage of time resting and a lower percentage of time foraging than the males in subgroup II (that were travelling in the less familiar area) ($U = 170.5$, $N_{old} = 29$, $N_{new} = 30$, $P <0.001$; $U = 297.0$, $N_{old} = 29$, $N_{new} = 30$, $P = 0.036$).

Fruits in general

Here I investigate whether familiarity influenced the efficiency with which individual mangabeys found edible fruits. I compared 1) the number of trees in which the individual males fed on fruit, i.e. the number of trees with edible fruit per 100m travelling, 2) the number of trees that were entered (irrespective of their fruiting state) per 100 m travelling, and 3) the percentage of time that the individual males ate fruit, between familiar and less familiar areas. I first investigated the monkeys' localisation efficiency of trees of a total of 28 fruit species that were regularly eaten within the observation period in both areas (more then 10 times in total). I pooled all trajectories from the individual males for analyses. For the period before the group split, the males did not enter significantly more trees with edible fruit or trees in general, in familiar area than in less familiar area ($U = 447.5$, $N_{old} = 23$, $N_{new} = 39$, $P = 0.988$; $U = 403.0$, $N_{old} = 23$, N_{new}

= 39, P = 0.507). Also no difference was found between the percentages of time that the males spent foraging for these fruits (U = 340.0, N_{old} = 23, N_{new} = 39, P = 0.114). For the period after the split, the males in subgroup I (that were travelling in the familiar area) did not enter significantly more trees with edible fruit or trees in general than the males in subgroup II (that were travelling in the less familiar area) (U = 393.0, N_{old} = 29, N_{new} = 30, P = 0.524; U = 370.0, N_{old} = 29, N_{new} = 30, P = 0.324). Also no difference was found between the percentages of time that the males spent foraging for these fruits (U = 392.0, N_{old} = 29, N_{new} = 30, P = 0.514).

Fig fruits

The above results suggest that the familiarity did not influence the efficiency with which individual monkeys found edible fruit in general. However, when I focussed my analyses on trees of the strangler fig *Ficus sansibarica*, whose fruit are highly preferred but widely distributed in space, I did find a difference in localisation efficiency between both areas. For the period before the split, the males entered significantly more trees with edible fruit in the familiar area than in the less familiar area (U = 380.0, N_{old} = 23, N_{new} = 39, P = 0.035). In addition I found that the males tended to spend a higher percentage of time foraging on these figs (U = 400.0, N_{old} = 23, N_{new} = 39, P = 0.097). However, no significant difference was found for the number of fig trees that were entered (irrespective of their fruiting state), (U = 372.0, N_{old} = 23, N_{new} = 39, P = 0.138). For the period after the group split, males in subgroup I did not enter significantly more *F. sansibarica* trees with edible fruit or trees in general than the males in subgroup II (U = 356.5, N_{old} = 29, N_{new} = 30, P = 0.164; U = 385.5, N_{old} = 29, N_{new} = 30, P = 0.442). Also no difference was found between the percentage of time that the males spent on feeding and foraging for these fruits (U = 378.0, N_{old} = 29, N_{new} = 30, P = 0.305).

Another fig species that is relatively common (3.8 ind. ha^{-1}, Chapman et al. 1999) and also high on the mangabeys' preference list (Waser 1974) is *Ficus exasperata*. The tree density of this species was much lower in the less familiar area. In fact, none of the males were observed to eat in a *F. exasperata* tree within the less familiar area within the entire observation period. In the period before the split, the males rarely fed in trees of *F. exasperata*. However, in the period after the split, the males of subgroup I had been observed to feed in *F. exasperata* trees on a regular basis (27% of all times that they had fed in any fruit tree). The males in subgroup I (that were travelling in the familiar area) entered significantly more *F.exasperata* trees with edible fruit or trees in general than the males in subgroup II (that were travelling in the less familiar area) ($U = 135.0$, $N_{old} = 29$, $N_{new} = 30$, $P < 0.001$; $U = 83.5$, $N_{old} = 29$, $N_{new} = 30$, $P < 0.001$).

Commonly eaten fruit

In addition, I conducted some more detailed analyses on the localisation efficiency of two fruit species that the males fed on most often in the period before the split (*Celtis durandii*) and after the split (*Uvariopsis congensis*). (The males had been observed to feed in these trees 36 and 66 % of all times that they had fed in any tree within each observation period, respectively). For the period before the split, males tended to enter significantly fewer *C. durandii* trees with edible fruit in familiar area than in less familiar area ($U = 334.0$, $N_{old} = 23$, $N_{new} = 39$, $P = 0.060$. However, no such tendency was found for the number of trees that were entered in general ($U = 349.5.0$, $N_{old} = 23$, $N_{new} = 39$, $P = 0.136$). For the period after the group split, the males in subgroup I (that were travelling in the familiar area) entered significantly fewer *U. congensis* trees with edible fruit or trees in general than the males in subgroup II (that were travelling in the less familiar area) ($U = 231.0$, $N_{old} = 29$, $N_{new} = 30$, $P = 0.002$; $U = 199.0$, $N_{old} = 29$, $N_{new} = 30$, $P < 0.001$).

Does fruit availability differ between both areas?

The above results suggest that the lack of long-term spatial memories of food tree locations within the less familiar area did not negatively influence the efficiency with which the monkeys found trees from fruit species or their fruits. In fact, the males localised more fruit of the most commonly eaten species, in the less familiar areas. The lack of long-term memories did seem to negatively influence the efficiency with which the monkeys located fruits of *F. sansibarica* within the early period after the shift. However, these results could also be an effect of differences in fruit availability between the familiar and less familiar area. For example, the familiar area may have simply had a higher density of fruit bearing *F. sansibarica* trees. In a similar way, a higher density of fruit bearing *U. congensis* trees in the less familiar area, could explain the higher success rates of finding edible fruit. In order to investigate this possibility I walked transects that were located at 15m parallel to the male's travel route. I found no significant difference in the number of fruit bearing *F. sansibarica* trees encountered within 5 m of the transect route per meter travelling, between the familiar and less familiar area ($U = 440.0$, $N_{old} = 23$, $N_{new} = 39$, $P = 0.686$). This was also true for the number of trees that carried ripe fruit ($U = 448.5$, $N_{old} = 23$, $N_{new} = 39$, $P = 1$), suggesting that monkeys' lower success in fruit finding in the less familiar area cannot be explained by differences in fruit availability, suggesting that a lack of spatial memories of previous fruiting states negatively influenced the localisation efficiency of edible figs. I did find a significant difference in the number of fruit bearing *U. congensis* trees (ripe) encountered within 5m of the transect route per meter travelling, between both areas ($U = 254.5$, $N_{old} =29$, $N_{new} = 30$, $P = 0.005$). To control for the differences in fruit density I calculated the *relative localisation efficiency* (RLE, see chapter 1). I found that the relative localisation efficiency was higher in the less familiar area than in the familiar area ($U = 198.0$, $N_{old} = 29$, $N_{new} = 30$, $P <0.001$), suggesting that the monkeys localisation efficiency of ripe *U. congensis* fruit was not negatively influenced by a lack of spatial memories.

Animal matter

Hladik (1975) stressed the importance of insect (animal protein) availability and its impact on the ranging behaviour of the tocque macaques (*Macaca sinica*). Since the diet composition and ranging behaviour of these macaques showed a number of similarities with the grey-cheeked mangabeys, I investigated the percentage of time that the individual males spent foraging for animal matter (insect larvae (e.g. weevil larvae and caterpillars), ants and snails). I found that in the period before the split the individual males tended to spend more time feeding on animal matter in the less familiar area than in the familiar area ($U = 320.0$, $N_{old} = 23$, $N_{new} = 39$, $P = 0.059$). However, no such tendency was found when I compared the time spent feeding on animal matter by the males in subgroup I while travelling in familiar area and subgroup II while travelling in less familiar area ($U = 381.5$, $N_{old} = 23$, $N_{new} = 39$, $P = 0.367$). The increase in time spent feeding on animal matter before the split cannot be explained by a significant decrease in time spent feeding on other protein sources; young leaves and flowers ($U= 356.5$, $N_{old} = 23$, $N_{new} = 39$, $P = 0.18$).

Why did the group shift their range and split?

One possible explanation for the shift could be that DJL significantly increased in the period before the shift (r_p = 0.310, N = 86, P = 0.004; fig. 10). This could have been related to a combination of a decrease in food availability and or an increase in group size or body mass (growing juveniles and or influx of males). The move to the south did not seem to have improved the situation. DJL was higher in the less familiar than in the familiar area and neither fruit localisation efficiency nor the number of tree species encountered per distance travelling increased (number of food tree species p. 100m travelling: U= 412.0 N_{old} = 23, N_{new} = 39, P = 0.595). In fact, when the group split, seven month after the shift, part of the group (subgroup II) that had moved even further south encountered significantly fewer food tree species per distance travelling than the individuals that stayed in the familiar area (subgroup I) (U= 289.5 N_{old} = 29, N_{new} = 30, P = 0.027). Therefore, I suggest that the shift was unlikely to be triggered by a discovery of a higher quality habitat (in relation to fruit availability/species diversity) in the less familiar neighbouring area. The overall lack of improvement in daily net energy intake could have caused the group to split. After the split, the DJL (8:00h – 17:00h) of subgroup I in familiar area was significantly shorter than the DJL (8:00h – 17:00h) of the complete group in familiar area before the split (t = 2.351, df = 176, P = 0.02). Also, I found that the males in subgroup I rested significantly more than the males before the split (U = 308.0, N_{before} = 62, $N_{subgroupI}$= 29, P <0.001). Surprisingly, however, no significant difference was found between DJL and resting time between the group before the split while travelling through less familiar area and subgroup II, while travelling through less familiar area (t = 1.355, df = 97, P = 0.178; U = 903.5, N_{before} = 62, $N_{subgroupI}$= 30, P = 0.825).

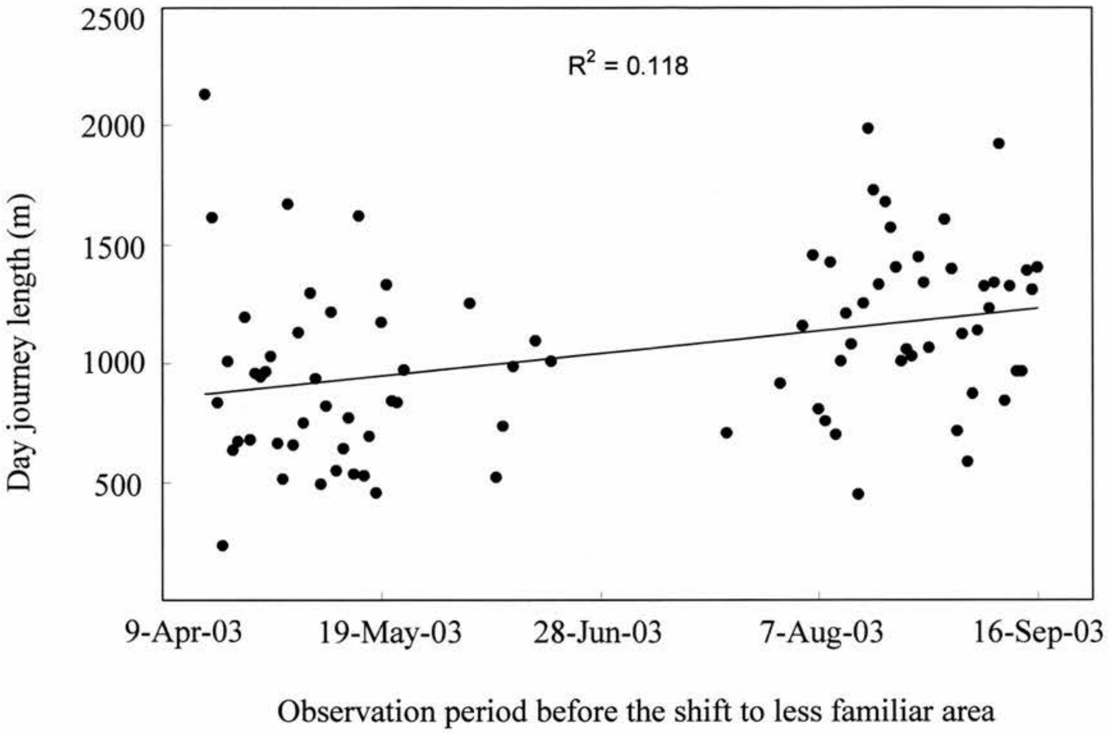


Fig. 10. Day journey lengths of the study group in the period before the shift into less familiar area.

DISCUSSION

Within this study I witnessed the unique event that a group of rain forest primates shifted their range after a discontinuous, yet regular observation period of 6 years. Seven month after the move into the unknown or less familiar area the group split. One part of the group remained travelling in the less familiar area, while the other part remained in the familiar area. This event gave me the unique opportunity to measure the behavioural consequences of a range shift, in particular those related to the lack of spatial memories of the locations of food trees, sleeping sites and suitable places for terrestrial travel and foraging.

I found that the mangabeys moved significantly longer distances (DJL) and explored more area per day in less familiar than in familiar area. This was true in the period before the group split as well as after the split when one of the subgroups had continued to proceed south into less familiar areas. Possibly, the difference in DJL was caused by a lack of knowledge on the locations of suitable sleeping sites in the less familiar area, within the first period after the shift. In this period the group regularly returned to the same sleeping site when travelling into the less familiar area. Possibly, this was the only site, the monkeys knew off as being suitable, which could have forced the group to walk longer distances to reach it in the evening. However later in time, I still found a difference between the DJL in both areas, yet the distribution of sleeping sites did not appear to be clumped anymore, suggesting that other factors may be responsible for this difference. Surprisingly, I found no indication that the range shift and a lack of spatial memories negatively influenced the number of fruit trees that were entered and fed in per distance travelling by individual males. In fact, for the species most commonly eaten within the observation periods (*Celtis durandii* and *Uvariopsis congensis*), the males were more efficient in finding trees with edible fruit in the less familiar areas than in the familiar areas. Even for the preferred and widely scattered fig species *Ficus sansibarica* I found no difference in the number of trees entered per distance travelling, between both areas. However, in the period right after the shift, the number of *F. sansibarica* trees that were fed in per distance travelling was significantly higher in the familiar than in the less familiar area. In addition, individual males tended to spend more time foraging on these figs in the familiar area. This could not explained by differences in the availability of *F. sansibarica* trees between both areas, suggesting that a lack of spatial memories hinder a correct prediction on the availability of edible figs (chapter 3; Janmaat et al. 2006b). In the period right after the shift males spent significantly more time feeding on animal matter in the less familiar area. This finding initially suggests that the group had a more difficult time finding particular fruit trees and therefore switched their foraging to animal matter. Similar compensative foraging was observed in potty nose monkeys (*Cercopithecus. nictitans*) and diana monkeys (*Cercopithecus diana*) that increased foraging on insects when fruit became more scarce (Eckhardt & Zuberbühler 2004). However, no decrease was found in the time that males spent foraging on other protein sources, like young leaves, or fruit. Neither were the males less efficient in locating fruit trees or finding fruits in general. One possible explanation for the increase in faunivory could be that the trees or plants in the less familiar area had a lower nutritional quality or digestibility levels and or lacked in sufficient protein sources, so that supplementary foraging on animal matter was necessary (e.g. Waterman 1974; Chapman et al. 2003; O'Driscoll Worman & Chapman 2005). An alternative explanation could be that the food supply in both areas was of equal quality, yet the lack of memories of the quality of specific individual feeding trees or species resulted in a less efficient nutrients intake. To make up for this, the monkeys had to increase foraging on animal matter and consequently travelled longer distances than when they had been foraging on high quality fruit (Hladik 1975). The gut passage time (transit time) for the grey cheeked mangabeys is longer than the average found for primates (22.7h versus an average of 14.4h; N=40; Lamberts 1998). Hence, for grey cheeked mangabeys it may be rather the quality i.e. the optimum mix of energy and nutrients and the digestibility of a given bulk of food, than the availability that affects their ranging behaviour. Primates are known to adjust their diet in reaction to time-or location-related quality differences within particular fruit species like *Celtis durandii* (Worman & Chapman 2005; Chapman at al 2003). Whether or not primates use detailed memories on the quality of individual trees (from previous feeding visits) remains topic of further investigations that could start by comparing the nutritional value and digestibility levels of food trees entered by adult versus presumably less experienced juveniles.

In the period before the split, I found no difference in the time that the males spent foraging or resting between less familiar and familiar areas. However, the males from subgroup I spent significantly less time foraging and significantly more time resting in the familiar area, than subgroup II did in the less familiar area. After the split no differences were found in either the time males spent foraging on fruits, *F.sansibarica* figs or animal matter, or the efficiency with which the males located edible fruits between both areas. However, I did find a significant difference in time that the males spend foraging on figs of *F. exasperata*. This highly preferred food source (Waser 1974) was basically absent in the less familiar area, and after the group split many *F. exasperata* trees were fruiting. I suggest that the access to these preferred fruits, that are produced in large crops, has enabled the monkeys in subgroup I to walk shorter DJL and to spend more time resting than the males from subgroup II who primarily fed on the small *Uvariopsis* trees that contained only a few fruits per tree. Another factor that could explain the observed differences in DJL, resting and foraging times could be group composition. Although both groups were approximately equal in size ($N_{\text{subgroup I}} = 10$, $N_{\text{subgroup II}} = 12$; equal number of cycling females), two females in subgroup I gave birth just before and after the split. Female primates are known to conserve energy during reproduction by increasing resting time (Harrison 1983; Rose 1994). Possibly, the two females had slowed down the group. Also subgroup II contained a higher number of juveniles (5 vs 2) that tend to have lower foraging success and preference for foraging on animal matter. Consequently they may need to travel further distances (Janson & van Schaik 2002; Hladik 1975). However, juveniles are seldom found at the beginning of a progression and there is no indication that juveniles lead the group (Waser 1985).

It is clear from the above results that it is difficult to be conclusive about the underlying triggers that determine a change in diet or DJL. A large number of factors such as the group composition or differences in food quality and its abundance could be of influence (Gillespie & Chapman 2001; Diaz & Strier 2003). Sometimes the direction of these influences are unexpected. When Sigg and Stolba (1981) compared the ranging behaviour of two groups in the overlapping areas of their home ranges, they found that rare visitors made shorter trips than the band that visited it often, i.e. was familiar to the area. Since both bands used and therefore knew the same water holes, they suggested that the regular visitors knew more sites off the direct route to the water holes and thus lengthened their march. Whatever direction we would expect the DJL to change in, it is clear that in this study I found the same changes within two comparisons, before and after the group had split. This strongly suggest that the increase in DJL and exploration rate was related to the range shift and therefore to a lack of spatial memories on relevant locations in the habitat in the less familiar area.

In addition to an increase in DJL and exploration rate another obvious behavioural difference was observed. The numbers of days in which one or more mangabey(s) were observed on the ground (when travelling, foraging or drinking) and the time spent on the ground was significantly lower in the less familiar than in the familiar area. This was true in the period before the group split as well as after. The frequency of terrestrial observations seemed to coincide with the monkeys' habituation to the area; the longer the group moved around in a particular area, the more often individuals were observed on the ground. I suggest that the lack of spatial knowledge of suitable drinking, foraging but also travel locations within the less familiar area restrained the monkeys from moving to the ground. This is not only thought to have consequences for the monkeys' foraging efficiency but it is also expected to bring about extra travel costs. Previous research on mangabey locomotion suggests that quadrupedal locomotion is energetically less costly than other forms of locomotion, such as leaping or tree swaying. An increase in terrestrial (quadrupedal) locomotion is therefore thought to decrease energy expenditure during travel. The idea that the mangabeys save energy by terrestrial travel was further supported by anecdotal observations of terrestrial travel at specific locations in primary forest that occurred only in uphill direction but not when the monkeys were heading downhill.

The shift in ranging area and the lack of extended spatial memories of these new areas is also expected to affect predation risk. Metzgar (1967) argues that predation risk is expected to be higher in less familiar areas for the following reasons 1) individuals who are familiar with their environment detect danger more readily (Brown 2001(escape response)); Windberg 1996; 2) animals that know the terrain can escape more effectively; (e.g. Manzer & Bell 2004) and 3) animals that are unfamiliar with their surroundings may show greater activity levels and hence be more prone to attack. Movement obviously has a strong impact on the likelihood of detection by predators. It is a cue to which many predators are highly tuned (Brown & Warburton 1997). Kibale primates are not hunted by humans, (Struhsaker 1997). The only potential primate predators in the area are chimpanzees (*Pan troglodytes*), leopards (*Panthera pardus*, golden cats (*Felis auratus*) and crowned eagles (*Stephanoaetus coronatus*). Chimpanzees have been observed to kill other primate species at Kanyawara, but not adult mangabeys. There is one observation of a hunt in which the chimpanzees chased a mangabey female with infant and ate the infant (pers. comm. Mangabey field assistant Richard Kaserengenyu and Chimpanzee field assistant Francis Mugurusi)). Leopards are extremely rare at Kanyawara and no evidence of mangabey predation by felids has been reported there (Olupot & Waser 2001). However, I did observe one series of alarm calls that were combined with mobbing behaviour in ground direction within this study (pers. observation). Yet, no alarm calls were elicited in responds to a moving fake leopard skin. The greatest predation risk comes from the crowned eagle. In fact, Struhsaker & Leakey (1990) showed that eagle predation has a more major impact on the mangbey population of Kibale: a minimum of 3.8% of males and 2.2 % of females are killed in this way each year. The observed increase in DJL in the less familiar area is therefore not only expected to increase the energy spent on travelling but it is also likely to increase the risk of predation.

In this study I witnessed a range shift that was not triggered by obvious human influences, such as hunting or logging pressure. Similar naturally occurring shifts have been observed in other primate species, like savannah baboons, but they are considered rare (Bronikowski & Altmann 1996). Most shifts in rain forest monkeys are known to occur after a group split, when one of the subgroups moves into a new range (Struhsaker T.T., Leland L. (1988); Cords, M. & T.E. Rowell. 1986; personal comm. M. Cords and T. Struhsaker). My study is unique in that the shift occurred seven months before the group split. The shift itself is consistent with Waser's conclusion that mangabeys are relatively unattached to particular feeding areas. Comparisons of the monkeys' movement patterns with a random walk model, indicated a slight site attachment, however, Waser suggested that the mangabeys come closer to a random walk prediction than many other animal species (Waser 1976). The results of this study clearly show that this nomadic-like behaviour does not go without costs. Both the energy expenditure on travel and possibly predation risk increased as a result of the shift in ranging area. Yet, if that many costs were involved, then why did the group decided to shift their range? One of the explanations could be that in the period before the shift the group's DJL increased significantly. Similar results were found in two groups of the closely related yellow baboons (*Papio cynocephalus*) right before they shifted their range (Bronikowski & Altmann 1996). Analogue to Bronikowski & Altmann I suggest that the mangabey group was suffering from a temporary decrease in habitat quality. Instead of eroding their time spent resting or socializing, they chose to explore new areas. In our case the shift may also have been triggered by a gradual increase in the group's body mass (due to growing juveniles and the influx of males). Unfamiliar males that have travelled in the less familiar area before may have guided the group into the less familiar area (pers.comm. Olupot). The group could have followed these males intentionally, yet the direction of the shift could also simply be a result of maintenance of minimal individual distances to conspecifics and a tendency of the new males to move south.

The exploration trip to the south did not bring much improvement though. The new habitat did not seem to be of better quality from a long-term perspective. The new area did have a temporarily higher density of ripe *U. congensis* fruit (chapter 1) however, it also had a substantial lower density of one of the preferred and highly profitable fig species *F. exasperata* and the trees species diversity in the new area was significantly lower. Tree species diversity has shown to be an important variable in the grey-cheeked mangabeys' ranging behaviour in earlier studies (Olupot et al. 1977). Olupot et al. (1977) found that the number of scan-sightings of a grey-cheeked mangabey group in a quadrat was positively related to the number of fruit species found in a quadrat. It was argued that high tree species diversity allows for a high dietetic diversity that may be essential in order to obtain sufficient nutrients of a variety of types as well as a variety of species over longer periods in time (Olupot et al. 1977; Chivers et al. 1984). After their exploration trip to a neighbouring area the DJL did not significantly decrease. Possibly this lack of improvement caused the group to split. However, as a result of the split, it was only subgroup I that decreased DJL. The difference between the DJL of subgroup II and that before the split was not significant. I therefore suggest that other events such as the birth of two infants, directly before and after the split, in subgroup I need to be considered as alternative explanation for the group split. Female spider monkeys (*Ateles geoffroyi*) with dependent infants were sighted in smaller subgroups and were more often solitary than other females (Chapman 1990). Chapman (1990) suggests that the females with dependent infants chose to forage in smaller groups to protect their infants from aggression by co specifics. The mangabey females may have been guided by similar triggers. However, predation is more likely to play a role. Anecdotal observations suggest that the mangabey subgroups were noticeably quieter and less male fighting was observed (pers. observations K.R.L. Janmaat & R. Chancellor). Possibly, the females induced the split in order to avoid losing their infant in fights but more likely to be less conspicuous and prone to predation

I conclude that the shift to less familiar area, that most likely coincided with a lack of spatial memories, had most clear consequences for the exploration rate, day journey lengths, and terrestrial behaviour. The two latter behavioural changes consequently increased the daily costs of travel (either by distance or type of locomotion). Cost of travel is an important selective pressure impinging on lifetime reproductive success of primates through its influence on net energy balance and limits to group size (Isbell 1999). For example, baboons (*Papio cynocephalus*) that fed on artificially high densities of foods (garbage dumps) were heavier than baboons that fed on naturally occurring foods (Altman et al., 1993). Examination of their activity budgets and diets indicated that the heavier baboons gained their greater weight by reducing travel distance rather than by increasing food intake (Altmann & Muruthi, 1988; Muruthi et al. 1991; Isbell 1999). Free-ranging female vervets (*Cercopithecus aethiops*) that are better fed are often younger when they have their first offspring and have shorter interbirth intervals than females that are less well fed (Whitten 1983; Cheney et al. 1988). Adding this up to the likely increase in predation risk due to increased travel activity, I conclude that a range shift into less familiar areas, i.e. a lack of spatial memories can have a negative effect on the monkeys' fitness. However, under certain conditions, such shifts may be the only effective adaptive behavioural responds to temporary changes in habitat quality or group composition.

SUMMARY CHAPTER 4

After six years of discontinuous, yet regular observations of a group of grey cheeked mangabeys (*Lophocebus albigena johnstoni*) in the Kibale rain forest, I observed a substantial shift in the ranging area. Seven months after moving into the unknown or less familiar area the group split permanently. One part of the group continued to travel in the less familiar area, while the other part remained in the familiar area. I measured the behavioural consequences of this event, in particular those related to the lack of spatial memories of the locations of food trees, sleeping sites and suitable places for terrestrial travel and foraging. I found that the mangabeys moved significantly longer distances (DJL) and explored more area per day in the less familiar than in the familiar area. Whether familiarity influenced foraging efficiency was less clear. No difference was found in the efficiency with which individual males located fruit or spent time foraging on fruit in general within both areas. However, right after the shift the males were less efficient in localising the highly preferred, yet widely scattered fruits of *Ficus sansibarica* in the less familiar area. In this same period the males also spent more time feeding on animal matter in the less familiar area. In the period right after the shift the group regularly returned to the same sleeping site when travelling in less familiar area. Familiarity significantly influenced the likelihood that individuals moved on the forest floor, to forage, drink or travel. I conclude that the mangabeys experienced higher travel costs and predation risk (due to either longer DJL's and or a lower frequency of terrestrial travel) within less familiar areas, while lacking extended long-term spatial memories.

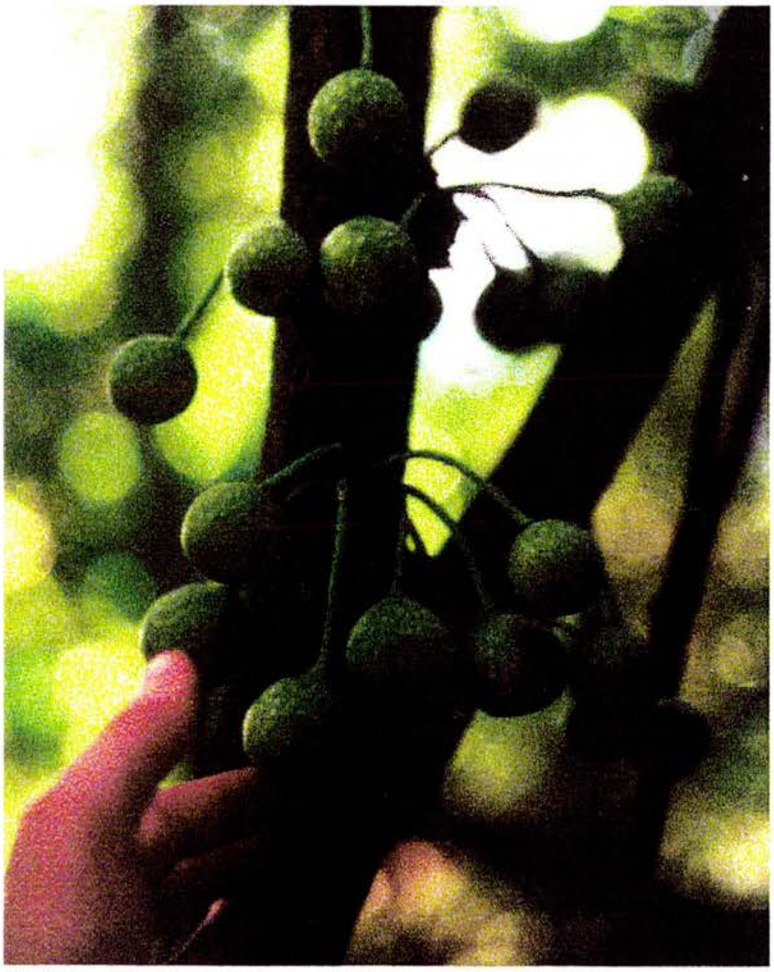
Possibly, the mangabey males were less efficient in localising edible fruits of *Ficus sansibarica* in less familiar areas because they had been unable to monitor them for longer periods in time. In the next chapters I investigate whether mangabeys are able to anticipate the emergence of edible fig fruits by monitoring trees and integrating the duration of revisit intervals and knowledge of maturation rates.

* * *

CHAPTER 5

FRUITS OF ENLIGHTENMENT?

CAN GREY-CHEEKED MANGABEYS PREDICT CHANGES IN THE FRUITING STATE OF RAIN FOREST FIG TREES?



Ficus sansibarica fruits

INTRODUCTION

"No field study can establish whether or not animals are capable of anticipatory thought. To do so one needs carefully controlled experiments to establish that the behaviour in question is learned, in the absence of any previous reinforcement...."
Emery & Clayton 2004a.

Fruit habitat hypothesis

Great apes exhibit various behaviours that apparently entail cognitive capacities beyond the reach of other primates. As a consequence many researchers now believe that a cognitive divide exists between great apes and the other primates (e.g. Byrne 1995; Russon et al. 1996; Parker & McKinney 1999; but see Tomasello & Call 1997). While trying to explain what selective pressures may underlie this divide researchers have been inspired by field observations of ape behaviours that were never or rarely observed in monkeys, such as tool making, teaching, nest building, clambering or complex food manipulation. (e.g. Povinelli & Cant 1990; Parker 1996; Byrne 1997). Others have been inspired by paleontological findings that suggest differences between the evolutionary settings of apes and monkeys, leading to hypotheses such as the fruit habitat hypothesis (Potts 2004). This idea focuses on differences in constraints imposed by habitat and diet onto apes and monkeys in a period of time in which the current great ape species are thought to have evolved. One crucial factor in great ape evolution is a dietary distinction (see also Milton 1988 and Byrne 1997). Studies on molar morphology and dental microwear and comparative behavioural studies of living primates indicate that apes were and are more dependent on ripe fruits than monkeys (Wrangham et al. 1998; Potts 2004). The hypothesis states that because ripe fruits are more complexly distributed in time and space a dietary dependence on ripe fruit has triggered enhanced cognition through complex foraging behaviour (Clutton-Brock & Harvey 1980; Milton 1981; Byrne 1997).

Prediction of fruit ripening

Unlike related hypotheses (e.g. Milton 1981; Byrne 1997), Potts proposes a potential adaptation that may have facilitated the finding of edible fruits, the ability to predict the occurrence of ripe fruits. This adaptation is substantially different from the ability to remember the location of fruit in time and space (spatio-temporal memory) as proposed by

Milton – an ability that has been observed in many other animal species (see Barton 2000 for review). The ability to anticipate and to predict future events could enable an individual to "travel in time" (Suddendorf & Corballis 1997; Roberts 2002). Anticipation of fruit ripening has received little attention in earlier cognitive studies, despite the fact that such a skill could create clear selective benefits, especially when a forager is searching for fruit that show no visual or olfactory signs of edibility. Rapid variation during the Pleistocene in the timing, length, and intensity of wet and dry seasons led to repeated forest contraction and expansion, i.e. periods of food scarcity and abundance, with consecutive changes in the spatial and temporal pattern of fruiting seasons (Potts 2004). Under extreme conditions of food scarcity and unpredictable synchronicity patterns, anticipation of the ripening of fruit in individual trees or tree patches, may be a highly beneficial trait, enabling individuals to out compete others for food. Phenological recordings of modern rain forests, of much shorter time frames, also show regular periods of fruit scarcity and a high degree of unpredictability of the times and locations of fruit appearance (Chapman et al. 1997; 1999). These conditions are likely to place a premium on individuals that are able to 1) remember trees or patches at which fist signs of fruiting were observed (flowers or unripe fruits) and 2) predict the optimal time of revisit.

Anecdotes of anticipatory behaviour in apes

Current information on anticipation of fruit ripening in wild primates are purely anecdotal (e.g. *Pan troglodytis*, Wrangham 1977 and *Pongo pygmaeus* Galdikas 1997): For example Wrangham (1977) writes: "Occasionally when individuals inspected a source they did not feed at the time but climbed straight up to feed on their return up to two days later". Understandably, little systematic research has been conducted on this topic. Long-term continuous following of individual apes over periods of ripening is nearly impossible. This might explain why anticipatory foraging behaviour in the wild has received so little attention (Barton 2000).

Aim of the study

The aim of this study is to test the fruit habitat hypothesis (Potts 2004). I investigated the ranging behaviour of one group of grey-cheeked mangabey monkeys relative to a number of pre-selected fruit trees within their home range. I collected data on the monkeys' visiting behaviour and speed of approach towards these trees as a function of the trees' fruiting state for a long and continuous observation period. The null hypothesis was that the mangabey monkeys could not anticipate the emergence of new fruits or, once the fruits have emerged, predict changes in fruit-quality. I pre-selected trees from the fig species *F. sansibarica* that were located in the rain forest of the Kanyawara research area, Uganda. Trees of *F.sansibarica* are thought to shown no synchrony in fruiting (Waser 1975).

Why *F. sansibarica* trees?

To reveal potential anticipatory behaviour that is related to fruiting states, I focussed on the monkeys' behaviour towards individual fig trees of the species *F. sansibarica*. Unlike the majority of rain forest tree species at Kanyawara (e.g. Chapman et al.1999; chapter 1), trees from this highly preferred food species does not show any synchrony in fruiting. This implies that each individual tree has a fruiting pattern that is independent from that of other trees of the same species. Therefore the monkeys cannot use the emergence of fruits in one tree individual as an indicator for fruit emergence in other individuals within the same species, like in synchronous species (Menzel 1991; chapter 1). In order to find fruits of *F. sansibarica* the monkeys are therefore challenged to use other strategies. Knowing that the edibility state of *F.sansibarica* figs cannot be detected by visual cues from outside the tree (Dominy et al unpublished manuscript; chapter 3), localisation efficiency by use of visual cues is expected to be limited. Experimental work on wild capuchin monkeys (*Cebus apella*) showed that monkeys can increase their foraging efficiency nearly treefold by knowing the location of a feeding platform in advance than to having to detect each platform anew (Janson & Di Bitetti 1997; Janson 1998). These studies suggest that as soon as detection distance decreases the monkeys will benefit more from using their memory skills. Hence, for *F. sansibarica* the mangabeys are expected to localise these figs more efficiently by remembering individual fruiting states of particular fig trees and possibly their potential ability to predict the maturation or depletion rates accordingly. In other words, anticipatory behaviour is most likely to be revealed when studying the monkeys while searching for fruit of *F. sansibarica* and possibly other fig species.

Behavioural data

Anticipation of fruit emergence

Results of an earlier study suggest that mangabeys do not monitor fig trees (Olupot et al. 1998). However, chapter 3 showed that mangabeys were able to remember previous fruiting states of *F. sansibarica* trees. (Janmaat et al. 2006b; chapter 3). When grey-cheeked mangabeys approach a fig tree without fruits they are less likely to visit it when the tree had been depleted recently, compared to when the tree never had fruit in recent periods, and thus has more potential to carry new fruits. These results can be interpreted in two ways. First, the monkeys may simply avoid recently depleted trees. Second, the monkeys prefer to visit the second group of empty trees because they are expecting to discover new fruits. In this chapter I investigated these possibilities by conducting more detailed analyses of the mangabeys' behaviour towards these two types of empty trees, i.e. depleted trees and previously empty trees. I conducted measurements on the angle and speed of approach and the time spent inside the trees (Rutte 1998). In addition, I investigated the lengths of the time intervals between a visit to a target tree and a subsequent time that the group came within 100 meter of the same tree. I investigated the likelihood of revisiting in relation to the time that had passed since the last visit for trees that did not carry fruit. In addition, I analysed the speed with which the study group approached target trees that recently grew fruit. The null hypothesis was that the group could not anticipate the emergence of new fruit and would therefore approach slower at the first feeding visit than at the subsequent visit. I also compared revisit intervals towards trees that carried inedible or unripe fruits and ripening intervals.

Anticipation of quality changes

To test whether mangabey monkeys anticipated increases or decreases in the quality of trees that carried fruits I compared the speeds with which the group approached target trees during successive visits.

Ecological data

In addition to the observational data I investigated the fruiting patterns of individual fig trees. In order to gain insight in the complexity of correct prediction of fruit emergence and ripening I investigated 1) the level of synchrony and 2) the timing and duration of fruit initiation intervals and non-fruiting periods. Potts (2004) argues that apes developed special anticipatory skills because they were more dependent on ripe fruits than other primates. The rarity of ripe fruits would have placed higher demands on the localisation skills of apes than that of monkeys, who supposedly had a much easier job, due to their ability to supplement their diet with unripe fruits. To investigate whether indeed the ability to correctly anticipate ripe fruit emergence is relatively more rewarding than the ability to correctly anticipate the emergence and development of fruit in general, I compared the availability of ripe fruit with that of fruit in general.

METHODS

Study species

I observed the ranging of one group of grey-cheeked magabeys, which was studied in a semi-logged moist evergreen forest of the Kibale National Park in Uganda (0°34'N, 30° 21'W, see Waser & Floody 1974 and Chapman et al. 1997 for an extended description of the study area). The group consisted of 20-27 independently moving individuals. Grey-cheeked managebeys are considered arboreal (Waser 1974), but our study group regularly foraged on the ground (chapter 4). The group was well habituated to human observers on foot, allowing observation from as close as 2 meters.

We focussed on the ranging behaviour in relation to trees of the strangler fig *Ficus sansibarica* (*Moraceae*, see chapter 3 for extended description). These figs are amongst the preferred foods of grey-cheeked mangabeys (Waser 1974, 1977; Barrett 1995; Olupot 1999). Individuals mainly eat ripe fruits but sometimes also the seeds of unripe fruits (Janmaat et al. 2006b, chapter 3). Unripe figs are also attractive to the monkeys because they often contain weevil larvae, such as *Omophorus stomachosus* (Waser 1977). Because the fruits of *F.sansibarica* can contain weevil larvae, the fruits are considered edible even when the fruits itself are not. Within this manuscript *edible fruits* will therefore refer to fruit that contains nutritious value to the mangabeys either in the form of ripe fruits or as weevil larvae or seeds. Individual trees can show marked differences in the amount of fruit produced during different fruiting periods, suggesting that there is little relation between the size of a tree and its crop (Chapman et al. 1992). Fruits show no obvious visual signs of ripeness, such as colour or size. As a consequence chimpanzees assess edibility of these fruits by entering trees and squeezing individual fruits (Dominy N.J., Lucas P. W., Wrangham R. W. & Ramsden L. unpublished manuscript). The edibility of unripe fruits is particularly difficult to assess, since these fruits produce no smell that can be detected by humans from further than 20 cm. Mangabeys identify infested fruits by turning them, presumably to check for the distinctive small black spots, indicative of larvae infestation. Long-range visual cues (the size of the tree and its crop) are unlikely to allow monkeys to make judgements about the suitability of these trees as a food source.

Data collection

Behavioural data

The method of data collection on the group's revisit behaviour and approach speed towards the pre-selected fig trees is described in chapter 3. During approaches we also analysed whether or not the individual closest to the tree was feeding (one-zero sampling, 1 minute intervals, Martin & Bateson 1986). Feeding was defined as any act of food manipulation, including examining mossy branches and epiphytes for insects, but not chewing while engaged in activities other than ingestion (see Waser 1974 for a more detailed description).

Phenology data

Phenological data on the fruiting state of Ficus trees were collected in three different ways. Firstly, me or my assistants walked five transects random in length, time and place, within the study area. In these transects we checked the fruiting state of a total of 316 Ficus trees that came into sight. Secondly, I determined the fruiting state of all target trees to which the study group approached within 100 m distance during the three continuous observation periods. Thirdly, I analysed long-term phenology data of 34 individual Ficus trees that were monitored fortnightly (2-weeks) for a continuous period of 16 years by the Kibale Chimpanzee Project (N = 399). In addition, I did analyses on phenology data of 27 Ficus trees that were monitored once a month for a continuous period of 5 years by the Fish and Monkey Project (N = 72). All trees had a larger DBH than that of the smallest Ficus tree seen fruiting, (Chapman et al. 1995; 1999). A *F. sansibarica* tree with unripe fruit was defined as a tree under which no ripe fruits were found or no smell of ripe fruits was scented. Ripeness of individual *Ficus sansibarica* fruits was determined by the level of elasticity, i.e. by squeezing the fruits.

Data analyses

A visit was defined as the entrance of at least one group member into the tree. Monitoring was defined as a visit without feeding. Ninety-one percent of all times that the group approached within 100 meters of particular trees were separated by at least one day, suggesting that they could be treated as independent events. In some rare cases, the group approached a particular tree two or three times in the same day; however, I only included these approaches in the analyses if the group had moved out of the 100 m circle between successive approaches. The coefficient of dispersion (variance/mean for the number of trees that were fruiting over the 16 years monitoring period) was used to represent the synchrony of fruiting events (Sokal & Rohlf 1981; Chapman et al. 1999). Data were analysed using Spearman and Pearson correlation analyses, Mann-Whitney U tests, Wilcoxon signed rank and the t-test, logistical regression analyses (Sokal & Rohlf 1995; Siegel 1956; SPSS 10). To determine the predictability of fruit initiation I used Shanon's diversity index (Zar 1996). Relative diversity ($0 > J' < 1$), (observed diversity as a proportion of maximum possible diversity) was used as a measure of uncertainty with which fruit initiated within any of the selected (two week) time periods within one year. All tests were two tailed. In each case we assessed evidence about specific hypotheses, so we did not adjust significance criteria using the Bonferroni method (Perneger 1998). To test whether the revisit probability of a fig tree was influenced by the time that had passed since the last visit I used logistic regression analyses using SPSS 10.0 (Field 2000). The statistical significance of a variable in regression can be judged either by the probability level associated with its parameter or by the change in the overall goodness of fit of the model due to the addition of that variable. The latter procedure depends less on specific assumptions needed for parameter estimation and thus is preferred; I provide both the probability that a given variable's asymptotic parameter equals 0 (second p-value), as well as the total model goodness of fit (first p-value)(measured by the chi-square statistic against the null hypothesis of homogeneity).

RESULTS

Do all Kanyawara figs fruit asynchronous?

Ecological Observations

If individual trees of the same species fruit synchronously in time the monkeys could use this knowledge to locate fruit bearing trees (Menzel 1991). Although *F. sansibarica* in the Kanyawara forest is considered as asynchronous (Waser 1975), seasonality has never been tested. Hence, I used the coefficient of dispersion to represent the synchrony of fruiting events to estimate the synchrony of fruiting events (CD; variance/mean for number of trees that were fruiting per month over 16 years of observation; Sokal & Rohlf 1981; Chapman et al. 1999). Results showed that individual trees of *F. sansibarica* fruited random/asynchronous in time (Fs: CD = 1.083). In contrast, the distribution pattern of fruiting periods of trees of the species *F. natalensis* and *F. exasperata* was clumped/synchronous in time (Fe: CD = 2.177; Fn: CD = 1.188; fig.1). In order to test whether (individual) trees fruit at fixed time periods within the year (for example in May), I plotted the timing of fruit initiation in table 1 and calculated the Shanon diversity indices. Table 1 presents the timing of fruit crop initiation over a period of 16 years. Table 2 presents the values of relative diversity (J') of timing of fruit initiation per individual tree as well as per species (Zar 1996). All trees have a J' value that is higher than 0.71 except for one tree of *F. natalensis* that fruited only once. Per fig species J' varies between 0.58 and 0.68. All J' values were closer to 1 than to 0, meaning that a good deal of uncertainty is involved in predicting the (two week) period in which fruit initiated in individual trees as well as within each species, selected at random. In sum, for *F. sansibarica* trees search by use of synchronicity (chapter 1) is unlikely to be rewarding, suggesting that monkeys will have to rely on more complex strategies to predict (ripe) fruit emergence.

Do monkeys anticipate the emergence of new fruit?

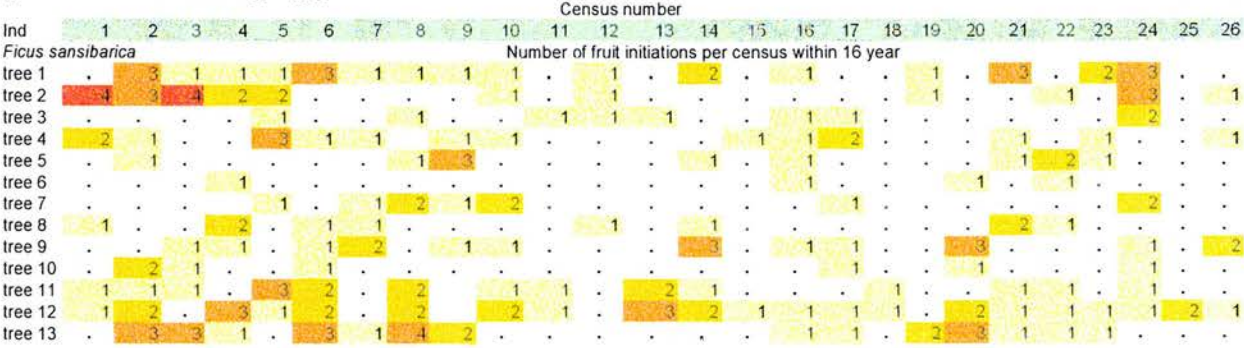
Behavioural observations

The group was followed during three continuous periods of 50, 60, and 100 days. Within these three periods the group came within a 100 meters of a total of 11, 20 and 28 *Ficus sansibarica* trees that carried fruits and 20, 24 and 31 *Ficus sansibarica* trees that did not carry fruits, respectively. I observed a total of 577 different approaches. Data of the three observation periods were pooled for analysis.

Behaviour in and around two types of empty trees

Recently depleted trees are expected to emerge new fruit at a later date than trees that have not had fruits yet. To investigate whether mangabeys have similar expectations I compared the group's behaviour towards a number of target trees as a function of time since the last depletion. As a first measure of expectation I determined the minimum angle between the direction at which the first individual of the group was first sighted by the observer under the tree and the direction of the last departing individual when it disappeared out of sight (similar to Rutte 1998; but not Janson 1998). Small angles suggest that the group made a detour from their daily travel path in order to visit the tree, while large angles suggest that the group encountered the tree as part of their route. I found that the angle between the direction of arrival and departure is significantly smaller for trees that carried edible fruits (n =45) than for trees that did not carry fruits (n = 35). (U = 2449, P = 0,049, N_1 = 59, N_2 = 64), indicating that the group made a detour in order to visit trees with fruits. However, no difference was found between trees that were depleted (n = 22) and trees that did not have fruits within the observation period (previously empty trees)(n = 45) (U = 382.500, p = 0.904, N_1 = 20, N_2 = 39).

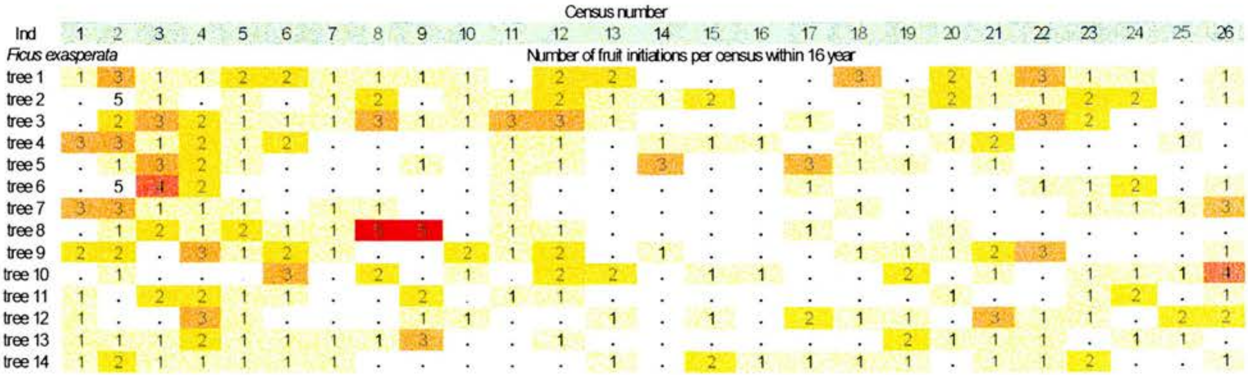
Table 1. Time of year of fruit crop initiation for *F. sansibarica* (N= 13), *F. exasperata* (N = 14) and *F. natalensis* (N=7) (top to bottom) individual in the sample over the total sampling period (16 year). Each of the 26 dots represents one 2-wk sampling period beginning at left with January and ending with December. The number 1 in a censuring period indicates that this tree showed one fruit initiation in this period over the 16-yr sample; the number 2 indicates that this tree showed two fruit initiations in this period over the 16-yr sample, and so on. Overall, data show that most individuals initiated fruit crops at many different times of year over the total sampling period.



Census number

Number of fruit initiations per census within 16 year

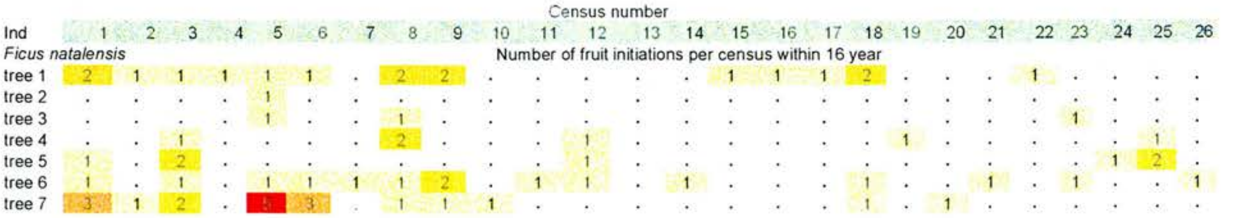
Ind	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Ficus sansibarica																										
tree 1	.	3	1	1	1	3	1	1	1	1	.	1	.	2	.	1	.	.	1	.	3	.	2	3	.	.
tree 2	4	3	4	2	2	.	.	.	.	1	.	1	.	.	.	.	.	.	1	.	.	1	.	3	.	1
tree 3	.	.	.	.	1	.	.	1	.	.	1	1	1	.	.	1	1	.	.	.	.	.	.	2	.	.
tree 4	2	1	.	.	3	1	1		1	1	.	.	.	.	1	1	2	.	.	.	1	.	1	.	.	1
tree 5	.	1	.	.	.	.	.	1	3	.	.	.	.	1	.	1	.	.	.	.	1	2	1	.	.	.
tree 6	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.		1	.	1	.	.	.	.
tree 7	.	.	.		1	.	1	2	1	2	.	.	.	.	.	.	1	.	.	.	.	.	.	2	.	.
tree 8	1	.	.	2	.	1	1	.	.	.	.	1	.	1	.	.	.	.	.	.	2	1	.	.	.	.
tree 9	.	.	1	1	.	1	2	.	1	1	.	.	.	3	.	1	1	.	.	3	.	.	.	1	.	2
tree 10	.	2	1	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	1	.	.
tree 11	1	1	1	.	3	2	.	2		1	1	.	2	1	.	.	.	1	.	.	1	1	.	1	.	.
tree 12	1	2	.	3	1	2	.	2		2	1	.	3	2	1	1	1	1	.	2	1	1	1	1	2	1
tree 13	.	3	3	1	.	3	1	4	2	.	.	.	.	.	.	1	1	.	2	3	1	1	1	.	.	.



Census number

Number of fruit initiations per census within 16 year

Ind	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Ficus exasperata																										
tree 1	1	3	1	1	2	2	1	1	1	1	.	2	2	.	.	.	.	3	.	2	1	3	1	1	.	1
tree 2	.	5	1	.	1	.	1	2	.	1	1	2	1	1	2	.	.	.	1	2	1	1	2	2	.	1
tree 3	.	2	3	2	1	1	1	3	1	1	3	3	1	.	.	.	1	.	1	.	.	3	2	.	.	.
tree 4	3	3	1	2	1	2	.	.	.	.	1	1	.	1	1	1	.	1	.	1	2	.	.	.	1	.
tree 5	.	1	3	2	1	.	.	.	1	.	1	1	.	3	.	.	3	1	1	.	1	.	.	.	.	.
tree 6	.	5	4	2	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	1	1	2	.	1
tree 7	3	3	1	1	1	.	1	1	.	.	1	.	.	.	.	.	.	1	.	.	.	.	1	1	1	3
tree 8	.	1	2	1	2	1	1	5	5	.	1	1	.	.	.	.	1	.	.	1	.	.	.	.	.	.
tree 9	2	2	.	3	1	2	1	.	.	2	1	2	.	1	.	.	.	1	1	1	2	3	.	.	.	1
tree 10	.	1	.	.		3	.	2	.	1	.	2	2	.	1	1	.	.	2	.	1	.	1	1	1	4
tree 11	1	.	2	2	1	1	.	.	2	.	1	1	.	.	.	.	.	.	.	1	.	.	1	2	.	1
tree 12	1	.	.	3	1	.	.	.	1	1	.	.	1	.	1	.	2	1	1	.	3	1	1	.	2	2
tree 13	1	1	1	2	1	1	1	1	3	.	.	1	.	.	.	.	.	.	2	1	1	1	.	1	1	.
tree 14	1	2	1	1	1	1	1	.	.	.	.	.	1	.	2	1	1	1	1	.	1	1	2	.	.	1



Census number

Number of fruit initiations per census within 16 year

Ind	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Ficus natalensis																										
tree 1	2	1	1	1	1	1	.	2	2	.	.	.	.	.	1	1	1	2	.	.	.	1	.	.	.	.
tree 2	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 3	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
tree 4	.	.	1	.	.	.	.	2	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	1	.
tree 5	1	.	2	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	2	.
tree 6	1	.	1	.	1	1	1	1	2	.	1	1	.	1	.	.	.	1	.	.	1	.	1	.	.	1
tree 7	3	1	2	.	5	3	.	1	1	1	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.

Table 2. Relative diversity (J') in the timing of initiation of fruiting in 34 individual fig trees of *F. sansibarica*, *F. exasperata* or *F. natalensis* (observed diversity (H') as a proportion of the maximum possible diversity (H'_{max}). J varies between 0 and 1, with increasing diversity and unpredictability when J is closer to 1.

Ind.	**Relative diversity in timing of fruit initiation (0 >J' <1)**		
	F. sansibarica	*F. exasperata*	*F. natalensis*
tree 1	0.81	0.84	0.88
tree 2	0.72	0.82	0.00
tree 3	0.93	0.79	1.00
tree 4	0.87	0.84	0.87
tree 5	0.82	0.80	0.80
tree 6	1.00	0.69	0.97
tree 7	0.82	0.82	0.71
tree 8	0.88	0.72	
tree 9	0.82	0.82	
tree 10	0.90	0.80	
tree 11	0.87	0.91	
tree 12	0.85	0.84	
tree 13	0.76	0.90	
tree 14		0.93	
All trees	**0.58**	**0.60**	**0.68**

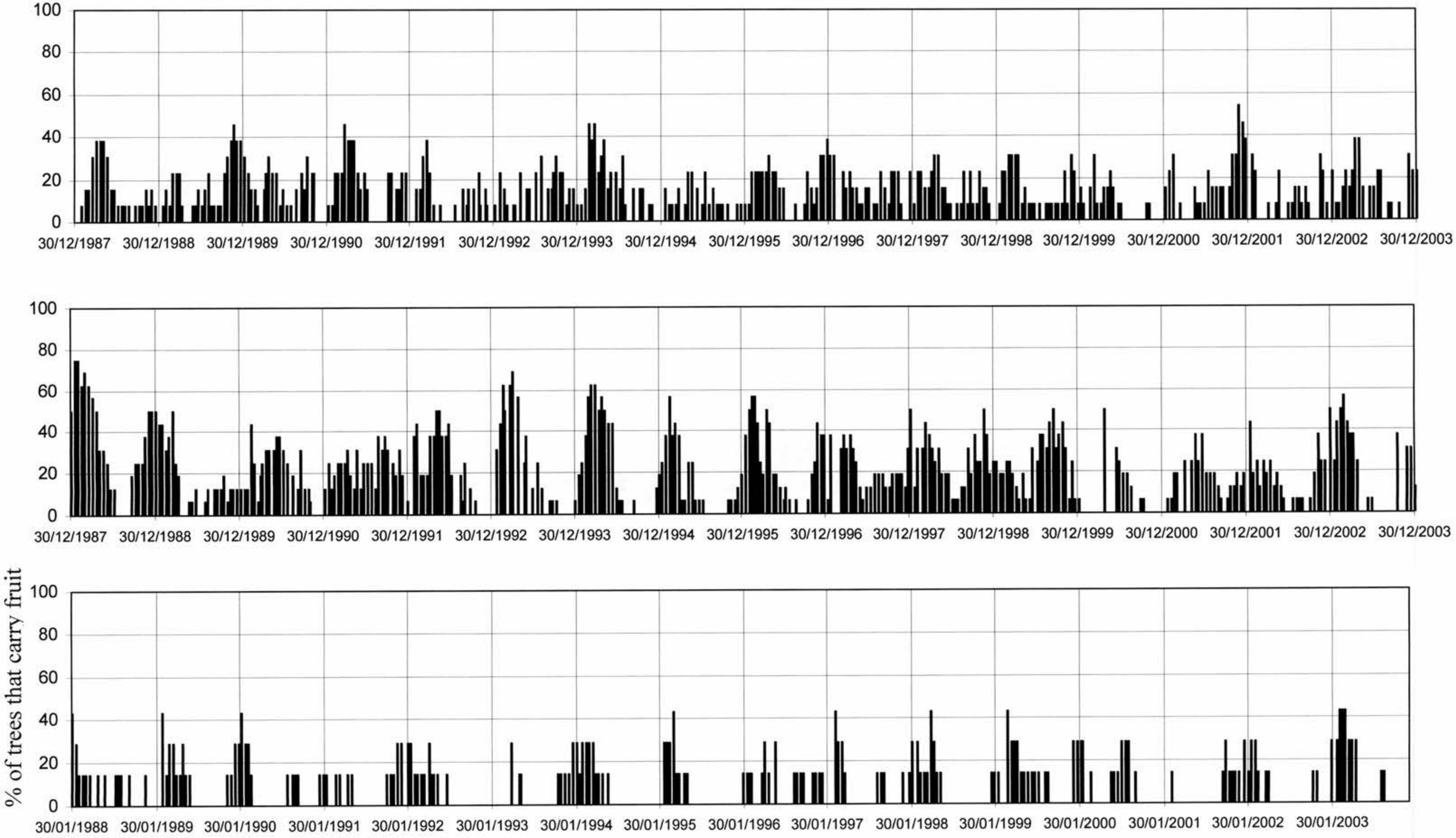


Figure 1. The distribution pattern of the fruiting periods of trees of the fig species *F. sansibarica*, *F. exasperata* and *F. natalensis* (top to bottom

Percentage of fig trees that carried fruit (ripe or unripe) out of all trees that were checked within the fortnightly transect for a period of 16 years.

As a second measure of expectation I measured the time that monkeys spent inside a tree, while walking along the branches in search for fruits. Fruits are rarely evenly distributed within a *Ficus sansibarica* tree, and the monkeys need time to search and detect fruit. I found no difference in time spent inside depleted ($n_{trees} = 6$) versus previously empty trees ($n_{trees} = 24$) ($U = 73.5000$, $p = 0.726$, $N_1 = 6$, $N_2 = 27$ (several visits per tree)). In addition, I found no significant correlation between the time spent in previously empty trees ($n_{trees} = 14$) and the revisit interval ($r_s = 0.334$, $N = 16$, $P = 0.206$).

In chapter 3 it was shown that the group approached trees with fruits significantly faster than trees that carried no fruits (Janmaat et al. 2006b, chapter 3). As a third measure of expectation I chose therefore the speed of approach. When I compared the speed with which the group approached and entered depleted versus previously empty trees I found no significant difference ($U = 90.5$, $p = 0.361$, $N_1 = N_2 = 15$). Because individuals may have been able to check the fruiting state from outside the tree, I also compared how fast the monkeys approached the tree to the point at which they could presumably see the tree (see methods chapter 3). No difference in approach speed was found ($U=215.0$, $N_1 = 15$, $N_2 = 29$, $P = 0.951$).

Revisit intervals of empty trees

I expected that the longer a tree had been without fruit, the higher the chance that new fruit would emerge. To further investigate whether the mangabeys had similar expectations and whether they were more likely to revisit a tree when the time that had passed since the last visit was longer I analysed the group's revisiting behaviour towards previously empty target trees. I determined the lengths of time that had passed in between approaches at which the group came into sight or continued to enter a previously empty tree and the subsequent time that the group came within 100 meter of the same tree (n=22). These intervals were named revisit intervals (if the tree was re-entered) or no-revisit intervals (if the tree was not re-entered). Intervals were named re-approach intervals (if the tree was approached into sight of the observer under the target tree again) or no-re-approach intervals (if the group did not come into sight of it again) (see fig. 2). Surprisingly, the results showed that the lengths of revisit and no-revisit intervals differed significantly ($U=2008$, $N_1 = 36$, $N_2 = 27$, $P = 0.000$). The same was true for the re-approach and no-re-approach intervals (U= 181, N_1 = 37, N_2 = 26, p=0.000). Figure 2 shows that both revisit and re-approach intervals are shorter than no-revisit and no-re-approach intervals. To investigate into more detail how the lengths of each interval influenced the likelihood of a revisit or re-sighting I conducted logistic regression analyses. Results showed that the probability of a revisit or re-sighting decreased with increasing lengths of the revisit and re-approach intervals (chi square $_{\text{revisit}}$ = 22.064, P <0.001, df = 1, ß = -0.079, P<0.001, df = 1; chi square $_{\text{resighting}}$, P < 0.001, df = 1, ß=-0.047, P = 0.001, df = 1). The results of these analyses indicated that the likelihood of a revisit of a tree that did not have fruits for longer periods decreased with the time that had passed since the last visit.

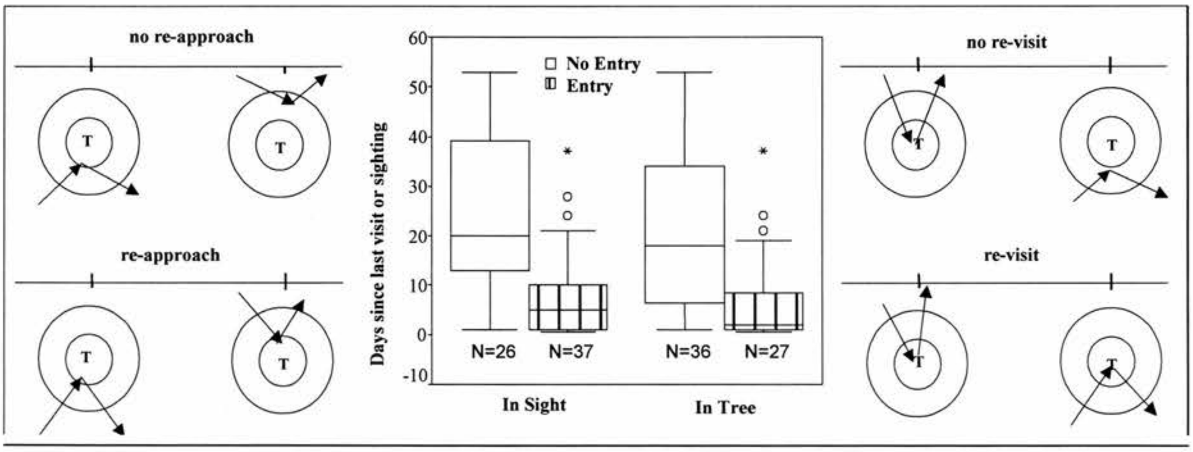


Fig. 2. The duration of revisit, no-revisit, re-approach and no-re-approach intervals of *Ficus sansibarica* trees without fruit (T), once they had approached within 100 meter (outer circle). Bars represent the median number of days that had passed since the last visit or approach into sight (inner circle), while the top and bottom of the boxes represent the 75 and 25 percentiles. The highest and lowest whiskers represent the highest and smallest values, which are not outliers. Circles and stars represent outliers and extreme values

According to a previous study on fruiting phenologies of two neotropical Ficus species (Milton et al. 1982) large fig trees initiate new fruit crops more frequently than small fig trees. No such effect was found for the fig trees of our study. (Since the majority of target trees are strangler figs I used the crown diameter as a measure of size). We found no significant correlation between the crown diameter and the frequency with which fig trees initiated fruit over a 16 years time period (crown: r_s = -0.088, P = 0.669, N = 26). Despite these negative results (that could be due to a small sample size) I continued to investigate

Milton's idea that monkeys may use a relation between tree size and frequency of fruit initiation. I therefore investigated whether trees that were either revisited or bypassed were different in size. I found that the group tended to be more likely to visit empty trees that are larger in size, however the difference in crown size between cases of revisit or bypass was not significant, (U = 2274.0, Nnv = 116, Nv = 47, P = 0.097). I found no significant correlation between revisit intervals and the crown size of the target trees, (rs= 0.092, N = 163, P – 0.242).

Speed towards trees with newly emerged fruit

Earlier studies on fig phenology showed that despite the highly asynchronous fruiting pattern of fig trees, individual trees have relatively predictable intervals between fruit initiation (Milton et al. 1982; Milton 1991). In theory, the monkeys could keep track of such individual fruit initiation cycles. This ability would be highly beneficial, as it would enable individuals to successfully predict the emergence of new fruit. To investigate whether the monkeys can anticipate the emergence of new fruit I analysed the speed of approach towards target trees with newly emerged fruit on successive visits. I compared

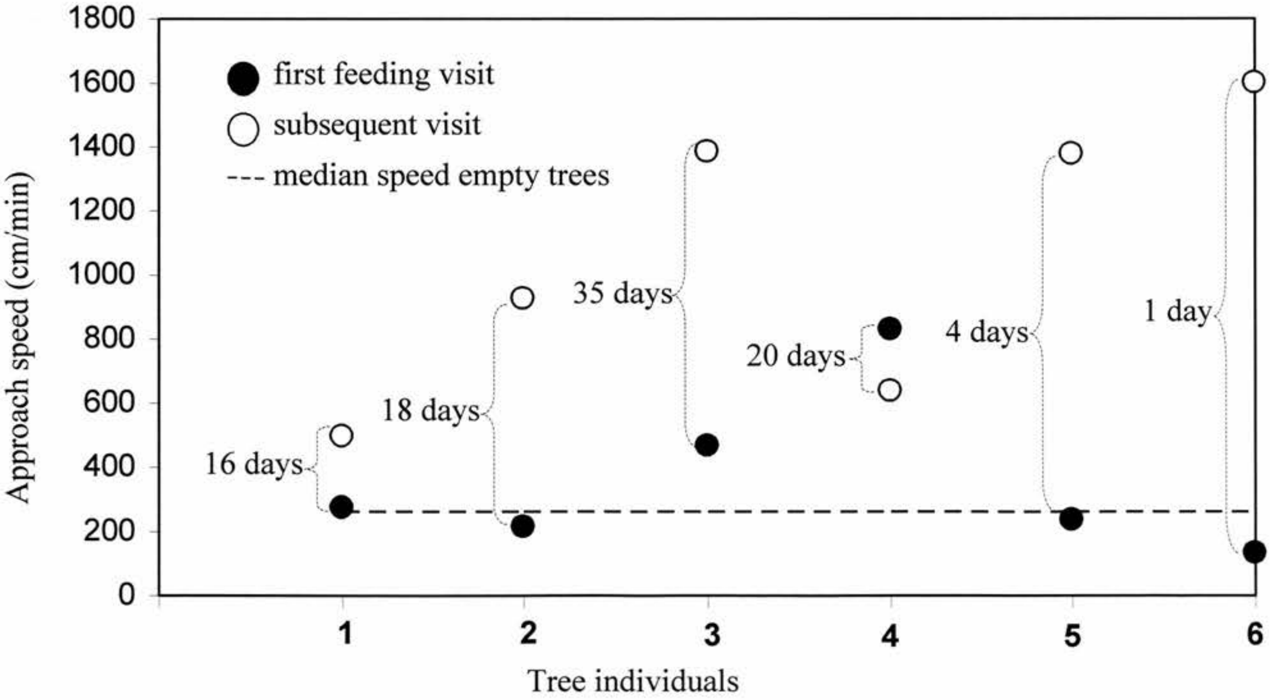


Fig. 3. Speed of approach towards six fruit bearing target trees of *F. sansibarica*. Closed circles represent the speed at first feeding visits. Black circles represents the speed on the subsequent feeding visit. Open squares are the median speed with which the group approached empty trees.

the speed of approach at first feeding visit with that of subsequent feeding visit. I defined a visit to be a first feeding visit when 1) edible fruit had emerged on the tree within the observation period and the group had not visited the tree before and when 2) the tree carried unripe fruits that contained weevil larvae, yet the group had not been within 100 m. of that tree earlier during the observation period (at least 40 days). When I compared the approached speed on the first feeding visit with speed on the subsequent visit I found a significant difference (Z = -1.992, P = 0.046, N = 6). Figure 3 shows that the speed of approach was significantly higher on the second than on the first visit. In addition, I compared the difference between the median speed with which the group approached empty trees with 1) speed on the first feeding visit, and 2) speed on the subsequent visit. I found that the speed with which the group approached at the first feeding visit differed significantly more from the median speed toward empty trees than the speed with which the group approached the subsequent time (Z = -1.992, P = 0.046, N = 6). This suggests that the monkeys did not expect to find fruit on the first feeding visit and were not anticipating the emergence of new fruit.

Is the monkeys' revisiting behaviour optimal in current environment?

Behavioural and ecological data combined

Revisit intervals of empty trees

One of my initial expectations was that the longer a tree had been without fruit the higher the chance that it would grow new fruit soon. This would be expected for neo-tropical fig species such as *F. yoponensis* and *F. insipida* that have fairly predictable fruiting initiation intervals (32.3 8 wk; 41.6 7.6wk; Milton et al. 1982). By analysing long-term data on the duration of non-fruiting periods and intervals between fruit emergence/initiation I investigated whether this assumption is also correct for Kanyawara figs. I first plotted the proportion of the emergence of new fruit against the time that has passed since the last depletion (Fig. 4). If I consider 16 years as a long enough period to correctly estimate the average distribution of non-fruiting period duration, the figure suggest, in contrast to my expectation, that the probability of emergence decreases with the time that has passed since the end of the previous fruiting bout. Second, I plotted the total of intervals between fruit crop initiations of each individual *F. sansibarica* tree (N = 13) of which the phenological state was checked fortnightly over a period of 16 years in figure 5 and table 3. Table 3 and figure 5 clearly indicate that the variation in the duration of between fruit initiation was high within and between individual trees (Between: Median = 32 wk; min/max value = 4/484 wk; ($\overline{X}$= 43 ± 50 wk). In a similar way table 4 and figure 6 show the total of non-fruiting periods observed for each individual *F. sansibarica* tree. Both the table and figure indicate that the variation in length of non-fruiting periods was high within and between individual trees. (Between: Median = 24 wk; min/max value = 2/476 wk; ($\overline{X}$= 35 ± 51 wk). The results of figure 4, 5, 6 and table 3 and 4 should be interpreted with caution, since some of the very short intervals may be a result of imprecise data collection, due to the unequal distribution of fruits in *F.sansibarica* trees. Because of this unequal distribution fruits may have been overlooked during some of the phenology checks. Yet even if I acknowledge some mistakes in data collection the overall picture still shows that the variation in length of both fruit initiation intervals and non fruiting periods was extremely variable, which is expected to complicate correct prediction of fruit emergence.

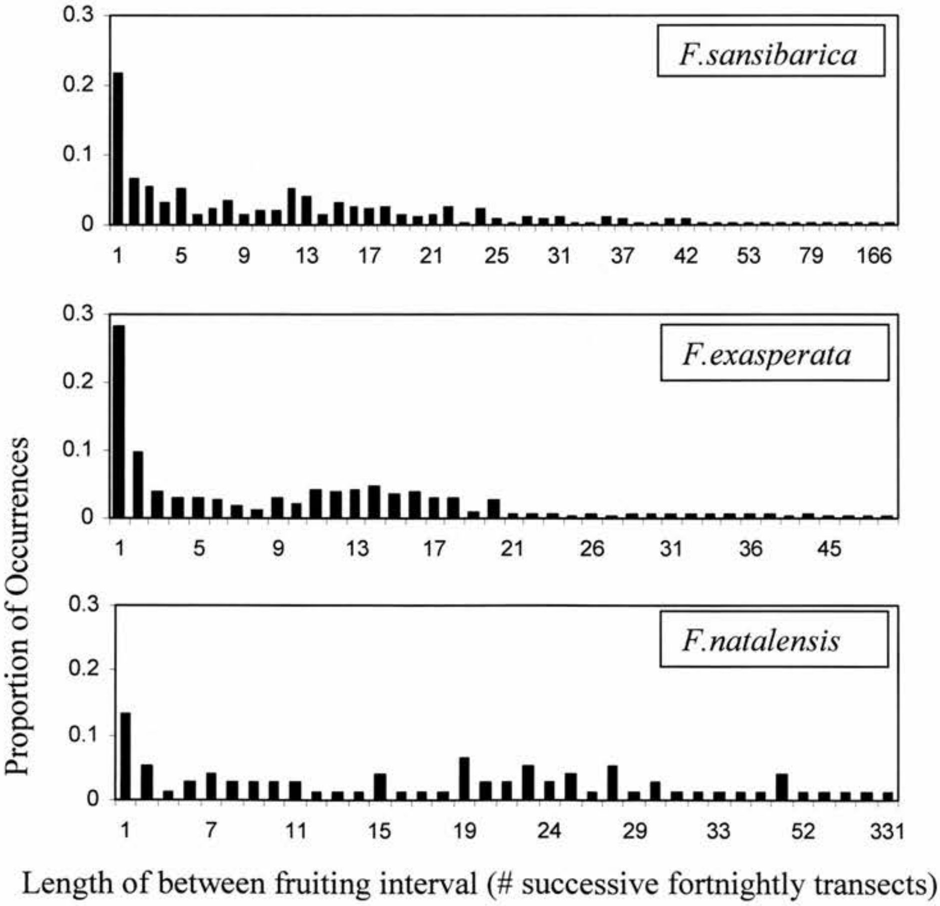


Fig. 4. Lengths of between fruiting interval and their proportion of occurrences (# interval$_i$ /tot intervals) within a total of 399 fortnightly phenological checks.

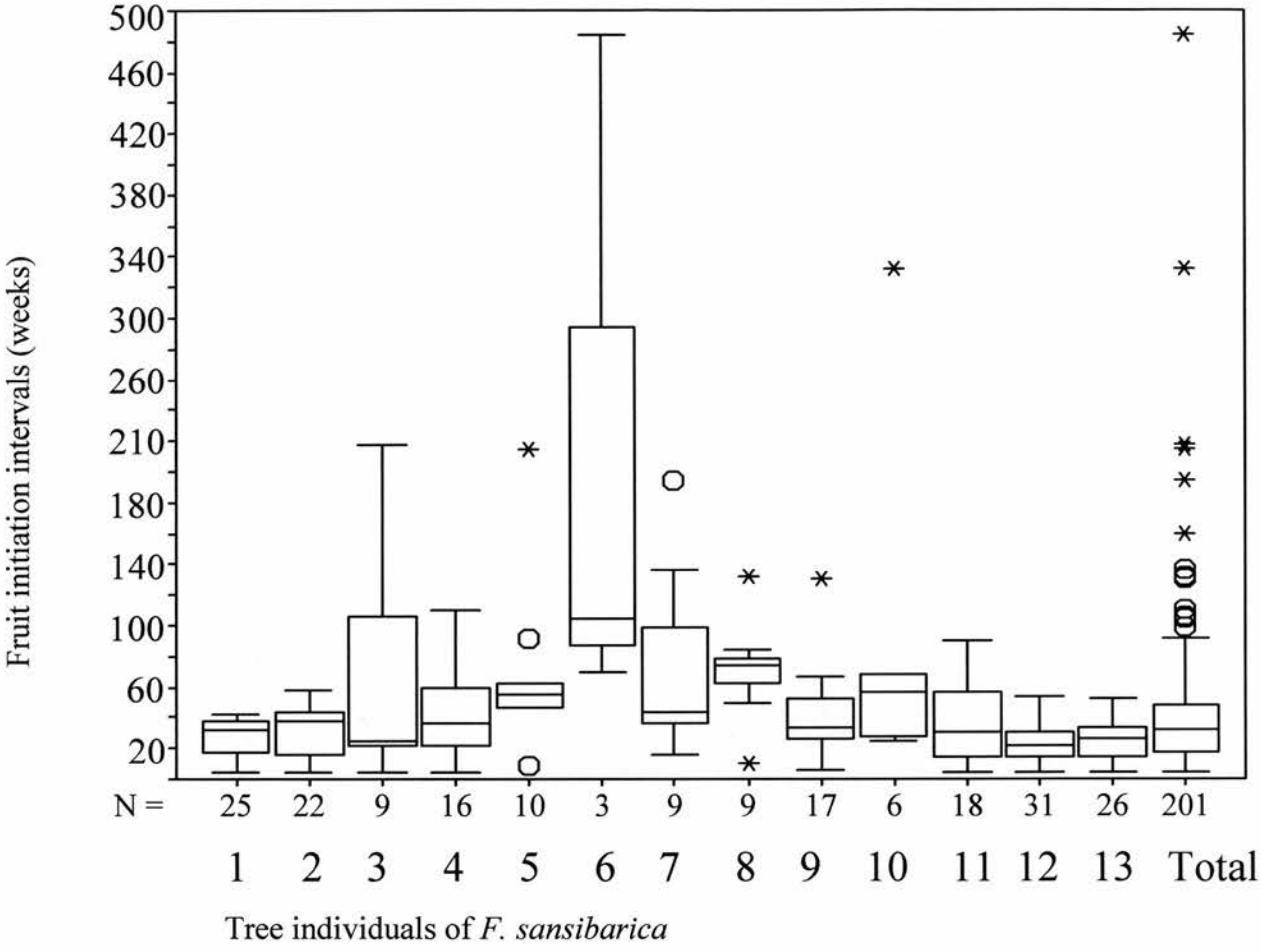


Fig. 5. Estimates of the lengths of intervals between fruit initiations of 13 individual trees of *F. sansibarica*.

For example, tree 1 initiated fruiting 25 times in 16 years. Bars represent the median estimate of the betwee fruiting interval, while the top and bottom of the boxes represent the 75 and 25 percentiles. The highest and lowes whiskers represent the highest and smallest values, which are not outliers.

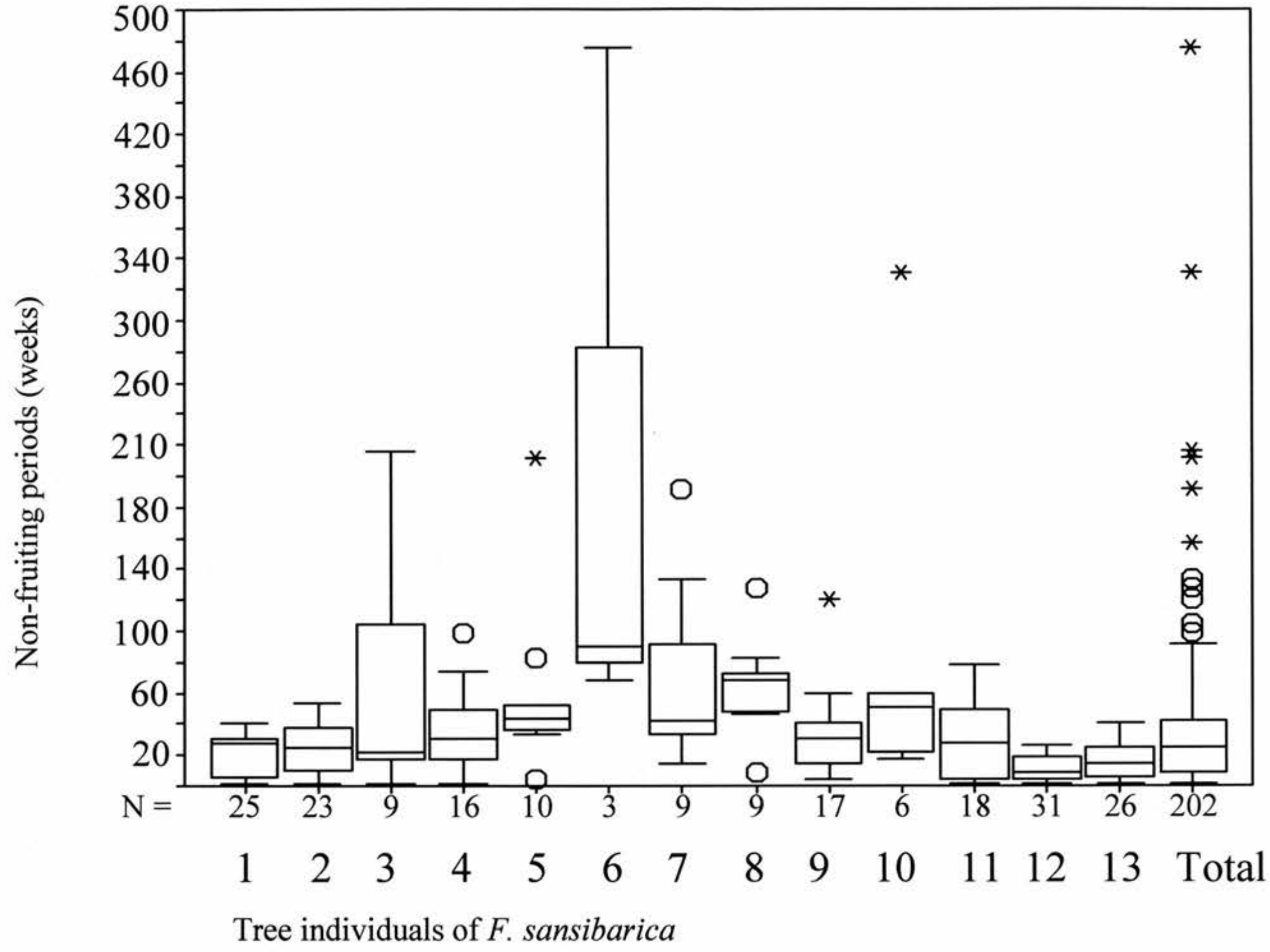


Fig. 6. Estimates of the lengths of non-fruiting periods of 13 individual trees of *F. sansibarica*. Bars represent th median estimate of the between fruiting interval, while the top and bottom of the boxes represent the 75 and 2 percentiles. The highest and lowest whiskers represent the highest and smallest values, which are not outliers.

Table 3. Fruit initiation intervals, of 13 *F. sansibarica* individuals, over the total sampling period. N = number of intervals between fruit initiations. Median = the median duration of initiation intervals (weeks). Each of the 243 dots represents one census period of 2 wk; the 243rd dot at the far right below represents the longest initiation interval of 484 weeks. To determine initiation intervals, begin counting dots from left to right until a number is reached. For example, over the 16-yr sample, tree 1 initiated 26 fruit crops, giving 25 intervals with a median of 32wk in duration between crops. There were two 4-wk intervals, two 10-wk intervals, one 12-wk interval, and so on.

Duration of intervals between fruit initiation (weeks)

Ind	N	Median	0					10					20					30					40					50					60					70					80
Ficus sansibarica																							Number of fruit initiation intervals of each duration																				
tree 1	25	32	.	.	2	.	.	2	1	1	.	3	1	.	.	.	.	2	1	2	3	2	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 2	22	37	.	.	1	.	1	.	.	1	3	1	.	.	.	1	.	1	.	1	1	1	2	1	2	1	2	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.
tree 3	9	24	.	.	1	.	.	.	.	.	.	.	.	2	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 4	16	36	.	.	1	1	.	.	.	.	1	1	.	.	.	1	.	1	.	2	.	1	.	.	1	.	1	.	.	.	.	1	2	.	.	.	.	.	.	.	1	.	.
tree 5	10	56	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	1	1	2	.	.	1	.	.	.	.	.	.	.	.	.
tree 6	3	104	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
tree 7	9	44	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
tree 8	9	74	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	1	.	1	1	1	.
tree 9	17	52	.	.	.	2	.	1	.	.	.	.	.	.	.	2	2	.	1	1	.	2	.	1	.	.	.	.	1	.	1	.	.	1	.	1	.	.	.	.	.	.	.
tree 10	6	56	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.
tree 11	18	31	.	.	3	1	.	.	.	1	1	.	1	.	.	.	.	2	1	.	.	.	.	.	1	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	2
tree 12	31	22	.	.	1	.	2	3	1	2	1	3	2	2	1	.	4	1	4	1	2	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 13	26	26	.	.	1	1	.	2	.	3	.	1	1	2	1	3	1	1	2	1	1	.	1	.	2	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Ind	N	Median					90					100					110					120					130					140					150					160	
tree 1			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 2			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 3			.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
tree 4			.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 5			.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 6			.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 7			.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 8			.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 9			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 10			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 11			.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 12			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 13			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Ind	N	Median				170					180					190					200					210					220					230					240		
tree 1			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 2			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 3			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 4			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 5			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 6			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 7			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 8			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Ind	N	Median		330					340					350					360					370					380					390					400				
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Ind	N	Median	410					420					430					440					450					460					470					480		484
tree 1			.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Table 4. Non fruiting periods, of 13 *F. sansibarica* individuals, over the total sampling period. N = number of intervals between fruiting periods. Median = the median duration of the non fruiting periods (weeks). Each of the 239 dots represents one census period of 2 wk; the 239rd dot at the far right below represents the longest non fruiting period of 476 weeks. To determine the length of non fruiting periods, begin counting dots from left to right until a number is reached. For example, over the 16-yr sample, tree 1 initiated 26 fruit crops, giving 25 non fruiting periods with a median length of 28wk in duration. There were two 2-wk intervals, two 4-wk intervals, three 6-wk intervals, and so on.

Duration of non-fruiting periods (weeks)

Number of non-fruiting periods of each duration

Ficus sansibarica

Ind	N	Median	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50	52	54	56	58	60	62	64	66	68	70	72	74	76	78
tree 1	25	28	.	2	2	3	.	.	2	1	.	.	1	.	.	1	[illegible]	3	2	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 2	23	24	.	2	1	1	2	.	2	.	.	1	.	1	2	.	.	1	.	1	3	2	.	2	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
tree 3	9	22	.	1	.	.	.	.	.	.	1	1	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 4	16	30	.	1	1	.	.	.	.	2	.	.	.	1	2	.	1	.	1	1	.	.	.			1	1	.	2	.	.	.	.	.	.	.	.	.	.	1	.	.
tree 5	10	44	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	2		2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 6	3	90	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
tree 7	0	42	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
tree 8	9	68	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	1	.	2	.	1	.	.	.
tree 9	17	30	.	.	2	.	2	.	.	1	.	.	1	1	1	.	.	2	1	1	.	.	1	.	.	1	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.
tree 10	6	51	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
tree 11	18	24	.	[illegible]	1	.	.	1	1	.	.	.	.	1	1	.	.	1	1	.	.	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	1	.	1	2
tree 12	31	8	.	[illegible]	4	3	[illegible]	3	.	1	1	1	2	3	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
tree 13	26	15	.	3	2	2	2	.	1	3	2	1	1	2	1	1	1	.	1	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Ind	80	82	84	86	88	90	92	94	96	98	100	102	104	106	108	110	112	114	116	118	120	122	124	126	128	130	132	134	136	138	140	142	144	146	148	150	152	154	156	158
tree 1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Ind	160	162	164	166	168	170	172	174	176	178	180	182	184	186	188	190	192	194	196	198	200	202	204	206	208	210	212	214	216	218	220	222	224	226	228	230	232	234	236	238
tree 1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Ind	240	242	244	246	248	250	252	254	256	258	260	262	264	266	268	270	272	274	276	278	280	282	284	286	288	290	292	294	296	298	300	302	304	306	308	310	312	314	316	318
tree 1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Revisit intervals of trees with inedible fruits

I compared the revisit and no-revisit intervals for trees that had inedible fruits at the previous visit (i.e. fruits that were not eaten). I found that the lengths of revisit and no-revisit intervals did not differ significantly (U = 186, N1 = N2 = 23, P = 0.081; fig. 7). However, Figure 7 shows that revisit intervals tend to be shorter than no-revisit intervals, suggesting a similar revisit pattern as for previously empty trees. Figure 8 shows the total of all ripening intervals of each individual *F. sansibarica* tree (N = 13) measured over a period of 16 years. Again intervals were highly variable within and between individual trees. The median of the total of the intervals lies between 2 and 6 weeks. This was higher than the median of the lengths of the revisit intervals of trees with inedible fruit. This indicates that the monkeys returned after time intervals that are within the median duration of fig fruit ripening. They also revisit before most fruits were expected to have ripened. Since the monkeys were known to feed on insect larvae and seeds of unripe fruit this behaviour seems to be beneficial in the current environment.

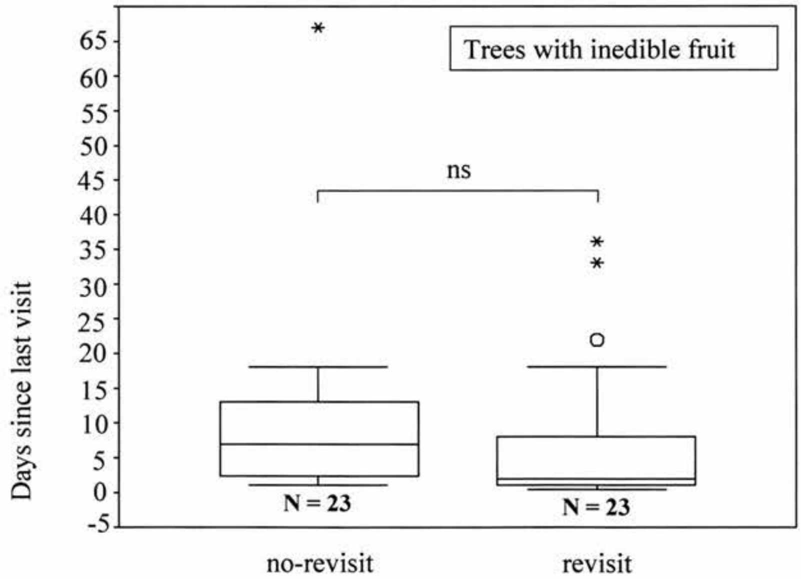

Fig. 7. The duration of revisit, no-revisit of *F. sansibarica* trees with inedible fruits (T), once they had approached within 100 meter (outer circle). Bars represent the median number of days that had passed since the last visit or approach into sight (inner circle), while the top and bottom of the boxes represent the 75 and 25 percentiles. The highest and lowest whiskers represent the highest and smallest values, which are not outliers. Circles and stars represent outliers and extreme values. Fruits are defined as inedible when they were touched but not eaten.

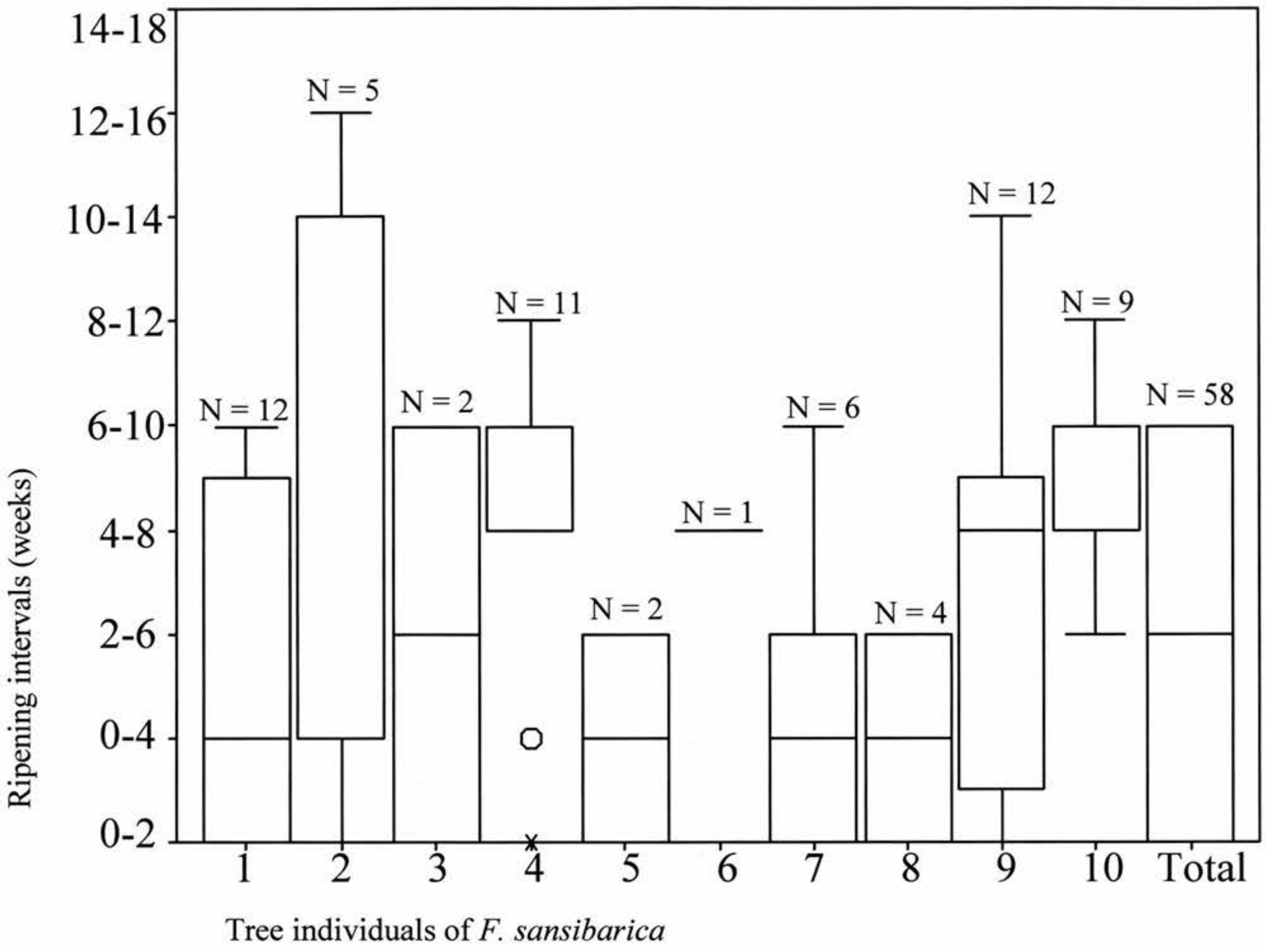

Fig. 8. Estimates of ripening intervals of 11 indiviual *F. sansibarica* trees. For example, tree 1 fruited 12 time: in 16 years. Bars represent the median estimate of the ripening interval, while the top and bottom of the boxe: represent the 75 and 25 percentiles. The highest and lowest whiskers represent the highest and smallest values which are not outliers.

Do monkeys anticipate changes in the edibility state of fruits?

Behavioural observations

To investigate whether mangabeys can anticipate changes in fruit quality once a tree carries fruit, I compared speeds with which the monkeys approached target trees with non-smelling unripe fruits on successive visits. In chapter 3 I showed that the speed with which the group approached trees that carried ripe or unripe fruits was significantly related to the quality value of the tree. Here I investigated whether speed of approach was also related to changes in quality value in particular trees. Quality (Q) is defined the cumulative number of monkeys inside the tree per minute, provided that at least one individual was eating fruits or larvae. In order to do so I compared approach speeds within two types of visits. Within the first type the quality of the tree had increased, i.e. current quality is higher than the quality of the previous visit. Within the second type of visit the quality of the tree had decreased since the previous visit. I found no significant correlation between both heights of increase or decrease and the log-10-transformed approach speed ($r_p = 0.306$, N = 33, P = 0.083, $r_p = 0.245$, N = 22, P = 0.271; fig. 9).

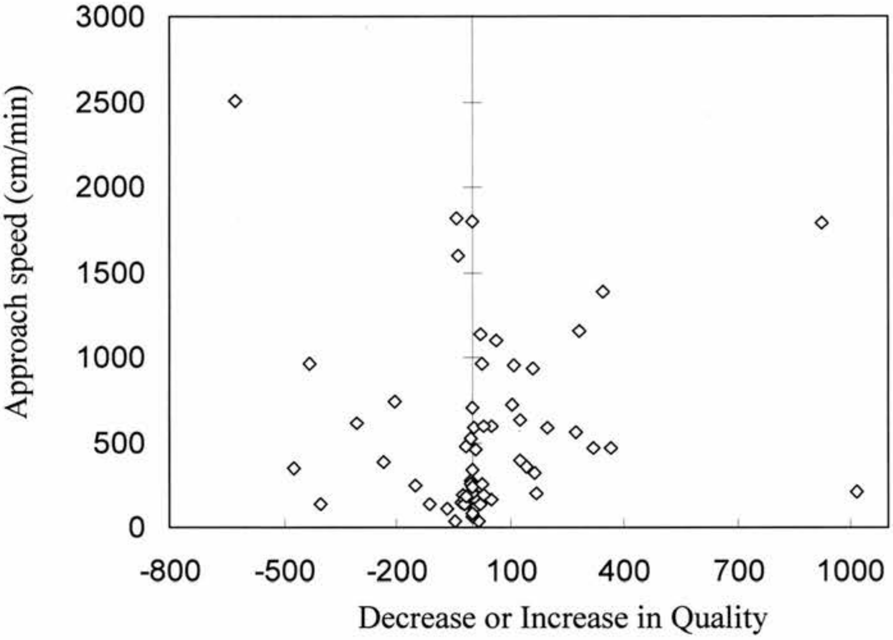

Fig. 9. The speed with which the group approached trees with unripe fruits is plotted against the difference in quality value between the current and previous visit.

In the next section I compared specific cases in which the quality values of successive visits remained relatively equal to cases where it became substantially different. I again only analysed visits towards trees with unripe fruits. I first selected cases in which the quality value (Q) of a subsequent visit remained equal; cases in which 1) previous and current quality was low, i.e. both below the median value ($Q < 52$) and 2) previous and current quality was high, i.e. both above the 75 percentile ($Q > 267$). I found that the log transformed speed with which the group approached trees that had remained relatively high in quality, since the previous visit, differed significantly from the speed with which they approached trees that had remained relatively low in quality (t = 4.813, df = 43, P = 0.000). Figure 10 shows that the speed is higher in cases in which both previous and current quality is high than in cases where the quality is low. In order to investigate the effect of the previous quality on the speed with which the group approached the subsequent time, I in addition selected cases in which the quality value had changed substantially; cases in which 1) previous quality was low (Q < 52) and current quality was high (Q > 267) and 2) previous quality was high (Q > 267) and current quality was low (Q < 52). I found that the speed (log transformed) with which the group approached trees that had substantially increased in quality, differed from the speed with which they approached trees that had substantially decreased in quality (t = -2.448, df = 12, P = 0.031). Figure 10 shows that the speed is higher in cases of significant quality increase than in cases of decrease. I again did not find a significant difference between the fruit quantity measured on both types of visits (U = 21.5, N1=6, N2 = 8, P = 0.653).

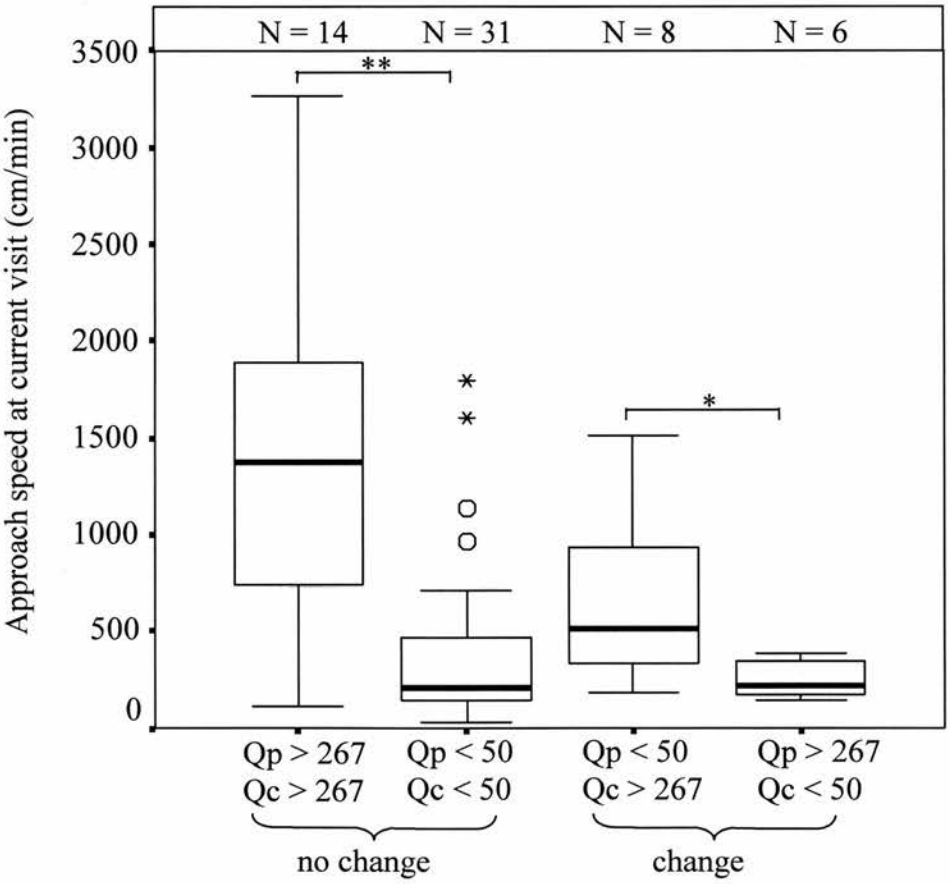

Fig. 10. Approach speed. Speed values for all visits in which the quality value of a fruit bearing *F. sansibarica* tree had either substantially changed since the previous visit or remained equal. The two boxes on the left represent cases in which quality value at the current visit (Qc) was equally high or low to that at the previous visit (Qp). The two boxes on the right represent cases in which the quality value at the current visit differed substantially from that at the previous visit. The outer right box represents the speed values at the current visit after an increase in quality, (i.e. current quality was higher than the 75 percentile (267) and the quality of the previous visit is lower than the median (52) of all quality values). The second right box represents the speed values after a decrease in quality. For both type of visits, bars represent the median speeds, while the top and bottom of the boxes represent the 75 and 25 percentiles. The highest and lowest whiskers represent the highest and smallest values, which are not outliers. Circles and stars represent outliers and extreme values.

In addition to the t-tests I did a two factor within subject ANOVA with comparable data (N = 6). The factors chosen are 1) quality on the current visit (>26: high, < 50: low) and 2) a substantial change between previous and current quality (Yes, No). The quality factor had a main effect that was significant beyond the 1 % level (F (1,5) = 74.314, P <0.0005, partial eta squared = 0.937. There was no significant effect of the change factor (F (1,5) = 0.582, P = 0.480, further indicating that the previous quality state had no effect on the speed with which the monkeys approached the tree.

Alternative explanations

In chapter 3 we found that 30 % of the variation in the average speed was explained by the average current quality values of target trees. This implies that a large part of the variation can still be explained by other factors. Approach speed could be influenced by many other factors such as for example the food availability in the area surrounding the target trees. When more food is found in the surrounding area, the monkeys eat more on the way, are less hungry and therefore travel slower towards the target tree. Additional analyses revealed that the speed with which the group approached all trees with fruits (n=32) was indeed strongly correlated with the percentage of feeding minutes observed during the approach (Kendall's Tau_b = -0.628,P < 0.0005). The relation found between average speed values and average quality values calculated from several visits (chapter 3) suggests that the approach speed was influenced by the characteristics of the tree (its quality) and not by the monkeys' hunger level. However, the relationship found between % of feeding and approach speed asks for more detailed investigation. For the days on which I had collected feeding data I conducted a partial rank correlation analysis (Kendall's Tau partial rank correlation; Siegel 1956, pg.260). Within this dataset approach speed and current tree quality were significantly related (Kendall's Tau_b = 0.328, N = 73, P <0.0005). When I kept the percentage of feeding constant approach speed and current tree quality were still significantly correlated ($T_{xy.z}$ = 0.233, Z = 2.9175, N = 73, P = 0.00352), indicating that the relation between approach speed and tree quality cannot be explained by the food availability in the surrounding area of the target tree. To further investigate whether the quality value is indeed representing the availability of edible fruit in the tree, and not the level of hungriness of the group, I compared the quality values of trees with unripe fruits (n = 15) with the percentage of edible fruits determined by 10 minutes focal observations, (i.e. the number of fruits that were toughed and eaten divided by the total number of fruits that are toughed (eaten and rejected) in the first 10 minutes of observation). This relation was highly significant ($r_s = 0.613$, $N = 18$ $P = 0.007$), suggesting that the quality value was a reliable measure for the number of edible fruits inside the target tree.

How rare are fruits eaten by apes?

Ecological observations

One of the underlying assumptions of the fruit habitat hypothesis is that ripe fruits are more rare than fruits in general and that ripe fruit dependent foragers need special adaptations to find them. To gain insight in the relative differences in probabilities of finding either ripe fruit or fruit in general, by random monitoring of trees, I compared the availability of ripe fig fruit versus fig fruit in general. First I walked five phenology transects in which I checked the phenological state of 77, 86, 105 and 48 trees of *Ficus sansibarica* at a random period in time and place. Out of all these trees I found that 26% of the trees carried fruits and 3% carried ripe fruits (table 5). Secondly, I checked the phenological state of a small number of individual trees of *F. sansibarica* (N = 13), *F. exasperata* (N = 14) and *F. natalensis* (N = 7) found on a two weekly basis for a continuous period of 16 years. Out of all the fortnightly checks of each individual tree we found fruit in 15, 21 and 9% of the checks, and ripe fruits in 2,4 and 3% of them, in the *F. sansibarica*, *F. exasperata* and *F. natalensis* respectively. Out of all monthly checks of each individual tree within the 5-year period fruit was found in 8 and 8% of the checks and ripe fruits in 2 and 4% of them for *F. sansibarica* (N = 11) and *F. exasperata* (N = 16), respectively. When I averaged the values measured in the first three data sets I estimated that the success rate during the monitoring of *F. sansibarica* trees was 16.3 out of 100 to find fruits and 2.3 out of 100 to find ripe fruits (table 3). When I compared the percentage of all the tree checks in which fruits were found with the percentage of all checks in which ripe fruits were found for each of the individual trees I found a significant difference for both the 16-years and 5- years data set (16-years dataset: Fs: $Z = -3.181$, $P = 0.001$, $N = 13$; Fe: $Z = -3.296$, $P = 0.01$, $N = 14$; Fn: $Z = -2.366$, $P = 0.018$, $N = 7$; 5-years dataset: Fs: $Z = -2.524$, $P = 0.012$, $N = 11$; Fe: $Z = -2.371$, $P = 0.018$, $N = 16$). Figure 10 shows that the percentage of checks in which ripe fruits were found, was lower than the percentage of checks in which fruits (ripe or unripe) was found.

How rare is fruit eaten by mangabey monkeys?

Ecological and behavioural observations

Apart from ripe fruits mangabeys also eat the seeds of or insect larvae inside young unripe fruit that have just emerged from the tree. To gain insight in the relative probabilities of finding fruits that are edible to mangabeys or contain edible food compared to fruits that is edible to apes, I determined the percentage of all visits towards target trees of *F.sansibarica* in which fruits were encountered and fruits were eaten. For a total of 192 visits to 54 fruit bearing *F.sansibarica* trees the fruits were eaten in 88.5 % of the cases. (In 39% of these feeding events the fruits were ripe). Knowing that the monkeys can eat in 88.5% of the times that fruits emerge from *F.sansibarica* trees I can re-estimate the success rate of finding edible fig fruit from the phenology data, which resulted in a success rate of 14.2 out of 100. This is 6 times higher than the success rate for finding ripe fruit.

Table 5. Percentages of checks in which ripe fruit (Fr), fruit in general (Ftot) out of the total of checks done within the two different methods. Each percentage is calculated separately for trees of *F. sansibarica* (Fs), *F. exasperata* (Fe) and *F. natalensis* (Fn). In the first Method we checked 316 trees that were checked once-only. In the second Method we checked 34 trees for a total of 399 times (IIa) and 27 trees for a total of 72 times (IIb).

Method	I	IIa			IIb		
Ficus species	Fs	Fs	Fe	Fn	Fs	Fe	Total
% Fr	3	2	4	3	2	4	3
% F_{tot}	26	15	21	9	8	8	15

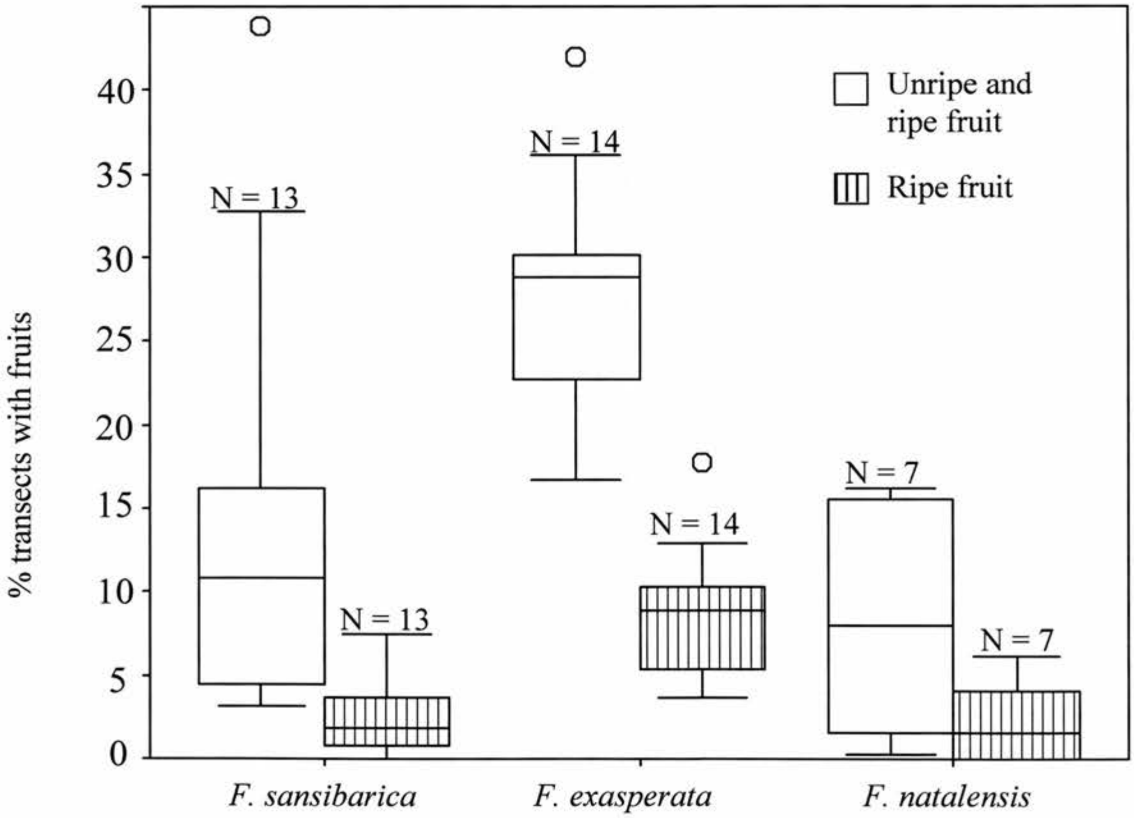

Figure 12. Median percentage of fortnightly transects (16 years) in which fruit was found. Blank boxes represent the percentage of transects in which fruits were found, shaded boxes represent the percentage of transect in which only ripe fruits were found. Bars represent the median percentage of transects in which trees with fruit were found, while the top and bottom of the boxes represent the 75 and 25 percentiles. The highest and lowest whiskers represent the highest and smallest values, which are not outliers.

DISCUSSION

Anticipation of the emergence of new fruit

In the first part of this study I investigated whether monkeys can anticipate the emergence of new asynchronously fruiting fig fruit. I found no indication that they can. I used three types of analyses. First, I investigated this question by comparing the behaviour of the monkeys towards recently depleted trees and trees that had not carried fruit for longer periods. I expected that trees that had been depleted recently would take longer to grow new fruits than trees that did not carry fruit for longer times. I found no indication, that the monkeys had similar expectations and I found no difference in behaviour of the monkeys towards the two tree types. When I calculated the angles between the directions in which the group approached and departed target trees, I found no difference between both tree types. Neither did I find a difference in the speed with which both tree types were approached and entered or the time that was spent inside them. Also, no relation was found between the revisit interval of a tree that did not have fruits for a longer time (previously empty trees) and the time that they spent inside that same tree. This suggests that the observed difference in visiting frequencies (chapter 3) was more likely a reflection of a strategy in which the mangabeys avoid depleted trees than of one in which mangabeys prefer to visit previously empty trees.

Second, I intended to investigate the question by analysing revisiting patterns of previously empty *F. sansibarica* trees to compare them with the between fruiting intervals calculated from the long-term phenology data. However, the median length of the between fruiting interval largely exceeded that of our observation period, so no comparison could be made. The analyses of the revisit behaviour did show however, that the monkeys did not expect that the chance of new fruit emergence increased with time. The likelihood of them revisiting previously empty tree did not increase with the time that had passed since the previous visit. Neither did I find convincing evidence that the monkeys were more likely to visit more frequently or return sooner to empty trees that were larger in size, i.e. trees that are more likely to have initiated new fruit crops according to other studies on neo-tropical figs (Milton et al. 1982).

Thirdly, I investigated whether the monkeys were able to predict fruit emergence by analysing approach speed towards trees that contained recently emerged fruits. We found a difference in the speed with which the study group approached trees with newly emerged fruits on successive visits. The finding that the speed on the first feeding visit was slower than the speed on the subsequent visit suggested that the monkeys were not expecting to find edible fruit on the first feeding visit. In sum, I did not find any indication that the mangabey monkeys were able to anticipate the emergence of new fruit, which is consistent with the fruit habitat hypothesis (Potts 2004).

The finding that the mangabeys did not seem to anticipate the emergence of new fruit, seems to make perfect sense from an ecological perspective. First of all, *F. sansibarica* showed to fruit a-synchronously, meaning that the monkeys cannot use the emergence of fruit in one tree as an indicator for the presence of fruit in other *F. sansibarica* trees. In addition, investigations on the predictability of the timing of fruit initiation did not show any indication that individual trees fruit at particular periods (months) of the year. The diversity indices calculated for 34 individual fig trees indicated a good deal of uncertainty involved in predicting the (two week) period in which individual trees and the species as a whole, initiated new fruit crops. Neither did the individual figs show to fruit at predictable intervals as had been observed in neo-tropical figs (Milton et al 1982; Milton 1991). I found an extreme high variation in the length of non-fruiting periods within and between individual trees, varying from 2 weeks up to 9 years within one tree individual. The standard deviation of the length of non-fruiting periods was higher than the mean. In a similar way I found an extreme high variation in the length of intervals between initiations of new fruit crops. The unpredictable character of fruit emergence and fruiting duration is unlikely to result in correct anticipations of fruit emergence by the monkeys.

The high variation in the fruit initiation intervals implies that revisiting after a week could be as rewarding as revisiting after two months. For ripe fruit frugivores, like apes, on the contrary, it would not pay to revisit shortly after a visit at which no fruits were found, since it takes at least between 2 to 6 weeks for the fruits to ripen, i.e. become edible, after they emerge. It would be interesting to investigate whether apes consequently revisit differently than mangabeys.

Analyses of revisit intervals to trees that did not carry fruit in the observation period showed that the likelihood of a revisit decreased with the time that had passed since the last visit. The median revisit interval of these empty trees was only 5 days. These results seem surprising at first. However, the results can be explained when considering the typical ranging habits of the mangabeys in the Kanyawara study area (described by Waser 1977). Our study group similar to Waser's group tended to "hang around" a good food patch for one or two weeks. After this they could travel up to 2 km to reach another food patch and often stayed there without returning to the previous area in between. Fig trees that carried no fruits that happen to be in the middle of such a patch then had a short revisit interval, probably because they simply were on the route to good food.

Anticipation of quality changes of fruit bearing trees

To investigate whether mangabeys can anticipate changes in fruit quality once the fruit is there, I first analysed the revisiting behaviour towards trees that carried inedible fruit (i.e. trees that were entered, yet no fruit was eaten). I found that the median revisit interval of trees with inedible or unripe fruits is much shorter than the median ripening interval of the 13 individual F. sansibarica trees measured over a 16 year period. This indicated that the monkeys returned within time intervals that were within the median ripening duration of fig fruit. They also revisit before most fruits were expected to have ripened. Since mangabeys were known to feed on insect larvae and seeds of unripe fruits this behaviour seems to be beneficial under current conditions.

Since it is not possible to assess when the fig fruits are edible to the monkeys by phenological observations (Janmaat et al. 2006b; chapter 3), we cannot compare the revisit intervals of the mangabeys with the optimal return intervals calculated from the phenology data. To answer the question whether monkeys can anticipate quality changes I therefore decided to use a second measure of expectation, namely the speed of approach. I compared speeds of approach on successive times that the group visited a pre-selected number of *Ficus sansibarica* trees with non-smelling unripe fruits. In chapter 3 I showed that the speed with which the group approached trees with (unripe) fruits was significantly correlated to the quality value of the tree. In this study I investigated whether speed of approach was also related to quality changes. Initially I found that speed of approach is not related to the height of increase and decrease of quality. Subsequently, I continued to compare specific cases in which the quality values of successive visits remained relatively equal to cases in which it was substantially different. I first selected cases in which the quality value (Q) of a subsequent visit remained equal; cases in which 1) previous and current quality was low, i.e. both below the median value ($Q < 52$) and 2) previous and current quality was high, i.e. both above the 75 percentile ($Q > 267$). I found that the speed with which the group approached trees that had remained relatively high in quality, since the previous visit was significantly higher than the speed with which they approached trees that had remained relatively low in quality. In order to investigate the effect of the previous quality on the speed with which the group approached the subsequent time, we selected cases in which the quality value had changed; cases in which 1) Previous quality was low ($Q < 52$) and current quality was high ($Q > 267$) and 2) Previous quality was high ($Q > 267$) and current quality was low ($Q < 52$). I found that the speed with which the group approached trees that had substantially increased in quality, since the previous visit, was significantly higher from the speed with which they approached trees that had substantially decreased in quality as well. In addition, two factors within subject ANOVA analysis did not reveal a significant effect of the type of quality change on the approach speed. In addition to the results in chapter 3 these results further support the hypothesis that the mangabeys can anticipate current fruiting states, even when the fruiting state is substantially different from the last observed fruiting state.

However, these results should be treated with care. Approach speed can be influenced by many factors, but foreknowledge, such as hunger level and scramble competition (pushing forward; van Schaik et al. 1983). Since the results from chapter 3 did not reveal any difference between the speed of approach measured early in the morning and later during the day the observed pattern is unlikely to be explained by the level of hunger of the monkeys. However, some may argue that the monkeys can be as hungry in the afternoon than in the early morning dependent on their stomach clearance rates. More convincing evidence that approach speed was influenced by the characteristic of the target tree and not by hunger state are the findings that showed a relation between average quality values and average speed of approach (chapter 3). However, only 33 % of the variation average approach speed was explained by the average quality of the tree, the remaining variation was unexplained. Within this study I suggested that the food availability in the surrounding area of the target trees could be another confounding variable. When I analysed a subset of data for which I collected the percentage of feeding of the individuals that were closest to the target tree during approach, I found that speed was negatively correlated with the percentage of feeding minutes. This finding is consistent with the interpretation that due to higher food availability in the surrounding area, the mangabeys ate more on the way, and therefore ate less once they arrived in the tree, resulting in a lower quality value. Realising that this alternative explanation existed, I conducted a partial rank correlation analyses for the subset of data on which I had collected feeding data. I found that even when the percentage of feeding during the approach was kept constant, approach speed and current quality of the approached tree was still significantly correlated, indicating that the relation between approach speed and tree quality cannot be explained by the food availability in the surrounding area of the target tree. This finding is further supported by the knowledge that *Ficus sansibarica* is a highly preferred food species. To further investigate whether the quality value is indeed representing the availability of edible fruit in the tree, and not the level of hungriness of the group I started collecting a second quality value, halfway the observation period, i.e. the ratio of the number of fruits eaten and rejected. The finding that the original quality value is highly correlated to the ratio of the number of fruits eaten and rejected strongly suggests that the original quality variable is a reliable measure for the number of edible fruits inside a tree and not simply a result of specific hunger levels. The finding that approach speed was significantly influenced by the current quality value even when the quality of the previous visit was significantly different is for the moment best explained by the hypothesis that individuals anticipated what they were going to find inside the tree.

In principle, the mangabeys could have relied on sensory cues. It is unlikely however that the mangabeys used visual cues to assess the value of the fruit bearing trees; to do so, they would have needed to detect either the small black spots on the figs, (that form the only visual sign of the presence of weevil larvae, yet not of their developmental state) or the edibility of the seeds, from before the point that the group entered the tree. Several other findings in chapter 3 support this belief. I found for example no correlation between the simple quantity of fruits in a tree, or the size of a tree, and the speed with which the group approached it (Chapter 3; Janmaat 2006b). Finally, it is unlikely that the monkeys could use olfactory cues to detect unripe fruits, as the unripe fruits produce almost no smell detectable to humans (chapter 3; Janmaat et al. 2006b). The most likely explanation for the observed behaviour therefore is that the monkeys anticipated the quality of the fruits in the tree without the use of sensory cues. This would imply that they were able to anticipate either the depletion rate of fruits and or the growth rate of weevil larvae or seeds inside the unripe fruits. It is difficult to explain, how the monkeys were able to anticipate decreases and increases in quality. For the cases of decrease, the monkeys might have integrated the number of days that had passed since the previous visit. Possibly, in the cases of quality decrease the time interval had been longer and the trees were more likely to be depleted. For the cases of quality increase, the monkeys might have known that these particular trees were infested by a larger number of weevil eggs than others. Or they might have known that the temperature since the time of the previous visit has been higher than that for other trees in other periods (Janmaat et al. 2006a; chapter 6). In order to investigate these potential explanations it is essential to do more detailed analyses on the particular cases of quality change. I therefore stress the need for further investigation and an increase of the size of the dataset. This would also allow me to further investigate the possibility of cueing by the males that are known to leave the group and feed alone in fig trees. Results of analyses on the sex ratio of individuals that were first to arrive at target trees did not suggest that the males cued the group towards particular high quality trees, (chapter 3; Janmaat et al. 2006b), however more research is needed to fully confirm this.

Further studies should also take into account the effect of foraging group size. Larger subgroups may approach faster due to the effect of scramble competition (van Schaik et al. 1983). At the same time large feeding groups will result in measurements of high quality values, providing another alternative explanation for the observed relationship between approach speed and current tree quality. For future studies I therefore advise to always use the second additional quality value: the ratio of the number of fruits eaten and rejected and possibly fruit intake rates for other fruit species. According to Janson individual fruit intake rate is not influenced by hunger levels or group size (Janson 1987; personal communication).

Is anticipation more rewarding for apes than for monkeys?

Lastly, I investigated to what extent ripe fruits are more difficult to find by random monitoring than fruits in general, as it was suggested in the fruit habitat hypothesis. The percentage of checks in which fig fruits were found were significantly higher than the percentage of all checks in which ripe fig fruits were found for each of the individual trees over a period of 16 years. The phenology transects, one that included a high number of trees that were checked over a limited time period, and a second that included a small number of trees that were checked over an extended time period (16 years and 5 years) both showed that the probability of finding ripe fig fruit can be on the average 5 times lower than the probability of finding fruits in general. For *F. sansibarica* it was 7 times lower. I estimated that our success rate of finding ripe fruits in all the *F. sansibarica* that were monitored was 2.3 out of 100. The success rate to find fruits in general was 16.3 out of 100. More detailed analyses that included observations of the mangabeys' feeding behaviour in which we measured which percentage of visits to fruit bearing trees of *F. sansibarica* the monkeys actually ate, resulted in a success rate to find fruit that is edible to the mangabeys of 14.2 out of 100. This suggests that the chance for ripe fruit dependent foragers like apes to find edible *F. sansibarica* figs is 6 times lower than it is for the mangabey monkeys to find edible figs. These results are consistent with the fruit-habitat hypothesis. These results are also congruent with the results a 5-years phenology study on 394 individual neo-tropical primate food trees (Milton 1988).

In sum, the results of the phenological data on fig trees is consistent with the idea that apes would benefit more from anticipatory skills than monkeys, simply because ripe figs were found to be more rare.

What are the selective benefits of anticipatory behaviour for monkeys?

Despite the fact that mangabeys can eat from unripe as well as ripe fruit and therefore have an easier job while searching for edible food, this study suggests that they did develop an ability to anticipate. Results of chapter 3 suggested that the mangabey group was able to anticipate differences in fruit quality. This study, in addition, suggests that the mangabeys were also able to anticipate substantial changes in fruit quality. These findings are inconsistent with the fruit-habitat hypothesis. So despite the confirmation that selective benefits of anticipatory behaviour initially seem to be higher for ripe fruit dependent frugivores such as apes, I find indications that anticipatory behaviour has evolved in a species that is much less dependent on ripe fruits, namely a monkey species. As a result of these findings I think that it is not the rareness or the complexity of the spatial and temporal distribution of ripe fruits that may have triggered the evolution of complex cognitive skills, such as anticipatory behaviour, in ripe fruit dependent foragers, like it was suggested by Milton (1981) and Potts (2004). Instead, I hypothesize that it is simply the level of competition and the opportunity/possibility to be earlier than other competitors that triggered anticipatory behaviour. Whether foragers search for either ripe fruits or unripe fruits with protein rich weevil larvae, an ability to anticipate could pay in both cases. This hypothesis also explains why I failed to find evidence for an ability to anticipate the emergence of new fig fruit. The emergence of fig fruit showed to be of such an unpredictable nature, that there simply is no way to be earlier than others and or to out compete them, and possibly for that reason the trait did not evolve.

SUMMARY CHAPTER 5

Great apes are more dependent of ripe fruits than monkeys. Hence, they are expected to experience greater benefits from an ability to anticipate the emergence of ripe fruit. This expectation resulted in the fruit habitat hypothesis. I tested this hypothesis by investigating whether monkey individuals indeed lack anticipatory skills and by estimating the relative benefits of an ability to predict the initiation of a fruiting bout. In order to do so I studied the ranging behaviour of one group of grey-cheeked mangabey monkeys relative to a number of pre-selected fruit trees within their home range. I collected data on the monkeys' revisiting behaviour and speed of approach towards these trees as a function of the trees' fruiting state. In addition, I analysed 16 years of phenology data on 34 individual fig trees. We found no difference in the monkeys' behaviour towards recently depleted target trees and target trees that had not carried fruit for longer times. The likelihood of a revisit did not increase with the time that had passed since the last visit. I found that the group travelled significantly slower to target trees that had recently grown edible fruits on the first feeding visit than on the subsequent visit. All these results taken together strongly suggest that the monkeys were unable to anticipate the initiation of a fruiting bout. Further analyses did suggest that once a fruiting bout had started, the monkeys were able to anticipate changes in the trees value. The speed at which target trees were approached was significantly related to the current quality value of these trees even when the quality of the previous visit was substantially different. Additional analyses showed that the monkeys were unlikely to have relied on cues available over long distances, auditory, visual or olfactory, in their anticipations. Combining the results from behavioural and ecological observations I conclude it to be unlikely that enhanced cognitive behaviour, like anticipatory behaviour was triggered by the complexity of the spatial and temporal distribution of ripe fruits only, like it was suggested in the fruit habitat hypothesis. Under current conditions, I consider variables such as the level of competition for fruit and the possibility to arrive earlier than competitors at fruits with nutritional value (ripe or unripe with insects), as more likely variables to favour such cognitive skills. Whether foragers search for either ripe fruits or unripe fruits with protein rich insect larvae, an ability to anticipate could pay in both cases.

In the next chapter I further investigate how the monkeys were able to predict changes in fruit quality. I investigate if they integrate past weather conditions in their anticipations.

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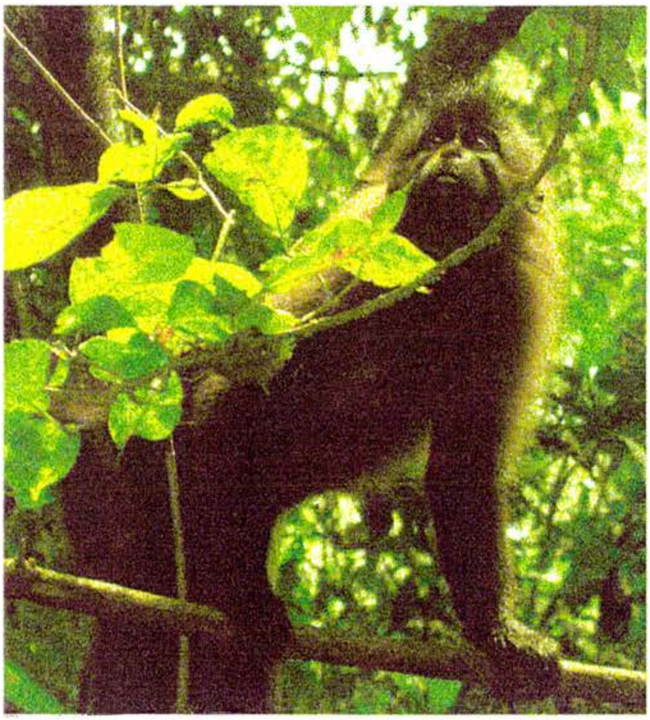
CHAPTER 6

MANGABEYS TAKE WEATHER INTO ACCOUNT WHEN SEARCHING FOR FRUITS

Results of this chapter are published in Current Biology (Janmaat et al. 2006a)



Juvenile grey-cheeked mangabey

INTRODUCTION

"The sun, with all those planets revolving around it and dependent on it, can still ripen a bunch of grapes as if it had nothing else in the universe to do". Galileo. (from: The two chief world systems: the ptolemaic and copernican, edited by S. Drake 1952).

Weather variables, such as temperature and solar radiation, are known to influence the ripening rates and growth of fruit (Morrison & Noble 1990; Wang et al.2000; Adams et al.. 2001; Diaz-Perez et al.. 2002; Spayd et al.. 2002; Graham et al. 2003; Houle 2004). Temperature can also affect the development of larvae that are extracted by primates from infested fruit (Mazzei et al. 1999; chapter 3; Janmaat et al. 2006b). I investigated whether grey-cheeked mangabeys (*Lophocebus albigena johnstonii*) of Kibale National Park, Uganda, take temperature and solar radiation into account when searching for figs. I predicted that monkeys would be more likely to revisit trees in which they had previously found fruits following a period of sunny and warm days, compared to after a cooler period with overcast skies.

I studied the ranging pattern of an observer-habituated monkey group in relation to a large number of pre-selected *Ficus* trees (N=80) throughout the group's home range. Data collection began as soon as the group entered a critical 100m-radius circle around a target tree and proceeded to the trunk. I then determined whether or not the tree carried fruit. As soon as the group re-entered the same circle for a second time, usually a few days later, I noted whether or not individuals proceeded to the trunk, i.e. whether they 'revisited' or simply 'bypassed' the tree.

The purpose of this study was to investigate whether the likelihood of revisiting or bypassing a target tree was related to the weather conditions experienced during the period since the previous visit. I thus determined the average daily temperature (maximum and minimum) and solar radiation (% high-level radiation) for the time interval between each visit and successive revisit/bypass. I expected averages to be higher during periods prior to revisits than bypasses, but only for trees that carried fruit at the previous visit.

METHODS

Study species

The group of grey-cheeked mangabeys was studied in the semi-logged moist evergreen forest of the Kibale National Park in Uganda (0°34'N, 30° 21'W) (Waser1974; Waser & Floody 1974; Chapman et al. 1997). The group consisted of 20-27 independently moving individuals that were well habituated to human observers. Figs (*Moraceae*) were amongst the most preferred foods of grey-cheeked mangabeys (Waser1974; Waser 1977; Barrett 1995; Olupot 1999). I focussed on the relatively common strangler fig *Ficus sansibarica* (density: 1.7 trees/ha (Chapman et al. 1999b)) that shows no synchrony in fruiting periods (Waser 1974; chapter 3; Janmaat et al. in press). Fruits can reach a diameter of 5.1cm, with no obvious visual signs of ripeness, such as specific colour or size. Chimpanzees and mangabeys assess edibility by squeezing individual fruits (chapter 3; Janmaat et al. in press). Unripe figs often contain weevil larvae, such as *Omophorus stomachosus* (Waser 1977), which are extracted and eaten by the monkeys.

Data collection

Prior to each observation period, I selected and labelled the maximum number of fruit bearing fig trees within the 623ha study area used by the group, such that individual trees were separated by at least 200 m (fig. 1). In regions without fruit-bearing trees, I identified fruitless trees using the same distance criterion. In areas that did not contain any *F. sansibarica* trees, I included trees of other closely related fig species, a total of 80 fig trees. The monkeys visited and re-approached only a subset of these, a total of 53 trees (N=22 with fruit, N=18 without fruit, N=13 changed fruiting state throughout the observation period). The majority of trees were of the species *F. sansibarica* (N=42), the others were *F. exasperata* (N=3), *F. sur forsk* (N=3), *F. stipulifera* (N=1), *F. natalensis* (N=2), *F. mucuso* (N=1) and *F. vallis-choudae* (N=1). For the final study period (January to May 2004; N=100 days) I also investigated whether average percentage of high-level solar radiation influenced revisiting behaviour. Within this period, the group re-approached 14 trees with fruit, 9 trees without fruit, and 6 trees that changed fruiting state.

I followed the monkey group for three continuous periods of 50, 60 and 100 days between 24 March 2003 and 30 April 2004. Two observers followed each group from the first movement in the morning to final resting-place at dusk. Whenever the group came within 100 metres of one of the target trees the primary observer stayed with the group while the other observer rushed to the target tree to estimate 1) the quantity of fruits, 2) the ripeness state and presence of weevil larvae inside fallen fruits, 3) whether other frugivorous animals or group members were present, and 4) whether or not the monkeys entered the tree. To exclude the potential use of auditory cues to discover fruit availability I only analysed approaches where no other primate or any other frugivorous species, such as black-and-white casqued hornbills (*Bycanistes subcylindricus*), were present before the arrival of the study group. Adult males sometimes feed on their own away from the group. In a previous study, I have shown that the group was unlikely to be cued by the behaviour of males (chapter 3; Janmaat et al. in press).

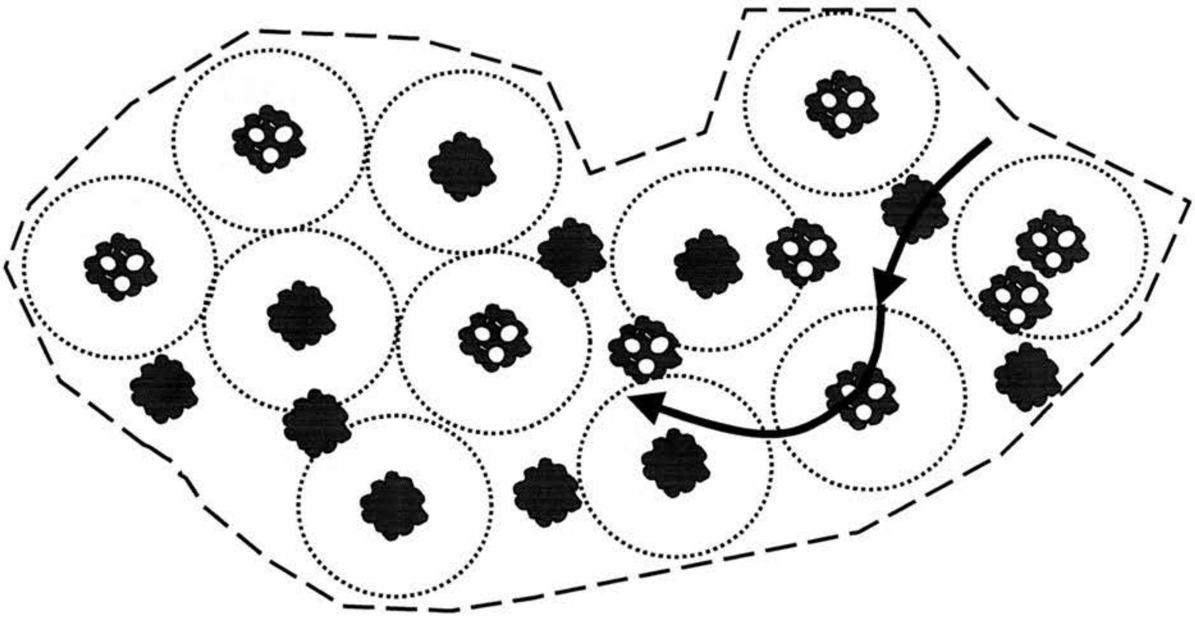


Fig. 1. Measuring revisiting behaviour. The diagram illustrates an example of part of the study group's daily route (arrows) amongst target trees, each surrounded by an imaginary 100m-radius circle (dotted line). Once the group entered the circle, one observer rushed to the tree to determine the fruiting state and whether the group came into sight and entered the tree. In this example, the group visited one target tree with fruit and bypassed one without fruit.

The ranging of the group was determined by measuring its position every 10 min using a global positioning system (Garmin 12XL) and a trail system. Day Journey Lengths were calculated from hand drawn daily maps (Waser 1975). Solar radiation was defined as the percentage of daily samples with high-level illumination (the upper threshold of a Gossen Lunasix 3 light meter when directed at the sun, 350,000 LUX). Samples were taken every 10 min between 07:30 and 17:30 hours. Temperature data were collected daily by the Kibale Fish and Monkey Project in the vicinity of the study area.

Statistical analyses

The median interval until the group re-approached a target trees was 5.0 days. The number of daily revisits was randomly distributed in time (dispersion coefficient=1.03 (Sokal & Rohlf. 1981; Chapman et al.1999b), suggesting that they were not restricted to particular periods of high fruit production. Whenever the group re-approached within a 100m of a target tree previously visited within the study period, I noted whether or not individuals proceeded to the trunk, i.e. whether they 'revisited' or 'bypassed' the tree. 95% of all repeated (<100m) approaches to target trees were separated by at least one day, suggesting that they should be treated as independent events. In some rare cases, the group revisited a particular tree two or three times in the same day. I only included these revisits in our analyses if the group had moved out of the outer circle between successive revisits.

Since most of our variables were not normally distributed I relied on non-parametric Mann Whitney U-test and Spearman correlation analyses for the main bulk of our analyses. All tests were two tailed. In each case I assessed evidence about specific hypotheses, and hence did not adjust critical alpha levels using Bonferroni procedures (Perneger 1998). Whenever an effect was found to be statistically significant, I conducted a follow-up analysis using logistic regression analyses with SPSS 10.0, provided variables were statistically independent from each other (Field 2000). The statistical significance of a variable in regression can be judged either by the probability level associated with its parameter or by the change in the overall goodness of fit of the model due to the addition of that variable. The latter procedure depends less on specific assumptions needed for parameter estimation and thus is preferred; I provide both the probability that a given variable's asymptotic parameter equals 0 (second p-value), as well as the total model goodness of fit (first p-value)(measured by the chi-square statistic against the null hypothesis of homogeneity).

RESULTS

Revisiting is influenced by weather

The average maximum daily temperature was significantly higher when the group revisited than when it bypassed a tree. This was only true for trees that carried fruit during the group's previous visit (with fruit: U=5476.0, $N_{revisit}$= 143, N_{bypass}=91, P=0.041; without fruit: U=2107.5, N_r=49, N_b=92, P=0.526; fig. 2).

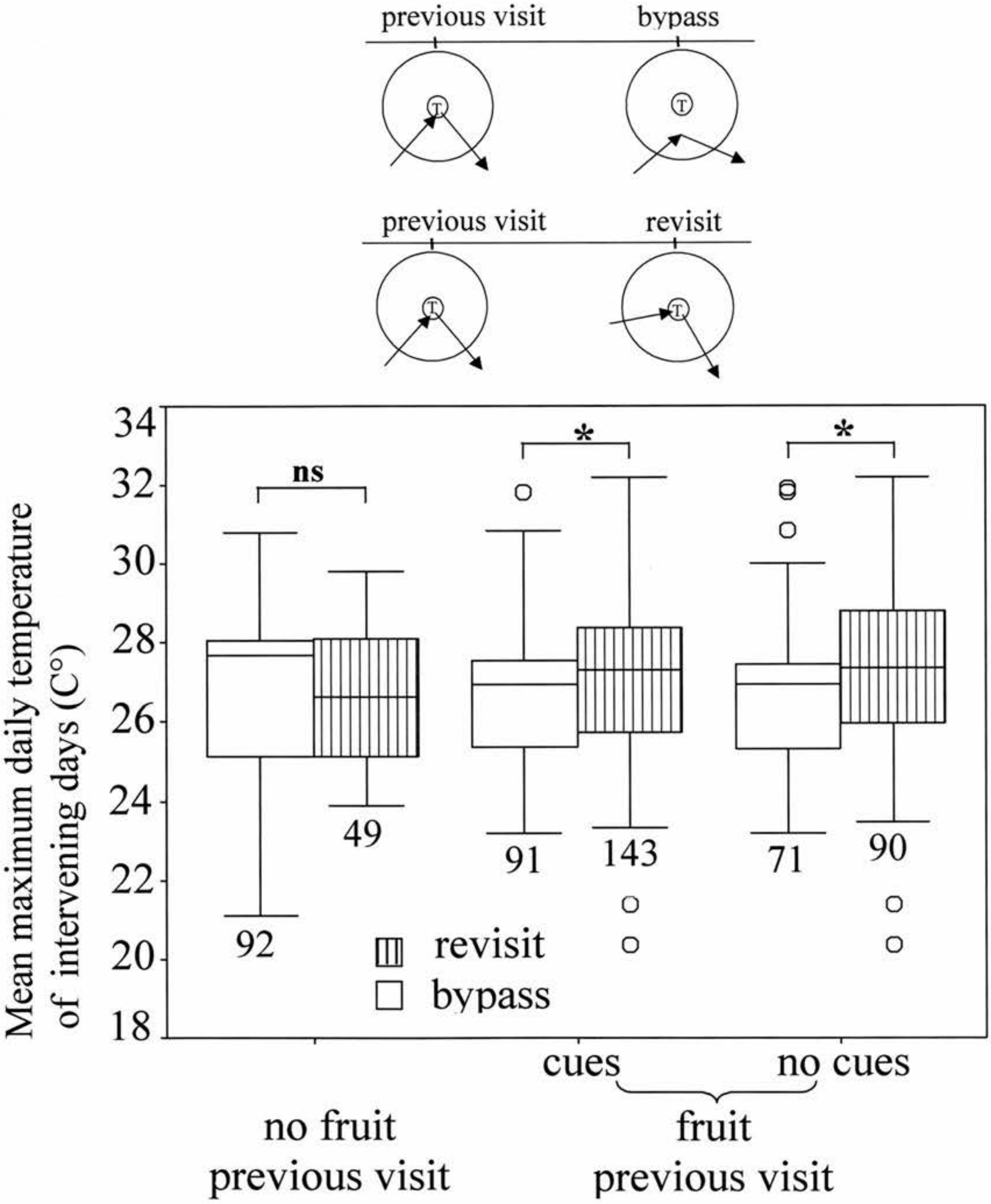


Figure 2. The influence of temperature on revisiting behaviour. Average daily maximum temperature determined for the intervening period between the time the group entered the 100m-radius circle and the time the group last visited the same tree. Shaded boxes represent average temperature values for revisits; white boxes represent bypasses. Different clusters refer to trees that 1) did not carry fruit at the previous visit, 2) carried fruit at the previous visit and 3) carried fruit at the previous visit but no longer offered any sensory cues. Bars represent the median values of the average temperatures; top and bottom of the boxes represent the 75 and 25 percentiles. Whiskers represent highest and lowest values; circles and stars represent outliers and extreme values.

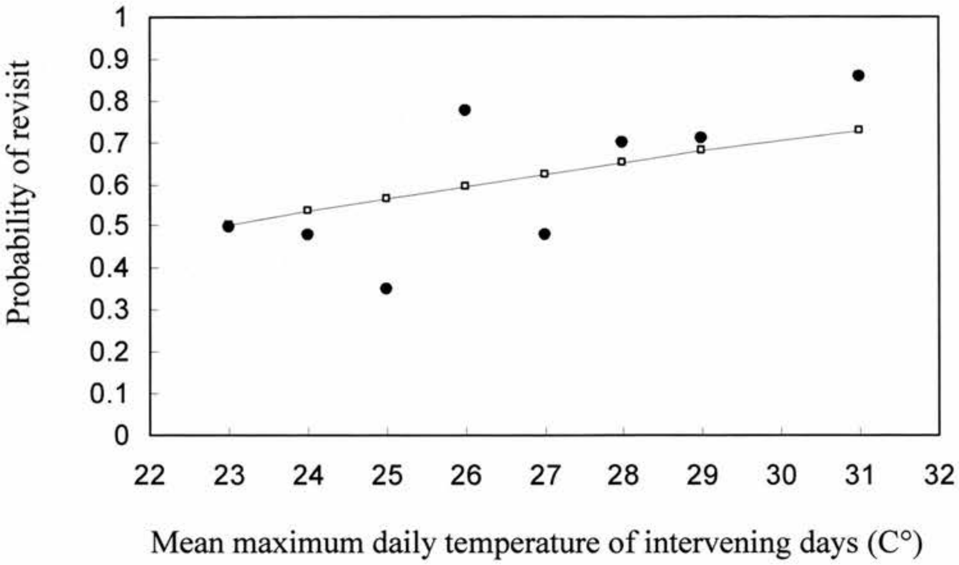


Figure 3. Probability of revisit as a function of the mean maximum temperature of the intervening days between a visit and a re-approach. Average temperatures were calculated between the first visit and the subsequent re-approach. For this graph temperature values were rounded to integers (e.g. 27° ranges from 26.5° to 27.4°). For each temperature interval, I calculated the observed revisiting probability (closed circles) as the proportion of times the monkeys entered the critical 100m-circle around a target fig tree and proceeded to the trunk (N= 8-48). This graph only considers temperature intervals with more than four data points. Predicted values (open squares) for the logistic regression were calculated as $Y=e^{\text{constant} + ß*X}/(1+ e^{\text{constant} + ß*X})$.

Logistic regression analyses showed that the probability of revisiting a tree increased with increasing average maximum temperature for trees that carried fruit (chi-square=3.938, P=0.047, df=1; ß=0.121, P=0.050, df=1; fig. 3). No significant relationships were found between the monkeys' foraging decisions and average daily minimum temperature measured at night (fruit: U=5951.0, N_r=143, N_b=91, P=0.271; no fruit: U=2112.0, N_r=49, N_b=92, P=0.539).

I also investigated whether the mangabeys returned earlier to a fruit-bearing target tree after warm periods compared to cooler ones. I found a negative relationship between the average maximum temperatures and the number of days between a current and previous visit (N=74; r_s=-0.260, P=0.025), but only for trees that had particularly high fruit cover of at least 25% during the previous visit. Trees with such large amounts of fruit were unlikely to be depleted at the day of re-approach. If all trees were included, the relationship was no longer significant (r_s=-0.09, P=0.171, N=231).

For the third data collection period (N=100 days), I additionally measured solar radiation. This second weather variable also influenced the monkeys' revisiting behaviour but effects were weaker. The average daily percentage of high-level radiation tended to be higher for revisits than for bypasses, again, only for trees that carried fruit at the previous visit (fruit: U=1735.5, N_r=93, N_b=46, P=0.071; no fruit: U=642.5, N_r=23, N_b =57, P=0.890; fig. 4). Additional logistic regression analyses did not reveal a significant relationship (chi-square=0.28, P=0.597, df=1; P=0.596, df=1). There was no correlation between the length of the revisit interval and the average percentage of high-level radiation (all fruit-carrying trees: r_s=-0.09, P=0.321, N=133; trees with >25% fruit cover: r_s=-0.223, P=0.136, N=46).

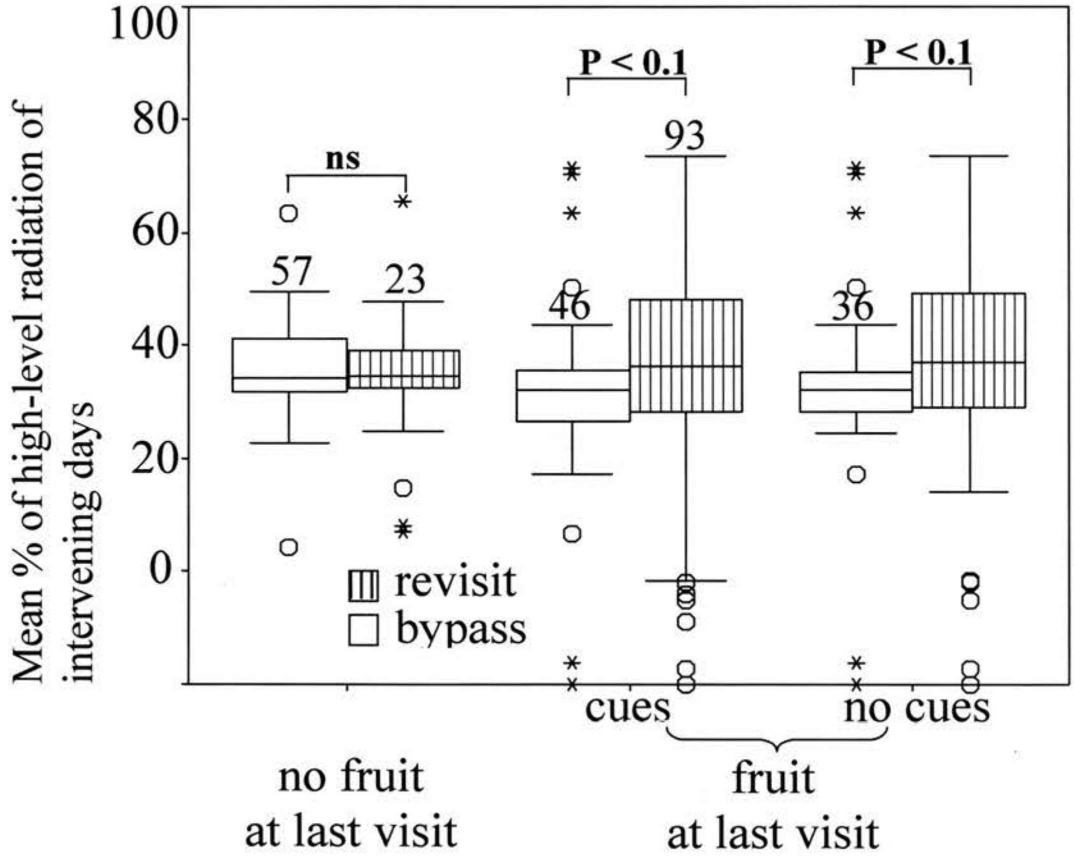


Fig. 4. The influence of solar radiation on revisiting behaviour. Average percentage of high-level solar radiation determined for the intervening period between the time the group entered the 100m-radius circle and the time the group last visited the same tree. Shaded boxes represent average radiation values for revisits; white boxes represent values for bypasses. Each cluster refer to trees that 1) did not carry fruit at the previous visit, 2) carried fruit at the previous visit and 3) carried fruit at the previous visit but no longer offered any sensory cues. Bars represent the median values of the average temperatures; top and bottom of the boxes represent the 75 and 25 percentiles. Whiskers represent highest and lowest values; circles and stars represent outliers and extreme values.

Is revisiting influenced by sensory cues?

An obvious alternative hypothesis suggests that the patterns described in figures 2 to 4 are the result of monkeys' responding directly to the physical presence of ripe fruits while approaching a tree. For example, monkeys may be more likely to revisit a fruit-bearing tree after warm and sunny weather, simply because they are responding to visual or olfactory cues emitted by ripe fruits. To address this point, I repeated the same set of analyses for a subset of trees that carried fruit at the previous visit, but excluding all trees that carried ripe fruits at the current revisit or bypass. The majority of these trees carried unripe fruit, while some others were already depleted. This subset of trees was still valuable to the monkeys because unripe fruits were often infested by weevil larvae (69% of trees with unripe fruit visited). As the developmental state of the larvae cannot be assessed from the outside monkeys have to inspect each fruit individually. Visual cues, in other words, do not offer reliable cues for foraging decisions with this subset of trees. Unripe fruit or the weevil larvae inside them did not emit any olfactory cues that could be detected from further than 20cm, making it extremely unlikely that monkeys were able to use olfactory cues to take foraging decisions from over 100m from a target tree.

For this subset of trees (N=31), revisits were associated with higher average daily maximum temperature than bypasses (U=2502.5, N_r=90, N_b=71, P=0.017, fig. 2). Additional logistic regression analyses for trees of this subset showed that the probability of a revisit increased with increasing average maximum temperature (chi-square=3.841, P=0.050, df=1; ß=0.144, P=0.054, df=1). A similar trend was found for the average percentage of high-level radiation (N=20; U=871, N_r= 63, N_b=36, P=0.056; fig. 4), although logistic regression analyses did not reveal a significant effect (chi-square=1.283, P=0.257, df=1; P=0.261, df=1).

Is revisiting influenced by weather conditions on particular days?

(a) Weather conditions during first visit

It could be the case that the monkeys returned earlier to a particular tree, if the weather conditions were favourable during the day of the initial first visit. For example, finding fruit during hot and sunny days may establish special memories in the monkeys compared to when finding fruits during cooler, cloudy days. According to this hypothesis, monkeys may simply remember particular days of first visiting a tree, rather than integrating temperature over several days. However, I found that daily maximum temperature measured at the first visit did not differ between subsequent revisits and bypasses (U=5723.0, N_b=91, N_r= 143, P=0.121), and further logistic regression analyses did not indicate a significant effect of this temperature value either (chi-square=1.946, P=0.164, df=1; P=0.163, df=1).

(b) Weather conditions during re-approach (revisit/bypass)

It may be the case that the monkeys' behaviour was driven by the weather conditions of the day of re-approach, rather than the temperature integral of the previous time period. For example, if monkeys are more active on hot days they will be more likely to come across trees with figs, regardless of weather conditions during the previous days. I found some support for this hypothesis because day journey length was significantly correlated with daily maximum temperature (r_p=0.247, N=210, P=0.001). However, the general increase in activity during hot days did not explain the monkeys' visiting patterns of fig trees. Day journey lengths leading to revisits did not differ significantly from those leading to bypasses (all trees: t =1.148, df=373, P=0.252; trees with fruit at previous visit only: t =1.197, df=193, P=0.233).

To further investigate this hypothesis I split the data and analysed the monkeys' behaviour on the day of re-approach and during all other days separately. I found no difference in the maximum daily temperature between revisits and bypasses on the day of re-approach (U=6001.0, P=0.316, N_r=143, N_b=91). Daily percentage of high-level radiation, however, tended to be higher on days of revisits than bypasses (U=1722.0, P=0.062, N_r=143, N_b=91). For all other days, the average maximum daily temperature was still significantly higher for revisits than bypasses (U=4876, N_r=127, N_b=91, P=0.049), but no effect was found for average radiation (U=1748.5, N_r=81, N_b=46, P=0.566).

I used multiple logistic regression analyses to investigate the effects of weather and activity on the monkeys' foraging behaviour. These analyses showed that the probability of revisiting increased significantly with percentage of high-level of radiation (hereafter RAD) on the days of revisit/bypass and with maximum temperature (hereafter Tmax; table 1) of the interval prior to the day of revisit/bypass. Adding either RAD or Tmax to the respective univariate models (1 and 2; table 1) increased the fit significantly (RAD: Δchi-square=4.130, df=1, P=0.042; Tmax: Δchi-square=6.527, df=1, P=0.011; table 1; block entry method). Adding day journey length (hereafter DJL) to control for an increase in activity (see rationale above) did not lead to relevant effects (Δchi-square=0.720, P=0.396; table 1). For trees that did not carry fruit during the previous visit, neither Tmax nor RAD was a significant predictor of revisiting probability (chi-square=1.829, P=0.401, df=1; RAD: P=0.669, df=1, Tmax: P=0.229, df=1).

(c) Weather conditions between first visit and re-approach

Finally, perhaps mangabeys remembered particularly hot days in the time period <u>between</u> first visit and revisit/bypass, rather than integrating an averaged value of maximum temperature over several days. However, when considering the highest temperature value for each time period only, I failed to detect any differences between instances of revisits and bypasses ($U=6162.5$, $N_r= 140$, $N_b=91$, $p=0.676$).

The average maximum daily temperature for all days between the first visit and subsequent re-approach, but excluding these days, was higher prior to revisits than to bypasses for trees with fruit (trees with fruit at previous visit: $U=2425.0$, $N_b=73$, $N_r=83$, $P=0.032$; trees with fruit at previous visit, but no ripe fruit at current visit only: $U=1141.0$, $N_b=57$, $N_r=57$, $P=0.006$). Differences for average radiation between cases of revisit and bypass were not significant ($U=881.0$, $N_b=33$, $N_r=56$, $P=0.715$; $U=525.0$, $N_b=26$, $N_r=41$, $P=0.923$).

Table 1. The relationship between the probability of revisiting and weather conditions. Results of logistic regression analyses (for 100 days period) illustrate the probability of revisiting of trees that carried fruit at the previous visit. RAD represents the daily percentage of high-level radiation on the days of revisit/bypass; Tmax represents the average maximum temperature values measured between the previous visit and the day of revisit/bypass (excluding the day of revisit/bypass). DJL is the day journey length travelled by the monkeys on the days of revisit/bypass (in metres).

Table 1 Model	Variable	Parameter estimate (SE)	Probability	Total model Chi-square (df)
1	Constant	-0.337 (0.416)	-	
	RAD	1.660 (0.699)	0.017	5.883 (1)
2	Constant	-5.477 (3.303)	-	
	Tmax	0.217 (0.119)	0.068	3.486 (1)
3	Constant	-7.219 (3.530)	-	
	RAD	1.808 (0.727)	0.013	10.013 (2)
	Tmax	0.244 (0.124)	0.049	
4	Constant	-7.935 (3.659)	-	
	RAD	1.824 (0.731)	0.013	10.733 (3)
	Tmax	0.245 (0.125)	0.050	
	DJL	0.001 (0.001)	0.399	

In sum, these additional analyses are consistent with the idea that the monkeys' foraging patterns could not be explained by events that took place on particular days, but that individuals integrated the weather conditions over larger periods of time.

DISCUSSION

The question of why primates, and especially humans, reveal more developed cognitive skills than other mammals has a long history in science. The most widely accepted notion has been that primates' superior cognitive abilities have evolved in the social realm. Many primate species live in complex societies and, the argument goes, this favoured the evolution of especially developed social skills (Byrne & Whiten 1988; Prop 1991). Although there is much empirical evidence in favour of the social intelligence hypothesis, very little work has been conducted to address its alternative, the idea that primate cognition has evolved to deal with problems of an ecological nature, such as foraging for food.

With this research I sought to address this anomalous gap. By following a group of wild monkeys from dawn to dusk in their natural habitat, I obtained an almost complete record of their foraging decisions in relation to their preferred food over three unusually long time periods. My data showed that the monkeys were more likely to revisit trees after a period of warm and sunny days compared to cold and cloudy days, provided they had found fruits during the previous visit. These findings are consistent with the idea that monkeys take foraging decisions based on episodic-like memories of whether or not a tree previously carried fruit, combined with a more generalised understanding of the relationship between temperature and solar radiation and the maturation rate of fruit and insect larvae. How exactly the monkeys managed to register the relatively subtle differences in average temperature values (fig. 2), however, remains elusive and a topic for further research.

The mangabeys' foraging behaviour shows similarities with those of some birds, such as Brent geese (*Branta bernicla*), finches (*Fringillid* sp.), and scrub jays (*Aphelocoma coerulescens*) (Cody 1971; Whiten & Byrne 1997; Clayton & Dickinson 1998; Emery & Clayton 2004). In these species, foraging decisions are influenced by the recovery rate of plants, the ripening rate of seeds, and the perishing rates of moth larvae and peanuts, respectively. Despite the similarities, my study is different in that I have shown that monkeys also take into account variation in weather conditions, rather than mere differences in elapsed time.

The fact that birds can demonstrate episodic-like memory when collecting cached food has led to a number of provocative theories concerning the evolution of cognitive abilities in non-human species (Clayton & Dickinson 1998; Emery & Clayton 2004). For non-caching species, such as non-human primates, a main selective benefit of episodic-like memories is to anticipate the emergence of new food sources, which is particularly relevant for fruit species that show no signs of synchronous ripening, such as figs (Waser 1974; chapter 3; Janmaat et al. 2006b). Kibale Forest has some of the highest primate densities ever recorded (Struhsaker 1972; Chapman et al. 1999a; Chapman et al. 2000) and competition for food is consequently high (Hauser & Wrangham1990; Houle 2004). The ability to take weather-related ripening of fruits into account could allow individuals to forage much more efficiently in order to thrive in an ecologically complex and highly competitive rainforest habitat (Struhsaker 1972; Chapman et al. 1999a; Chapman et al. 2000; Houle 2004).

SUMMARY CHAPTER 6

Temperature and solar radiation are known to influence maturation of fruits and insect larvae inside them (Morrison & Noble 1990; Mazzei et al.1999; Wang et al.2000; Adams et al. 2001; Diaz-Perez et al. 2002; Spayd et al. 2002; Graham et al. 2003; Houle 2004). I investigated whether grey-cheeked mangabeys (*Lophocebus albigena johnstonii*) of Kibale Forest, Uganda, take these weather variables into account when searching for ripe figs or unripe figs containing insect larvae. I predicted that monkeys would be more likely to revisit a tree with fruit following several days of warm and sunny weather compared to a cooler and more cloudy period. I pre-selected 80 target fig trees and monitored whether they contained ripe, unripe, or no fruits. I followed one habituated monkey group from dawn to dusk for three continuous observation periods totalling 210 days. Whenever the group came within a 100m circle of a previously visited target tree for a second time, I noted whether or not individuals proceeded to the trunk, i.e. whether they 'revisited' or simply 'bypassed' the tree. I found that average daily maximum temperature was significantly higher for days preceding 'revisits' than 'bypasses'. The probability of a revisit was additionally influenced by solar radiation experienced on the day of re-approach. These effects were only found for trees that carried fruit at the previous visit but not for trees that had carried none. I concluded that these non-human primates were capable of taking past weather conditions into account when searching for food. I discuss the implication of these findings for theories of primate cognitive evolution.

* * *

GENERAL DISCUSSION

"The argument that primate ranging habits, especially those of frugivores, place exceptional demands on cognitive abilities remains essentially a hand waving exercise, and there is little evidence to support it", Barton (2000).

EMPIRICAL EVIDENCE GAINED BY THIS STUDY

Aim of the studies

In this thesis I investigated what particular challenges primates encountered within their natural habitat and what strategies and cognitive skills they performed in order to deal with these challenges. In order to understand the observed relationship between levels of frugivory and relative brain and neocortex size in primates (e.g. Barton 1996; 2000), I focussed my studies on the cognitive challenges encountered by rain forest primates that were in search of fruit. I investigated a number of fruit localisation strategies in two frugivorous monkey species: the grey-cheeked mangabey (*Lophocebus albigena johnstonii*) in the Kibale National Park, Uganda and the sooty mangabey (*Cercocebus atys atys*) in the Taï National Park, Ivory Coast. The main aim of this study was to gain insight in the level of efficiency with which primates find fruit bearing trees and the type of strategies and skills that are used to optimise the timing of arrival at fruit trees.

Do monkeys know where fruits are?

The results of this thesis indicate that the mangabeys are relatively efficient in finding fruit of particular tree species. For both sooty and grey-cheeked mangabey groups, the likelihood of coming into sight, entering and or moving under pre-selected target trees of preferred fruit species was significantly higher if fruits were available than when trees were empty. In addition, target trees with fruit were approached significantly faster than trees without fruits (chapter 3). When I measured the number of trees that were encountered or closely approached (< 5m) per distance travelling by individual grey-cheeked mangabeys I found that the monkeys encountered or approached significantly more fruit bearing trees than human observers, who walked a fixed transect parallel to the monkey's route. This was true for fruit of the highly synchronically fruiting *Uvariopsis congensis* and the highly preferred yet a-synchronous fig species *Ficus sansibarica,* however, not for the moderately synchronically fruiting *Diospyros abyssinca*, that had much lower overall percentages of fruit-bearing trees within the season. This suggests that localisation efficiency differed among fruit species and that possibly the monkeys' did not search with equal efforts for each fruit species (chapter 1). Knowing that the monkeys were relatively efficient in finding fruits from particular fruit species, I continued to investigate how the monkeys knew where these particular fruits were located and what strategies they used to assess this knowledge.

What strategies do monkeys use to locate fruit?

Before generating hypotheses on the type of strategies used by the monkeys to find fruit, it is important to realize the difficulties of predicting the timing and duration of fruiting periods of individual rainforest trees. A number of factors make such predictions especially difficult. First, only a finite number of trees produce palatable fruits and mangabeys need to develop substantial botanical knowledge. Previous research has shown that grey-cheeked mangabeys consume the fruits of at least 54 different species (Waser 1977). Second, between-fruiting intervals may be considerably long (half a year to four years (e.g. Chapman et al. 1999; van Schaik 1986)) and weather conditions cause variation in the starting of a fruiting period, without obvious cues (e.g. Chapman 1999; Anderson et al 2005). Thirdly, within a tree's lifetime, the beginning and end of fruit production is extremely variable. Local soil and weather conditions determine the starting age, the moment of decay or collapse and the new tree species that can take its place, leading to a constantly changing spatio-temporal distribution of fruit (Milton et al. 1994; Chapman et al. 1997; Olupot 1998; Chapman et al. 1999). Finally, the nutritional quality of emerged fruit can vary substantially between and within species between different periods of the year and between different locations within the forest (Chapman et al 2004; O' Driscoll Worman & Chapman 2005). Nevertheless, a number of potential strategies can be used to help the monkeys to find fruits. In the next section I discuss evidence for the existence of a number of fruit-localisation strategies that could be used separately or in combination with each other by the mangabeys within the study areas.

Use of synchronicity

In the Kibale rain forest fruiting is known to be synchronous within 64% of the studied tree species (Chapman et al. 1999a), including two fig species that are highly preferred by the mangabeys (chapter 5). I therefore first investigated whether the monkeys use synchronicity as a conceptual tool to find rain forest fruit, in a similar way at it had been observed in more temperate zones (Menzel 1991). The results of the first chapter indicated that the mangabeys were not using memories of fixed species-specific synchronicity levels, in a way that search was activated after the encounter of one single fruit only. However, the results suggest that the monkeys used a more flexible search mechanism. The encounter of high densities of fruit bearing trees (high levels of local synchronicity) resulted in the entry of a larger number of trees of that same species per distance travelling than when fewer trees carried fruit. Yet, the encounter of high densities of fruit bearing trees also resulted in the monkeys entering a larger number of empty trees of that particular species in search for fruits. My findings suggest that the monkeys use a flexible searching mechanism that is triggered by the encounter of a specific threshold density of fruits of that same species. During this search the monkeys may use memories of the locations of these trees or patches of trees. Within a patch they may use a combination of search by sight and memories of the visual characteristics of the tree species itself (empty or filled with fruits) to locate individual trees. In addition, the monkeys may use memories of the nutritional quality of individual trees or tree patches (Chapman et al 2003; Chapman & Worman 2005).

How to find fruits that appear a-synchronically?

This particular search strategy would be highly inefficient for finding fruits with low synchronicity levels or a-synchrony. For these trees other strategies need to be considered. One of such species is *Ficus sansibarica,* belonging to the family of *Moraceae*. The trees of this fig species fruit in an a-sychronous manner with seemingly unpredictable fruit initiation intervals (chapter 5). Previous studies revealed that figs were highly preferred by the grey-cheeked mangabeys and profitable to exploit in terms of energy gain (which is suggested to stem mainly from its larger size rather than any major difference in calorie value) (Waser 1977; Barret 1995). Large fruit trees, like figs, were thought to strongly influence the mangabeys ranging behaviour and possibly increase their day journey lengths (Waser 1974, Barett 1995). Apart from ripe fig fruits, the mangabeys were particularly interested in the unripe fruits that contain insect larvae (69% of trees with unripe fruit visited) or edible seeds (chapter 3). Although a tree full of ripe fruits can be detected by use of smell, both ripe and unripe fruits produce no obvious visual nor olfactory cues that could be used to assess the edibility of individual fruits from outside the tree (chapter 3). The monkeys need to enter the tree to assess the edibility state of individual fruits by touch or other forms of close inspection (chapter 3). These characteristics make localisation of these fruits, especially that of the infested unripe fruits, a particular challenge. Despite this challenge, the group was more likely to visit pre-selected *F. sansibarica* trees that carried fruit than trees that carried none (chapter 3). In addition, individual mangabeys encountered more fruit bearing *F. sansibarica* trees per distance travelling than human observers did in a fixed transect that ran parallel to the monkey's travel route (chapter 1), suggesting that the monkeys used some strategy to increase localisation efficiency above a level achieved by walking a random route. Hence, I investigated the existence of several strategies that could help the monkeys to locate fig fruits in particular.

Use of auditory cues

Since fruit-bearing fig trees contained larger numbers of sympatric frugivores than empty trees (chapter 2), mangabeys were expected to benefit from tracking the auditory cues produced by these particular frugivores. Despite the suggestions made in a previous study that mangabeys used the loud calls of black and white casqued hornbills to discover fruits (Olupot et al 1998) the results in chapter 2 did not indicate that the mangabeys regularly used these cues to discover fruits at all. Neither did I find any evidence that the mangabeys used the calls of chimpanzees, given during feeding, that were broadcasted from 12 m. up a fig tree. Possibly, I did not find any evidence that the monkeys used these cues, because the monkeys used them in combination with a spatial-temporal memory. The mangabeys might have known that the experiment trees were empty or carried inedible fruits by using their memory, which stopped them from approaching the experimental cues. These results are consistent with conclusions made by Garber & Paciulli (1997) after studying the foraging skills of another rain forest primate *Cebus capucinus.* Garber & Paciulli claimed that if *Cebus capucinus* is given a choice between using a number of senses, remembered space is the most dominant "sense" used for finding food.

Use of spatial memory

I therefore continued to investigate whether the mangabeys used spatial memory to relocate fruit trees within the natural habitat and what aspects of these trees they were able to remember. I found evidence that the sooty mangabeys remembered the fruiting state of seasonal and preferred fruits of *Anthonota fragans* trees. Furthermore, the results strongly suggested that grey-cheeked mangabeys were able to remember previous feeding experiences and that they anticipated quality differences in fruiting states of trees from the preferred fruit species *Ficus sansibarica*. My selection of fruit species and tree types was such that the monkeys were unlikely to have been guided by visual and olfactory cues when arriving at the fig trees. Because I only analysed visits in which no other frugivores were observed inside the target trees before the group's approach, the monkeys' behaviour could also not have resulted from the use of auditory cues. My observations were therefore best explained by the hypothesis that the monkeys instead relied on spatial temporal memories of fruiting states when making foraging decisions (chapter 3). This hypothesis was further supported by the finding that the mangabeys were less efficient in finding edible fruits of *F. sansibarica* trees in less familiar areas of which they had fewer spatial memories than in more familiar areas (chapter 4). Perhaps the best evidence for the existence of a natural situation, in which monkeys solely depended on spatial memory, because no other cues were available, was found when I compared the mangabey's visiting behaviour towards two types of empty trees with different fruiting histories. I then found that the mangabeys were less likely to visit recently depleted trees than trees that did not carry fruit yet within the observation periods, indicating that the monkeys were using memories of past fruiting states when making foraging decisions (chapter 3).

Predicting fruit emergence, maturation and depletion rates

The finding that the monkeys were more likely to visit trees that did not carry fruit yet in previous visits, instead of depleted trees, suggested that the monkeys were anticipating an emergence of new fruit, i.e. the start of a fruiting bout. Further investigations showed however, that these results are better explained by the hypothesis that monkeys avoided the depleted trees (chapter 5). Analyses of long-term phenology data on fig trees (16 years) indicated that the timing of the emergence of fig fruit is very complex and irregular (chapter 5). It seems very unlikely that the monkeys would be able to predict the moment of fruit emergence. And the observational data on the monkeys' revisit behaviour also did not provide any evidence for such abilities (chapter 5). However, behavioural observations on approach speed did suggest that the monkeys were able to anticipate quality changes (the number of edible fruits) of fruit bearing trees between subsequent visits. How the monkeys could have been able to anticipate decreases in quality is not clear and a topic for further research. Possibly the monkeys estimated the depletion rate of fruit-bearing fig trees. How the monkeys were able to anticipate increases in quality was further investigated in chapter 6. In this chapter I found a strong indication that monkeys took weather variables into account when revisiting fig trees that were known to have carried fruits at the previous visit. The probability of a revisit of a fig tree, that was known to previously carry fruit, was best explained by past temperature values and solar radiation values of the morning before the revisit (Janmaat et al 2006; chapter 6).

Future studies related to my research question

The most surprising results from this thesis are perhaps the findings that suggest that mangabeys are able to predict changes in fruiting states by integrating time and weather variables with knowledge of previous fruiting states. Despite the clear benefit that such a cognitive skill could give in daily foraging, researchers remain sceptical about the ability of animals to "travel in time" (Suddendorf & Corbalis 1997; Roberts

2002; Gärdenfors 2006). This suggestion therefore is a clear topic for further investigation. The first step within these investigations should be to fully exclude the possibility that the monkeys used sensory cues. A fairly simple way to do so would be to conduct an experiment in which all the fruits are removed from particular target trees. This would be a rather tedious and dangerous job in the big *F. sansibarica* trees, however it may be possible for smaller exemplars. An alternative option would be to select trees of *F. capensis* that grow fruits on the trunk only.

The second step is to further investigate the role of cues that do not come from the fruit but from within the monkey group itself. Even though I followed the groups continuously for long periods, the mangabeys might have used knowledge from visits that were undetected by the observers. In both mangabey species males sometimes leave the group temporarily (Waser & Floody 1974; Olupot 1999; Range 2005) and solitary males have been observed to feed in fig trees up to 500 m from their group (chapter 3). The finding that fully-grown males were often the first to arrive near or at target trees suggested that they might lead the group towards good-quality trees. However, male early arrival was not significantly related to the fruiting state of the tree, suggesting that this was a by-product of males' peripheral foraging behaviour. These analyses are based on a rather small data set and it would be good to investigate this alternative explanation into more detail. A way to do this is to collar several males with a radio and g.p.s. device. This technique would enable the tracking of individual males for continuous long periods of several months. During these periods it could be investigated what happens when the male returns to the group after a solitary feeding visit. Do the females smell his mouth to check what he has been eating? Do they follow him the next time the group comes close to that same area? Also, it would allow monitoring the monkeys' visiting behaviour towards a much larger number of target trees within the duration of their fruit ripening periods. Furthermore, such continuous following periods would enable play back experiments from trees that are known to have carried inedible fruits during the male's previous visit. In addition, it would allow me to test whether the males use auditory cues of group members to locate fruit and whether individual approach speed is influenced by the arrival time of group members.

The monitoring of visiting behaviour towards a larger number of target trees would in addition enlarge the data set of particular visits that occur after substantial changes in the number of edible fruit (chapter 5). This would enable me to gain more insight in the question whether and if so, how the mangabeys anticipate changes in fruiting states. In addition, an increased data set would enable me to further investigate whether approach speed can be used as an indirect measure of expectation of fruit availability in these investigations. As mentioned in chapter 5, approach speed is likely to be influenced by many different variables but foreknowledge of fruit availability (see diagram 1), such as food availability in the surrounding area, the size of a foraging group (scramble competition) and the hunger level of the individuals inside a foraging group. To investigate whether approach speed is significantly influenced by foreknowledge of fruit availability it is most efficient to use a measure of fruit availability that is least related to the other confounding variables that may influence approach speed (such as hunger levels). In future studies I will therefore use the second fruit availability or quality value: the ratio of rejected and eaten fruits. For species that carry fruit that show visual signs of edibility, in which fruits are not rejected by touch, I could possibly just use the rate in which fruits are eaten.

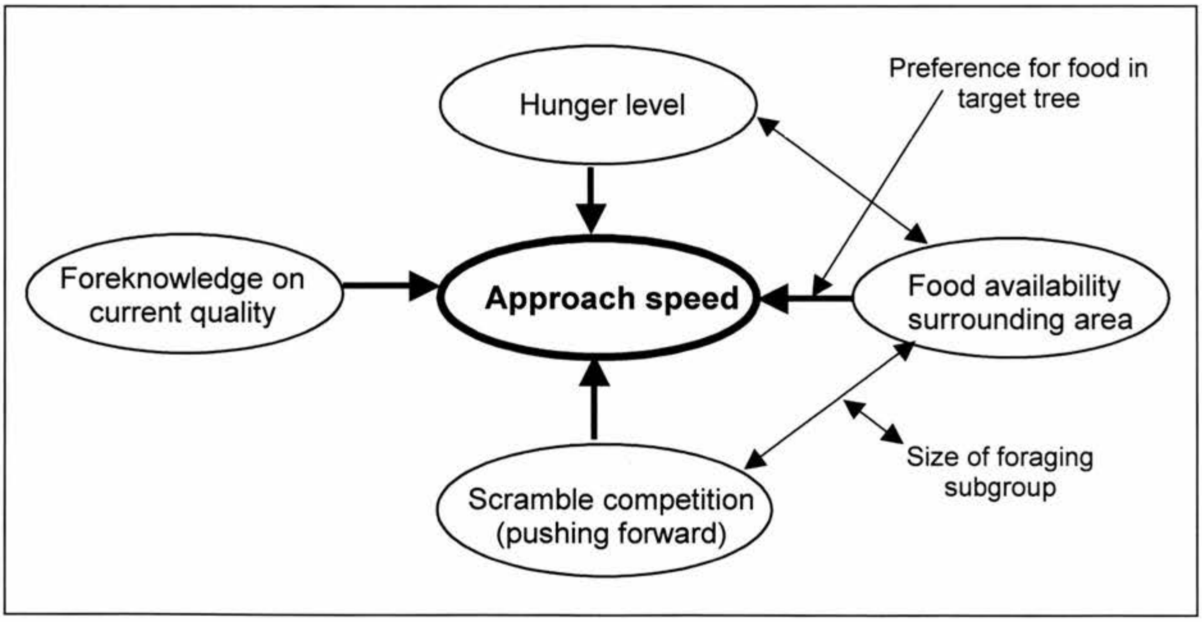


Diagram 1. Schematic diagram that represents the factors that could influence the speed with which a group of monkeys approaches a target tree.

Surprisingly, intake rates of individual fruits do not show to be influenced by hunger levels or group size (Janson 1987; personal communication). However, aggression levels inside the food tree can influence intake rates of individuals (Janson 1985). Measurements of aggression and feeding group sizes in trees that show visual signs of edibility are therefore considered important in future research. To minimize the potential influence of the food availability in the area surrounding the target tree on hunger levels and fluctuations in feeding group sizes it is in addition extremely important to select target trees of a food source that is highly preferred.

Lastly, I would find it interesting to investigate the monkeys' knowledge on the long term fruiting patterns of individual fruit trees. Analyses of 16 years of phenology data revealed impressive variation in fruit initiation frequencies between individual fig trees (chapter 5). To investigate whether primates and or other rain forest frugivores know and use these differences, it could be tested whether trees that fruit at high frequencies are monitored more frequently during non-fruiting periods than trees that fruit at low frequencies.

CONSEQUENCES FOR THEORIES ON THE EVOLUTION OF PRIMATE BRAINS

Primate brains differ significantly from those of most other mammals in their large size, particularly their larger cortices, and the higher proportion of the basal metabolism devoted to brain function (Armstrong 1983; Harvey & Krebs 1990). One of the proposed advantages of a large brain is the ability to perform intelligent behaviour that helps primates to solve problems in daily life. In the introduction of this thesis I discussed two competing types of "challenge" theories for the origin of primate intelligence. Using the comparative approach, primatologists searched for relationships between measures related to intelligence (i.e. relative brain or neo-cortex size) and measures of the complexity that primates are challenged with in their social and ecological environment, over a large number of primate species. Although the complexities faced in the social arena and their cognitive solutions gained far more attention, analyses free of phylogenetic bias showed that measures of brain size are related to both measures of social and ecological complexity (Barton 1996; 1999). When body size is taken into account, primate brain size is independently positively correlated with social group size but also the percentage of fruit in the diet (Barton 1999). This confirms results of earlier studies, in which a correlation in primates between diet and relative brain size was found (Clutton-Brock and Harvey 1980; Foley and Lee 1992). In addition, the size of one particular brain structure, the neocortex, is also correlated with both percentage frugivory and social group size when controlled for the size of the rest of the brain (contrast analysis; Barton 1996).

Why do fruit eating primates need relatively larger brains?

Fruit producing trees and primates have a long period of joined history in the course of evolution. It is suggested that as a result of long-term diffuse co-evolutionary interactions with flowering and fruiting plants, modern primates, together with bats and plant-feeding birds, first arose around the Paleocene-Eocene boundary (56 million years ago) and became the major seed dispersers of modern tropical flora during Eocene (Sussman 1991; 2004). Most primates eat fruit, yet some rely on them more than others (Smuts et al 1986). And as described earlier, the ones that have a larger percentage of fruit in their diet are likely to have a larger brain or neocortex ratios. The relation found between the level of frugivory and relative brain and neocortex size is not only apparent in primates. Fruit eating bats and rodents also have higher encephalisation than do insectivorous species (Harvey & Krebs 1990). It is therefore suggested, that a fruit dependent diet places particular demands on the cognitive capacities of foragers in general (Clutton-Brock & Harvey 1980; Milton 1981). In the next section, I will try to gain insight in the nature of these demands. What cognitive challenges do frugivorous primates encounter that folivorous primates do not? Is fruit localisation complex because fruits are widely dispersed in space and do frugivores consequently require an ability to map larger areas than folivores, like it was originally suggested by Clutton-Brock and Harvey (1980) and Milton (1981), or do other aspects of fruit need to be considered?

Complex spatial distribution of fruit?

Barton (2000) argues that the degree of frugivory remains significantly correlated with relative neocortex size even when home range size has been partialled out. It therefore seems to be frugivory per se, rather than the size of the ranging area that the animal must map, that is associated with relative neocortex size and absolute brain size. This is perhaps no real surprise when one tries to define the challenges encountered by frugivorous and folivorous primates in their natural habitat. If one considers the life styles and daily demands of both primate types it is difficult to determine what exactly makes one life more complex than the other. Possibly, frugivores need to store more information concerning efficient routes within the relatively larger areas (Clutton-Brock & Harvey 1977). But there is no reason to expect that primates ranging in larger areas need to remember a larger number of food trees or spatial information in general. As pointed out by Byrne (1975), remembering the toxicity level of the leaves of individual trees or parts of that tree may be as important for a folivore than remembering which trees can carry fruit for a frugivore. To me, a more obvious difference in complexity is that frugivores are confronted with a food source that is more *inviting* and *ephemeral*. Most ripe fruits are "designed" to attract seed dispersers and are therefore easy to digest and free of toxic compounds (e.g. Waterman 1977). However, they are only edible for short time periods (Milton 1988). Frugivores may therefore face higher levels of competition, as they have to share their food with a much larger number of animal species (Struhsaker 1997; Houle 2004). In addition, frugivores may experience higher levels of within group competition, since fruits, large fruits in particular, can be more easily defended than leaves (Dunbar 1987; Sterck 1995). In these competitive conditions early arrival is likely to pay and two cognitive capacities in particular may increase the foraging success of individuals: 1) an ability to remember and anticipate fruiting states and 2) the ability to spot fruits from far away distances and to judge their distance. Each of these capacities may be more developed in frugivorous than in more folivorous primates. Evidence for the existence for such capacities in primates and its usefulness in relation to fruit localisation is further discussed below.

Are frugivorous primates visually more specialised?

Barton (2000) argues that the variation in neocortex size is at least partly a product of selection on specific visual mechanisms. Since the majority of primate species live in forest habitats visual specialisation is not the first adaptation one thinks of as being useful (Smuts et al 1986). Experimental work on *Cebus apella* has shown that visual food detection of the forest monkeys is limited to 20 to 30 m due to dense vegetation (Janson & Di Bitetti 1997). Auditory and olfactory signals are generally regarded as more useful cues to discover and navigate towards food sources from large distances (Dominy et al 2001). However, there are reasons to be cautious. Olfactory cues are distributed by wind causing confusion on the original direction and the distance of the signal source. In addition, fruits that do not "want to be eaten", such as unripe fruits with undeveloped seeds, do not emit obvious smell (Janmaat et al in press; chapter 3). Auditory cues produced by other fruit eating foragers may be a more useful tool to find fruit. However, animal loud calls are often intermittent, so foragers can seldom follow a continuous signal from far away distances. This would not be a problem in an area with only few trees in which one can easily travel in a fixed bearing, however it becomes more difficult to travel straight to a sound source when there are 500 trees between the forager and the food source, that obscure long distance land marks (Rieser et al 1992; Loomis & Beall 1998). In addition, elevation differences, and variation in vegetation density and weather conditions influence the amplitude of the sound, which can make it difficult to judge whether the source is close by enough to be worth the travel. Visual signals may be much easier to work with, especially for the more arboreal primates. Visual detection can be limited especially when fruit is situated at the lower levels of the canopy such as fruit that grow in under story trees (also in Janson & Di Bitetti 1997). However, large emergent fruit trees like some figs can be spotted from much larger distances. Even for more terrestrial primates (like me) forest gaps caused by tree falls or swampy areas, and hills may allow foragers to spot fruit in trees at distances of over 150 m (personal observation).

Visual specialisation

Primates have specialized visual systems that differ from those of other mammals in various features and anthropoid primates are further distinguished by a suite of visual adaptations (Ross 2000). The eyes of primates are large and capable of high spatial resolution. Also they are orbital and mobile so they can scan the visual world moving to points of interest (e.g. Dominy et al 2001). These specialized eye movements give fine judgment of depth as well as pattern (Dominy et al 2001). It allows primates to estimate the distance to far away trees and to manipulate objects in three-dimensional space, facilitating hand mouth coordination while foraging on fruits or insects (Dominy et al 2001). In addition, trichromatic colour vision allows primates (apes, Old World and some New World monkeys) to distinguish coloured fruits more easily from the leafy background as well as young coloured leaves (Sumner & Mollon 2000; Dominy et al. 2001). Young leaves are particularly important for some frugivores as well - as a protein source.

Barton (2000) argues that it is a combination between primates' ability to deal with social complex behaviours, such as deception, and their visual specialisation, used to spot edible fruits, that explains the primates' relatively large brain. In addition, he adds that the elaboration of social skills also seems to have involved enhancements of visual mechanisms, for example, those involved in processing facial information about the identity, internal state, and intentions of the other individual. These skills require high degrees of visual acuity and the ability to store and recollect a wide range of facial or body expressions. Similarly, primates may need larger brains to store and recollect visual information on the location of particular trees that are important to them. The finding that monkeys use levels in synchronicity as a conceptual tool to locate fruit (chapter 1) further indicates that they can benefit from storing and quickly recollecting information on the visual appearance of fruit, yet also of the trees on which they can grow. Barton's idea is supported by Terrence Deacon who suggests that the loss of primates' ability to produce vitamin C, has increased the selection pressure on the evolution of visual skills in order to find fruits (Deacon 1997; personal comm.). Possibly this also increased the selection pressure to evolve memory and anticipatory skills.

Are primates able to remember and anticipate fruiting states?

Ripening rates of fruit and their quality is shown to be dependent on fluctuating weather variables (see chapter 1 and 6). Hence, an ability to use memory in a flexible way is likely to be advantageous. Especially frugivores that are dependent on fruit trees that show fairly irregular fruiting periods with no sign of synchrony, that in addition show no visual or olfactory signs of edibility of its fruit, are likely to benefit from the use of such episodic-like memory type. The results of this study suggest that frugivorous mangabeys can integrate memories of previous feeding visits and weather conditions while making foraging decisions. The mangabeys' foraging behaviour shows similarities with those of some birds, such as Brent geese (*Branta bernicla*), finches (*Fringillid* sp.), and scrub jays (*Aphelocoma coerulescens*) (Cody 1971; Whiten & Byrne 1997; Clayton & Dickinson 1998; Emery & Clayton 2004). In these species, foraging decisions are influenced by the recovery rate of plants, the ripening rate of seeds, and the perishing rates of moth larvae and peanuts, respectively. Despite the similarities, my study is different in that I have shown that monkeys also take into account variation in weather conditions, rather than mere differences in elapsed time. In addition, the results suggest that mangabeys can use memories of previous fruiting states to make predictions of the quality of the current fruiting states (when being within 100 m). In the competitive environment of the Kibale forest an ability to integrate memories of previous fruiting states and weather conditions to subsequently anticipate changes in fruiting states could allow individuals to forage much more efficiently than when they would be in absence of such cognitive specialisations.

Future directions in studies on primate cognitive evolution

Which primate benefits most from anticipatory skills or visual specialisation?

Whether the presence or absence of these cognitive specialisations indeed can explain the correlation between frugivory and measures of brain size remains a topic of further investigation. Instead of comparing measures of brain size with the level of frugivory, i.e. the percentage of fruit in the diet, the next step may be to create some finer measures of distinction. In order to make the right distinction it is necessary to determine which exact challenges could be tackled by using these cognitive specialisations and which type of primate would benefit most from them.

My study provides a clear illustration that it is not only the localisation of fruit that could be facilitated by the ability to use episodic like memory or anticipatory skills. These specialisations could also facilitate the localisation of another preferred and important food types, such as insect larvae. Grey-cheeked mangabeys belong to the second grade of frugivores that combine insects or other invertebrates and green pats of vegetals (like young leaves), in fairly small proportions, with a main complement of fruits and/or seeds (other species within this grade are: Cebus, Cercopithecus, Macaca, Papio, Pan (Hladik's classification 1975)). Hladik (1975) argues that despite the high percentage of fruits in the diet (59% for mangabeys), for this type of foragers it is the protein production that is the important determining factor in the ranging behaviour of these primates (see also Waser 1974; Olupot et al 1997). Preference for figs in grey-cheeked mangabey may therefore be explained by the high protein content (wasps and weevil larvae) inside them and not by the fruits at all. The proposed use of episodic like memory and anticipatory skills for larvae harvesting, indicate that these cognitive specialisations could benefit insectivores as well as frugivores (chapter, 3, 5 and 6). Similarly, folivores may benefit from the ability to integrate weather variables and elapsed time as well, since the nutritional value of particular leaves or unripe fruits is known to be influenced by past weather conditions (Chapman et al 2004; O' Driscoll Worman & Chapman 2005). The best way forward may be to determine the characteristics of those primates that would benefit most from these cognitive specialisations.

Which frugivore benefits most from anticipatory skills?

One particular aspect of frugivory that should be considered in future comparative studies is maybe not just the percentage of fruit in the diet but the characteristics of preferred fruits. Do preferred fruit species show high levels of synchronicity that can be localised by a fruit-density-induced localisation mechanism, like it was suggested in chapter 1, or do preferred fruit trees fruit asynchronously, like some rain forest figs? Possibly a comparison of brain size measures between frugivores 1) in seasonal and less seasonal areas or 2) with a fig dependent and fig independent diet, may provide insight in whether either prospective abilities or visual abilities correlate with measures of brain size. By focussing on the characteristics of preferred fruits we could also avoid the problem encountered when determining the levels of frugivory per primate species. Variation in the percentages of fruit in the diet shows large variation between and within primate populations of the same species that forage in different areas (Chapman et al 2002), complicating the determination of frugivorous versus folivorous species.

Ripe-fruit dependent frugivores

Another interesting comparison may be that of measures of brain size and levels of ripe-fruit dependency. This may provide further insight in the following question.

What explains the cognitive divide between monkeys and great apes?

Although the evolution of either one of or a combination of episodic-like memory, social skills and visual specialisation could explain the evolution of enhanced brain size in frugivorous primates or primates in general, one question remains unresolved. Great apes exhibit various behaviours that apparently entail cognitive capacities beyond the reach of other primates, such as tool making, nest building, clambering or complex food manipulation. (e.g. Byrne 1997; Parker 1996; Povinelli & Cant 1995). As a consequence many researchers now believe that a cognitive divide exists between great apes and the other primates (e.g. Russon et al 1996; Byrne 1995; Parker & McKinney 1999; but see Tomasello & Call 1997). However, great apes live in groups of a size and complexity comparable to monkeys and do not seem to require special social skills. It is also unclear why apes would need a more developed visual system. What else then can explain the cognitive divide between great apes and monkeys? One of the hypotheses (amongst others, see Byrne 1997) that tried to explain the difference between monkey and ape cognitive abilities is the *fruit habitat hypothesis* (Potts 2004). This recently developed hypothesis focuses on differences in constraints imposed by habitat and diet onto apes and monkeys in a period of time in which the current great ape species are thought to have evolved. One factor that is proposed to play a role in great ape evolution is a dietary distinction (see also Byrne 1997 and Milton 1988). Studies on molar morphology and dental microwear and comparative behavioural studies of living primates indicated that apes were and are more dependent on ripe fruits than monkeys (Potts 2004; Wrangham et al. 1998). The hypothesis states that because ripe fruits can be complexly distributed in time and space, a dietary dependence on ripe fruit has triggered enhanced cognition through complex foraging behaviour (Clutton-Brock & Harvey 1980; Milton 1981; Byrne 1997). One potential adaptation that is suggested to have facilitated the finding of edible fruits is the ability to predict the ripening of fruits. According to this theory, apes, unlike monkeys, should have developed anticipatory skills enabling them to be the first to arrive at trees when fruit had become edible. I tested this hypothesis by investigating the revisit behaviour of a monkey species to particular fruiting trees. As mentioned earlier the results from chapter 3, 5 and 6 suggest that grey-cheeked mangabeys are able to predict changes in fruit quality. These findings give reasons for further investigations, which could create convincing evidence for a rejection of the fruit habitat hypothesis.

Evidence of convergent cognitive evolution

Until recently, comparative studies on the cognitive skills of animals have been focussing on primates (e.g. Byrne 1995). Alternatively, comparisons of the cognitive skills in and with other groups of animals may help us to determine the environmental challenges (ecological and social) that triggered the evolution of enhanced brains. Recent research suggests that some birds (e.g. scrub jays) collect cached food using episodic-like memory (Clayton & Dickinson 1998; Emery & Clayton 2004b). Emery & Clayton (2001) also found that western scrub jays are able to project another birds' experience or "take its role". Ravens, apparently use insight when making and using tools to acquire otherwise unobtainable foods (Emery & Clayton 2004). For example hand-raised ravens encountered a novel problem (meat attached to string hanging form a perch). The only successful method was to pull the string up, place the foot on the string after each pull up and repeat this multiple times until the food was in reach, a solution some ravens reached on the first trial (that is, without recourse to trial-and error learning) (discussed in Emery & Clayton 2004b). This convergent evolution of episodic-like memory, role taking and insight in bird species is confusing. If birds are able to perform the same cognitive skills as primates why do they not have much larger brains? How is all that possible in a small bird brain but not in a primate brain of similar size? Emery and Clayton (2004) stress that the relative brain size of a crow (in relation to body size) is the same as that of a chimpanzee. Still, the brain itself is small and a much smaller proportion of the basal metabolism is devoted to brain function in birds (Harvey & Krebs 1990). Possibly bird brains are efficiently designed while primates inherited a very inefficient base structure, resulting in the evolution of relatively costly brains compared to those of birds? Of course other explanations are available. Primates are different from birds in several ways. First of all most primates are bigger, second they cannot fly but walk or jump which is relatively more costly (Schmidth-Nielsen 1972). Because of this, primates may have needed to develop a more sophisticated timing or visual system to assess the edibility state of food from far away distances and to judge whether the distance of travel is going to be worth the food reward. In human primates in particular, who evolved sophisticated language, communication may have accelerated the evolution of a new more complex competitive environment in which individuals were able to deceive each other in order to get food, in particularly complex ways while using language. I think this possibly could explain the evolution of 3rd 4th and 5th levels of intentionality in the human species (Dunbar 2005).

Alternatively, these new discoveries of complex cognitive skills in birds may mean that primatologists should place less emphasise on differences in brain size, but more on brain structure. Deacon argues that we cannot compare all animals to a single species-independent measure of intelligence: "brain size". To put things into perspective he argues: 'We do not consider ranking mammals as dolphins, rabbits, moles, horses, bats and gibbons according to some linear scale of locomotor efficiency. It is obvious that each species' locomotor abilities are specialised for locomotion through very different substrates'. 'It should be obvious that their mental abilities have been specialised to navigate in very different cognitive substrates which are at least as diverse as their different locomotor substrates' (Deacon 1990).

Imagination

In an article, that compared the cognitive skills of corvids and apes, Emery and Clayton (2004b) introduced a new division of cognitive complex behaviour. One of the proposed cognitive abilities that would separate corvids and apes from other animals was the ability to *imagine*. Imagination refers to the process by which scenarios and situations that are not currently available to perception are formed in the mind's eye. This ability, I think, deserves further attention, especially because it allows us to distinguish between cognitive abilities that are relevant in both the social and ecological arena. In addition, it can provide us with further insight in how to explain the cognitive divide between apes and monkeys. Imagination enables an animal to find solutions to problems. It could allow them to *see* how a nut will break once it is hit on it or how stinging nettles will not hurt when it is folded in a specific way, without trial and error (Boesch & Boesch 1984; Byrne 1995). Also it might enable animals to get into the mind of conspecifics, and to truly teach instead of tell, or use a conspecific's thoughts (intentions) for personal gain in relation to food acquisition or the avoidance of predation risk. At the same time it might enable an animal to make short cuts and walk routes that it has never tried before. Perhaps imagination even helps to correctly predict edibility states of fruit. It might allow recall of the last observed maturation state and the past weather conditions to consequently *see* the current fruiting state. The ability to imagine was suggested to be present in apes and corvids only (Emery & Clayton 2004).

What are the exact challenges?

The above example shows how comparative studies on cognitive skills can help us to understand the biological triggers in the evolution of the brain. Emery and Clayton (2004b) argue that corvids and apes share many cognitive abilities (such as imagination) because they face many of the same socio-ecological challenges, such as locating perishable food distributed in time and space or understanding the relationships between different individuals within large social groups. Similarly, one could say that scrub jays and mangabeys face an environment that rewarded similar skills, with the only difference that caching birds are rewarded by correctly predicting how fast food becomes degraded, while mangabeys are rewarded by correct predictions on how fast food becomes edible. Defining these exact challenges and the constraints that the social and ecological world imposes on each of the animal species, by observing animals within their natural habitat will clearly help us understand why similar cognitive skills and brain sizes evolved.

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