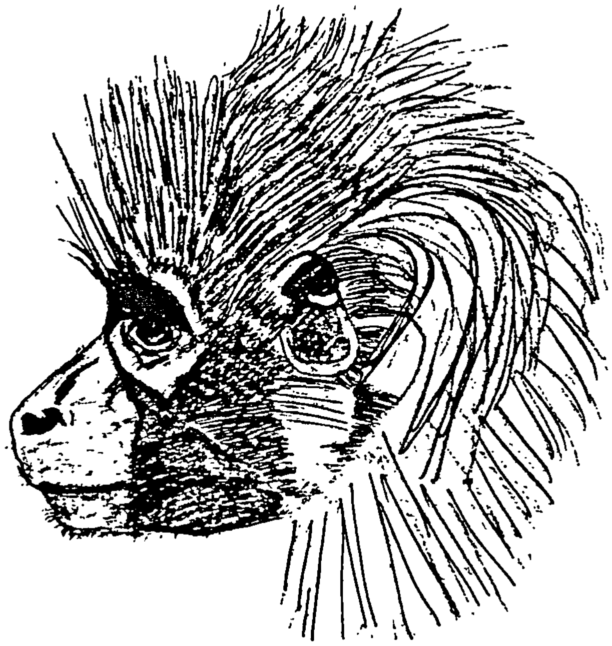

Cercocebus albigena

BEHAVIOUR AND ECOLOGY OF GREY-CHEEKED MANGABEYS (*CERCOCEBUS ALBIGENA*) IN THE LOPE RESERVE, GABON.

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Thesis submitted for the degree of Doctor of Philosophy

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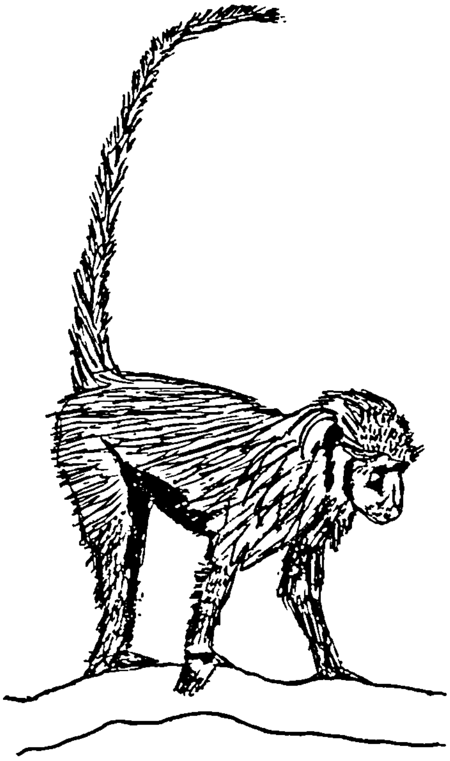


McDonald '94.

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ABSTRACT

Grey-cheeked mangabeys (*Cercocebus albigena*) are distributed across Central Africa, but have previously only been studied in detail at the eastern edge of their range in Uganda. Hence, little is known about this species from the western African rain forests, where forest composition and primate species are different from those in eastern Africa. The behaviour and ecology of grey-cheeked mangabeys was studied in the Lopé Reserve, Gabon over 18 months, between January 1991- June 1991 and September 1991- August 1992. Systematic data were collected mainly from one habituated group, and data were also collected opportunistically from other groups in the study area.

The mangabeys' diet is diverse, with 100 items of plant food from 75 species recorded. Overlap in the mangabey's diet with the seven other diurnal primate species at Lopé is high. Sixty-four percent of fruit-pulp, 51% of seed, 38% of leaf, 27% of stem and pith, and 15% of flower species in their diet are also eaten by at least one other species of diurnal primate. Mangabeys spent 36% of their time feeding, eating seeds. This is high, compared to studies in Uganda where seeds were relatively unimportant in the diet of grey-cheeked mangabeys. Seed-eating, may be a result of differences in forest composition, since there are a higher number of species from the family Leguminosae at Lopé. Alternatively, seed-eating may be a strategy for competing with sympatric primate species. This is the first time grey-cheeked mangabeys have been studied in areas where they coexist with both gorillas and chimpanzees, which at Lopé, both have a large proportion of succulent fruits in their diets. For more than half of the time mangabeys spent eating seeds, the

seeds were taken from immature fruit. Mangabeys, therefore, may be eating unripe seeds as a form of exploitation competition.

The overall home range size of the main group (18-23 members) was 225 ha, and a second group (18-20 members) had an estimated home range size of 156 ha. Use of different habitats was shown to be related to the availability in time (as assessed by phenological monitoring), and in space (as determined from strip sampling two 1 ha plots in two habitat types: savanna-edge and river-edge forests) of certain plant species. Comparisons with grey-cheeked mangabeys studied in Uganda revealed that home range size varied from about 10% to 200% of the size of those at Lopé.

Mangabeys spent an average of 80% of the time in association with at least one other primate species. Benefits of the associations are thought to be biased towards the *Cercopithecus* spp. since they followed mangabeys, but rarely vice versa. These species may benefit from decreased predation rates due to the mangabey's larger body and group size, and because mangabeys more actively defend against predators.

Forests at Lopé are highly seasonal, with periods of relative fruit scarcity in the long dry season. During this period, mangabeys spent a greater proportion of time feeding, their diet was less diverse consisting almost entirely of seeds, and mangabeys were observed in polyspecific associations less, than during the long rain season when fruit was relatively more abundant. The great variation in behaviour and ecology between the present study, and studies of grey-cheeked mangabeys in Uganda, highlights the ecological flexibility of this species, and emphasises the importance of both forest composition and primate community structure in shaping behaviour.

CHAPTER ONE: INTRODUCTION

Grey-cheeked mangabeys (*Cercocebus albigena albigena*, Gray 1850) are large arboreal primates which occur in the tropical rain forests in equatorial Africa. They have been the subjects of very few field studies compared to their relatives baboons and macaques. In the first part of this Chapter, I will introduce the study species and in the second, I will discuss the background that led to the formulation of my study in the Lopé Reserve, Gabon.

A: THE STUDY SPECIES

1. Taxonomy

The first evidence of mangabeys being known in Europe is a painting by Pieter Bruegel the elder (c.1562) of "two monkeys" which are probably white-collared mangabeys, *Cercocebus torquatus*. The name "mangabey" was first used by Buffon (1766, in Hill, 1974) to describe sooty (present taxonomy: *Cercocebus atys*) and white-collared mangabeys he had seen in London. He used this term because he believed them to be from Madagascar (since "Mangabe" means "a place north west of Tamatave" and is an island in Anongil Bay east of Madagascar, Hill, 1974). At first mangabeys were assumed to be *Cercopithecus* (eg. Buffon,1766, in Hill, 1974), until Geoffroy (1812, in Hill, 1974) put them into the separate genus; *Cercocebus*. This genus, however, also included green monkeys (*Cercopithecus sabaeus*), three species of macaque (*Macaca sinica, M.radiata* and *M.irus*) and a species of langur (*Presbytis aygula*).

The first record of a grey-cheeked mangabey, was that of an individual in the London Zoo. Gray (1850) was the first to describe it, and called it *Presbytis albigena,* thinking that it was a langur (Hill, 1974). There was debate over whether this was the correct classification, but it was not until du Chaillu brought back skins of grey-cheeked mangabeys from Gabon, that it was finally confirmed to be a mangabey, and given the name: *Cercocebus albigena.*

Today, the Old World monkeys (Cercopithecidae) are divided into two sub-families; *Colobinae* and *Cercopithecinae*. The latter contains 7-11 genera, including; mangabeys (*Cercocebus* or *Cercocebus* and *Lophocebus*), baboons (*Papio*), gelada baboons (*Theropithecus*), mandrills and drills (*Papio* or *Mandrillus*), macaques (*Macaca*), celebes macaques (*Macaca* or *Cynopithecus*), guenons (*Cercopithecus*), talapoins (*Cercopithecus* or *Miopithecus*), Allen's swamp monkey (*Cercopithecus* or *Allenopithecus*), and patas monkeys (*Erythrocebus*).

The basic taxonomy of the mangabey genus used today is that of Schwartz (1928, in Hill, 1974) with modifications from Schouteden (1944, in Hill, 1974) and Booth (1956, in Hill, 1974), but there continues to be discussion as to whether the genus *Cercocebus* should be divided into two groups; the 'Albigena' group, containing *C.albigena* and *C.aterrimus* and the 'Torquatus' group, containing *C. torquatus, C. atys* and *C. galeritus* (Schwartz, 1928). There is argument as to whether the Albigena group and the Torquatus group should be separate sub-genera (Elliot, 1913, in Hill), superspecies (Dobororuka and Badalec, 1966, in Hill, 1974), or genera (Groves, 1978). Groves (1978) suggested that there should be two genera for mangabeys, one with species *albigena* and *aterrimus,* and the other with species *torquatus, agilis* and *galeritus.* He suggested that the genus name *Lophocebus* (first used by Palmer in 1903, in Hill) to be used for the *albigena* and *aterrimus* group, and *Cercocebus* remain for the latter group.

These two groups are distinctive in many ways. Mangabeys in the 'Torquatus' group, are semi-terrestrial, whereas mangabeys in the 'Albigena' group are highly arboreal (Napier and Napier, 1967). Comparisons between their cranial morphology (Groves, 1978) also show these two groups to be very different, and biochemical and molecular studies (Barnicot and Hewett-Emmett, 1972; Cronin and Sarich, 1976; Dutrillaux *et al.*, 1979; Hewett-Emmett and Crook, 1978) suggest a diphyletic, instead of a monophyletic origin, of the two mangabey groups. This evidence has important implications for our understanding of the evolutionary history of mangabeys because it suggests that *Lophocebus* are more closely related to baboons, macaques and geladas, than the *Cercocebus*, which are more closely related to the *Cercopithecus* (Cronin and Sarich, 1976) (**Figure 1.1**). This taxonomic division of *Cercocebus* into two genera, however, has only been recognised by a few authors (eg. Gautier-Hion *et al.*, 1988a). Because the genus *Lophocebus* has not yet gained general acceptance, for the purposes of this thesis, the established classification will be used. Grey-cheeked mangabeys, therefore, will be referred to using the scientific name *Cercocebus albigena*.

The most widely used classification for mangabeys today, is that of Hill (1974), and Napier and Napier (1967) where the genus *Cercocebus* is divided into two superspecies: (1) the *Cercocebus torquatus* group, with three species: (i) white collared mangabeys (*C. torquatus*); (ii) sooty mangabeys (*C. atys)* (iii) agile mangabeys (*C. galeritus*), and (2) the *Cercocebus albigena* group, with two species: (i) grey-cheeked

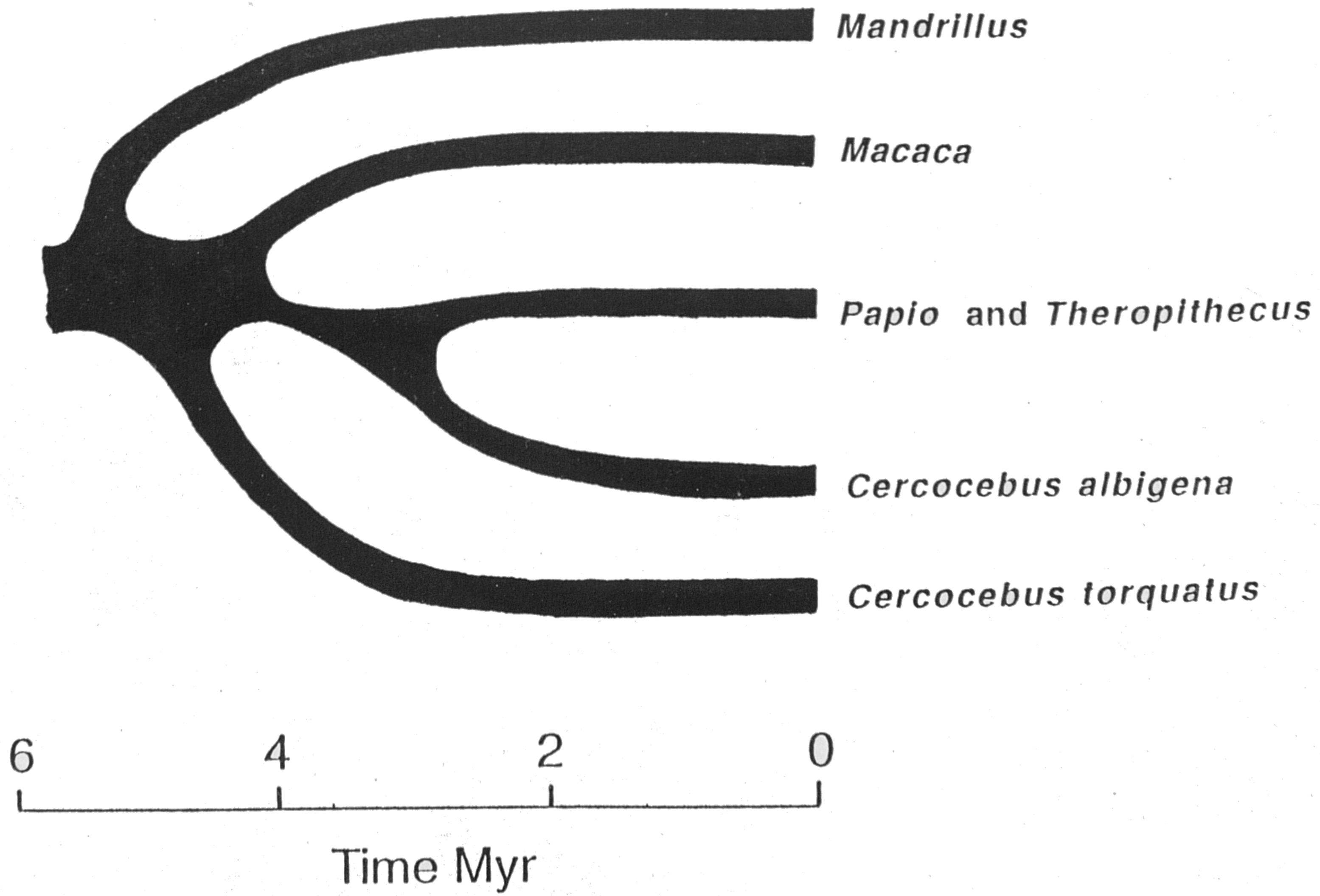


Figure 1.1 Cladogram derived from blood serum proteins (approximated from Cronin and Sarich, 1976) showing the evolutionary relationships of the two superspecies of mangabey (*Cercocebus albigena* and *Cercocebus torquatus*) to macaques (*Macaca*), mandrills (*Mandrillus*) and baboons(*Papio* and *Theropithecus*).

mangabeys (*C.albigena*), and (ii) black mangabeys (*C.aterrimus*). Within this structure, each species has two or three sub-species (**Table 1.1**). The subject of the present study was the subspecies *Cercocebus albigena albigena* (Gray, 1850).

The taxonomy of Napier and Napier (1967), including the common names provided, was used in the present study. The only modification made to this classification, is the addition of the "sanje crested mangabey" (subspecies *C.galeritus sanjei*). This subspecies was discovered by Homewood and Rodgers (1981).

2. Morphology

General

Detailed descriptions of the morphology of mangabeys are provided by Hill (1974), Groves (1978) and Napier and Napier (1967). The following is a description of the morphology of grey-cheeked mangabeys, as well as a brief outline of the morphological characteristics that most readily identify each of the other species.

Mangabeys, are large monkeys with long tails and dark fur. The average mass is about 9 kg for an adult male, and 6 kg for an adult female (Gautier-Hion and Gautier, 1976). Mean body length for adult males is about 576 mm (540-615 mm, n=15), or 886 mm (820-940 mm, n=15) including the tail, and about 503 mm (435-580 mm, n=14) for adult females, or 810 mm (740-895 mm, n=14) including the tail (Napier and Napier, 1967).

In addition to the differences mentioned above, the Albigena and Torquatus group of mangabeys differ in that (1) the hairs of the coat are longer in the Albigena group, (2) hairs are speckled in the Torquatus, but not in the Albigena group, and (3) the Albigena group have some form of a crest on their head,

Table 1.1 Classification of the genus: *Cercocebus*.

Superfamily:	**CERCOPITHECOIDEA**	**(Simpson, 1931)**	
Family:	**Cercopithecidae**	**(Gray, 1821)**	
Subfamily:	**Cynopithecinae**	**(Mivart, 1865)**	
Tribe A:	**Cercocebini**	**(Jolly ,1966)**	
Genus:	***Cercocebus***	**(Geoffroy, 1812)**	
Superspecies:	***C. albigena***	**(Gray, 1850)**	
Species:	*C. albigena*	(Gray, 1850)	Grey-cheeked mangabey
Subspecies:	*C. a. albigena* *C. a. zenkeri* *C. a. johnstoni*	(Gray, 1850) (Schwarz, 1910) (Lydekker, 1900)	
Species:	*C.aterrimus*	(Oudemans, 1890)	Black mangabey
Subspecies:	*C. a. aterrimus* *C. a. opdenboschi*	(Oudemans, 1890) (Schouteden, 1944)	
Superspecies:	***C.torquatus***	**(Kerr, 1792)**	
Species:	*C. torquatus*	(Kerr, 1792)	White-collared mangabey
Species:	*C. atys*	(Audebert, 1797)	Sooty mangabey
Subspecies:	*C. a. atys* *C. a. lunulatus*	(Audebert, 1797) (Temminck, 1853)	
Species:	*C. galeritus*	(Peters, 1879)	Agile mangabey
Subspecies:	*C. g. galeritus* *C. g. agilis* *C. g. chrysogaster* *C. g. sanjei*	(Peters, 1879) (Rivière, 1886) (Lydekker, 1900) (Homewood and Rodgers, 1981)	

whereas the Torquatus group has no crest.

Grey-cheeked mangabeys

Grey-cheeked mangabeys, have long and rough black fur with smoky grey underparts, and greyish-white cheeks and throat. The hair on the neck, breast and shoulders forms a mantle, or "cape" of 10-15 cm hairs which are brownish-grey (**Plate 1.1**). The tail has long and shaggy hair with shorter hair near the tip. The tail is often carried vertically over the head and has been described as semi-prehensile organ that is often seen to be wrapped around branches during rest or feeding (Tappen, 1960; personal observations).

The face of grey-cheeked mangabeys is black. They have tufts of hair above their eyes, and unlike other species of mangabeys, they have dark eyelids. Adult males have a black scrotum and a pink penis. The colour of the oestrus swelling in adult females, changes from flesh coloured to bright pink to purple, corresponding to different stages of the oestrus cycle (see *Chapter Four*). Sub-species of grey-cheeked mangabeys can be most easily identified by differences in the colour of the mantle, chest and legs. In *C. a. albigena* these parts are brownish-grey, in *C. a. zenkeri* they are brown and in *C .a. johnstoni,* they are black (Hill, 1974).

Other species of mangabey

The other species in the Albigena group, black mangabeys, are the darkest coloured of the mangabeys, with a glossy black pelage (Hill, 1974). Schwartz (1928) claimed that the skull of black mangabeys is narrower than that of grey-cheeked mangabeys, that grey-cheeked mangabeys possess a shoulder mantle, lacking

Plate 1.1. Adult male grey-cheeked mangabey (*Cercocebus albigena*):Illustrating brownish-grey cape.(Photo courtesy of Karen McDonald).

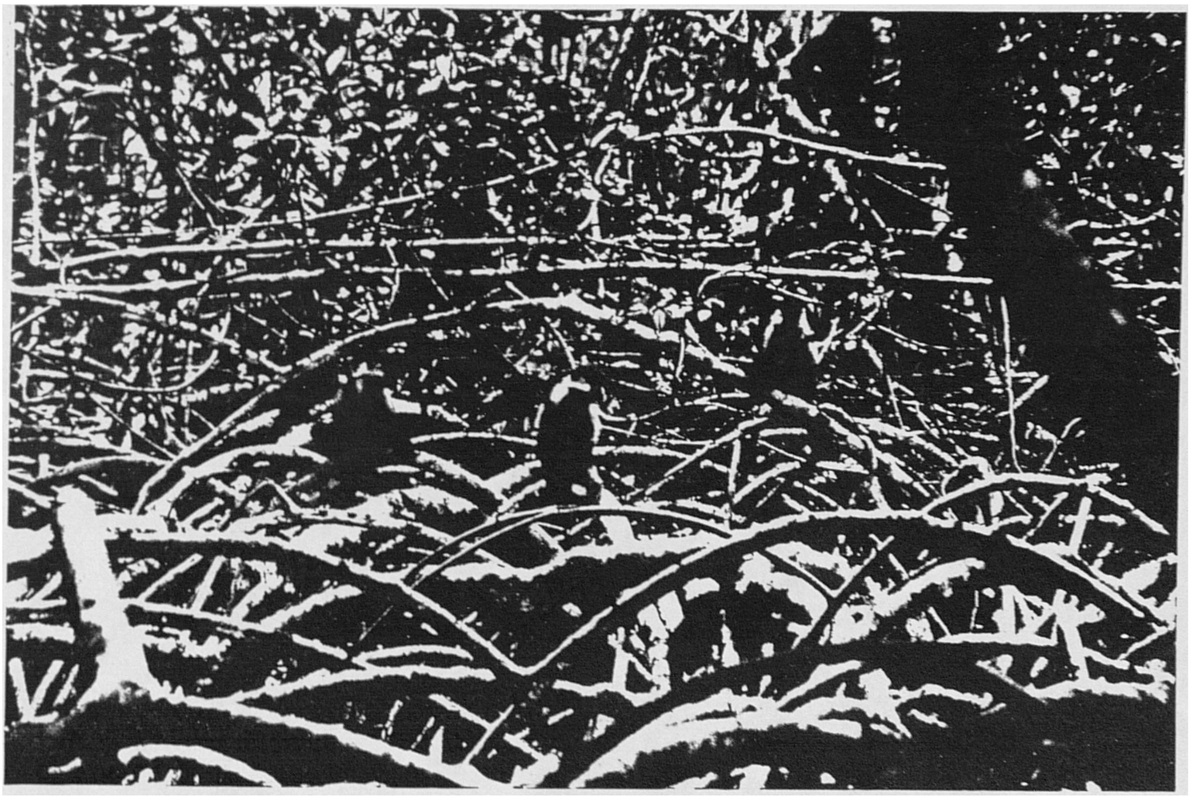


Plate 1.2 White-collared mangabeys (*Cercocebus torquatus*): Illustrating characteristic features of white cheeks and red cap.

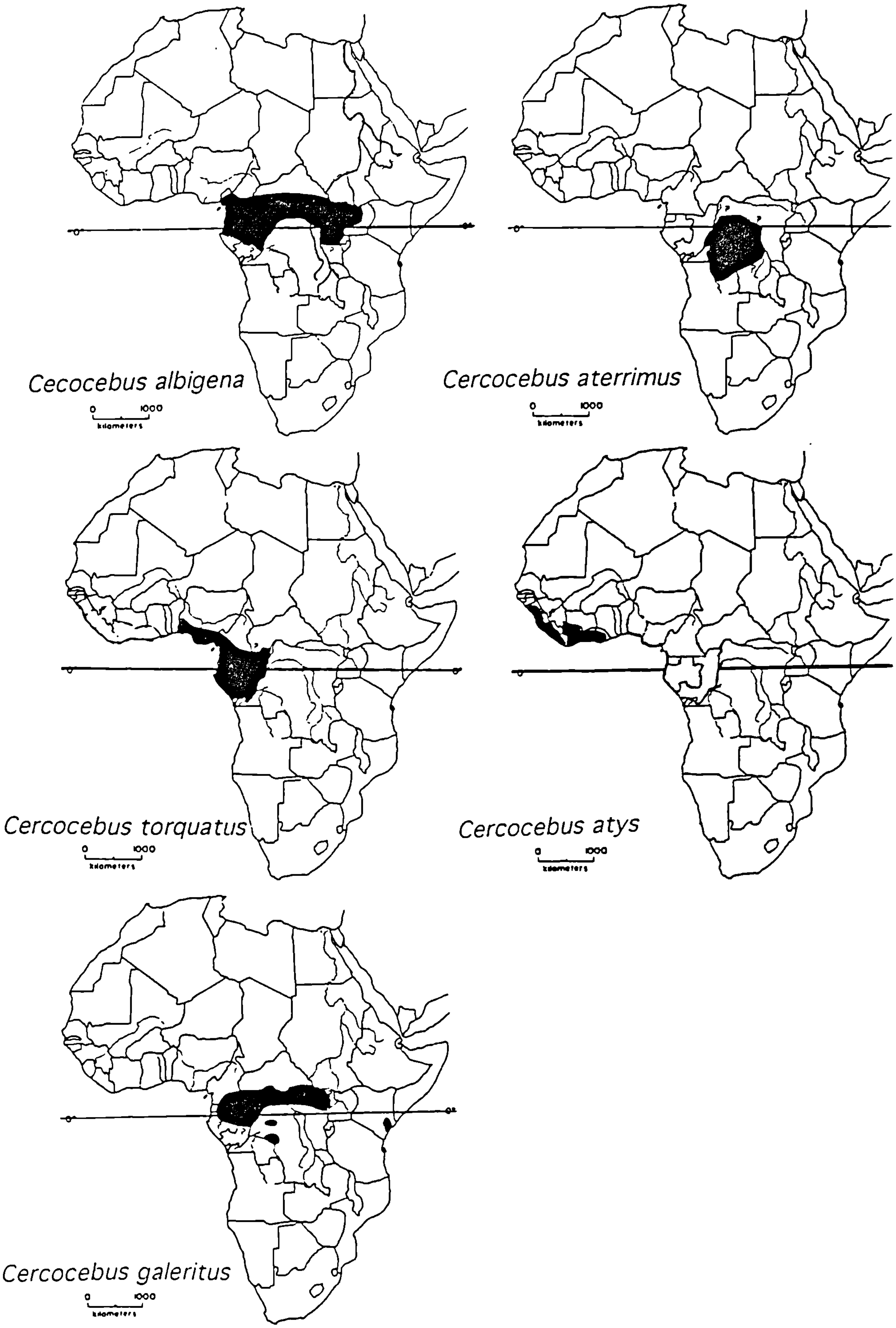
in black mangabeys, and that black mangabeys have a crest of hair on the top of their head which is more distinct than in grey-cheeked mangabeys. Groves (1978), however, points out that there is a great deal of variation and overlap in these characteristics between the species.

In the Torquatus group, for white-collared mangabeys, the most obvious identifying features are the white hairs around the neck and cheeks, white eyelids, white hair at the tip of the tail and chestnut-red hairs forming a cap on the top of the head (**Plate 1.2**). Sooty mangabeys are the darkest in the Torquatus group, with a dark smoky grey coat and a dark-brown cap. The face is flesh-coloured except for their white upper-eyelids (Hill, 1974). Agile mangabeys are most easily recognised by their coat, which has a "speckled olive appearance" (Hill, 1974). More details on the morphology of these species can be found in Hill (1974).

3. Geographical distribution and habitat

All mangabeys live in rain forests in Equatorial Africa. Their geographical range, therefore is mainly limited by that of the forest. The following provides a brief summary of the geographical distribution for each species (see also **Figure 1.2**), but more detailed summaries can be found in Hill (1974), Napier and Napier (1967), and Wolfheim (1983).

The distribution of grey-cheeked mangabeys extends through the lowland rain forests of Cameroon, Equatorial Guinea and Gabon, and then across Congo, north of the Congo River (Rahm, 1966, in Hill, 1974) to the eastern edge of their range in the forests surrounding Lake Victoria (Chalmers 1967). In Uganda they are found in some, but not all of the larger forest blocks.



Cecocebus albigena

Cercocebus aterrimus

Cercocebus torquatus

Cercocebus atys

Cercocebus galeritus

Figure 1.2 Geographical distribution of five species of mangabey: grey-cheeked mangabey (*Cercocebus albigena*); black mangabey (*Cercocebus aterrimus*); white-collared mangabey (*Cercocebus torquatus*); sooty mangabey (*Cercocebus atys*); agile mangabey (*Cercocebus galeritus*) (Napier and Napier, 1967; Wolfheim, 1983).

The ranges of the three subspecies of grey-cheeked mangabeys are poorly defined. *Cercocebus albigena albigena* are thought to range from the north bank of the lower Congo, northward through Gabon into adjacent parts of western Congo (Quris, 1976a; Hill, 1974; Wolfheim, 1983). *Cercocebus albigena zenkeri* have been observed to range in northern Cameroon and then eastwards into northern Congo as far as the Sangha river (Gartlan and Struhsaker, 1972; Hill, 1974; Wolfheim, 1983). *Cercocebus albigena johnstoni* are found in Congo, confined to the forest block between the Ubangi and the main stream of the Congo, and through Zaire, east of the Lualaba into Uganda (Freeland, 1977; Hill, 1974; Horn, 1987; Wallis, 1979; Waser, 1974; Wolfheim, 1983) (**Figure 1.3**). Grey-cheeked mangabeys are found typically in primary and secondary evergreen forest (Jones and Sabater Pi, 1968; Chalmers 1968b) although they are also found in swamp forests (Chalmers, 1968b), flooded forests (Gautier and Gautier-Hion, 1969) and coastal forests (Jones and Sabater Pi, 1968; personal observations).

The range of black mangabeys, *Cercocebus aterrimus,* is in Zaire, from the Congo River near 2°S, as far south as 7°30′S, 17°30′E, north to the Zaire River, and east to the Lualaba River (Horn, 1987a,b; Wolfheim, 1983). They are found on the west bank of the Lualaba-Zaire River, but north of this river they are replaced by grey-cheeked mangabeys (Horn, 1987a,b). Black mangabeys inhabit a variety of forest-types including semi-deciduous, gallery and swamp forests (Horn, 1987a,b).

White-collared mangabeys, *Cercocebus torquatus,* are found in Nigeria, southern Cameroon, Equatorial Guinea, Gabon and Congo and Central African Republic (Mitani, 1989; Wolfheim, 1983). They are typically found in mangrove, coastal, gallery and

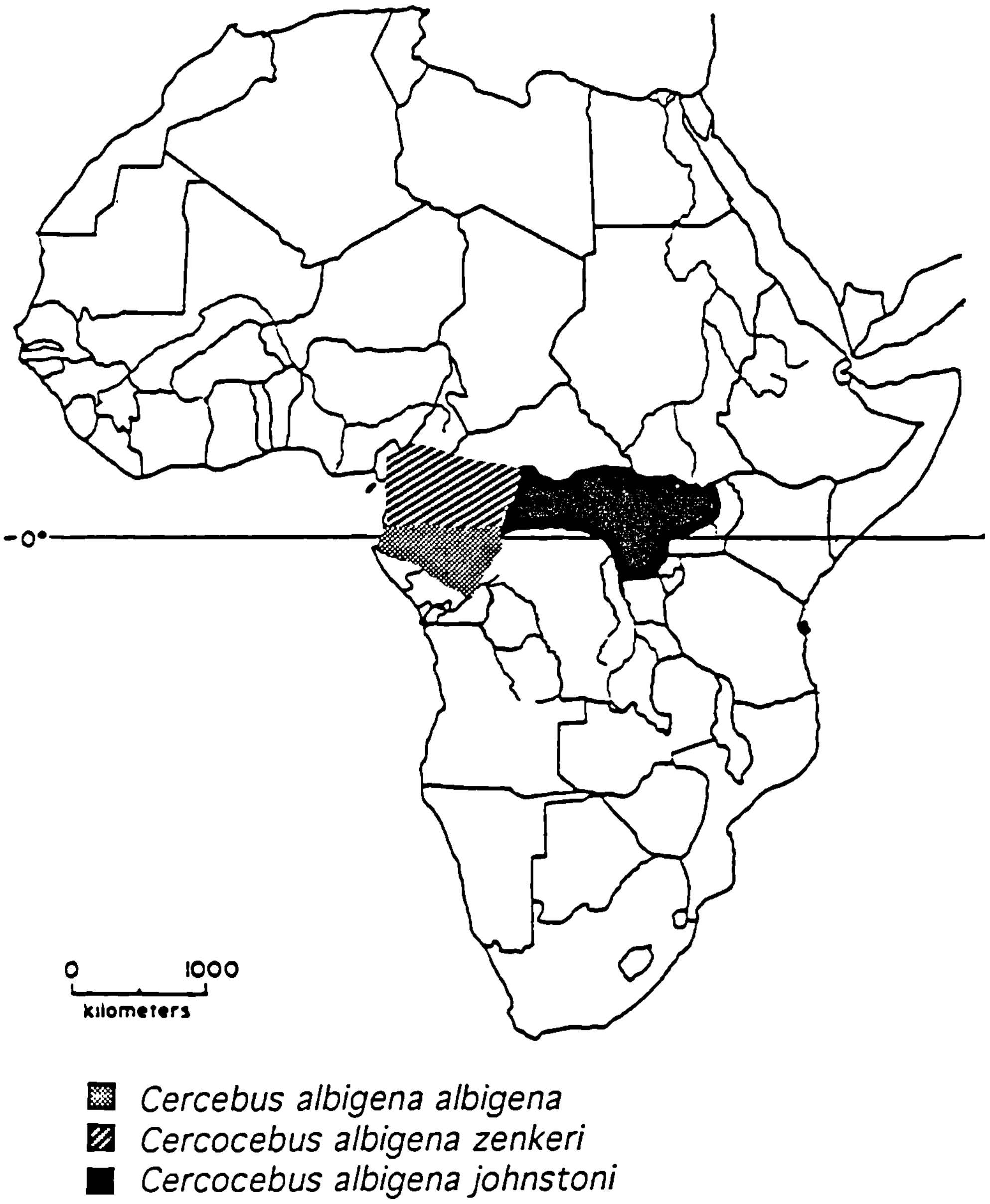


Figure 1.3. Geographical distribution of the subspecies of *Cercocebus albigena.*

inland swamp forests (Jones and Sabater Pi, 1968; Gartlan and Struhsaker, 1972), but are also found in primary forests (Jones and Sabater Pi, 1968; personal observations). They are listed as "vulnerable" in the IUCN Red Data Book (Lee *et al.*, 1988). Sooty mangabeys, *Cercocebus atys,* are found further to the north, inhabiting the coastal tropical forests of Senegal, Guinea, Sierra Leone, Liberia, Ivory Coast. They have been observed as far north as 12°30′N, 16°05′W in Senegal (Struhsaker, 1971; Wolfheim, 1983) The subspecies *C.atys atys* is found further to the north than the range of the subspecies *C.atys lunulatus* and their ranges are possibly overlapping (Hill, 1974).

Agile mangabeys, *Cercocebus galeritus* are found in Cameroon, Equatorial Guinea, Gabon, Congo, Central African Republic, Zaire, and Kenya (Gartlan and Struhsaker, 1972; Gautier and Gautier-Hion, 1969; Groves *et al.*, 1974; Homewood, 1975a,b; Quris, 1975; Wolfheim, 1983). Their northern limit and southern limit are thought to be 29°E in northeast Zaire and 4°S in Zaire, respectively (Wolfheim, 1983). They occur as far northwest as 2°57′N, 11°56′E in Cameroon, southeast as 2°15′S, 40°15′E in Kenya (Wolfheim, 1983). This species is listed as "endangered" in the IUCN Red Data Book (Lee *et al.*, 1988). The subspecies, *C.galeritus agilis* is widely dispersed in a narrow belt of forest in the Congo, from Cameroon in the west, to Lake Albert in the east and the subspecies *C. galeritus chrysogaster* is restricted to forests in the upper Congo (Hill, 1974). These western populations are often found in seasonally flooded forest (Gautier and Gautier-Hion, 1969; Quris, 1976). There is gap of about 1,200 km between their ranges, and the range of Tana river mangabeys, *Cercocebus galeritus galeritus,* in Kenya (Hill, 1974). Tana river mangabeys are endemic to gallery forests along the flood plain of the Tana River (Decker and Kinnaird, 1992). They live in small patches of seasonally flooded gallery forest and adjacent bush. The subspecies, sanje crested mangabey; *Cercocebus galeritus sanjei* has only been observed on the eastern side of the Uzungwa Mountains in Tanzania (7°76'S, 36°54'E), and lives in 'scarp' forest (Homewood and Rodgers, 1981).

B: BACKGROUND

Ecological studies of primates in their natural habitat did not begin until recently with Nissen's (1931) study on chimpanzees, Bingham's (1932) study on gorillas and Carpenter's (1934) study of howler monkeys (all cited in Richard, 1985). Early field studies were mainly descriptive (eg. DeVore, 1965) with little discussion of theoretical issues linking environment and behaviour and it has only been in the last 30 years that studies have begun to investigate this relationship (see Crook and Gartlan, 1966; Hall, 1962, for first studies).

During the 1960's it was frequently assumed that an animal's behaviour and ecology were products of species-specific strategies. More recently however, the ecological and behavioural flexibility of primates has been recognised. With an increase in the number of studies of the same species in different areas, and the same individuals over time, it has become clear that different environmental situations can produce different optimal strategies (Dunbar, 1988).

Partly because of the early interest in our evolutionary origins, there was a bias in the number of studies on those primates thought to be most intelligent and to most closely resemble humans (chimpanzees), and those living in open savanna conditions (baboons). The smaller, arboreal, forest living primates were generally ignored (Gautier-Hion *et al.*, 1988). In addition, intensive studies of primates living in tropical rain forests were probably avoided because work in the tropics was believed to be a difficult task due to the discomforts of the intense heat and humidity, insects, parasites and low visibility (Adams and McShane, 1992; Gautier-Hion *et al.*, 1988).

The few early studies on forest primates were mostly on New World monkeys (eg. Altmann, 1959). In the Old World, forest populations of macaques and langurs were studied, but much less intensively than populations of the same species living in more open habitats (Aldrich-Blake, 1970; Chalmers, 1968b). Chalmers (1967) aimed to balance this situation by studying grey-cheeked mangabeys (*Cercocebus albigena*) in Uganda. This was the first detailed field study of grey-cheeked mangabeys, and it was followed by several more field studies on this species during the next decade (Cashner, 1972; Freeland, 1977; Wallis, 1979; Waser, 1974).

The following section provides a brief review of these studies, as well as a description of other short-term and captive studies on the behaviour and ecology of mangabeys.

1. Previous studies

Long-term field studies of grey-cheeked mangabeys

There have only been five detailed field studies on grey-cheeked mangabeys in their natural habitat. Four of these were on mangabeys in the far eastern edge of their range in Uganda (Chalmers, 1967; Freeland, 1977; Wallis, 1979; Waser, 1974), and one was on mangabeys in Equatorial Guinea (Cashner,1972) (**Table 1.2, Figure 1.4**).

Table 1.2. General description of the study sites of previous studies on grey-cheeked mangabeys (*Cercocebus albigena*).

Study	**Chalmers (1967)**	**Waser (1974)**	**Freeland (1977)** **Wallis (1979)**	**Cashner (1967)**
Duration	Feb. 1964 to Nov. 1965	May 1971 to Nov.1974	Jan. 1975 to Sept. 1975 Aug. 1975 to May 1977	Sept.1967 to June 1968
Country	UGANDA	UGANDA	UGANDA	EQUATORIAL GUINEA
Location	Bujuko (0°22'N, 30°18'E) Mabira	Bwamba (Semliki) (0°48'N, 30°9'E) Lwamunda (0°22'N, 32°18'E) Kifu (0°24'N, 32°45'E) Kibale (Dura) (0°28'N, 30°22'E) Kibale (Kanyawara) (0°34'N, 30°22'E)	Ngogo (0°30'N, 30°25'E)	Ndjiakom (1° to 2°30'N and 9 to11°30'E)
Climate	rarely below 15°C at night 21°C to 27°C during day	mean minimum=16°C mean maximum=23°C	mean minimum=17°C mean maximum=24°C	mean minimum=21°C mean maximum=35°C
Annual rainfall	1026-1539 mm	1658 mm	1 475 mm	
Anthropoid primate species	*Cercocebus albigena* *Cercopithecus ascanius*	*Cercocebus albigena* *Cercopithecus ascanius* *Cercopithecus mitis* *Cercopithecus l'hoesti* *Colobus badius* *Colobus guereza* *Papio anubis* *Pan troglodytes*	*Cercocebus albigena* *Cercopithecus ascanius* *Cercopithecus mitis* *Cercopithecus l'hoesti* *Colobus badius* *Colobus guereza* *Papio anubis* *Pan troglodytes*	*Cercocebus albigena* *Cercopithecus pogonias* *Cercopithecus cephus* *Cercopthecus nictitans* *Colobus satanus* *Pan troglodytes* *Gorilla gorilla* *Mandrillus sphinx*

1. Present study: SEGC, Lopé Reserve, GABON: 0°10'S, 11°35'E.
2. Cashner (1972): Ndjiakom, EQUATORIAL GUINEA: 1-2°30'N, 9°30'-11°30'E.
3. Chalmers (1967): Bujuko and Mabira, UGANDA: 0°22'N, 30°18'E.
4. Waser(1974): Kanyawara, Kibale Forest, UGANDA: 0°30'N, 30°25'E
5. Freeland (1977), and 6. Wallis (1979): Ngogo, Kibale Forest. UGANDA: 0°30'N, 30°25'E

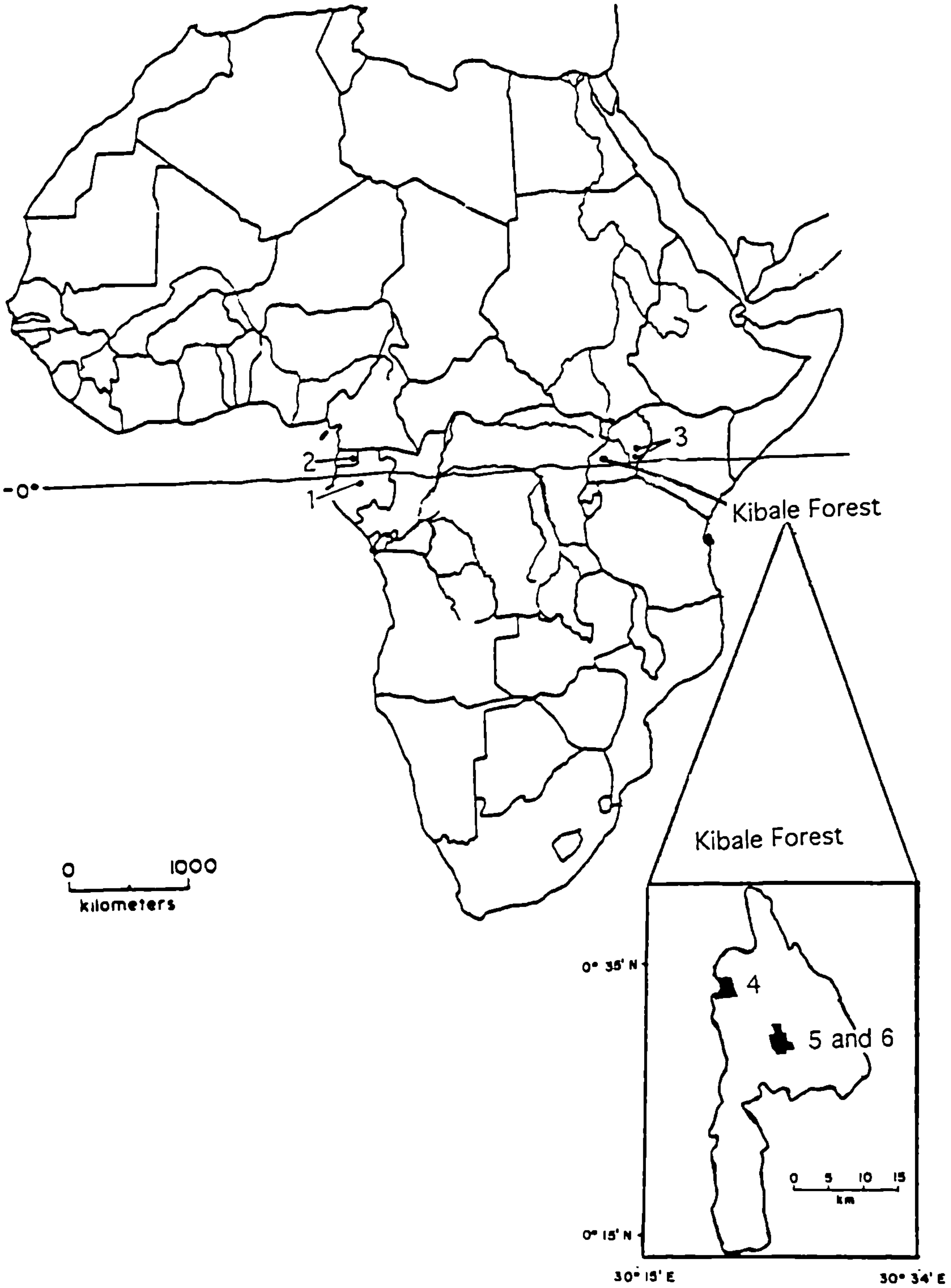


Figure 1.4. Map showing the location of the six long-term field studies on grey-cheeked mangabeys.

Chalmers (1967) was the first to provide information about grey-cheeked mangabey's visual and vocal communication (Chalmers, 1968 a), daily activities (Chalmers, 1968b) and social behaviour (Chalmers 1968c). The information he gave on ranging patterns, diet and interspecific relations, however, was limited . One of the problems with this study was that he was unable to follow the groups continuously due to dense ground vegetation.

Cashner (1972) studied both grey-cheeked mangabeys and white-collared mangabeys in Equatorial Guinea. This was the first long-term study of mangabeys living in western African forests. The study provided information on general aspects of the behaviour and ecology of mangabeys, although much of the data were only descriptive. Cashner (1972) did not follow habituated groups of mangabeys and therefore her understanding of the social relations within the group was only minimal. The most intriguing results of her study was that groups commonly contained only one adult male, and that groups sometimes peacefully aggregated to feed and travel. These results were surprising because in all other studies, mangabeys have been observed to generally live in multimale groups, which avoid each other (Chalmers, 1967; Waser, 1974). Although information on her study is available in her thesis (Cashner,1972), none of the results of her study have been published.

After a brief pilot study (Waser and Floody, 1974), Waser (1974) conducted a long-term study on grey-cheeked mangabeys at Kanyawara in the Kibale forest, Uganda. This was the most detailed of the five field studies on mangabeys. Unlike the studies by Chalmers (1967) and Cashner (1972), the groups which Waser (1974) studied were sufficiently habituated so that he could follow them continuously and recognise individuals. His study gave detailed information on aspects of their behaviour and ecology, including group size (Waser, 1977a), feeding (Waser, 1975a,1977a), ranging (Waser, 1977a, 1978a, Waser and Floody, 1974), activity patterns (Waser, 1975 a), polyspecific associations (Waser, 1980, 1982a, 1984, 1987) and especially on intergroup spacing systems (Waser, 1977b; 1978), and their vocal behaviour (Waser, 1975b, 1977b,1978a, 1982b). Waser (1978) provided some description of social relations within the group, but this was not the main focus of his study.

Wallis (1979) studied mangabeys at Ngogo, also in the Kibale forest in Uganda. His study provided mainly descriptive data on the ecology of mangabeys. He did, however, provide the most detailed information of the behavioural repertoire (Wallis, 1981), and especially the sexual behaviour (Wallis, 1983) of grey-cheeked mangabeys.

Freeland (1977) studied grey-cheeked mangabeys at the same location as Wallis (1979). Freeland (1979) examined relationships between social organisation and population density in relation to food density by comparing his data with that of Waser (1974). His other work (eg. Freeland, 1980) concentrates mainly on the effect of parasite contamination on behaviour, (especially ranging patterns).

Short term studies and brief observations

Several authors have given information on the behaviour and ecology of grey-cheeked mangabeys from brief observations or short studies. Jones and Sabater Pi (1968) published observations of grey-cheeked mangabeys in Rio Mbia in Equatorial Guinea (9° 55′E, 2°5′N). This study provided preliminary information on group size, ranging patterns, diet and associations with other species, although results were based on only 15.41 hours of observation from 12 visits to the area. Gautier-Hion (1977) examined the diet of grey-cheeked mangabeys in Gabon from information collected from the stomach contents of 18 mangabeys. Their study showed mangabeys to be very frugivorous, relying mainly on fruits from the family Myristicaceae during the long dry season. This information, however, was based on a very small sample size and was not supplemented with behavioural observations. All other studies on wild grey-cheeked mangabeys are based on very few encounters and only brief observations (Mitani,1991; Quris, 1976; Struhsaker, 1969).

Captive studies

Information is available on captive grey-cheeked mangabeys from several sources. Rowell and Chalmers (1970), and Chalmers and Rowell (1971) studied behaviour and recorded female reproductive cycles of grey-cheeked mangabeys in captivity. They observed changes in the behaviour of adult females during different stages of their menstrual cycle, but these results were based on a very small number of individuals (three adult females and one adult male). Danjou (1972), Deputte (1991), and Gautier-Hion and Gautier (1976) also gave information on the sexual behaviour and reproductive parameters of grey-cheeked mangabeys, and Deputte (1986; 1992) provided data on development and life history statistics.

Studies of other species of mangabey

Grey-cheeked mangabeys are the best known of the species of this genera, and little is known about other species. From captive studies, information is available for sooty mangabeys (Bernstein, 1971, a,b,1976; Busse and Gordon, 1983, 1984; Ehardt, 1988; Gust *et al.*, 1990; Gust and Gordon, 1991; Hadidian and Bernstein, 1979; Kyes, 1988) and information from field studies is available (1) for black mangabeys from Horn (1987a,b), (2) for white-collared mangabeys from the preliminary observations of Jones and Sabater Pi (1968) in Equatorial Guinea, a 15 month study by Mitani (1989) in Cameroon, and Cashner's (1972) study in Equatorial Guinea, (3) for sooty mangabeys, from the brief observations of Galat and Galat-Luong (1985) in Ivory Coast, and (4) for agile mangabeys from studies of their vocalisations by Quris (1973, 1980) in Gabon, and studies of their ecology, behaviour and conservation status by Quris (1975, 1976), Decker and Kinnaird (1992), Homewood (1975 a, b,1976, 1978), Homewood and Rodgers (1981), and Groves *et al.* (1974).

2.The present study

There have been no detailed field studies on grey-cheeked mangabeys now for over 15 years (although Louise Barrett is presently studying grey-cheeked mangabeys at Ngogo, Uganda). Although there has been an increase in the number of field studies on forest guenons in recent years (eg. Gautier-Hion *et al.*, 1988), still relatively little is known about mangabeys.

The above review of the literature reveals that most information on grey-cheeked mangabeys comes from populations in Uganda, and very little is known about this species living in western African forests. Studying the same species in different habitats is one of the best ways to study the effects of environment upon behaviour. In western African, forests are thought to be richer in plant species than forests in eastern Africa (Gautier-Hion, 1983) and the species composition of the primate communities differ. Grey-cheeked mangabeys in western Africa, therefore, coexist with a different set of potential competitors than mangabeys in eastern Africa. A study of grey-cheeked mangabeys living in forests in western Africa would therefore be interesting to examine how differences in forest composition and differences in sympatric primate species may affect their behaviour and ecology.

Gabon

Rain forest habitats in West Equatorial Africa have a high diversity of flora (Reitsma, 1988). Forests in Gabon, in particular, have a higher tree species diversity than rain forests in other parts of Africa, probably because this area was a refuge during the retraction of the forest in the Pleistocene (White, 1992). In terms of primates, Gabon has been described as one of the areas of greatest primate diversity (Chapman, 1983; Mittermeier and Oates, 1985) and has one of the largest populations of chimpanzees and gorillas in Africa (Tutin and Fernandez, 1983, 1984). Seventy-five percent of Gabon, comprising an area of 200,000 km2, is still covered in rain forest (Myers, 1991). The country has a low human population density (the population of Gabon is about 1.2 million with a density of about 4.6 people/km^2) and greater economic wealth compared to other countries in Africa (primarily from off-shore oil) (Breteler, 1988; White, 1992). For these reasons, it is an ideal country for studies of primates living in an intact rain forest ecosystem.

The Lopé Reserve and SEGC (The Station d'Etudes des Gorilles et Chimpanzés)

Few studies have looked at interspecific relationships between primates. This is especially important in tropical forests where diversity and complexity are great. In the Lopé Reserve, situated in the centre of Gabon, there are eight species of diurnal primates. At the SEGC study site, within the Reserve, research on chimpanzees (*Pan t.troglodytes*) and western lowland gorillas (*Gorillas g. gorilla*) has been in progress since 1984 (Tutin and Fernandez, 1993a). Black colobus (*Colobus satanus*) have also been studied at Lopé, 7 km from the SEGC study site (Harrison, 1986a,b). A study on mangabeys was therefore welcomed to contribute further to this growing data base on the primate community at Lopé.

Grey-cheeked mangabeys studied in Uganda were observed to be highly frugivorous, but these studies were done in areas lacking sympatric gorillas and chimpanzees (Wallis, 1979; Waser, 1977a). Gorillas at Lopé have a diverse frugivorous diet, which overlaps extensively with that of the chimpanzees (Tutin *et al.*, 1991a; Tutin and Fernandez, 1993a). At Lopé the forests are highly seasonal with periods of fruit scarcity during the long dry season (Williamson, 1988). Such periods could be critical for primates. It is important, therefore, to analyse their diets at times when fruit is limited, as it is at such times that the greatest niche differentiation between sympatric frugivores would be expected.

Research goals

The aim of this study, therefore, was to document in as much detail as possible, the behaviour and ecology of grey-cheeked mangabeys in the Lopé Reserve, Gabon. Specific research goals were to habituate a group of grey-cheeked mangabeys in the SEGC study area. From detailed observations of this group, and opportunistic observations of other groups, the main aims were:

(1) to monitor climatic changes over the period of the study (*Chapter Two*) in order to examine how these may affect the behaviour and ecology of mangabeys;

(2) to investigate differences in forest structure and plant species composition between different habitat-types within the mangabey's home range (*Chapter Three*) in order to examine how these may affect their use of space;

(3) to record group size and structure, and reproductive parameters of grey-cheeked mangabeys (*Chapter Four*);

(4) to describe in detail, the diet of grey-cheeked mangabeys and how it overlaps with the diets of other species of primates in the Reserve (*Chapter Five*);

(5) to determine the ranging patterns of the study group and to document the frequency and form of intergroup encounters (*Chapter Six*);

(6) to describe their social behaviour (*Chapter Seven*);

(7) to examine the relationships between grey-cheeked mangabeys and other primates within the study area, especially looking at factors that may influence the frequency of polyspecific associations between mangabeys and other arboreal primates (*Chapter Eight*);

(8) to compare the behaviour and ecology of grey-cheeked mangabeys at Lopé to populations of the same species studied

elsewhere.

These data will permit the definition of the mangabey's niche in the complex forest primate community and allow testing of hypotheses derived from ecological and evolutionary theory, thus contributing to an increased understanding of tropical forest ecosystems.

CHAPTER TWO: STUDY SITE AND GENERAL METHODS

A: STUDY SITE

1. General

Gabon lies on the equator on the West Coast of Africa and covers an area of 267, 667 km^2. There are no national parks in Gabon but there are five protected areas, three of which are faunal reserves. The Lopé Reserve is the largest of the faunal reserves, with 5,000 km^2 of rain forest and savanna, that has been administered by the Eaux et Forêts since 1946 (**Figure 2.1**). It has been designated a key area for primate research and conservation efforts (Oates, 1986).

The Station d'Etudes des Gorilles et Chimpanzés (0°10'S, 11°35'E) was founded by Tutin and Fernandez in 1983 after a 3-year nation-wide survey (Tutin and Fernandez, 1984). Research on chimpanzees and gorillas and their tropical forest habitat has been in progress since 1984.

In the north of the Reserve, close to the Ogooué River, savanna and gallery forests dominate. The proportion of forest increases southwards until about 15 km south of Ogooué where the forest becomes continuous. The SEGC camp is located about 500m from the edge of the continuous forest and the study area includes approximately 40 km^2 of uninhabited tropical rain forest, gallery forest, and savanna. The home range of the study group of mangabeys was located in the continuous area of forest in the SEGC study area (**Plate 2.1**). Savanna formed a natural barrier at the southern edge of their range. There was only one river that ran through the study area; the Koumbiane, although there were other, smaller and ephemeral streams.(Further details will be given about vegetation in *Chapter Three,* and more detailed description of

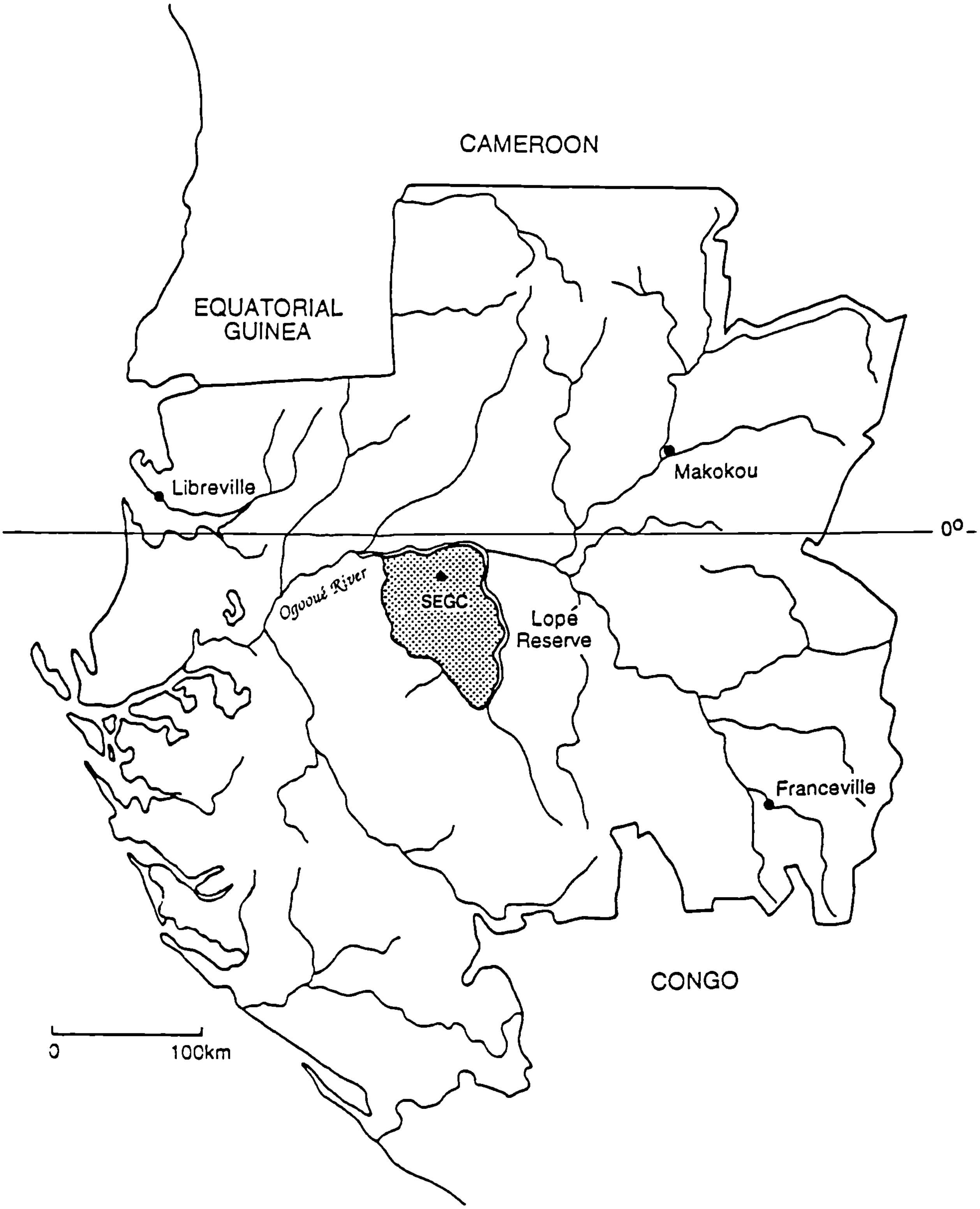


Figure 2.1. Map showing the location of the Lopé Reserve in Gabon and the Station d'Etudes des Gorilles et Chimpanzés (SEGC) in the Lopé Reserve (0°10'S, 11°35'E).

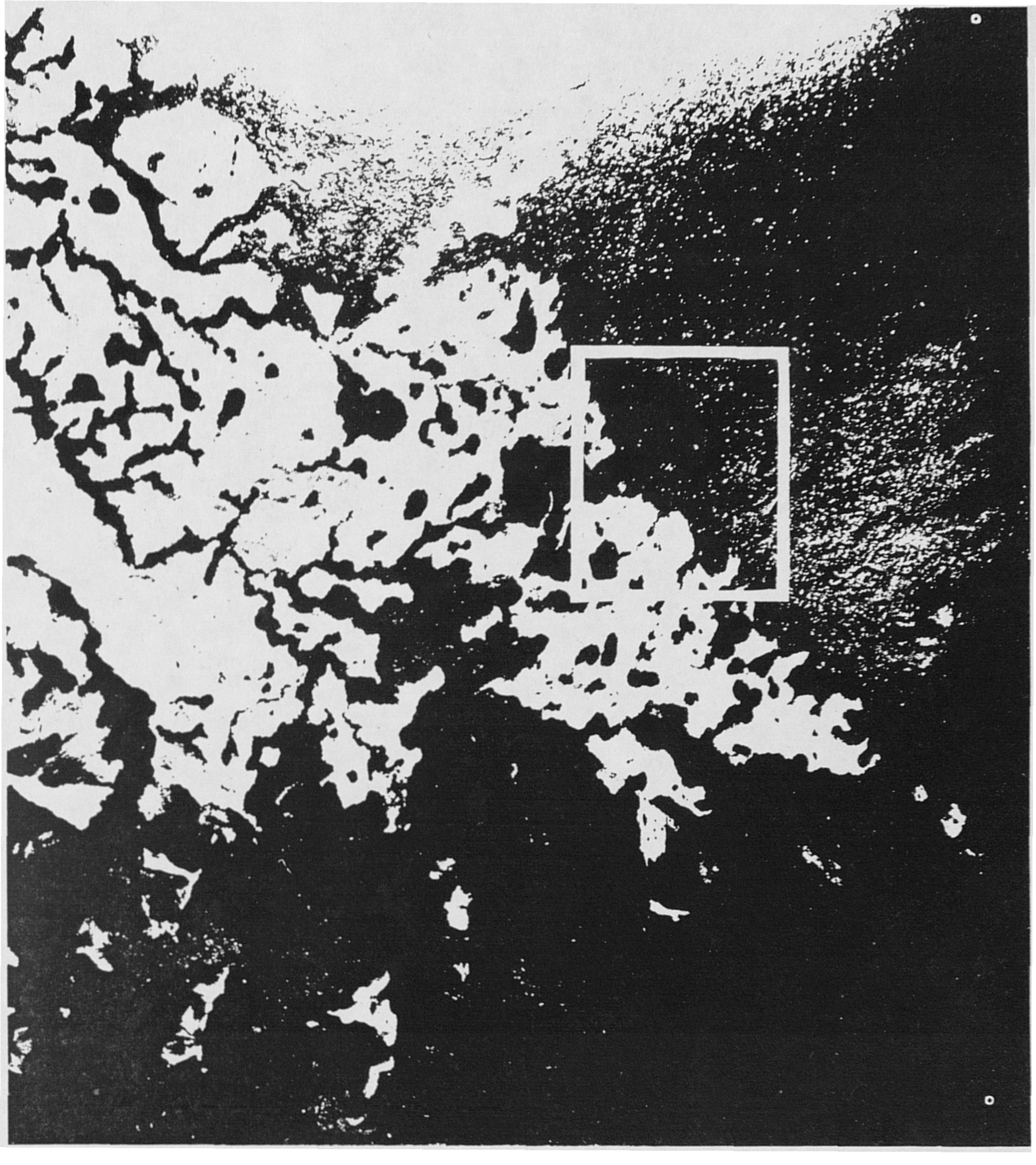


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Plate 2.1 Aerial photograph including the SEGC study area (1 cm=500m). The white box encloses the area of the photograph which encompasses the home range of the study group of grey-cheeked mangabeys.

their home range *in Chapter Six*).

Grey-cheeked mangabeys at Lopé, live sympatrically with seven other species of diurnal primates, including gorillas (*Gorilla gorilla gorilla*), chimpanzees (*Pan troglodytes troglodytes*), mandrills (*Mandrillus sphinx*), black colobus (*Colobus satanus*), crowned guenons (*Cercopithecus pogonias*), greater spot-nosed guenons (*Cercopithecus nictitans*), and moustached guenons (*Cercopithecus cephus*), as well as at least three species of nocturnal primates (Williamson, 1988).

2. Climate

Rainfall

Rainfall was collected in a rain-gauge at camp and measured each morning at 07:00. The rainfall during the period of this study was 1234 mm in 1991 and 1572 mm in 1992 (**Figure 2.2**). This falls within the normal range of rainfall at SEGC with an mean annual rainfall over 9 years (from 1984 to 1992) of 1506 mm (range: 1167 mm to 1851 mm) (**Figure 2.3**). During the study there was no rain in July 1991, and no rain in July and August 1992. This pattern is typical for SEGC and for Gabon in general, with a long dry season from mid-June to mid-September, a short rainy season from mid-September to mid-November, a short dry season from mid-November to mid January, and a long rainy season from mid January to mid-March.

Annual rainfall is relatively low in Gabon for tropical forests, and the Lopé itself is in an area with relatively low rainfall compared to most of the country. During the dry months, persistent cloud cover caused by the cold sea currents, and the associated reduction in temperature results in low evaporation rate and high humidity, thus permitting the evergreen forests to be maintained (Breteler, 1988). The

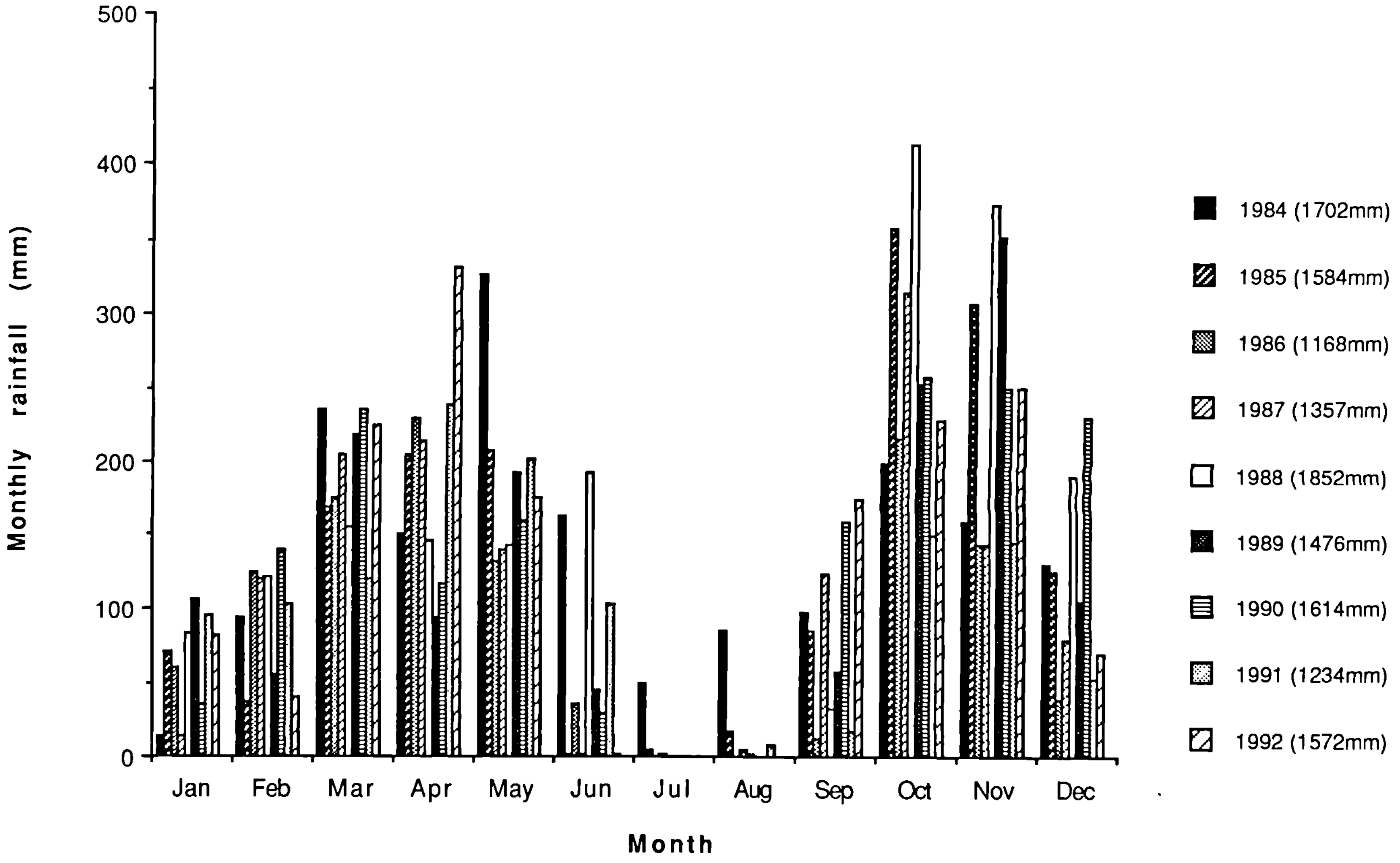

Figure 2.3 Rainfall at SEGC from 1984-1992

Lopé probably experiences reduced amounts of rainfall due to its location. It is surrounded by mountains, which may cause a rain shadow effect, and it is close to the Ogooué River, which is followed by a band of low rainfall (Hladik, 1973; White, 1992).

Temperature

A maximum and minimum thermometer, located inside the forest 1 m above the ground in the shade, recorded daily temperatures. During the two years in which the study was conducted, average low and high temperatures were 21.56°C (SD=0.75) and 28.57°C (SD=1.57) respectively, with the lowest monthly mean temperature in 20.2°C in July 1992 and the highest mean monthly temperature of 30.7°C in March 1992 (**Figure 2.4**). Mean monthly minimum and maximum temperatures over nine years (from 1984 to 1992) were 21.68°C (SD=0.66) and 29.21°C (SD=1.51) respectively, where temperatures were lowest during the long dry season (**Figure 2.5**).

Humidity

Humidity readings were taken using a standard wet and dry bulb thermometer. The thermometer was located in the shade, a few meters inside the forest. Humidity readings were recorded most frequently between 07:00-09:00 and 15:00-17:00, when researchers were entering or exiting the forest. From January 1991 to September 1992, the average relative humidity from 07:00 to 09:00 was 95.04% (SD=2.42) and from 15:00 to 17:00 was 79.91% (SD=7.43).

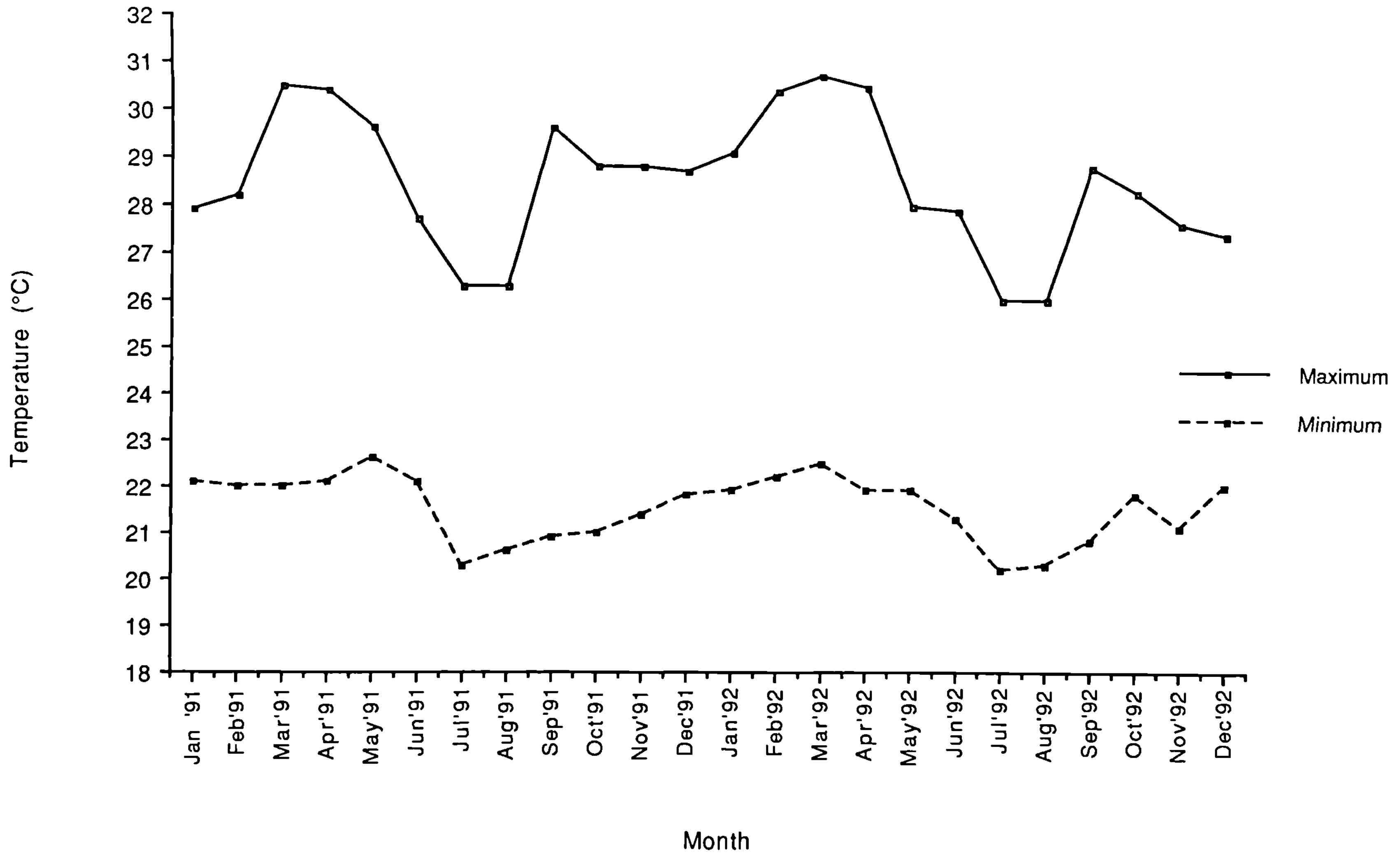

Figure 2.4. Maximum and minimum temperatures at SEGC during 1991 and 1992

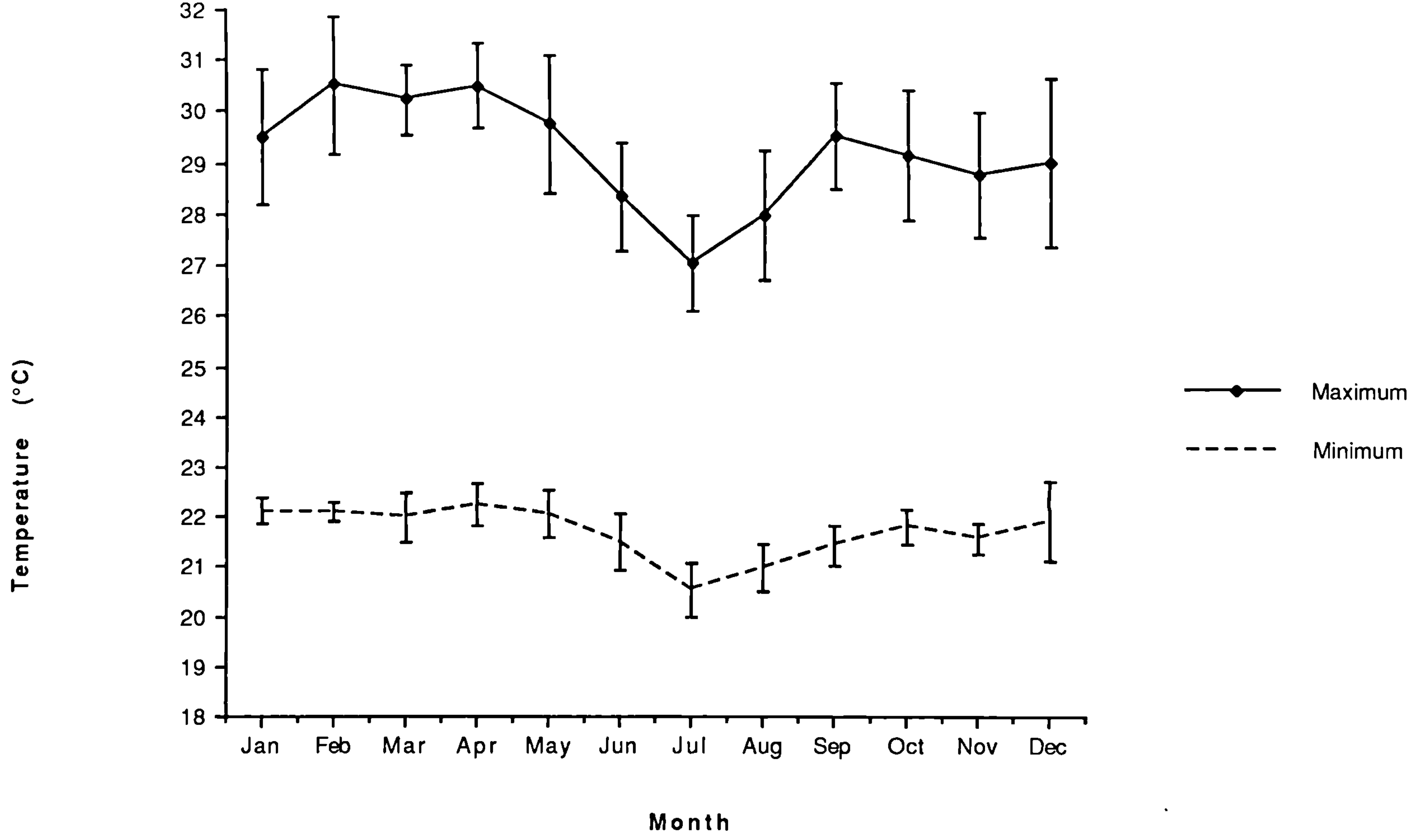

Figure 2.5. Mean minimum and maximum temperatures (°C) at SEGC from 1984-1992

B: METHODS

1. Equipment

Equipment included a compass, secateurs (used to cut through dense vegetation with minimum noise and minimum damage to the vegetation), and 10 X 40B Zeiss binoculars. Motorola HT90 "walkie-talkies" were carried by all researchers in the forest and used to report their location to the camp every hour, and to communicate information about the movement of animals, changes in weather etc. Field notes were taken on Nalgene water-proof notebooks, and data were recorded onto check-sheets (see below).

Aerial photographs of the study area with a scale of 1 cm: 500 m (**Plate 2.1**) were enlarged five times to the scale of 1 cm=100 m (**Plate 2.2**). These were used to draw maps, onto which streams and major animal paths were added for use as reference points (**Figure 2.6**). A watch was used, with an alarm set to beep at regular intervals to signal the beginning of a scan sample.

2. Habituation

In January 1991, a target group of mangabeys was chosen, primarily because they ranged in an area that had already been mapped and that was central to the main SEGC study area. This group of mangabeys ranged closest to camp, therefore minimising the time taken to reach the group in the morning. The group was found in the morning by walking the series of animal paths in the study area and listening for their vocalisations. The mangabey's characteristic long-call, the "whoop-gobble" (see *Chapter Seven*), can be normally heard from about 500 m, and even as far as 1200 m (Waser, 1977 b), although the distance depends on the terrain, forest type, and weather condition. Knowledge of the location of fruiting

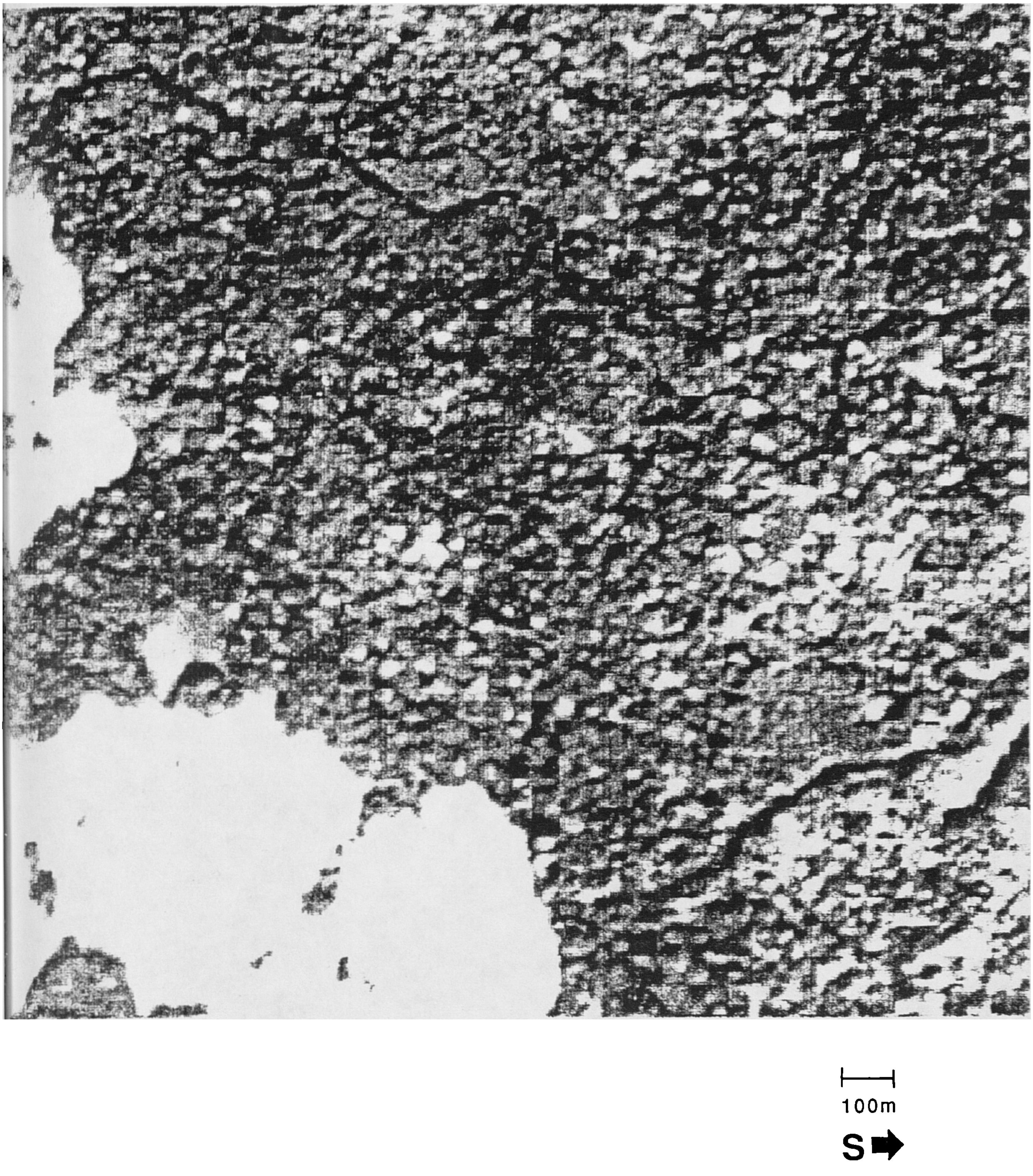

Plate 2.2. Forest encompassing the home range of the study group of grey-cheeked mangabeys (Cercocebus albigena) enlarged from the aerial photograph (see Plate 2.1).

Figure 2.6. Hand drawn map with superimposed grid-squares (1-grid-square=1 ha), drawn from the enlargement of the aerial photograph (see Plate 2.2). Shaded areas on the north edge of the map are areas of savanna, and black circles are rocky outcrops within the forest.

▬ ▬ shows position of the river-edge transect (see Chapter Three)

•••••• shows position of the savanna-edge transect (see Chapter Three) trees within the range of the mangabeys also helped to predict their movements. Once the group was located, they were followed for as long as possible.

At the beginning, I approached the group quietly, but tried not to get too close before they saw me since they seemed less alarmed when they first became aware of me at a distance. Initially, the first individual to see me alarmed with "chuckles" (see *Chapter Seven*). Most of the group fled, although the adult male often came to investigate and sit above me, threatening and displaying (see *Chapter Seven*). Once detected, I tried to move out into the open so that the mangabeys could see me and become habituated to my presence.

It is impossible to say when the mangabeys were "habituated" since this was a continual process. Analyses of the duration of contacts did not prove useful in determining when the group was sufficiently habituated, since it was not only how *long* I could remain in proximity with the group, but a combination of the duration of contacts, the distance to which I was able to approach them, and their behaviour towards me, that were important. By April 1991, I was able to walk directly under the trees in which mangabeys were feeding without seeming to affect their behaviour. They no longer alarmed with chuckles at my presence, unless I made sudden movements. Individuals in the group did not flee from me, or approach me to investigate, but instead, generally ignored me. Collection of ecological data, such as what food species were eaten and ranging data on the areas of the forest visited by the group, started in January 1991, but more detailed observations on, for example, social behaviour, activity patterns, and the frequency with which plant items were eaten, were used for analysis only from April 1991 onwards. Further details of this will be given in relevant chapters.

3. Field notes

General

Field notes were kept during all time spent in the forest. Time and location of entry and exit into the forest and start and finish times of visual contact with mangabeys were recorded, so that that field time and contact time could be calculated (**Figure 2.7**). Other researchers present, the names of all the paths followed and areas that were searched, were also recorded. All mammals that were encountered were noted, as well as details taken on the number of individuals, feeding observations and behaviour.

Arboreal primates

When I was not following the study group of mangabeys, whenever other primates were encountered, I recorded their location and whether there were any other species of primates within 50 m. (The criterion of 50 m is explained in more detail in *Chapter Eight*). Information was also collected on the average height of encountered groups of arboreal primates. Where possible the size and composition of the group was also recorded. Precise group counts were difficult for three main reasons: (1) monkeys did not always follow the same route through the canopy, and therefore, with only one observer, it was difficult to be certain that all individuals were counted; (2) group spread was sometimes so large that individuals on the periphery of the group were missed; (3) the canopy was usually dense and therefore visibility limited (see Aldrich-Blake,1970, for a discussion of the problems of observing forest primates). Groups were most easily counted when they crossed an open area, such as an old logging road,

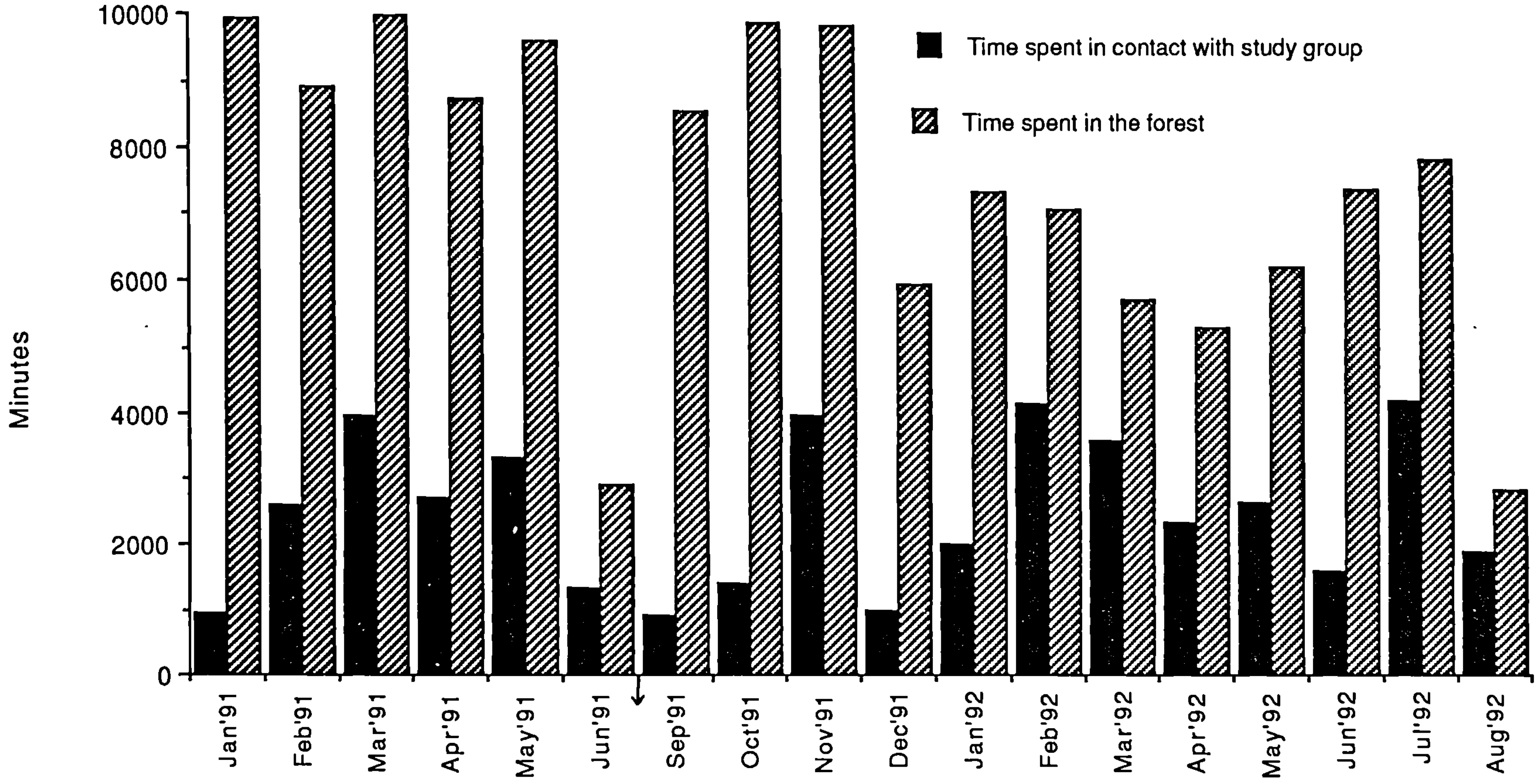

Figure 2.7. Graph showing time spent in the forest, and time spent in visual contact with the study group of mangabeys. The arrow indicates discontinuity between the months and will be used on graphs for the remainder of the thesis

or an area where there was only one travel route through the canopy. Group counts were only included in analyses if they were thought to be accurate ± 1 individual, and estimates were not used. (Further details of these methods are given in *Chapter Four* and *Eight*).

All foods seen to be eaten by monkeys were recorded, and the plant species and plant part noted as described below for the check sheet. (Further details of the methods of data collection on feeding behaviour, are described in *Chapter Five*).

4. Check Sheets

When the main group of mangabeys was contacted, the date, time, location and presence and identification of any other primates within 50 m were recorded. At 15 minute intervals, instantaneous scans (Altmann and Altmann, 1970) of seven minutes duration, or until five individuals (which ever come first), were sampled to record the following information:

Age and Sex of Subject

Methods for identifying different age and sex categories in grey-cheeked mangabeys have been provided by several authors (Cashner, 1972; Chalmers, 1968 b; Deputte, 1992; Wallis, 1979; Waser, 1974). Although there are some discrepancies about the age of the animals included in each class, they provide a useful framework for identifying general age classes.

Adult male

Male and female mangabeys were differentiated by their ischial callosities: in males, the ischial callosities form a continuous pad across the perineum, whereas in females, the pad is split in the median sagittal plane (Deputte, 1992). In captivity Deputte (1992) classified a male mangabey as adult, when his upper canines are twice as long as the upper incisor. This detail was not possible in the field and so an adult male was identified as a male mangabey of full body size, with full muscular development, an elongated face, large canines and full mane. Chalmers (1968 b) used these same criteria. The ages that have been assigned to adult males are: (1) greater than five years old (Danjou,1972; Wallis, 1979); (2) greater than five to seven years (Cashner, 1972; Chalmers, 1968 b; Waser, 1974), and (3) greater than seven years old (Deputte, 1992).

Adult female

Deputte (1992) defined an adult female, as a female with regular oestrus cycles. He classified adolescent females as those with irregular cycles. It was not always possible in the field to know when cycles were regular, especially when individuals were not identifiable. An adult female in the present study was classified as an adult from her first swelling onwards. In unknown groups, adult females were judged mostly on size and whether their callosities were clearly separated. The age of an adult female has been determined to be: (1) greater than five years old (Deputte, 1992; Danjou 1972); (2) greater than three years old (Chalmers, 1968 b); (3) greater than three to four years old (Wallis, 1979), and (4) greater than 4.5 years old (Cashner, 1972; Waser, 1974). Chalmers (1968 b) and Waser's (1974) estimates of age of maturation are probably lower than Deputte's (1992) because they include adolescent females in their category of adult females.

Sub-adult male

Sub-adult males can be distinguished from juveniles in that their scrotum is fully visible, but differ from adult males in that full body size has not yet been attained and muscular development is not yet complete. Chalmers (1968 b) defined a sub-adult male as a male mangabey that is sexually mature but not yet fully grown. This same criterion was used in this study. Sub-adult males have been estimated to be: (1) from five to seven years old (Deputte,1992); (2) three to six year old (Chalmers, 1968 b), and (3) four to five years old (Wallis 1979). The age limits were not known for Cashner's (1972) and Waser's (1974) class of sub-adult males.

Juvenile

In the present study, juveniles were mangabeys greater than 15 months. Females were no longer classified as juveniles once they became adult, and males, once they became sub-adult (see definitions given above). Individuals whose age was not known were judged by size, and the appearance of the mane on their shoulders. In juvenile males, the scrotum was not visible and in juvenile females the callosities were not clearly separated (Wallis, 1979).

Fifteen months was chosen for the present study, as the age above which mangabeys were juvenile, because before this age, mangabeys were still suckled and carried by their mothers.

This class is similar to Cashner's (1972) and Waser's (1974) class of "old juvenile" (older than 18 months) and Deputte's (1922) class of "juveniles 2" (older than one year). In other studies, juveniles have been judged to be older than about one year (Chalmers, 1968 b). Cashner's (1972) age limits for old juveniles were not known.

Infant

In the present study infants were individuals between birth and 15 months for the reasons given above. This includes Cashner's (1972), Deputte's (1992) and Waser's (1974) class of young infant, old infant and young juveniles (0-18 months). Chalmers' (1968 b) class for infants was animals less than one year.

Identification

The identity of individual mangabeys was recorded whenever it was known. Characteristics that proved to be most useful in identifying individuals were kinks in the tail, shape of the face, and the tone and pitch of individual chuckles. Identification of all individuals of the group was achieved after about nine months. A name was assigned to each monkey, and these were shortened to a three letter or number code (**Table 2.1**).

Even when all individuals were known, observations were sometimes too brief to recognise the focal subjects in a scan sample, although the age/sex class could be determined. For most analyses, therefore, only age/sex categories were used. Analyses were done at an individual level only when stated.

Reproductive status

I recorded if a female focal subject had a ventral infant or a perineal swelling. If a female was swollen, the stage of her swelling was recorded if known (see *Chapter Four* for more details).

Activity

The behaviour of the focal animal was recorded as one of the following mutually exclusive categories :

Table 2.1 Letter codes given to each individual in the study group of grey-cheeked mangabeys

Adult males:	PEI OTT (migrated into the group 5 November 1991)
Sub-adult males:	REG (reclassified as sub-adult in April 1992)
Adult females:	ALB BLA (mother of IN2) CHA LIP (mother of IN1) MAN (mother of WIN) ONT (disappeared December 1991) QUE (mother of QUC) STU YEL (mother of IN3) YUK
Juvenile males:	CAL (reclassified as sub-adult April, 1992) NEW TOR
Juvenile females:	BRI VIC TER
Infants:	WIN (infant of MAN, born 23 March, 1991), (reclassified as juvenile June 92) QUC (infant of QUE, born 18 April, 1991) (reclassified as juvenile June 92) NAP (born 6 February 1992) (disappeared 8 February 1992) IN1 (infant of LIP, born 3 June, 1992) IN2 (infant of BLA, born 9 June 1992) IN3 (infant of YEL, born 22 June 1992)

(i) Travel

Travel was recorded when the focal animal was mobile and was walking, running, climbing, or leaping.

(ii) Resting

The focal animal was recorded as *resting*, when stationary and inactive. The subject could be sitting, lying, or standing.

(iii) Grooming

Grooming was recorded when a subject used its fingers or mouth to examine and pick out particles in the fur, face or hands and feet, or ano-genital region of another mangabey or itself. Whether the focal animal groomed itself **(GRS)** , groomed another mangabey **(GRO)** or was groomed by another **(OGR)** was also recorded.

(iv) Playing

Play was recorded when mangabeys were engaged in wrestling, chases and grabbing in a non-aggressive way. Play was often accompanied by a play face where the mouth was open and lips covered the teeth.

(v) Feeding

Feeding was recorded when the focal animal was searching for, manipulating, holding, licking, biting, or placing food-items of plant origin in the mouth. Where feeding was recorded, the food species and part were also recorded where known (see below).

Food Species

The species of food ingested was recorded when it was known. When foods were not recognised, samples of the fallen remains of the food and a leaf from the tree were collected and brought back to camp for identification. When identifications could not be done in camp, samples were sent to the Missouri Botanical Gardens to be identified.

Plant Part

The following categories were used to represent the part of the food eaten:

Leaves: leaf buds, young leaves and mature leaves
Flowers : all parts of the flower and flower buds
Pulp: all parts of the fruit except the seed, (eg. arils, fleshy succulent pulp) and whether the fruit was ripe or immature, (determined by colour and size of the fruit).
Seeds : all parts of the seed and whether the seed was ripe or immature
Pith: inside of stems and branches

(v) Feeding on, or foraging for insects

The focal animal was manipulating, visually searching for, attempting to capture, handling or eating insect prey. The type of prey was recorded if known (eg. spider, caterpillar, ants) and the following categories of substrates used for foraging for insects were recorded:

Stick : dead woody branches of trees
Bark : outer sheath of tree trunks
Leaves : dead or living leaves of any plant
Pith : living fibrous material inside branches

Height of Subject and Tree

The subject's height above the ground and the height of the tree containing it were judged to the nearest metre.

Number of mangabeys in the same tree

The number of other mangabeys in the same tree as the focal subject was recorded.

Nearest Neighbour

The distance between the focal subject and the nearest member of the group under 15 m was estimated to the nearest metre. The distance of 15 m was chosen because above this distance, the identity of the nearest neighbour was not believed to provide useful information about affinity between individuals. The age and sex were recorded for the nearest neighbour using the same methods described above, used to determine the age and sex of the focal animal.

Location

A grid with squares 100m X 100m was superimposed onto the map of the study area, running parallel to latitude and longitude meridians (**Figure 2.6**). Every 15 minutes during follows of the main study group, the grid square occupied by the group was recorded and the path of their movement plotted onto the map. More details on these methods are given in *Chapter Six*.

Group spread

Group spread was estimated (1) from the distance between vocalisations from group members, (2) when the observer was stationary and the mangabeys travelled by, or (3) using two observers at edges of the group. At each scan sample it was recorded whether the group spread was large (> 100 m), medium

(50-100 m) or small (<50 m) or whether the group was divided into sub-groups. (See *Chapter Four* for a description of sub-groups).

Associations with other species of primates

Any lone primates, or primate groups observed within 50 m of a member of the study group of mangabeys was noted (see *Chapter Eight* for more details).

Other

Other behaviours not mentioned above were recorded *ad libitum*. These are described in *Chapter Seven*.

5. Field time

The number of scan samples taken each month, the number of individuals sampled in each scan, and the distribution of the scans over the day was highly variable (**Figure 2.8-2.10**). This is primarily due to the constraints listed below.

Buffalo

I was absent from the field during the months of July and August as a result of an accident I had while working in the forest. On June 13th 1991, I was attacked by an wounded buffalo and sustained injuries to my breast, ankle and hand. I was taken to a hospital in Franceville, where I received medical treatment. Ten days later, I was flown back to Canada, and then later, to Britain to recuperate. I returned to Gabon as soon as I could, at the end of August 1991.
From January 1991 until June 1991, I usually worked alone in the forest. After my accident I always worked with one other person. From October 1991 to December 1991, and from June 1992 to September 1992, I worked with other researchers at

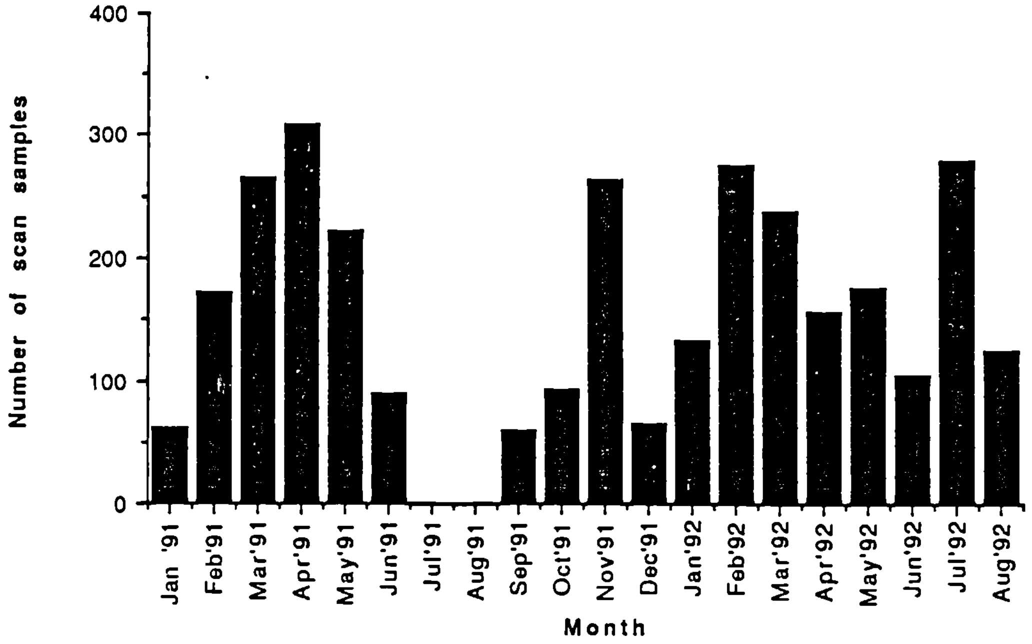

Figure 2.8. Number of scan samples taken during each month of the study

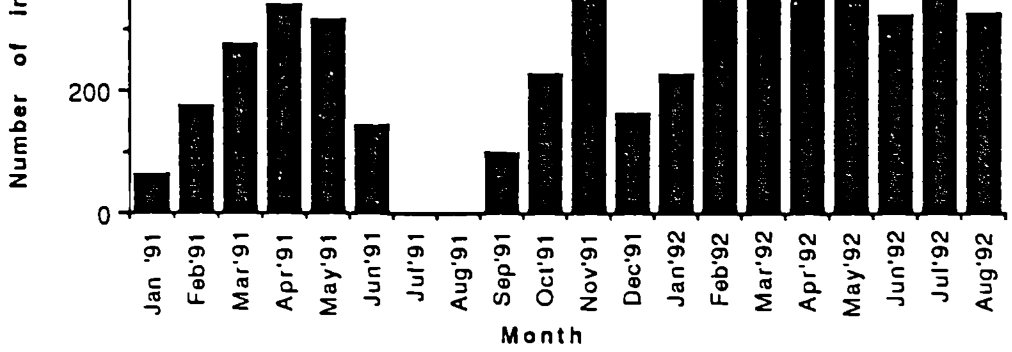

Figure 2.9 Number of individuals sampled during each month of the study

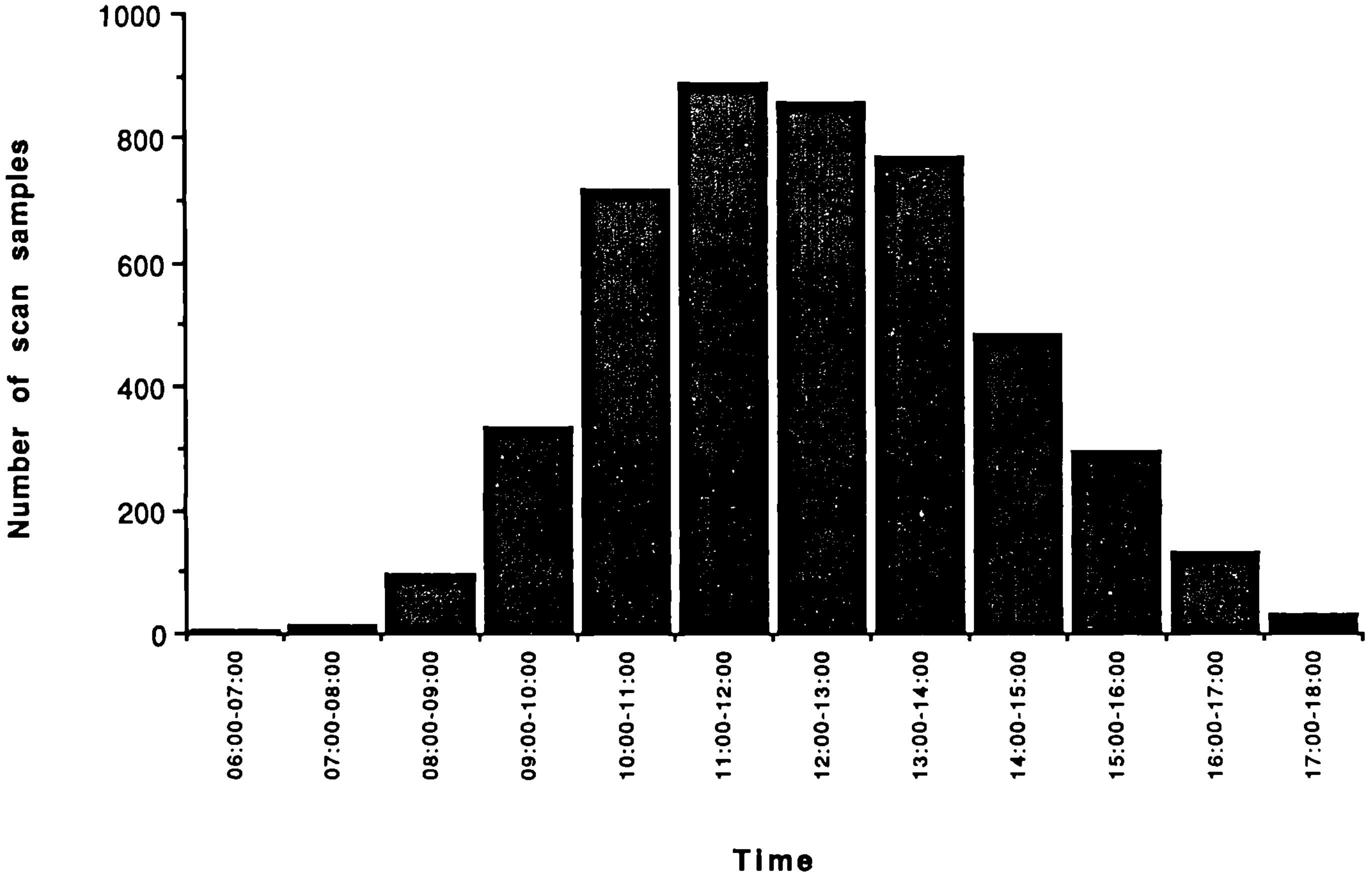

Figure 2.10 Number of scan samples taken during each hourly interval from September 1991 to August 1992 (n=4620)

SEGC. From January 1992 until June 1992, I was assisted by Francis Nzinga from the Lopé village. Due to logistical problems of travel to and from the village, while working with Francis, my field time was further cut to the hours between 09:00 and 15:00. The quality of my observations, however, were far greater than if I had been working a lone and having to divide my attention between watching the mangabeys and listening for buffalo and elephant.

Elephants

The density of elephants at Lopé, of 2.7 individuals per km^2, is higher than for most African forests and higher than in many savanna areas (White, 1992). Their density in the study area changed seasonally, with the lowest density during the long dry season and the highest during the long rainy season. This, combined with the low visibility on the ground due to the dense herbaceous vegetation, made avoiding them very difficult at times. The behaviour of elephants towards humans at Lopé was not always aggressive, but it was unpredictable, and this is what made them dangerous. Most often, they fled at the sight, sound or smell of a human being, and less often they charged.

The high density of elephants at Lopé affected this study in several ways:

(1) During the period of the study, elephants were encountered in the forest 176 times. General policy was to avoid proximity to elephants, therefore follows with the mangabeys were interrupted almost daily and sometimes had to be abandoned.

(2) Follows had to be terminated early enough to permit exit from the forest before nightfall (about 18:00). As elephant presence on, or close to paths sometimes necessitated long

detours, at least an hour had to be allowed for security reasons, unless the mangabeys were very close to the savannas.

(3) Despite their size, elephants can be very quiet and can move through the dense ground vegetation with apparent ease. Because visibility was limited by the dense ground vegetation, the main way of detecting elephants was by listening. Working during heavy rainfall was therefore dangerous since sound was obscured. Partially because of elephants and partially because of the danger of branches or trees falling during heavy rainfall, researchers at SEGC generally did not go in the forest under these conditions. This meant that days were sometimes missed, especially during the long rainy season.

6. Calculations

The problem of independent sampling has been addressed by many authors (eg. Martin and Bateson, 1986). In order to use statistical tests, each data point must be independent of one another. The appropriate time interval chosen between samples relies upon the nature of the behaviour being recorded. Preliminary observations of the mangabeys suggested that for information being collected in this study, a 15 minute interval between scan samples was appropriate. The duration of the bouts of behaviour recorded in this study were rarely continuous for more than 15 minutes. The problem of independence is discussed in more detail in relevant sections.

Data from check sheets were entered onto Excel 2.2 for Macintosh computers. This program was used to sort the data and to perform all simple calculations. StatView was used to perform all statistical analyses and Cricket Graph was used to create graphical illustrations of the results. Nonparametric analyses were used throughout most of the thesis (unless stated otherwise) because the data did not meet the assumption of normality and equal variance, usually because of small sample size (Siegel, 1956).

CHAPTER THREE: VEGETATION

INTRODUCTION

An understanding of the environment in which an animal lives, is essential in order to interpret its behaviour. The environment may provide clues to the ultimate causes of why a species has evolved to be the way it is today, since characteristics of an animal such as body size, gut morphology, or dentition, may have evolved as adaptations to selective pressures from the environment. The environment in which an animal lives also affects proximate aspects of its behaviour and ecology. The availability of food, in particular, has been shown to have profound influence on ranging patterns, diet, demography and social behaviour (eg. Struhsaker and Leland, 1979).

Where food is found and in *what quantities*, can affect where and how far an individual must travel in order to meet its nutritional requirements, as well as affecting group size and population density. For example, Mitani (1989) suggested that in Cameroon, the core area of the range of white-collared mangabeys shifted seasonally in relation to the spatial distribution of trees. *What* foods are available can also determines the diet of an animal. Homewood (1978) noted that in Kenya the diversity of the diet of Tana mangabeys decreased with increased fruit availability. Food availability can also affect demographic parameters, such as group size. For example, two subspecies of red colobus monkeys (*Colobus badius temminckii* and *C.b.rufomitratus*) living in dry woodlands are thought to live in smaller groups than another subspecies, (*C.b. tephrosceles*), because they live in areas of lower food densities (Struhsaker, 1975). Finally, social behaviours may be affected by food abundance and distribution. For example, aggression may increase if competition between individuals occurs when food is scarce (Kinnaird, 1992), or aggression may be greater with larger groups in smaller food patches (Waser, 1977 a).

The tropical forests in which mangabeys live are rarely uniform, and a great deal of variation may be found in tree species composition even within the home range of a single group. Topographical factors (eg. altitude), geomorphic factors (eg. closeness to water or to savanna) and historical factors (eg. tree falls or logging) may affect forest composition. In a study of vegetation at Lopé, White (1992) classified the forest into 20 categories. Observations during the first six months of the present study suggested that two of White's (1992) vegetation categories; savanna-edge and river-edge were particularly important in the ranging behaviour of mangabeys. These have also been observed to be important habitats for gorillas at certain times of year (see Williamson *et al.*, 1988). In the present study, the plant species composition of these particular habitats was examined in more detail.

One useful and commonly used method for studying the distribution and abundance of plant species, and forest structure, is by 'strip sampling', which involves measuring and identifying trees within a specified strip of vegetation. Two transects have already been cut within the SEGC study area (Williamson, 1988 and White, 1992), and another four transects have been cut outside of the study area (White, 1992). These transects were cut on compass bearings to sample a cross section of habitat types. In the present study two transects were cut. One transect was placed along the savanna-edge along the northern edge of the mangabey's home range, and another was placed along the edge of the main river in their home range (see *Chapter Two*), in order to compare species composition here with that from the transects already completed in the study area.

It is not only resource availability in *space,* however, that can affect an animal's behaviour, but also availability in *time*. The study of patterns of flower, fruit and leaf production of plants is called 'phenology'. In tropical rain forests plants do not always produce fruit in synchrony, and a great deal of variation in fruiting cycles has been observed between species and even between individuals of the same species. During periods of fruit scarcity, some sympatric primates decrease the overlap in their diets (Tutin *et al.*, 1991a; Gautier-Hion, 1980) and become reliant on certain "keystone" resources (Gautier-Hion and Michaloud, 1989; Terborgh, 1986; Tutin and Fernandez, 1993a). Changes in patterns of ranging have also been observed due to fluctuations in availability of food (Harrison, 1983a). Clearly, the study of phenology is also important in understanding primate behaviour and ecology.

One way of studying the effects of the environment upon behaviour is to study the same species living in different habitats. Forests in western Africa have been shown to be more diverse than eastern African forests and this has been used as an explanation for the generally higher quality diets observed for primates studied in countries in western Africa (Gautier-Hion, 1983). Information on forest structure is available from studies of mangabeys in Uganda from Waser(1974), Struhsaker (1975), and Freeland (1977, 1979). The botanical studies at Lopé used similar methods to these studies in Uganda, allowing direct comparisons to be made. A comparison between these habitats is useful for reference in future chapters of this thesis, and may aid in understanding differences or similarities between the behaviour of mangabeys at different study sites.

In summary, the main aim of this chapter is to examine the environment in which the study group of grey-cheeked mangabeys live, in order to provide information that can be used to interpret behavioural patterns discussed in the following chapters of this thesis. More specifically, the aims are; (1) to examine forest composition in two specific habitat-types; savanna-edge and river-edge forest, thought to be important to mangabeys; (2) to investigate patterns of fruit production; and (3) to compare the forest habitats of mangabeys at Lopé, to those of mangabeys studied in Uganda in order to facilitate comparisons of their behaviour and ecology made later in this thesis.

METHODS

A. TRANSECTS

Two 1 ha strips of forest were sampled. All trees with a diameter greater than 10 cm and whose trunk centre fell within a 5 m strip were measured; (1) for 2 km along the edge of the main river, the Koumbiane, in the home range of the mangabeys, and (2) for 2 km along the edge of the savanna at the northern boundary of the home range of the study group. The diameter of the trees were measured 1.3 m from the ground (dbh=diameter at breast height) or above any buttressed trunks or aerial roots. If the tree branched below 1.3 m then each trunk was measured individually. The river-edge transect was unbroken, but the savanna-edge transect was divided into three strips in order to avoid a forest corridor that was continuous with forest to the north.

Usually with this technique, the transect is placed along a compass bearing in order to sample all habitat-types. In the present study, transects were done to sample two particular habitat-types, so their locations were selected. Sampling river bank vegetation posed no difficulties. The depth of the river fluctuated depending on the season and location, from about 20-60 cm deep, but there was usually a distinct line of where the vegetation began, and the transect was placed here (**Plate 3.1**).

While in most areas, the savanna-forest boundary was distinct (eg. **Plate 3.2**) (probably as a result of annual burning of the savanna), in some areas, it was more difficult to define. To describe objectively where the transect was be placed, trees were measured in a 5 m wide strip as close to the savanna edge as possible but within forest where the average canopy height was greater than 10 m. This criterion was chosen because mangabeys rarely descend to feed below this height, so inclusion of plants below 10 m would have less biological relevance to mangabeys.

Trees were enumerated and labelled with aluminium forestry tags. For each tree the identity, location along the transect and dbh were recorded. For trees that could not be identified *in situ*, leaves, and where possible, the reproductive parts of the plants were collected and brought back to camp to be identified from Floras or with help of colleagues. When plants were still unknown, specimens were sent to the Missouri Botanical Garden to be identified.

Dbh's were used to calculate basal area of individual plants (assuming trunks were circular: $Area=\pi r^2$, where $r=radius=diameter \div 2$) which were summed to give the basal area of species or families. Basal area for plants with more than one stem was calculated by summing the basal areas of each stem.

There are a number of indices that may be used to calculate

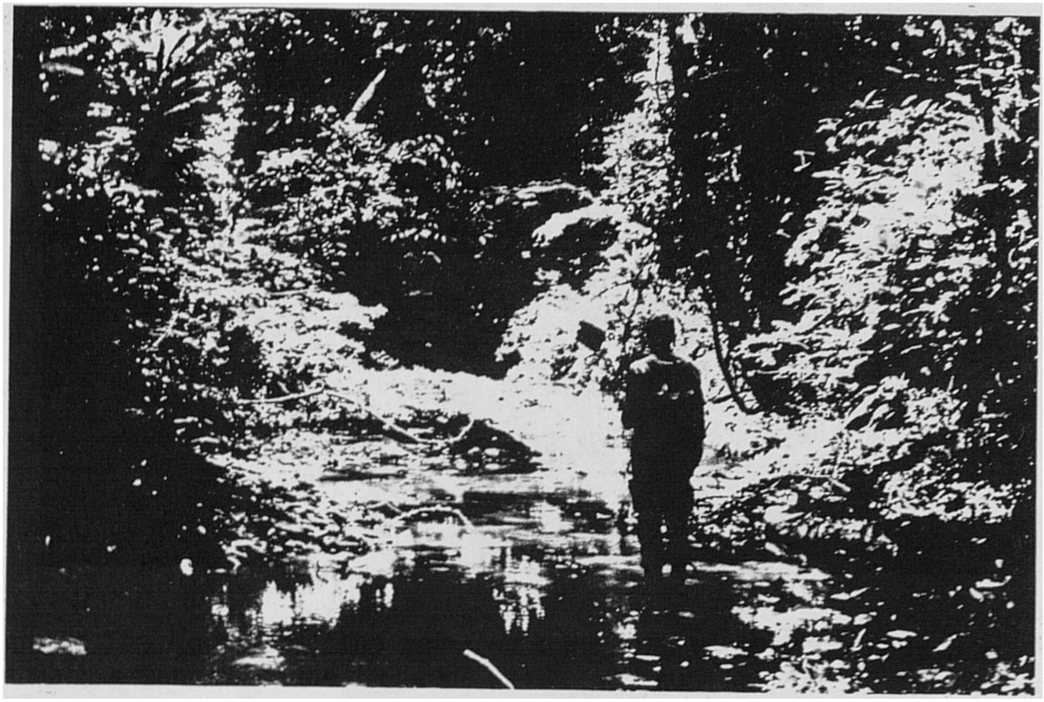

Plate 3.1 The 'Koumbiane': The main river in the home range of the study group of mangabeys along which the river-edge transect was cut.

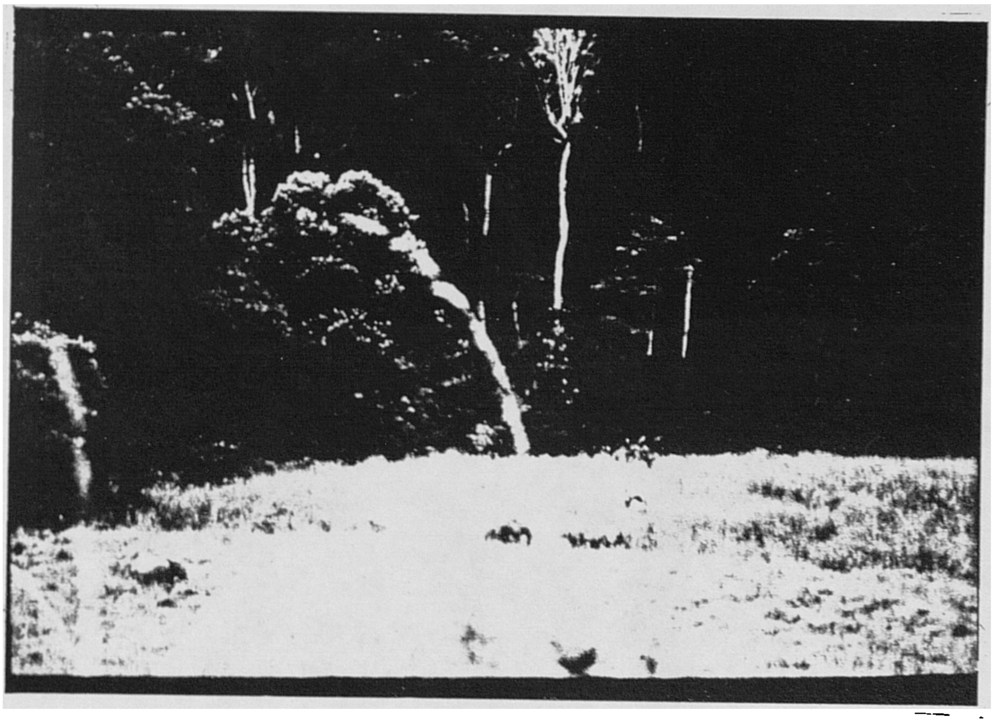

Plate 3.2 The savanna-edge boundary along which the savanna-edge transect was cut.

species diversity. Because the results of the present study were to be directly compared to other transects at SEGC, as well as to transects in other locations where mangabeys have been studied, it was important to have consistent diversity indices. The Shannon Diversity Index (Pielou, 1977) and the Simpson's Index (Simpson, 1949) were indices used by White (1992) at SEGC and by Waser (1974) and Struhsaker (1975) at Kibale, and were therefore used in this study to facilitate comparisons. The Shannon Diversity Index is calculated as follows:

$$H' = \Sigma \, pi(\ln pi) \qquad \textbf{Shannon index}$$

Where pi is the proportion of individuals found in the ith species. This index is designed to assess the variation in the number of species as well as variation in the number of individuals within each species. There are advantages and disadvantages to use different indices and therefore often more than one index is used to assess species diversity. The Shannon Index is sensitive to sample size (Rasmussen, 1980). The Simpson's index (Simpson, 1949) is less sensitive to sample size (Magurran, 1955) and therefore was also used as an index of diversity in the present study. The Simpson's index (Simpson, 1949) is calculated as follows:

$$D = \Sigma \, (n(n-1)/N(N-1)) \qquad \textbf{Simpson's index}$$

where n= the number of individuals in the ith species and N=the total number of individuals.

Because a community with few, evenly represented species can have the same diversity index as one with many, unevenly represented species, an index of evenness is also required. The J' of Pielou (1975) is an index frequently used as an index of evenness and is calculated by dividing the Shannon Index of diversity by the hypothetical maximum diversity, given the number of species *i.e.*:

$J'=H'/Hmax$ **J' of Pielou**

where H' is the Shannon index of diversity and $Hmax=\ln S$, where S is equal to the total number of species. This index was used in the present study so that results would be comparable to White (1992).

The degree of overlap between transects was assessed by the shared percent of species.

B. PHENOLOGY

Different methods have been used by different researchers in order to quantify variations in fruit production and availability, such as (1) recording the number of trees with fruit each month (e.g.Gautier-Hion *et al.*, 1985a); (2) systematically counting or weighing fallen fruits (e.g. Terborgh, 1983), and (3) estimating the crop size for individual trees as a proportion of the maximum potential score for that species (eg. Homewood, 1978).

Because data on the phenology of 60 species of plants from 25 families have been collected at SEGC monthly since 1984 (Tutin and Fernandez, 1993 b), this was the method used to estimate fruit availability for the present study. From January to June 1991 and from September 1991 to August 1992, I contributed to this data set. During the first week of every month, 10 individuals for each species were examined. Species were originally chosen because they were thought to be important foods in the diet of either, or both gorillas and chimpanzees. Methods of data collection have been described in detail already by Williamson (1988) and Tutin and Fernandez (1993 b). Each tree was examined using 10 X 40 binoculars and was scored for the relative quantity of ripe fruit, immature fruit, new leaves, mature leaves and senescent leaves, using a 10 point scale from 0-4 (*i.e.* 0, √, 0.5, 1, 1.5 ...4).(The √ is used in order to make up a 10 point scale, and represents an estimate between 0 and 0.5) Each tree therefore, had a possible score of 1-10, each species had a possible score of 100 (when there are 10 trees per species) and each month there was a possible fruit score of 6000. Total availability of fruit was calculated by summing "percentage fruit scores" for each species. These are the sum of the individual scores for each tree, expressed as a percentage of the maximum possible score for that species. The "percentage fruit scores" were thought to be the most accurate representation of fruit availability because this takes into account that individual trees may have large variation in their actual crop size, whereas recording only the number of trees with fruit does not. This will then be used as a measure of the availability of ripe fruit for the remainder of the thesis.

RESULTS

A. TRANSECTS

A total of 824 trees were encountered on both transects with 559 trees on the savanna-edge transect and 265 trees on the river-edge transect. In total, 89% of the trees (732 individuals) were fully identified, 10% (82 individuals) were identified to genus, 1% (eight individuals) were identified to family and 0.2% remained undetermined (two individuals).

1. Species richness and composition

In total 88 species were identified from 34 families. The savanna-edge transect had 60 species from 29 families and the river-edge transect had 61 species from 27 families. **Table 3.1** gives a list of the number of individuals of each species for both transects and for each transect. **Table 3.2** lists the number of individuals and the number of species in each family for both transects.

To give an indication of the importance of each species in terms of numbers, species were ranked by number of individuals. In **Table 3.1** the "top 10" species are

Table 3.1. Number of individuals and basal area for each species on transects

a=number of individuals on transect
b=basal area on transect (cm2ha-1)
Bold values=species in top 10

Family	**Species**	**Savanna transect**		**River transect**	
		a	**b**	**a**	**b**
ANACARDIACEAE					
	Lannea welwitschii	2	4057		
	Pseudospondias microcarpa			**16**	**51256**
	Trichoschypha acuminata	5	954		
	UNKNOWN	1	95		
ANNONACEAE					
	Artabotrys sp.			1	115
	Uvariastrum pierreanum	7	5524	5	2263
	Xylopia aethiopica	9	4061	**8**	6274
	Xylopia hypolampra	1	133		
	Xylopia quintasii	15	2851	**6**	1837
	Xylopia parviflora	1	266	1	117
	UNKNOWN liane			1	104
APOCYNACEAE					
	Rauvoulfia vomitoria	1	398		
	Tabernaetha crassa			1	127
BIGNONIACEAE					
	Kigelia africana	1	363		
	Newbouldia laevis	7	2253	3	1527
	Spathodea campanulata			1	4717
BOMBACACEAE					
	Ceiba pentandra	1	**10387**		
BURSERACEAE					
	Aucoumea klaineana	9	**44513**	1	**26880**
	Santiria trimera			3	3298

Table 3.1. Number of individuals and basal area for each species / cont.

Family	**Species**	**Savanna transect**		**River transect**	
		a	**b**	**a**	**b**
a=number of individuals on transect					
b=basal area on transect (cm2ha-1)					
Bold values=species in top 10					
CAESALPINIACEAE					
	Anthonotha macrophylla			4	1366
	Berlinia bracteosa	**47**	**36837**	**29**	**84130**
	Cassia mannii	1	227		
	Cryptosephalum staudtii	**91**	**43279**	**12**	7875
	Detarium macrocarpum	2	**10231**	2	**17601**
	Dialium lopense	3	658	1	1432
	Distemonanthus bethamianus			4	**14677**
	Hylodendron gabunense	3	6493	1	3848
	Julbernardia brieyi	**28**	**41795**	1	5178
CELASTACEAE					
	Euonymus congolensis	2	673		
CHRYSOBALANACEAE					
	Acioa sp. SEGC 499	2	414		
	Magnistipula sp. LJTW 0701	1	320		
DICHAPETALACEAE					
	Dichapetalum sp.	1	227		
EBENACEAE					
	Diospyros dendo	**30**	4150	**6**	1042
	Diospyros mannii	2	265	1	113
	Diospyros polystemon	1	434		
	Diospyros sp.	1	254		
	Diospyros suaveolens	1	109		
	Diospyros zenkeri	5	517		
ERYTHROXYLACEAE					
	Erythroxylum mannii	4	1818	3	800
EUPHORBIACEAE					
	Antidesma laciniatum	**31**	**10335**	3	436
	Discoglypremna coloneura			2	1217
	Maprounea membrenaceae			1	1656
	Phyllanthus discoides	2	352	5	3150
	Sapium ellipticum	1	254	2	2522
	Uapaca guineensis	**26**	**98446**		

Table 3.1. Number of individuals and basal area for each species / cont.

Family	**Species**	**Savanna transect**		**River transect**	
		a	**b**	**a**	**b**
a=number of individuals on transect					
b=basal area on transect (cm2ha-1)					
Bold values=species in top 10					
FLACOURTIACEAE					
	Caloncoba glauca			1	897
	Homalium letetui			1	1195
	Scottellia coriacea			2	3130
HYPERICACEAE					
	Psorospermum tenuifolium	1	219	4	828
IRVINGIACEAE					
	Irvingia gabonensis	1	176	1	278
	Irvingia grandifolia			4	**26842**
	Klainedoxa gabonensis	3	3424	1	108
LAURACEAE					
	Beilschmeidia sp.			1	254
LOGANIACEAE					
	Anthocleista sp.	1	201		
MELIACEAE					
	Carapa procera	1	384	1	607
	Trichilia prieureana	2	254	4	2229
MIMOSACEAE					
	Pentaclethra eetveldeana			1	3685
	Pentaclethra macrophylla	1	2173	3	3750
MORACEAE					
	Chlorophora excelsa			1	5608
	Ficus sp.			1	1909
	Myrianthus arboreus			**9**	**15366**
	Treculia obovoidea			3	3315
MYRISTICACEAE					
	Pycnanthus angolensis			1	**10207**
	Scyphocephalium ochocoa			1	8791
OCHNACEAE					
	Lophira alata	**95**	**48033**	**22**	**9545**
	Ouratea flava	2	173		

Table 3.1. Number of individuals and basal area for each species / cont.

a=number of individuals on transect
b=basal area on transect (cm2ha-1)
Bold values=species in top 10

Family	**Species**	**Savanna transect**		**River transect**	
		a	**b**	**a**	**b**
OLACACEAE					
	Ongokea gore	1	1019	1	6533
	Linociera aff.mannii	3	463		
PALMAE					
	Elaeis guineensis	1	745		
PANDACEAE					
	Panda oleosa			1	254
PAPILIONACEAE					
	LJTW 0950/0951	5	127	1	123
	LJTW 1000	1	1236		
	Milletia river sp.			**45**	**16666**
	Milletia savanna sp.	**28**	5126	1	283
PASSIFLORACEAE					
	Barteria fistulosa	**30**	4025	5	959
RUBIACEAE					
	Aidia ochroleuca	5	710		
	Nauclea diderrichii			3	1458
	Nauclea vanderguchtii	2	828	8	8263
	Tricalysia macrophylla			3	2835
SAPINDACEAE					
	Eriocoelum macrocarpum	2	1996	2	3314
	Lecaniodiscus cupanioides	1	346	3	2147
SAPOTACEAE					
	Omphalocarpum procerum	1	511		
STERCULIACEAE					
	Cola lizae	**21**	**11033**	4	4009
	Sterculia tragacantha	2	1191		
TILIACEAE					
	Duboscia macrocarpa			1	2206

Table 3.1. Number of individuals and basal area for each species / cont.

Family	Species	Savanna transect		River transect	
		a	b	a	b
a=number of individuals on transect b=basal area on transect (cm2ha-1) Bold values=species in top 10					
VERBENACEAE					
	Vitex doniana	3	1597		
FAMILY UNKNOWN					
	UNKNOWN K188			1	196
	UNKNOWN SS29	1	127		
OVERALL TOTAL		559	420062	265	393348
Number of species		60		61	
No.individs./No.spp.		9.32		4.34	
Shannon Weaver Index		3.02		3.39	
Simpson's Index		0.08		0.06	
Evenness		0.74		0.82	
Sum of values for 'top 10' spp.		427	354889	162	273171
Top 10 as % of total		76	84	61	69

Table 3.2. Number of individuals and basal area for families

	Savanna transect			River transect		
FAMILY	a	b	c	a	b	c
ANACARDIACEAE	8	4	5106	16	1	51256
ANNONACEAE	33	5	12835	22	6	10710
APOCYNACEAE	1	1	398	1	1	127
BIGNONIACEAE	8	2	2616	4	2	6244
BOMBACACEAE	1	1	10387			
BURSERACEAE	9	1	44513	4	2	30178
CAESALPINIACEAE	175	7	139520	54	8	136107
CELASTACEAE	2	1	673			
CHRYSOBALANACEAE	3	2	734			
DICHAPETALACEAE	1	1	227			
EBENACEAE	40	6	5729	7	2	1155
ERYTHROXYLACEAE	4	1	1818	3	1	800
EUPHORBIACEAE	60	4	109387	13	5	8981
FLACOURTIACEAE				4	3	5222
HYPERICACEAE	1	1	219	4	1	828
IRVINGIACEAE	4	2	3600	6	3	27227
LAURACEAE				1	1	254
LOGANIACEAE	1	1	201			
MELIACEAE	3	2	638	5	2	2836
MIMOSACEAE	1	1	2173	4	2	7436
MORACEAE				14	4	26198
MYRISTICACEAE				2	2	18998
OCHNACEAE	97	2	48206	22	1	9545
OLACACEAE	4	1	1482	1	1	6533
PALMAE	1	1	745			
PANDACEAE				1	1	254
PAPILIONACEAE	34	3	6490	47	3	17072
PASSILFORACEAE	30	1	4025	5	1	959
RUBIACEAE	7	2	1539	14	3	12556
SAPINDACEAE	3	2	2342	5	2	5461
SAPOTACEAE	1	1	511			
STERCULIACEAE	23	2	12224	4	1	4009
TILIACEAE				1	1	2206
VERBENACEAE	3	1	1597			
UNKNOWN	1	1	127	1	1	196
OVERALL TOTAL	559	60	420062	265	61	393348
Top 15 families	536	46	409154	238	48	374502
% overall	96	77	97	90	80	95

a: number of individuals in 1 ha sample
b: number of species in 1 ha sample
c: basal area in 1 ha transect

highlighted in bold type. *Berlinia bracteosa, Cryptosephalum staudtii, Diospyros dendo* and *Lophira alata* were species that were included in the "top 10" in both transects. The genus *Milletia* was also ranked in the "top 10" in both transects but was thought to be different at the species level on each transect. Other species included in the "top 10" on the savanna-edge transect included *Anthonotha macrophylla, Antidesma laciniatum, Barteria fistulosa, Cola lizae, Julbernardia brieyi,* and *Uapaca guineensis*, and on the river-edge transect; *Pseudospondias microcarpa, Xylopia aethiopica, Xylopia quintasii, Myrianthus arboreus,* and *Nauclea vanderguchtii.*

The family Leguminosae, (which includes subfamilies: Caesalpiniaceae, Papilionaceae and Mimosaceae) made up 11 species and 210 individuals (39% of the total sample of individuals) on the savanna-edge transect, and 13 species and 105 individuals (40% of individuals) on the river-edge transect. In terms of both number of species and number of individuals, the family Caesalpiniaceae was the most important, with seven species and 175 trees (31% of the total sample) trees for the savanna-edge transect and eight species and 54 trees (20% of the total sample) for the river-edge transect.

2. Basal area

The total basal area for the savanna-edge transect (42 m^2 ha^{-1}) was slightly greater than that of the river-edge transect (39 m^2 ha^{-1}). The "top 10" species in terms of basal area are highlighted in bold in **Table 3.1**. Species that accounted for most of the basal area on both transects included *Aucoumea klaineana, Berlinia bracteosa, Detarium* *macrocarpum* and *Lophira alata*. Species included only in the "top 10" on the savanna-edge transect were *Ceiba pentandra, Cryptosephalum staudtii*, Julbernardia brieyi*, Antidesma vogeliana*, Uapaca guineensis*, and Cola lizae** and species included only in the "top 10" species and for the river-edge transect were; *Pseudospondias microcarpa, Distemonanthus bethamianus, Irvingia grandifolia, Myrianthus arboreus*, Pycnanthus angolensis,* and *Milletia sp.*. (* marks species that were also included in the "top 10" in terms of number of stems).

The family Leguminosae made up 35% of the overall basal area on the savanna-edge transect and 41% of the river-edge transect. Caesalpiniaceae was the most important family in terms of basal area, making up 33% of the total basal area on the savanna-edge and 35% of the basal area on the river-edge transect. The "top 10" families in terms of basal area are highlighted in bold in **Table 3.2**.

3. Diversity and evenness

Different indices of diversity all indicate that savanna-edge habitat is less diverse than river-edge habitat (**Table 3.1**) The ratio of the individuals to species, the Shannon diversity index and the Simpson's index of diversity found the savanna-edge transect to be less diverse than the river-edge transect, and the 'top 10' species make up a larger proportion of the overall sample in the savanna-edge transect than on the river-edge transect. In addition, the percent of species, individuals and basal area in the top 15 families is greater for the savanna-edge transect. Fifty percent of the total number of individuals was made up of five species in the savanna-edge transect and six species in the river-edge transect. Species-area plots (**Figure 3.1**) show that at 1 ha

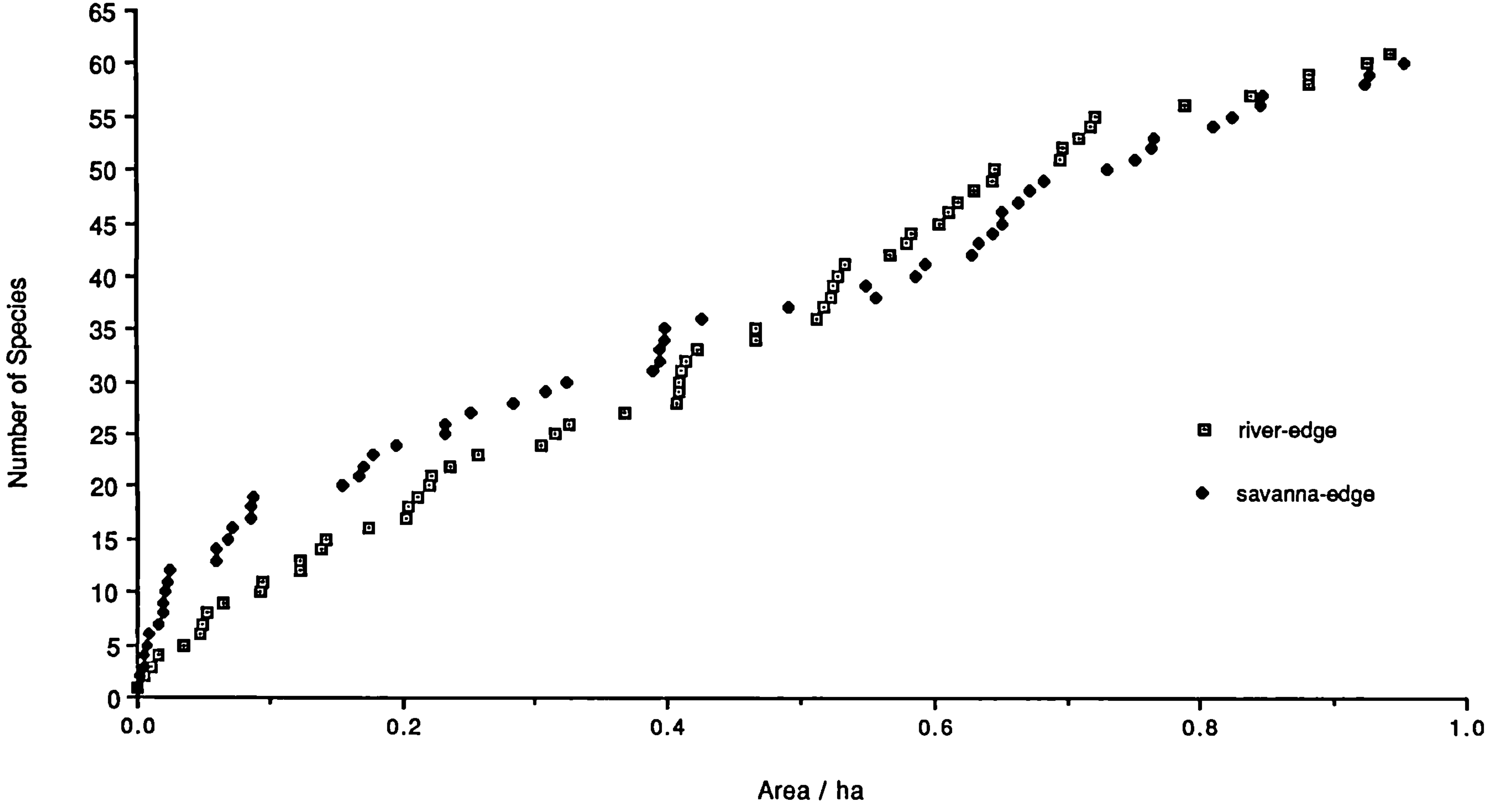

Figure 3.1 Species-area plots for savanna-edge and river-edge transects

both curves start to level out, although they are still increasing. The slopes of both curves are similar but the river-edge transect initially increased at a faster rate and then levelled off sooner than the savanna-edge transect, showing that the savanna-edge transect is less diverse.

Evenness was measured using the J′ of Pielou (1975, 1977) which showed evenness to be greatest in the savanna-edge transect.

4. Overlap

In total, 824 individuals and 84 species and 34 families were present in both sites. There were 32 species that were recorded on both transects forming 53% of all species on both the savanna-edge transect and river-edge transect.

5. Forest structure

The proportion of trees in each 10 cm diameter class (10-20 cm, 20-30 cm etc.) was strongly skewed towards 10 cm-20 cm dbh for the savanna-edge transect, with 52% of all plants measured with a dbh less than 20 cm, compared to only 35% on the river-edge transect (**Figure 3.2**). This may indicate differences in forest maturity. Plants may be generally smaller on the savanna-edge transect than the river-edge transect because they are younger. Alternatively, it may indicate simply a difference in species composition, where species characteristic of the savanna-edge do not generally grow as large as those characteristic of the river-edge.

Trees with a dbh greater than 100 cm included; one individual *Ceiba pentandra,* four individuals of *Uapaca guineensis* and three individuals of *Aucoumea klaineana* on the savanna-edge transect, and one individual of each *Aucoumea klaineana*, *Pycnanthus angolensis*, *Irvingia grandifolia*,

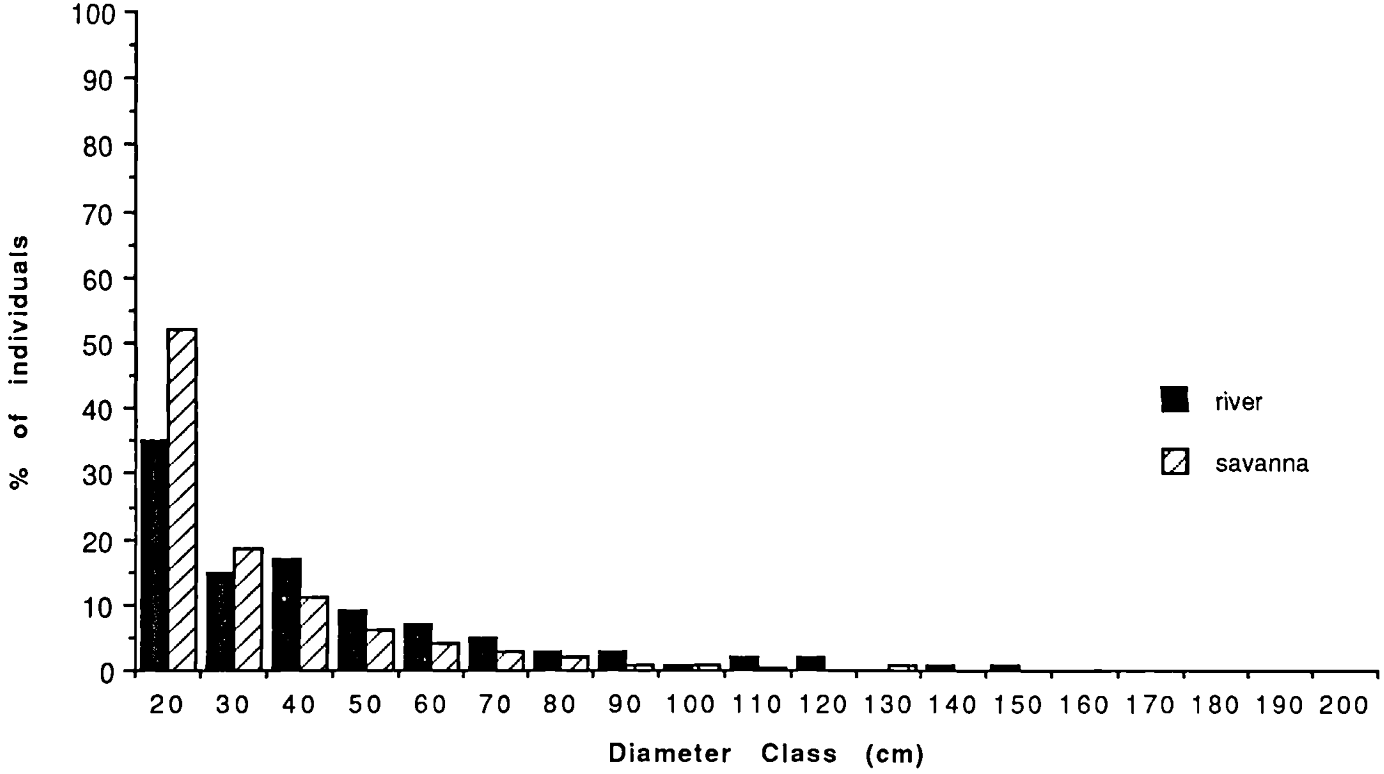

Figure 3.2: Diameter classes for plants >10cm dbh on transects

Scyphocephalium ochocoa, Detarium macrocarpum, Myrianthus arboreus, plus two individuals of *Pseudospondias microcarpa* and four individuals of *Berlinia bracteosa* on the river-edge transect.

On the savanna-edge transect 76 trees were recorded with multiple trunks (14% of the sample) compared to 48 trees (18% of the sample) on the river edge transect.

B. PHENOLOGY

Figure 3.3 shows the proportion of trees on the phenology circuit with fruit (ripe and immature) and **Figure 3.4** shows the amount of fruit as a proportion of what was estimated to be the potential fruit crop. From the graphs, the availability of ripe fruit was highest from October to April and was least during the long dry season in June, July and August in both years. The proportion of immature fruit was the highest during the long dry season, but did not fluctuate in availability as much as the ripe fruit.

In order to examine the changes in availability of ripe fruit between months, the following test was performed. Each month, each of the 60 species on the phenology circuit was given a score out of 100 for fruit availabiity (*i.e.* a score from 1-10 for 10 individuals for each species as described earlier). Species were examined between consecutive months to determine whether fruit availability was increasing (*i.e.* +) of decreasing (*i.e.* -). The number of species increasing or decreasing was compared between consecutive months using a binomial test (Siegel, 1956).

At the end of the long dry season (June, July and August) and the start of the short rainy season (September, October, and November) in 1991, there was a significant increase in the availability of ripe fruit, (from August to September:

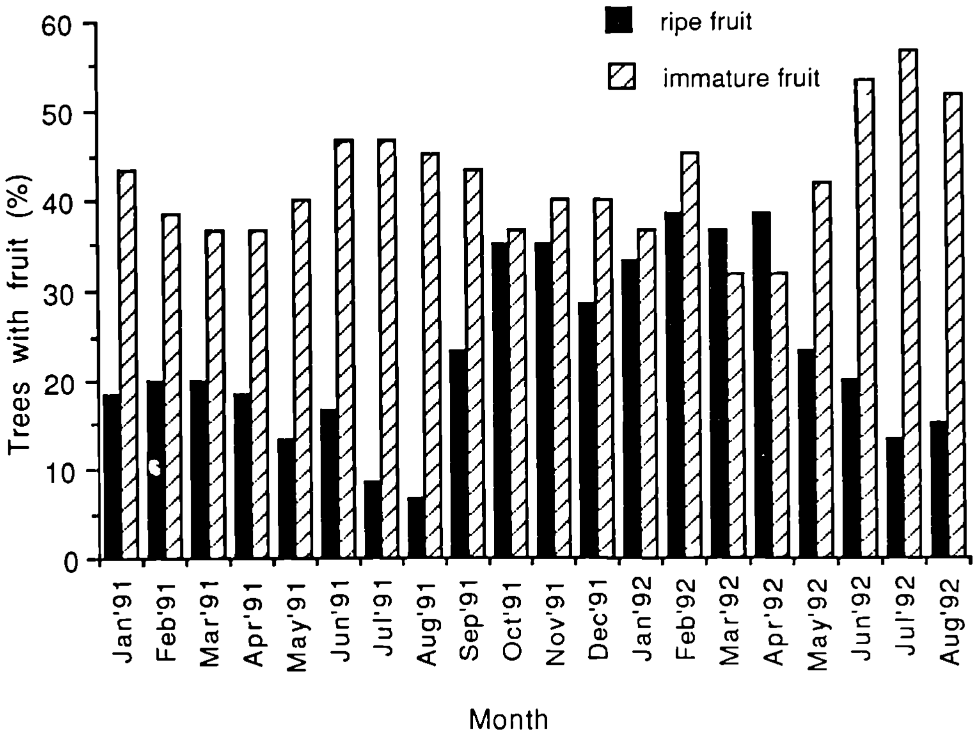

Figure 3.3 Proportion of Trees With Fruit on Phenology Circuit

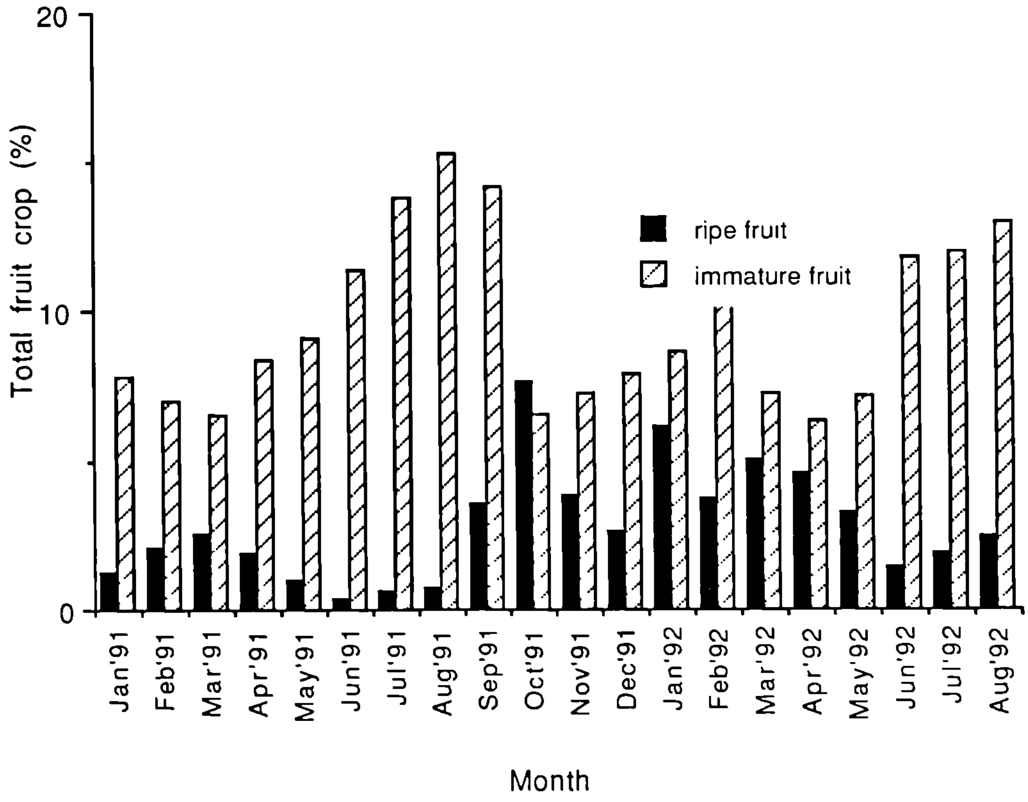

Figure 3.4. Amount of Fruit as a Proportion of the Potential Crop on the Phenology Circuit

p=0.001). At the end of the short rainy season and the start of the short dry season (December 1991, January 1992 and February 1992) there was a significant decrease in the availability of ripe fruit (from November to December 1991: p=0.017). From April to May 1992 the availability of ripe fruit decreased significantly (p=0.007) and did not increase significantly again before the termination of the study at the end of the long dry season in August 1992.

The long dry season was unusual in 1992, in that several species produced flowers and then fruits atypically (Tutin and Fernandez, 1993 b), including *Diospyros dendo, Diospyros polystemon, Pterocarpus soyauxii, Cola lizae, Dialium lopense*.

In order to look for environmental factors with which the production of fruit may be related, monthly rainfall and temperatures were tested for correlation with the availability of ripe fruit. During the period of the study, there were no significant correlations between the availability of ripe fruit and rainfall (r_s=0.24, n=18, p=0.34), maximum (r_s=0.52, n=18, p=0.03), or minimum monthly temperatures (r_s=-0.20, n=18, p=0.44).

DISCUSSION

A. TRANSECTS

There were obvious differences between the savanna-edge and the river-edge transect. Trees near the savanna-edge were found in greater numbers, with greater overall basal area, but were generally smaller in diameter than in the river-edge transect. There were equal number of species but more individuals per species in the savanna-edge transect and the savanna-edge transect was less diverse.

A more useful comparison to characterise these habitats types would be to compare the species composition of the savanna-edge and river-edge transects, to a transect in the study area that sampled a cross-section of habitat types. This would then highlight important species in each habitat type. Williamson (1988) sampled a 1 ha transect through the study area (1 km x 10 m), cut on a compass bearing, and White (1992) extended this to a 2.5 ha transect (5 km x 5 m) strip (measuring all trees >10 cm dbh). This transect traversed the southern end of the mangabey's home range and sampled trees across the drainage patterns, therefore encompassing different habitat types. This will be called the SEGC transect in the following discussion.

Data from the river-edge and savanna-edge transects represent only a small proportion of the overall home range of the study group of mangabeys (see Figure 6.7 in Chapter Six). The SEGC transect is probably more representative of the overall vegetation within the mangabey's home range because it samples a cross section of vegetation types and is not biased to one particular habitat, like the savanna-edge and river-edge transects. For this reason, the SEGC transect is used in subsequent chapters for calculations on spatial distribution and abundance of plant species (eg.Table 5.2, Chapter Five, for the selectivity index).The SEGC transect still only a sample of vegetation in the home range of the study group of mangabeys from which generalisations are made.

Savanna-edge

Compared to the SEGC transect, the savanna-edge habitat seemed to be characterised by a high density of small trees with low species diversity and uneven distribution (**Table 3.3**). The low diversity of plant species at the savanna-edge was not surprising given that in most tropical rain forests, there are usually fewer pioneering species than there are climax species (Whitmore, 1990). The savanna-edge transect shared 53% of its species with the SEGC transect; the same number as it shared with the river-edge transect. Species included in the "top 10" in the SEGC transect that were also in the "top 10" in the savanna-edge transects in terms of numbers of individuals were *Diospyros dendo, Lophira alata*

Table 3.3 Comparison of forests in different areas where grey-cheeked mangabeys have been studied.

Location	**SEGC Lopé GABON savanna-edge**	**SEGC Lopé GABON river-edge**	**SEGC Lopé GABON**	**Kanyawara UGANDA**	**Ngogo UGANDA**
Author	**Present study**	**Present study**	**White 1992 ***	**Waser 1977a ****	**Freeland 1979 *****
Size of sample	**1ha**	**1ha**	**2.5ha**	**5.78**	**3.025 ha**
Total no. indivs.	559	265	760	1667	1149
No.indivs/ha	559	265	304	288	369
Total basal area	42.01	39.33	29.59		
Total no. spp.	60	61	84	71	74
Total no. families	29	27	31		
No.individs./no.spp.	9.32	4.34	8.4		
Shannon Index	3.02	3.39	3.35	4.37	
Simpson's Index	0.08	0.06	0.08		
J' of Pielou	0.74	0.83	0.75	1.03	
No. indivs in 'top 10' spp.	427	162	528		
(% of total)	76%	61%	69%	75%	
Basal area in "top 10 spp.	35.5	27.3	56.1		
(% of total)	84%	69%	76%		
No. indivs in 'top 15' familes	536	238	681		
(% of total)	96%	90%	90%		
No. spp. in "top 15" families	46	48	65		
(% of total)	77%	80%	77%		
Basal area of "top 15" families	40.92	37.45	28.24		
(% of total)	97%	95%	95%		
No.spp. in 50% of indivs.	4 to 5	6	3 to 4	5	
Dominant family					
in terms of no. indivs.	Caesalpiniaceae	Caesalpiniaceae	Sterculiaceae		
in terms of species	Caesalpiniaceae	Caesalpiniaceae	Annonaceaea Rubiaceae		
in terms of basal area	Caesalpiniaceae	Caesalpiniaceae	Burseraceae		

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* White (1992) measured all plants > 10 cm dbh on a 4000 m X 5 m transect cut on a compass bearing

** Waser (1974) measured all plants >10m in height on a 8685 m X 5 m transect and combined his results with those of T.T. Struhsaker to give a sample of 5.78 ha and 1667 individuals.

***Freeland (1979) with T.T. Struhsaker, measured all plants > 10 m in height on a 6050 m X 5 m transect giving a sample of 3 ha and 1, 149 individuals.

and *Cola lizae*, and in terms of basal area were; *Lophira alata* and *Aucoumea klaineana*.

Several of the species encountered on the savanna edge transect are known to be characteristic of areas that have been disturbed either by logging, animals (eg. elephants) or natural disturbances (eg. tree falls) elsewhere in African forests. These species were *Rauvoulfia vomitoria, Ceiba pentandra*, *Lophira alata* (Whitmore, 1990), *Dialium* spp., and *Detarium macrocarpum* (Letouzey, 1968). Several trees are also characteristic of secondary forests, including *Distemonanthus bethamianus, Hylodendron gabunense* (Letouzey, 1968). White (1992) performed two types of multivariate analysis on data from his SEGC transect to identify habitat types. He identified trees that were characteristic of colonising and post-colonising forest. All of these species were encountered on the savanna-edge transect except *Pauridiantha efferata* and *Nauclea diderrichii*. White (1992) cites *Lophira alata* and *Aucoumea klaineana* as two important colonising species since they both have wind dispersed seeds and can establish in savanna conditions. *Lophira alata* was found in large numbers in the savanna-edge transect (95 trees in 1 ha, compared to 62 trees in 2.5 ha in the SEGC transect), but this was not found to be the case for *Aucoumea klaineana* (9 individuals in 1 ha compared to 61 individuals in 2.5 ha in the SEGC transect). Other species found in the present study to be important in terms of either basal area or numbers at the savanna edge were *Diospyros dendo, Antidesma laciniatum,* and *Milletia* spp. and *Detarium macrocarpum*.

The dominant family in the SEGC transect was Burseraceae but this family was the fourth most important on the savanna-edge transect. This may have been due to the small numbers of

Aucoumea klaineana, which accounted for a large proportion of the SEGC transect, both in terms of number of stems and basal area. An association between the family Caesalpiniaceae and poor soils has been observed by several authors (eg. Maisels *et al.*, in press; Maisels and Gautier-Hion, in press). Soils at the savanna-forest interface may be higher in pH and have less nutrients than further into the forest, accounting for the importance of this family compared to elsewhere in the study area.

There is a large literature concerning the process of colonising forest from savanna into mature forest. Trees typical of savanna-edge environments often have wind dispersed seeds and are species that can grow in poor soil, are light tolerant, grow quickly and may be fire resistant. In addition, pioneering species generally produce large amount of seeds, and their leaves tend to be short lived with few chemical defences against herbivores (Whitmore, 1990). Structurally, trees are usually smaller and branch lower than the same species further into the forest (White, 1992), although in the savanna-edge transect, the distribution of the number of individuals in each diameter class was similar to the SEGC transect.

In summary, savanna edge forests may be important for mangabeys for two main reasons: (1) because of the species composition, (*i.e.* a high proportion of Caesalpiniaceae and low diversity), and (2) because of the forest structure, (*i.e.* smaller trees branching low, and in high densities).

River-edge

The river-edge transect was more similar to the SEGC transect in terms of diversity, and species composition overlap, than the savanna-edge transect. Compared to the SEGC transect, the river-edge transect had a relatively low density of trees, but greater evenness and higher overall basal area than in the SEGC transect (**Table 3.3**). There were 38 species (63% of the river-edge transect) shared with the SEGC transect. In terms of the number of stems, species included in the "top 10" in the river-edge transect that were also included in the "top 10" in the SEGC transects were *Diospyros dendo, Xylopia hypolampra, Xylopia quintasii,* and *Lophira alata*. In terms of basal area, species included in the "top 10" in the river-edge transect that were also included in the "top 10" in the SEGC transects were; *Aucoumea klaineana, Pycnanthus angolensis,* and *Lophira alata* .

Certain species seemed particularly common in this habitat type. White (1992) identified trees that were characteristic of riverine areas and all of these except *Rinoria* spp. and *Marquesia excelsa* were encountered on this transect. Species on this transect known to be common close to water include *Berlinia bracteosa* and *Anthonotha macrophylla* (Letouzey, 1968). Other species found in the present study to be important in terms of either basal area or numbers at the river's edge were *Xylopia* spp., *Diospyros dendo, Lophira alata, Milletia* sp., *Detarium macrocarpum, Distemonanthus bethamianus,* and *Irvingia grandifolia*.

Burseraceae, the *most* important family on the SEGC transect was only third most important on the river-edge transect. Again, this may be attributed to the rarity of *Aucoumea klaineana* on this transect, compared to the SEGC transect. The dominance of Caesalpiniaceae at the river's edge may be related to poor soil conditions as was proposed for the savanna edge, but for different reasons. Soil is often eroded due to the action of water, decreasing the amount of topsoil and exposing the rocky surface beneath.

Forest structure differed at the river's-edge in that there were less individuals in the 10-20 cm height category on the river-edge transect than in the SEGC transect, but more individuals in the 40-50 and 50-60 cm classes. Species found near water often have special adaptations such as stilt roots (eg. *Uapaca guineensis*) and may have water dispersed seeds.

In summary, river edge forests may be important for mangabeys: (1) because of the forest composition, (*i.e.* the importance of Caesalpiniaceae), and (2) because of the forest structure, (*i.e.* a lower density of larger trees).

Comparison with other areas

Gabon was part of a forest refugia during the Pleistocene (Hamilton, 1988). Probably for this reason, Gabon has a large number of endemic species and high tree species diversity compared to other areas in Africa including the Korup Forest Reserve (Gartlan *et al.*, 1986) and the Douala-Edea Forest Reserve in Cameroun (Newbery *et al.*, 1986), and the Kibale Reserve in Uganda (White, 1992). Gabon's forests are characterised by (1) evergreen species, (2) the presence of *Aucoumea klaineana*, an important tree species for timber found almost exclusively in Gabon, and (3) the general importance of the family Caesalpiniaceae.

Reitsma (1988) sampled plots at four sites in various areas in Gabon, and found his plot in the Lopé Reserve to be less species diverse than other areas in Gabon. He attributed this to relatively poor soil and low rainfall because of Lopé's geographical location, as described in the previous chapter. White (1992) assessed forest composition and structure at five sites within the Lopé Reserve. He found the study area at SEGC to be the least diverse, with the least number of individuals per unit area. In 2.5 ha, White (1992) encountered 760 trees (304 tree per ha) and 84 species. The

Shannon Index of diversity was 3.35, less than four species made up 50% of the sample and the 'top 10' species in terms of number made up 76% of the sample. White (1992) suggests that forests at SEGC may have had lower species diversity compared to other areas in the Reserve as a result of the forest's close proximity to savannas. It may represent recent colonisation of savanna by forests since similar patterns have been observed elsewhere where forests are located adjacent to savanna regions. Sterculiaceae was the dominant family in terms of number of stems, and Burseraceae was the dominant family in terms of basal area on the SEGC transect. Leguminosae made up 9% of the sample in terms of number of stems, and 21% in terms of basal area.

Information on forest structure and composition are not available from all locations where mangabeys have been studied. Neither Cashner (1972) in Equatorial Guinea, nor Chalmers (1967) in Bjuko and Mabira in Uganda provided any detailed description of the vegetation in the areas where they studied mangabeys, so it is not possible to make useful comparisons here. In Chalmers' (1967) study, forest was classified as "semi-deciduous tropical rain forest". His study at Bujuko was confined to a valley with a swampy bottom where the upper slopes of the valley the forest turned in to cultivated land. The other study area at Mabira was 259 km^2 forest bordered by a tea estate. In Bujuko there had been some felling and clearing of the ground vegetation 14 years earlier, but at Mabira the interference was much less. Cashner (1972) gave very little description of the forest but does say that it had been selectively logged two years previous to the study.

Information on the forest composition and structure at Kibale, are available from Waser (1974, 1977a), Struhsaker(1975), and Freeland (1979) (**Table 3.3**). The Kibale forest has been classified generally as "moist evergreen forest". Waser (1974) studied mangabeys mainly at Kanyawara in the Kibale forest. His main study area was made up of secondary and colonising forest, swamps as well as primary forests. There had not been human interference for 50 years previous to his study. He cut a transect in the study area using the same methods described in the present study and combined his results with data from Struhsaker (1975) to get a sample of 1,667 trees in 5.78 ha of transect, (288 trees per ha). In this sample he found between 67 and 71 species (the range was due to the number of unknown species). The Shannon Index of diversity was 4.37, five species made up 50% of the sample, and the 'top 10' species in terms of number made up 75% of the sample. At Kanyawara, Legumes were of little importance compared with Lopé, forming only 3 % of the sample (Struhsaker, 1975).

Williamson (1988) calculated overlap indices between Lopé and other tropical forests in Africa. Species overlap between Williamson (1988) and Waser (1977a) in Uganda is 57 species (7.9%) of Williamson's (1988) sample. Freeland (1977) studied mangabeys in Kibale forest, but at a different location than Waser (1974); Ngogo. With T.T. Struhsaker he recorded 74 tree species in a sample of 1,149 trees in 3.025 ha (369 trees per ha, Freeland, 1979).

In summary, therefore, trees were found at highest densities at Ngogo, then Lopé, then Kanyawara. The Shannon Index shows tree species diversity to be greater at Kanyawara, than at Lopé, although the number of individuals/species was lower, and the overall number of species encountered was higher at Lopé

Trees at Lopé tended to be larger and taller than at

Kibale. At Kanyawara and Ngogo, 41% and 44% respectively of all trees enumerated were over 18 m high (Freeland, 1979), whereas at Lopé 47% to 53% of trees were greater than 20m (White, 1992).

B. PHENOLOGY

Fruit production in tropical rain forest varies seasonally (Janzen, 1967; Tutin *et al.*, 1991 b). Similarly to the data from transects, data on phenology come from a *sample* of trees in the home range of the study group. Although the sample forms only a small proportion of the overall home range, it nevertheless serves to give an indication of the overall availability of fruit in the area.

During the period of this study fruit was most abundant from November to March and least abundant during the long dry season from June to September. This pattern is consistent with long-term records of fruit production at SEGC, although there are inter-annual variations (Tutin *et al.*, 1991 b; Tutin and Fernandez, 1993 b; White, 1992; Williamson, 1988), and similar to patterns observed elsewhere in Gabon (eg. Gautier-Hion *et al.*, 1981, 1985a).

Tutin and Fernandez (1993 b) suggest that the atypical fruiting of several species during the dry season in 1992 was caused by unusual low temperatures in January 1992, as flowering may have been triggered by a drop in temperature below a critical value of 19°C (Tutin and Fernandez, 1993 b). A significant negative correlation was observed during the period of this study between the number of trees with immature fruit on the phenology circuit and the minimum monthly temperatures, concurring with the hypothesis that minimum temperatures play a significant role in regulating the timing of fruit production.

At Kibale in Uganda, where grey-cheeked mangabeys have been studied, seasonal changes were not as marked as in Gabon. Waser (1975a) stated that "synchronous, seasonal fruiting appears to be the exception among mangabey food plants". He also observed that many foods eaten by mangabeys came from tree species that "fruit either asynchronously and non-seasonally or synchronously but at very long and possibly irregular intervals. Thus mangabeys are faced with foods which fluctuate widely in availability, particularly within a small area, but which are not seasonal in their fluctuation." These differences in fruit production between forests where mangabeys were studied in Uganda and forests in the present study may have important consequences for their behaviour, as discussed in the following chapters.

SUMMARY

In this chapter, differences were highlighted between two specific habitat types within the home range of the mangabeys at Lopé, by sampling trees from two transects along savanna-edge and river edge. The characteristics of these habitats will be referred to in later chapters to help to explain patterns of range use by the mangabeys. Changes in the monthly availability of fruit were illustrated through a phenological study. Availability of ripe fruit was lowest and the availability of immature fruit was highest during the long dry season, a pattern typical in Gabon. The effects of this on the behaviour of mangabeys will be investigated in the following chapters. Finally, a comparison was made between the habitat in which mangabeys were observed in the present study, and in Uganda. Tree density at Lopé was found to be greater than at Kanyawara, but less than at Ngogo, and tree species diversity was greater a Kanyawara, than at Lopé. The consequences of this will be discussed when comparisons are made between studies of grey-cheeked mangabeys.

CHAPTER FOUR: DEMOGRAPHY AND REPRODUCTION

INTRODUCTION

Demography is the study of life history statistics such as birth, death and migration rates, as well as the structure of groups or populations in terms of age/sex categories (Dunbar, 1987). The study of demography is important in that it provides a link between the behaviour of an individual animal and its environment, social and otherwise. Demographic statistics may be affected by environmental conditions, such as resource availability and seasonality. In turn, demographic parameters may influence the social environment of an animal (Altmann and Altmann, 1979) which may affect social behaviour (Dunbar, 1979). Knowledge of demography, is therefore an essential prerequisite for the understanding of the behaviour of individuals, groups and populations.

There have been several studies of life history, and especially reproductive parameters for grey-cheeked mangabeys in captivity (Danjou, 1972; Deputte, 1986, 1991,1992; Gautier-Hion and Gautier, 1976; Rowell and Chalmers, 1970) but less detailed information is available from field studies (Chalmers, 1968 b; Gevaerts, 1992; Jones and Sabater Pi, 1968; Wallis, 1983; Waser, 1974). This chapter aims to look at the demography of grey-cheeked mangabeys at Lopé, discussing group size and composition, and life-history parameters. It is proposed that intraspecific differences in groups size are a result of differences in forest structure between study sites, and interspecific differences result from the body size, diet and arboreal lifestyle of grey-cheeked mangabeys.

METHODS

A. GROUP SIZE AND COMPOSITION

The population of grey-cheeked mangabeys in the SEGC study area consisted of several groups on which data was collected opportunistically. Most data came from the main study group, but the group sizes of two other unhabituated groups of mangabeys were also accurately recorded. The composition of the study group, and one of the unhabituated groups was known throughout the study. The methods for identifying different age/sex classes were provided in *Chapter Two*.

The factors that influence group size and structure, are births, deaths and migration. All of these parameters were recorded *ad libitum* for the study group. Although the age of infants from unhabituated groups was difficult to assess, infants less than one month old have characteristic bright pink faces, feet and perineal areas (Deputte, 1992). Therefore, for the unhabituated groups, only observations of infants less than one month old were used in estimates of dates of birth. In addition, it was necessary for observations of these infants to be from groups either in different parts of the study area, or far enough apart in time (*i.e.* one month) so as not to count the same infants twice.

B. REPRODUCTIVE PARAMETERS

Mangabeys exhibit swellings of the sexual skin that are correlated with stages of the menstrual cycle (Dixson, 1983). Because the identity of individual females was not always known, data on the duration of the stages of the oestrous cycle in the present study were limited. The number of females in the group with swellings was recorded each day that the main group of mangabeys were followed, and noted whenever possible for all other mangabey groups. For the study group, the identity of the female and her stage of swelling were also recorded whenever possible.

The different stages of the sexual swelling are described in detail by Wallis (1983), Deputte (1992) and Rowell and Chalmers (1970). The swellings go through four phases of quiescence, inflation, peak and deflation. The following is a summary of these stages:

Quiescence

The sexual skin includes the area ventral to the base of the tail, but not including the callosities or the anus (Wallis, 1983). It encompasses the major and minor labia, and the perineal body up to the anus (Hill, 1974). In its resting stage, the sexual skin is pale pink and flat. This phase lasts for about 11 days.

Inflation

The sexual skin increases in size and changes from pale pink, to bright pink, over the period of about eight days (Rowell and Chalmers, 1970: range=8-11; Danjou, 1972: range=8-13 days; Wallis, 1983: range=4-14)

Peak

This is the most obvious stage when the swelling is bright pink, rounded and shiny and characterised by the lack of colour around the vaginal orifice. It usually lasts only one day, but can last up to three days (Wallis, 1983: 87% of peak swellings lasted for 24 hours, n=46 swellings and 17 females).

Deflation

After the peak swelling, the skin immediately becomes a darker pink, and after two or three days it becomes wrinkled. The swelling then becomes an even darker pink to purple, and gets increasingly wrinkled and by about 10 days, the swelling is fully deflated (Wallis, 1983: mean=9.9, range=7-14, n=26 swellings).

RESULTS

A. GROUP SIZE AND COMPOSITION

The size of the study group at the start of data collection in January 1991 was 18, comprising one adult male, ten adult females, one sub-adult male, two juvenile males, three juvenile females and one infant male. During the course of the study, there were six births, two deaths and one immigration as well as changes in age classes during the study period. By March 1991, the infant (TOR) present in the group at the beginning of the study was thought to be about 15 months old and was therefore reclassified as a juvenile. The sub-adult male (REG) in the group was classed as an adult male and the juvenile male (CAL) was classed as sub-adult male in April 1992. In June 1992 the infants born in March 1991 (QUC) and April 1991 (WIN) were reclassified as juveniles. The size of the group, therefore, at the end of the study in August, 1992, was 23, comprising three adult males, nine adult females, one sub-adult male, four juvenile females, thre juvenile males and three infants (one male, two females) (**Table 4.1**). The group size, therefore increased over the period of the study (**Figure 4.1**).

The sex ratio of the study group, including all members,

Table 4.1 Groups sizes and composition of grey-cheeked mangabeys in the present study and previous field studies

STUDY	Present study GABON		Chalmers 1968b UGANDA		Waser 1974 UGANDA					Wallis 1979 UGANDA	Cashner 1972 EQUATORIAL GUINEA
GROUP	Group 1	Group2	Mabira	Bujuko	M	S	W	DS	SH	*	**
ADULT MALE	1 to 3	2	5	4 to 5	6 to 7	1	3	2	2	3	2
SUB-ADULT MALE	1	1	3	2	0	1	0	2	5	1	0
ADULT FEMALE	9 to 10	7	9 to 11	6	5	2	4	4	7	5	5 to 8
JUVENILE	5 to 7	6 to 9	4 to6	2 to 5	4	1	1	4	9	5	8 to 9
male	2 to 3			1 to 2						3	
female	3 to 4			1 to 2						2	
INFANT	1 to 3	2 to 4	2	1 to 2	0	1	1	0	2	1	2 to 4
male	1			1 to 2							
female	0 to 2										
UNKNOWN	0	0	0	0	0	0	0	0	3	0	2 to 4
GROUP SIZE	18-23	18-20	23-27	16-20	15-16	6	9	12	28	8 to 23	17 to 23

* from two identified groups

** mean composition from 10 groups=14.5. Freeland (1979) gives mean group size of 14.4 (n=5, range=7-21) for the same area

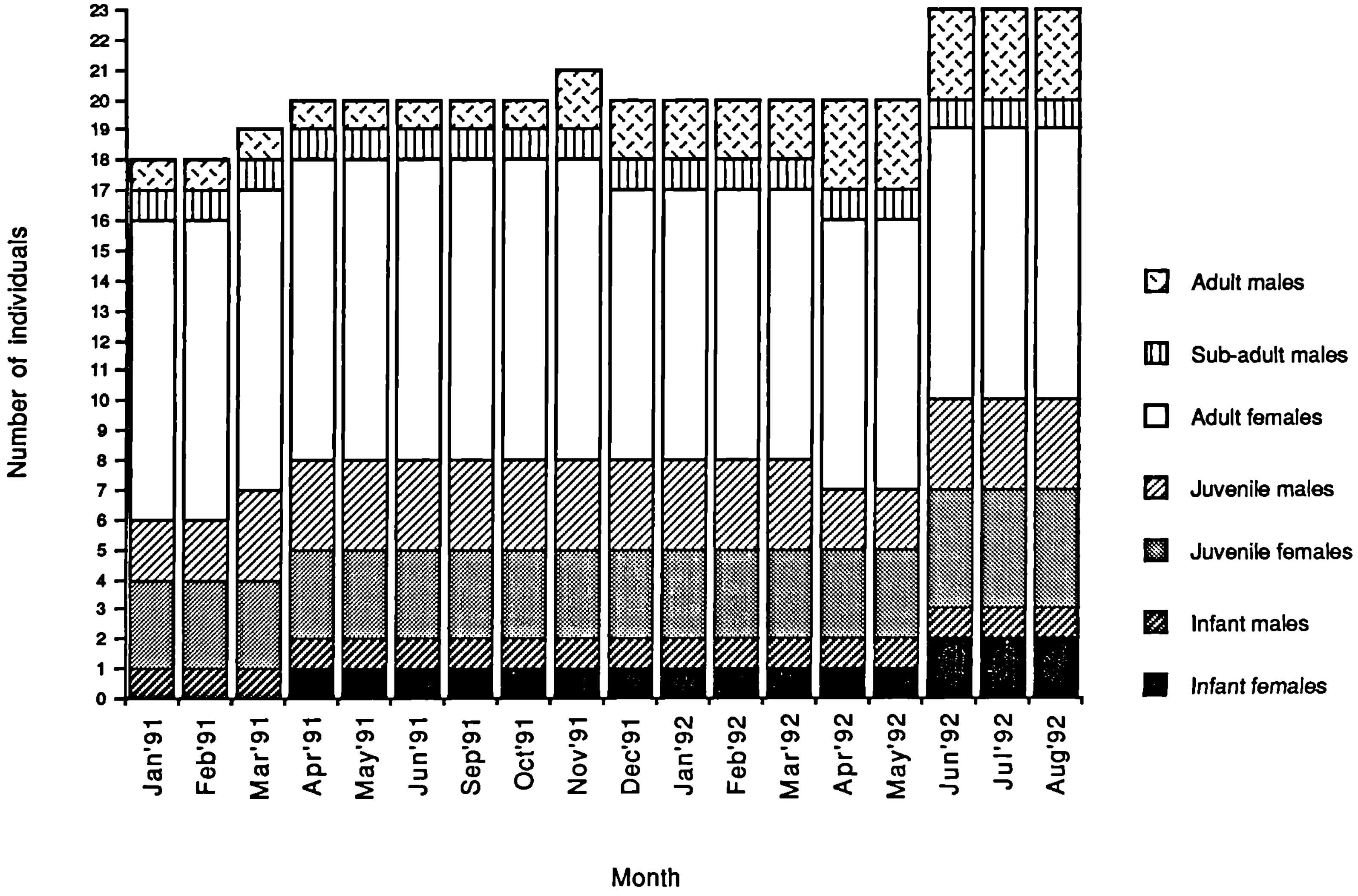


Figure 4.1 The number of individuals in each age/sex class in each month of the study

ranged from 1 : 2.6 (in January and February 1991) to 1:1.9 (in December 1992 to August 1992). The ratio of adult males to females changed from 1:10 in January 1991, to 1:3 at the end of the study.

Two other groups of mangabeys were accurately counted, both consisting of 18 individuals. The composition of only one of the groups was known, containing two adult males, one sub-adult male, seven adult females, six juveniles, and two infants. There were two births in this group and therefore the group at the end of the study consisted of 20 individuals. Although the study group of mangabeys had only one male at the beginning of the study, all other groups (n=7 groups) of mangabeys in the study area were observed to have a least two adult males.

1. Sub-groups

During 10% of scan samples in which group spread (see *Chapter Two*) was recorded (n=2883 scans, n=18 months), the study group of mangabeys was observed to split into two distinct sub-groups (**Figure 4.2**). The longest these groups remained apart was two hours. This occurred during all behaviours, and there was no significant difference between feeding behaviours (including the categories feeding and foraging for insects) and other behaviours (including travelling, resting, grooming and play), (Chi-square=1.94, df=1, p=0.16), indicating that these were not only foraging sub-groups. There was, however, a significant positive relationship between the availability of ripe fruit and the proportion of time the group were in sub-groups each month (r_S=0.56, n=18, p=0.02) suggesting that sub-grouping was not independent of the availability of food.

These sub-groups were generally consistent in their

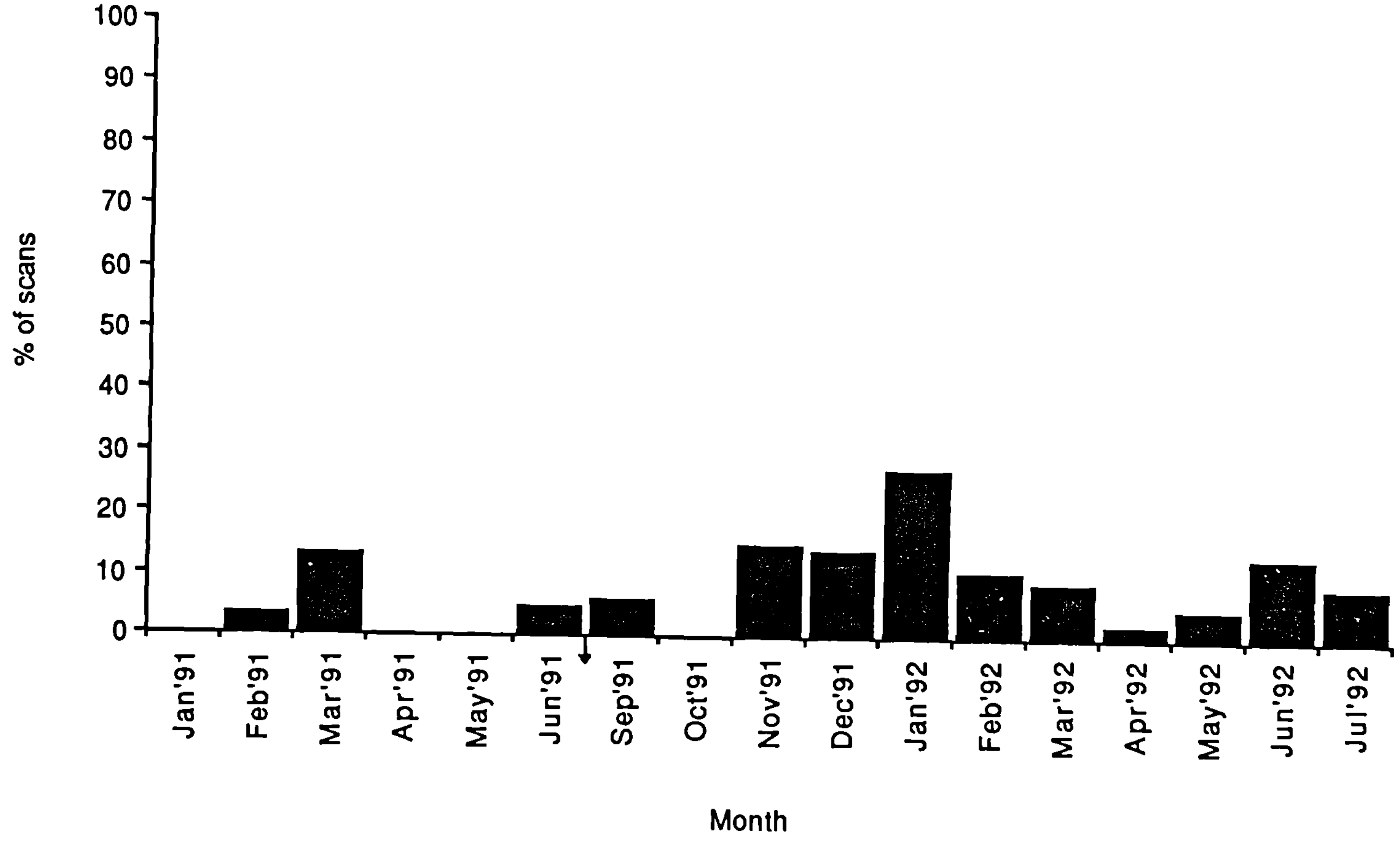


Figure 4.2 Percent of monthly scans that the study group of mangabeys were observed to divide into sub-groups.

composition. One sub-group of 11 to 16 individuals, contained the resident adult male PEI, the two adult females with the infants that were born in March and April 1991, three other adult females and five juveniles (plus two of the new infants). The adult female ONT who disappeared in December 1991 was also always in this sub-group. The other sub-group of six or eight individuals, consisted of the adult male REG, two recognisable females, STU and YUK, and two other females (plus one of the new infants). Also in this sub-group was a juvenile male who was frequently close to STU and was thought to be her offspring. The adult male who immigrated into the group in November 1991 (OTT), travelled with both of these subgroups.

As mentioned in *Chapter Two*, it is important for each consecutive scan to be independent in order to perform statistical tests, such as those used above. In *Chapter Five* evidence is provided to support that a duration of 15 minutes between scan samples is in fact long enough for scan samples to be independent for behaviour. It is possible, however, that a greater duration between samples is needed for sampling the behaviour of sub-grouping.

The problem of independent sampling is a reoccurring concern in many behavioural studies. Another concern is that of pseudoreplication, (*i.e.* where some individuals are sampled disproportionately to their representation in the group). *Chapter Five* addresses this problem in relation to social behaviour. Pseudoreplication may also present a problem, however, for sampling behaviour during sub-grouping. For example, if one particular individual is overrepresented in scan samples when the group is in sub-groups, and this individual has a tendency for a particular behaviour, then this may give a positive relation between this behaviour and sub-grouping, where a relationhip may not actually exist. Pseudoreplication is especially a problem for studies in forest habitats. Because visibility is low, recognition of individuals is often difficult, and the more conspicuous individuals, (eg. those which are most characteristic) may be sampled more than individuals which are more difficult to recognize. This would cause them to be overrepresenting in the sample.

A solution to this problem in more open habitats may be to randomly choose the individuals for scan samples previous to the study to ensure that all individuals are represented equally. In forest habitats this may mean loss of data, but will be considered for future studies.

2. Births

One infant was present in the main group at the beginning of the study in January 1991. His age was estimated to be about 12 months (± one month), and he was thus probably born in December to February 1990. Gestation length in mangabeys is about six months (see **Table 4.2**) and therefore the date of his conception was probably around June-August 1990. Six infants were born into the group during the 18 months of the study. A female was born on 23 March 1991 and a male on 18 April 1991. They were probably conceived between September and October 1990. Another infant was born on 6 February 1992, but disappeared by 8 February (see below). Three more infants were born into the group on 3 June 1992 (male), 9 June 1992 (female) and 22 June 1992 (female).

Including records for other groups of mangabeys in the study area (n=5 groups, n=12 births), births were concentrated in the period from January to July 1992 (**Figure 4.3**). In order to investigate if there was a relationship between births and environmental factors, the number of births each month was

Table 4.2. Reproductive parameters of grey-cheeked mangabeys

AUTHOR	**Study Captive(C) Field(F)**	**Oestrous cycle length (days)**	**Gestation (days)**	**Amenorrhea (months)**	**Interbirth interval (months)**
Present study	F	mean=31 SD=1.5 range=21-35 (n=12 cycles) (n=4 females)	181 181 186 (n=3 births) (n=3 females)	8 11 (n=2 births) (n=2 females)	36
Deputte 1991, 1992	C	mean=31 SD=8.5 range=11-72 (n=335 cycles) (n=9 females)	mean=175 SD=6.5 range=172-168 (n=25 births) (n=8 females)	mean=7.5*** SD=2.7 range=2.6-13.0 (n=17 births) (n=8 females)	mean=28*** SD=18 range=13-79
Wallis 1983	F	mean=47 SD=* range=8-184 (n=26 cycles) (n=7 females)	184 185 189 (n=3 births) (n=* females)	*	17 to 48
Rowell and Chalmers 1970	C	mean=31 SD=5.8 range=* (n=45 cycles) (n=3 females)	174 175 179 (n=3 births) (n=3 females)	3.9 4.7 (n=2 births) (n=3 females)	*
Waser 1974	F	mean=42 SD=6.4 range=29-75 (n=6 cycles) (n=** females)	172 176 164-177 (n=3 births) (n=* females)	10 (n=* births) (n=* females)	20
Danjou 1972	C	mean=29 SD=3.9 range=* (n=41 cycles) (n=* females)	*	*	*
Chalmers 1967	C	mean=28 SD=4.8 range=23-34 (n=7 cycles) (n=2 females)	*	*	*

*=data are not given in published work

**=most data are from one female (Waser, 1974)

***=data from females with surviving infants (Deputte, 1991)

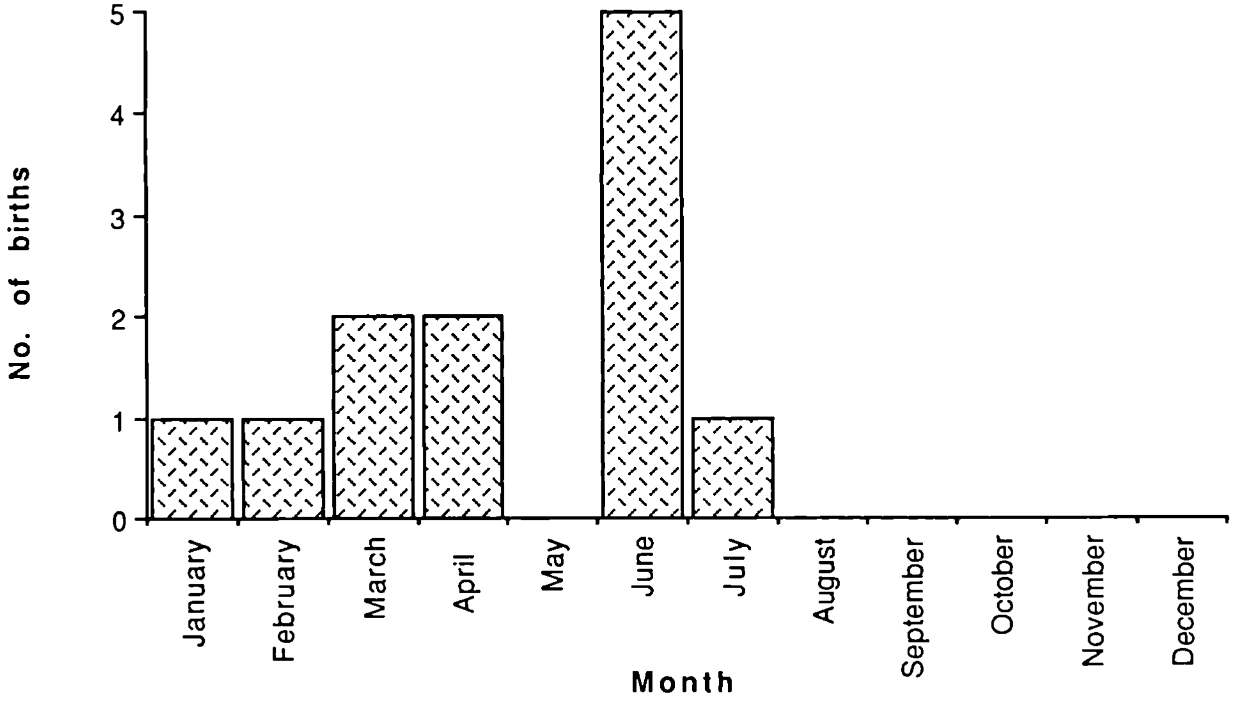


Figure 4.3 Number of births observed overall during the period of the study (n=5 groups, n=12 births)

tested for correlation with rainfall, temperature and fruit availability, but no correlations were observed (rainfall: r_s=0.13, n=18, p=0.68; maximum temperature: r_s=0.42, n=18, p=0.18; minimum temperature: r_s=0.38, n=18, p=0.22; availability of ripe fruit: r_s=0.10, n=18, p=0.98; availability of immature fruit: r_s=0.03, n=18, p=0.93).

3. Deaths

An adult female disappeared from the group in December 1991 and was never seen again. This female was thought to be old because of her scruffy appearance, low raspy chuckle and because she often moved more slowly than the rest of the group. These characteristics were also used by Waser (1978b) to describe an old female in his study group. However, unlike the female in Waser's (1978b) study, the female in the present study, was not post-reproductive because she was observed with a swelling the month before she disappeared. Although it is possible that she may have joined another group, this seems unlikely given that female transfer has never been recorded for grey-cheeked mangabeys. She was therefore assumed to have died. The other death in the study group was the infant born on the sixth of February 1992. This infant was seen to be weak and unable to cling well, and disappeared on 8 February, two days after its birth.

4. Migration

Males did not appear to transfer directly from one group to another, since lone males were observed in the study area. Lone males were observed twice when encountered randomly in the forest, and three times on the periphery of the study group during follows (see *Chapter Eight*). One immigration was observed during the period of the study. An adult male, OTT, migrated into the main study group during November 1991 and remained with the group for the rest of the study. The process of his entry into the group is described below.

OTT was first seen on 5 November 1991. The resident male PEI was 200 m from the rest of the group in consort with a swollen female (consorts are discussed in *Chapter Seven*). A few seconds after they had moved off towards the rest of the group, OTT appeared in the area they had just vacated. He showed typical behaviour of an unhabituated male, by giving penile displays and yawn threats (behaviours described in *Chapter Seven*) towards me but kept glancing in the direction that PEI and the swollen female had taken. He even stood bipedal at one point and peered into the distance. He seemed to be very nervous. After a few minutes, he left in the direction taken by PEI and the swollen female, and was not seen for the rest of the day.

OTT was not seen again until three days later on 8 November. He was sighted briefly about 200 m away from the study group, and moving towards them. A few hours later, he was seen on the periphery of the group, 300 m from where he was last sighted. Later, he reappeared, and was chased away from the group by the resident male, PEI. On 18 November, although OTT was not observed with the group, an unfamiliar whoop-gobble was heard from the direction of the group which may have been his.

On 23 November, an accurate count was obtained when the group passed through a gap in the canopy and OTT was not present. By 29 November, however, OTT was travelling, feeding, resting and grooming with the group, although he remained on the periphery. His strategy for entering the group was mainly by remaining close to adult females, particularly those with oestrous swellings (see *Chapter Seven*). On 26 November there were three swollen females in the group and OTT was seen to be associated with two of them on the periphery. The next time the group was followed, on 29 November, OTT was observed being groomed by a swollen female with another swollen female 5 m away in the same tree. On 3 December, a swollen female was observed with ejaculate on her swelling 1 m from OTT, who was grooming his genitals. It was therefore assumed that he was copulating with swollen females. Even once OTT became a permanent member of the group his strategy as an adult male was very different to that of the resident male (PEI) and this will be discussed in *Chapter Seven*.

No emigrations occurred during the period of the study, but during his transition to adulthood, the sub-adult male REG became increasingly peripheral to the group. This increased peripheralisation may have been a preliminary stage to his leaving the group (see *Chapter Seven*).

B. REPRODUCTIVE PARAMETERS

In the main group, adult females with swellings were observed during every month of the study, except April and May 1991. The maximum number of cycling females observed simultaneously in the study group was four. A total of 38 cycles were recorded for 11 females in the study group, but because individual females could not always be identified, and because the day of peak swelling was not always known, data were used from 12 cycles of four known females for whom the dates of peak swelling were certain. The mean cycle length was 31 days (S.D.=1.47, n=12 cycles, range 29-35 days, n=4 females) (**Table**

4.2).

The female with both the longest and shortest cycles was STU. Once ONT had left, STU was thought to be the oldest female in the group because of her raspy chuckle, and scruffy appearance. She was not observed with a swellings after 9 March, and therefore was assumed to have conceived. The adult female (QUE) resumed swelling on 23 November 1992, eight months after parturition (23 March 1991). She was observed with a swelling in December and January 1992, but did not cycle again, and so was assumed to have conceived. Adult female (MAN) was observed with a swelling on 23 March 1992, 11 months after parturition (April 18, 1991). She was observed only to cycle only once, and therefore had also probably conceived. Female (ALB) was believed to have just reached sexual maturity at the beginning of the study in January 1991. Her size was similar to those of the juveniles in the group, but in January 1991, she exhibited a sexual swelling. This swelling, however, was much smaller than those observed in fully adult females. The adult males did not show any interest in this female even during her peak swelling. In contrast, she showed great interest in them. (She was even observed to present to an adult male spot-nosed guenon, with whom the mangabeys were associated!) Adult male interest increased in her swellings and she was observed to copulate with OTT on 10 June 1992. She did not conceive, however, and continued cycling until the end of the study in August 1992. The behaviour of adult males towards ALB, and the continuation of her swellings throughout the study, suggests that female mangabeys have a period of adolescent infertility, as has been observed in captivity (Deputte, 1992).

Gestation length was known for three of the six pregnancies in the group (181, 181 and 186 days), but could not be precisely determined for the others. During the study period, six infants were born in 18 months, in a group containing an average of nine adult females. There was a breeding season from January to July which was monitored twice. Assuming no more infants were born until the following season, this yields an average of 0.33 infants per year, or projects that on average, each female gives birth once every three years (**Table 4.2**).

i.e. 6 infants per 9 females in 24 months
=0.67 infants per 1 female in 24 months
=0.33 infants per 1 female in 12 months
= 1 infant per 1 female every 3 years.

If only the annual cycle from September 1991 to August 1992 is examined, this yields an average of 0.44 births per female per year, that is one female will give birth to one infant every 2.3 years.

i.e. 4 infants per 9 females in 12 months
=0.44 infants per 1 female in 12 months
= 1 infant per 1 female every 2.3 years.

DISCUSSION

A. GROUP SIZE AND COMPOSITION

Comparison with other studies of grey-cheeked mangabeys

The groups of mangabeys accurately counted in this study had 18, 18-20 and 18-23 members. Group sizes at Lopé are slightly larger than the average group sizes reported for grey-cheeked mangabeys in Uganda of 15 (Wallis, 1979), 15 (Waser, 1974), 12 (Freeland, 1979), but similar to the 16-26 reported by Cashner

(1972) in Equatorial Guinea (**Table 4.1**). Comparing mangabeys in eastern African forests (Chalmers, 1968 b: 23 and 18; Freeland, 1979: 7, 12, 12, 20, 21; Wallis, 1979: mean=15; Waser, 1974: 15, 6, 9, 12, 28) and western African forests (present study: 20, 18, 18; Cashner, 1972; 17 and 22; Jones and Sabater Pi, 1968: 14 and 23), there is no significant difference (Mann-Whitney *U*-test=62.5, n=13 and 7, p=0.46). The median group size of mangabeys in eastern Africa is 15, compared to 18 in western African forests. Therefore, although the results are not significant, group sizes in western Africa do tend to be slightly larger, and a greater sample size may show this difference to be significant.

If there is a general trend for groups to be larger in western African forests, then this may be a result of differences in predation pressures, or differences in forest structure between study sites. If the predation pressure is greater in Gabon, then this may be a strong selective pressure for larger groups. By living in larger groups, an individual can decrease its chances of being taken by a predator because of an increase in the chance that a predator will be detected (Powell, 1974), deterred (Bertram, 1978), confused (Welty, 1934) and a statistical decrease in the probability of being attacked (Hamilton, 1971). The benefits of larger groups in avoidance of predation will be discussed in detail in *Chapter Eight*.

Unfortunately, very little information exists on the rates of predation between areas. The main predator of mangabeys is thought to be crowned hawk-eagles (*Stephanoaetus coronatus*) (Napier and Napier, 1967; Waser, 1980). During the present study, twenty-two flights of eagles over the main group were recorded. Three times an eagle was observed to swoop into the study group and land, but a successful predation was never observed. Waser (1980) observed less overflights or attacks during monthly follows (n=14), but whether this difference is significant is not certain.

Differences in forest structure have already been outlined in *Chapter Three* . A positive relationship is thought to exist between group size and food density (Wrangham *et al.*, 1993). In the present study, however, group sizes were slightly larger even though tree density was lower than at Ngogo. In addition, Freeland (1979) found mangabeys at Ngogo, to have similar group sizes to mangabeys at Kanyawara although forests at Ngogo have a higher density of food trees. This indicates that food density is not the only factor determining group size.

Differences in forests occur, not only in the amount of food available per unit area, but also how this food is distributed. Many species of fruiting trees in tropical rain forests, tend to have a more clumped than uniform distribution. Thus food sources for animals relying on the fruit of these trees are often "patchy in space" (Milton, 1988). Waser (1977 a) described the effect that this type of distribution of resources may have on group size. He explained that when food distribution is uniform, doubling the size of a group, doubles the area over which that group must travel to feed itself. When resources are clumped, however, an increase in group size does not necessarily mean an increase in the energetic requirements of travel for that group. This is because the distance between patches is the same, regardless if there are one or two animals. If this hypothesis is true, then group sizes may be larger in more patchy environments. Forests at Lopé are less even than forests at Kanyawara (*Chapter Three*), which may result in a more patchy distribution of trees, thus supporting this hypothesis.

Another factor which may limit group size, is patch size (Waser, 1977 a). It is possible that at Lopé, patch sizes are larger than at Kibale, but more detailed knowledge of the distribution and structure of food trees is needed to test both these hypotheses.

Sub-groups

If the size of a group exceeds the capacity of a food patch, then it may be advantageous for that group temporarily separate. This was observed in the present study, and was also observed by Waser (1977 a) and for other species of mangabey. Horn (1987b) observed that groups of black mangabeys frequently foraged in sub-groups of 9 or 10 individuals, containing at least one adult male in each sub-group, and that these groups would often sleep up to 400 m apart. He was not, however, able to confirm the stability of these subgroups. The present study shows that members of sub-groups remained constant, except for the adult male OTT who transferred between sub-groups depending on where there were swollen females. Formation of sub-groups has also been observed for white-collared mangabeys (Mitani, 1989, Jones and Sabater Pi, 1968) and agile mangabeys (Quris, 1975).

Although the division of the main group was observed to be temporary in the present study, the permanent fissioning of a group of mangabeys has been observed by Leland (unpublished data, cited in Struhsaker and Leland, 1979). It is possible that the mangabeys in the present study were in the process of a permanent fission. One of the sub-groups contained the male REG, who had recently reached adulthood. Further monitoring of this group is needed to confirm whether this separation will take place.

Comparison with other mangabey species

In general, size, terrestriality and frugivory are positively correlated with group size, where primates who are large, terrestrial and have relatively frugivorous diets live in larger groups than small, arboreal folivorous primate species (Clutton-Brock and Harvey, 1977; Milton and May, 1976). Competition may be greater between individuals in a group of arboreal primates where food is more clumped, than for terrestrial species feeding on more evenly dispersed resources, such as grasses. Comparison at a generic level indicates that terrestrial baboons and macaques have larger average group sizes than arboreal primates, such as grey-cheeked mangabeys (see Melnick and Pearl, 1987 for overview of other multimale *Cercopithecine* group sizes).

According to this hypothesis, semi-terrestrial mangabeys would be expected to have larger group sizes than the mainly arboreal grey-cheeked mangabeys, but the results do not support this. The study group of mangabeys were observed to spend more than an average of 96% of the time between 10 and 35 m (see *Chapter Six*). Black mangabeys are almost completely arboreal, spending 75% of their time between 12 and 30 m in trees, and have group sizes of 14-19 (Horn, 1987b). Of the more terrestrial mangabeys (see *Chapter One*), Homewood (1978) observed Tana River mangabeys, with average group sizes of 17 and 36, to forage for 73% of the time on the ground. Quris (1975) observed two groups of agile mangabeys with group sizes of 8-9 and 17-18, to be within five meters of the ground for 63.2% of the time. White-collared mangabeys, with group sizes of 21.11(S.E=2.55, n=9, range: 14-38) (Mitani, 1989), and 14-23 in Equatorial Guinea

(Jones and Sabater Pi, 1968) are observed on the ground for approximately 62% of the time (Mitani, 1989). Comparing the results for the arboreal species of mangabey (the present study; Cashner, 1972; Freeland, 1977; Horn, 1987b; Jones and Sabater Pi, 1968; Quris, 1976; Wallis, 1979; Waser, 1974) to the semi-terrestrial species (Homewood, 1978; Jones and Sabater Pi, 1968; Mitani, 1989; Quris, 1975), there was no significant difference in group size (Mann-Whitney *U*-test=104, n=22 and 9, p=0.496). Therefore, factors other than terrestrial versus arboreal habits appear to influence group size.

Crook and Gartlan (1966) suggested that habitat type can greatly affect group size, where primates living in more open habitats tend to have larger groups than those living in forest environments. This may be in order to decrease the predation risk, and may be an additional factor contributing to the larger group size of savanna-baboon compared to forest living mangabeys.

Births

In this study, there was no 'birth season' (*i.e.* births were not strictly confined to one part of the year, Jolly, 1972), although there may have been a 'birth peak' at Lopé from January to July (*i.e.* where births occur throughout the year but the majority of births occur within a few months, Jolly, 1972).

There is disagreement as to whether or not mangabeys exhibit a birth peak or season. Data from Uganda suggest that mangabeys do not have a breeding season or birth peak (Waser, 1974, Wallis, 1979; Chalmers, 1967) although Butynski (1988) reports a birth season of at least 9 months since from 29 births, only one infant was born from April to July. For mangabeys in Equatorial

Guinea, Cashner (1972) did not observe a birth peak (n=8 births), but Gevaerts (1992) observed considerable synchrony between the births of mangabeys with colobus and guenons in Zaire, and determined a birth season for mangabeys during July and August. In Gevaerts' (1992) study, the uteri of 134 female grey-cheeked mangabeys bought from markets in Zaire were dissected. The embryo, (when present) was weighed, and in order to determine the birth period, the weight of each specimen was compared to a standard growth curve.

In captivity in Europe, Deputte (1991) found a trend in births towards an autumn peak, but suggested that this could be a result of increased sexual behaviour in the spring due to their free access to both indoor and outdoor enclosures. Birth seasonality is also poorly defined in other species of mangabeys. Gust *et al.* (1990) found birth seasonality in sooty mangabeys and observed that swelling cycles and conceptions rarely occurred from April through September. Other Cercopithecinae, such as macaques, vervets, talapoins and mandrills have a birth peak, but baboons do not (Melnick and Pearl, 1987).

Birth seasonality is a reproductive adaptation whereby an animal adapts to seasonal changes in the environment such that births occur at the time most advantageous for both the mother and the infant in order to maximise reproductive success (Butynski, 1988). Seasonal reproduction can be affected by environmental factors such as availability of food, rainfall or temperature. Therefore birth seasonality might be expected to be greater in Gabon, where the climate is more seasonal, with longer periods without rain, greater extremes in temperature and more seasonal patterns in the availability of foods eaten by the mangabeys, than it is in Uganda, (see *Chapter Three* and *Chapter Five*). No relationship was found, however, between the distribution of births and these climatic factors. Other factors, such as diet, must also affect birth seasonality because different species of primates living in the same environment have great differences in birth seasonality (eg. vervets and baboons live in same environment, and vervets show a birth peak whereas baboons do not) (Melnick and Pearl, 1987). Developmental and phylogenetic constraints might also affect birth seasonality. For example, if the long interbirth interval is fixed, then mangabeys may be wasting their reproductive potential if they are confined to a strict birth season.

Migration

Lone males were also encountered by Wallis (1979) and Waser (1974) in Uganda. Wallis (1979), observed three adult males to enter his study group, although he did not observe the events leading up to the migration. Wallis (1979) speculates that the migrant males may have been peripheral to the group before his entry. The present study confirms this is indeed is the case. The adult male OTT was peripheral to the study group before entering and his acceptance into the group appeared to be facilitated by females in oestrus. In Waser's (1974) study, no males were observed to immigrate or emigrate from the main study group in 12 months.

B. REPRODUCTIVE PARAMETERS

In all species of mangabeys, females exhibit swellings during their menstrual cycle (Hill, 1974). These swellings have been shown to be related to hormonal changes and ovulation occurs at maximal tumescence (Aidara *et al.*, 1981). While the sample size in this study was small, the mean cycle length was considerably shorter than that observed by Chalmers (1967) and Waser (1974), although it does not differ greatly from captive studies on grey-cheeked mangabeys (**Table 4.2**). Chalmers (1968 b) noticed temporary cessation of cycling of the adult females in his group for four months. In the present study no adult females were observed to cycle during April 1991 and May 1991.

The reason why adult female primates exhibit obvious swellings is still debated (Hrdy and Whitten, 1987). Other species of primate also show obvious morphological changes of their sexual skin, and most of these species live in multimale groups (Clutton-Brock and Harvey, 1976). This relationship is especially notable for colobines. Out of 24 species in this family, the only three typically living in multimale groups, are also the only three in which females have sexual swellings. For other species, however, the relationship is not so clear.

For example, female hamadryas baboons and geladas exhibit swellings, but these species do not always live in multimale groups. Struhsaker and Leland (1979), however, argue that hamadryas baboons and geladas essentially *do* live in multimale groups because groups often aggregate together and females have the chance of being mated by other males. Other species, such as some species of macaques, live in multimale groups, but do not exhibit swellings (Hrdy and Whitten, 1987).

For species living in multimale groups, there are three main hypotheses to explain why swellings occur. The first hypothesis argues that by advertising the period when she is most fertile, a female encourages competition between males for copulations, and therefore ensures that she is copulated by the fittest male

(Clutton-Brock and Harvey, 1976). The second hypothesis proposes that by exhibiting a swelling , a female increases the chances of being mated by *more* than one male (Hrdy and Whitten, 1987). By increasing paternity uncertainty in this way, she may increase the chances of paternal care (Taub, 1980 a) or decrease the chances of infanticide (Hrdy, 1979). Finally, Hamilton (1984) suggests that the swelling *increases* paternity certainty by providing information about the stage of the cycle.

Evidence from observed copulations and ejaculate on swellings in the present study suggests that adult males have priority access to adult females with maximal swellings, but that sub-adult males and juveniles are allowed to copulate with adult females when their swellings are deflating (*Chapter Seven*). Adult male mangabeys formed consortships with adult females in oestrus during the peak stage of their swelling (see *Chapter Seven*). Thus one male appeared to be able to monopolise matings, giving evidence for either the first or third hypotheses.

Studies of grey-cheeked mangabeys in captivity (Chalmers and Rowell, 1971) and in the wild (Wallis, 1983), have observed that copulations ending in ejaculation were usually at maximal swelling, although Chalmers (1968c), observed three out of 11 copulations with non-swollen females. Copulations to ejaculation were most frequently observed for swollen females in captive studies of sooty mangabeys (Gust and Gordon, 1991; Gust *et al.*, 1990).

Interbirth interval

In the present study, the average number of births per female per year was about 0.33. This figure is similar to that observed by Wallis (1983) although longer than that observed for grey-cheeked mangabeys in captivity (Deputte, 1991, 1992) (**Table 4.2**), other species of mangabey (Gust et al., 1990; Hadidian and Bernstein, 1979; Homewood, 1975) (**Table 4.3**) and other Cercopithecine species (see Melnick and Pearl, 1987).

The interbirth interval comprises the period between giving birth and resumption of sexual swelling, the period from a female's first cycle to fertilisation, plus the gestation length. Amenorrhoea is the time from parturition to the first postpartum swelling, during which the female does not cycle. This is partly due to the suppression of menstrual cycles by lactation, although lactation may continue after a female resumes cycling. In the present study, adult females were first seen to have swellings eight and 11 months after parturition, which is comparable to the time reported in other field studies on mangabeys, but longer than observed during captive studies (**Table 4.2** and **4.3**).

Waser (1974) observed one female who did not become pregnant after nine cycles post amenorrhoea, although he found that most females conceived two to four months after resumption of cycles began. The length of gestation observed in the present study, is similar to that reported in other field studies (eg. Wallis, 1983), but longer that observed in captive studies (**Table 4.2**) and other species of mangabey (**Table 4.3**). There is a positive relationship between body size and gestation length in primates (Harvey *et al.*, 1987), however, gestation length for grey-cheeked mangabeys is similar, or even longer than some species of baboons and macaques which have larger body mass than mangabeys (see Melnick and Pearl, 1987; Harvey *et al.*, 1987 for summary tables).

The relatively long period of gestation and particularly of

Table 4.3. Reproductive parameters for other mangabey species.

SPECIES	AUTHOR	**Type of study Captive(C) Field(F)**	**Oestrous cycle length (days)**	**Gestation (days)**	**Amenorrhea (months)**	**Interbirth interval (months)**
Sooty mangabey *Cercocebus torquatus*	Gust et al., 1990	C	33	171	7	17
Sooty mangabey *Cercocebus atys*	Hadidian and Bernstein, 1979	C	35	167	5	13
Agile mangabey *Cercocebus galeritus*	Homewood, 1975	F	30	171	6 to 10	18 to 24

lactation, suggests that it is necessary for mangabey infants to be more developed at weaning, than is the case for baboons and macaques.The most obvious reasons why mangabey infants would need to be more developed at weaning is their arboreal lifestyle. Although mangabey infants were not seen to fall from trees during the present study, falls are not infrequently recorded for arboreal species of primate at Lopé. Of seven falls observed for black colobus at Lopé, older infants or young juveniles were involved (C.E.G. Tutin, personal communications). The average height of the canopy used by mangabeys was 20 m (*Chapter Eight*). Mangabeys were frequently observed to make spectacular leaps between trees, when they were at heights of 30 m or higher. Although by one year old, infants usually travelled alone, they were still observed to be carried ventrally for large jumps between trees, suggesting that these jumps may be difficult, or hazardous for small infants.

The idea that their arboreality contributes to a longer interbirth interval is supported by the observation that interbirth interval in mangabeys increases with increased arboreality of the species. The median interbirth interval for captive sooty mangabeys is 13 (range 4-26) (Hadidian and Bernstein,1979) and for wild agile mangabeys is 18 to 24 (Homewood, 1975), compared to 33 months for grey-cheeked mangabeys (this study; Wallis, 1983).

Another factor that may contribute to a longer dependency of infants on mothers is the low visibility in the canopy. Compared to the more open habitat of some savanna baboons where adult females can visually monitor infants at a greater distance, adult female mangabeys can easily lose sight of infants a few meters away. Infants would therefore be more vulnerable to predators or harassment form other group members. Possibly because of the dangers of arboreal life, infants were never observed to be carried dorsally as are infant baboons. It may therefore be more energetically demanding for an arboreal female to raise her infant than for a terrestrial species.

SUMMARY

This chapter gave data on the demography and reproduction of grey-cheeked mangabeys at Lopé. It is suggested that intraspecific differences in group size are a result of differences in forest structure between study sites. The genus *Cercocebus* has a smaller group size, in general, than closely related baboons and macaques. Although, differences between grey-cheeked mangabeys and terrestrial species of baboons and macaques may be explained by the hypothesis that terrestrial species have a larger group size than arboreal species (Clutton-Brock and Harvey, 1977), this relationship does not hold within the mangabey genera since the semi-terrestrial Torquatus mangabeys do not have a significantly larger group size than the arboreal Albigena mangabeys.

It is suggested that the arboreal lifestyle of mangabeys may also have effects on other aspects of their demography and reproduction, such as increasing the need for infants to be more mature at birth and independence than terrestrial species, therefore lengthening of the period of lactation and gestation of the mother, and increasing the interbirth interval as a result.

CHAPTER FIVE: FEEDING ECOLOGY

INTRODUCTION

Diet has been shown to be a good predictor of ecological parameters, such as ranging patterns (eg. Waser, 1977a), activity budgets (Clutton-Brock and Harvey, 1977), polyspecific associations (Peres, 1991) and group size and structure (Struhsaker and Leland, 1979) in animals, and therefore an understanding of dietary niche is important in any study of primate behaviour and ecology.

Previous studies have found that grey-cheeked mangabeys are highly frugivorous, although this assumption is based on very few studies. The most detailed information on the diet of grey-cheeked mangabeys comes from two studies in Uganda (Wallis, 1979; Waser,1974), but little information exists on the diet of grey-cheeked mangabeys in western Africa. Cashner (1972) provides food lists for grey-cheeked mangabeys in Equatorial Guinea, but the only other information available consists of (1) a list of 10 plant species observed to be eaten by grey-cheeked mangabeys in Equatorial Guinea (Jones and Sabater Pi, 1968), (2) nine feeding observations of grey-cheeked mangabeys in Cameroon (Mitani, 1991), and (3) data from the analysis of stomach's contents of 18 grey-cheeked mangabeys from Makokou in Gabon (Gautier-Hion, 1977).

The main variables which may influence diet are; (1) food availability; (2) inter- and intraspecific food competition; (3) food chemistry; and (4)morphological constraints, (eg. dental, cranial or gut). Food availability is in turn affected by forest composition and seasonality. Gautier-Hion (1983) suggested that because there is greater diversity and availability of succulent fruit in western African rain forests, primates in western African are more frugivorous than in eastern Africa. This hypothesis has been supported by observations that (1) forest guenons living in Gabon were observed to be less folivorous than related species in the Kibale Forest, Uganda (Gautier-Hion, 1983), and that (2) lowland gorillas in Gabon were observed to have the most frugivorous diet of any population studied to date (Williamson *et al.*, 1990). In the present study, therefore, grey-cheeked mangabeys were expected to have a larger proportion of succulent fruit in their diet than the grey-cheeked mangabeys studied in Uganda.

But diet can also be limited by competition from sympatric species. The diet of grey-cheeked mangabeys has not been studied in detail where they coexist with both gorillas and chimpanzees, and having to compete with these large bodied frugivores may be expected to affect their diet. Mangabeys at Lopé have been shown to have larger group sizes than at Kibale (*Chapter Four*) and therefore intra-specific competition may also be greater.

For competition to exists, it is necessary for resources to be limiting (Putman and Wratten, 1984). In Gabon, during times of year when fruit production is high, animals may not have to compete for food. During the long dry season, however, when ripe fruit is less abundant (see *Chapter Three*) there is evidence that competition may exist. Several species of primates, including gorillas (Rogers *et al.*, 1988; Tutin and Fernandez, 1993 a) in the Lopé Reserve, and guenons at Makokou (Gautier-Hion, 1980) turn to a more folivorous diet, and dietary overlap between species of primates tends to decrease.

The aim of this chapter is to document in as much detail as possible, the diet of the grey-cheeked mangabey in the Lopé

Reserve, in order to determine whether they are in fact more frugivorous than grey-cheeked mangabeys studied in Uganda, as predicted.

METHODS

A. ACTIVITY BUDGETS

Before looking at their diet, it is important to look at the overall proportion of time mangabeys spent feeding and how this may vary with time of day, months and seasons. The activity was recorded every 15 minutes during scan samples as described in *Chapter Two*. Behaviours recorded were rarely continuous for more than 15 minutes and therefore consecutive scan sample were probably independent. In order to test mathematically for this, the monthly proportion of time in each activity using 15 and 60 minute scan intervals was compared. Neither the proportion of time spent feeding (Chi-square=0.003, p=0.96), nor the proportion of time foraging for insects (Chi-square=1.64, p=0.20) were significantly different, indicating that samples were independent.

B. DIET

All foods observed to be eaten by mangabeys in the study area were recorded, but only information from scan samples during follows of the study group were used for frequency calculations. Foods observed to be eaten by mangabeys outside of scan samples, and observations from other researchers at SEGC were included in the overall list of food species eaten. The food type, species, and stage of ripeness of all foods eaten were recorded as described in *Chapter Two*. When mangabeys were observed feeding on "fruit", a distinction was made between whether they were feeding on "pulp", (including the arils and the succulent and fibrous material surrounding the seed), or "seeds" of the fruit. Researchers do not often differentiate between these parts, although they are nutritionally very different (eg. Cashner, 1972).

Data for analyses were not used until the mangabeys were sufficiently habituated to the presence of the observer, and until the observer could reliably identify feeding trees. Information therefore, from scans during the preliminary stages of the study, from January to March 1991 were ignored. Data for analyses came from scan samples from April 1991 to June 1991 and then from September 1991 until August 1992.

C. FACTORS THAT MAY INFLUENCE DIET:

1. Availability

(a) Availability in time

Information on the availability of fruit each month was generated from phenological monitoring of a sample of trees in the study area (see *Chapter Three*).

(b) Availability in space

Information on the availability of plant species in the SEGC study area came from SEGC transects (White,1992; Williamson, 1988) and the savanna and river-edge transects from the present study (see *Chapter Three*).

2. Chemical composition

The chemical composition for 54 fruits and 17 seeds from the Lopé Reserve is available from Rogers *et al*. (1990). Ten of the fruit and 10 of the seeds analysed were included in the diet of mangabeys, therefore the chemical composition of these foods can be compared with "important food items" to gorillas (as defined by Williamson, 1988), in order to determine if mangabeys are selecting or avoiding foods for different reasons than gorillas.

3. Diet overlap and competition with other diurnal primate species

For feeding observation for guenons, colobus and mandrills in the study area, the date and time of observation, food species, and food part were recorded. These observations were combined with SEGC records and information from a study of black colobus in the Reserve (Harrison, 1986 a, b) to give overall food lists. Comparisons were made between these food lists to measure overlap in plant species eaten for each plant part.

All information on gorilla diet comes from Williamson *et al.* (1990) and Tutin and Fernandez (1993 a) and all information on chimpanzee diet comes from Tutin and Fernandez (1993 a) unless otherwise stated. Ape foods were identified from faecal samples, feeding trail and direct observation. These methods were described in detail by Tutin and Fernandez (1985) and Williamson (1988).

RESULTS

A. ACTIVITY BUDGETS

1.Time of day

Because the number of scan samples varied over the time of day (*Chapter Two*), the proportion of time that the mangabeys were observed to be engaged in each activity was calculated for each hour of the day (**Figure 5.1**). When the day was divided into morning (08:00-11:00), midday (11:00-14:00) and afternoon (14:00-17:00), there was no significant difference in the amount of time spent feeding between morning and midday (Chi-square=0.67, df=1, p=0.41), morning and afternoon (Chi-square=0.47, df=1, p=0.49) and midday and afternoon (Chi-square=2.72, df=1, p=0.10). There was no significant difference in the amount of time they spent foraging for insects between morning and midday (Chi-square=0.70, df=1, p=0.40), although they spent significantly less time foraging for insects in the afternoon, than both the morning (Chi-square=10.46, df=1, $p<0.01$), and midday (Chi-square=8.92, df=1, p=0.01).

2. Seasonality

Because the number of scans varied between months (*Chapter Two*), the proportion of time that mangabeys were observed to be engaged in each activity was calculated for each month (**Figure 5.2**). Mangabeys spent a significantly greater proportion of their time feeding during the long dry season than in all other seasons, including the short rainy season (Chi-square=7.31, df=1, p=0.01), the short dry season (Chi-square=22.22, df=1, $p<0.01$), and the long rainy season (Chi-square=21.44, df=1, $p<0.01$). Differences between all other seasons were not significant. Mangabeys may have spent more time feeding during the long dry season because there was less succulent fruit available, and therefore they had to feed for longer to meet their nutritional requirements on lower quality food items. In order to test this, the proportion of ripe fruit available was tested for correlation with the proportion of time spent feeding. Although there was a trend in this direction, the relationship was not significant ($r_s=-0.42$, n=15, p=0.12).

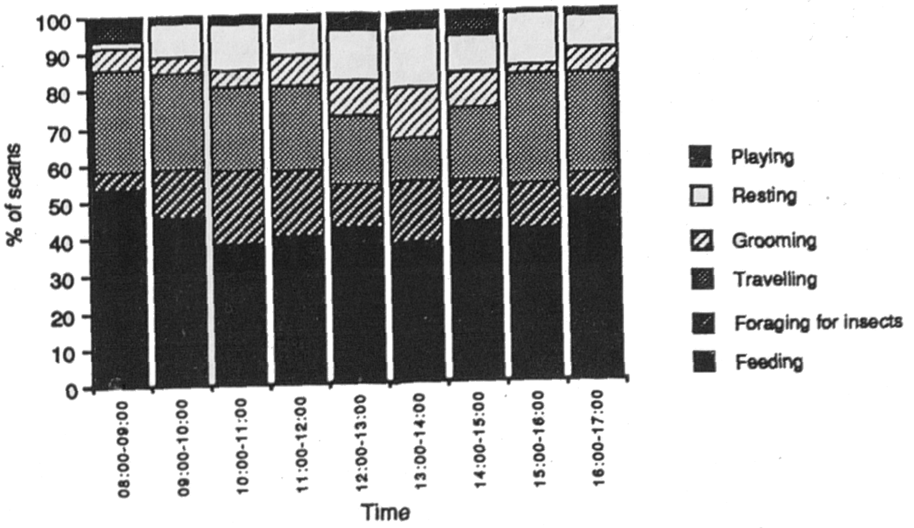


Figure 5.1. Percent of scans engaged in each activity during each hour of the day

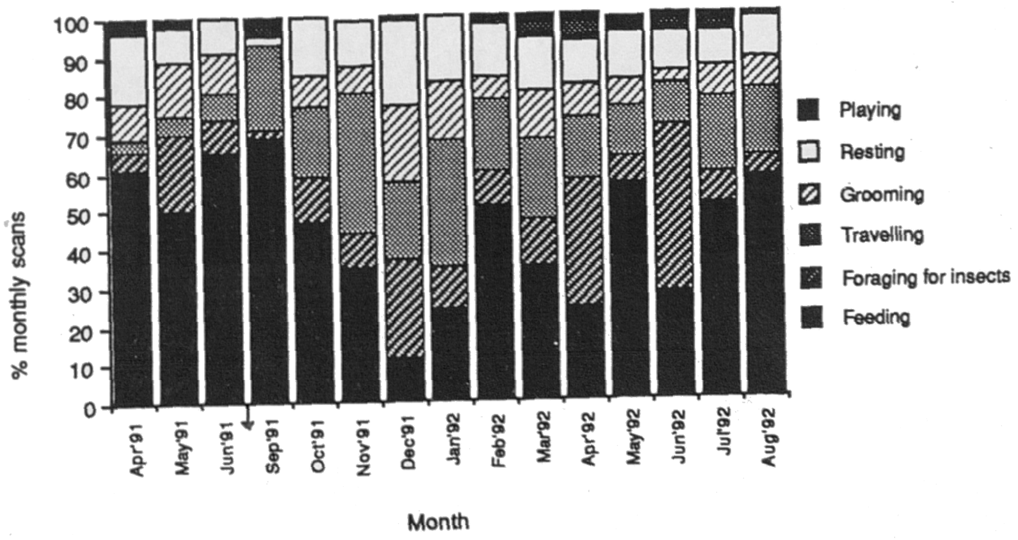


Figure 5.2 Percent of scans engaged in each activity during each month

Mangabeys spent the greatest proportion of time foraging for insects during the long rainy season, and this was significantly greater than during the short rainy season (Chi-square=6.7, df=1, p=0.01) and the short dry season (Chi-square=29.53, df=1, p<0.01). The proportion of time spent feeding on insects was tested for correlation with the availability of ripe fruit, and this relationship was found to be significant (r_s=0.524, n=15, p=0.05). The possible reasons for this are discussed below.

Because of the variability over time of day and months, in order to determine the overall percent of time engaged in each activity, the proportion of scans each activity was recorded was averaged over hours and months. Overall mangabeys spent an average of 43% of the time feeding and 10% of the time feeding on insects (**Figure 5.3**).

B. DIET

1. Food type

Because sample sizes varied between months, the percent of scans that mangabeys were observed to feed on each food type was averaged over all months (**Figure 5.4**). Mangabeys spent an average of 66% (S.D. =7.19) of all scans feeding on fruit. Because it had been predicted that mangabeys would eat a large proportion of succulent fruit, the most striking result was that they spent a greater proportion of time feeding on seeds (mean=36%, S.D.=7.86) than feeding on pulp (mean=30%, S.D.=6.12). The pulp was generally eaten when it was ripe, but seeds were eaten when they were both immature and ripe (**Figure 5.5**).

Mangabeys spent the majority of their time feeding on fruits (pulp and seeds) in all months except in June 1991, when new

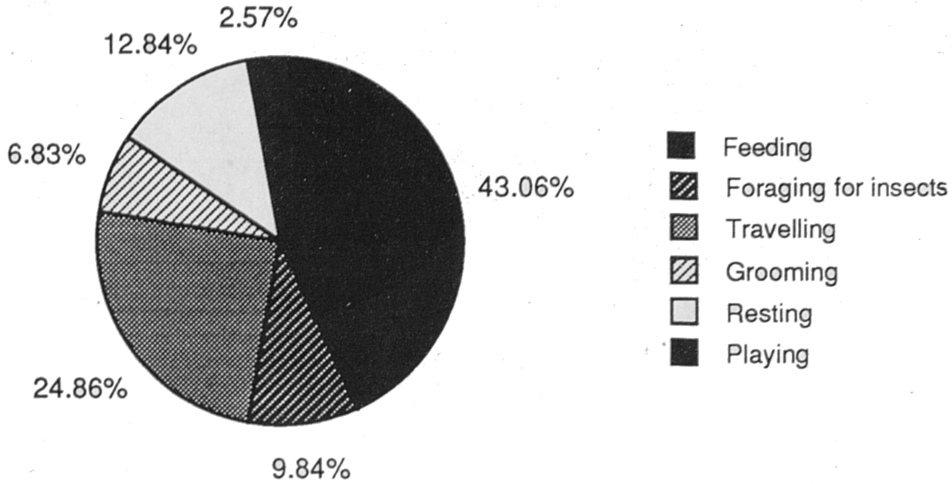


Figure 5.3 Overall proportion of time spent in each activity

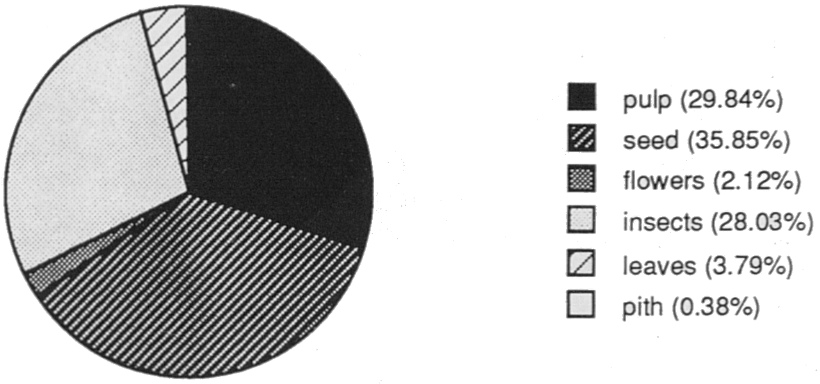


Figure 5.4 Average percent of scans that mangabeys spent feeding on each food-type

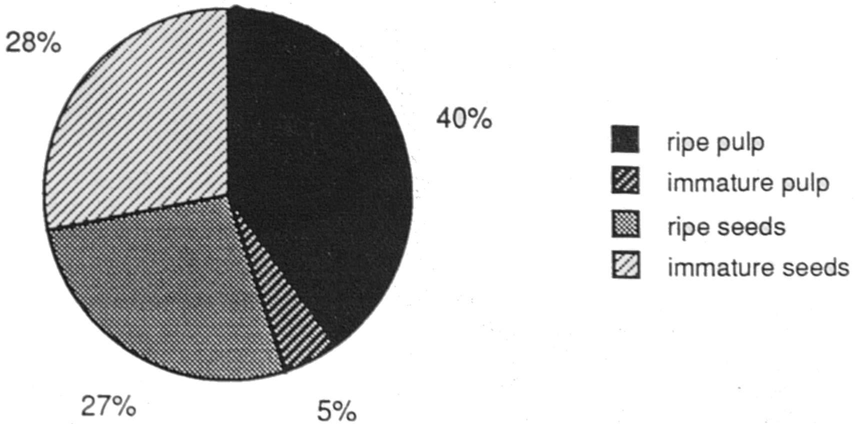


Figure 5.5 Average proportion of scans mangabeys spent eating ripe or immature pulp and seeds of fruit

leaves made up the majority of the diet, and in December 1991 and June 1992, when they spent a greater proportion of their time foraging for insects (**Figure 5.6**). Mangabeys may have been feeding on foods other than fruit during June of both years because this is the beginning of the dry season when fruit was becoming scarce. In order to investigate if mangabeys fed on fruit (pulp and seeds) according to its availability, the proportion of time spent feeding on each category was tested for correlation with the availability of ripe fruit, but there was no significant relationship here (fruit: $r_s=0.11$, $n=15$, $p=0.70$; pulp: $r_s=0.25$, $n=15$, $p=0.38$; seeds: $r_s=0.16$, $n=15$, $p=0.56$). However, comparing the long rainy season (when ripe fruit is most abundant), and the long dry season, (when ripe fruit is least abundant), significantly more time was spent eating seeds during the long dry season (Chi-square=78.50, df=1, $p<0.01$) and more time eating pulp (Chi square=106.00, df=1, $p<0.01$) and insects (Chi square=8.69, df=1, $p<0.01$) during the long rainy season. Therefore, although there was no month by month correlation, there was an overall seasonal trend.

The proportion of time spent feeding on different food-types was tested to see if any of the categories were related. The only significant relationship was a weak negative correlation between the amount of time spent foraging for insects, and the time spent feeding on seeds, ($r_s=-0.72$, $n=15$, $p=0.08$). Seeds and insects are generally high in protein. Mangabeys may have been able to get most of their protein requirements from seeds, which they ate most frequently during the long dry season when succulent fruit was scarce. During the long rainy season, when ripe fruit was most abundant, insects may have provided their protein requirements instead, thus explaining the positive correlation between the availability of ripe fruit and insect eating. Alternatively, insects may be scarce during the long dry season, when seed-eating is greatest. Unfortunately, information on insect availability is not available at Lopé.

The amount of time that mangabeys spent feeding on ripe and immature fruit was highly variable (**Figure 5.7**). During the long dry season, mangabeys spent 42% of all scans feeding on immature seeds, compared to only 7% during the long rainy season. The proportion of time they spent feeding on ripe and immature pulp was less variable. Fruit pulp was eaten immature for 2% of the time during the long rainy season, and 1% of the time in the long dry season, and this difference was not significant (Chi-square=0.02, df=1, p=0.89).

2. Food species and description

Plant foods

Mangabeys were recorded feeding on plant food for 1737 scan samples. During these scan samples, mangabeys were observed to feed on 100 different items from 60 known species, plus 15 unknown species from 24 taxonomic families (**Table 5.1**). Mangabeys ate 36 species of pulp, 30 species of seeds, 10 species of flowers, 18 species of leaves and 7 species of pith. Including observations of feeding outside of scan samples, and long-term data from records at SEGC, mangabeys were observed to feed on 55 species of pulp, 39 species of seeds, 12 species of flower, 22 species of leaf and 9 species of pith (**Appendix 5.1**).

The proportion of time that mangabeys spent feeding on each food species each month was averaged from April 1991 to September 1992 (**Appendix 5.2**) to give an overall proportion of

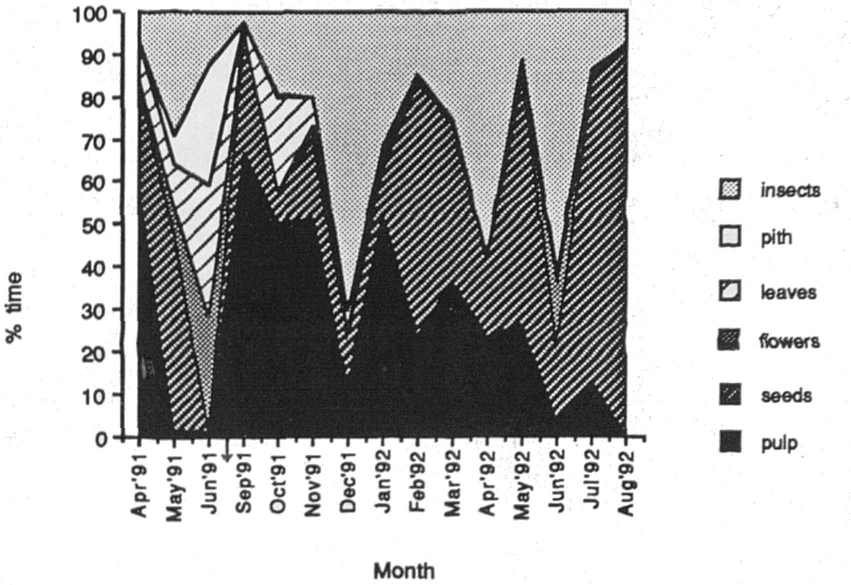


Figure 5.6 Proportion of time spent feeding on different types of food during each month.

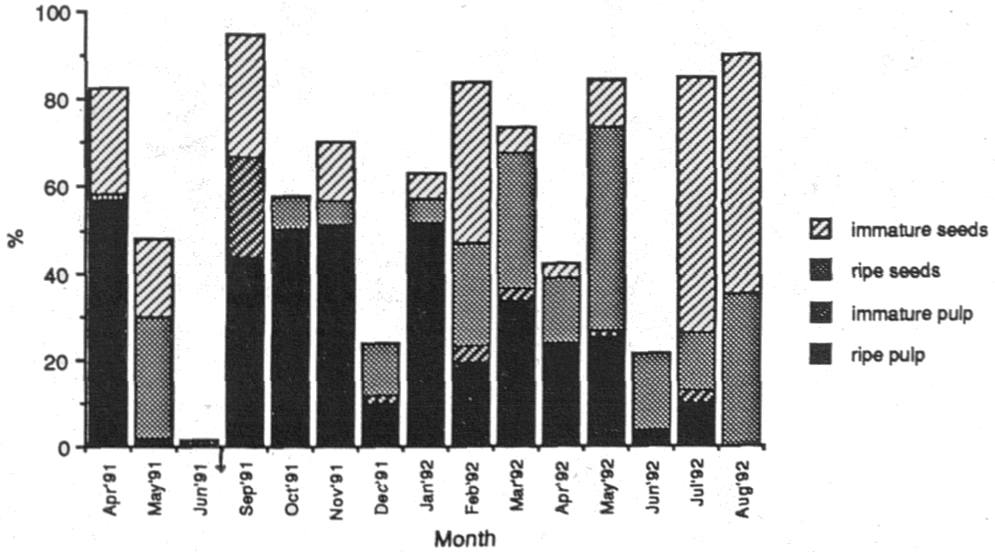


Figure 5.7 Proportion of time spent feeding on ripe or immature pulp and seeds of fruit

Table 5.1 List of food species, including the type of food observed to be eaten by grey-cheeked mangabeys during this study

Species	**Family**	**Part**							
		FRR	FRI	SDR	SDI	FL	NL	PTH	IN
Anthonotha macrophylla	CAESALPINIACEAE				√				
Aucoumea klaineana	BURSERACEAE				√	√	√		√
Baikiaea insignis	CAESALPINIACEAE			√					
Berlinia bracteosa	CAESALPINIACEAE				√				√
Blighia welwitschii	SAPINDACEAE	√							
Canarium schweinfurthii	BURSERACEAE	√					√		√
Ceiba pentandra	BOMBACACEAE						√		
Celtis tessmannii	ULMACEAE	√		√	√				
Cissus dinklagei	VITACEAE	√							√
Cola lizae	STERCULIACEAE	√						√	√
Cryptosepalum staudtii	CAESALPINIACEAE				√				√
Dacryodes buettneri	BURSERACEAE	√							√
Dialium lopense	CAESALPINIACEAE			√	√				
Diospyros cf. viridicans	EBENACEAE	√					√		
Diospyros dendo	EBENACEAE	√	√		√		√	√	√
Diospyros polystemon	EBENACEAE	√		√	√				
Diospyros zenkeri	EBENACEAE	√							
Distemonanthus bethamianus	CAESALPINIACEAE			√			√	√	√
Dichapetalum sp.	EUPHORBIACEAE	√							
Elaeis guineensis	PALMAE	√							
Eriocoelum macrocarpum	SAPINDACEAE			√					
Ficus mucuso	MORACEAE	√							
Ficus recurvata	MORACEAE	√							
Ficus thongii	MORACEAE	√							
Gambeya africana	SAPOTACEAE		√						
Ganophyllum giganteum	SAPINDACEAE	√							
Guibortia tessmannii	CAESALPINIACEAE			√					
Heisteria parvifolia	OLACACEAE	√							
Hylodendron gabunense	CAESALPINIACEAE			√					
Irvingia gabonensis	IRVINGIACEAE				√				√
Irvingia grandifolia	IRVINGIACEAE			√					
Klainedoxa gabonensis	IRVINGIACEAE	√			√				√
Landolphia cf heudelotii	APOCYNACEAE	√							
Lecaniodiscus cupanioides	SAPINDACEAE	√							√
Lophira alata	OCHNACEAE						√		√
Manniophyton sp.	EUPHORBIACEAE			√					
Millettia sp	PAPILIONACEAE						√		√
Monodora angolensis	ANNONACEAE	√							
Myrianthus arboreus	MORACEAE	√							
Nauclea diderrichii	RUBIACEAE	√				√			
Ongokea gore	OLACACEAE		√						
Parkia bicolor	MIMOSACEAE			√	√	√	√		
Parkia filicoidea	MIMOSACEAE					√		√	
Pentaclethra macrophylla	MIMOSACEAE				√	√	√		√
Piptadeniastrum africanum	MIMOSACEAE			√					√
Polyalthia suaveolens	ANNONACEAE	√							
Porterandia cladantha	RUBIACEAE		√						
Pseudospondias microcarpa	ANACARDIACEAE	√							
Pterocarpus soyauxii	PAPILIONACEAE			√	√	√	√		√
Pycnanthus angolensis	MYRISTICACEAE	√	√	√	√				√
Scottellia sp	FLACOURTIACEAE	√							
Scyphocephalium ochocoa	MYRISTICACEAE				√				√
Sterculia tragacantha	STERCULIACEAE	√	√					√	√
Tetrapleura tetraptera	MIMOSACEAE				√				
Uapaca guineensis	EUPHORBIACEAE	√	√						
Uvariastrum pierreanum	ANNONACEAE	√							
Vitex sp	VERBENACEAE					√			
Xylopia aethiopica	ANNONACEAE		√		√				
Xylopia hypolampra	ANNONACEAE	√			√				√
Xylopia quintasii	ANNONACEAE	√			√				√
Unknown May 1991	Unknown					√			
Unknown June 1991	Unknown							√	
Unknown November 1991	Unknown						√		
Unknown November 1991	Unknown						√		
Unknown November 1991	Unknown						√		
Unknown November 1991	Unknown						√		
Unknown November 1991	Unknown						√		
Unknown December 1991	Unknown						√		
Unknown December 1991	Unknown					√			
Unknown Februrary 1992	Unknown			√					
Unknown March 1992	Unknown							√	
Unknown May 1992	Unknown					√			
Unknown June 1992	Unknown						√		
Unknown July 1992	Unknown			√					
Unknown July 1992	Unknown			√					

FRR = ripe pulp, FRI = immature pulp, SDR= ripe seeds, SDI= immature seed, FL = flowers, NL= new leaves, PTH = pith, IN = insects time spent feeding for each species (**Table 5.2**). The most important species in terms of time spent feeding, are described below. The greatest proportion of feeding scans was from foods belonging to the family Caesalpiniaceae (17%) and Papilionaceae (14%). Foods from the family Leguminosae, (which includes the three families Caesalpiniaceae, Papilionaceae and Mimosaceae) made up 40% of all feeding scans (**Table 5.3**).

Mangabey foods were diverse in size and colour (**Table 5.4**). Most foods came from trees and lianes, and no feeding on shrubs or herbs was observed during this study. The size of plants that fruit were taken from varies from small plants less than 12 cm dbh (eg *Diospyros dendo*) to large plants with a dbh greater than 70 cm (eg. *Celtis tessmannii, Pterocarpus soyauxii*). When plants from which foods were taken were rated as lianes, or small (<25 cm dbh), medium (25-50 cm dbh) or large (50 cm+ dbh) trees, most foods came from large (48%) or medium trees (31%) and few from small trees (16%) or lianes (5%).

Pulp

For the majority of feeding scans mangabeys fed on either the succulent pulp (eg. *Canarium schweinfurthii*) or the arils of fruit (eg. *Blighia welwitschii*) (**Figure 5.8**). The fruits from which mangabeys ate the pulp, ranged in size from *Scottellia* sp., with fruits less than half a centimetre in diameter, to species like *Landolphia* sp., the size of a bowling ball. There was also a large variation in the colour of fruits. Many of the fruits are brightly coloured red or orange or yellow when ripe (eg. *Cola lizae*), but there are also fruits that remain dull in colour (eg. *Uvariastrum pierreanum*). In general, pulp came from fruits that seemed to fit the description of typical "monkey

Table 5.2. The proportion of feeding scans, the proportion on the transect and the selectivity index for each plant species eaten by mangabeys during the study

Species	Family	% Time Feeding	Rank	Proportion in transect	Selectivity Index	Rank
Pterocarpus soyauxii	PAPILIONACEAE	11.82	1	0.13	89.83	10
Cola lizae	STERCULIACEAE	9.61	2	23.55	0.41	63
Distemonanthus bethamianus	CAESALPINIACEAE	7.49	3	0.26	28.46	20
Diospyros dendo	EBENACEAE	6.06	4	3.82	1.59	56
Dialium lopense	CAESALPINIACEAE	5.13	5	0.01	513.00	1
Pycnanthus angolensis	MYRISTICACEAE	4.91	6	0.53	9.33	29
Elaeis guineensis	PALMAE	3.70	7	0.66	5.62	35
Parkia bicolor	MIMOSACEAE	3.05	8	0.13	23.18	21
Scottellia sp	FLACOURTIACEAE	3.01	9	1.05	2.86	46
Uapaca guineensis	EUPHORBIACEAE	3.00	10	0.01	300.00	2
Pentaclethra macrophylla	MIMOSACEAE	2.58	11	1.84	1.40	57
Aucoumea klaineana	BURSERACEAE	2.41	12	8.03	0.30	68
Nauclea diderrichii	RUBIACEAE	2.30	13	0.13	17.48	24
Berlinia bracteosa	CAESALPINIACEAE	2.29	14	1.05	2.18	49
Milletia sp.	PAPILIONACEAE	2.11	15	0.13	16.04	26
Piptadeniastrum africanum	MIMOSACEAE	2.02	16	0.13	15.35	28
Blighia welwitschii	SAPINDACEAE	1.80	17	0.01	180.00	3
Celtis tessmannii	ULMACEAE	1.78	18	0.01	178.00	4
Cryptosepalum staudtii	CAESALPINIACEAE	1.67	19	0.01	167.00	5
Unknown	Unknown	1.64	20	0.01	164.00	6
Xylopia quintasii	ANNONACEAE	1.62	21	5.00	0.32	66
Gambeya africana	SAPOTACEAE	1.58	22	0.01	158.00	7
Diospyros polystemon	EBENACEAE	1.53	23	5.00	0.31	67
Dacryodes normandii	BURSERACEAE	1.10	24	0.39	2.79	47
Lecaniodiscus cupanioides	SAPINDACEAE	1.08	25	0.53	2.05	50
Ficus mucuso	MORACEAE	0.97	26	0.01	97.00	8
Heisteria parvifolia	OLACACEAE	0.93	27	0.26	3.53	44
Scyphocephalium ochocoa	MYRISTICACEAE	0.90	28	0.01	90.00	9
Irvingia gabonensis	IRVINGIACEAE	0.89	29	0.53	1.69	54
Unknown	Unknown	0.89	30	0.01	89.00	11
Ficus thongii	MORACEAE	0.88	31	0.01	88.00	12
Xylopia hypolampra	ANNONACEAE	0.85	32	2.11	0.40	64
Manniophyton	EUPHORBIACEAE	0.80	33	0.01	80.00	13
Myrianthus arboreus	MORACEAE	0.71	34	0.01	71.00	14
Irvingia grandifolia	IRVINGIACEAE	0.59	35	0.13	4.48	38
Guibortia tessmannii	CAESALPINIACEAE	0.54	36	0.01	54.00	15
Uvariastrum pierreanum	ANNONACEAE	0.47	37	0.66	0.71	59
Unknown	Unknown	0.44	38	0.01	44.00	16
Klainedoxa gabonensis	IRVINGIACEAE	0.40	39	1.18	0.34	65
Drypetes	EUPHORBIACEAE	0.36	40	0.01	36.00	17
Parkia filicoidea	MIMOSACEAE	0.36	41	0.13	2.74	48
Ficus recurvata	MORACEAE	0.33	42	0.01	33.00	18
Canarium schweinfurthii	BURSERACEAE	0.32	43	0.01	32.00	19
Eriocoelum macrocarpum	SAPINDACEAE	0.27	44	0.53	0.51	60
Sterculia tragacantha	STERCULIACEAE	0.22	45	0.13	1.67	55
Vitex sp	VERBENACEAE	0.21	46	0.01	21.00	22
Ganophyllum giganteum	SAPINDACEAE	0.18	47	0.39	0.46	62
Lophira alata	OCHNACEAE	0.18	48	8.16	0.02	75
Tetrapleura tetraptera	MIMOSACEAE	0.18	49	0.13	1.37	58
Unknown	Unknown	0.18	50	0.01	18.00	23
Hylodendron gabunense	CAESALPINIACEAE	0.17	51	0.79	0.22	71
Unknown	Unknown	0.17	52	0.01	17.00	25
Unknown	Unknown	0.16	53	0.01	16.00	27
Diospyros cf.viridicans	EBENACEAE	0.13	54	0.26	0.49	61
Baikiaea insignis	CAESALPINACEAE	0.08	55	0.01	8.00	30
Landolphia cf.heudelotii	APOCYNACEAE	0.08	56	0.01	8.00	31
Polyalthia suaveolens	ANNONACEAE	0.08	57	0.01	8.00	32
Xylopia aethiopica	ANNONACEAE	0.08	58	2.76	0.03	74
Cissus dinklagei	VITACEAE	0.07	59	0.01	7.00	33
Ongokea gore	OLACACEAE	0.07	60	0.26	0.27	69
Porterandia cladantha	RUBIACEAE	0.07	61	0.66	0.11	72
Unknown	Unknown	0.07	62	0.01	7.00	34
Anthonotha macrophylla	CAESALPINIACEAE	0.05	63	0.79	0.06	73
Unknown	Unknown	0.05	64	0.01	5.00	36
Unknown	Unknown	0.05	65	0.01	5.00	37
Ceiba pentandra	BOMBACACEAE	0.04	66	0.01	4.00	39
Unknown	Unknown	0.04	67	0.01	4.00	40
Unknown	Unknown	0.04	68	0.01	4.00	41
Unknown	Unknown	0.04	69	0.01	4.00	42
Unknown	Unknown	0.04	70	0.01	4.00	43
Monodora angolensis	ANNONACEAE	0.03	71	0.01	3.00	45
Pseudospondias microcarpa	ANACARDIACEAE	0.03	72	0.13	0.23	70
Diospyros zenkeri	EBENACEAE	0.02	73	0.01	2.00	51
Unknown	Unknown	0.02	74	0.01	2.00	53
Unknown	ANNONACEAE	0.02	75	0.01	2.00	52

Table 5.3. Mean percent of feeding scans for each family

FAMILY	Mean % feeding scans
ANACARDIACEAE	0.03
ANNONACEAE	3.15
APOCYNACEAE	0.08
BOMBACACEAE	0.04
BURSERACEAE	3.83
CAESALPINIACEAE	17.42
EBENACEAE	7.74
EUPHORBIACEAE	4.16
FLACOURTIACEAE	3.01
IRVINGIACEAE	1.88
MIMOSACEAE	8.19
MORACEAE	2.89
MYRISTICACEAE	5.81
OCHNACEAE	0.18
OLACACEAE	1.00
PALMAE	3.70
PAPILIONACEAE	13.93
RUBIACEAE	2.37
SAPINDACEAE	3.33
SAPOTACEAE	1.58
STERCULIACEAE	9.83
ULMACEAE	1.78
VERBENACEAE	0.21
VITACEAE	0.07

Table 5.4 Description of fruits observed to be eaten by grey-cheeked mangabeys

		PART EATEN		TREE SIZE	FRUIT TYPE	FRUIT SIZE	SEED SIZE	FRUIT COLOUR
Species	Family	pulp	seed					
Anthonotha macrophylla	CAESALPINIACEAE		1	M	D	VL	L	BORWN
Aucoumea klaineana	BURSERACEAE		1	L	W	M	M	BROWN
Baikiaea insignis	CAESALPINIACEAE		1	L	D	VL	VL	BROWN
Berlinia bracteosa	CAESALPINIACEAE		1	M	D	VL	L	BROWN
Blighia welwitschii	SAPINDACEAE	1		L	A	L	M	ORANGE
Canarium schweinfurthii	BURSERACEAE	1		L	S	M	M	PURPLE
Celtis tessmannii	ULMACEAE	1	1	L	S	M	M	GREEN
Cissus dinklagei	VITACEAE	1		U	S	M	M	ORANGE
Cola lizae	STERCULIACEAE	1		M	S	L	L	RED
Cryptosepalum staudtii	CAESALPINIACEAE		1	S	D	L	M	BROWN
Dacryodes buettneri	BURSERACEAE	1		L	S	M	M	PURPLE
Dialium lopense	CAESALPINIACEAE		1	L	S	S	S	BLACK
Dichapetalum sp.	EUPHORBIACEAE	1		M	S	M	S	YELLOW
Diospyros cf.viridicans	EBENACEAE	1		S	S	S	S	RED
Diospyros dendo	EBENACEAE	1	1	S	S	M	M	RED
Diospyros polystemon	EBENACEAE	1	1	M	S	M	M	RED
Diospyros zenkeri	EBENACEAE	1		S	S	S	S	BLACK
Distemonanthus bethamianus	CAESALPINIACEAE		1	L	W	L	M	BROWN
Elaeis guineensis	PALMAE	1		M	S	M	M	RED
Eriocoelum macrocarpum	SAPINDACEAE		1	M	A	L	M	RED
Ficus mucuso	MORACEAE	1		L	S	M	S	GREEN
Ficus recurvata	MORACEAE	1		L	S	M	S	GREEN
Ficus thongii	MORACEAE	1		L	S	M	S	GREEN
Gambeya africana	SAPOTACEAE	1	1	L	S	L	L	YELLOW
Ganophyllum giganteum	SAPINDACEAE	1		L	S	M	S	YELLOW
Guibortia tessmannii	CAESALPINIACEAE		1	L	A	M	M	RED
Heisteria parvifolia	OLACACEAE	1		M	S	M	S	RED
Hylodendron gabunense	CAESALPINIACEAE		1	L	W	M	M	PINK
Irvingia gabonensis	IRVINGIACEAE		1	L	S	L	L	GREEN
Irvingia grandifolia	IRVINGIACEAE		1	L	S	L	L	GREEN
Klainedoxa gabonensis	IRVINGIACEAE	1	1	L	S	L	L	GREEEN
Landolphia cf heudelotii	APOCYNACEAE	1		U	S	VL	M	YELLOW
Lecaniodiscus cupanioides	SAPINDACEAE	1		M	S	M	M	BROWN
Lophira alata	OCHNACEAE		1	L	W	M	M	PINK
Manniophyton	EUPHORBIACEAE		1	S	D	M	S	GREEN
Milletia sp.	PAPILIONACEAE		1	S	D	L	M	BROWN
Monodora angolensis	ANNONACEAE	1		S	S	L	M	GREEN
Myrianthus arboreus	MORACEAE	1		S	S	VL	M	YELLOW
Nauclea diderrichii	RUBIACEAE	1		M	S	L	S	BROWN
Ongokea gore	OLACACEAE	1		L	S	M	M	YELLOW
Parkia bicolor	MIMOSACEAE		1	L	FP	VL	M	PURPLE
Parkia filicoidea	MIMOSACEAE		1	L	FP	VL	M	GREEN
Pentaclethra macrophylla	MIMOSACEAE		1	M	D	VL	L	BROWN
Piptadeniastrum africanum	MIMOSACEAE		1	L	W	VL	M	BROWN
Polyalthia suaveolens	ANNONACEAE	1		M	S	M	M	PURPLE
Porterandia cladantha	RUBIACEAE	1		S	S	M	S	ORANGE
Pseudospondias microcarpa	ANACARDIACEAE	1		M	S	M	M	PURPLE
Pterocarpus soyauxii	PAPILIONACEAE		1	L	W	M	M	YELLOW
Pycnanthus angolensis	MYRISTICACEAE	1	1	L	A	M	M	RED
Scottellia sp	FLACOURTIACEAE	1		L	S	S	S	RED
Scyphocephalium ochocoa	MYRISTICACEAE		1	L	F	L	M	BROWN
Sterculia tragacantha	STERCULIACEAE	1		M	S	M	M	RED
Tetrapleura tetraptera	MIMOSACEAE		1	M	FP	VL	S	BROWN
Uapaca guineensis	EUPHORBIACEAE	1		M	S	M	M	GREEN
Unknown	Unknown		1	M	D	M	S	BROWN
Unknown	ANNONACEAE		1	U	S	M	S	BROWN
Unknown	Unknown		1	M	W	M	S	GREEN
Uvariastrum pierreanum	ANNONACEAE	1		M	S	VL	S	BROWN
Vitex sp	VERBENACEAE	1		S	S	M	M	BLACK
Xylopia aethiopica	ANNONACEAE	1	1	M	A	M	S	RED
Xylopia hypolampra	ANNONACEAE	1	1	L	A	M	A	RED
Xylopia quintasii	ANNONACEAE	1	1	M	A	M	S	RED

KEY:
Fruit size - S=Small(<10mm), M=Medium (10-30mm), L=Large (40-100mm), VL=Very Large (>100m)
Seed Size-S=Small (<10mm), M=Medium (10-30mm), L=Large (>30mm)
Fruit type S=succulent, F=Fibrous,A=arillate,D=Dehiscent, FP=Fleshy Pod, W=Wind dispersed, O=Other

fruits" (Gautier-Hion *et al.*, 1985b) that are red or orange with a soft juicy pulp or aril.

The most important plant species from which mangabeys ate the pulp, was from a medium height tree called *Cola lizae*. The fruit is bright crimson when ripe and the mangabeys ate the thin layer of succulent mesocarp surrounding the seed. This species is endemic to Gabon and has a limited geographical distribution (Hallé, 1987). *Cola lizae* was discussed in detail, in relation to the diet of gorillas in the Lopé Reserve by Tutin *et al.* (1991 a).

Seeds

The majority of seeds were taken from fruits that were either succulent (24%) (eg. *Celtis tessmannii*), dehiscent pods (24%)(eg. *Pentaclethra macrophylla*), and wind dispersed (21%)(eg. *Piptadeniastrum africanum*), although seeds were also eaten from fruits with fleshy pods (9%)(eg. *Parkia bicolor*), arilated fruit (18%) (eg.*Guibortia tessmannii*), and fibrous fruits (3%) (eg. *Scyphocephalium ochocoa*) (**Plate 5.1**)(**Figure 5.9**). The most important species from which mangabeys ate the seed was *Pterocarpus soyauxii* . This is a large tree found dispersed through the study area, highly visible when it has seeds or flowers due to its large canopy and yellow colouration of the seeds and fruit. The common name of this species is "Padouk" and it is logged in Gabon for tropical hard word timber.

Flowers

Although flowers were not an important part of the mangabey's diet in term of the proportion of time spent feeding on them,

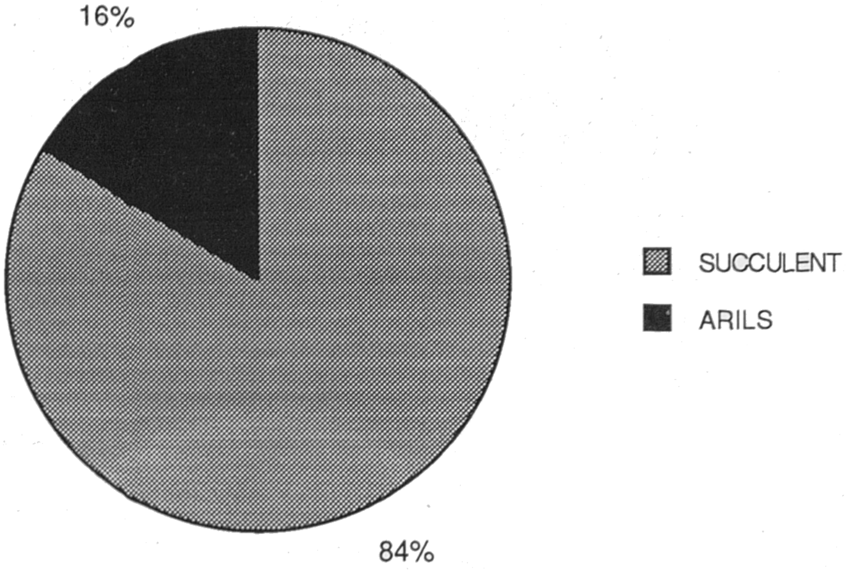


Figure 5.8 Proportion of species of each fruit-type from which pulp was eaten

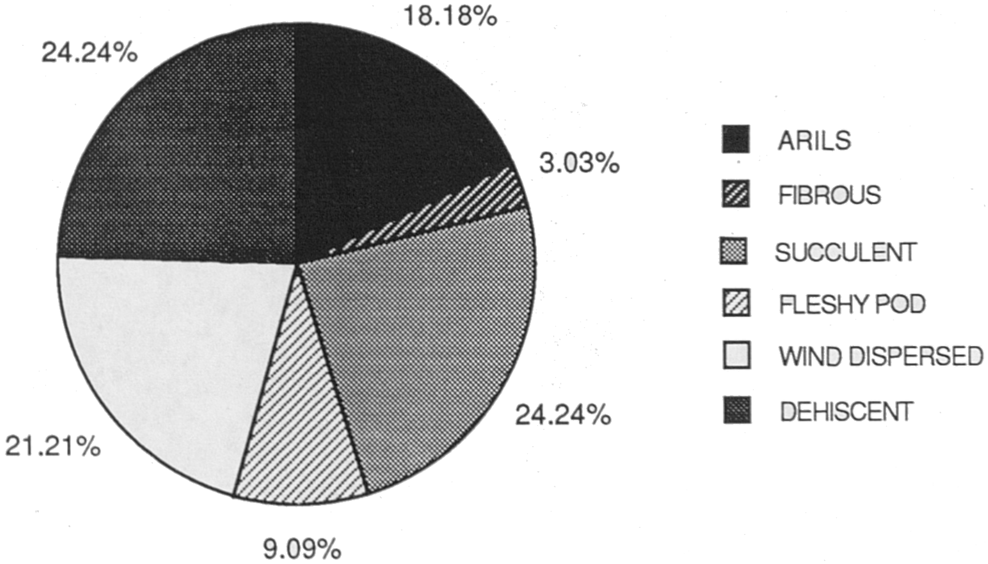


Figure 5.9 Relative number of species of each fruit-type from which seeds were eaten

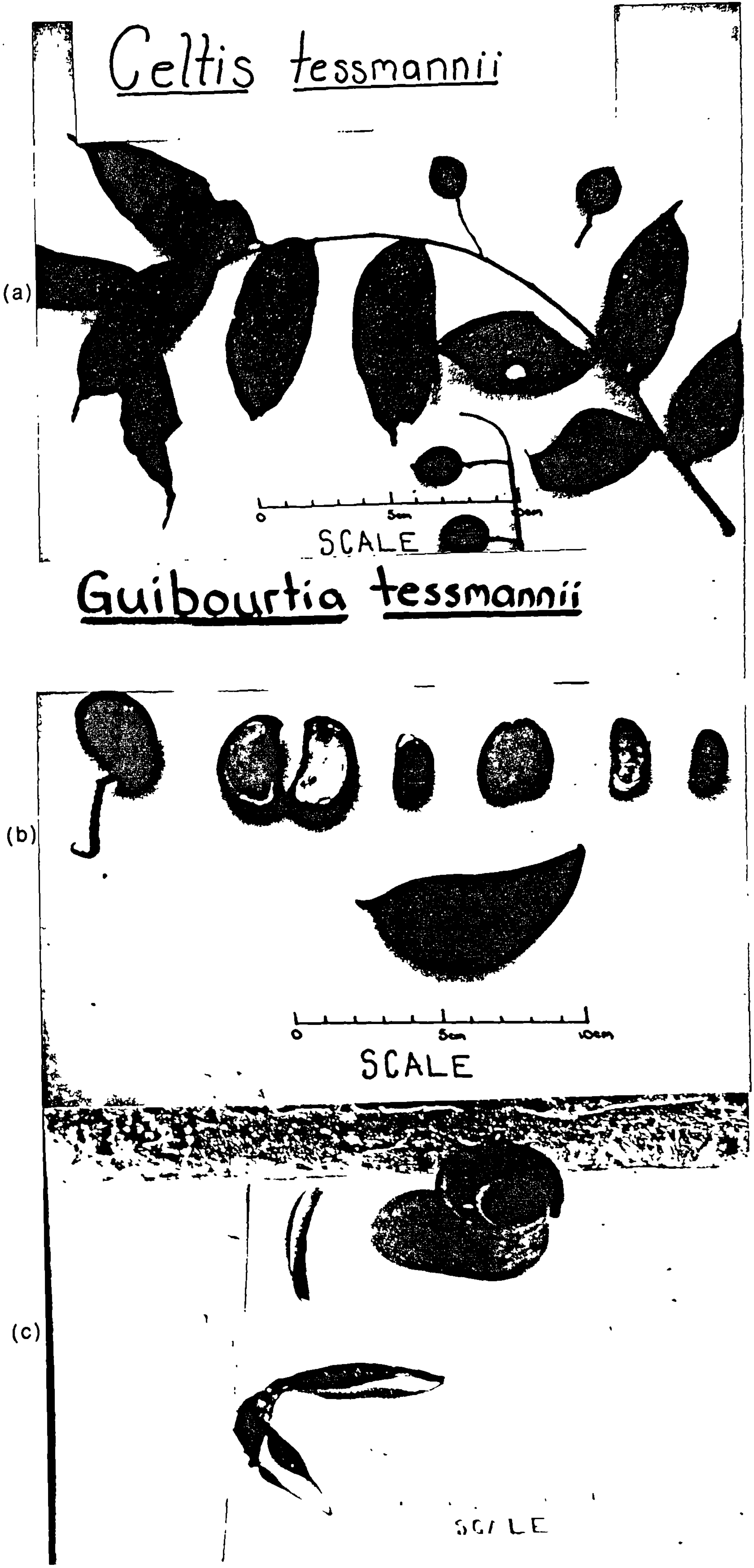


Plate 5.1. Fruit-types from which mangabey s ate the seeds (a) succulent fruit: *Celtis tessmannii*. (b) arilated fruit: *Guibortia tessmannii*. (c) dehiscent fruit: *Pentaclethra macrophylla*; wind dispersed fruit: *Piptadeniastrum africanum*, fleshy pods: *Parkia bicolor*.

they were eaten from a large number of species (n=16). The two most important species were; the yellow flowers of *Pterocarpus soyauxii* (this species is described above), and *Pentaclethra macrophylla* flowers, which were sweet tasting even to human observers.

Leaves

Leaves were not important in the diet of mangabeys in terms of the proportion of time spent feeding on them, but a large number of species were eaten (n=17). Only new leaves were eaten, probably because it is at this time that the chemical defences of the leaves are lowest. The species of leaf eaten most frequently by mangabeys were the new leaves of *Cryptosephalum staudtii* and *Milletia* sp.. *Cryptosephalum staudtii* was not observed on White's (1992) transect, but it was the second most common species in the savanna-edge transect (*Chapter Three*). Only one tree of *Milletia* sp. was encountered on White's (1992) transect, but this species was the most important species on the river-edge transect, both in terms of number of stems and and basal area (*Chapter Three*). This may have important effects on the ranging behaviour of mangabeys, as will be discussed in *Chapter Six*.

Pith

Pith was eaten from seven plant species. Pith feeding on *Cola lizae* was most frequently observed and is described below.

Insects

Mangabeys were recorded feeding on, or foraging for, insects for 589 scan. During these scan samples, at least 22 different species of plants were used. The most frequently used plant species were *Berlinia bracteosa, Cola lizae,* and *Aucoumea klaineana,* forming 68 % of all scans in which the mangabeys were observed foraging for insects (**Figure 5.10**).

Mangabeys spent 39% of all insect foraging observations, feeding on the pith of terminal branches, new leaves, flower buds, and flowers of *Berlinia bracteosa*. This species was often infested with caterpillars. It is unknown how much of the actually plant part is also ingested with the caterpillar, but because the main aim of feeding on the plant parts seemed to be to ingest the insect, all feeding observations on these parts of *Berlinia bracteosa* were recorded as "insect foraging". Ingestion of the plant parts seems to be as a by-product of feeding on the insects.

Feeding on ants on the back of *Cola lizae* leaves formed 16% of all observations of insect feeding and feeding on caterpillars inside *Aucoumea klaineana* leaves formed 13% of all insect feeding. Weaver ant (*Oecophylla longinoda*) were twice seen to be ingested by mangabeys.

Vertebrate prey

Mangabeys were never observed to feed on vertebrates. Once, however, they were observed to be mobbed by small birds, suggesting that possibly they had either eaten, or may be a potential predator of birds egg. On another occasion, an empty birds nest was found under a tree in which a mangabeys had just been foraging. Waser (1977 a) also reports that vertebrate feeding was unusual, but he did observe predation on birds eggs on one occasion, a small snake on another and also observed mobbing of mangabeys by birds.

Several times individuals were observed to poke their hands into holes and leap back as if something inside was trying to bite them. Whether they were trying to catch an animal inside the hole, was not certain.

3. Food processing

Plant food

Pulp

Fruits were selected according to ripeness in some species (eg. *Scottellia* sp.) by smelling or scrutinising individual fruits. Fruits were usually picked off the tree using the hands. Sometimes a whole branch was bitten off and carried to another tree to process individual fruits. This was especially noticed in smaller trees such as *Diospyros dendo.* Sometimes fruits were processed when they were still attached to a branch. For example, a juvenile male was observed to try to bite a *Landolphia* sp. fruit free from its source. He seemed to have difficulty in holding on to the 20 cm diameter fruit to prevent it from falling; and at the same time try to break it free from the stem. He finally bit into the fruit and ate it *in situ*, still attached to the branch.

Once fruits were freed, they were often rolled on a horizontal branch with the palm of the hand, a behaviour also observed by Chalmers (1967) and Waser(1974). Waser (1974) suggests this behaviour may be to break and separate the epicarp from the seed. Rolling of the fruit was especially noticed for *Diospyros* spp. fruits. Sometimes mangabeys would rub their hands or faces on a branch during feeding, as if to wipe off sticky or unpleasant substances. This was especially noticed during feeding on *Cola lizae*. Mangabeys bit into the red rubbery pod and then poured out the liquid inside the fruit before proceeding. If this liquid got onto their hands they tended to rub their hands vigorously up and down on the branch to wipe it off. Tutin *et al*. (1991 b) suggested that this liquid may be an ingestion inhibitor.

Some fruits had a fleshy pericarp and the seed was easily separated from the flesh (eg. *Elaeis guineensis*) and these were processed by biting off the flesh and discarding the seed, or biting pieces off the whole fruit including the seed, and ingesting both. Many fruits had a thin layer of mesocarp surrounding the stone. This had to be sucked, or scraped off, and therefore took a greater time to process (eg. *Celtis tessmannii*). These seeds were often packed into cheek pouches to be processed later (see "use of cheek pouches" below). Some seeds were too small to be separated and therefore were probably ingested with the fruit (eg.*Ficus* spp. and *Nauclea diderrichii*).

Seeds

For seeds from immature fleshy fruit, the fruit were usually bitten open and the seed picked out from the interior with the fingers and then ingested (eg. *Irvingia gabonensis, Celtis tessmannii, Diospyros polystemon*). Sometimes some of the the pulp was also ingested when a mangabey was biting through the fruit to reach the interior, but once the seed was eaten, the majority of the pulp was discarded (eg.*Scyphocephalium ochocoa*). Wind dispersed seeds such as *Pterocarpus soyauxii* seeds were generally eaten by biting the seed-part away from the wings and discarding the wings. Wind dispersed seeds were eaten at both immature and ripe stages.

Seeds from dehiscent pods and fleshy pods were also usually eaten immature. The pod was punctured with the teeth and then pried open with the hands and the seed inside ingested.

Seeds from fruit with arils (*Pycnanthus angolensis, Eriocoelum macrocarpum*) were crushed with the molars and the arils discarded (although arils were usually ingested from ripe *Pycnanthus angolensis* and seeds discarded). Seeds that were eaten ripe and the pulp discarded, included *Dialium lopense* and *Parkia bicolor*.

Flowers

Mangabeys pulled branches with flowers of *Pentaclethra macrophylla* towards themselves and then placed the branch between the lips and pulled it in a horizontal fashion, stripping the flowers off the branch. Flowers of *Pterocarpus soyauxii* were either picked off branches with the fingers and placed into the mouth, or picked off with the lips. Other flowers were generally pulled off the branch with the teeth or lips.

Leaves

Leaves were generally selected with the fingers, then plucked off the branch and placed in the mouth and ingested.

Pith

For both of the unknown species of pith eaten, and *Cola lizae*, the technique for extracting the pith was similar. Usually young trees no more than 12 cm dbh were selected. Mangabeys sat at the top of the tree and pulled apart the stems of the leaves to split the young trunk of the tree and reach the pithy inside. A chunk of about 10 cm long would then be bitten off and held in the hands and completely consumed.

Insects

Caterpillars (50%) and ants (17%) were most frequently eaten (**Figure 5.11**). Caterpillars from *Aucoumea klaineana* leaves were about 1 mm thick and 1 cm long. Caterpillars from *Berlinia bracteosa* were slightly thicker and about 3 cm long.

Mangabeys used various substrates to forage for insects (**Figure 5.12**). The most frequent substrate used were leaves (33%). For example, ants were picked off the back of *Cola lizae* leaves with the fingers and then placed into the mouth. Alternatively, insects were licked directly off the leaves. Some leaves of *Aucoumea klaineana* were adhered together with larval silk, containing caterpillars inside. Mangabeys were observed to pull a leaf off the tree, open it and lick the interior and then drop the leaf.

Weaver ant nests are found between leaves from trees or herbaceous vegetation. Mangabeys were observed to peel the leaves apart and lick the interior and then quickly discard the leaves, leaping back up again higher into the tree. Mangabeys were not observed either to crush the ants before eating them, as do chimpanzees, or ingests part of the nests as has been observed for gorillas at Lopé (Tutin and Fernandez, 1992). In both instances the nests were in herbaceous vegetation and the mangabeys descended to less than 2 m to pick and to process the nests. Mangabeys were twice seen foraging through leaf litter on the ground, presumably looking for insects under the leaves. On both occasions, nearly the whole group descended either to the ground or to less than 5 m in trees.

Mangabeys were frequently seen pulling strips of bark off

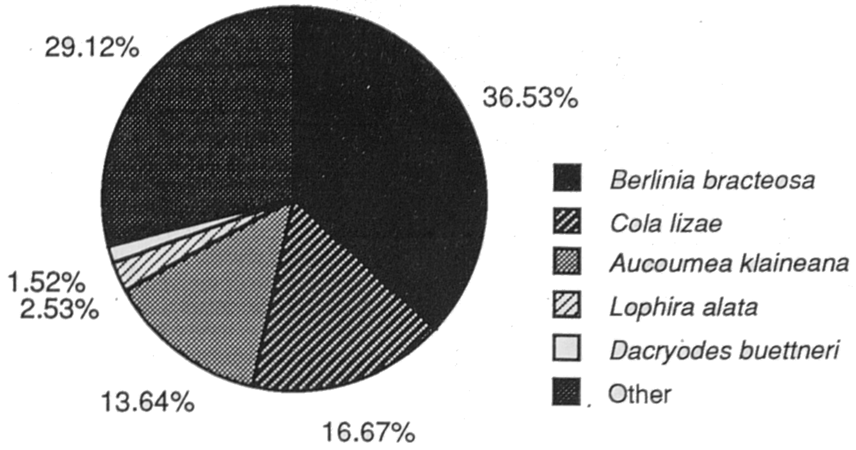


Figure 5.10 Percent of scans that each plant species were used for foraging for insects

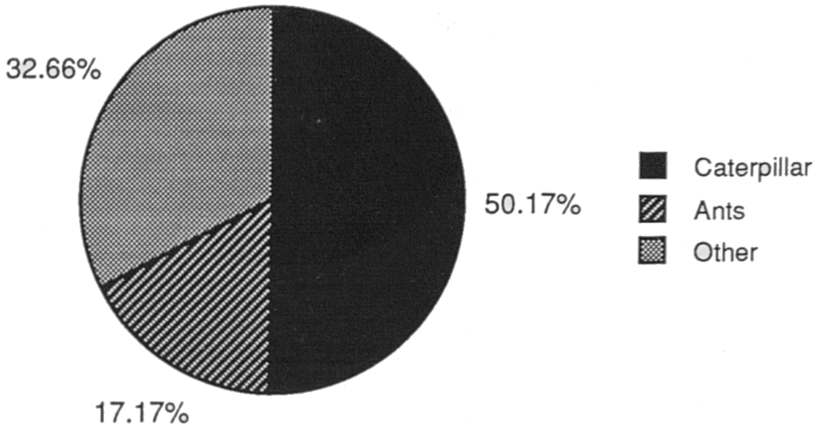


Figure 5.11. Percent of scans that mangabeys fed on each type of insect

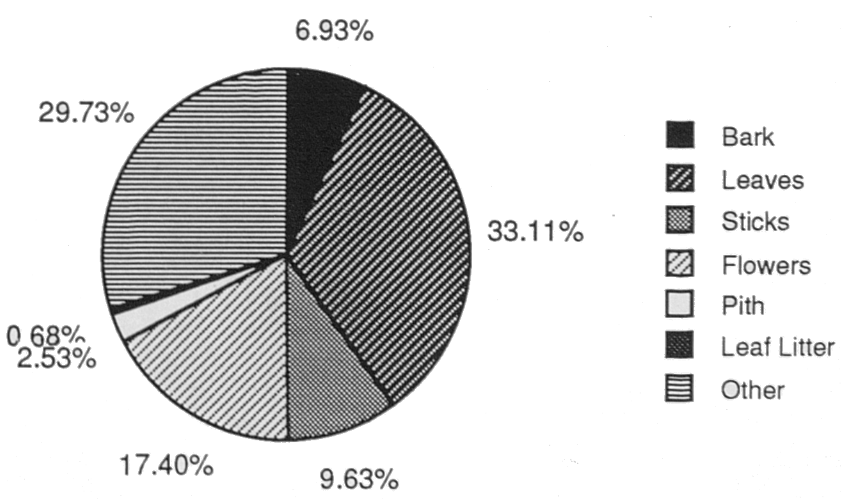


Figure 5.12 Percent of scans that each substrate was used for foraging for insects

trunks of trees and then picking off exposed insects under the bark. The bark of live trees (especially *Xylopia quintasii*) and dead or dying trees was pulled off to reach insects underneath (**Plate 5.2**). Insect infested dead sticks or branches were broken off a tree and then worked on for insects, either by poking a finger or tongue into the holes or breaking the stick even further to expose insects (usually ants) inside. The terminal branches of *Berlinia bracteosa* were ripped apart to obtain the caterpillars infesting this species. Flower buds of, for example *Berlinia bracteosa* were ripped apart to get to the caterpillars inside.

Fruit that the mangabeys selected were often insect-infested. In this case I scored feeding on the fruit-part, but probably both the insect and the fruit were equally important. This was most noticeable in *Canarium schweinfurthii* and *Dacryodes normandii*. Mangabeys selected insect infested fruits, ripe or immature, and bit out the part containing the insect and discarded the rest of the fruit.

Attempts at catching flying insects were seen several times, with mangabeys making swipes with their hands into the air and returning a closed fist to the mouth. These types of insects, however, were never identified.

Water

Drinking was recorded during 11 scans. All drinking was from depressions or holes in horizontal branches where rain water had remained. Two motor patterns were used: (1) lowering the head into the depression and drinking from the lips, or (2) putting the hand into the depression and licking or sucking water from the hand. Most of these observations were of drinking from one species: *Distemonanthus bethamianus*. It may be that (a) this species most frequently forms depressions or has holes in its branches (b) some nutrient may seep from the tree into the water.

During March 1992 when rainfall was low, mangabeys were observed twice in a polyspecific group on the ground. Vegetation was too dense to observe what they were doing, but post contact investigation revealed water splashed around the sides of small stream, suggesting that they had been drinking.

Use of cheek pouches

Cheek pouches were often filled with fruit, seeds, and leaves or stems while mangabeys were feeding, and then processed later, often in another tree (**Plate 5.3**). Although no quantitative data were taken on the use of cheek pouches, descriptive comments are made below.

The use of cheek-pouches appeared to be more frequent in mangabeys, than in the sympatric *Cercopithecus* spp., but this may be because mangabey's cheek pouches are larger and therefore more visible. Upon entering a tree, mangabeys often filled their cheek pouches first before beginning to process and swallow food. Food in the cheek pouches was either processed eventually *in situ* or mangabeys moved to another tree to process it. Use of cheek pouches seemed to depend on several factors:

(a) Intraspecific competition: Mangabeys used their cheek pouches more frequently (i) in smaller trees where only a few individuals could feed at a time, or (ii) for highly valued but uncommon foods, (eg.*Landolphia* sp. and *Myrianthus arboreus*).

(b) Characteristics of the fruit: If foods took a long time to process (eg. separating aril or flesh from the seed), then

Plate 5.2 Grey-cheeked mangabey feeding on insects underneath the bark of a dead tree.

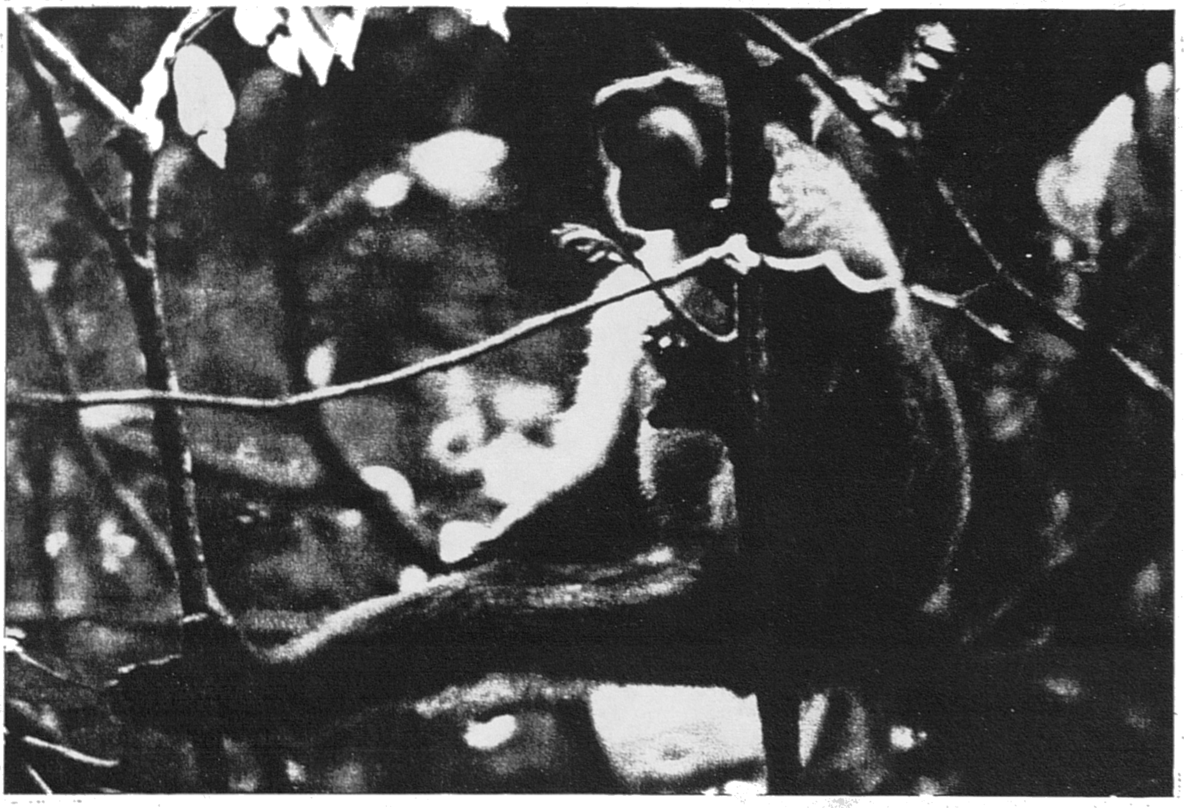


Plate 5.3 Grey-cheeked mangabey with distended cheek pouches. (Photo courtesy of Karen McDonald).

the use of cheek pouches allowed them to maximise the amount of food that they could harvest per unit time.

(c) Predator avoidance: If trees were low or cover either very dense or very open, then mangabeys seemed to prefer to harvest as much food as possible in a short period of time, and then process the food in another tree.

Fruits were pushed out of of the cheek pouches either by manipulation within the mouth without the hands, or with the back of the hand or wrist, pushing against the outside of the cheek and pushing the fruit from the pouch into the mouth.

Although mangabeys are seed predators for many species, they may act as important dispersal agents for others. Seeds can be dispersed by animals in a variety of ways, the most common being that the seed is ingested whole by the animal. The seed then passes intact through the digestive system of the animal and then is defecated later, usually at a distance from the original source. This method has two advantages. Firstly, the seeds is taken away from the mother tree, and therefore does not compete for resources such as light or nutrients. Secondly, the seed is deposited in the dung, which may provide a beneficial environment in which to grow (Tutin *et al*., 1991 b).

In mangabeys, some seeds may pass through the gut intact, such as those from *Ficus* spp. But mangabeys do not actually swallow many seeds whole. They *do*, however, carry fruit away from the seed's source in their cheek pouches, therefore enhancing its chance for survival. Advantages to dispersal in this way is that the seeds are scattered instead of being deposited in a clump (Tutin *et al*. 1991 b). Mangabeys may be important dispersers for many species in this way.

4. Monthly overlap in species eaten

The mean dietary overlap over all months was 13% (S.D.=12%, n=105, range:0-53%) (**Table 5.5**). The overlap between consecutive months (mean=28%, S.D.=10%, n=13, range:7-53%) was higher than between non consecutive months (mean=11%, S.D.=10%, n=92, range:0-52%), although this difference was not significant (Mann-Whitney *U*-test=180, n=13 and 92, p=0.48). Overlap between April, May, June in 1991 and April, May, June, 1992 (mean=16%, S.D.=14%, n=9, range:6-52%) was similar to overlap between other months (mean=16%, S.D.=12%, n=96, range:0-53%).

5. Dietary diversity and evenness

The 'top 10' food species in the mangabey's diet made up 59% of all feeding scans in the present study. Using the Shannon Diversity Index, annual dietary diversity in this study was 3.46 (range: 1.41 in June 1992 to 2.73 in November 1991). Dietary diversity was lowest during the months of June, July and August 1992 and highest for November 1991, and January, February 1992. The diet of the mangabeys was most diverse during the months in the long rainy season and least diverse during the long dry season (**Figure 5.13**). This may have been affected by the aseasonal fruiting of *Diospyros dendo* and *Pterocarpus soyauxii* during the long dry season in 1992. Because these species were preferred food items even in the long rainy season and because the availability of other fruits was limited, mangabeys may have specialised on these species, therefore decreasing the diversity indexes. There was, however, also low dietary diversity in June 1991 indicating that this may be a regular pattern.

In order to test if dietary diversity was related to the availability of ripe fruit, these variables were tested for

Table 5.5 Monthly percent of overlap in species eaten by grey cheeked mangabeys.

MONTH	May-91	Jun-91	Sep-91	Oct-91	Nov-91	Dec-91	Jan-92	Feb-92	Mar-92	Apr-92	May-92	Jun-92	Jul-92	Aug-92
Apr-91	11	12	0	2	15	15	0	4	7	11	11	12	7	10
May-91		15	12	8	16	8	10	17	19	20	12	52	17	26
Jun-91			0	6	8	6	6	7	7	9	9	6	9	3
Sep-91				29	3	0	0	3	4	3	3	8	5	6
Oct-91					22	10	1	1	8	3	2	7	4	2
Nov-91						30	7	10	12	10	8	18	10	9
Dec-91							7	15	22	6	0	8	1	3
Jan-92								25	23	14	2	0	5	0
Feb-92									53	38	17	18	26	21
Mar-92										50	13	22	24	21
Apr-92											39	22	19	17
May-92												15	26	24
Jun-92													42	31
Jul-92														32

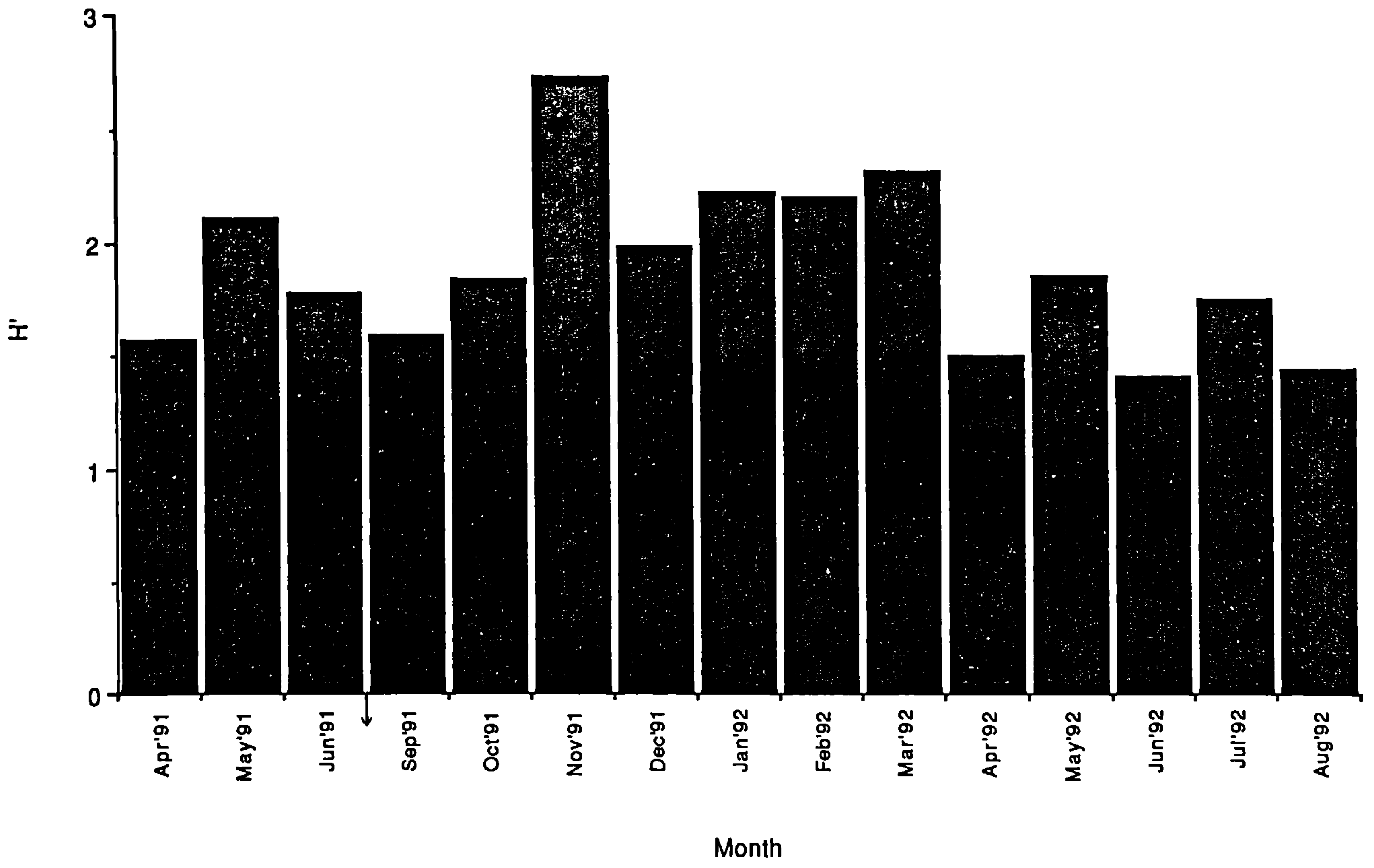


Figure 5.13 Shannon index of diversity for plant species eaten by grey-cheeked mangabeys from April 1991 to August 1992.

correlation. From September 1991 to September 1992 dietary diversity was found to be significantly correlated with the availability of ripe fruit (r_s=0.61, n=12, p=0.04). This relationship still existed from April 1991 to September 1992 but was only significant at the 10% level of significance (minimum temperature, r_s=0.47, n=15, p=0.08; fruit availability r_s=0.46, n=15, p=0.08).

C.FACTORS THAT MAY INFLUENCE DIET

There are three main factors which may influence the diet. These are discussed below.

1.Availability

(a)Availability in time

High diversity does not necessarily mean that the mangabeys were less selective as to which species they ate. It may simply mean that they ate what foods were available. In order to test if foods were eaten in relation to their availability in time, the proportion of time that the mangabeys spent feeding on a species was correlated with its fruit availability (see *Chapter Three*). This was done for the plant species included in the "top 10" in terms of feeding time. Phenological data were available for all of these species, except *Distemonanthus bethamianus, Elaeis guineensis* and *Scottellia* sp.. The only significant correlation was between the proportion of time spent feeding on *Diospyros dendo* and the availability of ripe fruit of this species, and this relationship was weak (r_s=0.48, n=15, p=0.07).

(b)Availability in space

Selectivity is not only affected by availability in time, but also by availability in space. In order to examine if mangabeys ate species in relation to their frequency in the study area, the percent of time spent feeding on the 'top 10' species in the mangabey's diet was tested for correlation with its relative frequency on the SEGC transect (White, 1992).

This method assumes that the amount of food available per tree is the same between species. This can be a dangerous assumption because the quantity of fruit a species produces may vary greatly. Plants just over 10 cm dbh may not be reproductively active. Some may be monecious (eg. *Diospyros* spp.), fruit crop size may vary depending on the strategy of the species, (*i.e.* some species produce abundant small fruit, eg. *Ongokea gore*, and others produce few, large fruit, eg. *Landolphia* sp.). It does, however, give a good general indication of selectivity. A significant correlation was found between the percent of time spent feeding on species, and the percent of those species on the transect (r_S=0.37, n=75, p<0.01), indicating that mangabeys were selecting species according to their representation in the environment.

A selectivity ratio was calculated by dividing the percent of feeding observations on each species, by the percent that the species represented on the transect in terms of number of stems (**Table 5.2**). When the plant species was not encountered on the SEGC transect, it was given a value of 0.01% since the denominator could not be zero. Many foods eaten from plant species that were common in the study area, dropped in rank of importance. The most spectacular examples of this were species *Cola lizae* which dropped in rank from 2nd to 63rd and

Diospyros dendo which dropped in rank from 4th to 56th most important species. Other foods that were eaten from relatively rare trees, rose in rank, such as *Blighia welwitschii* and *Celtis tessmannii*. Species that ranked among the 'top 10' most important species both in terms of feeding time and selectivity index were *Dialium lopense, Uapaca guineensis* and *Pterocarpus soyauxii*.

2. Chemical composition

Although mangabeys ate many foods in relation to their availability in the environment, as shown above, some foods stand out as selected positively (eg. *Dialium lopense, Uapaca guineensis* and *Pterocarpus soyauxii*). The key to understanding why certain foods are selected may lie in their chemical composition. Data on the chemical composition of some foods at Lopé are available from Rogers *et al*. (1990).

Examining the seeds included in the 'top 10' food species; the chemical composition of *Dialium lopense* seeds stands out because they have the second highest level of crude protein than all the other 186 food parts of 71 species analysed. *Parkia bicolor* seeds were the sixth highest in protein. The unripe seeds of *Diospyros dendo* were not outstanding in the amount of protein, sugar or lipid.

The ripe fruit pulp *Cola lizae* was the fifth highest in water soluble carbohydrates, and the ripe pulp of *Uapaca guineensis* was the 10th highest. Arils of *Elaeis guineensis* had the highest, and arils of *Pycnanthus angolensis* had the fourth highest, lipid content,. Although analysis was not available for *Pterocarpus soyauxii* from Rogers *et al*., (1990), information on the chemical composition of the seeds from this species is available from Harrison (unpublished data). In his analysis *Pterocarpus soyauxii* was found have eighth highest lipid content of 47 plant parts analysed. No data was available for *Distemonanthus bethamianus or Scottellia* sp..

Mangabeys seem to be able to tolerate high levels of tannins (eg. in the ripe flesh of *Myrianthus arboreus* and in the unripe seeds of *Diospyros dendo*). Overall, comparison between seeds and fruit eaten by mangabeys show that mangabeys are selecting seeds significantly higher in protein content than fruits (Mann Whitney *U*-test=2, n=8 and 9, p=0.02), and fruits slightly higher in fibre than the seeds (Mann Whitney *U*-test=6, n=8 and 8, p=0.09).

Comparisons of the chemical composition of the pulp of fruits eaten by mangabeys with the pulp of favoured gorilla fruits suggests that mangabeys selected a significantly higher amount of crude lipids (Mann Whitney *U*-test= 8, n=9 and 10, p=0.02). Comparisons of the chemical composition of seeds that mangabeys ate, with favoured gorilla seeds, suggests that mangabeys selected seeds slightly higher in protein than gorillas (Mann Whitney *U*-test=5, n=8 and 10, p=0.06) and slightly lower in tannins (Mann Whitney *U*-test=6, n= 8 and 10, p=0.09).

Certain foods may have been selected against because of their chemical properties. For example, ripe fruit from *Pentadesma butyracea* have alkaloids that may be avoided by mangabeys.*Pentadesma butyracea* was one of the 'top 10' foods of gorillas (Tutin and Fernandez, 1993 a), yet mangabeys were never observed to eat this species during the present study.

3. Diet overlap and competition with other primate species

There is large overlap between the species eaten for all diurnal primates in the Lopé (**Appendix 5.1**). Overlap in foods eaten is the greatest for the category of pulp (64%) then seeds (51%), leaves (38%), stems and pith (27%) and flowers (15%). *Cola lizae, Pterocarpus soyauxii, Diospyros dendo, Dialium lopense,* (all plant species included in the 'top 10' most important mangabey foods in terms of feeding time), were eaten by all eight diurnal species of primates at SEGC. In terms of plant part eaten, mangabeys were most similar in their diet to colobus because both primates spent a large proportion of their time feeding on seeds (**Figure 5.14**).

Because studies of the diets of sympatric gorillas and chimpanzees at SEGC have been ongoing since 1984, mangabeys can be compared in more detail to these species. Gorillas and/or chimpanzees feed on at least 72% of the species that mangabeys also utilised as a food source. Overlap between mangabeys and chimpanzees, and between gorillas and chimpanzees in the species eaten was identical (42% of species in the mangabey's diet).

Overlap in the plant species eaten by mangabeys and chimpanzees was higher for fruit pulp and flowers, but higher between mangabeys and gorillas for seeds and leaves (**Table 5.6**). Tutin and Fernandez (1993 a) classified certain plant species as "important " in the diet of gorillas and chimpanzees. The fruit species from which the mangabeys ate immature pulp or seeds, were generally those fruit that were classified a "important" in the diet of gorillas or chimpanzees or both. These included, *Gambeya africana, Cola lizae, Diospyros dendo, Diospyros polystemon, Celtis tessmannii, Irvingia gabonensis,*

Table 5.6 Percent of species eaten by grey-cheeked mangabeys also observed to be eaten by gorillas and chimpanzees, for each type of food.

PLANT PART	*Gorilla g. gorilla* % SPECIES OVERLAP	*Pan t.troglodytes* % SPECIES OVERLAP
PULP	70	78
SEED	26	18
FLOWERS	13	25
NEW LEAVES	40	20
OVERALL	42	42

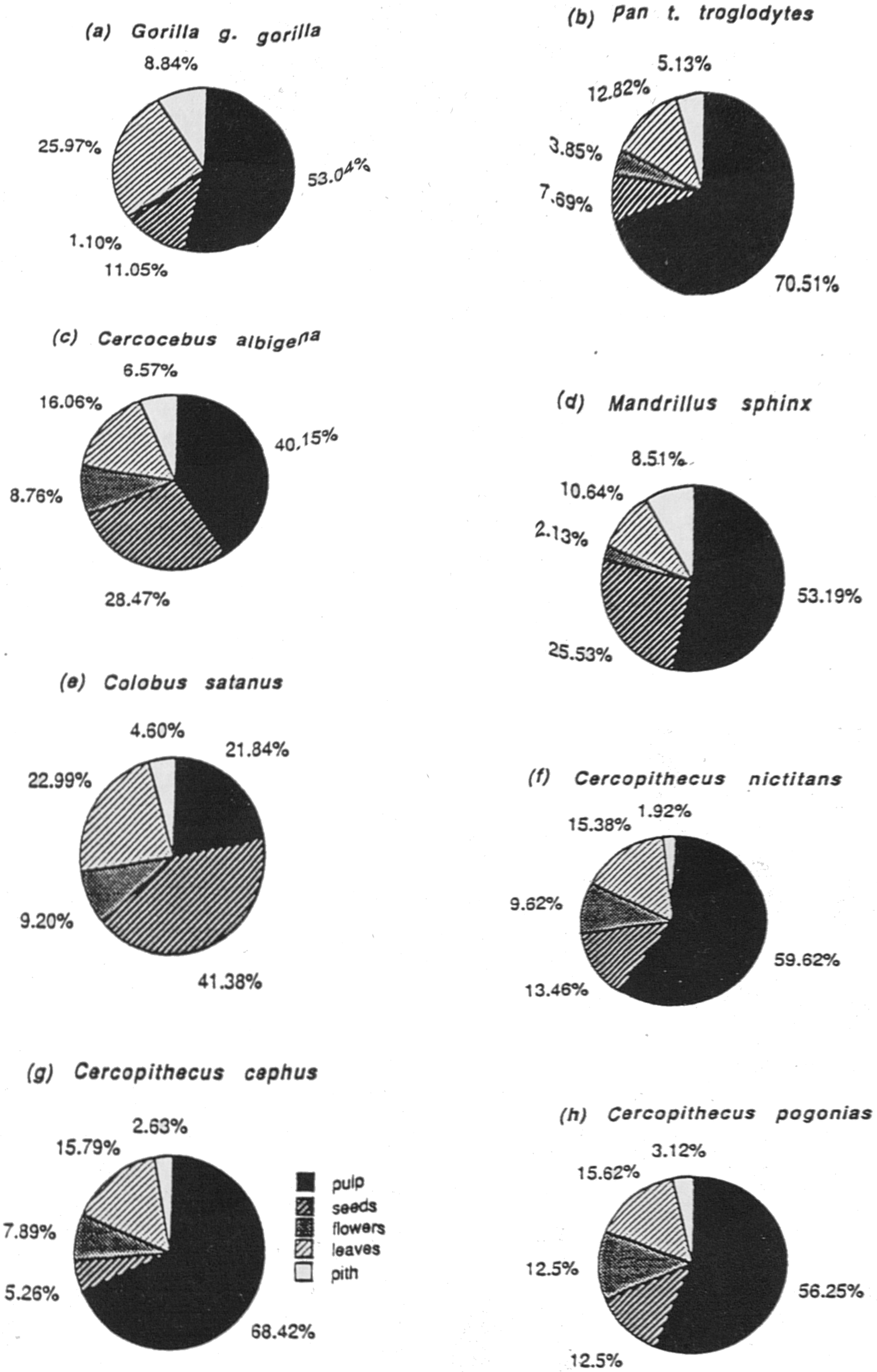


Figure 5.14. Proportion of food species eaten in each category for: gorillas (*Gorilla g.gorilla*); chimpanzees (*Pan t.troglodytes*); grey-cheeked mangabeys (*Cercocebus albigena*); mandrills (*Mandrillus sphinx*); black colobus (*Colobus satanus*); spot-nosed guenons (*Cercopithecus nictitans*); moustached guenons (*Cercopithecus cephus*) and crowned guenons (*Cercopithecus pogonias*).

and *Pycnanthus angolensis*. In addition, all of these fruits are eaten by five or more primate species at SEGC, suggesting that competition for these food species may have been high.

DISCUSSION

A. ACTIVITY BUDGETS

The proportion of time spent feeding overall in the present study (53%), was greater than that observed by both Waser(1977a) (42.5%), and Chalmers (1968 b) (46%). This could merely be a reflection of differences in methodology. Alternatively, the overall proportion of time mangabeys spent feeding in the present study may have been inflated due to the increase in time spent feeding during the long dry season. Mangabeys may have spent more time searching for food in the long dry season because food was scarce. In addition mangabeys may have spent more time feeding, because their diet consisted mainly of seeds during this time. Although seeds are high in protein, they are not as high in sugars and not as easily digested. It therefore may have been necessary for mangabeys to eat larger quantities of seeds to meet their energetic requirements. Because seeds often had to be separated from the surrounding unripe pulp, they may have also required a greater processing time.

Overall, the proportion of time that mangabeys spent foraging for insects in the present study (10%) was the same as that observed by Waser (1977) (10%).

B. DIET

The number of species observed to be eaten by mangabeys was greater than all other studies of mangabeys. Waser (1974) observed mangabeys to feed on 48 species plus 14 unknown species, Wallis (1979) observed 51 species, Freeland (1977) observed 29 species and Cashner (1972) observed about 35 species of plant to be used by mangabey as a source of food (**Table 5.7**). The proportion of fruit in the diet of the mangabeys in this study was comparable to that observed in other studies (**Table 5.8**), however, when the *part* of the fruit that is ingested is considered, *seeds* play a more important role in the diet of mangabeys at Lopé, both in terms of the proportion of time spent feeding on them, and in number of species eaten, compared to grey-cheeked mangabeys studied in Uganda (Chalmers 1967, Waser 1977a, Wallis 1979, Freeland 1977) and to mangabeys in northern Gabon (Gautier-Hion, 1977). Chalmers (1968 b) provides a short list of 11 of the most important foods eaten by mangabeys and no seeds are listed. Waser (1974) states that "seed-eating is not the rule" and that " although seed eating involves a fairly large number of species, with the exception of *Diospyros* these are not common items in the diet". Likewise, Wallis (1979) found that seeds only formed 7.9% of vegetable items in the mangabey's diet and that mangabeys only fed on two species to "any great extent". He found that seeds were eaten most frequently from unripe fruits and that "dry seeds" formed a very small part of the diet. Gautier-Hion (1977) reports that at Makokou in northern Gabon, it is usually fruit pulp, then arils and less often the seeds that are ingested by mangabeys.

The finding that seeds form a large proportion of grey-cheeked mangabey's feeding time in this study contradicts the hypothesis proposed by Gautier-Hion (1983) that primates in western African forests generally have more pulp in their diet than primates in eastern African forests. There are several possible explanations for this.

Table 5.7 Plant species observed to be eaten by grey-cheeked mangabeys in other studies

Malbrant et MacLatchy (1949)
Musanga sp.
Strophanthus sp.

Chalmers (1968)
Albizzia grandebracteata
Cassia sp.
Celtis duransii
Celtis zenkeri
cultivated maize
Ficus sp.
Maesopsis eminnii
Phoenix reclinata
Pycnanthus angolensis
Pygeum africanum
Sapium ellipticum
sweet potato
Treculia africana

Jones and Sabater(1968)
Anthrocaryon klaineanum
Caloncoba welwitschii
Conopharyngi crassa
Dacryodes macrophylla
Grewia coriaceae
Poga oloesa
Pycnanthus angolensis
Trichoschypha ferruginea
Uapaca guineensis
Xylopia quintasii

Cashner(1972)
Blighia unijuga
Celtis africana
Celtis durandii
Croton macrostchyes
Dacryodes macrophylla
Ficus dawei
Irvingia gabonensis
Manikara fouilloyana
Newtonia buchanini
Pachypodanthium staudtii
Piptadeniastrum mildbraedii
Premnegolensis
Pterygota mildbraedii
Pycnanthus angolensis
Ressantia sp.
Trichoscypha ferruginea
Uvariopsis congensis

Waser(1974)
Acanthaceae
Adenodolichos paniculatus
Albizia grandibracteata
Aningeria altissima
Aphania senegalensis
Apodytes dimidiata
Asclepidaceae
Balanites wilsoniana
Bersama abysinica
Blighia unijugata
Bosquela phoberos
Cassipourea ruwensorensis
Celtis africana
Celtis durandii
Chaetacme aristata
Chrysophyllum gorungosanum
Cordia millenii
Cyphomandra betacea
Diospyros abyssinica
Dracaena steudneri
Erythrina eriobotryoides
Fagaropsis angolensis
Ficus brachylepis
Ficus capensis
Ficus congensis
Ficus eribotryoides
Ficus exasperata
Ficus sp
Ficus sp.
Funtumia latifolia
Harungana madagascensis
Linociera johnsonii
Loranthus aurantracus
Lovoa swynnertoni
Markhamia platycalyx
Millettia dura
Mimusops bagshawei
Monodora myristica
Neoboutonia macocalyx
Newtonia buchanani
Olea welwitschii
Pancova turbinata
Parinari excelsa
Platycerium elephantotis
Premna angolensis
Pseudospondias microcarpa
Pterygota mildbraedii
Reissantia parvifolia
Ritchiea albersii
Spathodea niotica
Strombosia congensis
Strychnos mitis
Symphonia globulifera
Tabernaemontana holstii
Teclea nobilis
Tremaorientalis
Trichilia sp.
Tridactyle bicausata
Urera cmerooenensis
Uvariopsis congensis
Vangueria apiculata

Wallis(1979)
Albezia grandibracteata
Blighia unijugata
Celtis africana
Celtis durandii
Chrysophyllum albedum
Combretum sp.
Conopharangia sp.
Cordia abyssinica
Cordia cordifolia
Davyalis macrocalyx
Dictyandra aborescens
Diospyros abyssinica
Dombeya mukole
Erythrina abyssinica
Erythrina excelsa
Fagaropsis angolensis
Fern
Ficus brachyolipus
Ficus dawei
Ficus exasperata
Ficus mucosa
Ficus natalensis
Ficus sp.
Ficus vallischodea
Fungus sp.
Funtamia latifolia
Harrisonia abyssinica
Liana
Linociera johnsonii
Lovoa swynnertonii
Milletia dura
Miniusops bagshawei
Monodor myristica
Morus sp.
Olea welwitschii
Parinari excelsa
Parkia sp.
Piptadeniastrum africanum
Platycerium elephantotis
Premna angolensis
Pseudospondias microcarpa
Pteragota mildbraedii
Randia urcelliformes
Reissantia parvifolia
Spathoddea nilotica
Strombosia scheffleri
Unknown
Unknown
Uvariopsis congensis
Vine
Warburgia ugandensis

Gautier-Hion(1977)
Cissus dinklagei
Coelocaryon preussii
Pycnanthus angolensis
Uapaca sp.

Freeland(1979)
Aningeria altissima
Aphania senegalensis
Blighia unijugata
Bosquela phoberos
Celtis africana
Celtis durandii
Chrysophyllum albidum
Croton macrostachys
Erythina abyssinica
Fagaropsis angolensis
Ficus brachylepis
Ficus dawei
Ficus exasperata
Ficus natalensis
Ficus sp.
Ficus vallis-choudae
Linociera johnsonii
Maonodora myristica
Milletia dura
Mimusops bagwhawai
Morus lactea
Olea welwitschii
Orchid
Pancovia turbinata
Plyycerium sp.
Premna angolensis
Ressantia sp.
Spathodea nilotica
Unknown
Unknown vine
Unknown vine
Uvariopsis congensis
Warburgia ugandensis

Mitani(1991)
Anthonotha cf.cladantha
Eribroma oblongum
Grewia coroacea
Sacoglottis gabonensis
Xylopia quintasii

Table 5.8 Proportion of the diet of grey-cheeked mangabeys that each food-type was observed to be eaten, in the present and other studies.

	PART				
STUDY	FRUIT	LEAVES	FLOWERS	INSECTS	OTHER
Present study	66	4	2	28	0
Waser(1974)	59	5	3	26	3
Wallis(1978)	61	13	0	12	1
Struhsaker(1978)	59	8	0	0	0
Freeland (1979)	58	10	0	25	2
Gautier-Hion (1980)	83	6	5	6	0
Mitani (1991)	100	0	0	0	0

Hypothesis I: Availability in space

(a) There are less succulent fruits available at Lopé

Gautier-Hion (1983) proposed that monkeys of western African rain forests in Gabon eat mainly pulp because there are more fleshy fruit available. Their conclusions were based on data from Makokou, situated 200 km to the north-east of Lopé. It is possible that forests at Lopé are different, with less availability succulent fruit. This hypothesis, however, is refuted for two main reasons:

(1) White (1992) found that succulent fruits formed 61% of fruits at Lopé, a similar figure to the proportion of succulent fruits at Makokou in Gabon and Kibale in Uganda (about 60% at both sites, Maisels and Gautier-Hion, *in press*).

(2) Gorillas at Lopé have been observed to have a larger proportion of succulent fruit in their diet than gorillas studied elsewhere (Williamson *et al.*, 1990), which suggests that succulent fruit is not limited in the environment at Lopé.

(b) There are more seed-bearing trees at Lopé

Tree species bearing non-succulent fruits, such as those from the family Leguminosae (subfamilies: Caesalpiniaceae, Papilionaceae and Mimosaceae), are more important at Lopé in terms of number of stems (9%) (White, 192) than at Kibale (3%) (Struhsaker, 1975), therefore this may partially explain why mangabeys have a larger proportion of seeds in their diet at Lopé than at Kibale. However, there are an even greater proportion of trees from the family Leguminosae at Makokou (22.5%) (Reitsma, 1988) than at both Lopé and Kibale, and it is at Makokou where Gautier-Hion *et al.*, observed guenons to be more frugivorous, so there are obviously other factors involved.

(c) There are more seed-bearing trees in the home range of the study group

Maisels *et al.*,(in press) suggested a negative correlation between soil pH and the frequency of Caesalpiniodeae, a family of trees which produces non-succulent fruits. Caesalpiniaceae was not the dominant family on the SEGC transect (White, 1992), and was found in even lower proportions in the habitat at Lopé (5% of plants, White, 1992) than in Makokou (20.3%, Maisels and Gautier-Hion, in press). However, data from transect conducted along the river-edge and savanna-edge within the home range of the study group of mangabeys at Lopé (*Chapter Three*) showed that in these habitats, Caesalpiniaceae was in fact the dominant family. It is possible that because the home range of the study group of mangabeys bordered on the savanna edge and was traversed by a river, that for this particular group of mangabeys seed eating was important because there was less fleshy fruit available due to the location of their home range. Perhaps seeds would be less important for groups of mangabeys living further into the forest. This seems an unlikely explanation, however, given that the river-edge and savanna-edge habitats did not form a very large proportion of their home range (*see Chapter 6*).

(d) Tree density and diversity is lower at Lopé

In *Chapter Three* it was shown that tree density was higher at Ngogo than at Lopé. This may result in higher food densities at Ngogo, and therefore mangabeys may have been able to be more selective in their diet, and chose to eat succulent fruits. However, tree density was lower at Kanyawara than at Lopé, and mangabeys at Kanyawara ate very few seed, suggesting that there must be other factors involved other than trees density. In *Chapter Three* it was also shown that tree species diversity was greater at Kanyawara than at Lopé. Lower plant diversity may force mangabeys at Lopé to be less selective, and therefore include other items, such as seeds, in their diet.

Hypothesis II: Availability in time

(a) Fruit availability is more seasonal at Lopé

Availability of food, is not only affected by its spatial distribution, but also by its temporal distribution. Previous studies on mangabeys have found little seasonal dietary variation (eg. Waser, 1974). In the present study, however, there were large seasonal variation in terms of the proportions of food categories eaten, dietary diversity and food species eaten.

In *Chapter Three* it was shown that, forests are highly seasonal at Lopé and it is during the long dry season when the availability of ripe fruit is lowest. Seeds did not form the greatest proportion of the mangabeys feeding time during all months of the study. Mangabeys spent the largest proportion of time feeding on seeds during the long dry season, suggesting that seed-eating may be a strategy for coping with seasonal fluctuation in the availability of fruit. Feeding on seeds during the long dry season may have augmented the overall amount of time mangabeys were observed to feed on seeds. At Kibale, mangabeys did not seem to have the same period of hardship, and therefore could to continue to eat fruit pulp year-round.

In the present study, mangabeys had the lowest dietary diversity during the long dry season. When food is scarce, animals may either generalise and feed on a larger number of species of often lower quality food, or specialise and feed on a few key species. Homewood (1978) found that the dietary diversity of agile mangabeys increased as fruit availability decreased. The present study on grey-cheeked mangabeys found the opposite. When fruit was scarce, dietary diversity was at its lowest and they concentrated on few, important foods. Because the dietary diversity for mangabeys at Lopé, was low during the long dry season, this may have resulted in a lower overall dietary diversity than was observed for grey-cheeked mangabeys in Uganda. Waser (1974) determined a diversity index varying between 2.8 and 3.9 with an annual diet diversity of 4.2, whereas diversity ranged from 1.4 to 2.3 in the present study, with an overall dietary diversity of 3.46. Alternatively, differences in dietary diversity between study sites may merely reflect differences in habitat diversity, because as shown in *Chapter Three* the diversity of plant species at Lopé is lower than at Kibale in Uganda.

Species that fruit during times of fruit scarcity may form important "keystone" plant species for frugivores (Terborgh, 1986). Terborgh (1986) suggested that palm nuts and figs are important keystone resources in the New World, and suggested that figs may also be an important keystone resource in Asia and Africa. Waser (1974) and Cashner (1972) found feeding on figs to represent 16% of all feeding observations. In the present study, although figs were fed on whenever available within the mangabeys range, they only formed 2% of all feeding observations. There were only three known reproductively active fig trees within the mangabey's range and each fruited only once during the study period. Fruit was highly competed for, by other arboreal monkeys, birds and gorillas and chimpanzees, and the crop disappeared on all trees in a matter of days. Therefore, while figs may be "keystone" resources for primates in some areas in Africa where figs are abundant (eg. Kibale), this was not true for this study and Gautier-Hion and Michaloud (1989) has shown that this is not true for forest guenons at Makokou in Gabon.

Gautier-Hion (1977) suggested that *Polyalthia suaveolens* and Myristicaceae fruits may be keystone resources for mangabeys in northern Gabon. They found the aril of *Pycnanthus angolensis* in 40% of of stomach contents during long dry season. These species were not keystone resources for grey-cheeked mangabeys in the Lopé Reserve. Trees from the species *Polyalthia suaveolens* were found at low densities in the mangabey's home range and this was not an important food species for mangabeys (0.08% of all feeding scans). *Pycnanthus angolensis* was fed on for 5% of all feeding observations but because it did not ripen until the end of the long dry season, it did not provide a keystone resource for the mangabeys during times of fruit scarcity.

Elaeis guineensis produces fruits throughout the year and mangabeys were observed to feed on its fruit during eight months. It was also the seventh most important plant species overall in terms of feeding frequency. The fruit of *Elaeis guineensis* has already been proposed as a keystone resource for chimpanzees during the dry season (Tutin and Fernandez, 1993 a) and it may also be an important food for mangabeys during this time.

Hypothesis III: Competition

There is greater competition for food resources at Lopé

Finally, the availability of food is also affected by who else is competing for the same resources. Overlap in diets of diurnal primates at Lopé was shown to be high. It seems unlikely however, that mangabeys would show a shift in their dietary niche because of competition with forest guenons, since mangabeys have a larger body size and group size, and have never been observed to be supplanted from a food resource by the smaller bodied guenons. The dietary shift could, however, be a result of having to compete for resources with the large bodied great apes at Lopé. The diet of the mangabeys has never been studied in any detail where they coexist with both gorillas and chimpanzees. Gorillas and chimpanzees at Lopé are highly frugivorous (Tutin and Fernandez, 1993 a), therefore grey-cheeked mangabeys may have shifted their dietary niche to encompass a larger proportion of seeds in the diet in order to decrease competitive overlap with these species.

Mangabeys were observed to eat fruit-pulp most frequently when it had ripened. Fruit from which they ate unripe pulp and immature seeds, were usually those that have been classified as 'important' in the diet of gorillas and chimpanzees. It seems likely that if mangabeys are forced to compete with other species for certain fruits, then it may be to their advantage to harvest the fruit before their competitors. If they are indeed forced to feed on fruit before it has ripened then mangabeys may select the seed, which is high in protein instead of the unripe pulp which is often low in sugars and high in tannins (see Rogers *et al*. 1990).

Overall strategy

Previous studies imply that mangabeys show very little selectivity. Chalmers (1968 b) observed that mangabeys utilise some part of nearly every tree visited and Waser(1974) stated that the number of species utilised approached the number of trees enumerated on a random transect. However, Waser (1974) found that some trees were not used at all, and other uncommon species utilised frequently, indicating some degree of selectivity. In the present study, although there was a correlation between the proportion of time spent feeding on plant species and their abundance in the habitat, certain species were still highly selected for.

Nutritionally, mangabeys seem to be selecting fruit higher in lipids and seeds higher in protein content than gorillas. In this way their diet seems more similar to chimpanzees than to gorillas. Both mangabeys and chimpanzees exploit fruit high in lipid content, such as *Elaeis guineensis* and *Pycnanthus angolensis* but mangabeys also feed on *Scottellia* sp. and the arils of *Blighia welwitschii*, two fruits that neither gorillas nor chimpanzees seem to eat. Janzen (1975) remarked that animals who eat fatty fruits are usually those who rely on fruit as the major source of their diet, and animals who eat sugary fruit are usually those animals who also eat leaves and insects. Herbaceous vegetation forms a significant part of the gorillas diet, especially during the long dry season, but chimpanzees seem to depend on fruit as the major part of their diet throughout the year (Tutin and Fernandez, 1993 a). Gorillas select fruit with a higher sugar content and lower fat content than chimpanzees, thus supporting Janzen's (1975) hypothesis, but this pattern is less clear for mangabeys. The major source of the mangabey's diet at Lopé is fruit, but it is not only the pulp, but the *seeds* of the fruit that are important. Also contrary to his theory, insects played an important role in the diet of mangabeys.

Although mangabeys may be selecting fruit and seeds for high fat and low sugar content overall, foods may be selected at different times of year for different reasons. For example, a negative correlation was found between the time spent feeding on insects, and the time spent feeding on seeds. This suggests that seeds and insects may be selected for similar nutritional requirements (probably protein) and that one food-type may be selected in absence of the other, or one food type may not be necessary when the other is available.

The body morphology of the mangabeys suggests that they may have evolved as seed-eaters. Compared to the *Cercopithecus* species, mangabeys have heavy jaw musculature and strong dentition (Chalmers, 1968 b; Kay, 1981), morphological characteristics necessary for cracking hard seeds. Kay (1981) shows that the thickness of enamel on the molars of primates are usually correlated with seed eating. Grey-cheeked mangabeys have one of the largest enamel thickness of the 37 primates sampled. Similarly mangabeys have relatively large stomachs, intestine and caecum, perhaps because seeds are not so easily digested as succulent fruit. Chalmers (1968 b) also noticed that this specialised dentition of mangabeys may enhance niche differentiation. He noticed that mangabeys often fed on fruit that were difficult to crack open and that *Cercopithecus* monkeys did not eat.

Other mangabey species

Little information exists on the diets of other species of mangabeys. White-collared mangabeys have been observed to have a large proportion of fruit in the diet, but the fruit category is not divided into seeds and pulp (Homewood, 1978; Mitani, 1989). Black mangabeys, the closest relative of grey-cheeked mangabeys, have been observed to also have a large proportion of seeds in their diet. Horn (1987b) observed that the black mangabey spent 30.5% of the time feeding on seeds and nuts and 56.7% of the time feeding on the pulp of fruits, suggesting that seed-eating in mangabeys is not so unusual.

SUMMARY

In summary, the diet of grey-cheeked mangabeys in the present study was observed to be very different from the diet of grey-cheeked mangabeys studied in Uganda. Mangabeys at Lopé spent a large proportion of time feeding on seeds, and their diet was highly seasonal. From all the hypotheses suggested above, it seems most likely that mangabeys have a larger proportion of seeds in their diet than at Kibale, because:

(1) There are a larger number of species bearing trees from the family Leguminosae at Lopé (see page 56).

(2) Forests are more seasonal at Lopé. Mangabeys eat seeds during the long dry season when succulent fruit is scarce and this augments the overall proportion of seeds in the diet.

(3) Competition may be greater at Lopé, where mangabeys live sympatrically with gorillas and chimpanzees, which both have a high proportion of succulent fruit in their diets. Mangabeys may eat seeds as a form of exploitation competition, by eating the unripe seeds of fruit that is highly competed for.

These differences in diet between mangabeys in this study and those mangabeys studied in Uganda, warn us against making broad generalisations about the diet of any species. A growing number of studies comparing the feeding behaviour of the same species in different environments have found large variability in their diets, highlighting the flexibility of species in their ability to adapt to different circumstances.

CHAPTER SIX: RANGING BEHAVIOUR

INTRODUCTION

The way in which an animal uses space can be influenced by both environmental and social variables. Interspecific differences in ranging patterns have been found to be related to body mass, group size and gross dietary habits (Clutton-Brock and Harvey, 1977; Milton and May, 1976). For example, the size of the home range and the length of the day range have been shown to be positively correlated with body mass and negatively correlated to the proportion of foliage in the diet (Clutton-Brock and Harvey, 1977). Despite these general patterns, ranging behaviour has also been observed to vary widely within species (eg. Butynski, 1990). Intraspecific differences have been shown to be related primarily to differences in climate (eg. McKey and Waterman, 1982), the distribution and abundance of resources (eg. Altmann and Altmann, 1970; Gautier-Hion *et al*.,1981; Harrison, 1983a; McKey and Waterman, 1982), differences in habitat structure (Gautier-Hion *et al*., 1981; Harrison, 1983a), avoidance of other groups (Harrison, 1983b; Isbell, 1983; Struhsaker, 1975; Waser, 1976) and differences in group size (Waser, 1974). These variables may assume differences in their degree of importance to different species.

The ranging behaviour of grey-cheeked mangabeys has only been studied in detail at Kibale in Uganda by Waser (1974, 1976, 1977a) although home range size estimates are also provided by other authors (Chalmers, 1968b; Freeland, 1979, Wallis, 1979). Waser (1974, 1977a) found mangabeys to have the largest home range size of any arboreal primate and suggested that the distribution of food resources and intergroup avoidance were the main factors affecting their range use.

The aim of this chapter is to describe in detail the ranging behaviour of grey-cheeked mangabeys at Lopé, and to examine the effects of climate, distribution and abundance of food, diet, habitat structure and intergroup relations upon their patterns of range use.

METHODS

A: MEASUREMENTS OF RANGE USE

1. Range size

The home range of an animal is usually defined as : "the area in which an animal or group of animals habitually moves, feeds, and rests" (Richards, 1985). The method used to analyse ranging data may influence the estimation of the size of the home range (Altmann and Altmann 1970; Waser and Floody, 1974) so it is important to use analyses that are appropriate for the original method of data collection as well as useful for comparisons with other studies.

The advantages and disadvantages of different methods are discussed by many authors (eg. Altmann and Altmann,1970; Anderson,1982; Kenward, 1987; Kool and Croft, 1992; Olson,1986). The methods chosen to describe the home range size in this study were the 'grid-cell analysis' and 'minimum convex polygon analysis' for the reasons outlined below.

Grid-cell method (Siniff and Tester, 1965)

The grid cell technique was the main method used in this study. As described in *Chapter Two*, a grid with 1 ha squares was superimposed onto the map of the study area, and every 15 minutes during follows of the main study group, the grid square occupied by the centre of mass of the group, was recorded. The group's "centre of mass" was defined following

Waser and Floody (1974) as the "centre of the polygon enclosing all mangabey sightings in a given 5 minute sample period".

The grid-cell method was used in the present study because it has been suggested as being useful for habitat analysis and analysis of the interactions between groups (Harris *et al.*, 1990). It can be disadvantageous however, in that it ignores partial use of grid-squares and therefore may include large areas never actually visited by the group, resulting in an overestimation of the home range size (Kool and Croft, 1992). On the other hand, it could also result in an underestimation of home range size if grid squares were used but not recorded, because the centre of mass did not fall within the grid-square.

The size of the grid squares has been shown to affect the estimated home range size (Kool and Croft, 1992; Kenward, 1987; Olson 1986; Rasmussen 1980; Waser, 1976). Olsen (1986) advises use of the smallest grid size possible given the accuracy of mapping and the observation conditions. A grid size of 100m x 100m was chosen to be appropriate for the present study.

A second group (Group Two) was systematically followed on 5 days during the study. This group was also encountered frequently during searches for the main study group and its location was recorded whenever it was seen. From these observations, the home range size of this group was also estimated using the grid-cell method.

Minimum convex polygon (Southwood, 1966)

The paths of movement of the study group were also drawn onto the 1 cm:100m map. For the 'minimum convex polygon' method of analyses, a line is drawn around the outer limits of all the points visited by the group and the area enclosed by this line is the estimated area of the home range (Kool and Croft, 1992).

This is one of the earliest methods used to assess home range size (Kenward, 1987) and remains the technique most frequently used in studies of primates. It was therefore used in the present study because it is useful for comparisons with other studies. It has advantages when the number of observations are low, but is limited in that it may include areas rarely visited at the perimeters of the range. It therefore may encompass large areas never used, and so overestimate the home range size. Apparent differences in the size of the home range between studies could therefore reflect differences in the shape of the home range and not necessarily differences in their actual area (Kool and Croft, 1992).

This method was not used to estimate the home range size of Group Two for this reason. The home range of Group Two extended from the main forest into a gallery forest and a line enclosing all sightings of the group would incorporate large areas of savannas never entered by the group and therefore grossly overestimate the home range size.

2. Intensity

Neither the minimum convex polygon, nor the grid-cell method weight areas in the home range according to their use. Therefore, maps of "occupational densities" (Altmann and Altmann, 1970) of grid squares are useful in that they show areas of the home range that are used more frequently, versus those that are rarely visited. The "utilisation distribution" (Jennrich and Turner, 1969) or "occupation density" (Altmann and Altmann, 1970) technique calculates the minimum area encompassed within a specified percentage of scans. In the present study, the area occupied within 95% of all scans was determined to exclude areas rarely used. In this study 'core areas' were chosen to be regions that encompassed 50% of all scan samples. This proportion facilitated comparisons with studies of other primates.

3. Clumping

Although Jenrrich and Turner's (1969) method provides a useful measure of the size of core areas within the home range, it does not give information on how these areas are distributed within the range. An index of clumping is needed to assess the variation in the occupational density of grid squares.

The Shannon Index (see *Chapter Two*) is frequently used to examine the diversity in patterns of range use (Isbell, 1983; Struhsaker, 1975) and is therefore useful for comparison with other studies. Evenness was determined by the J' of Pielou (1975), by dividing the Shannon index H' by $H'max$, where $H'max=\ln(S)$, and S= the overall number of grid squares entered.

4. Consistency

An index of consistency measures the similarity in patterns of range use over time. In the present study, the same method was used as Struhsaker (1975) and McKey and Waterman (1982) where the shared percentages in each grid square were summed to give a percentage overlap between months.

B: FACTORS THAT MAY AFFECT RANGE USE:

1. Food availability

Food availability was determined each month from phenology data, as described in *Chapter Three*.

2. Diet

The proportion of different food types or food species in the diet of the mangabeys each month was determined as described in *Chapter Five*.

3. Habitat

White (1992) defined vegetation categories within the Lopé study area, by comparisons of the structure and composition of different areas of forest. For this analysis, the vegetation categories classified by White (1992) were collapsed into four main vegetation categories: "Savanna-edge forest", "River-edge forest", "Marentaceae forest" and "Rocky forest". The categories were chosen because they were thought to be biologically relevant to the mangabeys and so that habitat types were made broad enough to ensure accuracy in mapping. The following is a brief description of these vegetation types.

HABITAT A: Marentaceae Forest

This habitat type combines White's (1992) categories 3 to 6 and 11. The forest is generally more diverse in species, trees are generally taller and canopy cover greater than the other habitat types. Characteristic species include *Aucoumea klaineana, Cola lizae, Elaeis guineensis, Klainedoxa gabonensis* and *Lophira alata*.

HABITAT B: River-edge Forest

This habitat type combines White's (1992) categories 12 and 13. It includes areas next to streams and rivers and seasonal water courses and dry gulleys. Characteristic species in this habitat that provide food for mangabeys include *Berlinia* *bracteosa,Milletia* spp., *Myrianthus arboreus, Nauclea* spp. *Pseudospondias microcarpa,* and *Pycnanthus angolensis*. See *Chapter Three* for a detailed description of this habitat type.

HABITAT C: Savanna-edge Forest

This habitat type is the same as White's (1992) category two, and is forest which occurs adjacent to savannas. Trees are generally more abundant, but smaller and branching lower than in other areas of the forest and species diversity is low. Characteristic species of this habitat that provide food for mangabeys include *Antidesma laciniatum, Barteria fistulosa, Berlinia bracteosa, Cryptosephalum staudtii, Julbernardia brieyi, Lophira alata, Milletia* spp.,*Uapaca guineensis,* and *Xylopia* spp. See *Chapter Three* for a more detailed description of this habitat type.

HABITAT D: Rocky Forest

This habitat type combines White's (1992) categories 7 to 10. It includes areas adjacent to bare rocks or close to rocky outcrops usually on thin soil. The forest is dominated by trees less than 40 cm dbh. Characteristic species of this habitat type that are found in the diet of the mangabeys are are *Dichapetalum* sp.,*Diospyros* spp., *Ganophyllum giganteum, Heisteria parvifolia, Hylodendron gabunense, Lecaniodiscus cupanioides, Scottellia coriacea* and *Trichilia* cf.*prieureana* .

The aim was to test whether or not mangabeys utilised the habitat types in proportion to their abundance in the study area. Therefore, each of the grid squares from the annual home range was assigned to a habitat category according to its dominant vegetation type. The proportion of the annual home range filled by each of these habitat types was calculated and this provided the expected value for each category. Habitat selection indices were calculated using Jacob's preference index (P_i):

$$P_i=R_i-Q_i/\ R_i+Q_i \quad \text{(Jacob, 1974)}$$

where, R_i is the percent of scans that the mangabeys were observed in habitat i, Q_i is the percent of habitat i in the home range. When $P_i=+1$, the habitat is completely preferred, and when $P_i=-1$ habitat is completely avoided. $P_i=0$ shows that there is neither preference nor avoidance for this habitat

4. Other groups

The effects of conspecific groups on the ranging patterns of mangabeys were investigated by determining the degree of overlap in the home ranges of adjacent groups and the frequency and form of intergroup encounters. Either during searches for the study group, or during follows, the date, time and location were recorded for any sightings of another group of mangabeys within the home range of the study group, and whenever possible other groups were identified. When groups were more than 200 m away from the study group, relatively few changes in the behaviour of the mangabeys were noticeable, therefore intergroup encounters were defined as the study group of mangabeys coming within 200 m of another group of mangabeys. This criterion was also used by Waser (1976).

RESULTS

The study group's home range extended for about 2.5 km along the edge of the savanna and then back into the forest for about 1.5 km to the south. It also extended to the north through a narrow band of forest about 200 m wide. There was one main stream though the mangabey's range that ran close to the savanna edge, four minor streams as well as several ephemeral streams. The highest point in the home range was 321m located roughly in the geographical centre of the range. The lowest point was 200 m and located in the north-eastern area of the home range close to the savanna edge. The savanna edge was the only definable environmental feature which formed a boundary to the home range (See **Figure 2.6**).

The range of Group Two overlapped with the home range of

Group One (see under "Overlap with other groups and intergroup encounters") and then extended northward through a block of forest surrounded on both the east and west sides by savanna, and then into several bosquets. Their range included the same main river as Group One and there were also several minor rivers in their home range. A road bisected their range but this did not prove to be a barrier as the group were observed to freely cross the road through the canopy.

Home range:

1. Size

Grid square analysis

The annual home range size during the 12 months from September 1991 to September 1992 was 215 ha. During the first six months of the study, from January 1991 to June 1991, the mangabeys used 10 additional hectares that were not included in the above calculation, giving a total home range of 225 ha in 18 months.

If the home range included those grid-squares that were never used, but were surrounded on all four sides by squares that were used, then the annual and 18 month home range size increased to 223 ha and 234 ha respectively. The group was observed to enter seven out of these eight grid squares during *ad libitum* observation but because they were not systematically recorded during scan samples, they were left out of all calculations.

The home range size for "Group Two" was estimated to be at least 156 ha. The home range of this group may have extended further to the south than estimated here, but this group was not observed to range any further southwards into the home range of the study group.

When the cumulative number of new grid squares entered by the study group is plotted against time, the rate at which this asymptote is reached, or the slope of the curve, is a measure of the rate at which new quadrats are entered. In this study, the slope began to level off around seven months (**Figure 6.1**). During July 1992, nine new quadrats were entered, but no new quadrats were entered during the final month of August 1992. This is also an indication that the group were studied long enough to give an accurate estimation of their home range size.

Minimum convex polygon

The size of the annual home range, as determined by the minimum convex polygon, was 277 ha. This estimates the home range size to be 1.3 times larger than the annual home range estimate of 215 ha using the grid-square analysis.

2. Intensity

The proportion of time that the group of mangabeys was recorded in each grid square each month, was averaged from September 1991 to September 1992. This gave the average annual occupational density of each grid square (**Figure 6.2**). During 95% of all scans mangabeys were observed in 144 grid squares, or 67% of their total annual home range. During 50% of all scans the study group of mangabeys was recorded in only 32%, or 16% of the total annual home range, indicating that the mangabeys did not use their home range evenly.

***Monthly* range:**

1. Size

The size of the monthly range was highly variable, ranging from 19 ha in January 1991 to 90 ha in March 1991 (**Table 6.1**). Using the grid-square method, the mean number of

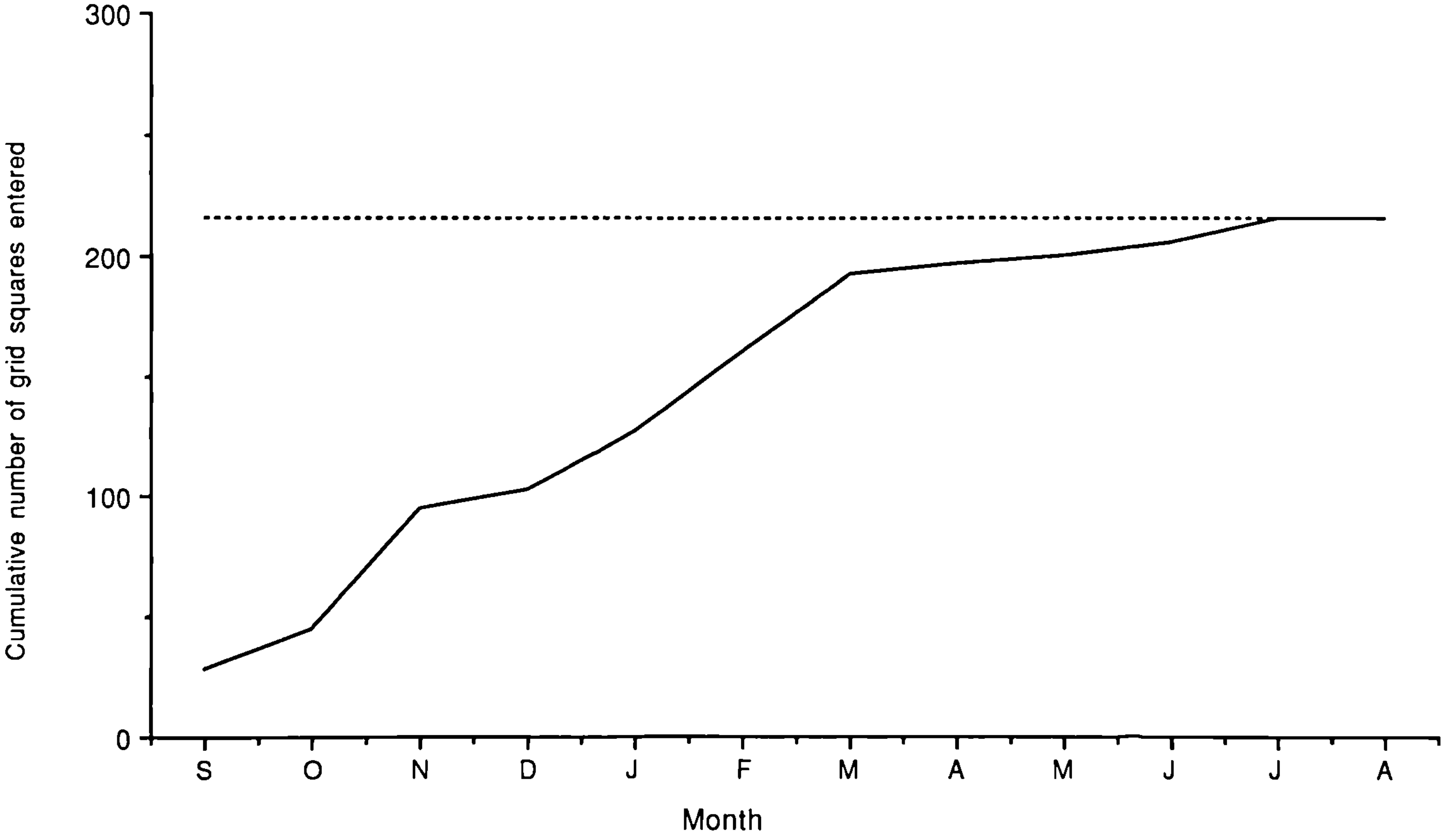


Figure 6.1 Cumulative number of 1 ha grid squares entered by the study group from September 1991 to August 1992.

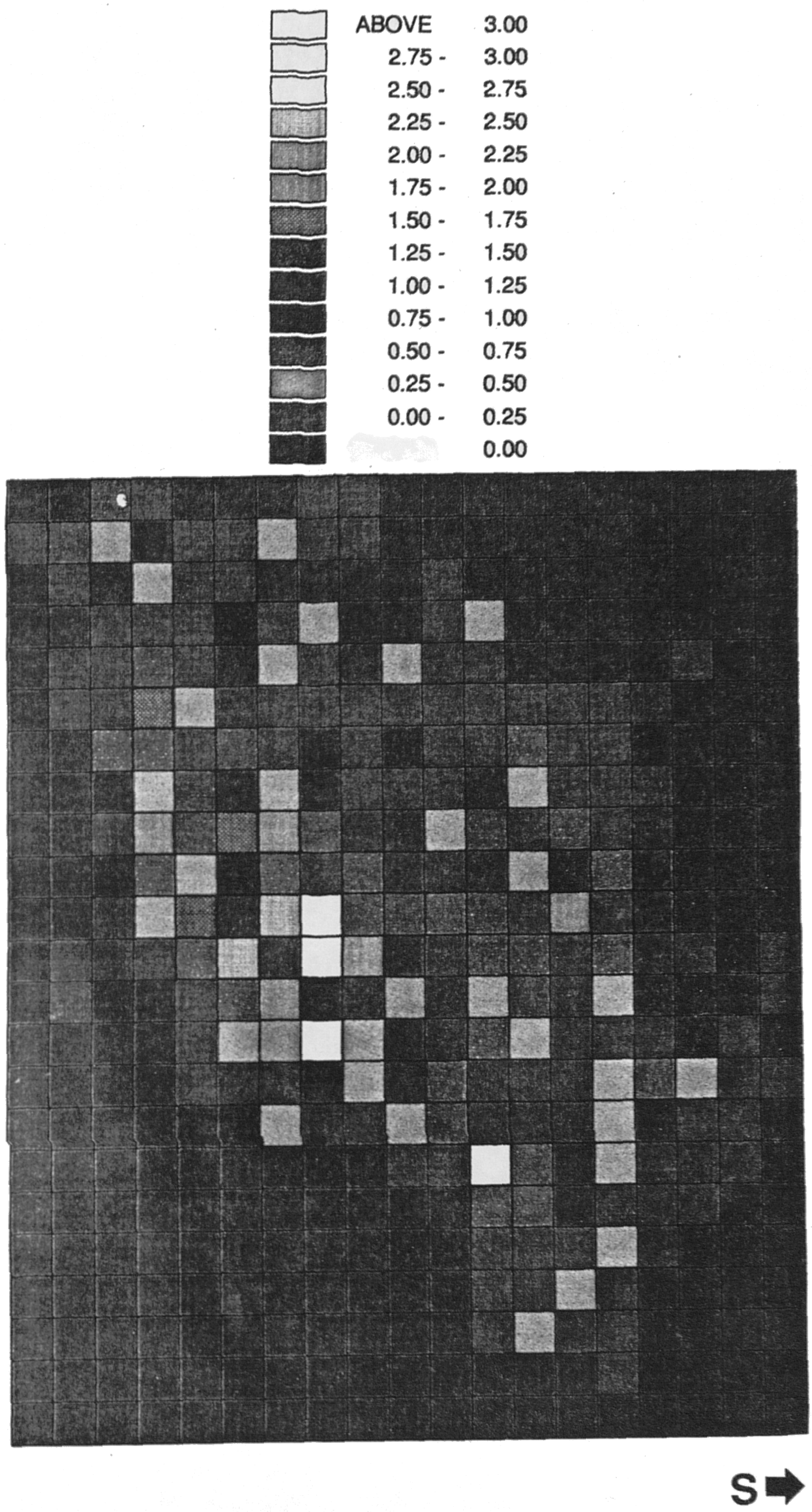


Figure 6.2. The mean percent of scans that the study group of mangabeys was observed in each grid square from September 1991 to August 1992. (Each grid square=1 ha)

Table 6.1 Monthly indicies of range use in the study group of grey-cheeked mangabeys

Month	No. grid squares used	% of range used in 95% of scans	% of range used in 50% of scans	Shannon index of diversity	J' of Pielou	Distance travelled (m) 09:30-14:30
Jan-91	19	84	21	2.64	0.90	-
Feb-91	36	75	17	3.06	0.85	-
Mar-91	90	46	17	4.07	0.90	-
Apr-91	72	79	13	3.70	0.87	-
May-91	46	76	20	3.45	0.90	-
Jun-91	27	81	11	2.84	0.86	-
Sep-91	28	89	25	3.11	0.93	-
Oct-91	19	74	16	2.40	0.82	390
Nov-91	77	83	18	3.96	0.91	1385
Dec-91	24	88	25	2.90	0.91	690
Jan-92	50	90	18	3.56	0.91	550
Feb-92	83	83	20	4.03	0.91	1274
Mar-92	96	88	20	4.25	0.93	1323
Apr-92	61	85	21	3.79	0.92	1110
May-92	48	81	23	3.62	0.94	550
Jun-92	35	86	14	3.11	0.87	500
Jul-92	67	79	13	3.63	0.86	600
Aug-92	25	76	12	2.62	0.81	580
18 MONTHS						
Mean	**50**	**80**	**18**			
S.D.	**26**	**10**	**4**			
12 MONTHS						
Mean	**51**	**83**	**19**			
S.D.	**26**	**5**	**4**			

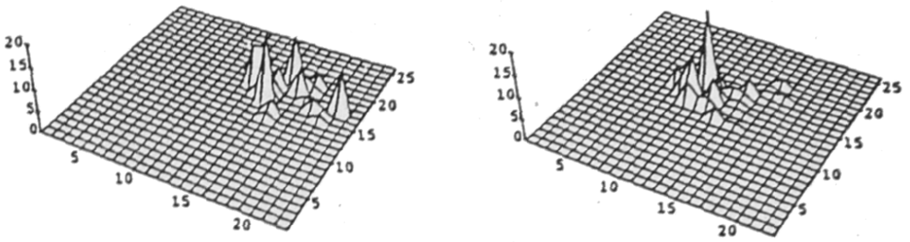
hectares used each month was 50 (S.D.=26, n=18, range=19-90) which is about one quarter of the annual home range. The variation in home range size was not attributable to monthly variations in rainfall (r_s=0.33, n=18, p=0.18) and there was no significant difference in range size between seasons (Chi-square =29.3, df=3, p=0.40).

2. Intensity

The intensity of range use was expressed as the mean monthly percentage of occupancy records per grid-square (**Figure 6.3**). During 95% of scan samples over an annual cycle, the group was observed in an average of 83% of the annual home range (S.D.=5%, n=12, range=74-90%). The core areas made up an average of 19% of the annual home range (S.D.=4, n=12, range=11-25%). There were no significant correlations between mean monthly rainfall and the number of grid squares occupied during 95% (r_s=-0.17, n=18, p=0.50) or 50% (r_s=0.19, n=18, p=0.45) of all scan samples. Mangabeys were, however, observed in a significantly smaller proportion of their monthly range in 95% of all scans during the long dry season than the short dry season (Chi-square=12.64, df=1, p<0.01), the short rainy season (Chi-square= 9.3, df=1, p<0.01), or the long rainy season (Chi-square=17.5, df=1, p<0.01) (**Table 6.1**), (**Figure 6.4**).

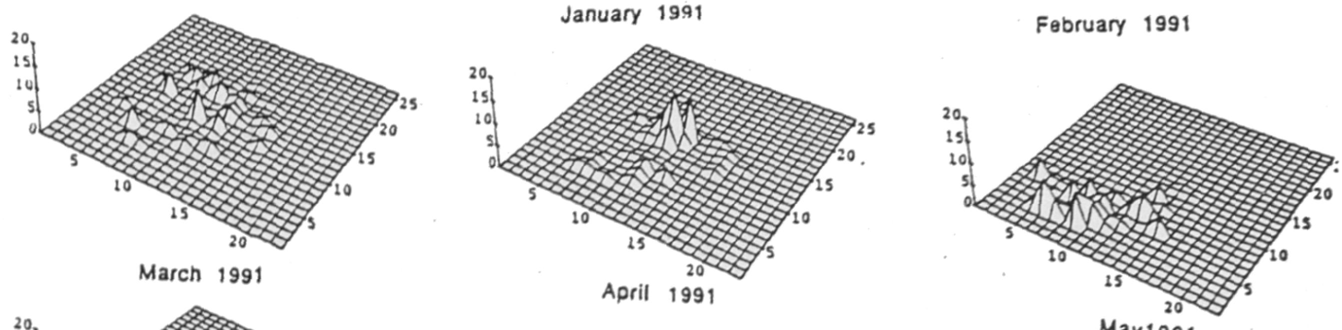
3. Clumping

The diversity of grid-square use was calculated for each month and found to be lowest in October 1991 and a highest in March 1992 (**Table 6.1**)(**Figure 6.5**). The diversity of range use was not related to rainfall (r_s=0.12, n=18, p=0.67), minimum (r_s=0.28, n=18, p=0.31) or maximum (r_s=0.30, n=18, p=0.28) temperature, but it was related to the dietary



January 1991

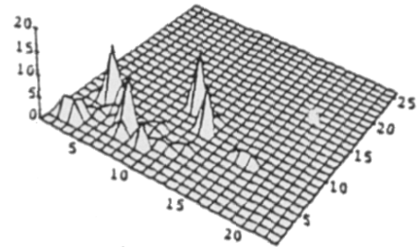
February 1991



March 1991

April 1991

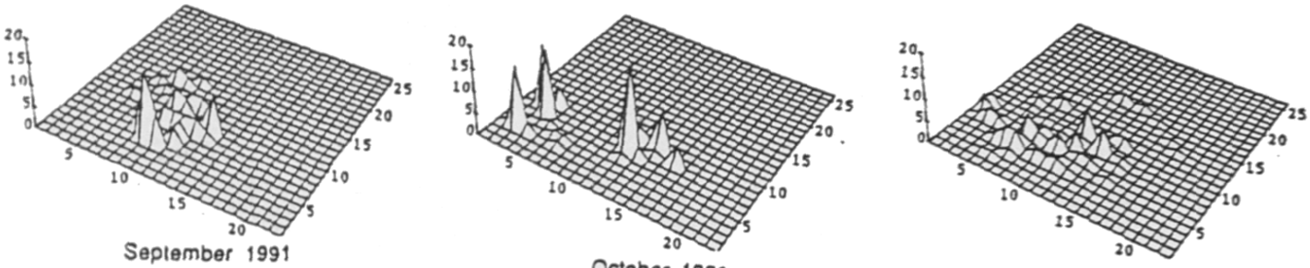
May1991



June 1991

July 1991

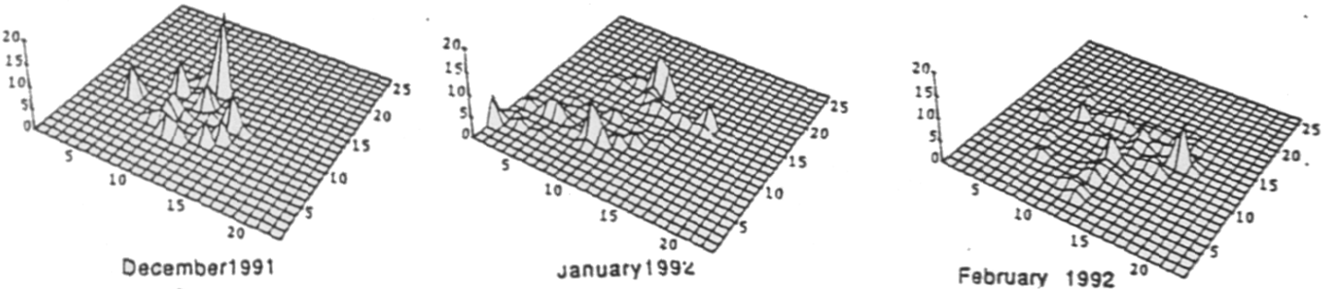
August 1991



September 1991

October 1991

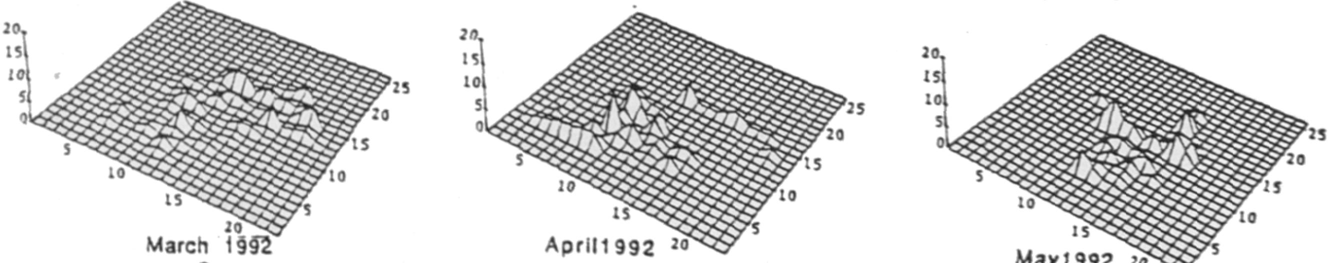
November 1991



December1991

January1992

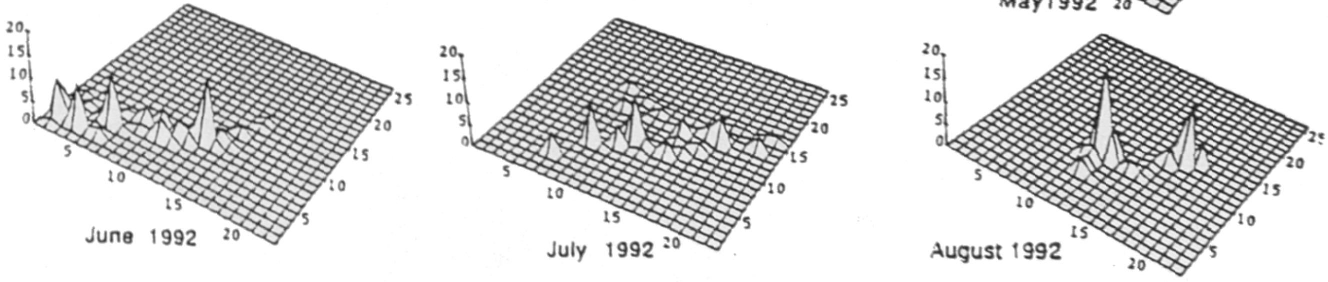
February 1992



March 1992

April1992

May1992



June 1992

July 1992

August 1992

Figure 6.3 The percent of scans that the study group of mangabeys was observed in each grid square each month. (Each grid square=1 ha).

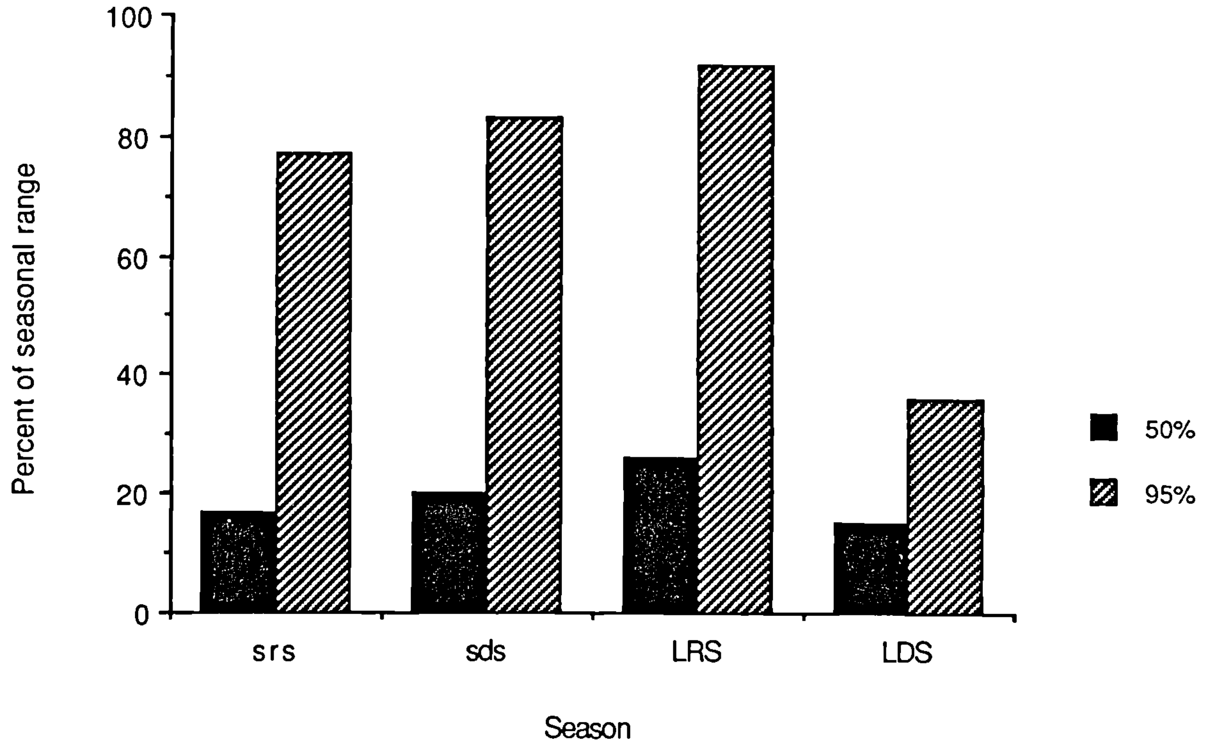


Figure 6.4 Percent of seasonal range used during 50% and 95% of monthly scan samples

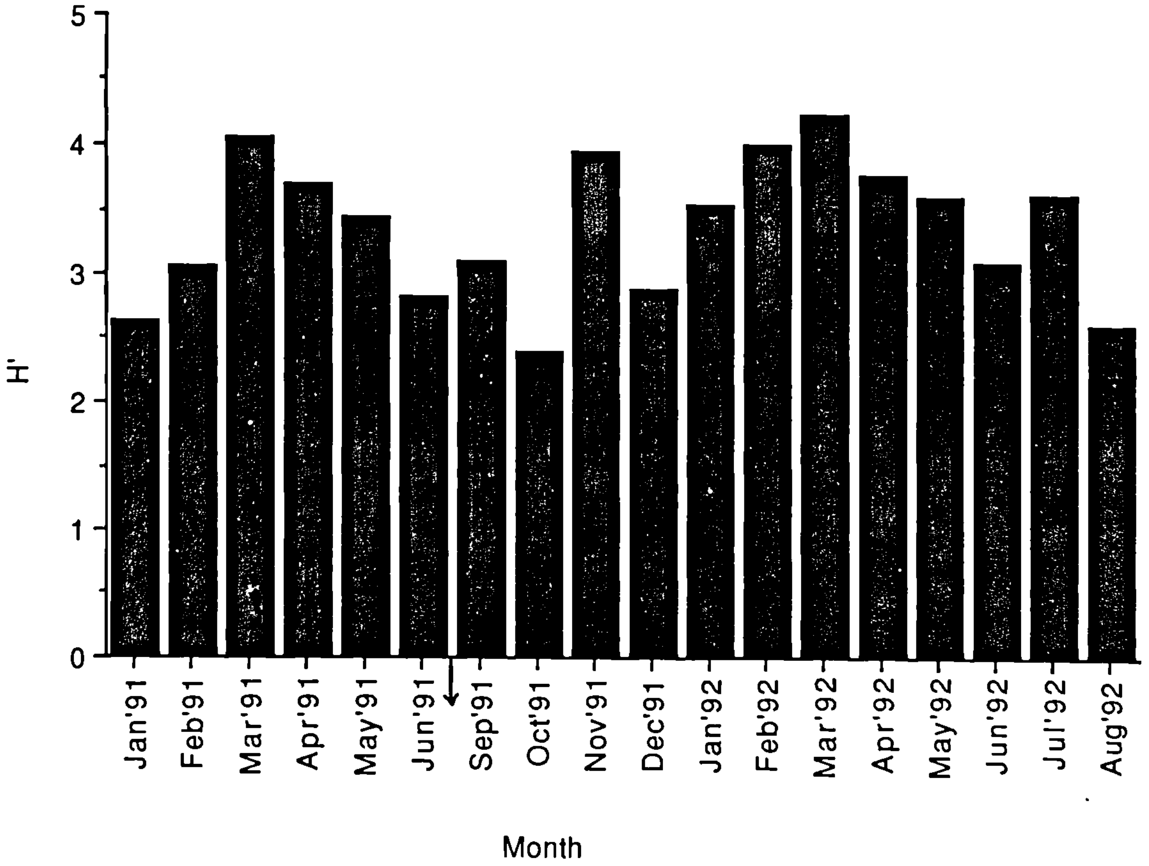


Figure 6.5 Shannon index of diversity of ranging patterns of the study group of grey-cheeked mangabeys from January 1991 to August 1992.

diversity (r_s=0.55, n=15, p=0.05). The diversity of range use also increased with increased monthly range size (r_s=0.514, p=0.03). Range use was most diverse during the long rainy season (H'=4.16) and least diverse during the long dry season (H'=3.995).

The evenness of range use was calculated for each month and found to be greatest in May 1992 and least in August 1992 (**Table 6.1**). Ranging patterns were less even in the long dry season (J'=0.82), than the short and long rainy season (J'=0.86), and the most even in the short dry season (J'=0.87).

4. Consistency

The percent of overlap in the monthly ranges, varied from 0% to 38% with an average overlap over one year of 15% (SD=9%, n=153) (**Table 6.2**). The average overlap in consecutive months (mean= 18%, S.D.=9%, n=16 range 7-38%) was higher than in non-consecutive month (mean=14%, S.D.= 9%, n=137, range= 0-35%). The mean overlap between the long rainy season in 1991 and 1992 was 26%, (S.D.=4%, n=9), which was higher than the overall mean, indicating that ranging was seasonal.

To investigate whether the degree of range overlap between pairs of months may reflect the degree of dietary overlap, the percentage of overlap in the diet (see *Chapter Five*) was tested for correlation with monthly overlap in range use, but this relationship was not significant (r_s=0.38, n=15, p=0.16).

Table 6.2 Percentage of monthly overlap in grid-sqare use

MONTH	Feb-91	Mar-91	Apr-91	May-91	Jun-91	Sep-91	Oct-91	Nov-91	Dec-91	Jan-92	Feb-92	Mar-92	Apr-92	May-92	Jun-92	Jul-92	Aug-92
Jan-91	9	4	4	0	0	0	0	2	0	2	4	10	3	13	2	4	7
Feb-91		22	24	1	0	0	0	4	26	15	15	7	2	16	0	1	0
Mar-91			38	17	16	22	4	16	17	24	31	26	22	23	12	22	13
Apr-91				15	7	19	4	20	26	18	29	24	23	32	13	20	17
May-91					21	21	12	32	12	15	19	10	18	11	19	16	6
Jun-91						10	25	18	1	7	6	10	15	6	16	19	11
Sep-91							9	19	25	11	16	16	35	13	18	12	21
Oct-91								11	5	3	7	5	12	9	11	6	9
Nov-91									13	19	25	20	30	13	19	20	15
Dec-91										15	13	8	15	18	14	8	9
Jan-92											21	17	16	13	10	22	14
Feb-92												29	17	30	16	30	27
Mar-92													32	19	9	23	19
Apr-92														12	15	19	13
May-92															15	24	23
Jun-92																7	11
Jul-92																	24

Daily range:

1. Size

As mentioned in *Chapter Two*, dawn-to-dusk follows were not possible in this study, so direct measures of the length of the day range of the group of mangabeys cannot be reported here. The longest time period between which the distance travelled could be calculated from continuous follows of the study group for each month was for five hours between 09:30 and 14:30, since this time period gave the largest sample size.

The average distance travelled from 09:30 to 14:30 during 11 months was 1056 m (S.D= 509.87) (**Table 6.1**). A longer distance travelled each day may indicate that a larger area is used overall. The relationship between the average daily distance travelled each month and monthly range size was significant (r_s=0.73, n=11, p=0.01). Mean day range length per month was also positively correlated with both the diversity of the monthly range use (r_s=0.77, n=11, p=0.01) and dietary diversity (r_s=0.62, n=11, p=0.04).

Although the mean distance travelled was not correlated with mean monthly rainfall (r_s=0.03, n=11, p=0.94), minimum (r_s=0.20, n=11, p=0.55) or maximum (r_s=0.27, p=0.43) temperatures, the mean distance travelled between 09:30 and 14:30 was smallest in the long dry season (820m) and highest during the long rainy season (1257m). Seasonal differences between distances travelled were not significant (F=1.089, df=3, p=0.37).but this may have been because the sample size was small (**Figure 6.6**).

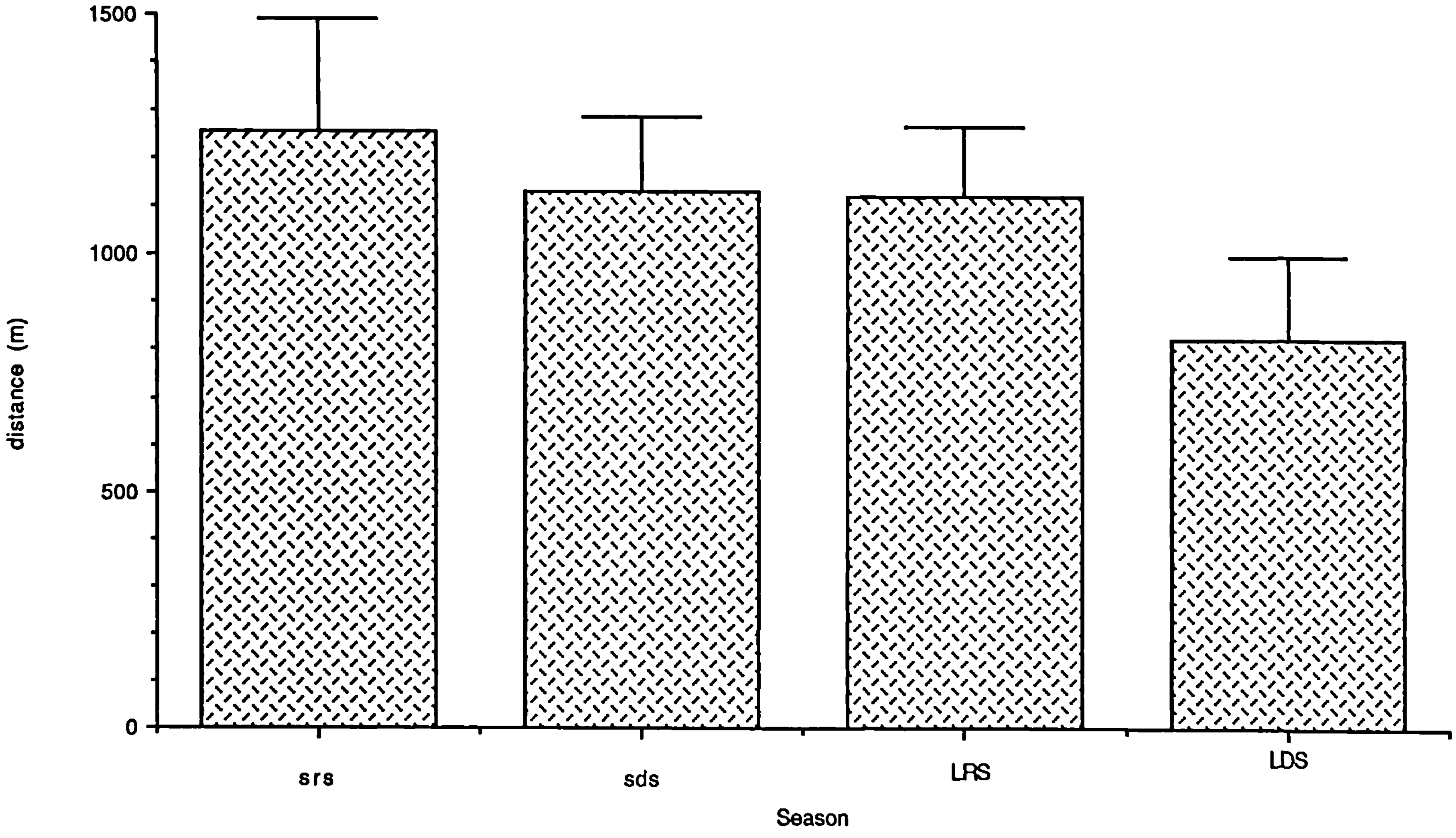


Figure 6.6 Mean seasonal distances travelled between 09:30 and 14:30 (with standard error bars).

B. FACTORS AFFECTING RANGE USE:

1. Food Availability:

The result above show that there are seasonal effects on the ranging patterns of grey-cheeked mangabeys at Lopé. During the long dry season the ranging patterns of the study group was less diverse, with shorter day ranges and a smaller area used in 95% of scans. These seasonal differences may be related to the availability of food, therefore, the percent availability of ripe fruit each month (as determined in *Chapter Two*) was tested for correlation with different measures of range use. There was a significant positive relationship between the availability of ripe fruit and the diversity of the range use ($r_S=0.48$, n=18, p=0.04), and a weak positive relationship between the availability of ripe fruit and the length of the day range ($r_S=0.56$, n=11, p=0.07), the size of the areas where the group spent 50% ($r_S=0.44$, n=18, p=0.07) and 95% of their time ($r_S=0.45$, n=18, p=0.06).

2. Diet

As seen in the previous chapter, diet is also related to food availability, therefore ranging behaviour may be expected to be related to the proportion of certain foods in the diet. The only significant relationship that was observed, however, was a negative correlation between the proportion of leaves in the diet of the mangabeys with the monthly range size ($r_S=-0.56$, n=15, p=0.03) and a negative correlation between the proportion of leaves in the diet and the diversity of range use ($r_S=-0.72$, n=15, p<0.01).

3. Habitat

Food availability is also related to habitat, where certain species may be more common in certain types of forests than in others. The home range of the study group was examined to determine the proportion and use of different habitat types in their home range. Each 1 ha quadrat in the mangabey's home range was assigned to one of the four habitats according to the dominant vegetation types (see pg. 125 for detailed description of the vegetation within each habitat-type). Although this was a subjective decision, because the categories were very general, the habitat type was usually obvious. White (unpublished data) independently categorised this area of SEGC into his vegetation categories and the results were very similar.

"Marentaceae forest" covered the largest area in the annual home range of the study group (67.91%), followed by "Rocky forest" (15.35%), "River edge forest" (8.37%), and "Savanna edge forest" (8.37%) (**Figure 6.7**). The proportion of time the mangabeys spent in each habitat type and selection ratios were calculated for each month. Overall "Rocky forest" was used significantly more than was expected by its representation in the home range and "Savanna edge forest" was used significantly less, as indicated by selectivity indices (**Table 6.3** and **Figure 6.8**).

The river edge habitat was most strongly selected for in May 1991, and in June 1992. The savanna-edge forest was strongly selected against in January, February, March, September and December 1991, and January and August 1992. The Marentaceae habitat was most strongly selected against in May and June 1991 and June, July 1992. Rocky forest was most strongly selected for in April 1991 and avoided in October 1991 (**Table 6.3**). Use of "River-edge forest" increased with increased use of "Savanna-edge forest" ($r_s=0.61$, $n=18$, $p=0.01$). This may have been because the main river in the home range of the mangabeys ran parallel to the savanna-edge and came close, to within 100m in some places. The use of "Marentaceae forest" decreased with use of both "River-edge forest" ($r_s=-0.50$, $n=18$, $p=0.04$) and "Savanna-edge forest" ($r_s=-0.69$, $n=18$, $p<0.01$) (**Figure 6.9**).

The use of "Marantaceae forest" varied significantly between seasons (Chi-square=15.80, df=3, $p<0.05$). The study group used this habitat more frequently than expected in the long rainy season (Chi-square=6.32, df=1, $p<0.05$) and less frequently than expected during the long dry season (Chi-square=9.32, df=1, $p<0.05$). The use of "River-edge forest" varied seasonally (Chi-square=14.82, df=3, $p<0.05$), and was used less frequently than expected in the short dry season (Chi-square=8.96, df=1, $p<0.05$) and more frequently than expected during the long dry season (Chi-square=4.82, df=1, $p<0.05$). The use of "Savanna-edge forest" varied significantly between seasons and was used less frequently than expected during the short dry season (Chi-square=6.94, df=1, $p<0.05$) and more frequently than expected during the long dry season (Chi-square=4.01, df=1, $p<0.05$). Finaly, the use of "Diospyros forest" also varied seasonally (Chi-square=75.81, df=3, $p<0.05$). This habitat type was used less frequently than expected during the short rainy season (Chi-square=55.89, df=1, $p<0.05$), and more frequently than expected in both the long rainy season (Chi-square=7.22, df=1, $p<0.05$) and the long dry season (Chi-square=12.59, df=1, $p<0.05$) (**Figure 6.10**).

In order to investigate whether habitat choice was affected by the availability of food species important in the diet of mangabeys ('important species' being those that were included

Table 6.3 Percent of monthly scans and selection ratios for each habitat type

Month	% monthly scans in each Habitat type				Selectivity index for each Habitat type			
	Marentaceae	River	Savanna	Diospyros	Marentaceae	River	Savanna	Diospyros
Jan-91	67.74	1.16	0.00	30.65	0.00	-0.66	-1.00	0.30
Feb-91	64.74	0.00	0.00	35.26	-0.02	-1.00	-1.00	0.36
Mar-91	65.66	6.42	0.00	27.55	-0.02	-0.11	-1.00	0.25
Apr-91	50.49	8.09	0.97	40.45	-0.15	0.01	-0.78	0.42
May-91	40.27	30.77	13.57	15.38	-0.26	0.59	0.26	-0.03
Jun-91	40.00	28.57	3.81	27.62	-0.26	0.56	-0.35	0.25
Sep-91	56.67	26.67	0.00	16.67	-0.09	0.54	-1.00	0.01
Oct-91	65.59	25.81	4.30	4.30	-0.02	0.53	-0.30	-0.59
Nov-91	72.25	9.13	5.70	12.93	0.03	0.07	-0.17	-0.12
Dec-91	74.25	7.58	0.00	18.18	0.04	-0.03	-1.00	0.05
Jan-92	72.18	1.50	0.00	26.32	0.03	-0.68	-1.00	0.23
Feb-92	49.64	9.78	3.62	36.96	-0.16	0.10	-0.38	0.38
Mar-92	58.40	6.72	7.56	27.31	-0.08	-0.09	-0.03	0.25
Apr-92	61.54	10.90	4.49	23.08	-0.05	0.15	-0.28	0.17
May-92	49.15	12.43	2.26	36.16	-0.16	0.22	-0.56	0.37
Jun-92	40.00	28.57	3.81	27.62	-0.26	0.56	-0.35	0.25
Jul-92	38.35	13.62	10.04	37.99	-0.28	0.26	0.11	0.40
Aug-92	63.20	4.00	0.00	32.80	-0.04	-0.33	-1.00	0.33
Mean	58.44	13.06	3.48	25.03				
S.D.	12.15	9.07	3.25	10.47				
No. grid-squares in annual home range	146.00	18.00	18.00	33.00				
% of annual home range	67.91	8.37	8.37	15.35				
Annual selectivity index	-0.07	0.04	-0.55	0.18				

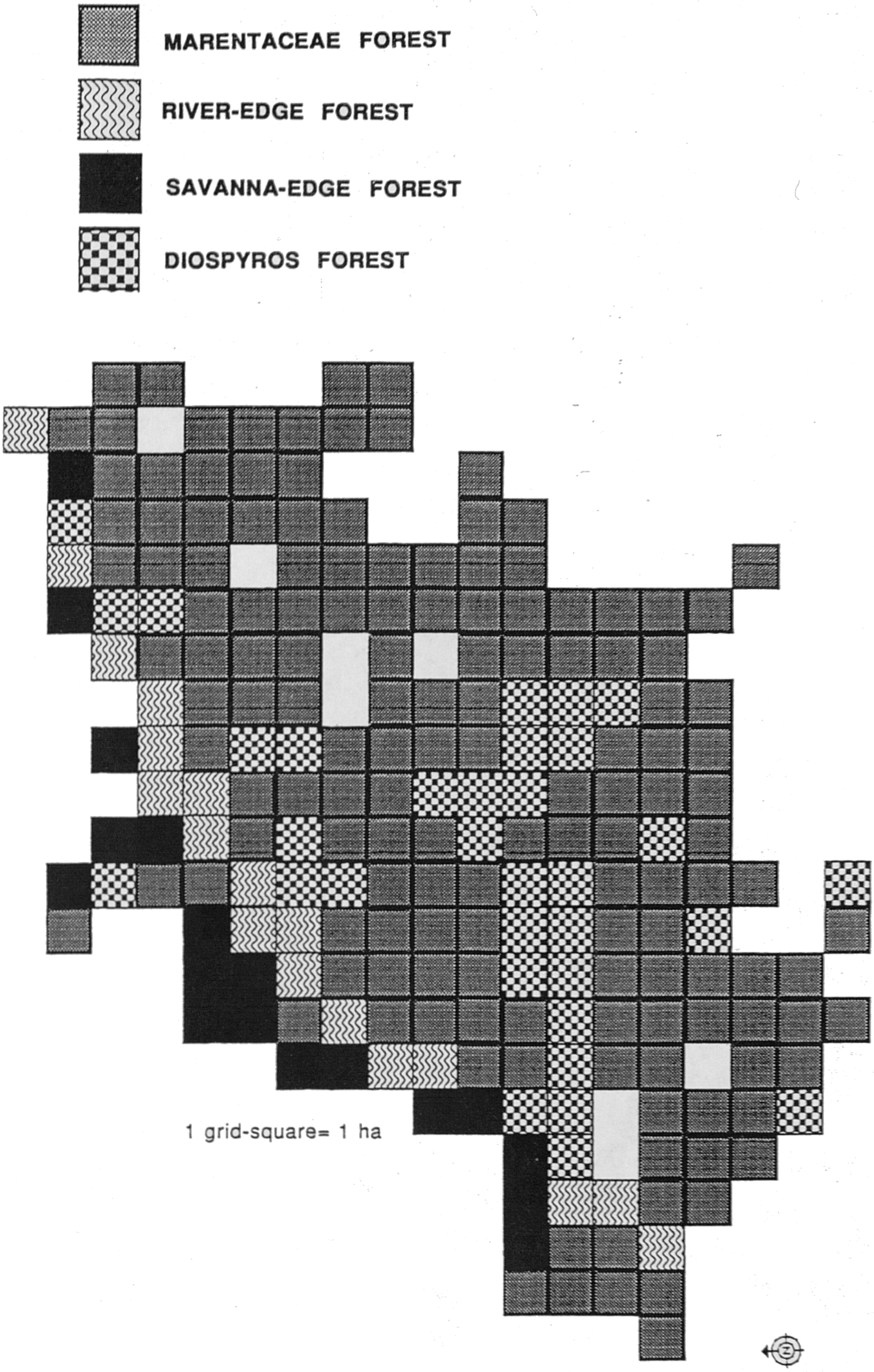


Figure 6.7 Map showing the grid squares of each habitat-type in the annual home range of the study group of mangabeys.

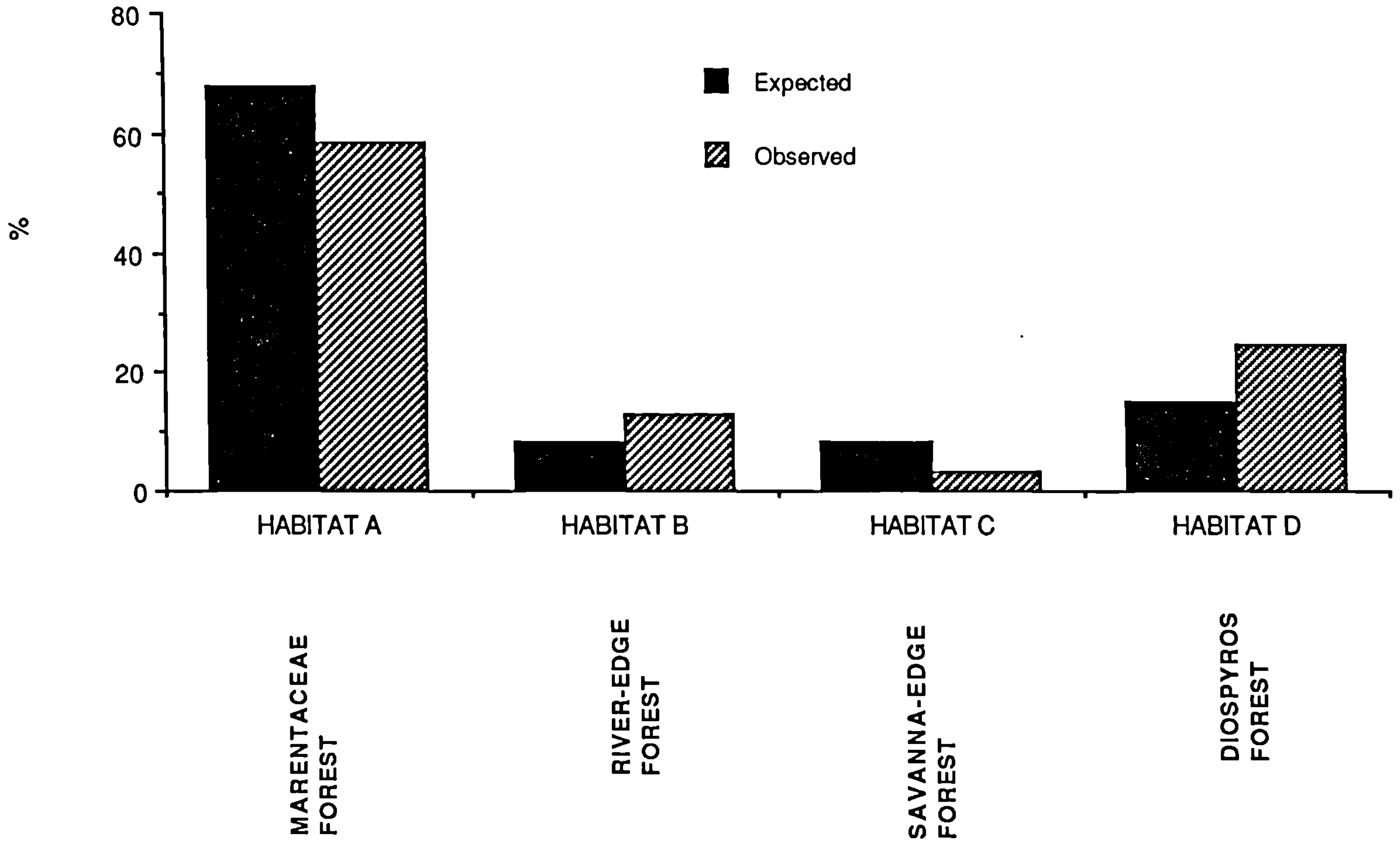


Figure 6.8 Expected and observed proportion of time the study group of mangabeys used each habitat-type.

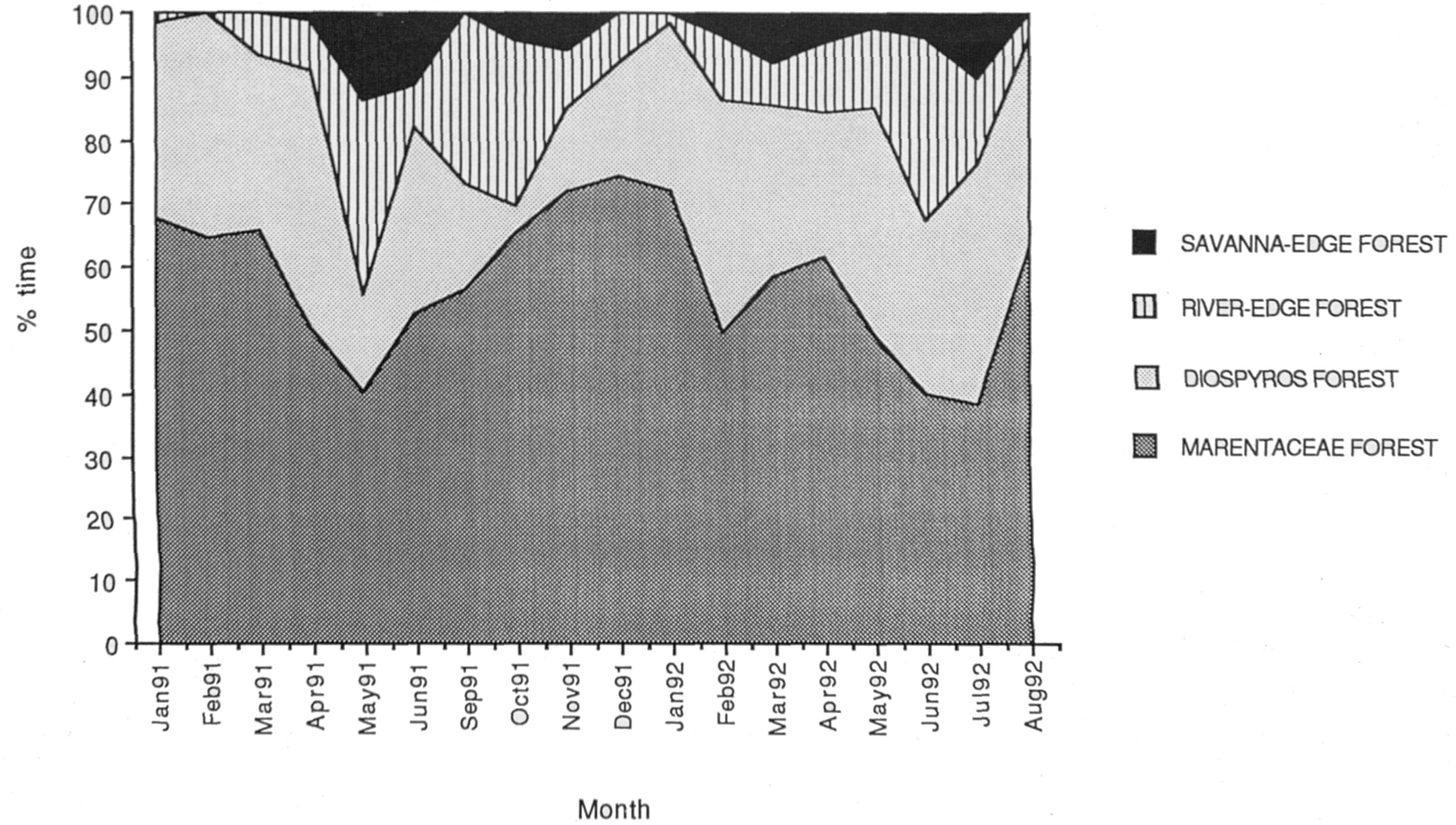


Figure 6.9 Monthly variations in the proportion of time the study group of mangabeys spent in each habitat-type.

in the 'top 10' species in terms of time spent feeding), the proportion of time that mangabeys spent in each habitat type was tested for correlation with the availability of these species (as determined by Phenological monitoring: see *Chapter Three*). The proportion of time that mangabeys were observed in each habitat type was also tested for correlation with the monthly percent of time that mangabeys were seen to feed on each of these 'important' species (see *Appendix 5.2*).

The amount of time that mangabeys were observed in the "River-edge" habitat was significantly correlated with and the amount of time spent feeding on *Pycnanthus angolensis* fruit (including pulp and seeds) (r_S=0.53, n=15, p=0.04), but not the availability of its fruit (r_S=0.12, n=18, p=0.62). The "Savanna-edge habitat" was positively related with the availability of *Uapaca guineensis* fruit(r_S=0.56, n=18, p=0.15), although not the time spent feeding on this species (r_S=0.12, n=15, p=0.66). *Uapaca guineensis* is one of the species characteristic of both savanna-edge and river-edge habitat types. The amount of time that the mangabeys were observed in the "Rocky forest" habitat was weakly positively correlated with the availability of *Diospyros dendo*, (r_S=0.44, n=18, p=0.07) but strongly positively correlated with the time spent feeding on this species (r_S=0.69, n=15, p<0.01). *Diospyros dendo* is a characteristic species of this habitat type (White, 1992). The use of "Marentaceae forest" was not significantly correlated with the availability, or the time spent feeding on any of the "top 10" food species (although habitat types could not be correlated with the availability of *Distemonanthus bethamianus* or *Elaeis guineensis* fruits, as these trees were not monitored for fruit production).

Mangabeys spent the greatest proportion of time feeding on

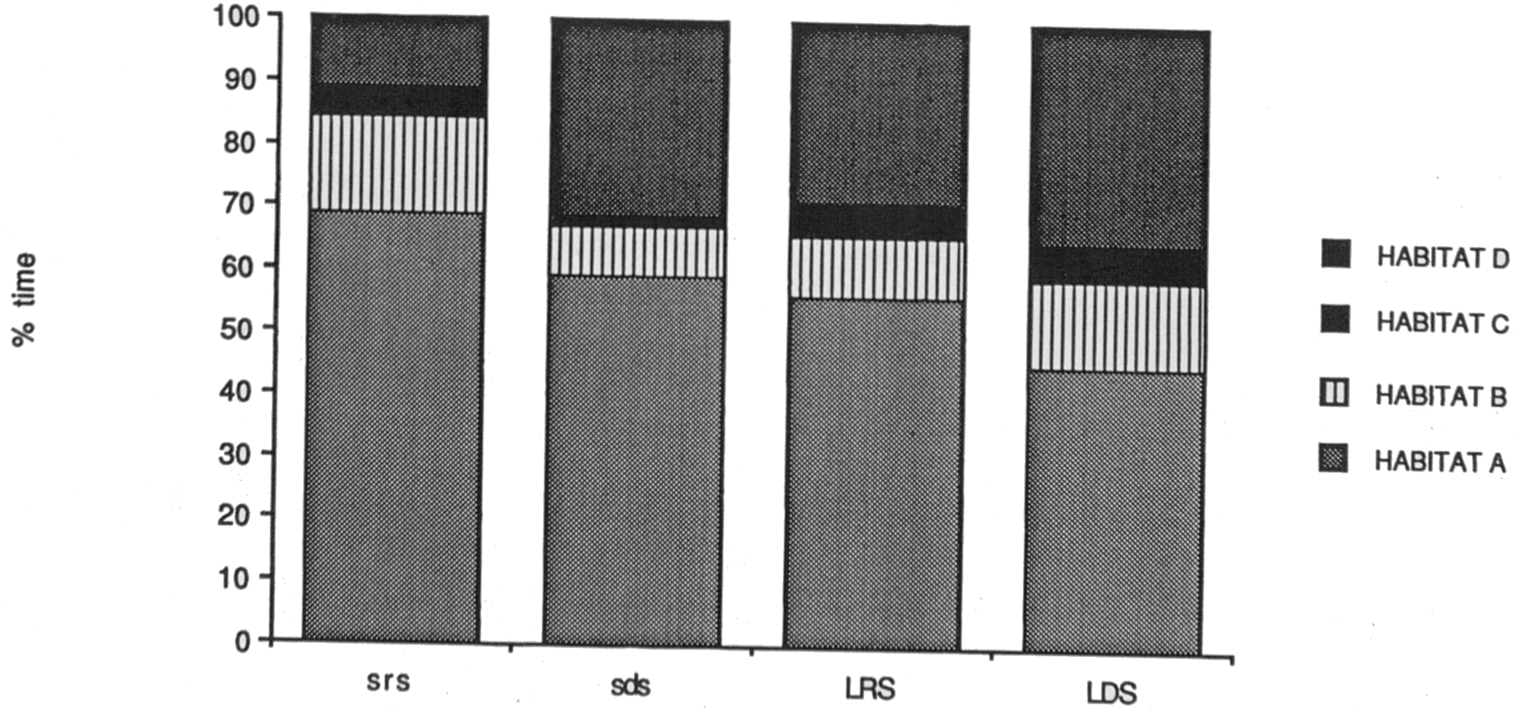


Figure 6.10 Percent of scans that the study group of mangabeys was observed in each habitat-type during each season

the new leaves of *Cryptosepallum staudtii* (a tree species especially common at the savanna-edge) (*Chapter Three*) in June 1991. Savanna-edge habitat was positively selected during this months. Likewise, mangabeys spent the greatest proportion of time feeding on new leaves of *Milletia sp.,* (a species especially common of river-edge habitat) (*Chapter Three*) in October 1991, a month when river-edge habitat was positively selected.

4. Range overlap with other groups and intergroup encounters

At least five other groups of mangabeys were observed to enter 59 grid-squares within the home range of the study group, making up 26.22% of the total home range over 18 months and 27.44 % of the annual home range (**Figure 6.11**). Because these groups were not followed systematically, it is likely that this is an underestimate of the true home range overlap.

The overall annual selectivity of the areas of overlap was calculated to be 0.09, showing that these areas were neither selected for nor against. The average use of these overlapping areas over 12 months was 34.11% (SD=10.72). The month with the highest selection ratio was February 1991 and 1992, and August 1992 (**Table 6.4**). The percent of monthly scan samples that the study group was observed in the overlapping areas was significantly higher during the dry season than during the short rainy season (Chi-square=11.49, df=1, p<0.01), and the long rainy season (Chi-square=8.84, df=1, p<0.01), and the time spent in the overlapping areas was greater in the short dry season than in during the short rainy season (Chi-square=4.51, df=1, p=0.03).

Waser (1976) developed a formula to test whether encounters

Table 6.4 Percent of scans spent in areas of overlap with other groups, selection ratios for those areas and frequency of intergroup encounters for each month

Month	% of scans in overlapping areas grid squares	Selection Ratio	Number of Intergroup Encounters	% of scans in intergroup encounter
Jan-91	24.19	-0.04	1	1.61
Feb-91	58.96	0.38	6	14.45
Mar-91	25.66	-0.01	1	1.89
Apr-91	22.33	-0.08	0	0.00
May-91	31.67	0.09	1	0.90
Jun-91	19.10	-0.16	1	1.12
Sep-91	33.30	0.12	3	11.67
Oct-91	20.43	-0.12	1	1.08
Nov-91	28.14	0.04	1	0.38
Dec-91	37.87	0.18	4	6.06
Jan-92	29.32	0.06	1	0.75
Feb-92	39.49	0.20	0	0.00
Mar-92	31.51	0.09	0	0.00
Apr-92	21.79	-0.09	2	1.90
May-92	35.03	0.14	0	0.00
Jun-92	32.38	0.11	0	0.00
Jul-92	37.63	0.18	0	0.00
Aug-92	62.40	0.41	3	2.40
18 MONTHS				
Total	**591.20**	**1.50**	**25**	**44.21**
Mean	**32.84**	**0.08**	**1**	**2.46**
S.D.	**11.86**	**0.16**	**2**	**4.15**
12 MONTHS				
Total	**409.29**	**1.31**	**15**	**24.24**
Mean	**34.11**	**0.11**	**1**	**2.02**
S.D.	**10.72**	**0.14**	**1**	**3.51**

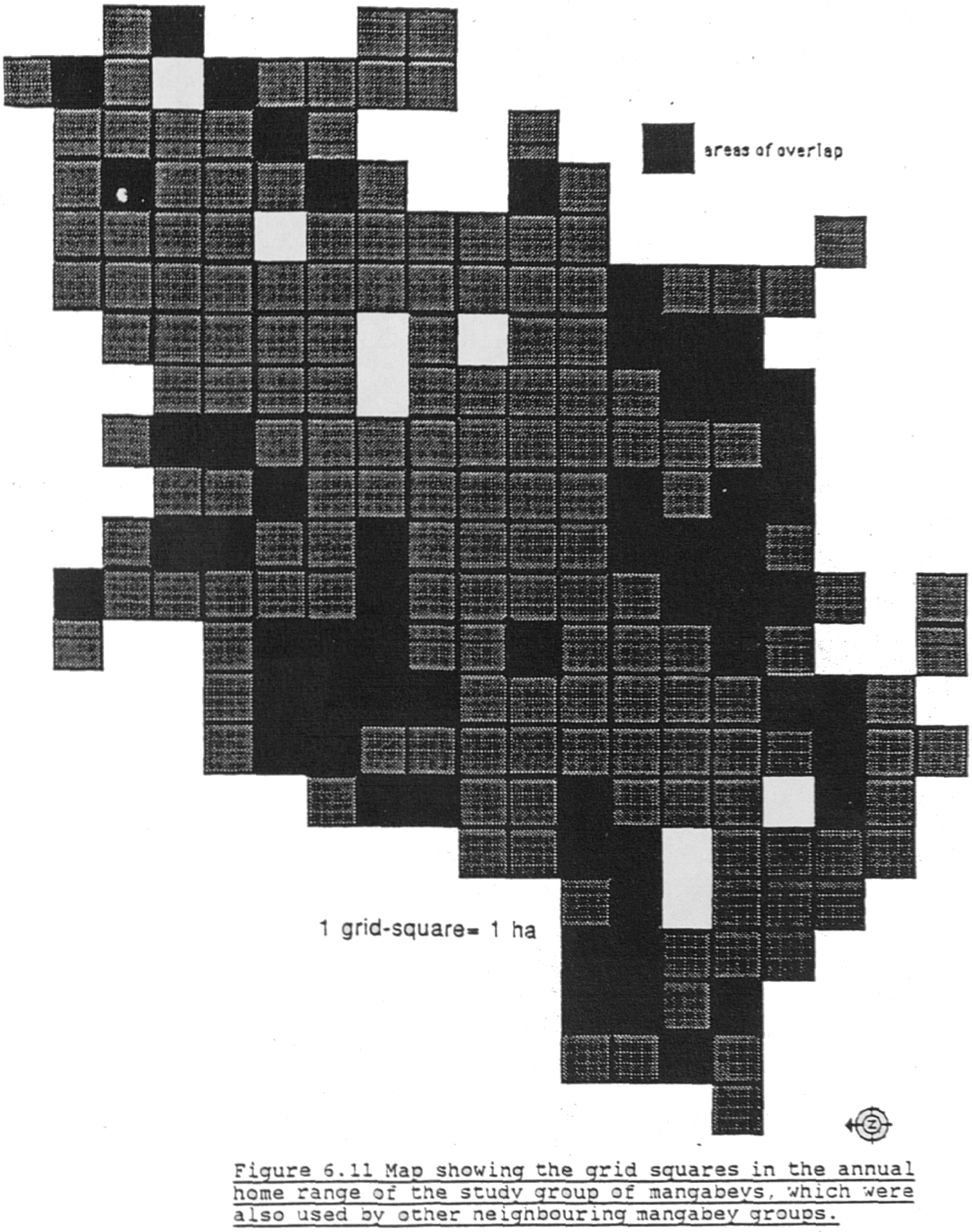


Figure 6.11 Map showing the grid squares in the annual home range of the study group of mangabeys, which were also used by other neighbouring mangabey groups.

occur more frequently than expected by chance:

$f=4\ p\ v\ /\pi\ (2d+s)$ Waser (1976)

where f is the frequency of expected encounters, p is the density of the groups in the area (p=0.265 group/km^2 for other groups), d is the distance criterion (d=0.200 km), s is the groups spread (s=0.120 km) and v is the velocity with which groups travel (v=0.049 between scan samples=0.196km/hr). This velocity was calculated by averaging the annual mean distance travelled, over the time of day (**Figure 6.12**). This equation predicts that 0.034 encounters should be observed during each hour of observation. During 18 months, the study group was observed for 618 hours and therefore 21 encounters were expected. During 12 months, the study group were observed for 394 hours, and therefore 14 encounters were expected. There were 25 encounters observed during the 18 months and 15 during the year. Therefore the frequency of intergroup enounters was very similar to that expected.

The number of scans that the study group were observed within 200m of another group was also recorded. Waser (1987) provides another formula to test if the duration of intergroup encounters is any more or less frequent than expected given the density of groups:

$T=(\pi^2/2)\ p\ r^2$ (Waser, 1987)

where p is the density of the groups in the area (p=0.265 group/km^2 for other groups), r=ri+rj+d, where r=the radii of groups i and j (r=0.060 km), and d is the distance criterion (d=0.200 km). This equation predicts that the study group should be observed within 0.200 km of another group of mangabeys during 13% of all scans. The percent of scans the study group was observed within 0.200 km of another group of

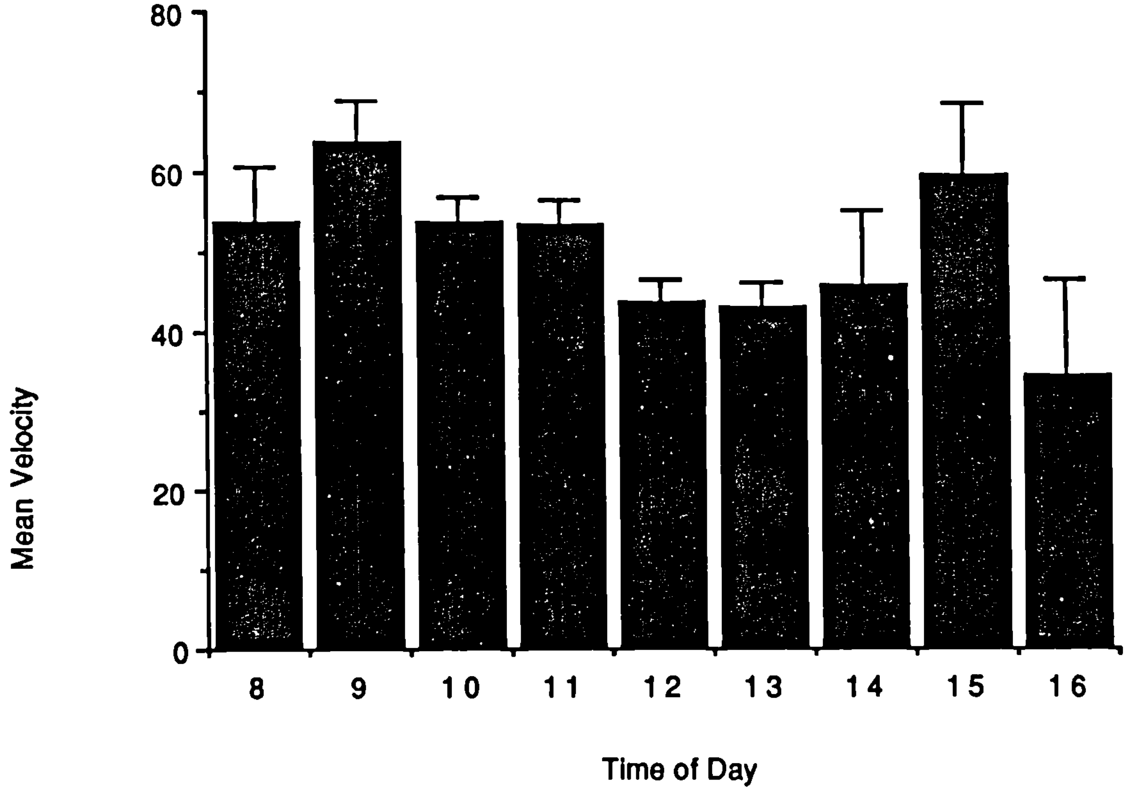


Figure 6.12 Mean velocity (m/15 minutes) travelled during each hourly interval of the day, with SE bars

mangabeys was calcuated for each month (**Table 6.4**). This was averaged across months to give a mean of 3% and 2% of all scans, during 18 months and 12 months respectively, that the study group were observed within 0.200 km of another group of mangabeys. These values are less than the predicted values. Therefore, although the study group encountered other groups of mangabeys as expected, the duration of the encounters was less than expected.

The number of encounters was highest during February September and December 1991, and April and August 1992. The location of all intergroup encounters was recorded (**Figure 6.13**). Although there was a peak in the amount of time spent in overlapping areas and the number of intergroup encounters in August 1992, December 1991 and February 1991, the relationship between these two variables was not significant (r_S=0.09, n=18, p=0.72).

Behaviour of the mangabeys during encounters was extremely variable. Whoop-gobbles (see *Chapter Seven*) were emitted from both groups on 22 of the 25 encounters (88%),and during four encounters, adult males were seen to move rapidly through the canopy towards the other group. The path of the males through the trees was usually low and loud grunts were emitted as they approached.

In 21 encounters, the groups approached each other when they were within vocalising distance. In four encounters it was not clear how the encounter began. During four encounters the study group withdrew; during 6 encounters, the other group withdrew (all of which were Group Two); and during 13 encounters, both groups withdrew. During two encounters, there was no apparent reaction, although both groups were within hearing distance of each other.

The most frequent encounters took place between the study group and the group to the north of their range (Group Two). Group Two was observed to overlap at least 31 ha with the study group and at least 32 ha with another group to the north, so the overlap comprised 40% of their overall estimated home range. This group was unusual in that its home range was made up of an area of forest bordered by savanna on the east and west side, which joined two main block of forests. Its home range, therefore, could only overlap with two groups.

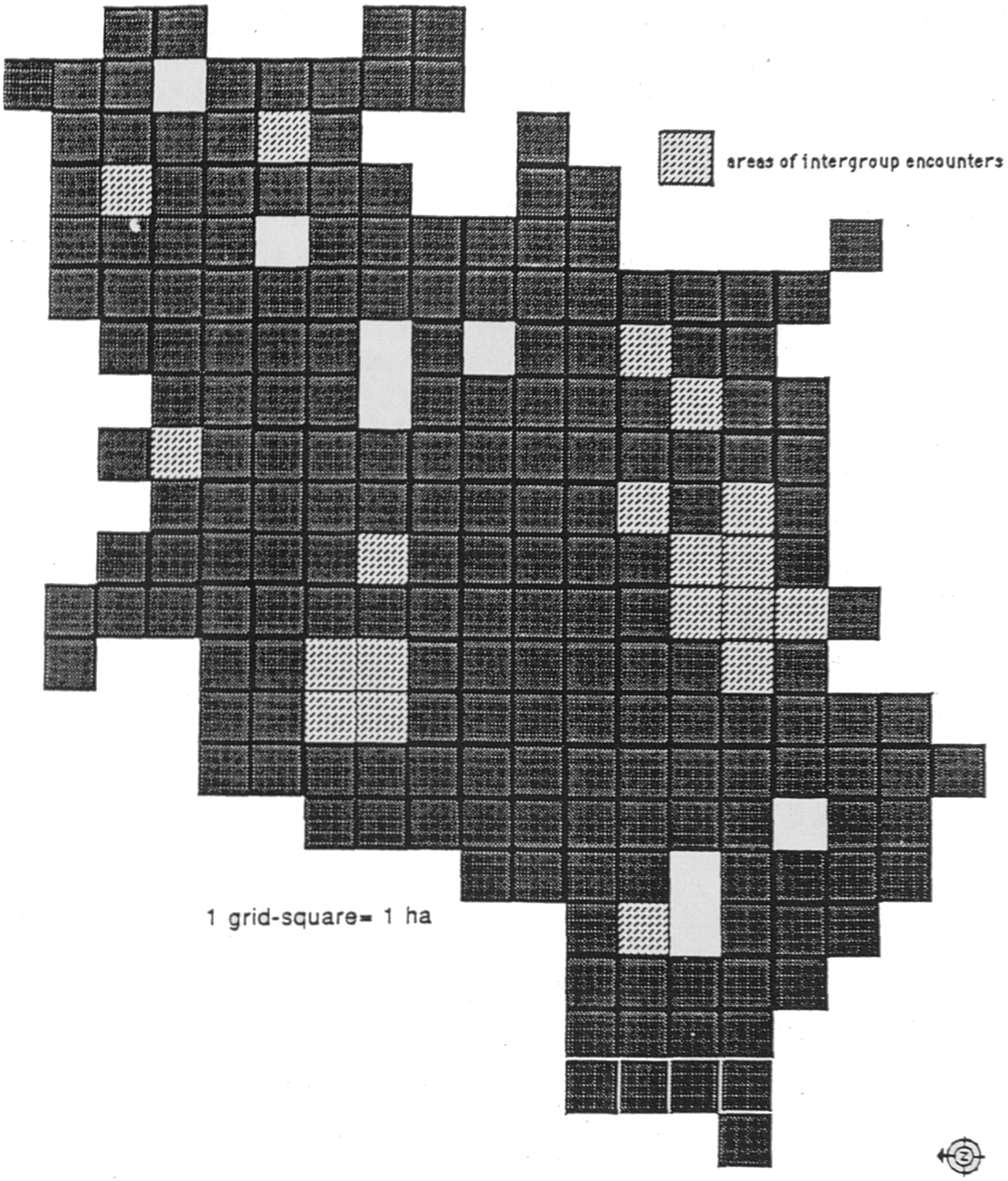


Figure 6.13 Map showing the grid squares in the home range of the study group of mangabeys where intergroup encounters occurred.

DISCUSSION

In summary, two groups of grey-cheeked mangabeys at Lopé were observed to have a home range size of 225 ha and 156 ha over 18 months. Not all of the home range was used used each month and seasonal changes were observed in range use. The results suggests that food has a great influence on ranging patterns because (1) ranging diversity increased with increased dietary diversity (2) ranging diversity increased with an increased availability of ripe fruit (3) monthly range size decreased with an increase in the proportion of leaves in the diet, and (3) use of certain habitats was significantly correlated with the availability of fruit from species characteristic of that habitat type, or the proportion of time spent feeding on those species. Ranging patterns did not appear to be greatly affected by other groups of mangabeys, since use of areas of overlap, and the frequency of intergroup encounters was not any more or less frequent than expected by chance.

Comparison to other studies of grey-cheeked mangabeys

Home range size

The mangabeys at Lopé had a home range only about half the size of the mangabeys studied by Waser(1974) at Kanyawara, and slightly larger than the home range size of mangabeys observed by Freeland (1979) (**Table 6.5**). The higher density of trees at Ngogo than Lopé, and Lopé than Kanyawara (see *Chapter Three*), may mean that mangabeys do not have to travel so far to visit the same number of trees, resulting in relatively smaller home ranges with increasing tree density. Home range size for mangabeys in the present study, was

Table 6.5 Measures of ranging behaviour of grey-cheeked mangabeys in other studies

Country	UGANDA	UGANDA	UGANDA	UGANDA	EQUATORIAL GUINEAE	GABON
Study Site	**Bujuko**	**Kanyawara**	**Nogogo**	**Nogogo**	**Ndakon**	**Lopé**
Source	Chalmers (1967)	Waser (1974)	Freeland (1977)	Wallis(1979)	Cashner (1974)	Present study
Home range size (ha):						
gird-square	NA	286 ha in 12 months	140 ha	250 ha	NA	215 ha/12 months
minumum convex polygon	NA	410 ha in 15 months	175-200 ha	NA	at least 200 ha	277 ha in 12 month
arbitrary line enclosing all sightings	13ha in 22 months	NA	NA	NA	NA	NA
Day range (m)	"group frequently moved over its entire home range in one day"	1135	1299	NA	884	1056 (from 09:30-14:30)
Mitani and Rodman (1979) Index of defendability	NA	0.50	0.97	NA	0.55	0.62
% home range overlap	"groups overlapped slightly"	72%	11%	NA	100%	26.22%
No.intergroup encounters	None					
within 100m	None	1 in 160 days	NA	NA	NA	NA
within 200m	None	4 in 160 days	NA	NA	NA	25 in 18 months
within 500m	None	11 in 160 days	NA	NA	24 in 65 days	NA
Population density						
Grey-cheeked mangabeys						
biomass kg/km2		60*	129**	129**		41****
indivs./km2	77	9*			22	10****
group/km2		0.6*	1.31**	1.31**		.43-.69***
All diurnal primates						
biomass/km2		2652*	1954**	1954**		419****
indivs./km2		546*				52.1****
group/km2		19*	6.49**	6.49**		4.02-7.14***

* data from Waser (1987)
** data from Butynski (1990)
*** White (personal communications)
****White (1992)

slightly smaller, however, than the home range sizes observed by Wallis (1979), who also studied mangabeys in Ngogo. In eastern Uganda, Chalmers (1967) observed mangabeys to have a home range less than 10% of the mangabeys in the present study. These differences are less easily explained.

Another differences between Lopé in Gabon and the study sites in Uganda, is the climate and its effects on the predictability of resources. In Uganda, the seasonal changes are not as marked as in Gabon. During the long dry season in 1992 at Lopé, there was no rainfall for almost three months, compared to only 10 days during Waser's (1974) study. Waser(1977a) observed that the relatively even distribution of rainfall throughout the year released many tree species from a synchronized annual pattern of phenology and that many of the species used for food by mangabeys came from trees that "fruit either asynchronously and non-seasonally or synchronously but at very long and possibly irregular intervals." At Lopé there is marked seasonal fluctuation in food availability, and long term phenological monitoring of trees at Lopé has shown that fruiting is synchronous and seasonal for many species (Tutin *et al*., 1991b). 'Important' foods in the diet of the mangabeys in this study all fruit seasonally, except *Elaeis guineensis* . Because trees fruit synchronously and seasonally at Lopé, the availability of food may be more predictable both in time and space than for mangabeys living in Uganda. Because the fruiting of trees is seasonal in Gabon, and because ranging is related to food availability, the group may return to areas occupied the previous season, resulting in a smaller home range size than at Kanyawara, where the fruiting of trees is not as seasonal. This is supported by the observation that overlap between the long rainy season in 1991 and 1992 was greater than the mean overlap between months, whereas Waser (1975a) observed no such patterns.

In addition to the factors mentioned above, the differences in range size between study sites may also be affected by the differences in the composition of the primate community and the primate density between study sites. Information is not available from all studies on primate species density, but what data is available suggests that home ranges may be larger in areas where there are more competing species and a greater overall primate biomass. At Kanyawara and Lopé, there are a similar number of anthropoid primate species (n=8), but the total anthropoid primate biomass at Kanyawara (3133 kg/km^2, Butynski, 1990) is greater than at Lopé (418 kg/km^2).

Anthropoid primate densities at Ngogo, are smaller than at Kanyawara, though much greater than at Lopé (1954 kg/km^2). Data on primate densities are not available from Chalmers' (1967) study, but the only other anthropoid primate species was the redtailed monkey (*Cercopithecus ascanius*). Range sizes were smallest in Chalmers' (1967) study where mangabeys have to compete with only one other primates species, and largest at Kanyawara, where primate biomass is greatest, and intermediate at Lopé where primate biomass is intermediate. Therefore the number of competing species, or the overall primate biomass may have a significant effect.

Finally, group size has been shown in other studies to affect the home range size, where larger groups use larger areas for their home range (Clutton-Brock and Harvey, 1977). In the present study, however, home ranges were smaller and group sizes larger, than in Waser's (1974) study where home ranges are larger and group sizes smaller. In addition, the mangabeys studied by Waser (1974) had a similar home range size to Chalmers, yet the difference between their home range sizes were enormous. These comparisons, therefore, *do not* support the hypothesis proposed by Clutton-Brock and Harvey (1977). This is probably because there are other factors involved, such as those mentioned above.

The very small home ranges described mangabeys studied by Chalmers (1967) in Uganda are puzzling. During part of Chalmers' (1967) study, he could only make observation from permanent paths or roads because the undergrowth in the forest was impenetrable. Chalmers (1967) points out that "on the days when the group was not seen in the whole day it was nevertheless possible to hear it and so to know its approximate position", but Waser and Floody (1974) question the validity of his estimates. Alternatively, Wallis (1979) suggests the small home ranges in Chalmers' (1967) study may be due to human pressures on the area. The home range of the mangabeys observed by Chalmers (1967) was surrounded on three sides by plantations in which the mangabeys were sometimes observed to feed. The mangabeys in Chalmers (1967) study therefore, *may have had* a *more* predictable and constant source of food, allowing them to have a smaller home range.

Home range overlap and intergroup behaviour

Not only are there large differences in the home range sizes of mangabeys studied at different locations, but there are great differences in the degree to which their ranges overlapped. In the present study the home range of the mangabeys overlapped almost a third the amount of the mangabeys studied by Cashner (1972), a half the amount of mangabeys studied by Waser (1974), a similar amount to those studied by Wallis (1976), but at least three times the degree of overlap in the mangabeys studied by Chalmers (1967) (**Table**

6.6).

There were also differences between studies in the behaviour of mangabeys towards other conspecific groups. In the present study, mangabey groups did not encounter each other any more or less often than would be predicted by chance. They also did not select for or against areas that were shared with other groups. Waser (1976), however, observed that groups encountered each other less often than expected by chance and that they showed "mutual avoidance", Chalmers (1968b) observed mangabeys to completely avoid other groups, whereas Cashner (1972) observed groups to approach each other and to merge together.

These differences may be explained partly by the differences in the home range sizes. The costs of defending a territory can be measured in terms of the energy it requires to monitor the home range and the energy and risk of its actual defence. The benefits of defending a territory are to protect resources from exploitation by other groups. It is only worth defending a territory if the benefits outweigh the costs (Harrison 1983b; Struhsaker, 1975), that is, when it is "economically defendable". Theories of optimal territory size predict that as the home range size becomes larger, the territory will become too big to utilise all resources within the range. The cost of defence becomes greater because the area over which the group must patrol is larger, therefore demanding more energy. The number of adjacent groups may increase, thus making the area more difficult to defend. Mitani and Rodman (1979) state that "to maintain a territory, group members must encounter the perimeter of their range frequently enough to monitor potential intruders". Most animals that exhibit territorial behaviour are those that can cover their whole home range in a day. The "index of defendability" proposed by Mitani and Rodman (1979) is the ratio of day-range length to home-range size. In a comparison across primate species, they found that territories are more defendable if this ratio is high and species with ratios of less than one are usually non-territorial. In the present study, mangabeys have a similar day range length but a smaller home range size, resulting in a higher "index of defendability" than the mangabeys studied by Waser(1974) and so would be more likely to defend a territory.

In addition, the maintenance of an exclusive home range is not likely to be adaptive for animals which feed on resources like fruit, that are concentrated in space and intermittent in time. Differences between studies in the defendability of resources can also depend on resource quantity and distribution in time and space (Davies and Houston, 1978). Because the density of trees, and the predictability that a given area will contain food at a given time is higher at Lopé than at Kanyawara, there may be more incentive for the mangabeys at the Lopé to defend an area and this may partially explain why intergroup encounters were more frequent.

The mangabeys studied by Chalmers (1967) showed a very high "index of defendability" and this may explain why their overlap with neighbouring groups was so low. Chalmers (1967) saw no intergroup encounters, but this does not mean that their territory was not defended. Defence of a territory does not necessitate conflict. Both Chalmers(1967) and Waser (1974) suggest that the long call of the mangabey, the "whoop-gobble"(see *Chapter Seven*), plays a role in intergroup spacing.

Surprisingly, although the mangabeys studied by Cashner (1972) live in a similar climate and have a similar home range size to the mangabeys in this study, their home range overlap was virtually complete. Mangabey groups were observed by Cashner (1972) to come together and mix peacefully throughout the day. There are at least three possible explanations for this.

Firstly, it is possible that these were not separate groups, but sub-groups, and that Cashner(1972) was observing fission-fusion of a single group. Because the group spread for grey-cheeked mangabeys is so large, it is easy to mistake one group for two if the identity of all individuals is not known. Second, if they were separate groups, it may be that food was so abundant in the habitat that mangabeys did not have to compete for resources, and therefore there was no need for any sort of territorial behaviour. This hypothesis is also supported by the high frequency of polyspecific associations in Cashner's (1972) study. Finally, it is possible that the low density of gorillas and chimpanzees in the area decreased the competition for resources.

Freeland (1979) also suggested that as tree density increases, the home range size decreases and overlap between adjacent groups is smaller. But he also suggested that group size does not increase, resulting in similar densities of mangabeys. Freeland (1979) proposed that this may be an adaptation for disease control. In the present study, however, although range size did decrease and overlap between adjacent groups was smaller, the group size *did* increase, as shown in *Chapter Four*, therefore Freeland's (1979) hypothesis seems unlikely.

Comparison to other mangabey species

Very little data exists on the home range sizes of other species of mangabeys. Horn (1987b) reports a home range of 48 ha and 70 ha for two groups of black mangabeys, and a home ranges overlap of 60% to 70%. As shown in *Chapter Four*, black mangabeys have similar group sizes to grey-cheeked mangabeys (mean=17.5, n=4) (Horn, 1987b), but they have a higher population density (4 groups per km^2) than grey-cheeked mangabeys in the present study and in Uganda (Cashner, 1972; Chalmers, 1967; Freeland, 1979; Wallis, 1979; Waser, 1974). The two main field studies of agile mangabeys, *Cercocebus galeritus* report very different home range sizes of 35 ha in Kenya (17-53 ha) (Homewood,1978) and 198 ha in Gabon (Quris, 1975).

Compared to other arboreal primates, grey-cheeked mangabeys have generally the largest home range size (see Smuts *et al.*, 1987 for comparisons with range sizes for other primates). This is probably related to a combination of their large body size, large group size and diet. Larger animals, in general have to eat more food and therefore would be expected to have larger home ranges. Although there are other arboreal primates with a larger body mass (e.g. *Colobus spp.*), and similar group size (e.g. *Cercopithecus pogonias*), it is probably the combination of the large body size *and* large group size and their reliance on *fruit* (pulp and seeds) that necessitates a larger home range size for mangabeys in order for them to to meet their energetic requirements. Fruit is a resource that is often found in patches, unevenly distributed throughout their range in both time and space. Animals feeding on resources that are patchily distributed (like fruit) are expected to have a larger range in order to find enough food, than animals feeding on resources (like leaves) that are distributed evenly and abundantly year-round (Clutton-Brock and Harvey 1977; Waser, 1977 a).

SUMMARY

In summary, the large body size and group size of mangabeys, and their highly frugivorous diet necessitates a large home range size in order for all group members to meet their energetic requirements. Large range size increases overlap between groups and decreases the likelihood of territorial behaviour. Differences between study sites can be explained by differences in density and of trees species, predictability of resources through seasonality, and differences in sympatric primate species.

CHAPTER SEVEN: SOCIAL BEHAVIOUR and TRIADIC MALE-INFANT INTERACTIONS

PART I: SOCIAL BEHAVIOUR

INTRODUCTION

More is known about the social behaviour of Cercopithecines that live in multimale groups than any other primate class (Melnick and Pearl, 1987). Most information on social relationships comes from studies on baboons, macaques and vervets, and mostly from terrestrial species living in open savanna-habitats. Very little is known about forest living and arboreal multimale Cercopithecines (Moreno-Black and Maples, 1977). Because mangabeys are closely related to baboons, their behaviour has frequently been compared (eg. Chalmers, 1968 c, Wallis, 1981), but as little is known about mangabeys, these comparisons are only in their preliminary stages.

Only three papers discuss their social behaviour in the wild in detail (Chalmers 1968a, c; Wallis, 1981), although some information can be found in the unpublished theses of Chalmers (1967), Wallis (1979), Waser (1974) and Cashner (1972). Descriptions of the behaviour of grey-cheeked mangabeys in captivity can be found in Chalmers and Rowell (1971), Deputte (1992), and in the unpublished theses of Danjou (1972) and Deputte (1986). The behaviour of captive sooty mangabeys is discussed in Ehardt (1988) and Kyes (1988).

The purpose of this chapter, therefore, is to investigate in detail, the social behaviour of grey-cheeked mangabeys. In Part I of this chapter, the behavioural repertoire, of grey-cheeked mangabeys is described. The frequency of affiliative, agonistic and sexual behaviours and associations between individuals are given in order to examine the roles of individuals or age/sex classes in the group. In Part II, the relationship between adult males and infants will be examined in more detail.

METHODS

A. SOCIAL BEHAVIOUR

1. Behaviour recorded during scan samples

All information on social interactions came from a single study group habituated to the presence of observers. Frequency of behaviours were recorded for each age/sex class (see *Chapter Two*) and because adult males were recognised throughout the study, they were considered individually.

Grooming and *play* were the only behaviours to occur frequently enough to allow them to be recorded during scan samples. These behaviours were therefore included in the six mutually exclusive categories recorded during scan samples, as described in *Chapter Two*.

Grooming:

This behaviour was defined in *Chapter Two*. When the focal animal was grooming, the identity of the grooming partner, whether the focal animal was the groomer (GRO subject grooms other), being groomed (OGR=other grooms subject), or whether the subject was grooming itself (GS=groom-self) was recorded.

Playing:

This behaviour was also defined in *Chapter Two*. When the focal animal was playing, the identity and age/sex categories of those playing with the focal animal were also recorded.

2. **Behaviour recorded** *ad libitum*

All other behaviour occurred too infrequently to be recorded during scan samples and so instead were recorded *ad libitum*. The following provides a description of behaviour recorded this way.

(a) Affiliative behaviour :

Affiliative behaviour was defined as "all patterns implying 'friendliness' from greeting rituals to those expressing marked personal preferences between individuals" (*Bertrand*, 1969)

Non-sexual present:

The subject presents its ano-genital region to another, usually more dominant animal, with forelimbs slightly flexed, sometimes glancing over its shoulder towards the monkey to which it is presenting. This behaviour is also described by Wallis (1981) who specifies that the tail is held vertically and curled posteriorly.

Grooming present:

The presenter stands with all four limbs straight and presents its flank towards another animal. The behaviour is usually followed by grooming between the two animals. Wallis (1981) specifies that the tail is held vertically and the tip of the tail is curled anteriorly in during this present.

"69 embrace":

A term invented by Wallis (1981), the '69 embrace' describes when " the juvenile moves towards the seated animal and thrusts its head into the crotch of the seated animal. The hind legs are then thrown up, so that the juvenile performs a head stand in the lap of the adult. When the head is in the crotch, it is twisted and on performing the head stand the body follows this twist to bring the juvenile's ventral surface into contact with that of the adult. The juvenile's legs and tail are at level with the adult's head. The adult then embraces the abdominal region of the juvenile with both forelimbs. The embrace is released after 5 to 10 seconds. The juvenile *then rights itself and either sits* with, grooms or moves away from the adult."

Standing embraces:

This type of embrace occurs when two monkeys approach each other on a branch. When they are parallel to each other, they pause. One monkey places its arm over the back of the other; likewise the second monkey places its arm over the back of the first. This position is held for a few seconds, then released. The animals then continue along the branch, in opposite directions. This behaviour has not been previously described in mangabeys.

Mutual embraces:

During a mutual embrace, a seated animal is approached by another, who crouches in front of it, and the two embrace each other with their ventral surfaces in contact.

Lip-smacking:

When lip-smacking, the neck is stretched forward and the slightly pouted lips are rapidly opened and closed.

Non-Sexual mount:

During a non-sexual mount, a juvenile or sub-adult male mounts an adult male, thrusting the pelvis against the side of the adult male. This behaviour has not been previously described in mangabeys.

(b) Agonistic behaviours:

Agonistic behaviour was defined as "those activities directed against another animal which cause physical insult, effect withdrawal or otherwise intimidate the others", and "behaviours which communicate or demonstrate an acknowledgement or acceptance of another animal's dominance" (Bertrand, 1969).

Chase:

A chase occurs when one individual pursues another animal, usually running.

Supplant:

For a supplant, one animal approaches another animal, usually at a walking pace. The approached animal leaves (sometimes leaping away), and the approaching animal takes its place.

Displace:

A displace is similar to a supplant but the approaching animal does not remain in the place previously occupied by the approached animal.

Lunge:

The animal rapidly lurches forward onto one forelimb. The direction of movement is aimed at another individual (described in more detail by Wallis, 1981).

Yawn:

During a yawn the animal slowly opens its mouth with its head slightly tilted back. The lips are retracted exposing the teeth. This gesture is held for a few seconds. Yawns are described in more detail by Wallis (1981).

Penile display:

During a penile display, the mangabey sits with its legs widely spread and knees bent. In males, the penis is often clearly visible; flaccid or erect.

Fast head shake:

Described by Wallis (1981), a fast head shake occurs when the head is shaken from side to side several times a second over 1 to 5 seconds.

Mane erection:

For a mane erection, the adult male clearly erects the hairs on the back of his neck and shoulders (described by Wallis,1981).

Grab:

During a grab, one animal reaches towards and grabs hold of another animal with either one or both hands.

Bite:

This is recorded when one animal bites another, regardless of whether any obvious bodily harm is done.

Branch shake:

An animal bounces on a branch with all four limbs straight, causing the branch to shake. Occasionally, thinner branches are also shaken with the hands. This behaviour has not been previously recorded in mangabeys.

Ignore

While remaining seated, the individual suddenly and forcefully turns its back, so that the body and head are twisted to face in the other direction. This position is frozen for about four seconds and then the individual suddenly jerks back to face the individual to whom the behaviour is being directed. This has not been previously described for mangabeys.

(c) Sexual behaviour

Sexual behaviour was defined as any behaviour related to mating.

Sexual presenting:

In this type of present, the forelimbs are straight and the presenter does not glance over the shoulder. Wallis (1981) also describes this behaviour and specifies that the tail is curved anteriorly over the back.

Ano-genital inspection:

An adult male visually or olfactorily inspects the swelling or surrounding area of an adult female who is sexually presenting to him. This behaviour is also described by Wallis (1981).

Head flag:

Wallis (1981) describes this behaviour as being performed by a seated male towards a female during the peak of her swelling. He turns his head back over his shoulder five or six times in two to three seconds. This gesture is usually followed by the swollen female approaching and presenting to the adult male.

Sexual mounting and copulations:

Sexual mounts and copulations are described in detail in Wallis (1981, 1983). The male approaches the adult female from behind, places his feet on the calves of the female, and grasps her hips with his hands. He inserts his penis into her vagina and then thrusts several times. Ejaculation corresponds with a pause in the thrusting. Copulations are described in more detail in (Wallis, 1981).

Sexual harassment:

Sexual harassment occurs when one or more animal jumps on, slaps, or grabs at either one or both members of a copulating pair.

Consort behaviour:

Females in oestrus are often observed on the periphery, up to 300 m away from main body of the group. Although occasionally alone, during the peak of their swellings they are usually accompanied by an adult male.

(d) Vocalisations

The vocal behaviour of grey-cheeked mangabeys has already been the subject of intense investigation by Waser (1974, 1975 b, 1976, 1977b,1982b) and Waser and Waser (1977), and Brown (1989), and therefore will not be discussed in any detail in the present thesis. The vocal repertoire of grey-cheeked mangabeys is described below, but no quantitative data is given on the frequency or context of these vocalisations.

Chalmers (1968 a) described five main classes of grey-cheeked mangabey vocalisations and the contexts in which they were heard. These included: *whoopgobbles, chuckles, grunts, screams* and *barks*. Waser (1977 b) used Struhsaker's (1969) term; *staccato bark,* for Chalmers' (1968 a) *chuckle* because he believed it to describe this vocalisation more accurately. He also added another vocalisation; the *loud grunt*, since he believed it to be significantly different from the *grunt* both in form and in context. During the present study, an additional variation of the grunt was recorded; the *rapid grunt*, but no other major differences were noted. The list of vocalisation classes are as follows:

Whoopgobble (Chalmers, 1968a):

This vocalisation consists of a "whoop" sound lasting less than a second (0.3 s: Chalmers, 1968a), then a pause of about 3-5s, and then a "gobble" consisting of a series of staccato pulses (Waser, 1975). Whoopgobbles are often given in pairs, with about 17 s between the first "gobble" and the second "whoop". Chalmers (1968) described this behaviour:

> "On the whoop, the body jerks forward slightly, the lips remain closed and are pushed forward in a pout, and the cheeks billow out. During the pause between the whoop and the gobble, the monkey sits tensed, the shoulders shake very slightly and the eyes are half closed. During the gobble, the shoulders shake violently up and down, the head is slightly raised and the mouth remains almost closed."

This vocalisation is generally audible up to 500 m, although can be sometimes heard up to 1200 m Waser (1977b), depending on factors such as the forest type, topography and the level of background noise. Spectrograms are provided by Chalmers (1968a) and Waser (1977b).

Chuckles (Chalmers, 1968a) or *Staccato barks* (Waser, 1977 b):

These vocalisations consist of a rapid succession of pulses (six pulses, each between 0.04-0.09 seconds: Chalmers, 1968) of sound, descending in pitch: "ah-ah-ah-ow". Each bout can last up to 5 s (Chalmers, 1968). The mouth is opened with the lips retracted for the "ah" and then the lips are closed over the teeth for the "ow" (**Figure 7.1**). Spectrograms are also provided by Chalmers (1968) and Waser (1977b, 1982).

Grunts (Chalmers, 1968a):

Grunts are deep rough sounds ("hoh, hoh, hoh, hoh"), often given by more than one individual in the group simultaneously. While giving this vocalisation, the neck is slightly extended, with mouth slightly opened. Grunts vary in volume and speed and tone. Their speed within a bout ranges from about 0.17 s to 0.67 s and each bout may last up to 10 minutes (Chalmers, 1968) (**Figure 7.1**). Spectrograms are also provided by Chalmers (1968) and Waser (1977b).

Loud grunts (Waser, 1977 b)

In loud grunts, the pulses of sound (i.e. each "hoh") are are slower and louder than for *grunts*. A spectrogram of this vocalisation is provided by Chalmers (1968a) and Waser (1977b).

Rapid grunts

During this vocalisation, pulses of sound ("hoh") are emitted in rapid succession, ascending then descending in pitch and intensity (**Figure 7.1**).

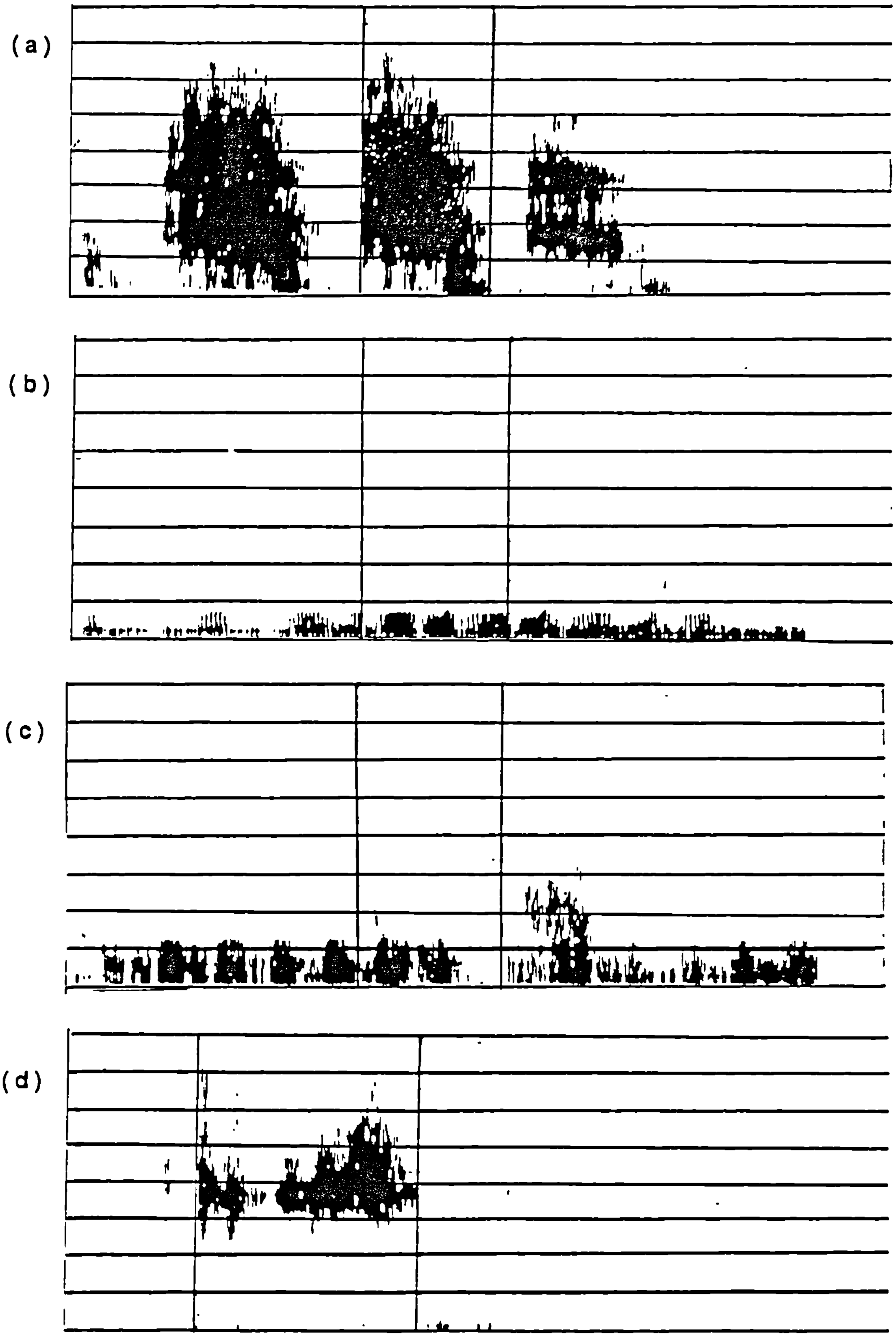


Figure 7.1 Sound spectrograms of: (a) chuckles: cursors enclose: 0.45 s;(b) grunts: cursors enclose 0.5s; (c) rapid grunts: cursors enclose 0.5s;(d) a scream: cursors enclose 0.75 s. Height of the graphs=8 kHz.

Screams (Chalmers, 1968a):

Screams are loud and high pitched sounds, with the energy dispersed across a wide range of frequencies (Chalmers, 1968a) (**Figure 7.1**). Spectrograms can also be found in Chalmers (1968a) and Waser (1977b).

Barks (Chalmers, 1968a)

Barks are a short explosion of noise, usually very deep. They are sometimes followed by a deep inspiration, giving a double bark and may be repeated several times. During this vocalisation, the mouth is slightly opened and the teeth remain covered by the lips (Chalmers, 1968a).

Other

Infrequent vocalisations are: *soft rattling growls* (Waser, 1977b), and *post-copulatory grunts*, *hurrs* and *icks* (two soft infant calls) and *gurgles* (a high intensity grunt)(Chalmers, 1968a).

B. ASSOCIATIONS BETWEEN AGE/SEX CLASSES

Spatial proximity has often been used in primatology as a measure of affinity between individuals (Smuts, 1985). In the present study, therefore, the age, sex and identity of the focal animal was recorded, together with its distance from (to the nearest metre), and identity of, its nearest neighbour, in order to give and indication of the affiliation between different age/sex classes and the frequency with which they associate. The number of other group members in the same tree as the focal animal was also noted. This data illustrate whether certain age/sex classes were more likely to be found with many members of the group, or only with a few other individuals.

Statistics

A Chi-square analysis was used to determine whether each age/sex class was sampled in proportion to their representation in the group and whether behaviours between individuals occurred more or less frequently than would be expected. Expected values were calculated as the average number of each age sex category during the study. This was : 2 adult males, 9 adult females, 1 sub-adult male, 6 juveniles, 2 infants

RESULTS

A: SOCIAL BEHAVIOUR

Grooming:

Table 7.1 to **7.3** shows the frequency of grooming that occurred between age/sex class pairs. **Table 7.1** shows grooming frequencies when groomers were the focal animals. **Table 7.2** shows grooming frequencies when focal animals were being groomed and **Table 7.3** shows the frequency of grooming dyads. Sample size in each dyad was too small to allow statistical comparison of the observed and expected frequencies of grooming. In general, however, adult females were observed to groom other individuals more than they were groomed themselves, whereas infants were groomed more frequently than they groomed others. Grooming was most frequent between adult females and between adult females and adult males.

Play:

Play was most common among juveniles (n=42 scans), but was

GROOMED

G R O O M E R

	ADULT MALES				ADULT FEMALES			SUB-ADULT MALES	JUVENILES	INFANTS	TOTAL
	total	PEI	OTT	REG	total	in oestrus	with infants				
ADULT MALES											
total	1				7	1			1	1	10
PEI	1		1		1				1	1	4
OTT					2						2
REG											0
ADULT FEMALES											
total	7	3	4		6		2	2	5	28	48
in oestrus	3	1	2					2	1		6
with infants	2	1	1		3		1		2	14	21
SUB-ADULT MALES					1					1	2
JUVENILES	1	1			5	1	2	1	3	1	11
INFANTS					3		3				3
TOTAL	9	4	4	0	22	2	7	3	9	31	74

Table 7.2 Number of scans that each age/sex class (as a focal subject) was observed to be groomed by other age/sex classes.

GROOMER

G R O O M E D

	ADULT MALES				ADULT FEMALES			SUB-ADULT MALES	JUVENILES	INFANTS	TOTAL
	total	PEI	OTT	REG	total	in oestrus	with infants				
ADULT MALES											
total	1				8	1		1	1		11
PEI					3			1	1		5
OTT	1				4						5
REG											0
ADULT FEMALES											
total	2	1			27		1	1	4	2	36
in oestrus	1				1				1		3
with infants					7		1		1	2	10
SUB-ADULT MALES					1				1		2
JUVENILES					6		1		3		9
INFANTS	1				17			1	1	1	21
TOTAL	4	1	0	0	59	1	2	3	10	3	79

Table 7.3 Frequency of grooming dyads between age/sex cateories

AGE/SEX CLASS	ADULT MALE	ADULT FEMALE	SUB-ADULT MALE	JUVENILE	INFANT
ADULT MALE	2	39	1	2	3
ADULT FEMALE		71	7	40	46
SUB-ADULT MALE			0	2	0
JUVENILE				8	2
INFANT					3

also observed between juveniles and infants (n=19), juveniles and adult females (n=3), juveniles and sub-adult males (n=1), infants and adult males (n=1), and among infants (n=27). Play involved chases and leaps in the canopy, tail pulling, and wrestling. Play was often repetitive. For example, jumping through the same gap in the canopy again and again. Outside of scan samples, an adult female was once observed using an object for playing with her infant. She dragged a small broken branch with the leaves still attached in front of the infant and when the infant tried to pounce on it, she pulled it away. Interspecific play was also observed and will be described in *Chapter Eight*.

(a) Affiliative behaviour

Non-sexual present:

Presenting was observed 10 times during this study; when a juvenile got in the way of an aggressive interaction, attempted to pass an adult male on a branch, or was approached by an adult male. The behaviour was directed towards adult males eight times, once towards an adult female and once toward a juvenile. This behaviour appeared to be an appeasement gesture, or recognition of status.

Grooming present:

This behaviour was observed 13 times and was performed by all age/sex classes except sub-adult males. This present was only directed towards adult females, sub-adult males and adult males. Grooming followed this type of present 11 times.

"69 Embrace":

The "69 embrace" was observed eight times. It was initiated by juveniles and adult females toward adult and sub-adult males, other adult females and juveniles. This type of embrace appeared to be used as a type of greeting, and was sometimes followed by grooming (n=3), but other times (n=5) the individuals just remained seated next to each other following the embrace.

Standing embrace:

This was observed three times, twice by a juvenile towards an adult female. and once by an adult female towards and adult male. This embrace was also probably a type of greeting, used when individuals were in motion and passing each other on a branch.

Mutual Embrace:

This was only observed twice, both times by a juvenile towards an adult female. This type of embrace was used for reassurance, especially after aggressive interactions.

Lip-smacking:

This was only ever seen to be directed at infants. It was performed three times by adults and twice by juveniles. All age/sex classes were curious about small infants, but were also timid of them. Lip-smacking may have been used as a signal to the mother, and other group members with reproductive investment in the infant, that the performer's intentions were good, in order to avoid any agonistic interactions.

Non-Sexual mount:

This behaviour was performed once by a sub-adult male and once by a juvenile. On both occasions, the younger individuals had found themselves obstructing the path of an adult male. It therefore seemed to be used as an appeasement gesture.

(b) Agonistic behaviour

Forty-nine cases of agonistic behaviour were observed within the group during the study. The frequency of agonistic interactions between age/sex classes was too small to allow statistical comparisons. The following is a list of those agonistic behaviours and the frequency with which they were recorded.

Chase:

Thirteen chases were observed. Adult males were observed to chase other adult males four times, juveniles four times and a sub-adult male once. Adult females were observed to chase a sub-adult male once, and another adult female once. Juveniles were observed to chase an adult female once and another juvenile once. Chases were used either to displace an individual from an area, to gain access to either food or a swollen female. Chases were different from supplants in that the chaser followed the individual he was chasing away from the area, before returning to take its place. Chases were also used in other contexts, such as a between adult males as a demonstration of dominance.

Supplant:

Supplants were observed 17 times. Adult males supplanted other adult males twice, juveniles five times, a sub-adult male once, and an adult female once. Adult females supplanted juveniles four times and other adult females four times. Supplants were used to gain access to a food source, swollen female, or grooming partner, or to reinforce dominance relations.

Displace:

Five displaces were observed, twice between adult females, twice between adult males, and once when OTT displaced an infant. The displace seemed to function to advertise or reinforce dominance relations between individuals.

Lunge:

Lunges were observed five times, all by the adult male PEI. PEI lunged towards an adult female after she had retrieved her infant from him, twice towards juveniles (once after the juvenile had repeatedly "grooming presented" towards him), and twice towards a sub-adult male when the sub-adult male approached him on the branch. The lunge was used as an advertisement of aggressive intent. If the individual to whom the lunge was directed, did not either change its behaviour or leave, then the individual was chased. Thus, the lunge may have decreased the number of more overt aggression in the group by functioning as a "warning" before more aggressive behaviour followed.

Yawn:

Yawns were observed three times; once by PEI towards a juvenile after the juvenile had mounted a swollen female, and twice by REG towards PEI. This behaviour was frequently observed by unhabituated adult males towards observers. Yawns were often used in combination with other behaviours, such as penile displays, ignores, or branch shakes and were therefore assumed to be a type of display or threat.

Penile display:

This was never observed between individuals in the group, but like the yawn threat, was regularly directed towards the observer by unhabituated adult males. Juveniles and adult females were also observed to adopt the same 'legs apart', sitting position and to use this in the same context as adult males.

Fast head shake:

This behaviour was observed *once between two adult males*, and once when directed at the observer. It was directed towards the observer when an adult female of the group, suddenly became aware of the close proximity (5 m) of the observer.

Mane erection:

This was sometimes performed by adult males following yawn threats and appeared to function as a display.

Grab:

Juvenile males were twice observed to grab adult females. One grab occurred when an adult female approached a group of individuals grooming, one of which was a juvenile male. The juvenile chased the adult female away from the group and grabbed at her as she ran away.

Bite:

Biting was observed only three times; once when an adult female bit her infant when it tried to cling to another adult female; once when an infant bit its mother when she would not let it suckle; and once when a juvenile male bit an adult female when she tried to approach him on a branch.

Branch shake:

This was observed only among adult males when directed towards other adult males and during intergroup encounters. The frequency of this behaviour was not recorded.

Ignore:

This behaviour was observed to be directed by one male, towards another three times and frequently towards the observer in the early stages of habituation. It was frequently used in combination with yawn threats and branch shaking.

Of the 49 cases of agonistic behaviour, 29 involved adult males, 19 involved adult females, 4 involved sub-adult males, 18 involved juveniles and 3 involved infants. Adult males were the only age sex class to be involved in agonistic behaviour more frequently than expected by chance (Chi-square=25.94, df=1, p<0.01).

Of the 29 cases involving adult males, OTT was the aggressor six times, PEI 16 times and REG five times. Agonistic behaviour was directed towards OTT six times, towards PEI three times and towards REG once. Adult females acted aggressively 12 times and were receivers of aggression 15 times. Sub-adult males received aggression four times but were never observed to direct aggression at other individuals.

(c) Sexual behaviours

Sexual presenting:

This was observed eight times by swollen females and was directed towards adult males six times and juveniles twice.

Ano-genital inspection:

Ano-genital inspection occurred after three of the observed sexual presents and was always followed by a mount.

Head flag:

This behaviour was only performed once by OTT towards a swollen female. The female did not approach following this behaviour.

Sexual mounting and copulations:

Sexual mounts were observed 18 times: three times by the adult male OTT, four times by sub-adult males (once to a female with a deflating swelling and once to a female during her first cycle) and 11 times by juvenile males. Copulation to ejaculation was only observed twice, although females were observed with ejaculate on their swelling eight times. The number of observed copulations in this study was thought to be small because swollen females travelled at the periphery of the group (see below).

Sexual harassment:

Adult females were observed to harass the copulating pair by slapping and grabbing at them in four out of the 18 sexual mounts observed. In every case this terminated the copulation.

Consort behaviour:

PEI was observed in consort with 10 different females during the 18 months that the group was followed, and OTT was observed in consort with females 10 times in the 10 months that he was observed within the study group. The length of consorts varied from a few hours, to a few days. The pair was observed up to 300 m from the group and generally remained silent.

(d) Vocalisations

Whoopgobble

Although the resident adult male, PEI, whoopgobbled the most frequently, all adult males gave this vocalisation. Whoopgobbles were given after major disturbance in the group, especially; (1) after the overflight of an eagle, (2) during intergroup encounters, (3) after an aggressive interaction within the group. They were also given, however, for no apparent reason.

Chuckles

Considerable variation in this vocalisation was noted, both between and within individuals. Variations occurred in the pitch, the number of pulses of sound, and whether the vocalisation ended in the "ow". The chuckle of adult males often ended in a distinctive "honk" sound, and would often continue into grunts. Chuckles were given in potentially alarming situations, but ranged from mild alarm, eg. elephants moving in the vegetation, to severe alarm: eg. overflights of eagles. Chuckles were also given in alarm to the alarm calls of other animals (see *Chapter Eight*). After duiker alarms, mangabeys gave chuckles in rapid succession.

Grunts

Grunts were given by all age/sex classes except infants. They occurred during all activities and appeared to function as a form of a contact call, whereby members of the group could monitor each other's location. If one individual grunted, other individuals in the group often grunted immediately after. Chalmers (1968a) suggested that this call may also function to pacify. During his study, aggression was significantly less if one or both individuals involved an agonistic encounter grunted.

Loud grunts

As was observed by Waser (1977 b), loud grunts were given either by a temporarily separated adult male as he rejoined the group, or during major disruptions of the group. The context of this call was less specific in the present study, however, and mangabeys gave loud grunts in other situations. For example loud grunts were exchanged between groups when they were within audible distance of each other, and loud grunts were given when a group of crowned guenons approached and joined the study group of mangabeys in a polyspecific association, or during intergroup encounters.

Rapid grunts

In the study group, rapid grunts were only heard to be given by the adult male, PEI, during the overflight of an eagle. He gave this vocalisation while chasing eagles or while monitoring the eagle. This vocalisation was also heard to be given by other males in the study area during overflights of eagles. Because the male often temporarily leaves the group in pursuit of the eagle, this call may inform the other group members of his location. Alternatively, the vocalisation may be used to frighten the eagle.

Screams

Screams were mainly given mainly by infants, but also by juveniles and females and sub-adult males. Screaming occurred during eagle overflights and aggressive interactions. and may act to startle the attacker, or communicate to others, imminent danger.

Other

Soft rattling growls were given mainly by juveniles and females during the overflight of an eagle, but were also given during the overflight of other birds, possibly because they were mistaken for eagles. *Hurrs* and *icks* were given by infants younger than six months.*Post-copulatory grunts*, and *gurgles* were not heard during this study.

B. ASSOCIATIONS

The number of times each age/sex class was sampled as focal animals was calculated and compared to the expected number of times each age/sex class should have been sampled based on the average group composition for the duration of the study (**Table 7.4**). Adult males (Chi-square=40.82, df=1, p<0.01), and infants (Chi-square=6.28, df=1, p=0.01) were sampled more frequently than expected, and sub-adult males (Chi-square=31.3, df=1, p<0.01), and juveniles (Chi-square=25.42, df=1, p<0.01) were sampled less frequently than expected. Adult females were sampled as expected (Chi-square=0.20, df=1, p=0.66). In order to overcome this bias in sampling, each age-sex category was examined individually (**Table 7.5** and **Table 7.6**). Mean nearest neighbour distances (**Table 7.7**) and mean number of other monkeys in the same tree as the focal animal (**Table 7.8**) were also calculated for each age/sex category.

Table 7.4 Sampling frequency of each age/sex class as focal animals compared to expected values based on group composition

	ADULT MALE	ADULT FEMALE	SUB-ADULT MALE	JUVENILE	INFANT	TOTAL
OBSERVED	305	798	28	392	222	1745
EXPECTED	175	785	87	523	175	1745
Chi-square	40.82	0.2	31.3	25.42	6.28	
p	<0.01	0.66	<0.01	<0.01	0.01	

Table 7.5 Nearest Neighbour distances for each age/sex class.

NEAREST NEIGHBOUR

		ADULT MALES				ADULT FEMALE				SUB-	JUVENILE	INFANT	TOTAL
						in	with			ADULT			
		PEI	OTT	REG	TOTAL	oestrus	infant	neither	TOTAL	MALE	TOTAL		
	ADULT MALES												
F	PEI	NA	4	2	6	12	14	39	65	4	22	26	123
O	OTT	10	NA	5	15	21	7	30	58	2	5	1	81
C	REG	4	5	NA	9	0	2	18	22	0	3	0	34
A	TOTAL	11	10	7	35	42	35	114	191	8	38	33	305
L	ADULT FEMALES												
A	in oestrus	13	22	1	43	11	1	19	31	4	13	4	95
N	with infant	32	27	5	66	3	31	26	60	0	22	64	192
I	neither	38	28	17	106	6	26	234	266	14	73	52	511
M	TOTAL	83	57	23	195	20	58	279	357	18	108	120	798
A	SUB-ADULT MALES	1	0	0	1	3	0	18	21	1	5	0	28
L	JUVENILES	29	4	5	46	7	20	117	147	6	163	30	392
	INFANTS	20	1	0	26	1	39	78	116	1	21	58	222

Table 7.6 Chi-square values showing whether each age/sex class were nearest neighbours more (+) or less (-) frequently than expected ($p<0.05$).

NEAREST NEIGHBOUR

		ADULT MALES				ADULT FEMALE				SUB-ADULT MALE	JUVENILE TOTAL	INFANT
		PEI	OTT	REG	TOTAL	In oestrus	with Infant	neither	TOTAL			
	ADULT MALES											
F	PEI	NA	NA	NA	0.02	NA	0.04	NA	0.80	0.49	6.30 -	5.23 +
O	OTT	NA	NA	NA	7.17 +	NA	0.26	NA	7.81 +	0.69	18.63 -	6.80 -
C	REG	NA	NA	NA	3.36 +	NA	0.73	NA	2.15	2.06	5.76 -	4.25 -
A	TOTAL	NA	NA	NA	7.63 +	NA	0.15	NA	14.63 +	2.83	32.64 -	0.01
L	**ADULT FEMALES**											
A	In oestrus	3.93 +	12.48 +	1.73	30.61 +	NA	2.24	NA	1.82	0.12	8.69 -	2.78
N	with Infant	12.79 +	0.59	2.70	12.15 +	NA	12.04 +	NA	NA	10.37 -	22.98-	29.98 +
I	neither	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
M	TOTAL	13.99 +	2.42	5.79-	53.52 +	NA	2.73	NA	1.19	10.62 -	74.3 -	7.28 +
A	**SUB-ADULT MALES**	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
L	**JUVENILES**	1.52	11.56 -	10.18-	0.28	NA	8.00 -	NA	7.82 -	8.29 -	20.48 +	1.96
	INFANTS	2.16	9.59 -	12.33-	0.21	NA	2.16 +	NA	1.09	9.59 -	33.19 -	35.89 +

Table 7.7 Mean distance to the nearest neighbour for each age/sex class and individual adult males

Adult males	Mean	SD	N
PEI	3.01	3.81	129
OTT	6.77	7.96	92
FEG	6.47	7.99	36
OVERALL	4.46	6.09	324
Adult females			
IN OESTRUS	3.77	4.60	104
WITH INFANTS*	1.86	2.93	199
NEITHER WITH INFANTS NOR IN OESTRUS	3.14	3.91	560
OVERALL	2.92	3.85	862
Juveniles	2.63	3.32	76
Sub-adult male	3.67	3.43	568
Infants	0.84	1.20	444

*Not including ventral infant

Table 7.8 Mean number of other mangabeys in the same tree as the focal subject for each age/sex cateory and individual adult males

Adult males	Mean	SD	N
PEI	4.32	3.12	133
OTT	3.22	2.85	77
FEG	3.02	2.06	46
OVERALL	3.92	3.03	355
Adult females			
IN OESTRUS	3.62	2.87	87
WITH INFANTS*	5.16	3.19	208
NEITHER WITH INFANTS NOR IN OESTRUS	3.93	2.96	708
OVERALL	4.16	3.05	1002
Juveniles	4.84	3.27	546
Sub-adult male	3.86	2.34	36
Infants	5.50	3.20	189

*Not including ventral infant

1. Adult males

Overall

Adult males were more often found closer to adult females (Chi-square=14.63, df=1, p<0.01) and adult males (Chi-square=7.63, df=1, p=0.01) but less often next to juveniles (Chi-square=32.64, df=1, p<0.01) than would be expected by chance. They were found next to infants (Chi-square=0.01, df=1, p=0.91) and sub-adult males (Chi-square=2.83, df=1, p=0.09) and females with infants (Chi-square=0.15, df=1, p=0.70) as expected.

Resident adult male (PEI):

PEI was the only adult male in the group at the beginning of the study in January 1992. Infants were his nearest neighbours more than expected (Chi-square=5.23, df=1, p=0.02), and juveniles less than expected (Chi-square=6.30, df=1, p=0.01). Proximity to all other age/sex classes did not differ from expected values. The average distance to his nearest neighbour was 3.01 m (S.D.=3.81, df=1, n=129) and the average number of individuals in the same tree as him was 4.32 (S.D.=3.12, df=1, n=133).

Immigrant male (OTT):

OTT migrated into the group in November 1991. He associated more frequently with adult males (Chi-square=7.17, df=1, p=0.01) and adult females (Chi-square=7.81, df=1, p=0.01) than expected, but less frequently with juveniles (Chi-square=18.63, p<0.01) and infants (Chi-square=6.80, df=1, p=0.01). He associated with sub-adult males (Chi-square=0.69, df=1, p=0.41) and adult females with infants (Chi-square=0.26, df=1, p=0.61) as expected.

The an average distance to OTT's nearest neighbour of 6.77

(S.D.=7.96, n=92) was greater than PEI's, probably because when he was not in association with swollen females, he remained on the periphery of the group. The average number of monkeys sharing the same tree reflects this because it is lower than that of Prince (mean=3.22, S.D. = 2.85, n=46).

REG:

REG was a sub-adult male in the group at the beginning of the study in January 1991 and was reclassified as an adult male in April 1992. As an adult he spent significantly more time than expected in association with adult males (Chi-square=3.36, df=1, p=0.07), but less time than expected with juveniles (Chi-square=5.76, df=1, p=0.02) and infants (Chi-square=4.25, p=0.04). He was observed with adult females (Chi-square=2.15, df=1, p=0.14), adult females with infants (Chi-square=0.73, df=1, p=0.39) and sub-adult males (Chi-square=2.06, df=1, p=0.15) as expected. As a sub-adult, the distance to his nearest neighbour was 3.1m (SD=3.18, n=10). During his transition to adulthood he became increasingly peripheral and the average distance to his nearest neighbour when he was an adult male was 6.47 m (SD=7.90, n=36). His increased peripheralisation was also reflected in the number of other individuals in the same tree when he was a sub-adult (mean=5.30, SD=2.54, n=10) compared to the situation in adulthood (mean=3.02, SD=2.06, n=46).

Comparison of the three adult males

OTT was found significantly more frequently with swollen females as his nearest neighbour than both PEI (Chi-square=8.42, df=1, p<0.01) and REG (Chi-square=5.52, df=1, p=0.02). PEI had infants as his nearest neighbours significantly more frequently than both OTT (Chi-square=17.73, df=1, p<0.01) and REG (Chi-square=8.61, df=1, p<0.01) and juveniles more frequently as his nearest neighbour, than OTT (Chi-square=6.41, df=1, p=0.01). There was no significant difference in the number of individuals in the same trees as the adult males, but nearest neighbours to PEI were significantly closer than both OTT (z=3.48, p<0.01) and REG (z=2.19, p<0.05).

2. Adult females

Overall

Adult females had nearest neighbours of adult males (Chi-square=53.52, df=1, p<0.01) and infants (Chi-square=7.28, df=1, p=0.01) more frequently than expected, but juveniles (Chi-square=74.30, p<0.01) and sub-adult males (Chi-square=10.62, df=1, p<0.01) less than expected. They associated with other adult females (Chi-square=1.19, df=1, p=0.28) and adult females with ventral infants (Chi-square=2.73, df=1, p=0.10) as expected. They associated more frequently with PEI than expected (Chi-square=13.99, df=1, p<0.01), with OTT no more or less than expected (Chi-square=2.42, df=1, p=0.12) and REG less than expected (Chi-square=5.79, df=1, p=0.02).

Adult females with infants

Adult females with infants associated with adult males (Chi-square=12.15, df=1, p<0.01), other adult females (Chi-square=4.50, df=1, p=0.03), other adult females with infants (Chi-square=12.04, df=1, p<0.01) and infants (Chi-square=29.98, df=1, p<0.01) more than expected, but sub-adult males (Chi-square=10.37, df=1, p<0.01) less than expected. They associated with PEI more than expected (Chi-square=12.79, df=1, p<0.01), but with OTT (Chi-square=0.59, df=1, p=0.44) and REG (Chi-square=1.73, df=1, p=0.19) as expected .

Adult females in oestrus

Adult females with swellings were observed to associate with adult males more than expected (Chi-square=30.61, df=1, p<0.01), and juveniles less than expected (Chi-square=8.69, df=1, p=0.03). Infants (Chi-square=2.78, df=1, p=0.10), adult females in general (Chi-square=1.82, df=1, p=0.18) and sub-adult males (Chi-square=0.12, df=1, p=0.73) were associated with as expected. Females with swellings associated with both PEI (Chi-square=3.93, df=1, p=0.05) and OTT (Chi-square=12.48, df=1, p<0.01) more than expected, and they associated with OTT significantly more frequently than they associated with PEI (Chi-square=8.42, df=1, p<0.01). They associated with REG as expected (Chi-square=2.70, df=1, p=0.10).

3. Sub-adult males

Sub-adult males associated with all age/sex classes as expected (Chi-square=8.03, df=4, p=0.09, n=28)

4. Juveniles

Juveniles were found more often than expected next to other juveniles (Chi-square=20.48, df=1, p<0.01), but less often than expected next to adult females (Chi-square=7.82, df=1, p<0.01), adult females with infants (Chi-square=8.00, df=1, p<0.01) and sub-adult males (Chi-square=8.29, df=1, p<0.01). They were observed as frequently as expected next to infants (Chi-square=1.96, df=1, p=0.16) and adult males (Chi-square=0.28, df=1, p=0.59), but they associated with OTT (Chi-square=11.56, df=1, p<0.01) and REG (Chi-square=10.18, df=1, p<0.01) less than expected and PEI as expected (Chi-square=1.52, df=1, p=0.22).

5. Infants

Infants were observed more frequently than expected in association with adult females with infants (Chi-square=2.16, df=1, p=0.14) and other infants (Chi-square=35.89, df=1, p<0.01), but less frequently than expected with sub-adult males (Chi-square=9.59, df=1, p<0.01) and juveniles (Chi-square=33.19, df=1, p<0.01). They associated as would be expected with adult females (Chi-square=1.09, df=1, p=0.30) and adult males (Chi-square=0.21, df=1, p=0.65), although they associated less than expected with OTT (Chi-square=9.59, p<0.01) and REG (Chi-square= 12.33, df=1, p<0.01) and as would be expected with PEI (Chi-square=2.16, df=1, p=0.14).

DISCUSSION

A: SOCIAL BEHAVIOURS

Many of the behaviours observed in this study were similar to those reported in two earlier studies (Chalmers, 1968 a; Wallis, 1981), but some differences were evident. "Lip-smacking" was most similar to that observed by Chalmers (1968a), although the present study, this behaviour was never seen during agonistic encounters, nor was it accompanied by shaking of the head. Wallis (1981) reported never having observed this behaviour, but suggested that it could be similar to his "exaggerated chewing" category, a behaviour that was never observed in this study. "Non-sexual presents" were frequently observed in this study, yet Wallis (1981) and Chalmers (1968a) report that this behaviour was uncommon. The "penile display" as described by Wallis (1981) was frequently observed in the present study, however, it was usually directed towards the observer and not other members of the group.

Behaviours observed in this study, but not reported in other studies include the 'standing embrace', 'displace', 'branch shake' 'ignore' and 'non-sexual mount', 'consort behaviour' and 'sexual harassment'. The 'standing embrace' is similar to an embrace described by Strum (1987) for baboons. Strum states that sideways embraces are more common for adults, and frontal embraces are used more for reassurance than just greeting. 'Displace' and 'branch shake' are behaviours that have been recorded for stumptail macaques (*Macaca arctoides*) (Bertrand, 1969). Branch shaking has been reported in other primates, such as red colobus (*Colobus badius*) (Struhsaker, 1975). 'Ignore' is similar to a behaviour described by Bertrand (1969) when a macaque feigned indifference. It is also similar to 'back-turning' in baboon (Strum, 1987). 'Non-sexual mount' has also been observed in stumptail macaques (personal observations), and pig-tailed macaques (Castles, personal communications) but in macaques it appears to aid in alliance formation between adult males rather than a signal of submission. 'Consort behaviour' and 'sexual harassment' were not included in lists of the behavioural repertoire by Wallis (1981) or Chalmers (1968a), and these will be discussed below.

Behaviours not observed in the present study but observed by Wallis (1981) or Chalmers (1968a) include 'teeth bare', 'exaggerated chewing', 'straight arm raise', 'mutual inspect', 'open mouth o', and '69 ventral cling'. It is possible that variation in, or the absence of, behaviours represent cultural differences. Differences in behaviours or gestures between populations have been observed in other primates. For example, chimpanzees have been observed to display a stereotypic pattern of mutual grooming at Mahale in Tanzania (McGrew and Tutin, 1978) and Kibale Forest in Uganda (Ghiglieri, 1984) but not at Gombe in Tanzania.

The vocalisations recorded in the present study were generally similar to those described in other studies (eg. Chalmers, 1968a; Waser, 1977b), with the exception of the rapid grunt. This vocalisation seemed to be specific to adult males in the presence of eagles. Predator-specific alarm calls have been recorded in other primate species (eg. Seyfarth *et al.*,1980) and it would therefore not be unusual if they also existed in mangabeys, although more detailed study is needed of this vocalisation. The vocal repertoire has been compared between species of mangabeys. Waser (1982b) found the whoopgobble of black mangabeys to be almost identical to that of grey-cheeked mangabeys. The whoopgobble of agile mangabeys differs on a superficial level, but is similar in its temporal pattern. Further comparisons within between species of mangabey, between mangabeys and baboons, and discussions of the frequency, context and function of these calls can be found in (Chalmers, 1968 a; Waser, 1974, 1975b, 1976, 1977b, 1982b; Waser and Waser, 1977).

The behavioural repertoire of mangabeys is similar to both baboons and macaques (Chalmers, 1968 a; Wallis, 1981; Waser, 1982b). Most baboons, macaques and mangabeys have frequent social interactions, conspicuous gestures, yet dull dark fur and face. In this way they differ noticeably from sympatric guenons, who are more discrete in their behaviours, but have distinctive brightly coloured facial patterns and markings (Rowell, 1988). These markings give instant information about where the individual is and what direction it is looking or travelling. Rowell (1988) describes the social organisation of forest guenons, the "monitor-adjust" method, whereby individuals monitor the position of other individuals in the group and what they are paying attention to. They then adjust their own behaviour accordingly. Baboons macaques and mangabeys differ in that they use overt specialised signals instead, such as gestures and vocalisations. These differences in social organisation cannot necessarily be attributed to habitat differences, because mangabeys and forest guenons live sympatrically, as do vervets and baboons. Instead, they probably represent two different strategies for communication and group cohesion.

B: ASSOCIATIONS

Infants and Juveniles

The physical and behavioural development of infants and juveniles is a topic which has already received much attention (Deputte 1992; Chalmers, 1967) and so was not a focus of the present study. The results show that transition from infant to juvenile was marked by a decrease in the number of individuals in the same tree and a increase in the average distance to nearest neighbours. Juveniles tended to associate more with juveniles than any other group members, and all members of the group associated with juveniles less than expected. Chalmers (1968c) also observed that association between adult females and juveniles was less than expected.

Adult females

In all Cercopithecinae species, it is usually the male which transfers between groups. Females remain in their natal group all of their lives and form long-lasting stable relationships with each other. A linear dominance hierarchy is known to exist for female baboons and macaques (except perhaps in hamadryas baboons, see Byrne *et al.*, 1989) and this hierarchy is based on matrilines. Infants born into the group take on similar dominance rank to their mothers. Because adult females were not easily recognised in the present study (see *Chapter Two*), relationships between individuals were difficult to assess and a dominance hierarchy was not determined. A dominance hierarchy has been observed for mangabeys in captive studies, and more detailed study of their social relationships in the wild may confirm this (Ehardt, 1988).

Changes in the behaviour and relationships of females in the present study were observed when adult females had infants and when they were in oestrus.

Adult females with infants

A special association was observed among adult females with infants. They associated more than expected and were sometimes observed to "babysit" each other's infants, when one mother left to forage in another tree and another mother remained with both infants. The existence of "babysitting" behaviour may give an adaptive advantage to adult females giving birth to infants synchronously. In this study the first two infants were born only a month apart, and the other three surviving infants were born in the same month.

Females with infants associated more often with the resident adult male PEI than the immigrant male OTT. Females with infants preferentially associating with the resident male over an immigrant male has also been observed in other species of mangabeys (Ehardt, 1988) and in baboons (Busse and Hamilton, 1981).

Adult females in oestrus

Behaviours of adult females in oestrus differed in significant ways from females who were not cycling. Evidence from nearest neighbour distances and the number of individuals in the same tree as the focal individual, confirms that oestrous females were more peripheral to the group than non-oestrous females, or females with infants. Data from grooming frequencies and nearest neighbour frequencies shows that oestrous females were found more often interacting with, or in association with adult males than non-oestrous females or females with infants. In particular, they were found in association with the adult male OTT more often than with PEI.

The peripheralisation of swollen females and their close association with adult males was a striking feature in the behaviour of mangabeys in the present study. Wallis (1983) observed that adult males and swollen females formed "pair-bonds" but little attention has been paid to this. He noticed that two or three days before peak swelling one or more of the adult males began to follow the swollen female at a distance of about 20 m. Chalmers (1967) did not observe consort pairs in his study in Uganda, although in captivity, Chalmers and Rowell (1971) noticed changes in the behaviour of oestrous females and that the frequency with which adult males approached swollen females increased with the size of her swelling and decreased when the swelling decreased.

Savanna baboons are known to form temporary pair-bonds or consorts where a male monopolises a female during or around ovulation. The length of consorts depends on the dominance of the male, and the intensity of male-male competition, (eg. Rasmussen, 1983; Smuts, 1985). Consorts have also been observed in macaques (eg. Takahata, 1982), but not as frequently as in baboons, and consorts are generally absent in vervets and talapoins (Melnick and Pearl, 1987).

The purpose of consorts is not certain although there is much speculation. The female may choose to remain peripheral to the group to increase the chances of extra-group copulations and the adult male may be forced to follow the female if he wants to prevent this. Alternatively, the pair may remain peripheral in order to avoid aggression from other adult males in the group. In the present study, however, PEI formed consorts even when he was the only adult male in the group, so this explanation seems unlikely. Alternatively, the pair may be attempting to avoid harassment from other individuals in the group during copulation. In the present study, harassment of a copulating pair was observed during 22% of observed sexual mounts in the group. Sexual harassment has also been observed in two other studies (Struhsaker and Leland,1979; Wallis,1979), suggesting that this may be the most likely reason for the pair remaining peripheral.

Adult and sub-adult males

All mangabeys in the wild have been observed to live in multimale groups, although there may be a greater tendency towards single male groups of grey-cheeked mangabeys in Equatorial Guinea (Cashner, 1972, Jones and Sabater Pi, 1968). From an adult male's point of view, the costs involved in allowing another male into the group are increased competition for food and mates. The benefits of having more than one male are; aid in avoidance of, and defence against predators, defence against other groups (Clutton-Brock and Harvey, 1976; Crook, 1972; Goss-Custard *et al.*, 1972), and additional knowledge of the location and availability of food resources (Struhsaker and Leland, 1979).

Agonistic behaviour is usually highest between adult males in multimale groups, probably because they are likely to be unrelated and because they are in competition for females. One of the ways in which males can decrease aggression when living together is through a dominance hierarchy. Very little is known about the relationship between adult males in mangabey groups. This study provided a unique opportunity to study the strategies of individual males in a group of grey-cheeked mangabeys because of the immigration of a new male into the single-male study group, and the development of a sub-adult into a fully adult male during the study. Transfers between groups have been noted in other studies (eg. Wallis, 1979; Waser, 1974), but have not been observed directly.

Observations from this study combined with observations from other studies suggest that individual males have very different roles in the group. Although a general dominance hierarchy was not obvious, OTT was found in association with oestrous females more frequently than PEI. Differences in copulatory success have also been observed in other studies of grey-cheeked mangabeys (Struhsaker and Leland, 1979; Waser, 1977b). For example, Waser (1977b) observed one of the three males in his study group completing 66% of all copulations. However, both Waser and Wallis (personal communications in Struhsaker and Leland,1979) observed that more than one male may copulate with a single female during one oestrous cycle and Bernstein (1976) found no evidence that higher ranking males successfully out-competed other males in the number of completed copulations in captivity.

PEI remained more central to the group than OTT as measured by nearest neighbour distances and the number of other monkeys in the tree, and he was nearest neighbour to adult females with infants, infants and juveniles more frequently than OTT. Preference for associating with older, lower ranking, and longer-term residents of the group has been observed in other studies of grey-cheeked mangabeys. Chalmers (1967) noticed that adult females preferentially groomed and spent time close to the oldest and lowest ranking male. A similar effect was noted by Bernstein (1976) between an old low-ranking male and the alpha females. Ehardt (1988) observed that interactions between individuals in a group of grey-cheeked mangabeys with three adult males were related to the age and dominance of the male and there was a preference for grooming older members of the group. This relationship has also been observed for olive baboons (Smuts, 1985).

PEI was the only male who participated in predator defence and intergroup encounters. This is contrary to the findings of Waser (1974) who observed that adult males that 'whoop-gobbled' while approaching other groups, were most frequently the younger and more dominant of their group. Wallis (1979) also observed the two top ranking males defend the group against eagles (primarily crowned hawk-eagles). Because PEI had an investment in infants in the group, he might have been expected to defend the group against predators more than OTT. OTT might have been expected to defend the group against other groups if he had special interest in oestrous females. It may be, however, that there is no need to defend females from males in other groups, but only from those males travelling alone or seeking to immigrate.

Thus it seems that there are reasons why each male is tolerant of the presence of other males in the group. The migrant male gets priority access to oestrous females, and benefits from the presence of the other adult males in the areas of predator detection, group defence and knowledge of food sources. The resident adult male usually has reproductive investment in the offspring in the group and therefore benefits by staying to protect his infants from predators. Furthermore, he may also find opportunities to copulate with swollen females. Males may be deterred from leaving their groups by the potential dangers of travelling alone, or attempting to enter new groups, especially if they are older and less fit.

It is also possible that the resident adult male remains in order to protect his offspring from infanticide from other adult males. Shortly after OTT entered the group, PEI was observed to pick up and carry infants in the presence of OTT. This behaviour has also been observed in baboons and macaques and is discussed in the next section.

PART II:TRIADIC MALE-INFANT INTERACTIONS

INTRODUCTION

For Cercopithecine species living in multimale groups, the relationship between adult males and infants is more uncertain compared to species living in single male groups since the paternity of the offspring is often unknown. In multimale Cercopithecines, adult males have been observed to interact with infants by grooming them, sharing food, and even by carrying them (Whitten, 1987), but one of the most controversial behaviours that has been observed is when an adult male carries an infant during an interaction with another adult male. This behaviour has been called "agonistic buffering" (Deag and Crook, 1971), "kidnapping" (Popp, 1978 in Whitten, 1987), "triadic male-infant interactions" (Taub, 1980b), "infant carrying" , (Busse and Hamilton, 1981), "infant use" (Strum, 1984), "countercarrying" (Hamilton, 1984), and "tripartite relations" (Kummer, 1967). The term "triadic male-infant interactions" (Taub, 1980b) will be used in this study because it is descriptive and implies least about underlying mechanisms.

This behaviour has provoked considerable discussion due to the difficulty of interpreting who benefits from the interaction. Hypotheses explaining 'triadic male-infant interactions' can be divided into three main arguments: an adult male will carry an infant during a potential or actual conflict with another adult male to (1) decrease the chances of aggression from the other adult male (Hrdy, 1976; Stein, 1984; Strum, 1984), (2) protect the infant from aggression from the other adult male (Busse and Hamilton, 1981; Hrdy, 1974; Packer and Pusey, 1985; Stein, 1984), or (3) benefit the relationship between him and the infant's mother, in order to increase the chances of future copulations (Smuts, 1985).

Observations of 'triadic male-infant interactions' come mostly from the study of baboons. It has been observed in *Papio anubis* (eg. Packer, 1980; Popp, 1978 in Whitten, 1987), *Papio cynocephalus* (eg. Stein, 1984), *Papio ursinus* (eg. Busse and Hamilton, 1981), *Papio hamadryas* (eg. Kummer, 1967), and *Therpithecus gelada* (eg. Dunbar and Dunbar, 1975). The behaviour is not as common in macaques (Stein, 1984) and has only been observed in four out of 19 species in this genus, including barbary macaques (*Macaca sylvanus*) (Deag and Crook, 1971), java macaques (*Macaca fuscata*) (Itani, 1959), stump-tailed macaques in captivity (*Macaca arctoides*) (Gouzoules, 1975), and bonnet macaques (*Macaca radiata*) (Silk and Samuels, 1984).

Mangabeys, closely related to baboons and macaques in morphology (Hill, 1974), behaviour (Chalmers, 1968 a; Wallis, 1981) and genetics (Cronin and Sarich, 1976) are usually ignored in any discussions despite the fact that adult males have been observed to carry infants in both grey-cheeked mangabeys *Cercocebus albigena* (Chalmers, 1968c; Wallis, 1979, Waser, 1974; Struhsaker and Leland, 1979) and sooty mangabeys *Cercocebus torquatus atys* (Bernstein, 1971a; Busse and Gordon, 1984). 'Triadic male-infant interactions' have been reported for sooty mangabeys in captivity (Busse and Gordon ,1984), but the possibility of this being an aberrant behaviour due the effects of a captive environment can not be ruled out. The only published report of triadic male-infant interactions is from Chalmers (1968 c) who reports adult males being attacked by other adult males whilst carrying infants. This is the first study to document in detail, triadic male-infant interactions for mangabeys in the wild.

METHODS

The relationships between infants and adult males was discussed in the previous chapter through nearest neighbour distances and frequencies of affiliative and aggressive interactions. This chapter describes instances in which adult males were observed to carry infants.

RESULTS

In the previous chapter, it was established that PEI was the probable father of infants born in March and April 1991, since OTT did not migrate into the group until one year after the date when the infants were conceived. It was also established that PEI had infants and juveniles as his nearest neighbours more frequently than OTT, but OTT had adult females in oestrus as his nearest neighbours more frequently than PEI. The only male observed to carry infants was PEI (n=12). In 7 out of 12 observations, PEI was in conflict with another adult male. The following gives a brief summary of each instance in which PEI was observed carrying an infant.

The first observations occurred almost a year after the commencement of data collection; one month after OTT joined the group. The infants were between eight and 10 months old.

Observation I

December 3rd 1991 : In this first example, PEI did not successfully carry the infant although he attempted to. Another unknown adult male was seen on the periphery of the study group.

PEI was sitting on a branch with two infants and the mother of one of the infants as his nearest neighbours. The new male approached PEI and at the same time, one of the infants ran towards PEI. He made a scooping movement as if to pick up the infant and then went to the edge of the branch and yawn threatened the new male. The mother picked up one of the infants and carried it off and PEI was left with the other infant. He left the tree, followed closely by the infant and a juvenile. The new male approached and then left the group.

Observation II

December 24th 1991: During an intergroup encounter an infant leapt into PEI's lap. PEI stood and walked a few paces carrying the infant ventrally. The infant dangled and did not cling properly and then finally leapt off PEI onto its mother.

Observation III

One hour later the other group was still audible. PEI was with a oestrus female when OTT approached him. Suddenly a female infant appeared and presented to PEI. He grabbed the infant and pulled her close and started to groom her. PEI then tried to approach the swollen female while holding the infant. All moved into denser vegetation and observation was obscured. Suddenly OTT came charging out of the vegetation and continued to run away from the group at high speed. Another observer about 200m from the group, saw OTT pass overhead at high speed heading away from the group.

Observation IV

28th January 1992 : OTT was sitting alone in a tree. PEI rapidly approached and supplanted him. Fifteen minutes later PEI was observed walking along a branch carrying a female infant. He sat down and she sat in his lap. They were followed by a male infant and an adult female.

The following observations occurred one month after three new infants were born into the group.

Observation V

14th July 1992: A crowned hawk eagle flew overhead. PEI began to vocalise at the eagle and tried to grab one of the young infants from an adult female. There was a lot of screaming from the infant's mother, and he did not succeed in obtaining the infant. PEI charged off after the eagle. His alarm vocalisations could be heard about 200m from the group. During his absence, OTT attacked a small juvenile male who fell 8 m.

Observation VI

About 3 hours later, PEI was observed suddenly to charge into a group of adult females and grab a young infant from one of them. Two minutes later he was observed sitting on a horizontal branch with the infant in his lap. He looked down at it and pulled its arm roughly. It squealed and then tried to move away, but was still unsteady. PEI let the infant start to crawl away but then grabbed it again, stood up, held it ventrally, and moved off carrying it. Its mother was about 10m away and followed PEI and the infant to a different tree.

Four minutes after PEI had taken the infant, he reappeared, this time without the infant, but followed by two older infants. He lay down on a branch and they played at his feet.

Observation VII

22nd July 1992: PEI was sitting next to an adult female with a ventral infant. The infant moved off its mother and reached towards him. PEI lip-smacked at the baby and then picked it up and carried it off ventrally. The baby did not cling properly and eventually fell off onto the branch. The mother rushed over and picked it up and moved back to her original position. PEI then lunged at the mother and she jumped with the infant into another tree below. OTT suddenly appeared coming towards PEI. He supplanted PEI who jumped into the tree below following the mother and infant.

Observation VIII

24th August 1992: PEI was observed carrying an infant ventrally. He sat on a branch and the infant moved off him. His nearest neighbours were three young infants together on the same branch. One of the infants approached PEI and he gently reached towards it, but the infant moved away. Another infant approached PEI's back and grabbed a handful of hair and climbed onto him. After 5 minutes, the infants moved off into another tree.

Observation IX

Three hours later during group travel, PEI was observed carrying an infant ventrally again. It moved off him and onto its mother and the group continued on.

Observation X

27th August 1992: PEI and OTT were in the same tree on either side of the trunk. Both were out in the open facing each other. The distance between them was about 10 m. PEI had an infant in his lap. He yawn threatened twice towards OTT and then groomed the infant. The two males appeared nervous and to be monitoring each other. Two minutes later PEI bent over the infant hiding it from view and turned his back on OTT. After two minutes, an adult female approached PEI and sat 10m above him in the same tree. The infant squealed and there were chuckles from other members of the group. After a further minute, PEI left the tree carrying the infant ventrally. OTT also left the tree in which he was sitting and followed PEI. Alarm chuckles were then heard from PEI.

Observation XI

About an hour and a half later PEI was sitting with a small infant in the open. OTT was in a different tree about 30m away and they seemed to be watching each other. After 5 minutes, the infant crawled off PEI and remained away for about 3 minutes. Suddenly, the infant fell to a branch below and there were grunts from other members of the group. PEI reached down and hauled the infant back up and the held it ventrally again. Eight minutes later, PEI left the tree still holding the infant ventrally.

Observation XII

17th September 1992: While searching for the study group, another group of mangabeys was encountered on the periphery of the study group's home range. As they fled from the observers, an adult male was seen carrying an infant ventrally.

Of these 12 interactions, four were initiated by the infant, two were initiated by the adult male and in six the initiator was not known. Six instances of infant carrying were observed during conflict with another adult male, one occurred when there was a predator present and one occurred when an unhabituated group fled from the observers. These observations are summarised in **Table 7.9.**

DISCUSSION

Although there are few cases, it is important to document the occurrence of triadic male-infant interactions in mangabeys to show that this behaviour is not confined to baboons and macaques alone. Because they are closely related, it is not surprising to find that a pattern that occurs in macaques and baboons also occurs in mangabeys. It is also not surprising that triadic male-infant interactions in mangabeys are less well known since mangabeys have been studied less intensively than baboons and macaques, and because observation conditions are often difficult.

There are only two published accounts of adult male grey-cheeked mangabeys carrying infants (Chalmers, 1968c; Struhsaker and Leland, 1979), although information from unpublished theses show that it is common, and 'triadic male-infant interactions' are widespread (Chalmers, 1967; Wallis, 1979; Waser, personal communication; Struhsaker and Leland, 1979). Struhsaker and Leland (1979) noted that in Uganda adult males carried infants "occasionally in situations apparently involving agonistic buffering". "Agonistic buffering" is the term first used by Deag and Crook (1971) to describe interactions in which low-ranking adults held infants to decrease the likelihood of aggression from higher ranking adults. Chalmers (1967, 1968c) reported extensive carrying by adult males of infants 2.5 to 5 months old and described 'triadic male-infant interactions', although he did not call it such:

Table 7.9 Observations of adult males carrying infants.

Observation	Circumstance*	Infant initiated	Adult male initiated
I	a	YES	NO
II	a	YES	NO
III	a	YES	NO
IV	a	UNKNOWN	UNKNOWN
V	b	NO	YES
VI	c	NO	YES
VII	a	YES	NO
VIII	c	UNKNOWN	UNKNOWN
IX	c	UNKNOWN	UNKNOWN
X	a	UNKNOWN	UNKNOWN
XI	a	UNKNOWN	UNKNOWN
XII	b	UNKNOWN	UNKNOWN

a: during a potential conflict with another adult male (including intergroup encounter)
b: in the presence of a predator (including humans for non-habituated group and crowned hawk eagles)
c: unknown

> "14 conflicts between adult males over infants were seen in the Bujuko group; i.e. one male while sitting with or carrying an infant was attacked by another male. This contrasts with the complete lack of aggression seen towards the mother during transfer of the infant from the mother to the male. In addition, two males who initially carried infants, both at that time sustained wounds. As these were the only wounds seen in either group during the whole study, it possibly indicates that infants provided a major source of conflict between adult males."

Although there is little published, in three out of the four main field studies on grey-cheeked mangabeys, adult males were recorded carrying infants and triadic male-infant interactions were observed (Chalmers, 1967; Wallis, 1979; Waser, personal communication). Cashner (1972) was the only study of wild grey-cheeked mangabeys that did not observe infant carrying by males. This may have been because most of the groups Cashner (1972) observed had only one adult male.

Wallis (1979) recorded triadic male-infant interactions in his unpublished thesis. The behaviour appeared at a time when one adult male (OLH) was overthrowing another adult male (RAT):

> "...there were some interesting observations of agonistic buffering where RAT carried an approximately 2 year old juvenile 1/4 his size when he was chased by OLH. RAT kept the juvenile close to himself even when he was not being chased by carrying or dragging it, and when he fed, he sat with his foot on he juvenile's tail. This behaviour was observed on 2 consecutive days and the juvenile was in contact with RAT for the majority of those days.

Waser (personal communication) observed adult males carrying infants, but that adult male-infant interactions were fairly complex, occurring not only in male-male conflict situations but also during periods of alarm (crowned hawk-eagle overflights) and on at least one occasion following a prolonged (several days) absence of the male from the study group. Triadic male-infant relationships are not limited to only one species of mangabey, but have also been recorded in captive studies of sooty mangabeys. Busse and Gordon (1984) observed infants being carried by adult males, and in 62 out of 65 observations the "recently deposed alpha male carried an infant in the presence of the newly ascendant dominant male". Bernstein (1976) also observed that adult male sooty mangabeys in captivity carried infants ventrally, but that "male carriage of infants seemed to occur in response to the stress of the infant rather than the stress of the males themselves" and that "male motivation did not seem to involve agonistic buffering."

Various hypotheses have been proposed to explain why adult males may carry infants in the presence of another adult male, and these are outlined below.

Hypothesis 1: "Infant Exploitation"

The first hypothesis states that an adult male carries an infant for his own immediate (proximate) advantage (Popp, 1978 in Whitten, 1987; Packer, 1980; Stein, 1984; Strum, 1984). Evidence for this hypothesis comes from observations in baboons that males carrying infants are *less* likely to (a) be threatened by other males (eg. Packer, 1980), and (b) retreat from an interaction with a more dominant male (Stein, 1984), but are *more* likely to (a) direct aggression towards a more dominant adult male (eg. Packer, 1980; Stein, 1984), (b) be successful at supplanting another adult male (Packer, 1980), (c) initiate aggression towards a higher ranking male (Stein, 1984), and (d) resist aggression from another adult male for longer (Stein, 1984).

There are also several hypotheses to explain the mechanisms of why an adult male would be less likely to be attacked when carrying an infant. Maynard Smith and Parker (1976) hypothesise that in a fight, the opponent who is more likely to gain from winning should be more willing to fight. Applying their theory to this situation; if an adult male is holding his own offspring he has more to gain in terms of his reproductive fitness from winning a fight, than the attacking adult male, and therefore the attacking male should defer (eg. Packer and Pusey, 1985).

Another theory is that a male attacking an infant-carrying male, might subsequently provoke retaliation from other members of the group who may be related to the infant (Stein, 1984; Strum, 1984). This has been observed in 6 different troops of baboons (eg. Smuts, 1985).

Finally, if the adult male is carrying the offspring of the other adult male, then the other adult male may be less likely to attack since he would risk injuring his own offspring.

Hypothesis 2: "Infant Protection"

The second hypothesis suggests that adult males carry infants in the presence of another adult male in order to protect the infant. This hypothesis would predict that the adult male would be genetically related to the offspring he is carrying, but the evidence for this is conflicting. In some studies on baboons the adult male and the infant he carried were genetically related (eg. Busse and Hamilton, 1981; Packer,1980), but in other studies carriers were most likely to be fathers during only 40% (Packer and Pusey, 1985) and 50% (Smuts, 1985) of all interactions.

Hypothesis 3: "Cultivation"

A third hypothesis suggests that males carry infants to benefit, or to "cultivate" their relationship with the mother of the infants, therefore increasing the chances of future copulations (Smuts, 1985). This hypothesis emphasises sexual investment instead of paternal care investment. It predicts that adult males would only carry infants when the mother would be likely to be watching; that the adult female should not show distress when the adult male is carrying the infant, and that the adult male should carry infants for whom he provides care in other contexts. The genetic relatedness between the adult male and infants should not be important.

As mentioned above, carrier adult males are not always related to the infants they carry. Several authors have observed that adult males tend to carry infants that are usually offspring of the females with whom they have close relationships and the same infants that they provide care for, but not necessarily infants to whom they are genetically related (eg. Smuts, 1985; Packer, 1980; Strum, 1984). In addition, some studies have found that adult males who carried infants were more likely to copulate with the mothers of the infants when they were cycling than other adult males who did not carry infants (eg. Smuts, 1985). In some studies adult female baboons did not, in general, seem distressed when the adult male carried their infants (Smuts, 1985; Busse and Hamilton, 1981). In other studies, however, responses of females to males carrying their infants varied and females sometimes did show signs of distress (Stein, 1984).

Evidence from this study

The resident male, PEI was the only adult male who was observed to carry infants, and in at least four out of the 12 cases he was more likely than OTT to be the the father since OTT did not enter the group until nine months after the infants were born. This, in combination with evidence that infants sometimes actively participated in these interactions, allows rejection of the hypothesis that an adult male carries the offspring of the other adult male in order to protect himself from being attacked. In this study it could not be determined if the adult male was less likely to be attacked when carrying an infant than when not, since the number of attacks was too low.

Adult females with infants were sometimes observed to show distress when PEI attempted to carry their infant. In the previous section it was shown that PEI was observed as the nearest neighbour of mothers more frequently than OTT. However, when one of the adult females with infants recommenced cycling, this female showed preference for OTT over PEI by presenting to him more often and remaining close to him when her swelling was maximum. This suggests it was unlikely that PEI was carrying the infant to better a relationship between him and the mother to increase the likelihood of future copulations.

The most likely reason that PEI carried infants was in order to protect them. Evidence supporting this is that (1) infants sometimes initiated these interactions, ruling out exploitation alone, and (2) PEI was observed attempting to carry infants in situations requiring his protection, such as during the overflight of crowned hawk eagles and in the presence of OTT.

Waser (personal communications) also observed that adult males carried infants during periods of alarm, suggesting a protective role of the adult males towards the infants. In nearly every overflight of crowned hawk eagles, PEI was the only adult male to chase the eagle and to follow it away from the group. In these situations PEI may not only have carried an infant to protect it from eagle attack, but also to ensure its safety from attack by the immigrant male, that might otherwise have taken place in PEI's absence. This hypothesis is consistent with the observation that OTT attacked the youngest juvenile male in the group during the temporary absence of PEI from the group during an overflight of an eagle.

In baboons, attacks on infants are often by adult males who have recently immigrated into the group (eg. Collins *et al.*, 1984) and it is frequently the resident adult males who were in the group when infants were conceived who carried infants in encounters with the immigrant males (eg. Collins, 1986). Waser (personal communications) observed that it was usually the older, less dominant male who carried infants and Chalmers (1968c) noted that especially when the infant was young, only one adult male was observed to carry infants, although he did not specify the status of this male. For Wallis (1979) and Busse and Gordon (1984) although both adult males were already present in the group, triadic male-infant interactions occurred during changes in the dominance status of these males, indicating that infant carrying may be most frequent when the infant is in fact in danger from either a new adult male in the group, or a new dominant male in the group.

If an adult female's infant survives, then it may be up to eight months before she starts to cycle again (see *Chapter Four*), whereas if her infant dies, adult female mangabeys have been observed to start cycling again within 37 days (Deputte, 1991). Thus the newly immigrant male, or recently dominant adult male may improve his chances of impregnating an adult female by killing her offspring. Although infanticide has never been observed in mangabeys in the wild, in a captive group of sooty mangabeys, adult males attacked and bit three new born infants and one of these infants died (Busse and Gordon, 1983). An adult male was also observed stalking and chasing an eight month old infant in the group. Bernstein (1971b) observed infanticide in sooty mangabeys when a dominant male in one group attacked and killed a two month old infant in another group during an experimental merging of groups. Busse and Gordon (1983), and Bernstein (1976) also suggested that adult male mangabeys carry infants to protect them rather than to exploit them.

There now seems to be general agreement that males may carry infants for multiple reasons, or different reasons at different times. The benefits may be for both infants and males (Packer, 1980; Stein, 1984; Strum, 1984; Smuts, 1985). This is probably the case for mangabeys, though more detailed study is necessary to resolve the issue.

SUMMARY

In summary, many of the behaviours described in this chapter are similar to those described for baboons and macaques. Wallis (1983) provided the first outline of the behavioural repertoire of grey-cheeked mangabeys, and the present study has expanded this list, and described in detail for the first time in grey-cheeked mangabeys, behaviours such as consorts and triadic male-infant interactions. Nearest neighbour distances revealed that the three adult males: PEI, OTT and REG were very different in their relationships with other members of the group. PEI was found more often in close proximity with infants and adult females with infants, than the other two males, and OTT was more often associated with females in oestrus than PEI and REG. These different strategies of adult males in multimale groups have also been observed for other mangabey groups and other Cercopithecines.

CHAPTER 8. POLYSPECIFIC ASSOCIATIONS

INTRODUCTION

Different species living sympatrically, sometimes join together to feed, travel, rest and even interact socially. These "mixed species" or "polyspecific" associations have been observed in a variety of taxa including fish (eg. Ehrlich and Ehrlich, 1973; Landeau and Terborgh, 1986; Wolf, 1985); birds (eg. Morse, 1970; Munn and Terborgh, 1979; Wiley, 1980), ungulates (eg. FitzGibbon, 1990; Leuthold, 1977; Sinclair, 1985), bats (eg. Bradbury, 1975) and primates (eg. Gautier and Gautier-Hion 1969; Struhsaker, 1981; Terborgh, 1983).

In primates, polyspecific associations are most common among small to medium sized, diurnal, frugivorous (Peres, 1991), forest living and arboreal species (Gautier-Hion, 1988b) living in Africa (Struhsaker, 1981) or South America (Klein and Klein, 1973). They have been recorded in New World primates for the genera *Saimiri*, and *Cebus* (eg. Terborgh 1983; Podolsky, 1990), *Cacajo* (eg. Mittermeier and Coimbra-Filho, 1982) and *Saguinus* (eg. Buchanan-Smith, 1990, Castro and Soini, 1977; Garber 1988; Heymann, 1990; Norconk, 1990; Pook and Pook 1982; Terborgh 1983; Yoneda, 1984) and in Old World primates, for *Cercopithecus* spp. (eg. Cords, 1990a,b; Dunbar and Dunbar, 1974; Galat and Galat-Luong, 1985; Gartlan and Struhsaker, 1972; Gautier, 1985; Gautier and Gautier-Hion, 1969; Gautier-Hion, 1983, 1988b; Gautier-Hion and Gautier, 1974; Gautier-Hion *et al.*, 1983; Gautier-Hion and Tutin, 1988; Mitani 1991; Struhsaker, 1981; Waser, 1980, Whitesides, 1989), *Colobus* spp. (eg. Galat and Galat-Luong, 1985; Oates and Whitesides, 1990; Struhsaker, 1975), and *Cercocebus* (eg. Cashner, 1972; Jones and Sabater Pi, 1968; Wallis,1979; Waser, 1980). Polyspecific association among Asian species of primates are rare (see MacKinnon and MacKinnon, 1980). Associations are thought to be the most common between species from the same genus, especially forest guenons, *Cercopithecus* spp. (Gautier-Hion, 1988b) and tamarins, *Saguinus* spp. (Terborgh, 1983). Associations between species of different genera are less frequent (Peres, 1991), but have been observed between genera of several New World primates (eg. Peres, 1991; Terborgh, 1983), and between different genera of Old World monkeys (eg. Oates and Whitesides, 1990; Waser, 1980).

Because polyspecific associations are common, they are probably adaptive. Many authors have proposed functional explanations for polyspecific associations, the two most common being an increase in foraging success and a reduction in predation risk. Although these benefits may be great, association are likely to incur costs as well as benefits, and the most obvious cost is increased competition.

Grey-cheeked mangabeys, have been observed to form associations with sympatric species, but these associations have only been studied in detail in Uganda (Waser, 1980, 1982a, 1984, 1987). Waser (1974) observed them to associate with *Cercopithecus* spp. and *Colobus* spp. and described these associations as "infrequent" and "impermanent" only occurring with one species; the red-tailed guenon (*Cercopithecus ascanius*) more than expected by chance encounters in the forest. In Gabon, mangabeys live sympatrically with a different community of primates than in Uganda (*Chapter Two*). At Lopé mangabeys form polyspecific associations with spot-nosed guenons (*Cercopithecus nictitans*), crowned guenons (*Cercopithecus pogonias*), moustached guenons (*Cercopithecus cephus*) and black colobus (*Colobus satanus*) and although the associations formed between the three *Cercopithecus* spp. have been described in detail for populations at Makokou (about 200 km to the north east of Lopé in Gabon), mangabeys have generally not been included in these discussions (eg. Gautier and Gautier-Hion, 1969; Gautier-Hion and Gautier, 1974; Gautier-Hion *et al.*, 1983).

The aim of this chapter is to describe, in detail, the polyspecific associations between mangabeys and other primate species at Lopé, testing the proposed hypotheses of foraging success and predator avoidance as explanations for their occurrence. These costs and benefits do not necessarily apply equally to all species participating in the association. Polyspecific associations may range from mutualistic to parasitic (Peres, 1991), therefore variations in the frequency of associations between different species will be examined and related to ecological and behavioural parameters to determine their effects on the frequency of the associations.

METHODS

Polyspecific associations defined

In this study polyspecific associations were defined as when individuals from two different species are spatially intermixed or within 50m of each other. The distance of 50m was chosen because it was the longest distance to which I could accurately detect the presence or absence of another species and because this is the distance most frequently used in other studies of polyspecific associations in arboreal African primates. It therefore allows direct comparisons of results (Mitani, 1991;

Oates and Whitesides 1989; Waser 1980).

Frequency of polyspecific associations

Data on polyspecific associations were collected using two different methods:

Method One: Censuses

During searches for the study group of mangabeys, during transect work, collecting phenology data, tracking gorillas (*i.e.* all time spent in the forest when I was not with the study group of mangabeys), I recorded all encounters with primates. The date, time, location, species identity, height of the first visible individual, and whether species were alone or within 50m of another species were recorded. If the same group of any species was encountered a second time during the day, the encounter was not recorded, so that no group was recorded more than once in a day to ensure independence of samples. Groups were assumed to be different if (1) I was aware of more than one group simultaneously, or (2) groups of guenons were encountered at least 1 km apart, and groups of colobus were encountered at least 2 km apart. The latter criterion is based on the assumption that (i) the home range sizes of guenons at SEGC were similar to those studied at Makokou (see Gautier-Hion, 1988b: home range sizes were 80 ha for spot-nosed guenons; 100 ha for crowned guenons; and 90 ha for moustached guenons), and (ii) the home range size of black colobus at SEGC was similar to colobus studied by Harrison, 7 km north of SEGC (1986a), and (iii) the shape of home ranges was approximately square.

Never more than one group of mandrills was recorded in a day, so this was not a problem for ensuring independence of observations of this species.

Method Two: Follows

During continuous follows of the study group of mangabeys, a scan sample was conducted every 15 minutes and information was collected as described in *Chapter Two*. During the scan samples the presence or absence, and the species identity of any other primate within 50m of the study group was recorded.

Only data on associations between mangabeys, colobus, crowned guenons, spot-nosed guenons, moustached guenons and mandrills were used in calculations (**Plate 8.1**). None of these species associated with gorillas (*Gorilla g. gorilla*) or chimpanzees (*Pan t. troglodytes*) also present at Lopé, although occasional encounters between the species did occur. These encounters will be described below.

Lone males

For forest guenons, mangabeys and mandrills, it is usually the adult males who transfer out of their natal group upon reaching sexual maturity. Lone individuals of all these species were observed to associate with monospecific or polyspecific groups of other species. Although data on the frequency of these associations were collected, they were not used in calculations for the reasons described below. Other researchers have not included lone males in general calculations of association frequency either because sample sizes were not large enough (Mitani, 1991) or because " the potential advantages and disadvantages of interspecific associations may be very different for these solitary animals than with social groups" (Oates and Whitesides, 1980).

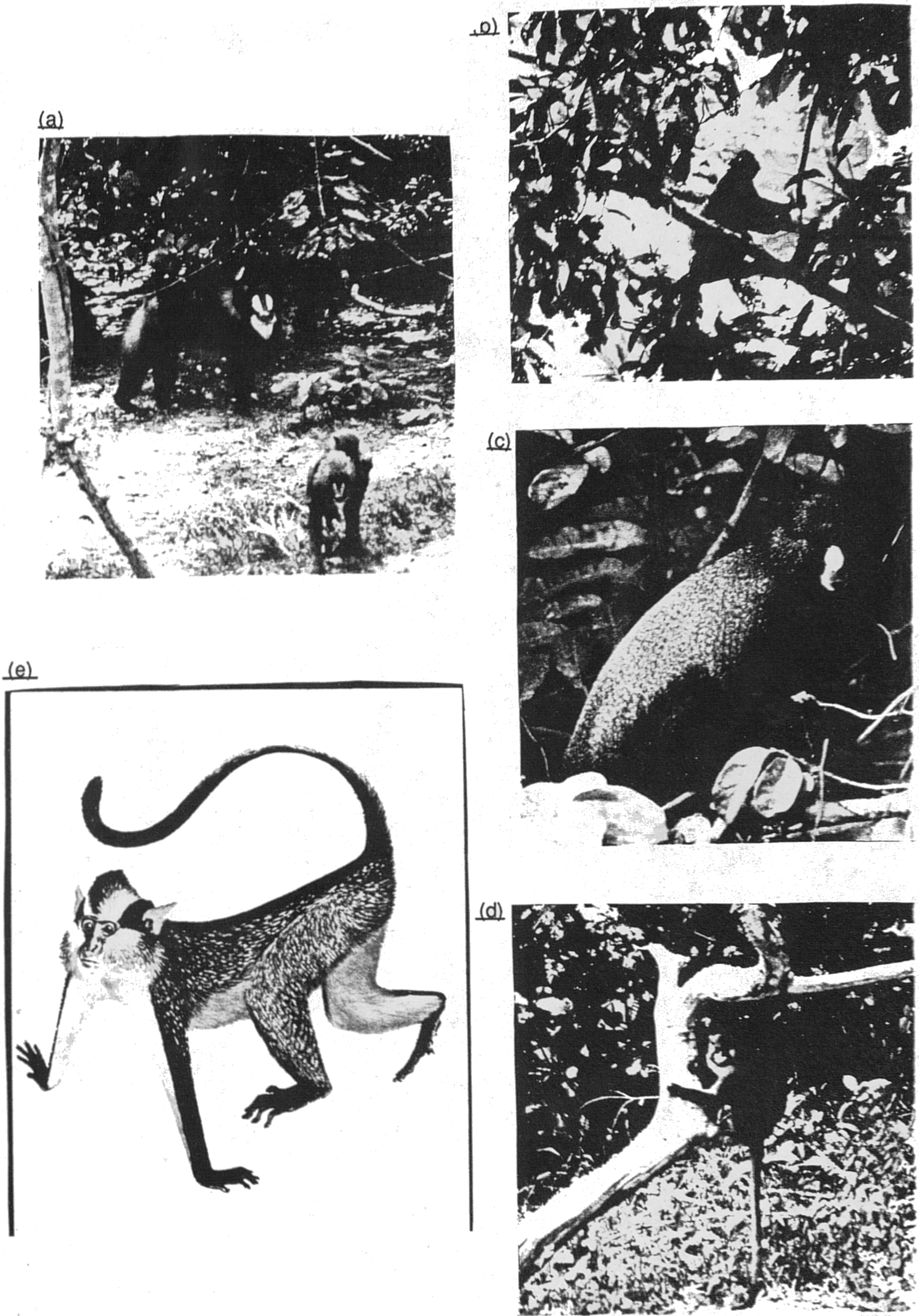


Plate 8.1. Five species of primates at Lopé which were observed in polyspecific association with mangabeys: (a) mandrills (*Mandrillus sphinx*); (b)black colobus (*Colobus satanus*); (c) spot-nosed guenon, (*Cercopithecus nictitans*); (d) moustached guenon, (*Cercopithecus cephus*); (e) crowned guenon, (*Cercopithecus pogonias*)(illustration by Jonathan Kingdon in Gautier-Hion *et al.*, 1988).

RESULTS

1. Frequency of polyspecific associations

Censuses

Overall

Data was collected over 18 months, but where specified, data from only 12 months were used in order to control for the possible effects of seasonality. During 18 months, 797 encounters with primate groups were recorded, and during 12 months, 523 encounters were recorded. During both 18 months and 12 years, species encountered most frequently were; spot-nosed guenons, then mangabeys, colobus, crowned guenons, moustached guenons, and then mandrills. The encounter rates reflected the density of primate species at SEGC (White,1992), except for mangabeys for which encounter rates were probably elevated since they were the main focus of the study.

Because sample sizes were uneven between months, the average amount of time spent in association was calculated for each month. To avoid the effects of seasonality, the average frequencies of associations were calculated over one year from September 1991 to August 1992. Collapsing the data across species, monkeys were associated with one or more species in 48% of all encounters. The proportion of time spent in association decreased with the number of species involved in the association, where 52% of encounters were with monospecific groups, 29% of encounters with bispecific groups, 10% of encounters with trispecific groups, 7% of encounters with quadrispecific groups, and 2% of encounters with pentaspecific groups (**Figure 8.1**).

The species observed mono-specifically most frequently was

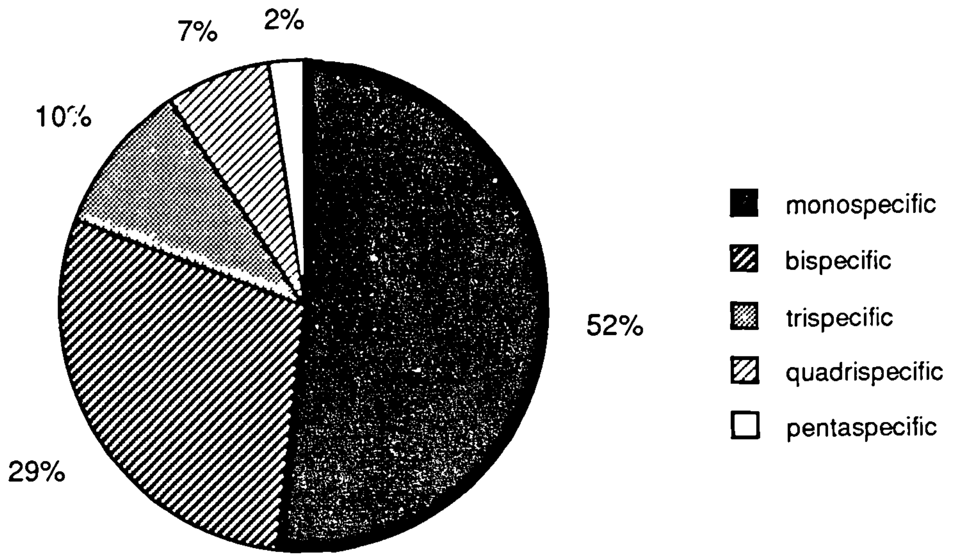


Figure 8.1 Average percent time all species were observed alone or in association from September 1991 to August 1992

colobus (mean=52%, S.D.=3%), then spot-nosed guenons (mean=39%, S.D.=15%), then moustached guenons (mean=23%, S.D.=16%), then mangabeys (mean=20%, S.D=11%), then crowned guenons (mean=2%, S.D.=4%). The most frequent association occurred between mangabeys and crowned guenons, forming 56% of all observed associations. Bispecific associations of groups of spot-nosed guenons and moustached guenons formed 12%, and trispecific associations of mangabeys, crowned guenons and spot-nosed guenons also fo~med 12% of all observed associations.

Grey-cheeked mangabeys

During one year, mangabeys were encountered; 20% of encounters in monospecific groups, 39% of encounters in bispecific groups, 20% of encounters in trispecific groups, 17% of encounters in quadrispecific groups, and 4% of encounters in pentaspecific groups (**Figure 8.2**). They species observed most frequently in association with mangabeys was crowned guenons (mean=63%, S.D.=15%), then spot-nosed guenons (mean=47%, S.D.=14%), then moustached guenons (mean=20%, S.D=15%), then colobus (mean=16%, S.D.=10%), then mandrills (2%, S.D.=4%) (**Figure 8.3**). Because the frequency of one species associating with mangabeys could have influenced the association of another species, frequencies of associations of each species with mangabeys were tested for correlation. There was a significant positive correlation over 18 months between spot-nosed guenons and moustached guenons (r_S=0.67, n=18, p<0.01) as to the amount of time they spent in association with mangabeys, but there were no significant correlations between any other species. Because associations between spot-nosed guenons and moustached guenons were the second most frequent, this may indicate affinity

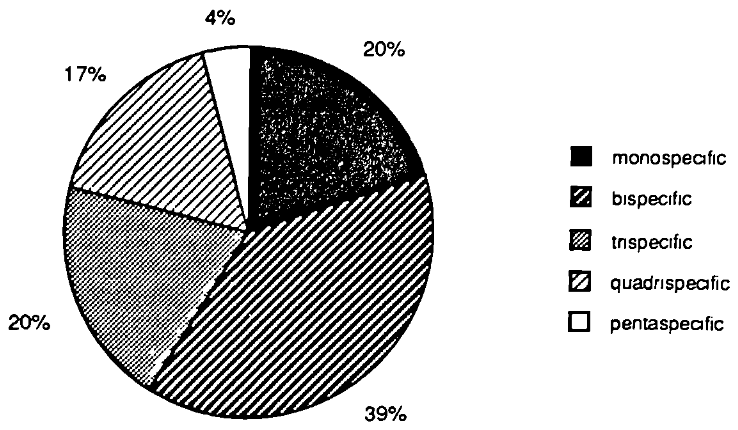


Figure 8.2 Average percent time Cercocebus albigena were observed in monospecific or polyspecific groups from September 1991 to August 1992 (method: "census")

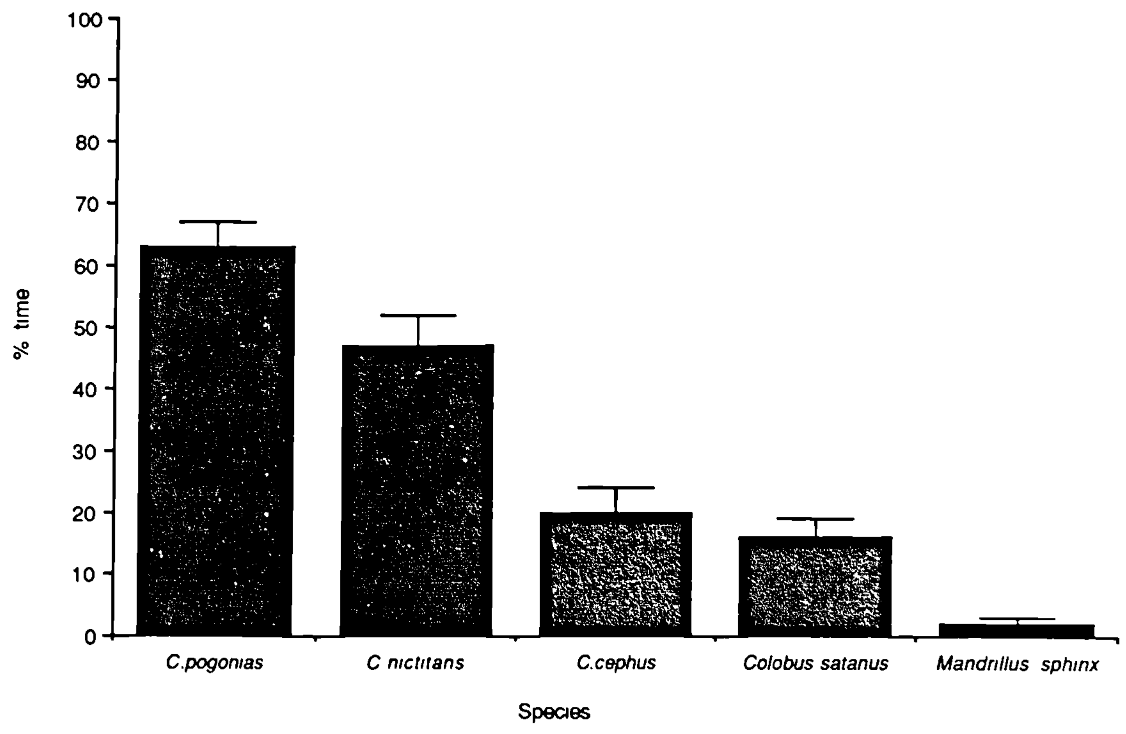


Figure 8.3 Average percent time that each species were observed in association with Cercocebus albigena from September 1991 to August 1992 (method: census).

between these species, and may explain why the amount of time they spent associating with mangabeys was related. Alternatively, the same costs and benefits for associating with mangabeys may apply to both guenons, and changes in these would affect the association frequencies of both species in a similar way.

Follows

During 18 morths, the association status of the study group of mangabeys was recorded for 3609 scans, and over 12 months, 1971 scans. During, the 12 months, the proportion of time mangabeys spent in association decreased with the number of species involved in the association. Mangabeys were in monospecific groups for 40% of scans, bispecific groups for 32% of scans, trispecific groups for 20% of scans, quadrispecific groups for 6% of scans, and pentaspecific groups for 2% of scans. (**Figure 8.4**).

Mangabeys were most frequently observed associated with crowned guenons (mean=49%, S.D.=21%), then spot-nosed guenons (mean=32%, S.D=19%), then colobus (mean=9%, S.D.=6%), then moustached guenons (mean=7%, S.D=7%), then mandrills (1%, S.D.=2%) (**Figure 8.5**). Mangabeys most frequently associated in bispecific groups with crowned guenons (22%, S.D.=11%) or in trispecific groups with both crowned guenons and spot-nosed guenons together (16%, S.D.=17%). There was a significant correlation over 18 months in the proportion of time that crowned guenons and spot-nosed guenons spent in association with mangabeys (r_s=0.54, n=18, p=0.02), but not for any other species.

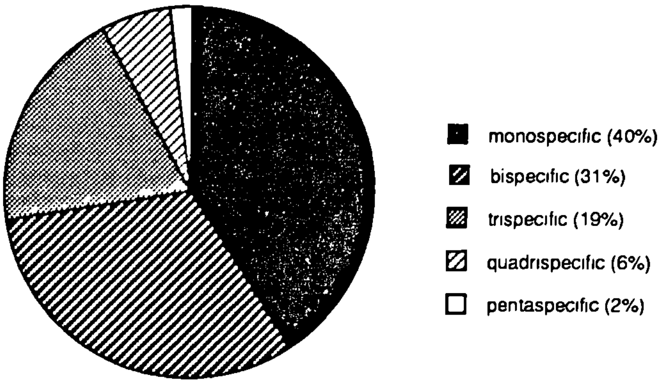


Figure 8.4 Average percent time that Cercocebus albigena were observed in monospecific or polyspecific groups from September 1991 to August 1992 (method, "follows")

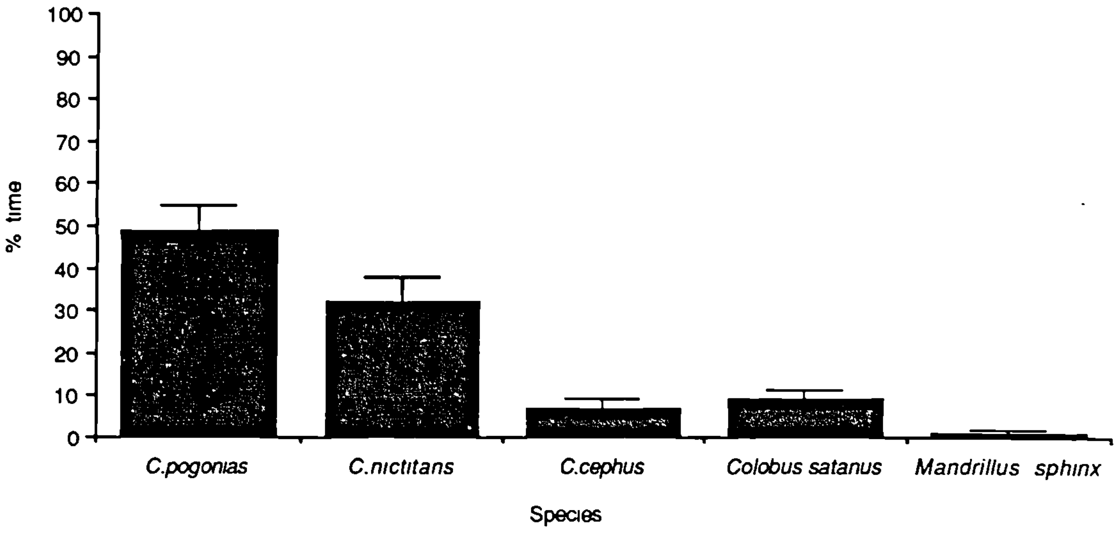


Figure 8.5 Mean percent of time that grey-cheeked mangabeys were observed in association with each species from September 1991 to August 1992.

Lone Males

During censuses, lone male mangabeys were encountered twice, once in April 1991 and once in October 1991 but no other species were detected nearby. During follows, lone male mangabeys were observed on the periphery of the study group three times. One of these males were observed to enter the study group.

During censuses, lone male crowned guenons were observed five times and were always associated with mangabeys, either with monospecific groups of mangabeys (n=2) or bispecific groups of mangabeys and nictitans (n=1) or mangabeys and colobus (n=2). During follows of the main study group, a recognisable lone male crowned guenon was observed associating with the mangabeys for 105 scans. He associated with the study group for six consecutive days plus two separate days in November 1991 and then one full day in February 1992. He was first observed in November 1991 and last observed in March 1992. He was most frequently observed when the study group was also in association with spot-nosed guenons (53% of scans when he was present), but was also observed when the study group were alone(42%) or in association with colobus (5%). He did not associate with the study group when they were in association with other groups of crowned guenons. He was seen most frequently with the study group in November 1991, which corresponds to the month with the lowest proportion of time that mangabeys spent in association with groups of crowned guenons.

Lone spot-nosed guenons were recorded during census data (n=13), but were never observed during follows. During censuses, they were always observed alone and never in association with another species group.

Lone moustached guenons were observed 11 times during censuses. They were observed alone (n=3), with spot-nosed guenons (n=2), with a bispecific group of mangabeys and spot-nosed guenons (n=2), a bispecific group of spot-nosed guenons and colobus (n=2), and with a trispecific group of mangabeys, crowned guenons and spot-nosed guenons (n=2). A recognisable lone moustached guenons associated with the group for 29 scans during follows of the study group of mangabeys. He was first observed in February 1992 and was still lone in August 1992. He was observed in association with the study group for two consecutive days during February 1992 and was most frequently observed with mangabeys when they were in associations with crowned guenons and spot-nosed guenons (48%), although he was also observed with monospecific groups of mangabeys (28%), or bispecific groups of mangabeys and crowned guenons (21%), and with a quadrispeciefic group of crowned guenons, spot-nosed guenons and colobus (3%).

During census, lone mandrills were encountered five times, either alone (n=4), or in association with a group of mangabeys (n=1).

A lone adult male mandrill was observed in association with the study group of mangabeys during at least four scans in May 1991 and at least four scans in April 1992.

Gorillas and chimpanzees

During follows, gorillas and chimpanzees were only within 50 m of the study group in 1.3% and 0.4% of scans, respectively. During censuses, gorillas were encountered 49 times, and chimpanzees were encountered 28 times, and during these encounters there were other species of primates within 50 m, eight and three times, respectively. Arboreal monkeys were observed to move into trees with fruit, minutes after gorillas had been feeding in them (eg. *Pterocarpus soyauxii, Diospyros polystemon* and *Diospyros dendo* trees) but monkeys were never observed to feed in the same tree as apes, to travel together, or to interact socially.

Comparison of data collection methods

Because two methods were used in this study to measure the frequency of associations between species, it was possible to compare the methods to see if they gave similar results and to determine whether they showed similar variation over months. Overall, the percent of time that mangabeys were observed in association was consistently higher using data from censuses than from follows. There was no significant difference, however, between mean values of the percent of time that mangabeys were observed alone over N=18 months (Mann-Whitney *U*-test=119, n=18 and 18, p=0.48), with crowned guenons (Mann-Whitney *U*-test=126, n=18 and 18, p=0.49) moustached guenons (Mann-Whitney *U*-test=86, n=18 and 18, p=0.47), spot-nosed guenons (Mann-Whitney *U*-test=109, n=18 and 18, p=0.48), or colobus (Mann-Whitney *U*-test=119, n=18 and 18, p=0.48). The percent of time mangabeys spent with mandrills each month was too low to allow for any useful comparisons. Correlations, comparing the mean frequency that species were observed with mangabeys each month using the two method, were significant for crowned guenons over N=18 months (r_S=0.72, n=18, p<0.01), moustached guenons (r_S=0.60, n=18, p<0.01) and colobus (r_S =0.50, n=18, p=0.04), but not spot-nosed guenons (r_S =0.23, n=18, p=0.37).

Because differences between the two methods in the frequency of associations may reflect differences between groups which might have a tendency to associate at different frequencies, two groups of mangabeys were compared in their association frequencies.The first group (Group One) of mangabeys was the study group and the second group (Group Two) was the group that ranged adjacent to, and overlapping the study group's range. The range of Group Two extended into a block of forest that was surrounded on either side with savanna. The frequency of associations has already been analysed for Group One as described above for *follows*. Data on the frequency of associations for Group Two were collected using the *census* methods. As shown above these methods do not give significantly different results and therefore the frequency of associations between Group One and Group Two were compared.

Results showed that Group Two tended to be associated with more species at the same time, than Group One. The percent of time that Group One was found in monospecific and bispecific groups was greater than for Group Two while the percent of time Group Two was observed in quadrispecific and pentaspecific was greater than for Group One (**Figure 8.6**). Group One associated more frequently with colobus than Group Two, whereas Group Two associated more frequently with spot-nosed guenons and crowned guenons than Group One, but these differences are not great. What is striking is that Group Two associated more than three times the amount of time with moustached guenons than did Group One.

The differences between the frequencies with which different groups associated may reflect differences in habitat structure in their home range. The home range of Group Two was bordered on two sides by savanna, therefore increasing the amount of savanna edge-habitat in the home range. Moustached guenons prefer lower

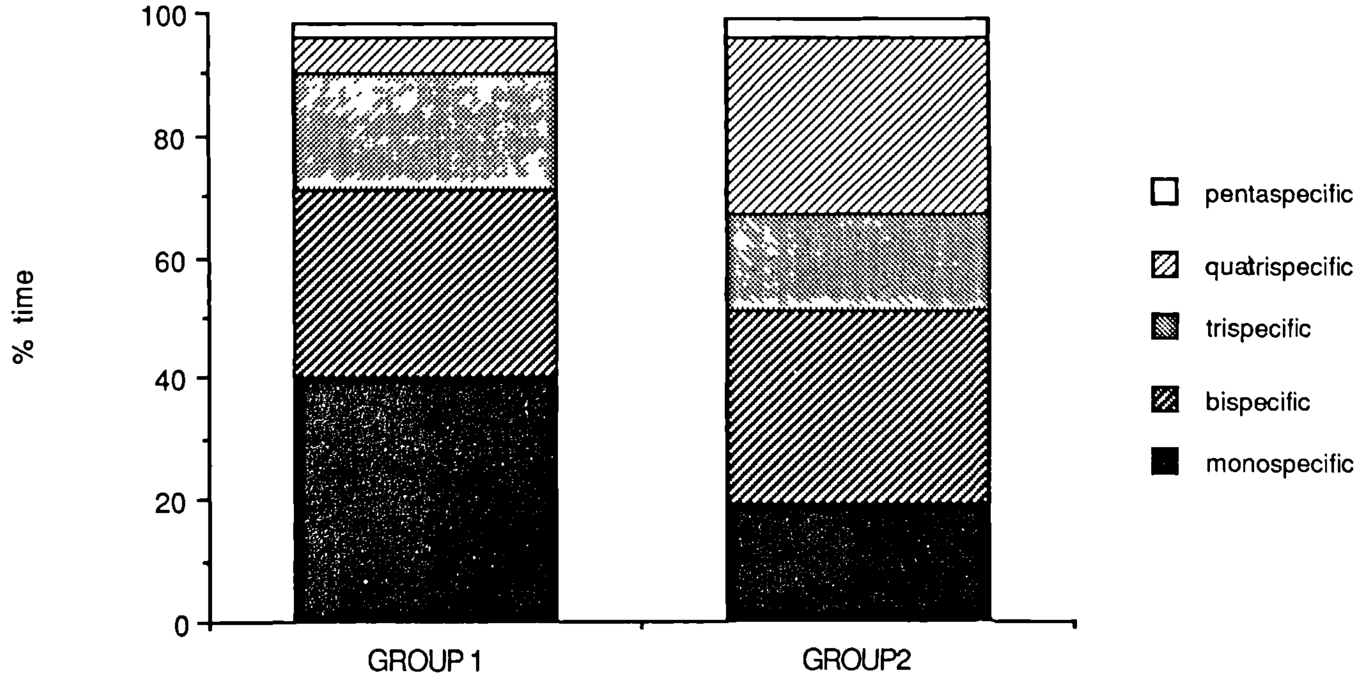


Figure 8.6 Comparison between the average percent time two groups of grey-cheeked mangabeys were observed in monospecific or polyspecific groups.

forest, with dense understory (Gautier-Hion *et al.*, 1983) common of forests which grow adjacent to savannas (*Chapter Three*, White, 1992), and therefore the density of moustached guenons may have been greater in the home range of Group Two, resulting in higher frequencies of associations with this species during censuses.

There are advantages and disadvantages of both methods for estimating associations frequencies. Struhsaker (1981) found that census methods exaggerated the frequency of associations over longitudinal studies. Contrary to Struhsaker (1981), for the present study, the census method was thought to be more accurate for two reasons. Firstly, although the study group of mangabeys were habituated, the other species were not, and therefore may have been reluctant to join the study group while I was observing them. This may have decreased the overall frequency with which mangabeys were observed in associations during *follows*. This is supported with data from the present study, where the census data shows mangabeys to be in polyspecific association more frequently than data from follows (**Figure 8.7**)

Secondly, the census method was considered to be better because it sampled a larger number of groups. Differences between groups of the same species in tendencies to associate have also been observed in other studies (Gautier-Hion *et al.*, 1983). For this reason also, the census method is better in that it samples a greater cross-section of groups. In the following discussions therefore, data on frequencies from the census method will usually be used, except for investigations of the relationships between activity and time with the association state, since data on activity were only collected during follows

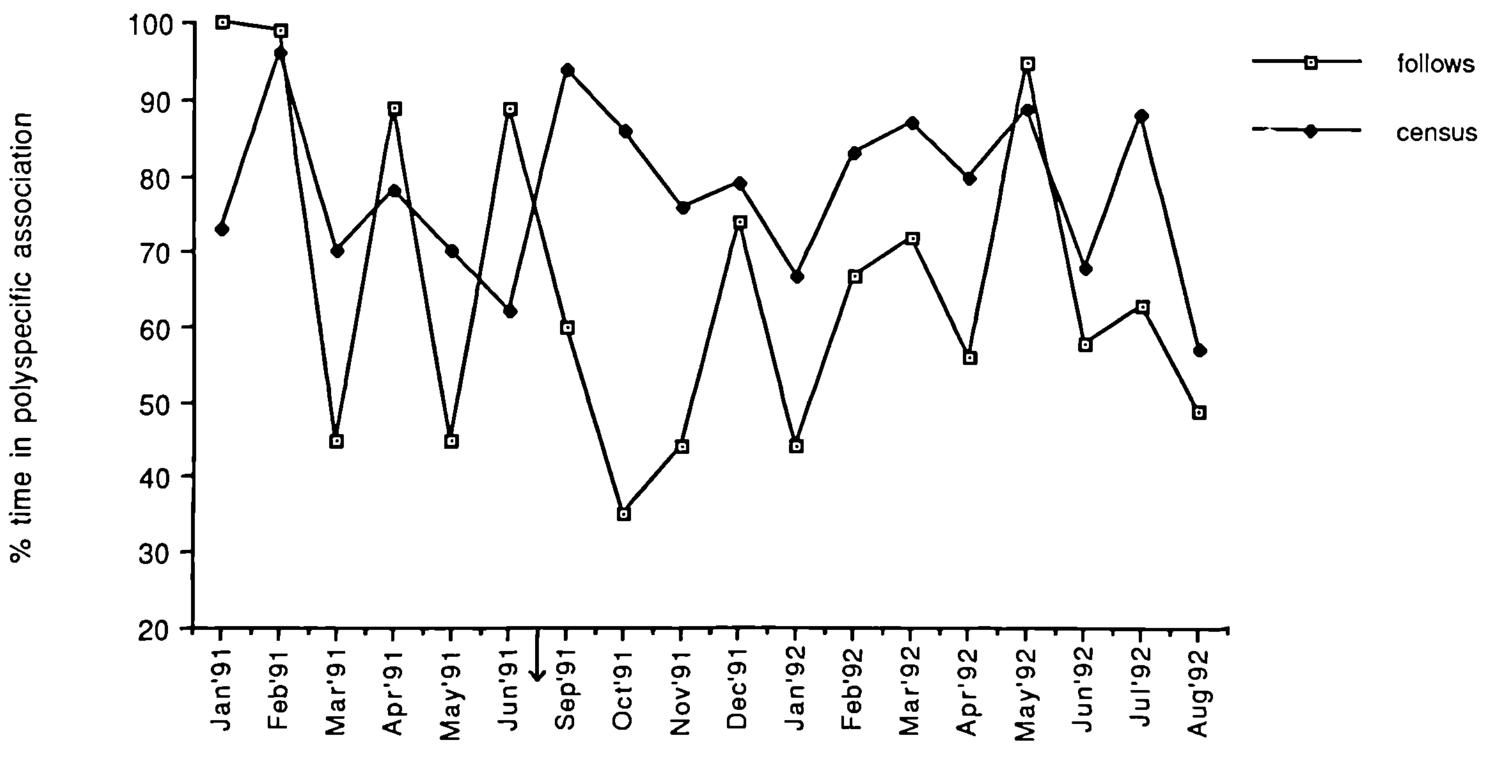


Figure 8.7 Comparison of "census" and "follows" methods in estimating the frequency that grey-cheeked mangabeys were in polyspecific associations

and not during censuses.

2. The Null Hypothesis

The above section shows the frequency of associations between species, but it is not clear whether these associations occur more frequently than expected by chance. Before examining the costs and benefits of associations, it is necessary first to test the null hypothesis that polyspecific associations may occur only as a result of random encounters in the forest. Many studies have been criticised for assuming that polyspecific associations have some ecological or behavioural significance, without first testing this null hypothesis. Several researchers have proposed methods for testing for this. Methods using only the frequency of encounters (Gartlan and Struhsaker,1972; Gautier and Gautier-Hion,1969; Jones and Sabater Pi, 1968; Quris,1976), ratios of the number of observations of a species in association to the total number of sightings (Gartlan and Struhsaker,1972; Gautier and Gautier-Hion, 1969; Struhsaker,1975), or Fager's index of affinity (Fager, 1957; Gartlan and Struhsaker,1972; Gautier and Gautier-Hion,1969; Quris,1976; Struhsaker,1975), do not accurately predict whether associations occur more frequently than expected by chance because they assume that the observer has equal probability of contacting all species. This assumption is usually false given that the density of individual species within the study area are usually variable.

To calculate expected frequencies with which new associations would be formed between species, Waser (1980) used a model normally applied in physics for predicting the collision frequencies of gas molecules: the"Perfect Gas model" (Waser, 1980). This method is useful in situations where associations are formed and broken frequently, but in situations where associations are long lasting or semi-permanent, the frequency with which associations are formed or broken are low, even if the associations are significant. Waser (1987), therefore proposed another model to compare the observed frequency of associations between species to the expected frequency of associations. This model also predicts that associations should occur in proportion to the density of other groups present.

$T = (\pi^2 / 2) \times (Pj) \times (r)^2$ (Waser, 1984, 1987)

where, T is the time spent in association, Pj is the density of species j (calculated by dividing number of individuals/km^2 by mean group size in White, 1992), and r = ri + rj + d, where ri and rj are the radii of group i and j (**Table 8.1**), and d is the criterion distance (50m).

The expected frequencies using this formula were calculated and compared to the average observed frequencies. The ranges of the expected frequencies were set by variations in species densities within the study area provided by White (unpublished data). Although mandrills were observed in polyspecific associations, they were not tested for significance because their densities in the study area was highly seasonal. Large groups of mandrills were observed travelling through the study area in some months, but during other months, they were not observed. Because the main factor affecting the frequency with which they were observed to form associations was therefore mainly when they were in the study area, mandrills were not included in the following discussions.

Using Waser's (1984, 1987) formula, all species were observed to associate significantly more frequently than expected by

Table 8.1 Ecological correlates of five sympatric arboreal primates.

	Cercocebus	*C.pogonias*	*C.nictitans*	*C.cephus*	*Colobus*
1 Estimated Group Spread (m)	120	60	60	30	50
2 Density of groups/km2 range	0.53 0.43-0.69	0.43 0.31-0.6	1.77 1.47-2.29	0.67 0.48-1.02	1.05 1.04-1.69
3 Home Range Size (ha)	225 (n=1)	55-100	55-80	30-90	184 (n=1)
4 Average Group Size ±SD	median=18.00 n=3	13.82±4.64 n=11	10.50±2.63 n=16	6.4±1.65 n=10	12.58±3.56 n=19
5 Average body mass (kg)	41.0	11.9	79.6	13.0	106.7
Average height (m)±SD	20.0±3.1 (n=12 months)	21.0±5.8 (n=14)	18.7±5.8 (n=44)	13.3±6.4 (n=14)	20.4±6.3 (n=37)

1 Group spreads estimated as described for Cercocebus in Chapter Two.

2 Density estimates from White (1992) (no.indivs km-2/mean group size) and range of density from White (unpublished data)

3 Home range size of Cercocebus from this study, Cercopithecus spp. from Gautier-Hion (1988) and Colobus from Harison (unpublished data)

4 Average group sizes calculated as described in Chapter Two

5 Primate body masses from Gautier-Hion and Gautier (1974), Harrison (1988b)

random encounters, except associations between with mangabeys and colobus and spot-nosed guenons and colobus (**Figure 8.8, Table 8.2**).

Now that it is clear which species associate more than expected by chance encounters, it is possible to discuss the benefits that each species might gain from associating. Before going any further, however, it must be emphasised that polyspecific associations do not always benefit each species equally. Several studies have shown that benefits may be biased towards one species, usually the species that initiates and maintains the association. In the present study it was difficult to judge who initiated the associations, but data collected on order of movement of species in the polyspecific troop show that mangabeys were most frequently the leader (78%, n=50). This suggests that the following analysis of costs and benefits should be assessed considering the advantages and disadvantages of associating foremost to the *Cercopithecus* spp..

The benefits species incur by forming polyspecific associations can be divided into two main categories, including *foraging benefits* and *decreased risk of predation*. These will be considered in turn.

3. Benefits of polyspecific associations

Increased foraging success

The "foraging benefits hypothesis" can be broken down into five specific hypotheses:

Table 8.2 Observed vs expected values for the percent of time pairs of species spent in association.

The range of expected values are based on density variations from White (unpublished data).

	Cercocebus albigena		***C.pogonias***		***C.nictitans***		***C.cephus***		***Colobus satanus***	
	Observed	**Expected**	**Observed**	**Expected**	**Observed**	**Expected**	**Observed**	**Expected**	**Observed**	**Expected**
Cercocebus albigena	NA	NA	63	3 - 6	47	14 - 22	20	4 - 8	16	9 - 15
C.pogonias	88	4 - 7	NA	NA	53	9 - 13	33	2 - 5	27	6 - 9
C.nictitans	37	4 - 7	30	2 - 4	NA	NA	23	2 - 5	17	6 - 9
C.cephus	39	3 - 5	50	1 - 3	67	7 - 10	NA	NA	17	4 - 7
Colobus satanus	23	4 - 6	27	2 - 3	31	8 - 12	12	2 - 4	NA	NA

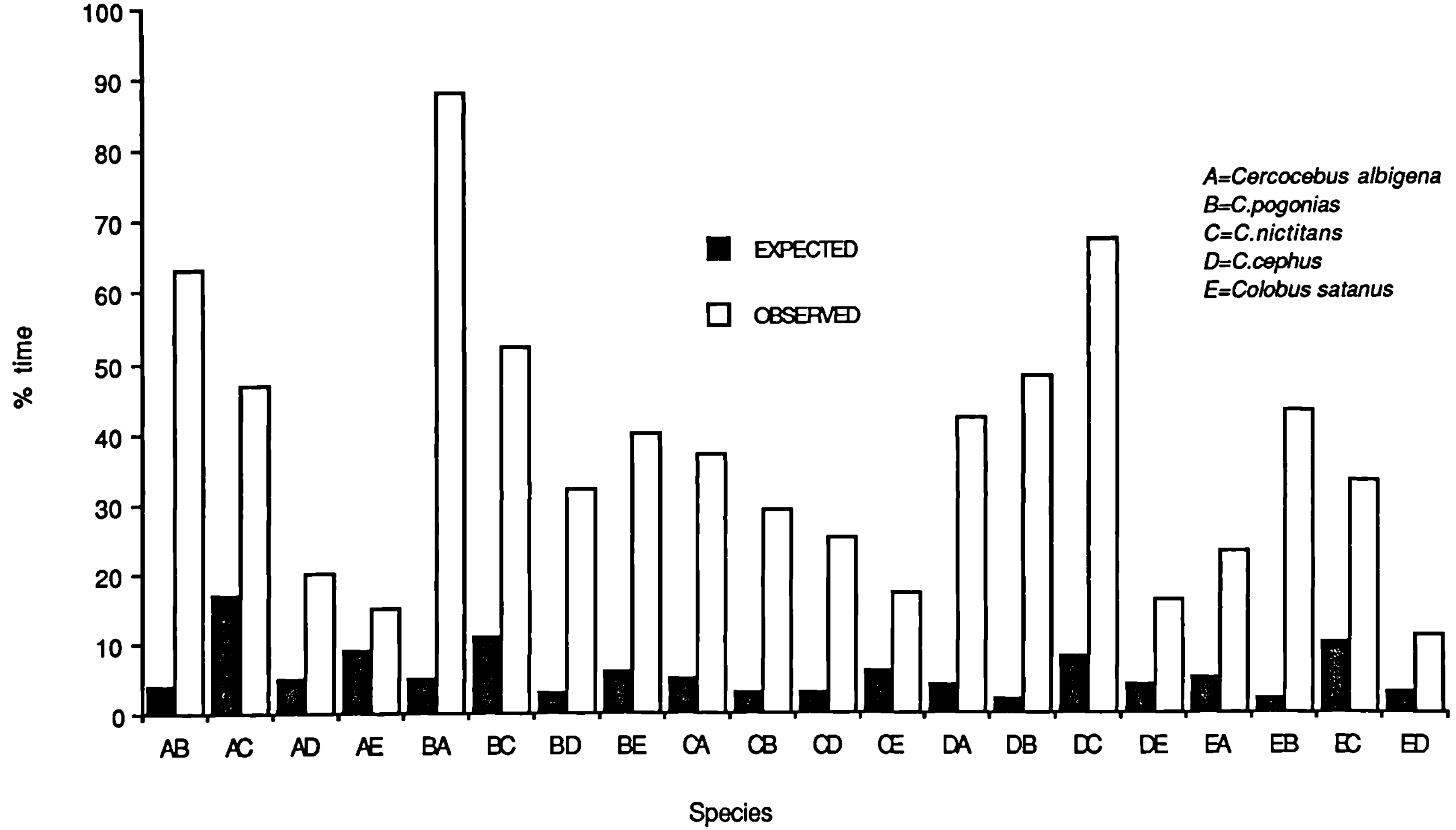


Figure 8.8 Observed and expected frequencies with which each species pair were observed in association

Foraging hypothesis I: One species may gain access to otherwise inaccessible food by associating with another (Waser, 1987; Struhsaker, 1981; Terborgh, 1983).

This hypothesis predicts that mangabeys associate most frequently when feeding and this was supported by the results. Using data from follows, mangabeys spent more time in associations when feeding than when resting, grooming and playing (Chi-square=4.21, df=1, p=0.04) although not when they were travelling (Chi-square=1.58, df=1, p=0.21) (**Figure 8.9**).

Waser (1974) and Wallis (1979) observed that *Cercopithecus* spp. in Uganda opened hard-to-crack fruit and by following mangabeys, and that *Cercopithecus* spp. gained access to fruits that had been opened by mangabeys, which they were unable to open themselves. This was never observed between primates in the present study, although it may have been a cause of some of the inter-taxa associations observed. For example forest duikers (*Cephalophus*) were frequently observed under monospecific or polyspecific groups of primates and fed on fruit dropped by monkeys (eg.*Pterocarpus soyauxii* seeds and *Irvingia gabonensis* fruit). Elephant (*Loxodonta africana*) may have been attracted by the sound of dropping fruit remains (especially *Pentadesma butyracea* fruit) when monkeys were feeding, but no conclusions can be drawn as to whether these associations were more frequent than random encounters.

A type of food that may have been made more accessible to other primate species in associations was insects, (see *Foraging hypothesis III*):

Foraging Hypothesis II: One species gains knowledge of the location of a food patch by associating with another (Gartlan and Struhsaker, 1972).

This hypothesis may explain why mangabeys were also observed in associations when travelling. It predicts that associations are especially beneficial for species with larger home ranges so that they could learn the location of fruiting trees from species with smaller home ranges (Cords, 1990a) who use areas more intensively and therefore probably have a better knowledge of where food is located. Because mangabeys were the species observed to lead polyspecific groups for 78% of the time, yet they were the species with the largest home range (**Table 8.1**), this hypothesis does not gain any support and alternative hypotheses should be considered.

Foraging hypothesis III: One species may feed on insects flushed by another species (Gautier-Hion and Gautier, 1974; Klein and Klein, 1973; Munn and Terborgh, 1979).

It was mentioned above that mangabeys associated significantly more when they were feeding than when they were playing, resting or grooming. Mangabeys were observed in associations even more frequently, however, when they were foraging for insects than when they were feeding (Chi-square=6.65, df=1, p=0.01,), travelling (Chi-square=8.56, df=1, p<0.01) and resting, grooming and playing (Chi-square=16.22, df=1, p<0.01) (**Figure 8.9**). Although they spent more time in association when foraging for insects, they did not, spend significantly more time foraging for insects when in association than when not in association (Mann Whitney U=0.95, n=12 months, p=0.37).

The frequency of polyspecific associations was observed to vary with the time of day (**Figure 8.10**). When the day was

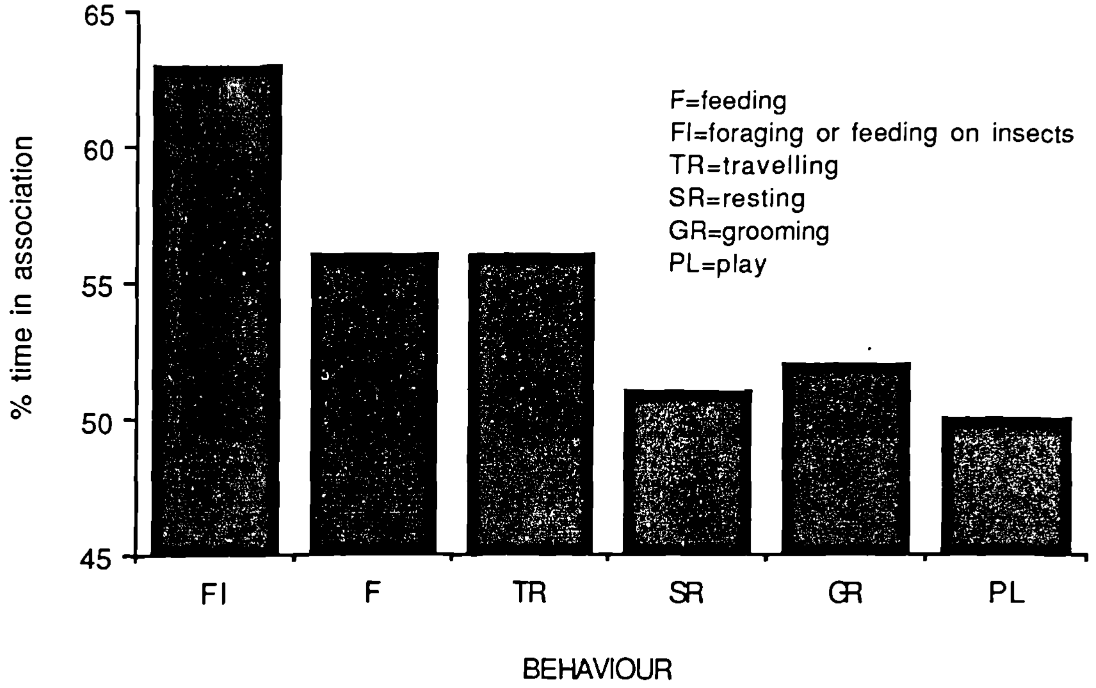


Figure 8.9 Percent time grey-cheeked mangabeys were observed in polyspecific associations while engaged in each behaviour (method: "follows")

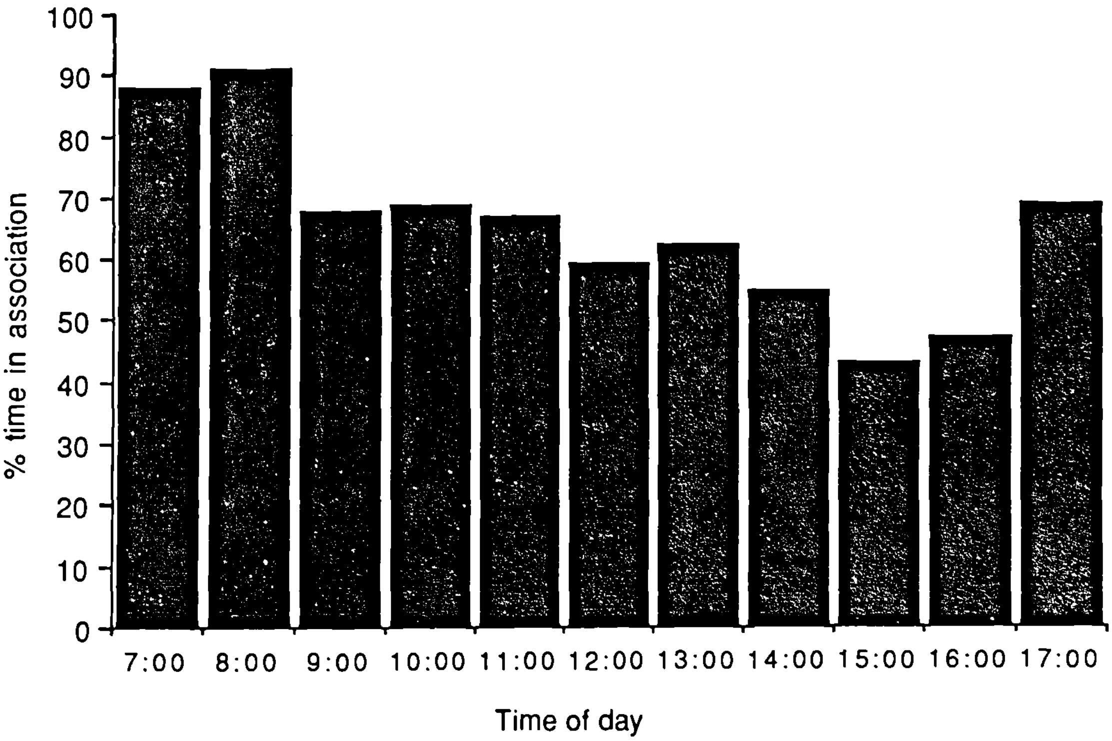


Figure 8.10 Percent time that grey-cheeked mangabeys were observed in polyspecific associations during different times of day (method: "follows")

divided into morning (08:00-11:00), midday (11:00-14:00) and afternoon (14:00-17:00), the proportion of time mangabeys were in polyspecific associations was significantly less in the afternoon than the morning (Chi-square=37.20, df=1, p<0.01), and midday (Chi-square=31.22, df=1, p<0.01), but there was no difference between the proportion of time spent in association between morning and midday (Chi-square=2.42, df=1, p=0.12).

Mangabeys spent 10% of their time overall foraging for insects. As described in *Chapter Five*, different methods were used for extracting the insects and a variety of substrates were used. Gautier-Hion (1978, 1980) found that crowned guenons had a larger proportion of insects in their diet than both spot-nosed guenons and moustached guenons and analysis of stomach's contents showed that crowned guenons tended to concentrate more on mobile insects (such as grasshoppers) than spot-nosed guenons and moustached guenons. Crowned guenons, therefore may have benefited the most by associating if this increased prey-capture rates. This may explain why crowned guenons had the highest frequency of associations.

Unfortunately, there were no direct observations of one primate species eating prey exposed by another in the present study. Hornbills were frequently seen following groups of monkeys and were observed snapping at the air to capture insects, suggesting that monkeys do flush insects.

There are three other hypotheses which suggest that foraging success may increase by associating with another species, but none of these hypotheses seem plausible in the present study.

Foraging hypothesis IV: By collectively exploiting food patches, previously used areas are avoided, therefore allowing maximum resource renewal (Cody, 1971).

This hypothesis seems most likely for species sharing a similar sized home range (eg. Buchanan-Smith, 1990). In such species, knowledge of which patches had been exploited would be accurate, but in species with (1) different sized home ranges, and (2) large overlap in home ranges with adjacent conspecific groups, exploitation of patches by other groups cannot be ruled out. Mangabeys, forest guenons and colobus at Lopé, have different sized home ranges (**Table 8.1**). Furthermore, mangabeys share approximately 25% of their home range with other groups of mangabeys (*Chapter Six*). This hypothesis, therefore seems an unlikely explanation for associations between mangabeys and other species.

Foraging hypothesis V: Polyspecific groups may jointly defend a territory better than monospecific groups (Terborgh, 1983).
Territoriality in polyspecific groups is most likely to occur between groups that require similar resources and have similar home range sizes (Peres, 1991) since this would increase the benefits for both parties involved. Home range sizes of mangabeys and guenons differed greatly (**Table 8.1**) and joint territoriality was never observed in the present study. Groups of guenons were even observed to transfer between groups of mangabeys during intergroup encounters (n=2 intergroup encounters), therefore this hypothesis also seems unlikely as an explanation for polyspecific associations.

All the hypotheses discussed above attempt to explain the benefits of polyspecific associations through an increase in foraging success. Foraging success cannot be the only explanation for the occurrence of these associations, however, because species have been seen to form associations when not only feeding, foraging, or travelling (eg. Gautier-Hion *et al.*, 1983; Struhsaker, 1981) and this was also observed in the present study. In addition, there was no direct relationship between dietary similarity and the frequency of associations between species.

The diets of all sympatric species at Lopé were examined in *Chapter Five*. Colobus, with whom mangabeys shared the largest number of food species was the only species with whom mangabeys did not associate more than expected by chance. When the proportion of time spent feeding on plant parts was examined, the diet of mangabeys was intermediate between colobus and crowned guenons. Mangabeys were observed in associations the most frequently with crowned guenons and the least frequently with colobus. This suggests that although foraging benefits may be an important reason for polyspecific associations, they are not the only reason. Benefits of predator avoidance may also have an important role.

Decreasing the risk of being predated

The known predators of the arboreal monkeys in Gabon, are crowned hawk eagles (*Stephanoaetus coronatus*), leopards (*Panthera pardus*), pythons (*Python sebae*), golden cats (*Felis aurata*), chimpanzees (*Pan t. troglodytes*) and humans (Gautier-Hion *et al.*, 1983). There are several ways by which associating with other species may decrease the risk of predation:

Predation Hypothesis I: "Safety in numbers" (Hamilton, 1971)

According to this hypothesis, there is a statistical decrease in the probability of any individual being taken by a predator with increased group size. This hypothesis predicts that primates living in smaller groups would be more likely to associate than species living in larger group. In order to tests the effects of group size on the tendency to associate, data were collected on the group sizes of primates as described in *Chapter Two* (**Table 8.1**). Moustached guenons had the smallest group size, followed by spot-nosed guenons, then colobus, crowned guenons, and then mangabeys. When group sizes were examined in relation to association frequency, the relationship was in fact the reverse of what was expected. Crowned guenons had the largest group size of all the guenons, yet they were observed in associations the most frequently, and moustached guenons, with the smallest group size, associated the least frequently. Although group size may explain general advantages of living in a larger group, there are probably additional ways in which polyspecific associations are beneficial.

Predation Hypothesis II: The "confusion" effect (Welty, 1934)

According to this hypothesis, predator success is reduced as a result of confusion of the predator by the flight pattern of groups under pursuit. This has been demonstrated experimentally to be true in fish (Landeau and Terborgh, 1986) and although this hypothesis seems likely, it was not observed in the present study.

Predation Hypothesis III: More "eyes and ears" (Powell, 1974)

This hypothesis simply states that a large number of individuals are more likely to detect an approaching predator than just one individual. In the present study, all species participating in the associations were observed to respond to each other's alarms calls, therefore if an individual of one species detected a predator and alarmed, then other primate species also benefited from their knowledge. Monkeys were also observed to respond to the alarm vocalisations and chest-beats of gorillas, alarm calls of forest duikers (*Cephalophus* spp.), and to various birds, including Hadada Ibis(*Bostrychia hagedash*) and Blue Touracos (*Corythaeola cristata*), and therefore this could also be an explanation for associations between these species.

This hypothesis, however, predicts that group size should be related to the tendency for a species to associate and as shown above, this was not observed in the present study. It may not only be group size that affects a species' vulnerability to predators, but also other factors, such as body size, ability to detect and deter predators and habitat preference. If predation pressure is an important reason for forming associations then these variables should be related to the frequency of associations. Each of these will be factors will be discussed in turn.

Body size

It has been suggested that smaller primates may be more vulnerable to predation by eagles than larger primates (Gautier-Hion and Tutin, 1988), therefore the amount of time each species spent in association with mangabeys was examined to see if it was related to body mass (**Table 8.1**). Except for moustached guenons, smaller-bodied species associated with mangabeys more than larger species. When the amount of time that each species spent in association overall was considered, however, there was no clear relationship with body size. Moustached guenons are the smallest primates, yet they associated the least overall.

Mangabeys are the second largest species, yet they were observed in associations the second most frequently overall.

Ability to detect predators

It has been proposed that not only do polyspecific associations increase the chances that predators are detected simply by increasing group size, but also because individual species may specialise in the way that predators are detected (Terborgh, 1983: Baldwin and Baldwin,1972; Cashner, 1972; Gartlan and Struhsaker, 1972; Gautier and Gautier-Hion, 1969; Gautier-Hion *et al.*, 1983). It has been proposed that more efficient predator detection results from a greater vertical spread of individuals and interspecific division in the ability to detect certain types of predators (Gautier-Hion and Tutin, 1988). In order to test if species used different parts of the canopy, the average heights of each species were calculated (**Table 8.1**). Crowned guenons were found highest in the canopy, then mangabeys and colobus, spot-nosed guenons, and moustached guenons in decreasing order of height. Because of these differences in heights, crowned guenons may be expected to be more alert to aerial predators and moustached guenons more specialised for detecting ground predators. This has been confirmed by Gautier-Hion *et al.*(1983) at Makokou.

In the present study, because aerial predators could not always be confirmed, and because observation of ground predators was so rare, the most useful measure of species-specific antipredator behaviour was the reaction of non-habituated groups of primates to humans. The reaction of primate species in polyspecific groups was noted 43 times for mangabeys, 36 times for crowned guenons, 25 times for spot-nosed guenons, 18 times for moustached guenons, and 12 times for colobus. Moustached guenons were the first detect my presence most frequently (67%), then crowned guenons (47%), spot-nosed guenons (40%), mangabeys (26%) and colobus were never the first to detect my presence.

Antipredator behaviour

Once predators had been detected, the reaction of species varied considerably. The antipredator behaviour of the *Cercopithecus* spp. have been described by Gautier-Hion (1988) at Makokou, and by Gautier-Hion and Tutin (1988) at Lopé and these antipredator behaviours were observed to be similar in the present study.

When guenons fled from predators, they fled in the trees and were never observed to flee along the ground. An adult male spot-nosed guenon was once observed to chase a crowned hawk eagle, as has also been observed by Gautier-Hion and Tutin (1988). Moustached guenons were observed to abandon polyspecific groups in the presence of predators and remain still and silent, as has also been observed by Gautier-Hion *et al.* (1983). In the present study, crowned guenons adopted different strategies depending on with which species they were associated . When they were with spot-nosed guenons or mangabeys, they fled with the polyspecific group. When associated with colobus, crowned guenons fled only a short distance and then adopted the moustached guenon's strategy of remaining still and silent. They may have behaved in this way with colobus, because even non-habituated groups of colobus rarely fled from humans in the study area and therefore in order to maintain their association with colobus, crowned guenons were not able to flee.

Compared to colobus and forest guenons at Lopé, mangabeys are relatively more conspicuous and vocal. Adult males from the group actively participated in defence against predators by alarming at, and chasing aerial predators, and following, monitoring and threatening ground predators (see also Gautier-Hion and Tutin, 1988). Adult males responded to ground-alarm vocalisations from other members of the group and alarms of duikers by investigation of the area. Two adult males were observed to lunge at and threaten a genet (*Genetta* sp.) which was foraging in the same tree as the mangabeys group. Although genets are not known predators of arboreal monkeys, this observation still demonstrates the active role of adult male mangabeys in antipredatory behaviour. Because of their larger body size, mangabeys may have been more successful in deterring predators than guenons, but since no successful predation attempts were observed during this study, this theory could not be tested. In 1988, a chimpanzee was observed eating a juvenile mangabey and the group remained above the chimpanzees alarming (SEGC records). Unfortunately, the events leading up to this predation were not observed.

A group of mandrills in a pentaspecific association was the first to alarm at a crowned hawk eagle during a predation attempt on the polyspecific group. In reaction to humans, mandrills emitted alarm vocalisations and other mandrills responded by either leaping into a nearby tree, or by fleeing a short distance. The response of mandrills to a leopard was also observed. A sub-adult male remained in a tree about 12m off the ground repeatedly alarming at a leopard in the vegetation below him.

The reaction of lone individuals to predators were similar across all species. Lone adult males, even when associated with other species, were never observed to alarm and fled silently without alarming.

Habitat type

Not only do the characteristics of the primates themselves affect the risk of predation, but factors in the habitat may also affect their vulnerability. In *Chapter Seven,* the home range of the mangabeys was divided into four main vegetation categories and two of these (savanna-edge and river-edge forests) were described in detail in *Chapter Three*. Factors such as average tree height, tree density or ground visibility may affect the degree to which predators can be detected, therefore a Chi-square analysis was performed to investigate whether species associated more or less frequently in different habitat types.

The only two species which appeared to be affected by habitat type were colobus and moustached guenons. Moustached guenons associated less frequently when they were in 'Savanna-edge' habitat than when they were in 'Marentaceae' forest, although this was not quite significant (Chi-square=3.11, df=1, p=0.08). In 'Savanna-edge' habitat, trees are smaller, in higher density (see *Chapter Three*), and branch lower (White, 1992). In the present study moustached guenons were observed in this habitat-type more frequently than all other arboreal primate species (Chi-square=18.64, df=1, p<0.01). Their preference for this habitat type has also been noted by Tutin (unpublished data), and Gautier-Hion *et al*. (1983).

Gautier-Hion *et al*. (1983) also observed that moustached guenons associated more frequently outside of this habitat type, but believed that moustached guenons entered other habitat types because they were "drawn" into other areas when they are in associations. In the present study it seemed more likely that moustached guenons sought to be in polyspecific associations because they were outside of this habitat type. Moustached guenons may have relied on the dense savanna-edge habitat for protection from predators and therefore been more vulnerable in more open areas and needed the increased security of a larger group .

The opposite was true for colobus, who associated more frequently when they were in 'Savanna-edge' habitat than when they were in all other habitat types (Chi-square=4.05, df=1, p=0.04). In addition, a significant negative correlation was observed between the amount of time the study group of mangabeys were observed in association with colobus and the amount of time the study group of mangabeys spent in 'Marentaceae' forest (r_S=-0.641, n=18, p<0.01). It is possible that colobus may have been more vulnerable to ground predators in the low vegetation at the savanna-edge, but no evidence of this was observed.

Thus far, the many benefits of polyspecific associations have been examined. As recognised earlier, there may also be costs involved in associating with other species; namely increased competition. The effects of competition on the frequency of polyspecific associations will now be examined.

4. Costs of polyspecific associations: Competition

There are several ways of testing whether competition has an important influence on polyspecific associations. The first two tests involve examining whether the use of horizontal and vertical space differ for mangabeys in and out of associations.

Horizontal use of space: Group spread

Inter-individual distance, or group spread, has been observed to increase when competition increases, therefore a Chi-square was performed to test if mangabeys were observed with a larger group spread when they were in association with other species. The spread of the study group of mangabeys was measured as described in *Chapter Two* and was observed to be smaller when they were not in association than when they were in associations (Chi-square=20.08, df=1, p<0.01), suggesting that competition is greater in associations.

An alternative hypothesis for this, however, is that a larger group spread may actually be an additional benefit of associating with other species. If different age/sex classes have different nutritional needs and preferences for different food types, associating with other species may allow them to exploit different resources without increasing the risk of predation (Tutin, personal communications).

Vertical use of space: Height

The heights of mangabeys in scan samples of the study group were recorded as described in *Chapter Two*. The average height in the canopy was calculated each month for when mangabeys were in association (mean=22, n=12, S.D.=3) than when not (mean=19, n=12, S.D.=1). Mangabeys were higher in the canopy when in polyspecific associations, although this difference was not significant (Mann-Whitney *U*-test=46, n=12, 12, p=0.46). Differences in the height of the canopy used when in polyspecific associations may indicate a shift in their ecological niche and therefore be evidence of competition (Gautier-Hion *et al.*, 1983)

Seasonality

If competition does exist, then polyspecific associations would be expected to be the least frequent when competition is highest. As shown in *Chapter Three*, the availability of ripe fruit was found to be the lowest during the long dry season. Comparing the amount of time that mangabeys spent in association between seasons, mangabeys associated less during the long dry season than in all other seasons (Chi-square=33.64, df=1, p<0.01) (**Figure 8.11**).

Interspecific behaviours

Behaviours between individuals can be an indication of the degree of competition, where aggressive interactions may be expected to be greater between species who are in greater competition. Direct interspecific behavioural interactions were rare (n=12) and most interspecific behaviours were affiliative. Play was observed between a bispecific group of colobus and spot-nosed guenons (n=1), and mangabeys and crowned guenons(n=1). Trispecific play was observed between mangabeys, crowned guenons and spot-nosed guenons (n=1) and between a trispecific group of mangabeys, spot-nosed guenons, and moustached guenons (n=1). Play bouts were between juveniles and infants in the groups.

Interspecific grooming was observed two times. Although a lone adult male crowned guenon was observed to try to solicit grooming three times, he was only observed to be groomed once by an infant mangabeys. Grooming was also observed between a lone

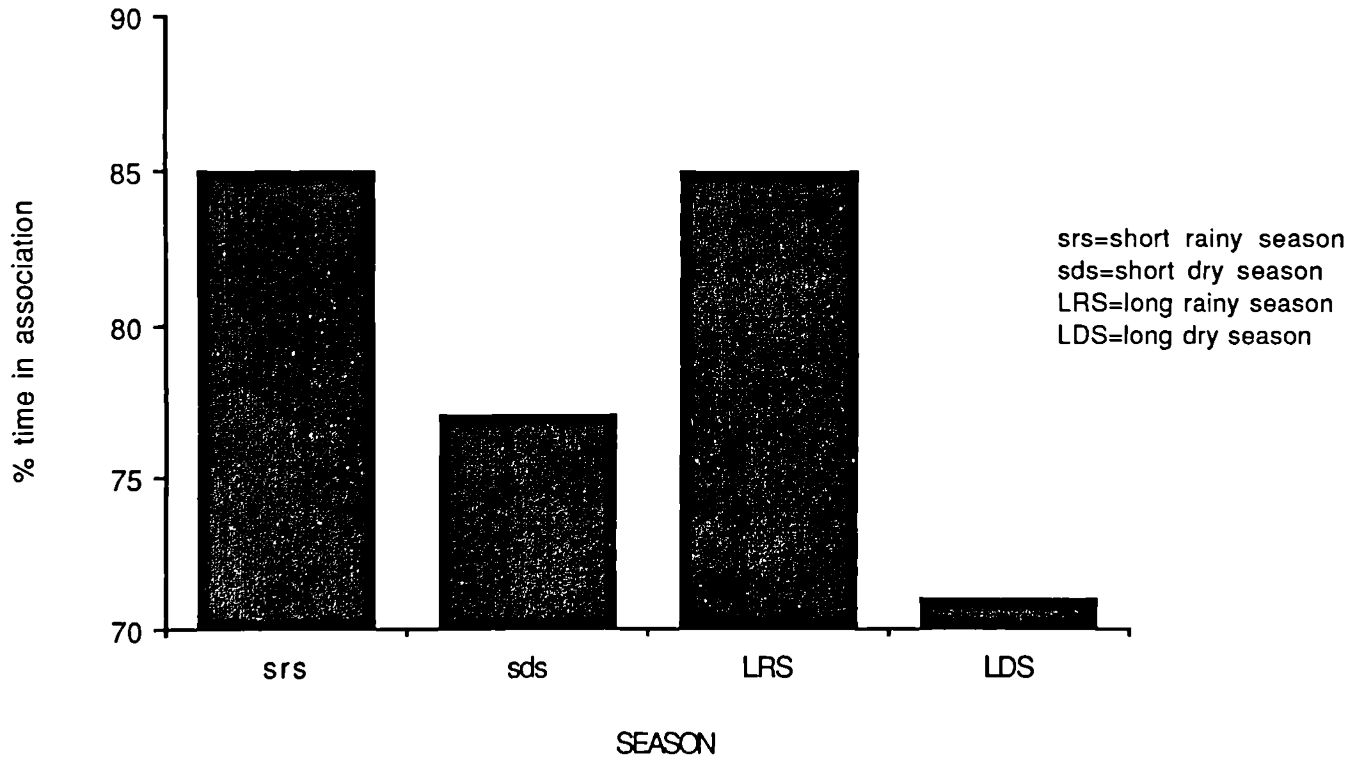


Figure 8.11 Percent time that grey-cheeked mangabeys were observed in polyspecific associations during each season (method: "census")

moustached guenons and a juvenile mangabey. Interspecific sexual behaviour was only observed once when a young adult female mangabey with a sexual swelling presented to an adult male spot-nosed guenon.

Interspecific agonistic behaviour was observed five times between mangabeys and colobus : (1) An adult male mangabey was observed to supplant an adult female colobus with a ventral infant. The female leapt out of the way when the adult male mangabeys approached. (2) The study group of mangabeys was observed to supplant a group of colobus from a *Pterocarpus soyauxii* tree where they were feeding. The group of colobus returned to the tree once the mangabeys had left. (3) An adult female mangabey walked directly towards an adult female colobus with a new infant, and the female colobus leapt aside, seemingly alarmed. (4) The female mangabey continued along the branch towards the other colobus and all the colobus moved out of the way and allowed her to pass. (5) Another adult female mangabey walked through the group of colobus supplanting several individuals. She sat down close to the group of colobus and the colobus left the tree. Colobus were only species towards whom mangabeys were observed to direct aggression and they were the only species with whom mangabeys did not associate more than expected by chance. These observations indicate that competition may also play an important part in determining the frequency of polyspecific associations.

DISCUSSION

Clearly, polyspecific associations are a complex trade-off between the benefits of increased foraging success and decreased predation risk, and the costs of competition. The benefits of associations are obviously not equal for all individuals. Peres (1991) observed that associations can range from parasitic, to commensal to "proto-cooperative" . In the present study it appeared that because other species followed mangabeys, it was these species that probably benefited the most from the associations, although mangabeys probably gained some benefits from the associations, such as increased rates of predator detection with the increased group size and predator detection specialisations of species involved in the associations. These benefits may have outweighed the costs that would be involved in deterring other species from associating with them. Buchanan-Smith (1990) observed that even though saddle-back tamarins (*Saguinus fuscicollis*) followed red-bellied tamarins (*Saguinus labiatus*) during associations between these two species in Bolivia, *S.labiatus* still played some role in maintaining the associations. This illustrates that even though one species may lead an association, this does not necessarily mean the relationship is parasitic.

Associations between all species were greater than expected by chance for associations between colobus and mangabeys, and colobus and spot-nosed guenons. Evidence that associations incurred some sort of foraging benefits was that associations occurred most frequently when mangabeys were feeding and especially when they were foraging for insects. Crowned guenons, the *Cercopithecus* species with the highest proportion of insects in their diet, were the species observed to associate the most frequently, both with mangabeys, and overall. Several studies have suggested that one species may eat insects flushed by another species (Gartlan and Struhsaker, 1972; Gautier-Hion and Gautier, 1974) but other studies have challenged this as a benefit of polyspecific associations (eg. Terborgh, 1983). Peres (1991), however, has recently shown that saddle-back tamarins (*Saguinus fuscicollis avilapiresi*) more than doubled their prey yield by associating with moustached tamarins (*Saguinus mystax pileatus*).

Because association frequencies between species were not directly related to the degree of dietary overlap, and because mangabeys were also observed in associations when they were engaged in other behaviours, it is likely that there were other benefits involved as well, such as a decreased predation risk. Although the frequency of association was not related to group size, it is possible that interspecific differences between species, such as body size, habitat preference and antipredator behaviours, may have accounted for variations in the frequency of associations. Except for moustached guenons, which appeared to rely more on habitat structure for predator avoidance, there was a direct relationship between body mass and the amount of time species were observed to associate with mangabeys, where the large bodied colobus associated the least and the small bodied crowned guenons associated the most frequently. This relationship did not exist, however, for the frequency with which species were observed in associations overall. Mangabeys were probably a desirable species with which to associate, given their relatively large body size, conspicuousness, active antipredator behaviour and large group sizes, and this is reflected in the observation that mangabeys was the species with which both crowned guenons and spot-nosed guenons associated the most frequently.

There was evidence that competition was higher in associations. When in associations, mangabeys had a larger group spread and used a higher level of the canopy and they associated least frequently during the long dry season.

Lone Males

The benefits involved for lone males associating with other species may be different than the benefits gained by groups of species associating together. Lone males probably benefit from a decreased probability in being predated for the same reasons given above, but in addition may also benefit from social interactions to which they would not have access if they were alone. In the present study the only interspecific grooming observations were between juvenile mangabeys and lone males of other species. Waser (1974) also observed lone males of other species to be groomed by mangabeys.

Lone males were not observed to vocalise and alarm at predators during the present study. Lone males were therefore probably parasitic on polyspecific associations, but the costs involved in chasing them away were probably greater than the costs of the small increase in competition for resources with one extra individual in the group.

Other studies

Very limited data exist on the participation of mangabeys in polyspecific associations from other studies. Although data exist from studies in Uganda (see below) the only quantitative data from western Africa are frequencies of observations of mangabeys alone or in association with other primates during survey work in Cameroon (Gartlan and Struhsaker, 1972, n=8 encounters; Mitani 1991, n=41 encounters), Gabon (Gautier and Gautier-Hion, 1969, n=11 encounters; Quris, 1976, n=7 encounters), Equatorial Guinea (Cashner, 1972; Jones and Sabater Pi, 1968, n=12 encounters; Waser, unpublished data, n=3 encounters; Whitesides, 1989).

In Equatorial Guinea, Cashner (1972) studied associations between mangabeys and the same species observed in the present study. She also observed that associations between mangabeys and crowned guenons were particularly common and suggested that they may live in "stable bispecific groups". Summing all the published data, Waser (1982a)reports that in western Africa mangabeys associated with *C.erythrotis* (or its close relative moustached guenons) for 41% of all sightings, spot-nosed guenons; 44% and crowned guenons (or the closely related *C.mona*) in 62% of all sightings. This the same ranking of the frequency with which related species were observed with mangabeys in the present study.

Waser (1982) suggested that in western African forests, grey-cheeked mangabeys participate in polyspecific associations to a greater extent than mangabeys in eastern African forests. Gautier-Hion *et al.*(1983) suggested that overall, associations between primate species tend to last longer in western African forests. Comparisons between the present study and studies of mangabeys in Uganda confirm this hypothesis. In eastern Uganda where Chalmers (1967) studied mangabeys, they lived sympatrically with only redtailed monkeys (*Cercopithecus ascanius*). He observed encounters between mangabeys and this species but did not give any details on the frequencies of associations. Wallis (1979) and Waser(1980) reported the same ranking in the frequency with which mangabeys were observed to associate with sympatric species, although both authors believed that associations occurred more frequently at Ngogo, than in

Kanyawara. Waser (1980) observed his study group of mangabeys within 50 m of other primate species during 56% of all scan samples. This is not very different from the 60% of all scan sample in which the study group of mangabeys was observed in association in the present study. Densities of primates at Kibale, however, are much higher (564 individuals/km^2, 2652 kg/km2, Waser, 1987) than at Lopé (62 individuals/km^2, 418.7 kg/km2, White, 1992), thus increasing the likelihood that species would be observed within 50m of each other. When Waser (1987) used his "gas model" to determine which species associated more than by chance given their densities in the forest, he found associations only between red-tailed monkeys (*Cercopithecus ascanius*) and mangabeys were significant. In addition Waser (1980) observed mangabeys to associate in relation to their dietary overlap, suggesting that species may have been associating only because of random encounters or convergence at a common food source.

Waser (1980) suggested that associations in western Africa are different in kind, rather than in degree and this hypothesis is supported by the present study. Waser (1980) described association between mangabeys and other species at Kibale as "impermanent" and lacking spatial structure. He observed no tendency for any one species to follow another or to lead movements. In the present study mangabeys were observed to lead associations and this was also observed by Cashner (1972) for grey-cheeked mangabeys in Equatorial Guinea. Various hypotheses have been proposed to explain the differences between associations formed by mangabeys in western African forests and those in eastern African forests. Waser (1980) suggested that the geographical variation may be due to "learning". If differences in the frequencies of polyspecific associations were only "cultural" , however, then one would not expect such great variations between adjacent groups of mangabeys as observed in the present study between mangabeys in Group One and Two. Waser (1982a) suggests that the hunting pressures from humans is greater in western Africa and therefore the benefits for associating are greater in western Africa to decrease the risk of predation. Although this may be true in some areas of western Africa, no hunting exists in the study area of SEGC and frequencies of polyspecific associations are still high. As shown in *Chapter Four*, predation pressure may be greater at Lopé than at Kanyawara, but more data is needed to test this hypothesis.

I suggest that associations were observed to be more frequent in the present study than for mangabeys in Uganda for several reasons. Firstly, data from *Chapter Five*, suggests that dietary overlap is probably greater between mangabeys and other primates at Lopé than for mangabeys studied in Uganda. High dietary overlap may be a prerequisite for associating in the first place, if benefits gained from associations are related to foraging. More data on feeding frequencies are needed from *Cercopithecus* spp. at Lopé, however, to confirm this. Secondly, as shown in *Chapter Three*, tree density is higher at Lopé, therefore, during most of the year, competition may be less than at Kanyawara. This may also explain the higher frequency of associations at Ngogo than at Kanyawara, where tree densities are even higher (*Chapter Three*).

SUMMARY

In summary, I agree with Waser (1980) that polyspecific associations are "behaviourally complex". The frequency with which mangabeys participated in polyspecific association did seem to reflect variations in the competition between species for resources, but it would be naive to attribute any one cause to polyspecific associations, especially in an environment so complex as a tropical rain forest ecosystem. Polyspecific associations appear to be a widespread phenomenon, highly plastic and adaptable to varying conditions.

CHAPTER NINE: DISCUSSION

This study provides information on the behaviour and ecology of grey-cheeked mangabeys, a species about which very little is known, and for which most of our knowledge comes from studies in Uganda, conducted over 15 years ago (Chalmers, 1967; Freeland, 1977; Wallis, 1979; Waser, 1974). The results of the present study help to define the mangabey's niche in the complex forest primate community at Lopé and permit the testing of hypotheses derived from ecological and evolutionary theory. The goals of the present chapter are: (1) to briefly outline the main results of this study to give a general description of the behaviour and ecology of grey-cheeked mangabeys at Lopé; (2) to compare these results to other studies on grey-cheeked mangabeys and look for general patterns and account for their similarities and differences; (3) to look at the niche of grey-cheeked mangabeys in the forest primate community at Lopé, and (4) to put this study into a broader context by comparing the behaviour and ecology of mangabeys with other species of primate.

Grey-cheeked mangabeys at Lopé

Grey-cheeked mangabeys at Lopé are highly arboreal primates, living in multimale groups with a median group size of 18. They showed no obvious birth peak, but all births occurred between January and July (n=5 groups). Systematic data were collected on the feeding behaviour of the main study group. They were mainly 'frugivorous' in that they spent 66% of their feeding time eating fruit. When the *part* of the fruit eaten was considered, however, they spent 55% of their time feeding on seeds and 45% of their time feeding on fruit pulp. The proportion of different types of foods eaten was highly variable, with seeds forming the majority of the diet especially during the long dry season. Although there were strong correlations between the foods eaten and their frequency in the habitat, certain foods were selected for. Analysis of the chemical composition of foods revealed that mangabeys favoured fruit pulp high in lipids and seeds that were high in protein.

The annual home range size of the main study group was 215 ha, and mangabevs used less than one quarter of this home range each month. The overall home range size over the 18 months was 225 ha. The home range size of a second group was estimated to be 156 ha. Ranging patterns were seasonal. Use of certain habitat types was positively correlated with the availability of, or the time spent feeding on, foods from tree species characteristic of that habitat type. Habitat-types influenced by proximity to rocky outcrops were preferred, whereas those close to the savanna-edges were strongly avoided during most months. The study group shared 26% of its home range with at least five other groups of mangabeys. Areas of overlap were neither selected for nor against. In addition, encounters between groups did not occur more or less frequently than expected by chance. Interspecific groups therefore did not seem to practice mutual avoidance as has been described in other studies (eg. Waser, 1974).

The study of social behaviour concentrated on adult males and their relationships with each age/sex class in the group. Initially, the main study group contained only one fully adult male, but in November 1991 a new adult male migrated into the group. This immigrant male was observed more often in close proximity to females in oestrus than the resident adult male, who was observed more often in close proximity to infants, and adult females with infants. The resident adult male was observed to pick up and carry infants in situations of potential conflict with the new adult male; a behaviour previously recorded for baboons and macaques, but not described in detail for mangabeys.

Finally mangabeys in the study area were observed to spend an average of 80% of their time in association with at least one other group of arboreal primate. Associations between all pairs of species occurred significantly more than expected by chance, except for those between black colobus and mangabeys, and between black colobus and spot-nosed guenons. Other arboreal primate species followed mangabeys and rarely vice versa. The benefits of the associations, therefore, appeared to be greater for the other species. Mangabeys may have benefited from an increase in the rate of predator detection arising from an increased group size or differing 'species-specific' abilities in detecting predators, eg. moustached guenons more readily detected ground predators than other arboreal species (*Chapter Eight*). The smaller forest guenons probably achieved more benefits however, by associating with mangabeys than the reverse, since mangabeys have (1) larger bodies, (2) larger groups, (3) are more conspicuous, and (4) more actively participate in predator defence than forest guenons. In addition to the benefits of decreased predation risk, other species may have also gained benefits in increased foraging success. Associations with mangabeys were most frequent when mangabeys were foraging for insects, suggesting that the other primate species may have gained access to insects exposed or flushed by the mangabeys.

For a deeper insight into mangabey ecology it is useful to compare and contrast the findings of the present study with other studies. The most detailed previous studies of grey-cheeked mangabeys have come from Uganda (Chalmers, 1967; Freeland, 1977; Wallis, 1979; Waser, 1974), where they live in a different forest among an almost completely different community of primate species.

Comparisons to other studies

An increasing number of studies of primates have made intraspecific comparisons of the same species living in different conditions (eg. Butynski, 1990; Clutton-Brock and Harvey, 1977; Maisels and Gautier-Hion, in press). What is apparent from these studies is that primates are not static in their ecology or rigid in their behaviour as was once believed, but highly flexible and adaptable to environmental variations. Of course there are methodological problems with such comparisons, due to differences in, for example, the sampling methods or the duration of the study. This may mean that subtle differences are more difficult to define, but gross differences in ecological parameters such as diet, group size or range size are more likely to be real effects. Although the most detailed data in the present study came mainly from one group, data were also collected on other groups in the study area so that generalisations about the population are possible. The present study attempted to identify the main environmental factors responsible for the observed differences between populations of grey-cheeked mangabeys.

One of the most surprising differences between the present study and other studies of grey-cheeked mangabeys, was the heavy reliance on seeds in the diet exhibited by Lopé mangabeys. This was surprising in that it was previously believed that primates living in western African forests generally have a larger proportion of succulent fruit in their diet than similar primate species in eastern African forests because forests are generally more diverse with a higher availability of succulent fruit in western Africa (Gautier-Hion, 1983). Seed-eating has been viewed as a 'last resort' for primates (Gautier-Hion *et al.*,1992), and it has been suggested that monkeys are mainly fleshy-fruit eaters where fleshy fruit are available (Maisels and Gautier-Hion, in press).

In *Chapter Five* several explanations were offered for the seed-eating behaviour of mangabeys. To summarise: (1) Seed eating may have been a form of "exploitation competition" whereby mangabeys ate the seeds of immature fruits before the fruits were eaten by gorillas and chimpanzees. The seeds may have been eaten instead of the whole fruit because unripe pulp is often high in secondary plant chemicals, such as alkaloids (see Rogers *et al.*, 1990). Both gorillas and chimps are highly frugivorous at Lopé. At the locations where the mangabeys were studied in Uganda, the only apes present were chimpanzees, so mangabeys may have been able to expand into a more frugivorous niche due to a "competitive release" in the absence of gorillas. (2) Seeds may have formed a larger proportion of the mangabey's diet because there were more seed-producing tree species of the family Leguminosae at Lopé than where mangabeys were studied in Uganda (see *Chapter Three*). (3) The overall proportion of seeds in the diet of mangabeys at Lopé was inflated due to a heavy reliance on seeds during the long dry season, when succulent fruit was scarce. (4) Mangabeys may eat more seeds at Lopé because the diversity of tree species is lower than at Kibale, and therefore mangabeys cannot be so selective in their diet. Other reasons why mangabeys may have such a large proportion of seeds in their diet may rely on the chemical and physical properties of the foods themselves. For example seeds may have a higher food value, or lower handling time, than the available fruit pulp.

Other differences between mangabeys in the present study and mangabeys studied in Uganda were the differences in ranging behaviour, relationships with neighbouring groups and group sizes. Compared to mangabeys studied by Waser (1974), mangabeys in the present study had smaller home ranges, less home range overlap with neighbouring groups, more frequent intergroup encounters and larger groups. At Lopé, tree density is higher than at Kanyawara (see *Chapter Three*). This may mean that mangabeys at Lopé did not have to use such a large area to meet their nutritional requirements as at Kanyawara. Because the home range was smaller, it may have been easier to monitor, thus resulting in less overlap between the home ranges of adjacent groups and an increase in the number of intergroup encounters. Freeland (1977) also studied grey-cheeked mangabeys in a location where tree species density was higher than at Kanyawara. These mangabeys also had smaller home ranges and shared less of their home range with other groups than mangabeys studied by Waser (1974), suggesting that plant density may be an important factor affecting ranging behaviour.

Mangabeys at Lopé may have also had smaller home ranges because many of the trees which provided food for mangabeys, fruited synchronously and seasonally (*Chapter Five*). Their patterns of ranging therefore, were also seasonal, and they returned to areas occupied during the same season, the previous year. At Kanyawara, synchronous, seasonal fruiting was the exception for plants providing food for mangabeys (Waser, 1975 a) and therefore mangabeys may have been forced to travel into new areas to find food.

Finally, there were differences between studies in the amount of time mangabeys spent in association with other primate species. The density of anthropoid primates is much greater at Kibale (546 individuals/km^2) than at Lopé (62 individuals/km^2) (Waser, 1987; White, 1992). Since this would increase the likelihood of random encounters, the amount of time mangabeys were observed in association with other species was expected to be greater at Kibale. This hypothesis was not supported however, since it was at Lopé that mangabeys spent a greater proportion of their time in polyspecific associations. The reasons for this are not clear. Predation pressure may be greater at Lopé, and therefore polyspecific associations may be more common due to an increased predation avoidance from living in larger group (see *Chapter Eight*). Alternatively, associations may be more frequent in Gabon because the diets of arboreal species are more similar, and therefore species are more likely to gain benefits from increased foraging success.

Although the number of studies on grey-cheeked mangabeys is small, comparisons between studies reveal great variation in their behaviour and ecology, highlighting the ecological flexibility of the species. This emphasises the overall importance of both the forest structure and primate community structure in shaping behaviour.

Grey-cheeked mangabeys in the forest primate community at Lopé

At Lopé, mangabeys share the forest with seven other diurnal primate species. Although there is large overlap in the diet of these species (*Chapter Five*), morphological and behavioural differences may allow them to partition resources, thereby exploit different ecological niches, and therefore coexist. The 'competitive exclusion principle', first outlined by Gause (1934), states that where species are competing for a limited resource, one species will exclude the other in the areas where their niche's overlap (Richards, 1985). This principle predicts that either one species will become extinct in the area of overlap, or the area will be divided between the two. The latter results in one or both species undergoing an ecological shift which enables the two species to coexist sympatrically (see Richards, 1985, pp. 368).

Although many studies on primates imply this principle is a cause of niche differentiation (Charles-Dominique, 1977; Gautier-Hion, 1978; Struhsaker, 1978), the practical (Wiens, 1977) and philosophical (Peters, 1976) validity of this theory has been challenged. It has been argued that the theory is tautological and based on false assumptions. One of the main assumptions is that resources are limited. Several authors have argued that in tropical rain forests resources are not limited and therefore competition does not exist (Schoener, 1974).

Evidence from the present study, however, suggests that competition may exist between sympatric primate species at Lopé, and that competition is highest especially during the long dry season when the availability of ripe fruit is lowest. This will be discussed below.

Comparison between eight sympatric species at Lopé

It is first necessary to show the ways in which these sympatric primate species differ and how this may aid in niche differentiation. The most obvious difference between primate species at Lopé is the great variation in their body mass, from the 2 kg moustached guenon, to the 200 kg adult male silverback gorilla (see White, 1992 for body masses). Body size may allow niche differentiation in several ways. Firstly, Clutton-Brock and Harvey (1977) have shown that body mass is positively related to the proportion of foliage in the diet. This is not obvious for the primate community at Lopé. For example, chimpanzees have a low proportion of foliage in their diet compared to black colobus, yet black colobus are less than one third the average weight of an adult chimpanzee (see White, 1992). Secondly, body mass may affect the degree of insectivory, where smaller bodied primates tend to be more insectivorous (Clutton-Brock and Harvey, 1977). Data were not collected on the proportion of insects in the diet of species other than mangabeys in the present study, but Gautier-Hion (1978) observed the smaller bodied moustached guenons to be more insectivorous than the larger bodied spot-nosed guenon. Finally, body size may restrict habitat use, where larger bodied primates may not be able to use areas of the canopy with fragile supports (Gautier-Hion, 1980). In the present study, differences were found in the average heights of arboreal primates (*Chapter Eight*). Gorillas, chimpanzees and mandrills harvest most of their foods arboreally, (Lahm, 1986; Tutin and Fernandez, 1993a; Williamson, 1988; personal observations) however the ability of these species to utilise foods in both arboreal and terrestrial habitats may permit resource partitioning.

There are many other differences in the primate species at Lopé which may aid in niche separation, such as species differences in dentition. For example, mangabeys have relatively thick enamel on their molars, which is possibly an adaptation for cracking hard seeds (Kay, 1981). Colobus have molars with higher cusps and deeper basins than mangabeys and guenons, specialised to cut and grind tough fibrous foods (Richards, 1985). Differences, however, are less pronounced between other species (eg. between gorillas and chimpanzees, Tutin and Fernandez, 1993a).

Gut morphology also shows great variation between species. Black colobus, for example have a compartmentalised stomach, which functions similarly to the stomach of cows (Milton, 1993). The stomach has four chambers. The food is initially passed into the fore chamber, where the relatively low acidity permits fermentation by anaerobic bacteria. This allows greater extraction of energy from fibre and thus permits colobus to have a more folivorous diet (Struhsaker and Leland, 1979). Gorillas do not have polygastric stomachs, but have long colons with many entodiniomorph ciliates which aid in cellulose digestion (Collet *et al.*, 1984). This permits gorillas to exploit more fibrous fruits, mature leaves and stems (Rogers *et al.*, 1990).

Finally, differences group structure and behaviour may aid in niche differentiation. For example, the ability of mangabeys to *temporarily divide into sub-groups and* the fission-fusion societies of chimpanzees, may allow them to be more flexible in the patch sizes they exploit (*Chapter Four*).

Evidence for competition

These differences in themselves, however, are not evidence for competition. Competition will only exist if resources shared by species are limited. In *Chapter Five* it was shown that dietary overlap between sympatric species at Lopé is high, and that overlap was greatest for the category of fruit pulp. For most of the year at Lopé, succulent fruit is abundant, but during the long dry season (June, July and August), rainfall is very low, or even absent, and the availability of succulent fruit is scarce (*Chapter Two* and *Three*). Because fruit availability is low during the long dry season and because many of the primates at Lopé rely on fruit-pulp as a major part of their diet (*Chapter Five*), competition for resources may be expected to be greatest during this time.

Results from the present study showed that although fruit pulp formed a significant proportion of the diet of the mangabeys during most of the year, in the long dry season, mangabeys ate almost exclusively seeds. Similarly, Tutin and Fernandez (1993a) showed that although both gorillas and chimpanzees have a large proportion of fruit in their diets during most of the year, during the long dry season, chimpanzees continue to eat succulent fruit, while gorillas turn to an almost exclusively folivorous diet. Although variations in the diet of forest guenons, were not documented in the present study, Gautier-Hion (1980) showed that at Makokou, guenons ate the largest proportion of leaves during the long dry season. During most of the year, the diets of the guenons were very similar, but during the long dry season their diets diverged the most (Gautier-Hion and Gautier, 1979). These results may simply show that species' diets become specialised during the dry season. However, the fact that each species specialises on a *different* resource, may give evidence for competition.

Further evidence for competition from the present study comes from observations that:

(1) One of the costs of living in larger groups is increased competition (Krebs and Davies, 1981). Mangabeys were involved in polyspecific associations significantly less during the long dry season, suggesting that during this time competition was greater. (2) Mangabeys were observed to supplant groups of black colobus from fruiting trees. Of all seven species, the diet of mangabeys was most similar to that of black colobus (*Chapter Five*) therefore this may illustrate a form of 'interference competition' (also called 'contest' or 'direct' competition) (Nicholson, 1954) where one animal prevents the other's use of a resource through aggression (Wrangham *et al.*, 1993). (3) Mangabeys ate the seeds of immature fruits that were classified as 'important' foods in the diet of either or both gorillas and chimpanzees (Tutin and Fernandez, 1993a). This may have been a form of 'exploitation competition' (also called 'scramble' or 'indirect' competition) (Nicholson, 1954) whereby mangabeys are exploiting a resource before others.

Mangabeys do not only share resources with diurnal primates at Lopé, but also with many other animals in the Reserve. For example, more than 75% of the plant species eaten by mangabeys, were also observed to be eaten by forest elephants at Lopé (White *et al.*, 1993). At Makokou, Emmons *et al.* (1983) showed that the frugivorous community at Makokou was extremely large and Gautier-Hion *et al.* (1980) showed the overlap in the diets between taxa to be extensive. The definition of the mangabey's niche in this forest community is therefore complex and more information is needed on all species involved before more detailed conclusions can be drawn about their interrelationships.

The community approach was an important advancement in the study of primate ecology and behaviour (Moreno-Black and Maples, 1977). Species can modify each other's densities, diets, and behaviour (Waser, 1987). It is therefore essential to study any animal, not in isolation, but as an interacting part of their biotic environment.

Comparisons of grey-cheeked mangabeys with other primate species

Jolly (1972) suggested that within each major phyletic group of primates are species which have evolved to fill similar ecological niches, and several authors have looked for ecological parallels between Old World and New World species (eg. Struhsaker and Leland, 1979). Mangabeys in particular, have been compared to spider monkeys (*Ateles*) (Struhsaker and Leland, 1979). They have similar body masses and are both largely frugivorous, although spider monkeys have a higher proportion of succulent fruit in their diet and mangabeys eat more insects. Like mangabeys, spider monkeys have large home ranges of about 100 ha to 389 ha depending on the species (Robinson and Janson, 1987). Group sizes and structure are also similar. Spider monkeys, however, live in multimale groups with an average group size of 15-25 members (Robinson and Janson, 1987) compared to the median group size of 18-23 for mangabeys in the present study.

Robinson and Janson (1987) claimed that mangabeys and spider monkeys differ in two main ways: (1) In spider monkeys it is usually adult females that transfer between groups, whereas in mangabeys it is usually the males. (2) Spider monkeys divide into independently moving subgroup but mangabeys do not. Spider monkeys usually forage individually or in sub-groups of two or three individuals with the group spread over about 800 m (Struhsaker and Leland, 1979). The present study has shown that mangabeys also divide into sub-groups, although the distance between these subgroups and the size of the sub-groups differ from spider monkeys. The reason for the differences in the size of the sub-groups may be a result of difference in patch sizes of important food resources. One of the common foods of spider monkeys, especially during times when other fruit is scarce, is a tree with a small canopy, and found in widely dispersed, small patches. At Lopé, food patches generally consisted of single large trees (eg.*Pterocarpus soyauxii*), or common smaller trees (eg.*Diospyros dendo*). Few trees limited the number of monkeys that could feed simultaneously to such an extent as for spider monkeys, (except perhaps the oil palm, *Elaeis guineensis*). More detailed comparisons, however, of the structure of the habitat and distribution of food may prove useful.

Parallells have also been drawn between other species of Old World and New World primates. For example *Colobus* spp.have been compared with *Brachyteles* (both leaf eaters) and *Cercopithecus cephus* have been compared with *Cebus* (species with similar group sizes and similar proportion of food -types in their diets) (Robinson and Janson, 1987). *Brachyteles* are most similar to *Colobus badius* because these species typically have more than one male in the group and it is the adult females which transfer between groups (Struhsaker and Leland, 1979). These species are different however, in that *Brachyteles* exhibit fission-fusion of groups, a behaviour not observed for colobus.

Although there may be parallells in the ecological niches of these species, there are also major differences. It seems that social structure, in particular, is probably influenced by other factors (Struhsaker, 1969). Although grey-cheeked mangabeys live in the same environment as the seven other species of primates at Lopé, their social structure and behaviour is more similar to their close relatives, the baboons, even though baboons generally live in very different environments.

The common ancestor of baboons and mangabeys was probably arboreal (Jolly, 1972). Dunbar (1988) argued that the ancestor was probably a frugivore since folivory is a derived strategy which requires morphological specialisations. The evolution to baboons from this ancestral Old World Monkey probably occurred in two steps; firstly with a move to greater terrestriality within the same environment, and secondly a move to exploit the more open woodland habitats. This probably occurred during the retraction of the forests during the Pleistocene era. Both increased terrestriality and living in more open habitats has been shown to be correlated with a larger body size (Clutton-Brock and Harvey, 1977) and increased group size, for protection from ground predators. This may explain therefore, why savanna baboons have a greater body mass than mangabeys, and generally live in larger groups.

It was suggested in *Chapter Three* that arboreality and decreased visibility may also affect the behaviour and ecology of mangabeys in other ways. Mangabeys have a greater interbirth interval than baboons. Low visibility and the danger of falling from the canopy may necessitate dependence of infants upon mothers for a longer duration in mangabeys than for baboons. Decreased visibility may also affect communication between individuals in the group. Mangabeys rely more heavily upon vocal communication and exaggerated gestures, whereas baboons can use more subtle gestural communication (Rowell, 1988). Baboons are not observed to form polyspecific associations as frequently as mangabeys (eg. Dunbar and Dunbar, 1974). This may be because the baboon's larger group size no longer necessitates added vigilance from other species, or it may be because there are fewer primate species in the same habitat with which they can associate.

Mangabeys and baboons have also been compared in their behavioural repertoire and visual communication systems (Chalmers, 1968a and b; Wallis, 1983; Rowell, 1988), their vocal communication systems (Chalmers, 1968b; Rowell, 1988; Waser, 1982 b) and their sexual behaviour (Rowell and Chalmers, 1970; Wallis, 1983). As little information is available on mangabey social behaviour, comparisons are still relatively superficial and in their preliminary stages. More detailed comparisons of the social behaviour of mangabeys and baboons offer opportunity for giving deeper insight into how an evolutionary transition from a forest to an open savanna habitat, and an arboreal to terrestrial lifestyle, can affect social structure and behaviour, and may even hold implications for a greater understanding of human evolution.

Conservation

The differences found between the behaviour and ecology of grey-cheeked mangabeys in the present study and mangabeys studied in Uganda warns against making generalisations about the ecology of single species. It emphasises the need for deeper understanding of how species respond to environmental changes, as well as studies of ecological communities and not just individual species (Raemaekers and Chivers, 1980).

With 90% of all primate species living in the tropical forests of Africa, Asia and South and Central America, and these forests disappearing at the rate of 10 to 20 million hectares per year (Mittermeier and Cheney, 1987), about 50% of all primate species are endangered of extinction (Wolfheim, 1983). This stresses the urgency of research since understanding of tropical forest ecosystems is an essential prerequisite for conservation. If in the future, primates are going to be confined within protected areas, then knowledge of the ecology of primate species is necessary in order to best select areas for parks. Synecological data are needed to determine whether habitats will be able to support populations. Knowledge of species' adaptability to change is necessary to aid in determining conservation priorities since some species may be less adaptable than others.

Gabon is an exceptional country in that 75% of the forest still remains relatively undisturbed (Myers, 1991). There are several reasons why Gabon's forests have remained intact for so long. Gabon gains most of its income from offshore oil, the exploitation of which does not directly affect the forests. Gabon has a low human population (about 1.2 million people and a population density of 4.6 people/km^2) and therefore the pressures from human inhabitation on the land are not as great as they are in some African countries (see Mittermeier and Cheney, 1987).

The need for conservation efforts in Gabon, however, is now greater than ever. As oil prices drop, the importance of timber as an income will probably increase, thus threatening primate populations by destruction of their habitats. In 1987 the Transgabonais Railway was built which traverses the country linking the two main cities in Gabon. One of the effects that the railway had on the country was to open new areas for exploitation of timber. The railway has facilitated its extraction, as well as facilitated the trade of bush meat. Although direct damage to the forest through logging may be slight, with on average only one or two trees of mainly one species removed per hectare (White, 1992), the damage is often greater in indirect ways, especially through the building of logging roads, and making areas more accessible for hunting.

The present study has shown how the environment can affect a primate species, but primates can also play a major part in structuring the forest by, for example seed dispersal (Gautier-Hion, 1984; Gautier-Hion *et al.*, 1985 b, 1992; Rowell and Mitchell, 1991), seed predation (Gautier-Hion *et al.*, 1985 b, 1992) and pollination (Gautier-Hion, personal communications). The present study has also shown the complex inter-relationships between primate species living in the same habitat. The removal of one species through extinction, therefore, may have repercussions for the tropical forest ecosystem as a whole.

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Appendix 5.1 Food species eaten for each food-type for eight diurnal primate species at Lopé.

A= Pan.t.troglodytes									
B=Gorilla g.gorilla									
C=Cercocebus albigena									
D=Cercopithecus pogonias									
E=C.nictitans									
F=C.cephus									
G=Colobus satanus									
H=Mandrillus sphinx									
FRUIT		**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**
Species	**Family**								
Aframomum leptolepis	ZINGIBERACEAE	•	•						•
Aframomum longipetiolatum	ZINGIBERACEAE	•	•						
Aframomum sp.nov	ZINGIBERACEAE	•	•						
Antidesma sp.251	EUPHORBIACEAE		•						
Antidesma laciniatum	EUPHORBIACEAE	•				•	•		
Antidesma vogelianum	EUPHORBIACEAE	•	•						
Antrocaryon klaineanum	ANNONACEAE	•	•						
Atractogyne gaboni	RUBIACEAE	•							
Baillonella toxisperma	SAPOTACEAE	•	•						
Barteria fistulosa	PASSILFORACEAE	•	•	•				•	
Beilschmeidia fulva	LAURACEAE	•							
Beilschmeidia sp. No.140	LAURACEAE	•							
Blighia welwitschii	SAPINDACEAE			•					
Canarium schweinfurthii	BURSERACEAE	•		•		•			
Carapa procera	MELIACEAE			•					
Celtis tessmannii	ULMACEAE	•	•	•		•	•		•
Chlorophora excelsa	MORACEAE			•					
Cissus dinklagei	VITACEAE	•	•	•	•	•			•
Cissus leonardi	VITACEAE		•						
Cola lizae	STERCULIACEAE	•	•	•	•	•	•	•	•
Dacryodes buettneri	BURSERACEAE	•		•	•	•	•	•	
Dacryodes igaganga	BURSERACEAE	•							
Dacryodes klaineana	BURSERACEAE	•							
Dacryodes normandii	BURSERACEAE	•	•	•					
Detarium macrocarpum	CAESALPINIACEAE						•		•
Dialium 118	CAESALPINIACEAE		•						
Dialium eurysephalum	CAESALPINIACEAE	•	•						
Dialium lopense	CAESALPINIACEAE	•	•		•	•	•		•
Dialium pachyphyllum	CAESALPINIACEAE	•							
Diospyros abyssinica	EBENACEAE	•	•		•				
Diospyros dendo	EBENACEAE	•	•	•	•	•	•	•	•
Diospyros mannii	EBENACEAE	•	•						
Diospyros piscatoria	EBENACEAE	•							
Diospyros polystemon	EBENACEAE	•		•	•		•	•	•
Diospyros soyauxii	EBENACEAE	•							
Diospyros sp.286	EBENACEAE	•	•						

FRUIT cont.		A	B	C	D	E	F	G	H
Species	**Family**								
Diospyros viridicans	EBENACEAE		•	•				•	
Diospyros zenkeri	EBENACEAE	•	•	•		•	•		•
Discoglypremna coloneura	EUPHORBIACEAE	•							
Dichapetalum sp	EUPHORBIACEAE	•	•	•		•			
Duboscia macrocarpa	TILIACEAE	•	•	•					•
Elaeis guineensis	PALMAE	•		•	•	•			•
Enantia chlorantha	ANNONACEAE	•	•	•					
Eremospatha cabrae	PALMAE	•	•						
Eriocoelum macrocarpum	SAPINDACEAE							•	
Ficus ?ingens	MORACEAE	•							
Ficus barteri	MORACEAE		•						
Ficus bubu	MORACEAE	•							
Ficus macrosperma	MORACEAE	•	•						•
Ficus mucuso	MORACEAE	•	•	•		•	•		
Ficus polita	MORACEAE	•	•	•					
Ficus recurvata	MORACEAE	•	•	•			•		
Ficus sp. No.441	MORACEAE	•							
Ficus sp.408	MORACEAE	•							
Ficus sp.443	MORACEAE	•	•						
Ficus thonningii	MORACEAE	•	•	•					
Gambeya africana	SAPOTACEAE	•	•	•		•		•	
Gambeya subnudum	SAPOTACEAE	•	•						
Ganophyllum giganteum	SAPINDACEAE	•	•	•	•	•			
Garcinia afzelii	GUTTIFERAE	•							
Grewia coriacea	TILIACEAE	•	•						
Guibortia tessmannii	CAESALPINIACEAE								•
Heisteria parvifolia	OLACACEAE	•	•	•		•	•	•	•
Irvingia gabonensis	IRVINGIACEAE	•	•	•	•	•	•	•	
Irvingia grandifolia	IRVINGIACEAE	•	•	•				•	
Klainedoxa 208	IRVINGIACEAE		•						
Klainedoxa gabonensis	IRVINGIACEAE	•	•	•		•			•
Klainedoxa microphylla	IRVINGIACEAE	•							
Landolphia cf.heudelotii	APOCYNACEAE	•		•					
Lecaniodiscus cupanioides	SAPINDACEAE	•	•	•		•		•	
Mammea africana	GUTTIFERAE	•	•						
Mangifera indica	ANACARDIACEAE	•	•						
Manilkara?fouilloyara	SAPOTACEAE	•							
Maranthes gabunensis	CHRYSOBALANACEAE					•			
Megaphrynium gabonense	MARENTACEAE	•	•						
Megaphrynium macrostachya	MARENTACEAE	•	•						
Monanthotaxis congoensis	ANNONACEAE	•	•						•
Monodora angolensis	ANNONACEAE	•	•	•					
Mussaenda debeauxii	RUBIACEAE		•						
Myrianthus arboreus	MORACEAE	•	•	•		•	•	•	•
Nauclea diderrichii	RUBIACEAE	•	•	•	•	•	•		•
Nauclea latifolia	RUBIACEAE					•			

FRUIT cont.		A	B	C	D	E	F	G	H
Species	**Family**								
Nauclea vanderguchtii	RUBIACEAE	•	•	•					
Ongokea gore	OLEOSA			•		•			
Parkia bicolor	MIMOSACEAE	•	•	•					
Parkia filicoidea	MIMOSACEAE	•	•	•					
Pentadesma butyracea	GUTTIFERAE		•	•		•	•	•	
Plagiostyles africana	EUPHORBIACEAE	•	•						
Polyalthia mannii	ANNONACEAE	•		•	•	•			
Porterandia cladantha	RUBIACEAE	•	•	•			•		•
Pseudospondias longifolia	ANACARDIACEAE	•	•	•		•	•		
Pseudospondias microcarpa	ANACARDIACEAE	•	•	•	•	•			•
Psidium guineensis	MYRTACEAE	•	•			•			
Psorospermum tenuifolium	HYPERICACEAE						•		
Psychotria peduncularis	RUBIACEAE	•	•						
Psychotria vogeliana	RUBIACEAE	•	•						
Ptychopetalum petiolatum	OLACACEAE	•	•						
Pycnanthus angolensis	MYRISTICACEAE	•		•	•	•	•		•
Renealmnia macrocolea	MYRISTICACEAE								•
Rutidea duuissii	RUBIACEAE		•						
Sacoglottis gabonensis	HUMIRIACEAE		•						
Santiria trimera	BURSERACEAE	•	•		•		•	•	
Scottellia sp.	FLACOURTIACEAE			•		•		•	
Scyphocephalium ochocoa	MYRISTICACEAE			•				•	
Scytopetalum sp168	SCYTOPETALACEAE	•	•						
Sorindeia cf.juglandifolia	ANACARDIACEAE		•						
Staudtia gabunensis	MYRISTICACEAE	•		•	•			•	
Sterculia tragacantha	STERCULIACEAE			•					
Strombosiopsis tetrandra	OLEOSA							•	
Treculia africana	MORACEAE	•	•	•					
Trichoschypha acuminata	ANACARDIACEAE	•	•				•		
Trichoschypha patens	ANACARDIACEAE	•	•						
Uapaca ?acuminata	EUPHORBIACEAE		•						
Uapaca cf.sansibarica	EUPHORBIACEAE	•	•						
Uapaca guineensis	EUPHORBIACEAE	•	•	•	•	•	•		•
Uapaca heudelotii	EUPHORBIACEAE	•							
Uapaca sp.299	EUPHORBIACEAE	•	•						
Uapaca vanhouttei	EUPHORBIACEAE	•	•						
Uavaria sp.SEGC 162	ANNONACEAE	•		•			•		
Uavaria sp.SEGC 256	ANNONACEAE	•	•						
Uvariastrum pierreanums	ANNONACEAE	•	•	•					•
Vitex doniana	VERBENACEAE	•	•						
Xylopia aethiopica	ANNONACEAE	•	•	•					
Xylopia hypolampra	ANNONACEAE	•	•	•					
Xylopia quintasii	ANNONACEAE	•	•	•					
SEGC117	ANNONACEAE	•							
SEGC182	ANNONACEAE	•							
SEGC288	RUBIACEAE		•						

FRUIT cont.		A	B	C	D	E	F	G	H
Species	**Family**								
SEGC291	RUBIACEAE		•						
SEGC318	SAPOTACEAE		•						
SEGC347	PASSILFORACEAE	•							
SEGC36	APOCYNACEAE		•						•
SEGC385	APOCYNACEAE	•							
SEGC428	ANNONACEAE	•							
SEGC431	MENISPERMACEAE	•							
SEGC46	APOCYNACEAE		•						
SEGC56	CELASTRACEAE		•						
SEGC58	APOCYNACEAE		•						
Sub-total		**104**	**90**	**54**	**17**	**31**	**24**	**19**	**25**
Unidentified foods		**6**	**6**	**1**	**1**	**0**	**2**	**0**	**0**
Total		**110**	**96**	**55**	**18**	**31**	**26**	**19**	**25**

SEEDS		A	B	C	D	E	F	G	H
Species	**Family**								
Anthonotha macrophylla	CAESALPINIACEAE			•				•	•
Aucoumea klaineana	BURSERACEAE			•	•	•			
Berlinia bracteosa	CAESALPINIACEAE			•				•	
Ceiba pentandra	BOMBACACEAE							•	
Celtis tessmannii	ULMACEAE			•		•	•	•	
Cissus dinklagei	VITACEAE								•
Coelocaryon preussi	MYRISTICACEAE							•	
Cryptosephalum staudtii	CAESALPINIACEAE	•	•	•					
Desbordesia glaucescens	IRVINGIACEAE							•	
Detarium macrocarpum	CAESALPINIACEAE		•						
Dialium lopense	CAESALPINIACEAE	•	•	•				•	•
Dichapetalum? unguiculatum	DICHAPETALACEAE		•						
Diospyros dendo	EBENACEAE	•	•	•					•
Diospyros polystemon	EBENACEAE	•	•	•				•	
Diospyros suaveolens	EBENACEAE		•						
Diospyros viridicans	EBENACEAE							•	
Diospyros zenkeri	EBENACEAE		•						•
Distemonanthus bethamianus	CAESALPINIACEAE			•	•	•		•	•
Duboscia macrocarpa	TILIACEAE	•	•						
Eriocoelum macrocarpum	SAPINDACEAE			•				•	
Erythroxylum mannii	ERYTHROXYLACEAE							•	
Gambeya africana	SAPOTACEAE							•	
Gambeya subnudum	SAPOTACEAE							•	
Guibortia tessmannii	CAESALPINIACEAE	•		•					
Haumania liebrechtsiana	MARENTACEAE	•	•						
Heisteria parvifolia	OLACACEAE			•				•	
Hylodendron gabunense	CAESALPINIACEAE		•	•		•			
Hypselodelphis violacea	MARENTACEAE	•	•						
Irvingia gabonensis	IRVINGIACEAE	•		•				•	
Irvingia grandifolia	IRVINGIACEAE			•				•	

SEEDS cont.		A	B	C	D	E	F	G	H
Species	**Family**								
Julbernardia brieyi	CAESALPINIACEAE	•	•	•				•	
Lophira alata	OCHNACEAE							•	
Mammea africana	GUTTIFERAE							•	
Manniophyton sp379	EUPHORBIACEAE		•	•					
Maranthes gabunensis	CHRYSOBALANACEAE							•	
Megaphrynium macrostachya	MARENTACEAE								•
Milletia	PAPILIONACEAE			•					
Monodora	ANNONACEAE			•					
Myrianthus arboreus	MORACEAE			•					
Newtonia leucocarpa	MIMOSACEAE			•					
Ongokea gore	OLEOSA			•				•	
Parkia bicolor	MIMOSACEAE			•				•	
Parkia filicoidea	MIMOSACEAE			•					
Pentaclethra eetveldeana	MIMOSACEAE			•				•	
Pentaclethra macrophylla	MIMOSACEAE			•				•	•
Pentadesma butyracea	GUTTIFERAE		•	•		•		•	
Piptadeniastrum africanum	MIMOSACEAE		•	•		•			
Plagiostyles africana	EUPHORBIACEAE							•	
Pterocarpus soyauxii	PAPILIONACEAE	•	•	•	•	•	•	•	•
Pycnanthus angolensis	MYRISTICACEAE			•				•	•
Scottellia sp.	FLACOURTIACEAE							•	
Scyphocephalium ochocoa	MYRISTICACEAE			•				•	
Staudtia gabunensis	MYRISTICACEAE				•			•	
Sterculia tragacantha	STERCULIACEAE								•
Strombosiopsis tetrandra	OLEOSA							•	
Swartzia fistuloides	CAESALPINIACEAE								•
Tetrapleura tetraptera	MIMOSACEAE			•				•	
Treculia africana	MORACEAE	•							
Trichilia monadelpha	MELIACEAE		•						
Trilepisium madagascariense								•	
Xylopia aethiopica	ANNONACEAE			•					
Xylopia hypolampra	ANNONACEAE			•					
Xylopia quintasii	ANNONACEAE			•					
Sub-total		**12**	**18**	**35**	**4**	**7**	**2**	**35**	**12**
Unidentified foods		**0**	**2**	**4**	**0**	**0**	**0**	**1**	**0**
Total		**12**	**20**	**39**	**4**	**7**	**2**	**36**	**12**
FLOWERS		A	B	C	D	E	F	G	H
Species	**Family**								
Aucoumea klaineana	BURSERACEAE	•	•	•					
Barteria fistulosa	PASSILFORACEAE							•	
Berlinia bracteosa	CAESALPINIACEAE			•	•	•	•	•	•
Campostyles mannii	FLACOURTIACEAE							•	
Cola cf. gigantea	STERCULIACEAE							•	
Distemonanthus bethamianus	CAESALPINIACEAE	•							
Duboscia macrocarpa	TILIACEAE						•		

FLOWERS cont.		A	B	C	D	E	F	G	H
Species	**Family**								
Irvingia gabonensis	IRVINGIACEAE	•							
Millettia sp.	PAPILIONACEAE							•	
Nauclea diderrichii	RUBIACEAE			•					
Parkia bicolor	MIMOSACEAE			•					
Parkia filicoidea	MIMOSACEAE			•					
Pentaclethra macrophylla	MIMOSACEAE	•		•					
Pentadesma butyracea	GUTTIFERAE			•					
Piptadeniastrum africanum	MIMOSACEAE					•			
Pterocarpus soyauxii	PAPILIONACEAE	•	•	•	•	•	•	•	
Pycnanthus angolensis	MYRISTICACEAE					•			
Treculia africana	MORACEAE	•							
Uapaca guineensis	EUPHORBIACEAE					•			
Vitex doniana	VERBENACEAE			•	•				
Sub-total		6	2	9	3	5	3	6	1
Unknowns		0	0	3	1	0	0	2	0
Total		6	2	12	4	5	3	8	1

LEAVES		A	B	C	D	E	F	G	H
Species	**Family**								
Anchomanes difformis	ARACEAE		•						
Anisotes macrophylla	ACANTHACEAE	•	•						
Anthocleista ?vogelii	LOGANIACEAE		•						
Ataenidia conferta	MARENTACEAE	•	•						
Aucoumea klaineana	BURSERACEAE			•	•		•	•	
Berlinia bracteosa	CAESALPINIACEAE		•	•	•	•	•	•	
Canarium schweinfurthii	BURSERACEAE			•	•	•		•	
Ceiba pentandra	BOMBACACEAE			•				•	
Celtis tessmannii	ULMACEAE		•						
Chlorophora excelsa	Milicia excelsa		•	•		•			
Cissus dinklagei	VITACEAE		•						
Cola lizae	STERCULIACEAE	•	•						
Combretum platypterum	COMBRETACEAE		•						
Coryanthe sp.373	RUBIACEAE		•						
Costus afer	ZINGIBERACEAE		•						
Cryptosephalum staudtii	CAESALPINIACEAE	•	•	•			•	•	•
Dacryodes buetnerri	BURSERACEAE			•					
Detarium macrocarpum	CAESALPINIACEAE		•						
Dialium lopense	CAESALPINIACEAE	•	•		•	•			
Diospyros cf.cinnabarina	EBENACEAE	•							
Diospyros dendo	EBENACEAE			•					
Diospyros viridicans	EBENACEAE		•	•					
Distemonanthus bethamianus	CAESALPINIACEAE	•		•				•	
Dichapetalum sp			•						
Eremospatha cabrae	PALMAE		•						
Ficus 407	MORACEAE		•						
Ficus cf.dicranostyla	MORACEAE	•							

LEAVES cont.		A	B	C	D	E	F	G	H
Species	**Family**								
Ficus mucuso	MORACEAE		•						
Halopegia azurea	MARENTACEAE		•						
Haumania liebrechtsiana	MARENTACEAE	•	•						•
Heisteria parvifolia	OLACACEAE		•						
Heisteria sp.110	OLACACEAE		•						
Hypodaphnis zenkeri	LAURACEAE							•	
Hypselodelphis violacea	MARENTACEAE	•	•						•
Irvingia gabonensis	IRVINGIACEAE							•	
Irvingia grandifolia	IRVINGIACEAE							•	
Julbernardia brieyi		•	•						
Leptoderris sp.57	PAPILIONACEAE	•	•						
Lophira alata	OCHNACEAE		•	•		•	•	•	
Marantachloa cordifolia	MARENTACEAE		•						•
Marantachloa filipes	MARENTACEAE		•						
Marantachloa purpurea	MARENTACEAE		•						
Megaphrynium gabunense	MARENTACEAE	•	•						•
Megaphrynium macrostachyu	MARENTACEAE	•	•						
Milletia sp.	PAPILIONACEAE	•	•	•				•	
Myrianthus arboreus	MORACEAE							•	
Onchoba spinosa	FLACOURTIACEAE		•						
Ongokea gore	OLACACEAE	•							
Parkia bicolor	MIMOSACEAE			•					
Pausinystalia macroceras	RUBIACEAE		•					•	
Pavetta puberula	RUBIACEAE		•						
Pentaclethra eetveldeana	MIMOSACEAE		•						
Pentaclethra macrophylla	MIMOSACEAE	•	•	•				•	
Pentadesma butyracea	GUTTIFERAE							•	
Plagiostyles africana	EUPHORBIACEAE					•			
Psorospermum tenuifolium	HYPERICACEAE	•							
Pterocarpus soyauxii	PAPILIONACEAE		•	•				•	
Pycnanthus angolensis	MYRISTICACEAE							•	
Scyphocephalium ochocoa	MYRISTICACEAE		•						
Sterculia tragacantha	STERCULIACEAE	•						•	
Swartzia fistuloides	CAESALPINIACEAE		•						
Testulea gabonensis	LUXEMBURGIACEAE		•						
Vitex doniana	VERBENACEAE						•		
Xylopia parvifolia	ANNONACEAE		•						
SEGC No. 319			•						
SEGC No. 369			•						
SUB-TOTAL		**19**	**46**	**15**	**4**	**6**	**5**	**18**	**5**
UNKNOWNS		**1**	**1**	**7**	**1**	**2**	**1**	**2**	**0**
TOTAL		**20**	**47**	**22**	**5**	**8**	**6**	**20**	**0**

STEM		**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**
Species	**Family**								
Aframomum leptolepis	ZINGIBERACEAE	•	•						•
Aframomum longipetiolatum	ZINGIBERACEAE	•	•						
Aframomum sp.nov	ZINGIBERACEAE	•	•						
Anchomanes difformis	ARACEAE		•						
Berlinia bracteosa	CAESALPINIACEAE			•	•	•	•	•	
Cissus dinklagei	VITACEAE			•					
Cola lizae	STERCULIACEAE	•		•				•	
Costus afer	ZINGIBERACEAE	•							•
Diospyros dendo	EBENACEAE			•					
Distemonanthus bethamianus	CAESALPINACEAE			•					
Elaeis guineensis	PALMAE	•							
Eremospatha cabrae	PALMAE	•	•						
Halopegia azurea	MARENTACEAE		•						
Lophira alata	OCHNACEAE							•	
Marantachloa cordifolia	MARENTACEAE		•						
Marantachloa filipes	MARENTACEAE		•						
Marantachloa purpurea	MARENTACEAE		•						
Megaphrynium gabunense	MARENTACEAE		•						
Megaphrynium macrostachyum	MARENTACEAE		•						
Palisota ambigua	COMMELINACEAE		•						
Pycnanthus angolensis	MYRISTICACEAE							•	
Renealmia cincinnata	MYRISTICACEAE		•						
Renealmia macrocolea	MYRISTICACEAE	•	•						•
Sterculia tragacantha	STERCULIACEAE			•					
Trachyphrynium braunianum	MARENTACEAE		•						•
SEGC NO.351	PALMAE		•						
SUB-TOTAL		**8**	**16**	**6**	**1**	**1**	**1**	**4**	**4**
UNKNOWN		**0**	**0**	**3**	**0**	**0**	**0**	**0**	**0**
TOTAL		**8**	**16**	**9**	**1**	**1**	**1**	**4**	**4**

Appendix 5.2 Number and percent of scan samples each species and plant part were observed to be eaten each month.

MONTH	SPECIES	No. scans each month							% of scans each month							MEAN %
		PART							PART							
		FRR	FRI	SDR	SDI	FL	NL	PTH	FRR	FRI	SDR	SDI	FL	NL	PTH	
Mar-92	Anthonotha macrophylla	0	0	1	0	0	0	0	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.05
Apr-91	Aucoumea klaineana	0	0	0	0	0	6	0	0.00	0.00	0.00	0.00	0.00	0.10	0.00	
May-91	Aucoumea klaineana	0	0	0	0	0	1	0	0.00	0.00	0.00	0.00	0.00	0.01	0.00	
Jun-91	Aucoumea klaineana	0	0	0	0	0	8	0	0.00	0.00	0.00	0.00	0.00	0.12	0.00	
Nov-91	Aucoumea klaineana	0	0	0	0	4	0	0	0.00	0.00	0.00	0.00	0.02	0.00	0.00	
Apr-92	Aucoumea klaineana	0	0	0	1	0	0	0	0.00	0.00	0.00	0.01	0.00	0.00	0.00	
May-92	Aucoumea klaineana	0	0	0	5	0	3	0	0.00	0.00	0.00	0.03	0.00	0.02	0.00	
Jun-92	Aucoumea klaineana	0	0	0	0	0	3	0	0.00	0.00	0.00	0.00	0.00	0.04	0.00	
Jul-92	Aucoumea klaineana	0	0	0	4	0	2	0	0.00	0.00	0.00	0.01	0.00	0.01	0.00	
									0.00	0.00	0.00	0.05	0.02	0.20	0.00	2.41
Aug-92	Baikiaea insignis	0	0	2	0	0	0	0	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.08
Apr-91	Berlinia bracteosa	0	0	0	14	0	0	0	0.00	0.00	0.00	0.23	0.00	0.00	0.00	
May-91	Berlinia bracteosa	0	0	0	7	0	0	0	0.00	0.00	0.00	0.09	0.00	0.00	0.00	
Jul-92	Berlinia bracteosa	0	0	0	1	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Aug-92	Berlinia bracteosa	0	0	0	6	0	0	0	0.00	0.00	0.00	0.03	0.00	0.00	0.00	
									0.00	0.00	0.00	0.34	0.00	0.00	0.00	2.29
Jan-92	Blighia welwitschii	10	0	0	0	0	0	0	0.27	0.00	0.00	0.00	0.00	0.00	0.00	1.80
Nov-91	Canarium schweinfurthii	8	0	0	0	0	1	0	0.04	0.00	0.00	0.00	0.00	0.01	0.00	0.32
Nov-91	Ceiba pentandra	0	0	0	0	0	1	0	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.04
Feb-92	Celtis tessmanni	0	0	0	15	0	0	0	0.00	0.00	0.00	0.09	0.00	0.00	0.00	
Mar-92	Celtis tessmanni	1	0	12	0	0	0	0	0.01	0.00	0.09	0.00	0.00	0.00	0.00	
Jan-92	Celtis tessmanni	0	0	0	3	0	0	0	0.00	0.00	0.00	0.08	0.00	0.00	0.00	
									0.01	0.00	0.09	0.17	0.00	0.00	0.00	1.78
Oct-91	Cissus sp.	1	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.07
May-91	Cola lizae	0	0	0	0	0	0	8	0.00	0.00	0.00	0.00	0.00	0.00	0.10	
Jun-91	Cola lizae	0	0	0	0	0	0	4	0.00	0.00	0.00	0.00	0.00	0.00	0.06	
Oct-91	Cola lizae	0	0	0	0	0	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.01	
Dec-91	Cola lizae	0	1	0	0	0	0	0	0.00	0.07	0.00	0.00	0.00	0.00	0.00	
Jan-92	Cola lizae	5	0	0	0	0	0	0	0.14	0.00	0.00	0.00	0.00	0.00	0.00	
Feb-92	Cola lizae	29	8	0	0	0	0	0	0.16	0.05	0.00	0.00	0.00	0.00	0.00	
Mar-92	Cola lizae	40	0	0	0	0	0	0	0.31	0 00	0.00	0.00	0.00	0.00	0.00	
Apr-92	Cola lizae	49	0	0	0	0	0	1	0.49	0.00	0.00	0.00	0.00	0.00	0.01	
May-92	Cola lizae	3	0	0	0	0	0	0	0.02	0.00	0.00	0.00	0.00	0.00	0.00	
Jul-92	Cola lizae	9	0	0	0	0	0	0	0.03	0.00	0.00	0.00	0.00	0.00	0.00	
									1.15	0.11	0.00	0.00	0.00	0.00	0.18	9.61
May-91	Cryptosepalum staudtii	0	0	0	0	0	3	0	0.00	0.00	0.00	0.00	0.00	0.04	0.00	
Jun-91	Cryptosepalum staudtii	0	0	0	0	0	12	0	0.00	0.00	0.00	0.00	0.00	0.18	0.00	
Mar-92	Cryptosepalum staudtii	0	0	0	1	0	0	0	0.00	0.00	0.00	0.01	0.00	0.00	0.00	
Apr-92	Cryptosepalum staudtii	0	0	0	0	0	1	0	0.00	0.00	0.00	0.00	0.00	0.01	0.00	
Aug-92	Cryptosepalum staudtii	0	0	0	0	0	2	0	0.00	0.00	0.00	0.00	0.00	0.01	0.00	
									0.00	0.00	0.00	0.01	0.00	0.24	0.00	1.67
Nov-91	Dacryodes buettneri	11	0	0	0	0	3	0	0.06	0.00	0.00	0.00	0.00	0.02	0.00	
Jan-92	Dacryodes buettneri	1	0	0	0	0	0	0	0.03	0.00	0.00	0.00	0.00	0.00	0.00	
Feb-92	Dacryodes buettneri	11	0	0	0	0	0	0	0.06	0.00	0.00	0.00	0.00	0.00	0.00	
									0.15	0.00	0.00	0.00	0.00	0.02	0.00	1.10
Feb-92	Dialium lopense	0	0	0	4	0	0	0	0.00	0.00	0.00	0.02	0.00	0.00	0.00	
Mar-92	Dialium lopense	0	0	1	3	0	0	0	0.00	0.00	0.01	0.02	0.00	0.00	0.00	
Apr-92	Dialium lopense	0	0	22	0	0	0	0	0.00	0.00	0.22	0.00	0.00	0.00	0.00	
May-92	Dialium lopense	0	0	95	0	0	0	0	0.00	0.00	0.48	0.00	0.00	0.00	0.00	
Jul-92	Dialium lopense	0	0	3	1	0	0	0	0.00	0.00	0.01	0.00	0.00	0.00	0.00	
									0.00	0.00	0.72	0.05	0.00	0.00	0.00	5.13
Apr-91	Diospyros dendo	3	0	0	0	0	0	0	0.05	0.00	0.00	0.00	0.00	0.00	0.00	
Apr-92	Diospyros dendo	0	0	0	3	0	0	0	0.00	0.00	0.00	0.03	0.00	0.00	0.00	
May-92	Diospyros dendo	25	0	0	0	0	0	0	0.13	0.00	0.00	0.00	0.00	0.00	0.00	
Jul-92	Diospyros dendo	2	6	0	36	0	0	1	0.01	0.02	0.00	0.12	0.00	0.00	0.00	
Aug-92	Diospyros dendo	0	0	0	94	0	0	0	0.00	0.00	0.00	0.56	0.00	0.00	0.00	
									0.18	0.02	0.00	0.70	0.00	0.00	0.00	6.06
Feb-92	Diospyros polystemon	0	0	0	7	0	0	0	0.00	0.00	0.00	0.04	0.00	0.00	0.00	
Mar-92	Diospyros polystemon	0	0	1	0	0	0	0	0.00	0.00	0.01	0.00	0.00	0.00	0.00	
Apr-92	Diospyros polystemon	0	0	0	3	0	0	0	0.00	0.00	0.00	0.03	0.00	0.00	0.00	
May-92	Diospyros polystemon	24	0	0	4	0	0	0	0.12	0.00	0.00	0.02	0.00	0.00	0.00	
Jul-92	Diospyros polystemon	0	0	3	0	0	0	0	0.00	0.00	0.01	0.00	0.00	0.00	0.00	
									0.12	0.00	0.02	0.09	0.00	0.00	0.00	1.53
May-92	Diospyros viridicans	0	0	0	0	4	0	0	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.13
Jul-92	Diospyros zenkeri	1	0	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
May-91	Distemonanthus bethamianus	0	0	32	0	0	7	0	0.00	0.00	0.39	0.00	0.00	0.09	0.00	
Jun-91	Distemonanthus bethamianus	0	0	0	0	0	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.02	
Nov-91	Distemonanthus bethamianus	0	0	9	0	0	0	0	0.00	0.00	0.05	0.00	0.00	0.00	0.00	
Feb-92	Distemonanthus bethamianus	0	0	1	0	0	0	0	0.00	0.00	0.01	0.00	0.00	0.00	0.00	
May-92	Distemonanthus bethamianus	0	0	6	0	0	2	0	0.00	0.00	0.03	0.00	0.00	0.01	0.00	
Jun-92	Distemonanthus bethamianus	0	0	31	0	0	0	0	0.00	0.00	0.39	0.00	0.00	0.00	0.00	
Jul-92	Distemonanthus bethamianus	0	0	1	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Aug-92	Distemonanthus bethamianus	0	0	24	0	0	0	0	0.00	0 00	0.14	0.00	0.00	0.00	0.00	
									0.00	0.00	1.01	0.00	0.00	0.10	0.02	7.49
Jan-92	Dichapetalum sp.	2	0	0	0	0	0	0	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.36

Appendix 5.2 Number and percent of scan samples each species and plant part were observed to be eaten each month / cont.

MONTH	SPECIES	No. scans each month							% of scans each month							MEAN %
					PART							PART				
		FRR	FRI	SDR	SDI	FL	NL	PTH	FRR	FRI	SDR	SDI	FL	NL	PTH	
Apr-91	Elaeis guineensis	7	0	0	0	0	0	0	0.11	0.00	0.00	0.00	0.00	0.00	0.00	
May-91	Elaeis guineensis	1	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	
Oct-91	Elaeis guineensis	2	0	0	0	0	0	0	0.02	0.00	0.00	0.00	0.00	0.00	0.00	
Nov-91	Elaeis guineensis	19	0	0	0	0	0	0	0.10	0.00	0.00	0.00	0.00	0.00	0.00	
Dec-91	Elaeis guineensis	2	0	0	0	0	0	0	0.13	0.00	0.00	0.00	0.00	0.00	0.00	
Mar-92	Elaeis guineensis	4	0	0	0	0	0	0	0.03	0.00	0.00	0.00	0.00	0.00	0.00	
Apr-92	Elaeis guineensis	6	0	0	0	0	0	0	0.06	0.00	0.00	0.00	0.00	0.00	0.00	
Jun-92	Elaeis guineensis	6	0	0	0	0	0	0	0.08	0.00	0.00	0.00	0.00	0.00	0.00	
Jul-92	Elaeis guineensis	2	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	
									0.55	0.00	0.00	0.00	0.00	0.00	0.00	3.70
Feb-92	Eriocoelium macrocarpum	0	0	7	0	0	0	0	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.27
Oct-91	Ficus mucosa	14	0	0	0	0	0	0	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.97
Jul-92	Ficus recurvata	15	0	0	0	0	0	0	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.33
Sep-91	Ficus thonningii	5	0	0	0	0	0	0	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.88
Sep-91	Gambeya africana	0	9	0	0	0	0	0	0.00	0.24	0.00	0.00	0.00	0.00	0.00	1.58
Jan-92	Ganophyllum giganteum	1	0	0	0	0	0	0	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.18
Jan-92	Guibortia tesmannii	0	0	3	0	0	0	0	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.54
Nov-91	Heisteria parvifolia	16	0	0	0	0	0	0	0.09	0.00	0.00	0.00	0.00	0.00	0.00	
Jan-92	Heisteria parvifolia	1	0	0	0	0	0	0	0.03	0.00	0.00	0.00	0.00	0.00	0.00	
Mar-92	Heisteria parvifolia	1	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	
Jul-92	Heisteria parvifolia	6	0	0	0	0	0	0	0.02	0.00	0.00	0.00	0.00	0.00	0.00	
									0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.93
May-92	Hylodendron gabunense	0	0	5	0	0	0	0	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.17
Nov-91	Irvingia gabonensis	0	0	0	25	0	0	0	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.89
Nov-91	Irvingia grandifolia	0	0	4	0	0	0	0	0.00	0.00	0.02	0.00	0.00	0.00	0.00	
Dec-91	Irvingia grandifolia	0	0	1	0	0	0	0	0.00	0.00	0.07	0.00	0.00	0.00	0.00	
									0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.59
Nov-91	Klainedoxa gabonensis	0	0	0	1	0	0	0	0.00	0.00	0.00	0.01	0.00	0.00	0.00	
Jan 92	Klainedoxa gabonensis	2	0	0	0	0	0	0	0.05	0.00	0.00	0.00	0.00	0.00	0.00	
									0.05	0.00	0.00	0.01	0.00	0.00	0.00	0.40
Jun 92	Landolphia	1	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.08
Jan-92	Lecaniodiscus cupanoides	6	0	0	0	0	0	0	0.16	0.00	0.00	0.00	0.00	0.00	0.00	1.08
Jan-92	Lophira alata	0	0	0	0	0	1	0	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.18
Feb-92	Manniophyton	0	0	6	0	0	0	0	0.00	0.00	0.03	0.00	0.00	0.00	0.00	
Jul-92	Manniophyton	0	0	26	0	0	0	0	0.00	0.00	0.09	0.00	0.00	0.00	0.00	
									0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.80
Jun 91	Millettia	0	0	0	0	0	3	0	0.00	0.00	0.00	0.00	0.00	0.05	0.00	
Oct 91	Millettia	0	0	0	0	0	26	0	0.00	0.00	0.00	0.00	0.00	0.27	0.00	
									0.00	0.00	0.00	0.00	0.00	0.32	0.00	2.11
May-92	Monodora sp	1	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.03
May 91	Myrianthus arboreus	1	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	
Sep-91	Myrianthus arboreus	3	0	0	0	0	0	0	0.08	0.00	0.00	0.00	0.00	0.00	0.00	
Mar 92	Myrianthus arboreus	2	0	0	0	0	0	0	0.02	0.00	0.00	0.00	0.00	0.00	0.00	
									0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.71
Oct 91	Nauclea didderichi	17	0	0	0	0	0	0	0.18	0.00	0.00	0.00	0.00	0.00	0.00	
Nov 91	Nauclea didderichi	28	0	0	0	0	0	0	0.15	0.00	0.00	0.00	0.00	0.00	0.00	
Mar 92	Nauclea didderichi	0	0	0	0	1	0	0	0.00	0.00	0.00	0.00	0.01	0.00	0.00	
May 92	Nauclea didderichi	2	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	
									0.34	0.00	0.00	0.00	0.01	0.00	0.00	2.30
May-92	Ongokia gore	0	1	0	0	0	0	0	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.07
Apr-91	Parkia bicolor	0	0	0	1	0	0	0	0.00	0.00	0.00	0.02	0.00	0.00	0.00	
Nov-91	Parkia bicolor	0	0	0	0	0	1	0	0.00	0.00	0.00	0.00	0.00	0.01	0.00	
Dec 91	Parkia bicolor	0	0	2	0	0	0	0	0.00	0.00	0.13	0.00	0.00	0.00	0.00	
Feb 92	Parkia bicolor	0	0	31	0	2	0	0	0.00	0.00	0.18	0.00	0.01	0.00	0.00	
Mar-92	Parkia bicolor	0	0	7	4	0	0	0	0.00	0.00	0.05	0.03	0.00	0.00	0.00	
Aug 92	Parkia bicolor	0	0	5	0	0	0	0	0.00	0.00	0.03	0.00	0.00	0.00	0.00	
									0.00	0.00	0.39	0.05	0.01	0.01	0.00	3.05
Jan 92	Parkia filicoidea	0	0	0	0	1	0	1	0.00	0.00	0.00	0.00	0.03	0.00	0.03	0.36
Apr-91	Pentaclethra macrophylla	0	0	0	1	0	0	0	0.00	0.00	0.00	0.02	0.00	0.00	0.00	
May 91	Pentaclethra macrophylla	0	0	0	1	1	0	0	0.00	0.00	0.00	0.01	0.01	0.00	0.00	
Jun 91	Pentaclethra macrophylla	0	0	0	0	19	0	0	0.00	0.00	0.00	0.00	0.29	0.00	0.00	
Nov-91	Pentaclethra macrophylla	0	0	0	5	0	0	0	0.00	0.00	0.00	0.03	0.00	0.00	0.00	
Apr 92	Pentaclethra macrophylla	0	0	0	1	0	0	0	0.00	0.00	0.00	0.01	0.00	0.00	0.00	
Aug 92	Pentaclethra macrophylla	0	0	0	0	0	3	0	0.00	0.00	0.00	0.00	0.00	0.02	0.00	
									0.00	0.00	0.00	0.07	0.30	0.02	0.00	2.58
Apr 91	Piptadeniastrum africanum	0	0	1	0	0	0	0	0.00	0.00	0.02	0.00	0.00	0.00	0.00	
Dec 91	Piptadeniastrum africanum	0	0	3	0	0	0	0	0.00	0.00	0.20	0.00	0.00	0.00	0.00	
Feb 92	Piptadeniastrum africanum	0	0	3	0	0	0	0	0.00	0.00	0.02	0.00	0.00	0.00	0.00	
Mar 92	Piptadeniastrum africanum	0	0	9	0	0	0	0	0.00	0.00	0.07	0.00	0.00	0.00	0.00	
									0.00	0.00	0.30	0.00	0.00	0.00	0.00	2.02

Appendix 5.2 Number and percent of scan samples each species and plant part were observed to be eaten each month/ cont.

MONTH	SPECIES	No. scans each month							% of scans each month							MEAN %
					PART							PART				
		FRR	FRI	SDR	SDI	FL	NL	PTH	FRR	FRI	SDR	SDI	FL	NL	PTH	
Jun-92	Polyalthia suavoelense	1	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.08
May-92	Porterandia cladantha	0	2	0	0	0	0	0	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.07
May-92	Pseudospondias microcarpa	1	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.03
May-91	Pterocarpus soyauxii	0	0	0	0	5	0	0	0.00	0.00	0.00	0.00	0.06	0.00	0.00	
Sep-91	Pterocarpus soyauxii	0	0	0	0	0	1	0	0.00	0.00	0.00	0.00	0.00	0.03	0.00	
Nov-91	Pterocarpus soyauxii	0	0	0	0	3	0	0	0.00	0.00	0.00	0.00	0.02	0.00	0.00	
Feb-92	Pterocarpus soyauxii	0	0	0	30	0	0	0	0.00	0.00	0.00	0.17	0.00	0.00	0.00	
Mar-92	Pterocarpus soyauxii	0	0	23	0	0	0	0	0.00	0.00	0.18	0.00	0.00	0.00	0.00	
Apr-92	Pterocarpus soyauxii	0	0	12	0	0	0	0	0.00	0.00	0.12	0.00	0.00	0.00	0.00	
May-92	Pterocarpus soyauxii	0	0	0	15	0	0	0	0.00	0.00	0.00	0.08	0.00	0.00	0.00	
Jun-92	Pterocarpus soyauxii	0	0	0	0	31	0	0	0.00	0.00	0.00	0.00	0.39	0.00	0.00	
Jul-92	Pterocarpus soyauxii	0	0	11	160	0	0	0	0.00	0.00	0.04	0.52	0.00	0.00	0.00	
Aug-92	Pterocarpus soyauxii	0	0	29	0	0	0	0	0.00	0.00	0.17	0.00	0.00	0.00	0.00	
									0.00	0.00	0.51	0.77	0.47	0.03	0.00	11.82
May-91	Pycnanthus angolensis	0	0	0	4	0	0	0	0.00	0.00	0.00	0.05	0.00	0.00	0.00	
Sep-91	Pycnanthus angolensis	0	0	0	11	0	0	0	0.00	0.00	0.00	0.29	0.00	0.00	0.00	
Oct-91	Pycnanthus angolensis	19	0	9	0	0	0	0	0.20	0.00	0.09	0.00	0.00	0.00	0.00	
Nov-91	Pycnanthus angolensis	1	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	
Jun-92	Pycnanthus angolensis	0	0	4	0	0	0	0	0.00	0.00	0.05	0.00	0.00	0.00	0.00	
Jul-92	Pycnanthus angolensis	0	4	0	4	0	0	0	0.00	0.01	0.00	0.01	0.00	0.00	0.00	
Aug-92	Pycnanthus angolensis	0	0	4	0	0	0	0	0.00	0.00	0.02	0.00	0.00	0.00	0.00	
									0.20	0.01	0.17	0.35	0.00	0.00	0.00	4.91
Apr-91	Scottellia sp.	28	0	0	0	0	0	0	0.45	0.00	0.00	0.00	0.00	0.00	0.00	3.01
Feb-92	Scyphocephalim ocochoa	0	0	0	21	0	0	0	0.00	0.00	0.00	0.12	0.00	0.00	0.00	
Mar-92	Scyphocephalium ocochoa	0	0	0	2	0	0	0	0.00	0.00	0.00	0.02	0.00	0.00	0.00	
									0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.90
Jun-91	Sterculia trgacantha	0	1	0	0	0	0	0	0.00	0.02	0.00	0.00	0.00	0.00	0.00	
Nov-91	Sterculia trgacantha	2	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	
Jul-92	Sterculia trgacantha	0	0	0	0	0	0	2	0.00	0.00	0.00	0.00	0.00	0.00	0.01	
									0.01	0.02	0.00	0.00	0.00	0.00	0.01	0.22
May-91	Tetrapleura tetrapta	0	0	0	2	0	0	0	0.00	0.00	0.00	0.02	0.00	0.00	0.00	
Jul-92	Tetrapleura tetrapta	0	0	0	1	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
									0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.18
Oct-91	Uapaca guineensis	7	0	0	0	0	0	0	0.07	0.00	0.00	0.00	0.00	0.00	0.00	
Nov-91	Uapaca guineensis	26	0	0	0	0	0	0	0.14	0.00	0.00	0.00	0.00	0.00	0.00	
Dec-91	Uapaca guineensis	3	0	0	0	0	0	0	0.20	0.00	0.00	0.00	0.00	0.00	0.00	
Mar-92	Uapaca guineensis	0	5	0	0	0	0	0	0.00	0.04	0.00	0.00	0.00	0.00	0.00	
									0.41	0.04	0.00	0.00	0.00	0.00	0.00	3.00
Mar-92	Uvariastrum pierreanum	9	0	0	0	0	0	0	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.47
Apr-91	Vitex sp.	0	0	0	0	1	0	0	0.00	0.00	0.00	0.00	0.02	0.00	0.00	
Jun-91	Vitex sp.	0	0	0	0	1	0	0	0.00	0.00	0.00	0.00	0.02	0.00	0.00	
									0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.21
Nov-91	Xylopia aethiopica	0	1	0	0	0	0	0	0.00	0.01	0.00	0.00	0.00	0.00	0.00	
Jul-92	Xylopia aethiopica	0	0	0	2	0	0	0	0.00	0.00	0.00	0.01	0.00	0.00	0.00	
									0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.08
May-91	Xylopia hypolampra	0	0	0	7	0	0	0	0.00	0.00	0.00	0.09	0.00	0.00	0.00	
Nov-91	Xylopia hypolampra	8	0	0	0	0	0	0	0.04	0.00	0.00	0.00	0.00	0.00	0.00	
									0.04	0.00	0.00	0.09	0.00	0.00	0.00	0.85
Sep-91	Xylopia quintasii	9	0	0	0	0	0	0	0.24	0.00	0.00	0.00	0.00	0.00	0.00	
Aug-92	Xylopia quintasii	0	0	0	1	0	0	0	0.00	0.00	0.00	0.01	0.00	0.00	0.00	
									0.24	0.00	0.00	0.01	0.00	0.00	0.00	1.62
May-91	UK	0	0	0	0	2	0	0	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.16
Jun-91	UK	0	0	0	0	0	0	16	0.00	0.00	0.00	0.00	0.00	0.00	0.25	1.64
Nov-91	UK	0	0	0	0	0	1	0	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.04
Nov-91	UK	0	0	0	0	0	5	0	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.18
Nov-91	UK	0	0	0	0	0	2	0	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.07
Nov-91	UK	0	0	0	0	0	1	0	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.04
Nov-91	UK	0	0	0	0	0	1	0	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.04
Dec-91	UK	0	0	0	0	0	2	0	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.89
Dec-91	UK	0	0	0	0	1	0	0	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.44
Feb-92	UK	0	0	1	0	0	0	0	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.04
Mar-92	UK	0	0	0	0	0	0	1	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.05
Mar-92	UK	1	0	0	0	0	0	0	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.05
Jun-92	UK	0	0	0	0	0	2	0	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.17
Jul-92	UK	0	0	0	1	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Jul-92	UK	0	0	1	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02