POPULATION SIZE AND STRUCTURE OF THE NGOGO CHIMPANZEE COMMUNITY IN THE KIBALE FOREST, UGANDA AND THE IMPACT OF TOURISM

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Abstract

Although both species of chimpanzees, the common chimpanzee (*Pan troglodytes*) and the bonbobo (*Pan paniscus*) show a so-called fission-fusion social organisation, they differ significantly in the details of social relationships between and within genders. These differences have been linked to ecological differences between the species' habitats. Common chimpanzees living in forested habitats were put forward as providing a link between common chimpanzees in less forested habitats and bonobos.

In this study, the Ngogo community of Kibale Forest in Uganda was investigated to determine whether it is justified to say that forest-living chimpanzees exhibit characteristics in their social organisation which resemble both the common chimpanzees in less forested habitats and the bonobos. From January 1992 to June 1993, focal animal samples on adult males, anoestrous and oestrous females yielded data on party size and composition, social interactions and time budgets. Statistical analysis suggested that the Ngogo chimpanzees resemble common chimpanzees from other habitats in party size and composition, intra- and intersexual relationships more than bonobos, whereas their time budget resembles more that of bonobos. A comparison with data from the literature suggests that intraspecific variation of social organisation may be as great as interspecific variation.

In the second part of the study, the impact of habituation and tourism on the Kanyancu community of chimpanzees in the Kibale Forest was monitored. From February 1992 to June 1993, chimpanzees' initial reactions to contacts with human observers were recorded together with other factors such as numbers of observers present and the method used to locate the chimpanzees. On 54 occasions with various numbers of observers (and/or tourists) present, activity rates were recorded for the observed individuals. Numbers of observers present (up to 5) had no impact on the chimpanzees' initial reaction, and the only significant change in activity caused by higher numbers of observers (up to 15) was an increasing vocalisation rate. As visitor satisfaction declines with groups of more than six to eight people it is suggested that tourist groups viewing chimpanzees should be kept at a maximum number of 10 (including guides).

Contents

Chapter 1: General Introduction

Chapter 2: Study Area and Methods

Chapter 3: Size and Structure of the Ngogo Community

Chapter 4: Gender Relationships

Chapter 5: Time budgets

Chapter 6: Habituation

Chapter 7: Discussion

List of Tables

List of Maps and Figures

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Chapter 1

General Introduction

1.1 The importance of chimpanzee studies

Common chimpanzees (*Pan troglodytes* Blumenbach, 1799) and bonobos (*Pan paniscus* Schwarz, 1929) are becoming increasingly threatened by habitat loss, hunting and commercial exploitation (Goodall, 1994; Lee et al, 1988; Malenky *et al.*, 1989; Teleki, 1989). It thus becomes the more important that we learn as much as possible about these species' behaviour under natural conditions, so that we learn how to protect them better and how to look after them better when they are in captivity. In addition, observations of apes, our closest relatives, can shed light on features of human evolution (e.g. Ghiglieri, 1989; Wrangham, 1987). DNA-DNA hybridization experiments have indicated that chimpanzees and bonobos are even more closely related to humans than they are to gorillas (Sibley & Ahlquist, 1984), and chimpanzees have already been instrumental in re-defining "what is human" several times (Goodall, 1986).

This study was implemented in two distinct but related sections, a behavioural and an applied section. The results of the behavioural study helped to define priorities for habituation of chimpanzees in different habitats for ecotourism.

1.2 Behavioural studies of chimpanzees and bonobos

1.2.1 Common chimpanzee behaviour as perceived from Gombe

Although common chimpanzees are distributed from West to East Africa in 3 subspecies (Lee *et al.*, 1988), most data come from two long-term studies on the eastern subspecies, *P.t. schweinfurthi* (Giglioli, 1872) in Gombe National Park and Mahale Mountains National Park, both situated in Tanzania (e.g. Goodall, 1986; Nishida, 1990).

These data indicate that chimpanzees live in so-called communities (or unit-groups, Nishida, 1968; Nishida *et al.*, 1990). The members of a community share a common home range and neighbouring communities are usually hostile towards each other (Bygott, 1979; Goodall *et al.*, 1979; Nishida, 1979; Nishida *et al.*, 1985; Wrangham, 1979). Within a community, chimpanzees have what has been termed a fusion-fission organisation (Goodall, 1986; Nishida, 1968, 1979). This means that they live in temporary associations of varied size and composition (Goodall, 1968, 1986; Halperin, 1979). Females transfer between communities, whereas males stay in their natal communities (Hiraiwa-Hasegawa *et al.*, 1984; Nishida *et al.*, 1985; Nishida *et al.*, 1990; Pusey, 1979). Therefore the males of one community are related to each other, whereas females are usually unrelated outside mother/daughter and sister relationships (Wrangham & Smuts, 1990). Females lead more solitary lives in which they are less sociable compared to males, who spend more time with other chimpanzees and groom each other more frequently (Goodall, 1968; Halperin, 1979; Muroyama & Sugiyama, 1994; Nishida, 1979; Wrangham & Smuts, 1980).

Chimpanzee males have relatively strong dominance hierarchies (Bygott, 1979; Takahata, 1990b) and may form alliances to improve their status in the dominance hierarchy or to maintain it (Goodall, 1986; Nishida, 1979, 1983; Riss & Goodall, 1977; Uehara *et al.*, 1994). In contrast, hierarchy relationships among females are not very clear. If there are dominance relationships, it is usually the older female who is more dominant (Bygott, 1979). Adult males are invariably dominant over females (Bygott, 1979). Mating patterns are either opportunistic (the female mates with all males present) or possessive (one male maintains exclusive copulation rights) (Goodall, 1986; Hasegawa & Hiraiwa-Hasegawa, 1983, 1990; McGinnis, 1979; Takahata, 1990a; Takasaki, 1985; Tutin, 1979).

Chimpanzees have been shown to use a variety of tools (Goodall, 1968, 1986; McGrew, 1979; Wrangham, 1977) and to hunt, kill and eat a number of mammalian species (Goodall, 1968, 1986; McGrew, 1979; Nishida & Uehara, 1980; Wrangham 1974, 1977; Wrangham & van Zinnicq Bergmann Riss, 1990). Apart from these hunting forays, chimpanzees are predominantly frugivorous with leaves, flowers, pith, bark and insects as additional food items (Goodall, 1968, 1971; Nishida, 1968; Wrangham, 1977).

1.2.2 Common chimpanzee behaviour as perceived from other study sites

Studies at other sites have indicated that the basic structure of temporary associations within a relatively stable community as reported from Gombe can be applied to other chimpanzee populations all over this species' wide geographical distribution. For example, populations at Kasakati in Tanzania (Suzuki, 1969), Bossou in Guinea (Sugiyama & Koman, 1979), in the Tai Forest in the Ivory Coast (Boesch, 1991), on Mt Assirik in Senegal (Tutin *et al.*, 1981), and in the Budongo and Kibale Forests in Uganda (Ghiglieri, 1984; Reynolds & Reynolds, 1965; Sugiyama, 1968, 1969; Wrangham *et al.*, 1992), all follow this pattern.

However, considerable intraspecific variation in a range of behavioural parameters lies hidden beneath the blanket of fission-fusion society. In Bossou, Tai, and on Mt Assirik (Sugiyama & Koman, 1979; Boesch, 1991; Tutin *et al.*, 1981), parties are reported to be more cohesive than at Gombe or Mahale, i.e. a greater proportion of the community is together at any one time. In Bossou, the males seem to transfer between communities rather than the females (Sugiyama & Koman, 1979). Social relationships among and between the sexes are not the same everywhere, either: in Bossou, Tai and the Ngogo community in the Kibale Forest, affiliation between females was reported as higher than at Gombe, whereas affiliation between males was lower (Boesch, 1991; Ghiglieri, 1984; Sugiyama, 1988). The causes for these differences are not well understood; differences in habitat quality or predation pressure are proposed as possible factors (Sugiyama, 1988; Boesch, 1991).

1.2.3 Bonobo behaviour

Although bonobos and common chimpanzees show the same fission-fusion organisation (Badrian & Badrian, 1984; Kano, 1980, 1982, 1983; Kuroda, 1979; White, 1988), the details of their social organisations show remarkable differences. As with the common chimpanzee, it is the female bonobos who transfer to other communities (Furuichi, 1989; Kano, 1982a). This being so, the degree of relatedness within the sexes should be similar in both species of chimpanzees (also suggested by Gerloff, 1995). However, the relationships within and between sexes seem to be completely different.

Bonobo parties are reported to be more cohesive (Badrian *et al.*, 1981) and bigger than in common chimpanzees (Kano, 1980, 1982; Kuroda, 1979; White &

Wrangham, 1988). Bonobo females are more sociable than the males (Kano, 1980, 1982, 1983; Kuroda, 1979; White, 1989). For instance, females are less solitary (Badrian & Badrian, 1984; Furuichi, 1987; Kano, 1982a, 1983; Kuroda, 1979). Moreover, grooming occurs more often between males and females, or among females, than between males (Badrian & Badrian, 1984; Kano, 1980, 1983; Muroyama & Sugiyama, 1994). Both sexes have a number of greeting behaviours that are not observed in common chimpanzees such as genito-genital rubbing between females (Badrian & Badrian, 1984; Idani, 1991; Kano, 1980, 1983, 1992; White & Lanjouw, 1988), rump contact and mounting between males (Kano, 1980) and ventro-ventral copulation between males and females (Kano, 1980, 1992; possibly Kuroda, 1984b; Patterson, 1979; Savage-Rumbaugh & Wilkerson, 1978; Savage & Bakeman, 1979; Thompson-Handler *et al.*, 1984).

Although researchers speak of dominance/subordinance relationships between male bonobos (Ihobe, 1992; Kano, 1980; Kano & Mulavva, 1984), the rate of agonistic interactions between them is low (Badrian & Badrian, 1984; Kano, 1983) and the rank order has been described as "not strictly linear" (Kano, 1992, p.182). They only rarely join forces in aggression against other males (Ihobe, 1992). Also, the dominance relationships between males and females are not clear-cut. In the African ape with the smallest degree of sexual dimorphism (Kuroda, 1979; but see also Leigh & Shea, 1995), "the female has about the same rank as the male" (Kano, 1992, p.182).

While males do not behave submissively towards single females, they may do so towards an aggregation of females (Furuichi, 1989). Females have priority of access to food (Kano & Mulavva, 1984) and may form alliances and attack males (Kano, 1992).

Bonobos are promiscuous (Kano, 1980; 1992); no possessive mating patterns have been observed to date (Kano, 1992). They have been shown to use tools only as a protection against rain (Kano, 1982b). Their diet is predominantly fruit (Badrian & Malenky, 1984; Kano, 1979; Kano & Mulavva, 1984; White, 1992), but they do hunt occasionally at least at two sites, Lomako and Lilungu (Badrian & Badrian, 1984; Badrian & Malenky, 1984; Hohmann & Fruth, 1993; Sabater-Pi & Veà, 1994).

1.3 The effect of habitat

Habitats and habitat ecology not only shape the evolution of physical and physiological traits, but also the evolution of behaviour and social organisation (for example, Dunbar, 1988; Krebs & Davies, 1991). The differences in details of social organisation between common chimpanzees and bonobos are intriguing and various attempts have been made to explain them, all hinging on the premise that bonobos live in a "richer" habitat and can therefore "afford" larger parties (Chapman *et al.*, 1994). The increased consumption of terrestrial herbaceous vegetation (THV), increased utilization of larger food patches and a reduced, temporal habitat variability for bonobos compared to common chimpanzees were all put forward to explain the presumed lower feeding competition in bonobos and the consequences of living in bigger groups (Badrian & Badrian, 1984; Malenky, 1990 as quoted in Chapman *et al.*, 1994; White & Wrangham, 1988; Wrangham, 1986).

Considering the data on common chimpanzees from sites other than Gombe or Mahale, it becomes evident that there are indeed parallels in party size, cohesion and social relationships between the common chimpanzees in Bossou, Tai, and the Ngogo community in Kibale on the one hand and bonobos on the other (Badrian *et al.*, 1981; Boesch, 1991; Ghiglieri, 1984; Kano, 1980, 1982, 1983; Kuroda, 1979; Sugiyama, 1988; Tutin *et al.*, 1981; White, 1989). This converges on White & Wrangham's (1981) prediction that "forest-living *Pan troglodytes* will feed in larger parties than *P. troglodytes* living in Gombe and other mixed habitats with poorly-developed forest", because all three communities live in tropical forests. However, the habitat at Bossou is isolated and severely disturbed with regenerating secondary forest stages and cultivated fields (Sugiyama & Koman, 1987; Sugiyama, 1988). The data coming from this chimpanzee community can not be considered representative for forest chimpanzees. In the Tai forest, leopard predation is higher than at other chimpanzee sites and has been put forward as a possible conflicting factor in determining the form of chimpanzees' social relationships (Boesch, 1991).

Kibale seems to be the most appropriate site for a comparison with bonobos, but results from the two chimpanzee communities studied in the Kibale Forest seem to be contradictory. Ghiglieri (1984) described the Ngogo community as having strong social bonds between females and between males, although the mean size of travelling parties was smaller than at Gombe. In contrast, Wrangham *et al.* (1992) found that the Kanyawara community have social relationships very similar to communities of common chimpanzees in poorer habitats. These authors argue that Ghiglieri's methods and definitions influenced his results. According to their preliminary data from Ngogo, there is no difference in party size or social relationships between the two communities (Wrangham *et al.*, 1992).

This study aims to provide new data on the Ngogo community in the Kibale Forest, employing the definitions and methodology of both Ghiglieri (1984) and Wrangham *et al.* (1992) to make the results comparable to both studies. It will therefore enable us to determine whether the Ngogo chimpanzees as representatives of forest-living common chimpanzees do, in fact, exhibit social characteristics more similar to bonobos or to other common chimpanzee communities living in non-forest habitats.

1.3.1 Hypothesis and predictions

This study will enable us to test the hypothesis that forest-living common chimpanzees have a social organisation more similar to bonobos than to other common chimpanzee communities in non-forest habitats. If this hypothesis is true

- the Ngogo chimpanzees should have bigger and more cohesive parties than chimpanzee communities in non-forest sites;

- females should affiliate with each other more than males affiliate with each other; or

- females should affiliate with males more than males affiliate with each other;

- males should affiliate with each other less than with females.

If this is the case, it needs to be discussed why two chimpanzee communities in the same forest should differ so much (Wrangham *et al.*, 1992). If it is not the case, habitat quality will have to be re-assessed in its hitherto assumed significance for the evolution of details in chimpanzee and bonobo social organisation.

1.4 The effect of habituation and tourism

As humans can pose severe threats to wild animal species, a very important habitat feature is whether it contains humans or not and which functions these humans have. As human populations steadily increase in most habitat countries, animal species which are able to tolerate the presence of humans in their habitat have a better chance of long-term survival. This is particularly the case if the species is a threatened one and if it is attractive to tourists, because tourists can be made to pay for the pleasure of seeing these species and the species therefore pay for their keep, so to speak. The resulting concept is called eco-tourism, a revenue-generating sustainable conservation measure (for example Boo, 1990; Giannecchini, 1993; Burnie, 1994).

The challenge of ecotourism is to combine the demands of tourists with the needs of local populations and the conservation of protected areas and species (Giannecchini, 1993). Whether ecotourism takes the form of bird watching, game viewing or trekking, it may have a negative impact on the physical and biological environment. Boobies (*Sula* sp.) in the Galapagos were shown to change their behaviour in response to tourists (Burger & Gochfeld, 1993). Human traffic led large mammals to avoid certain areas and to change their activity periods in Borneo (Griffiths & van Schaik, 1993). Cheetahs

(*Acinonyx jubatus*) in Ambosele National Park interrupt hunts, abandon their prey and are even driven to infanticide when surrounded by tourist minibuses (Mather, 1989). The cutting of firewood for trekkers in the Himalayas has led to serious deforestation (Bjonness, 1980), and Asian rhinos (*Rhinoceros unicornis*) were shown to spend less time feeding and more time on alert when visited by tourists (Lott & McCoy, 1995).

In order to avoid such problems, it is necessary to monitor the impact of ecotourism from the outset so that changes in the environment and in animals' behaviour can be detected before irretrievable damage occurs.

Gorillas and chimpanzees are particularly attractive to tourists because of their physical, behavioural and genetic closeness to humans. They can be viewed in African rain forest countries such as Zaire, Rwanda and Uganda. Grauer's gorillas (*Gorilla gorilla graueri*) were habituated for tourism in the Kahuzi-Biega National Park in Zaire as early as 1966 (Murnyak, 1981). Gorilla tourism proved so successful in Rwanda, that the revenue generated by the mountain gorillas (*G. g. beringei*) made up an important part of the gross national product (Aveling & Aveling, 1981; Harcourt, 1984). Tourists can visit chimpanzees in Tanzania at Gombe and in the Mahale Mountains (Crowther & Finlay, 1991); in Zaire at Tongo

(Mühlenberg et al., undated), and in Uganda in the Kibale Forest and elsewhere.

However, because of their closeness to humans, great apes also suffer the greatest risk from contact with humans, for example through human diseases which are also infectious to apes (Goodall, 1971, 1986). Apart from this obvious problem, there is always the danger that chimpanzees or gorillas change their natural behaviour because they are in regular contact with humans. Wrangham (1974), for example, has shown that aggressive interactions among chimpanzees increased in the artificial feeding area at Gombe and that the chimpanzees hunted baboons more frequently after having been fed at the artificial feeding site. Other reactions to frequent exposure to humans might include shifts in daily activity patterns and changes in ranging behaviour. As the goal of conservation is to conserve natural behaviour of species, these dangers need to be avoided. Therefore, monitoring habituation is of paramount importance, both to ensure that habituation does not have an adverse effect on the animals to be conserved and to determine progress and identify potential problems at an early stage. Results of monitoring studies can be used to develop habituation guidelines and to make habituation comparable between sites.

1.4.1 Hypotheses

This study provides the first data on chimpanzees' reactions to tourists. The process of chimpanzee habituation was monitored at two sites in the Kibale Forest for two chimpanzee communities, the Ngogo and the Kanyancu community. Responses to visitor (tourist) groups of different sizes were monitored at Kanyancu only. The aim was to provide objective data on which ecotourism regulations for chimpanzees could be based.

The hypotheses were that the degree of habituation would increase over time and that the number of observers present would have an impact on the chimpanzees' reactions.

Intersite comparisons were made both within Kibale and with Lopé in Gabon (Tutin and Fernandez, 1991) in order to throw light on the question as to whether the habituation process of chimpanzees is also affected by habitat.

1.4.2 Wider applicability

Unfortunately, no quantitative data on bonobo responses to humans are available in the literature (but see Badrian & Badrian, 1984; Kano, 1983). As yet, bonobo habitats in the depths of Zaire are not easily accessible to tourists. With the expansion of the tourism market, however, it may be only a matter of time before tourists begin to arrive at bonobo sites in appreciable numbers. Bonobos are as much at risk from humans as chimpanzees for the afore-mentioned reasons; therefore they will need to be as carefully protected and managed as chimpanzees.

As these two species are so closely related and their behaviour is similar in many respects, guidelines for the habituation of chimpanzees may turn out to be a useful help for the habituation of bonobos, either for research or for tourism, until such a time when monitoring programmes for bonobos have been set up and guidelines been developed for this species. Once this has been achieved, it will be possible to compare the habituation process between the two species and to determine yet again the potential impact of habitat quality.

Chapter 2

Study area and methods

2.1 Study area

2.1.1 Kibale Forest National Park

Kibale Forest National Park was established as a Forest Reserve in 1932 and regazetted as a National Park in 1994. It is one of nine principal remaining forests in the Albertine Western Rift region of western Uganda (Fig. 2.1). Kibale is located southeast of Fort Portal, in the Administrative District of Kabarole (0°13' to 0°41'N and 30°19' to 30°32'E).

Kibale Forest National Park (KFNP) has an area of 560 km^2. 134 km^2 of the southern section of the NP overlaps a 360 km^2 game corridor (the Kibale Forest Corridor Game Reserve) giving a total research area of 786 km^2. The corridor links Kibale with the Queen Elizabeth NP and its contiguous protected areas. Kibale is bordered on the west and east by agricultural land and in the north and north-east by tea plantations. KFNP is located on undulating terrain on the main Uganda plateau. It is drained by the Mpanga and Dura rivers in a southerly direction towards Lake George (Wing & Buss, 1970;

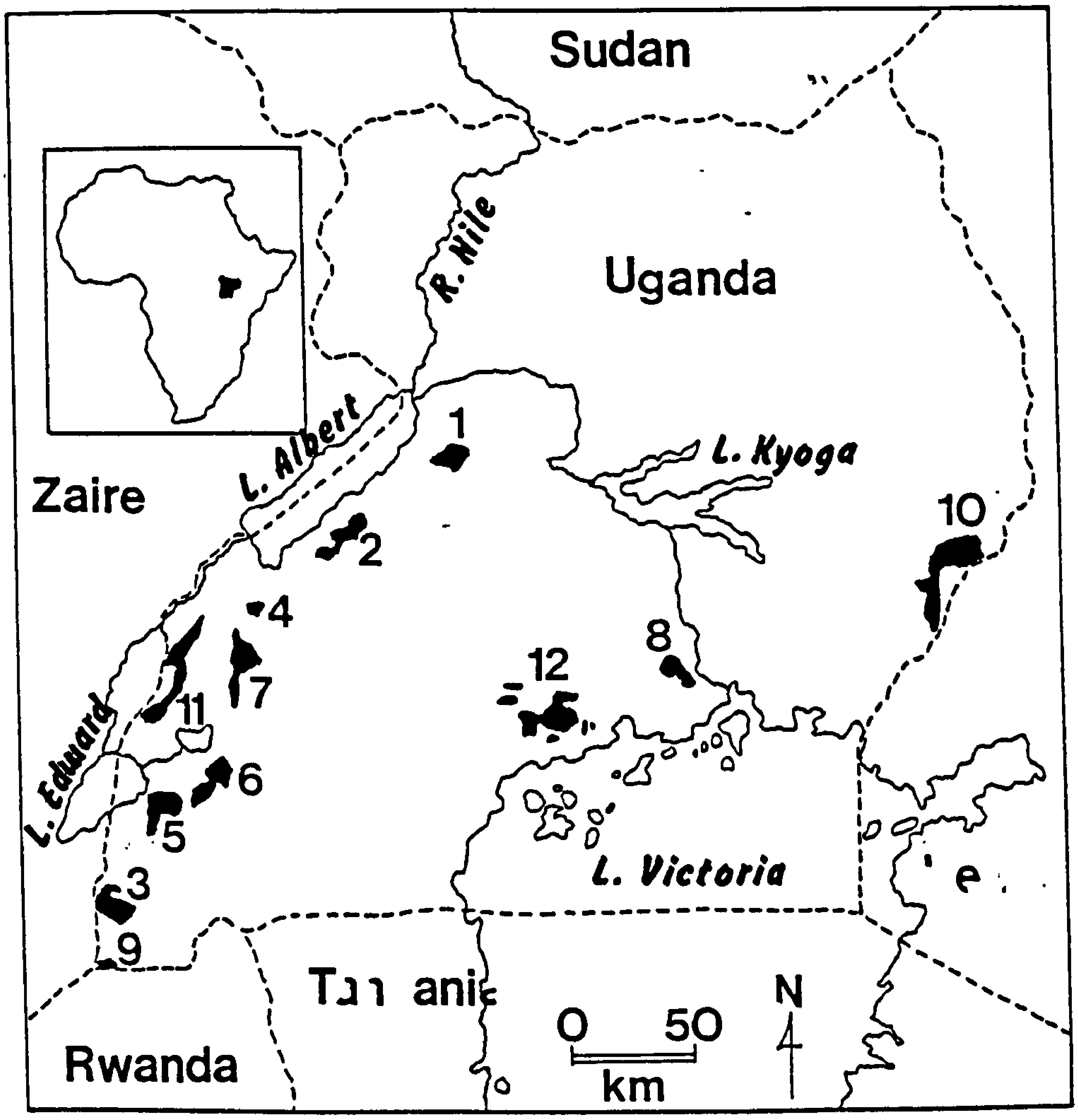

Figure 2.1: Principal remaining forests in Uganda.

Most remaining forests are scattered through the Albertine Rift region: these include Budongo (1), Bugoma (2), Bwindi/Impenetrable (3), Itwara (4), Kalinzu-Maramagambo (5), Kasyohn-Kitomi (6), Kibale (7), Mgahinga (9) and Ruwenzori (11). Two large forests remain n the Lakeshore region, Mabira (8) and West Mengo (12), and isolated forest remains on Mount Elgon (10).

Struhsaker, 1975). Its north-south extension is approximately 58 km with an altitudinal range from 1,590 m to 1,110 m. 83% of its area lie between 1,250 and 1,500 m, 12% are below 1,250 m and 5% above 1,500 m. The annual mean temperature ranges between 14-15°C minimum and 26-27°C maximum. Annual rainfall is between 1,100 and 1,600 mm (Howard, 1991). The region is characterized by four distinct annual seasons: two wet seasons (from March through May and from September through November) alternating with two dry seasons in between (Figure 2.2).

Between 60-70% of the National Park is occupied by various types of forest vegetation (Skorupa, 1988). In the north it can be classified as medium-altitude moist-evergreen forest, and at lower altitudes in the south as medium-altitude moist semi-deciduous forest (Langdale-Brown et al., 1964; Osmaston, 1959; Wing and Buss, 1970; for details see Kingston, 1967). Grassland, swamp vegetation, woodland thicket and colonizing forest occupy the remainder (Skorupa, 1988). The grassland communities resemble those found in savanna woodland with *Pennisetum purpureum*, *Imperata cylindrica* and *Cymbopogon afronardus* as dominating species. The grasslands occupy the hilly summits and were probably formed by past human settlement and disturbance. Presently, the grasslands are maintained by poachers' fires. These in effect prevent successful natural re-colonization by tree seedlings.

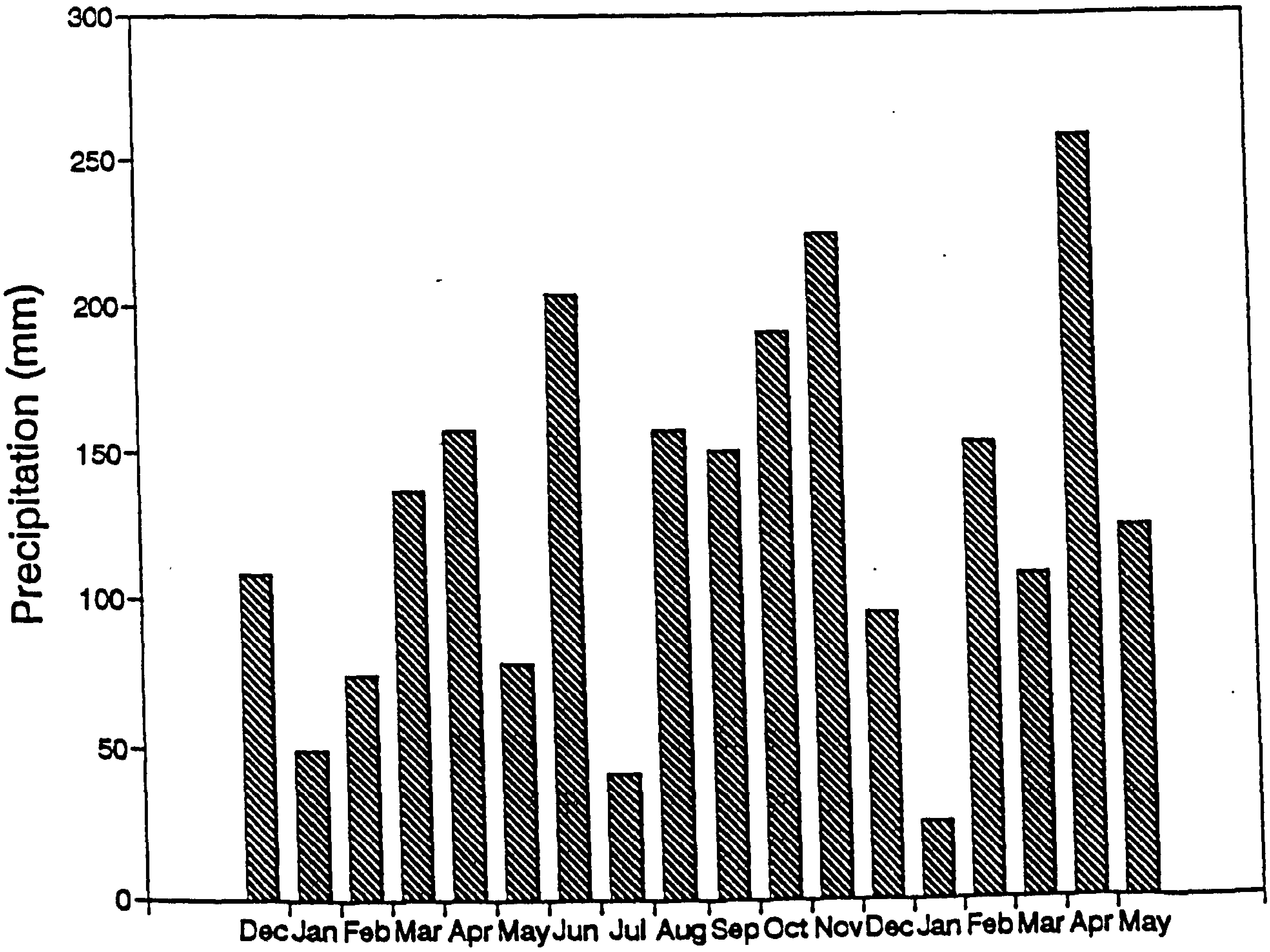

Figure 2.2: Precipitation at Ngogo.

After Ghiglieri 1984, p.19. Total precipitation 2336 mm.

The avian and mammalian fauna of Kibale National Park is diverse. It includes over 300 species of forest birds, 59 large mammals, 19 small rodents and an unknown number of bat species. The mammals range in size from the dwarf bushbaby (*Galago demidovi*) to the African savannah elephant (*Loxodonta a. africana*). In addition to the eastern chimpanzee *(Pan troglodytes schweinfurthi*), the primate list of Kibale includes eight other diurnal species: red colobus (*Colobus (badius) tephrosceles*), black and white colobus (*Colobus guereza*), redtail monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), L'Hoest's monkeys (*C. l'hoesti*), vervets (*C. aethiops*), gray-cheeked mangabeys (*Cercocebus albigena*) and olive baboons (*Papio anubis*) (Ghiglieri, 1984; Howard, 1991).

2.1.2 Study Sites

There are three working stations in the Kibale National Park: Kanyawara, Ngogo and Kanyancu (Figure 2.3).

Kanyawara

From 1970-1987, the Kanyawara Forest Station provided the headquarters for the New York Zoological Society's Kibale Forest Project. Facilities established at Kanyawara became the basis for the establishment of the Makerere University Biological Field Station (MUBFS) in 1987. Between 1970-94 Kanyawara was the study site for

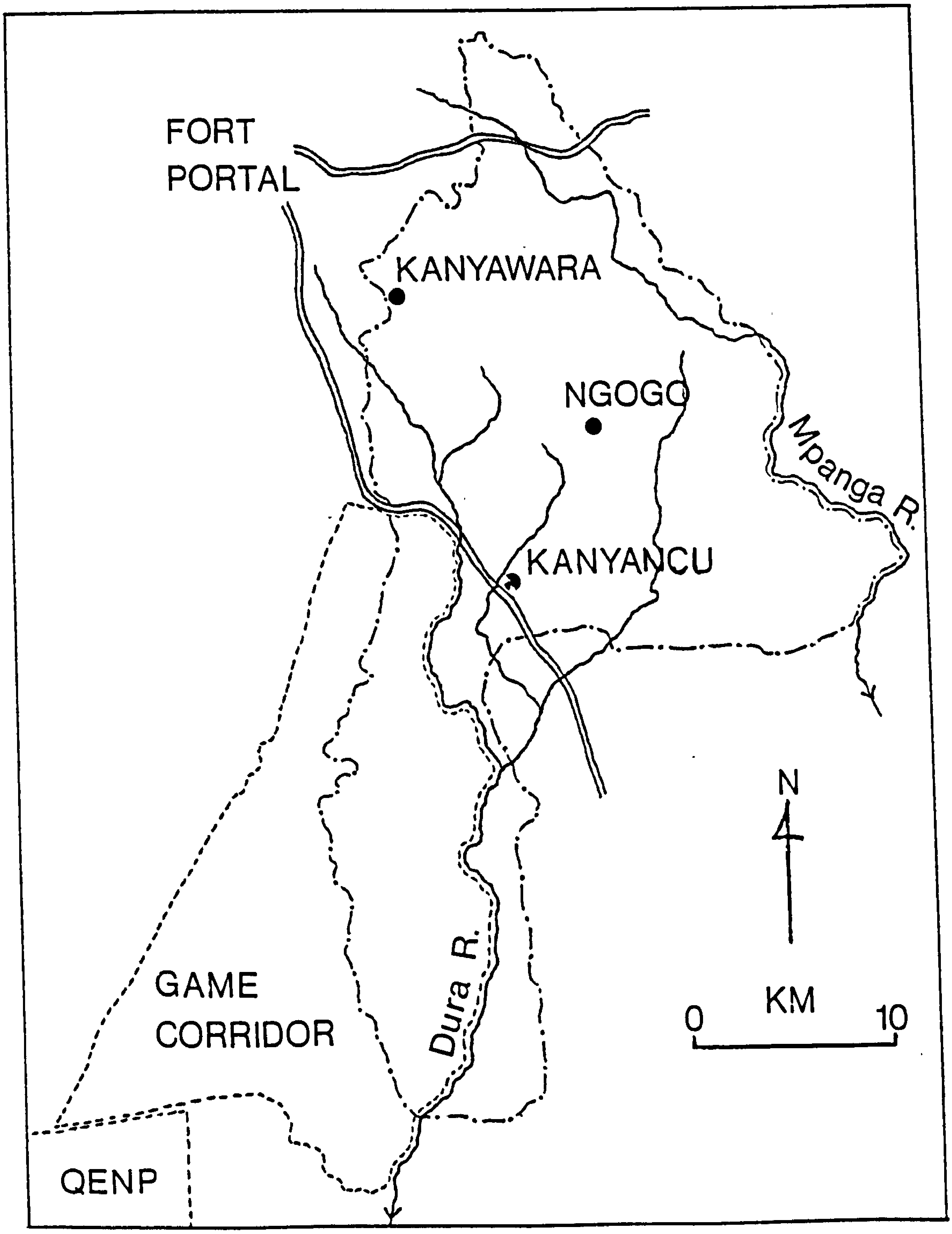

Figure 2.3: Kibale Forest National Park working stations.

The KFNP is connected by a deforested Game Corridor to the large savanna woodland areas of the Queen Elizabeth National Park.

over 50 research projects on various aspects of forest ecology and particularly primatology (for example Butynski, 1990; Skorupa, 1988; Struhsaker 1975). Chimpanzees have been studied at Kanyawara since 1983 (Wrangham et al., 1992).

The forest at Kanyawara was mostly logged (at felling intensities of 14-21 m^3/ha timber) during the late 1960s. Some felled areas have been heavily degraded subsequent to logging by a combination of arboricidal treatment of non-timber trees, windthrows and elephant damage. Large areas are dominated by dense herbaceous growth and non-woody vegetation, notably *Acanthus*. Some grasslands around Kanyawara were planted with exotic softwoods (*Pinus caribaea*, *Cupressus*, *Arucaria*) in the late 1960s. Valley bottoms are dominated by swampy vegetation with papyrus (Cyperus papyrus) in permanently waterlogged areas.

Unlogged high forest at Kanyawara persists only in the western section of a former forest research plot (RP 703), which has a total area of around 16 km^2. This forest is a mixture of deciduous and evergreen tree species dominated by *Chrysophyllum gorungosanum*, *Celtis africana*, *Markhamia platycalyx* and *Diospyros abyssinica*. Typical associates in low numbers are *Parinari excelsa*, *Strombosia scheffleri*, *Aningeria altissima*, *Mimusops bagshawei*, *Newtonia buchananii*, *Lovoa swynnertonii* and *Olea welwitschii*. Shade tolerant herbs and shrubs such as

Palisota schweinfurthii and *Pollia condensata* characterise the sparse undergrowth.

Ngogo

Ngogo (0°29' to 0°31'N; 30°24' to 30°26'E) is situated about 10 km southeast of Kanyawara on the eastern side of a former Nature Reserve (Ghiglieri, 1984). When Kibale Forest was gazetted as a Forest Reserve in 1932, Ngogo was set aside as a Nature Reserve. Felling operations stayed at a distance of approximately 8 km from Ngogo, so it can be said that the forest at Ngogo has not been disturbed since the 1930s (Ghiglieri, 1984).

Ngogo is about 150 m lower than Kanyawara and more sharply undulating, but both areas are similar in the relative areas described as valley bottom, hillside and hilltop (Butynski, 1990). It is divided by a system of trails running North-South and East-West at intervals of between 25 and 200 m (Figure 2.4). The main forest in the former Nature Reserve is dominated by *Olea welwitschii*, *Pterygota mildbraedii* and *Piptadeniastrum africanum*. *Lovoa swynnertonii*, *Diospyros abyssinica*, *Markhamia platycalyx*, *Celtis durandii*, *Celtis africana* and *Wurburgia ugandensis* are predominant in some areas. Swamp forest occurs in the west of the former Nature Reserve and is dominated by sedges such as papyrus (*Cyperus papyrus*) and other herbaceous forms with an occasional tree such as *Ficus dawei*, *Neobutonia macrocalyx*, or

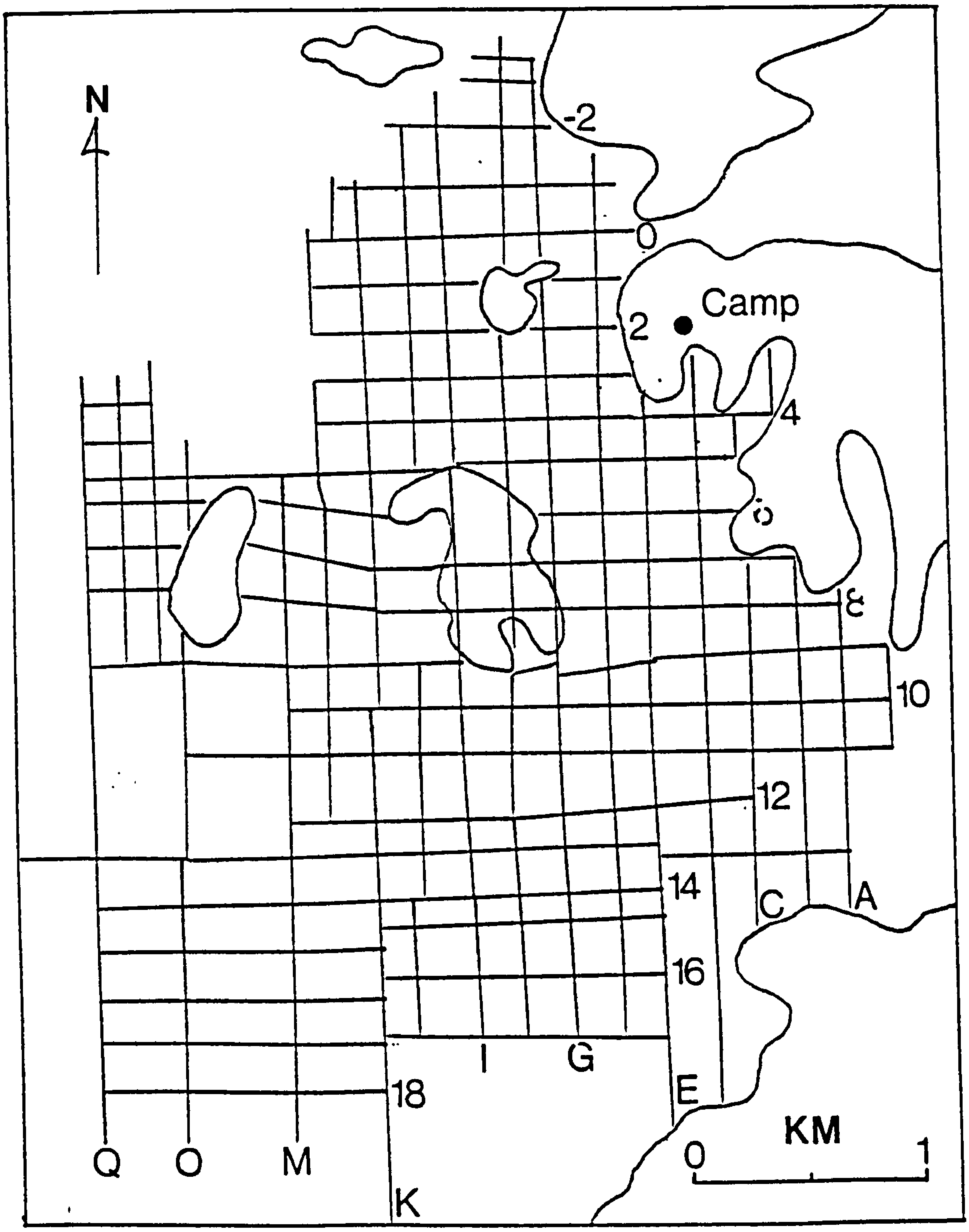

Figure 2.4: Outline of the trail system at Ngogo.

Principal trails only are shown (100x100m grid or larger intervals). Additional trails at smaller intervals are present in most of the grid system north of line 12. Irregular outlines illustrate the location of grasslands.

Symphonia globulifera in wide valley bottoms (Ghiglieri, 1984). The high forest to the north of Ngogo camp and in the area covered by the trail system resembles the high forest at Kanyawara in that it is dominated by *Chrysophyllum gorungosanum*, *Celtis africana* and *Markhamia platycalyx*. A feature that distinguishes Ngogo from Kanyawara is the presence of a large number of fig (*Ficus* sp.) trees, notably *Ficus mucuso* which does not occur at Kanyawara. Hill-tops are covered with grasslands (Butynski, 1990; Ghiglieri, 1984).

Ngogo was the major site for this study. Trails have been extended since Ghiglieri's times (85 km, Ghiglieri, 1984, p. 18) and now approximate 130 km. Chimpanzees were studied at Ngogo by Ghiglieri (1984) during 436 hours of contact from December 1976 to May 1978 and from March 1981 to May 1981.

Kanyancu

Kanyancu was established as an ecotourism development in 1991. It is situated approximately 12 km south of Ngogo. The tourist camp is located on the Kamwenge road from Fort Portal to Bigodi in the south-centre of the National Park.

Similarly to the other sites, the vegetation at Kanyancu forms a mosaic of high forest, swamp forest and grassland. In composition, the forest is more similar to the one at Ngogo, however there are several characteristics that distinguish the vegetation at Kanyancu from the other two sites in the Kibale Forest. Due to the proximity of the Kanyancu and the Dura rivers there is a higher proportion of swamp vegetation at Kanyancu. This varies from *Pandanus ugandaensis* swamp along the Dura River itself to large areas of palms (*Phoenix reclinata*) and sedges in low-lying seasonally flooding valley bottoms. High forest is restricted to hill slopes and is in places dominated by almost monotypic stands of *Piptadeniastrum africanum*, with high densities of large fig trees, especially *Ficus mucuso*.

Kanyancu was the site for the study on the impact of habituation and tourism on chimpanzees. The trail system approximates 52 km, extending on both sides of the road (Figure 2.5). Chimpanzees had not been studied previously at Kanyancu.

2.2 Observation Methods

2.2.1 The habituation process

Levels of habituation at the three KFNP sites

Following Tutin and Fernandez (1991) I defined habituation as the acceptance by wild animals of a human observer as a neutral element in their environment. At a number of study sites chimpanzees have been habituated with the help of provisioning (Goodall, 1986; Nishida,

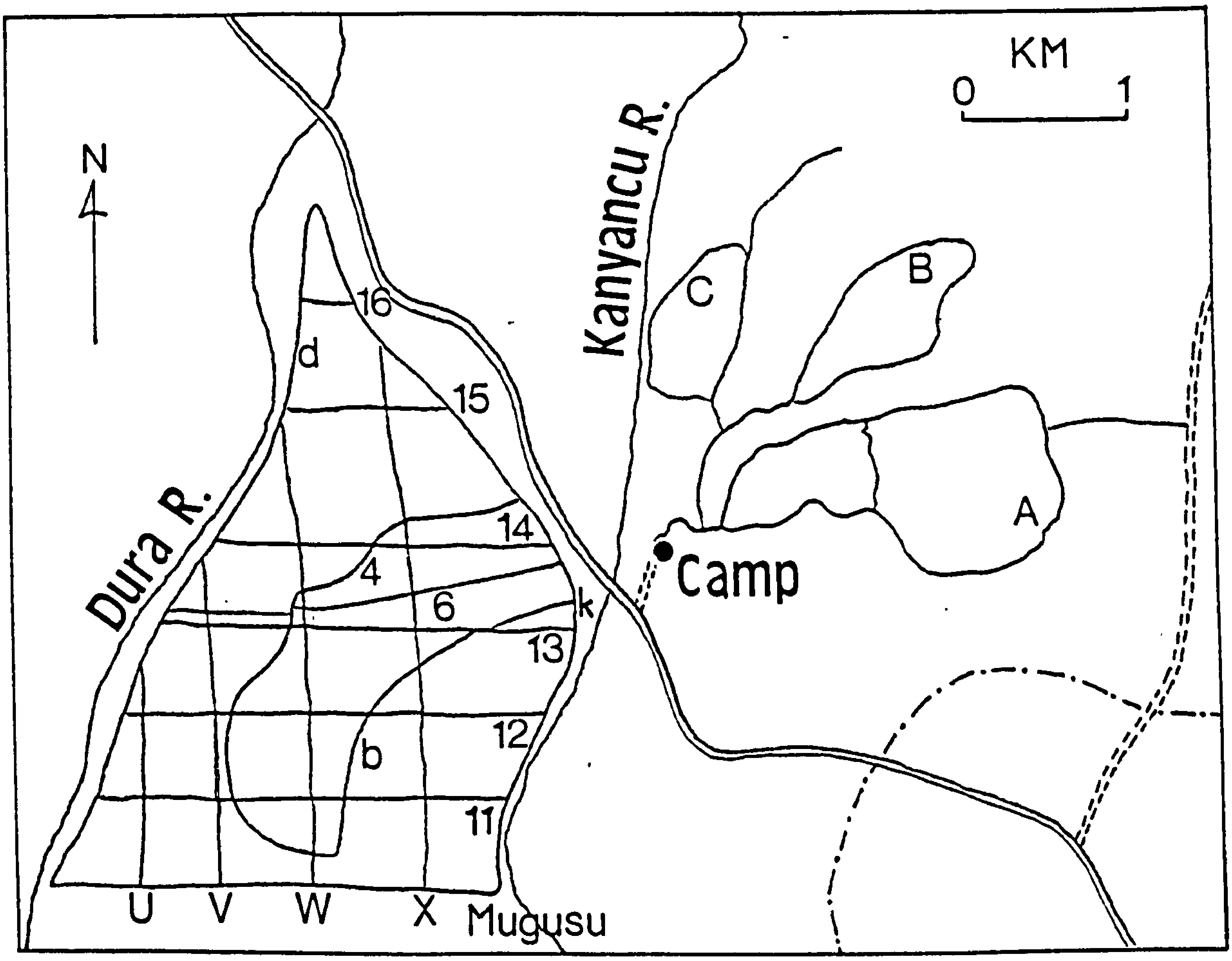

Figure 2.5: The trail system at Kanyancu.

Solid double line represents the Fort Portal to Bigodi road; dashed double line is the access track to Ngogo camp. Single dashed line is the border of the National Park.

1990). This was not the case in Kibale (Wrangham *et al.*, 1992): neither Ghiglieri at Ngogo in 1976 nor Isabirye-Basuta at Kanyawara in 1983 nor MUBFS personnel at Kanyancu in 1991 used incentives to attract chimpanzees to a certain area. Without provisioning, the habituation process has proved to be prolonged.

Whereas work on the chimpanzees at Kanyawara has been more or less continuous since 1983 (Wrangham *et al.*, 1992), Ghiglieri's study occurred only between December 1976 and May 1981. Work was resumed at Ngogo in 1989, when Ugandan field assistants started observing chimpanzees on a fairly regular basis (Wrangham, pers. comm.). When the current study started in January 1992, chimpanzees were still rather unhabituated. Hence considerable time was spent trying to locate chimpanzees. Table 2.1 records time spent in the forest compared to the time spent with chimpanzees. A contact is defined as an encounter with a party, temporally separated from other contacts in time by at least 30 min of silence (no vocalisations, no movements) or spatially separated by at least 5 minutes' walk. A party is defined as all individuals within 50 m (Wrangham *et al.*, 1992), not counting dependent offspring. As the vegetation was often dense and visibility therefore restricted, it was not always possible to be rigorous about distances.

Following initial surveys during 1990, MUBFS personnel began working on the habituation of chimpanzees

Table 2.1: Monthly summaries of observations at Ngogo

Month	Time in the forest (hours)	# contacts	Duration of all contacts (hours)	Mean duration of contact (hours)
Jan 92	179.45	11	42.47	3.86
Feb 92	153.32	15	42.15	2.81
Mar 92	155.38	17	40.12	2.36
Apr 92*	202.90	33	65.22	1.96
May 92*	380.67	40	125.38	3.51
Jun 92*	164.20	15	34.90	2.18
Jul 92*	276.82	46	89.07	1.94
Aug 92*	99.35	15	19.08	1.73
Sep 92*	122.13	18	30.62	1.70
Oct 92	91.78	6	5.00	0.83
Nov 92*	189.88	26	78.77	3.03
Dec 92*	146.73	20	63.25	3.16
Jan 93*	92.50	15	31.45	2.10
Feb 93*	225.33	24	92.50	3.85
Mar 93*	381.38	35	121.00	3.46
Apr 93*	191.85	22	96.17	4.37
May 93*	80.40	15	38.92	2.59
Jun 93*	+	2	0.53	+

* Data collected by the author plus field assistants.
+ Data not available.

at Kanyancu in July 1991. Tourism was opened in January 1992. The Kanyancu part of this study started in February 1992 and was completed in June 1993.

Documenting the habituation process

The process of habituation was to be documented at both Ngogo and Kanyancu. A data sheet was filled in each time chimpanzees were located. The following data were taken on the 'first detector', that is the first chimpanzee to detect the observer:

A. Location on map (grid reference provided by the labelled trail system)
B. Density of vegetation (for definitions see Table 2.2)
C. Location method (for definitions see Table 2.3)
D. Number of observers present
E. Number of animals in the party
F. Age/sex class (*male/female adult*, *subadult*, *juvenile*, *infant* for definitions see Table 2.4)
G. Reaction (*flight*, *charge*, *approach and wait for another*, *stealthy retreat*, *loud vocalisation*, *soft vocalisation*, *hide*, *curiosity*, *ignore*; for definitions see Table 2.5)
H. Distance from the observer at detection
I. Distance to the next chimp at detection
J. Height above ground at detection (in 5 m intervals)
K. Activity before and after the contact (for definitions see Table 2.6)
L. Communicative impact (whether the first detector

Table 2.2: Definitions: Density of vegetation

Dense Forest: Forest of short trees or tall trees with enough undergrowth to make walking difficult.
Open Forest: Forest of tall trees with little undergrowth so that walking is relatively easy.
Clearing: Patch without tall trees, caused by treefall; depending on age with a more or less thick stand of short trees and undergrowth.
Grassland: Discernible patch of elephant grass (*Penisetum purpureum*) in a forest of tall trees; may contain thickets, short trees and a few tall trees. Virtually impenetrable.
Swamp: Boggy area surrounding creeks and rivers.

Table 2.3: Definitions: Location method

Vocalisations: After hearing chimpanzee calls, a compass bearing was taken and the observer moved in the direction of the vocalisations. New bearings were taken when more calls were heard and if they seemed to have changed direction. This process was repeated till the source of the vocalisations was reached. If calls from more than one party could be heard, the observer tried to reach the closest one. Pant-hoots (Goodall, 1986) can carry a considerable distance.

Tree vigil: During the search for chimpanzees the observer would come across fruiting trees known to attract chimpanzees, especially big Ficus mucuso. The observer would then place herself under the tree or with view of its canopy to wait for chimpanzees to visit the tree. If the tree proved to attract many chimpanzees, a tree vigil could last over several days from dawn to dusk until the fruit crop was exhausted.

Feeding noises: Same procedure as with vocalisations, except that the observer moves in the direction of feeding noises, i.e. the tearing of branches, stripping of leaves off branches or munching noises. These sounds would not carry very far, though, and the observer would already have to be within approximately 50 m to be able to hear them.

Faeces: As chimpanzee faeces are readily distinguishable from baboon or other faeces, the observer would search an area thoroughly after having found fresh chimpanzee faeces.

Nests: Chimpanzees usually build nests in which they spend the night. If the observer succeeds in following the chimpanzees until they build their night nests, the probability that they will spend the night at that location is high, and the observer will be able to find them at the same place in the morning. However, the Ngogo chimpanzees were so poorly habituated that the author succeeded in "nesting" them only 5 times in 18 months.

Chance: Neither chimpanzees nor the observer were aware of each other until visual contact was established.

Table 2.4: Definitions of life stages

Infants: 0-4 years; black body colour with white tail tuft; pink face, hands and feet; carried by mother, no younger siblings. Small body size (<10 kg).

Juveniles: 4-9 years; black or brown body colour; white tail tuft still present but reduced; face, hands and feet pinkish-brown blotchy. Bigger than infants (between 10 and 20 kgs). Often have younger siblings. May still travel with mother but do not ride on her any more. May travel with other individuals or on their own.

Subadults: Males: 9 to 15 years. Females: 9 to 13 or 14 years. Black or brown body colour; no tail tuft; Face, hands and feet brown, black, possibly blotchy. Slim body build.

Adults: Males: more than 15 years of age; brown or black body colour; muzzle grey or white. Lower back may turn first brown then grey and white. Face, hands and feet brown, black, possibly blotchy. Testicles very large. Massive body build. Females: more than 14 years of age; brown or black body colour; muzzle grey or white. Lower back may turn first brown then grey and white. Face, hands and feet brown, black, possibly blotchy. Solid body build but not as massive as adult males. Very large perineal swellings during oestrus.[1] Often accompanied by dependent offspring.

Note: Adapted from Goodall (1986) and Ghiglieri (1984), with emphasis on physical characteristics.

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[1] The term "oestrus" was originally used as a scientific synonym for "heat", a behavioural term (Heape, 1900, as discussed in Rowell, 1972). Eventually, this term came to include all the physiological changes relating to ovulation, although research showed that the timing of heat relative to ovulation could vary in some species (e.g. Everett, 1961). In chimpanzees, heat is characterised by a large perineal swelling, and throughout the text the terms "in oestrus" and "oestrous" are used to describe those females who possess such a swelling (whether it is fully or only partly inflated at the time) and the term "anoestrous" is used to describe females without such swelling. The usage of these terms may be considered arguable as higher primates have a menstrual rather than an oestrous cycle (Rowell, 1972).

Table 2.5: Definitions: Reactions to the observer (adopted from Tutin and Fernandez, 1991)

Flight: Rapid jumping or sliding out of a tree or running at speed along the ground causing much noise.

Charge: Rapid noisy running approach, either direct or oblique, towards the observer.

Approach and wait for another: After a glance or stare at the observer, chimp moves directly to another chimp and makes physical contact, or turns towards another chimp and waits for it to approach before both move away from the observer.

Stealthy retreat: Slow, cautious and almost silent descent from tree or avoidance on the ground.

Loud vocalisation: Wraaghs, waas or screams*.

Soft vocalisation: Hoo or whimper.

Hide: Either moving behind vegetation (sometimes hiding the whole body, but often only the face) or pulling vegetation in front of body or face to form a screen.

Curiosity: Includes two or more of the following elements: staring, head swaying, moving to obtain a clearer view of the observer, chest beating, slapping a tree trunk and clapping hands, or a hand and foot.

Ignore: No discernible reaction shown; after glancing or staring at the observer, the individual continues with previous activity.

* Terminology after Goodall (1986).

Table 2.6: Definitions: Activity before and after contact

Feeding plants: Foraging, processing, ingesting or chewing plant parts (leaves, fruit, bark, flowers, wood, seeds), including the chewing of fig wadges, which could go on for a considerable length of time after the figs were put into the animal's mouth.
Feeding meat: Processing, ingesting or chewing meat.
Grooming: Working through another chimpanzee's fur either with hands or mouth or both.
Playing: Play-chase, play-wrestle, tickling.
Copulating: Mounting or being mounted and thrusting, irrespective of whether intromission is achieved or not.
Travelling: Moving on the ground at a more than leisurely pace.
Consorting: Only refers to the male partner in parties of one male and an estrous female.

Table 2.7: Definitions: Communicative impact (adopted from Tutin and Fernandez, 1991)

All: First detector alarms all others in the group.
None: First detector does not alarm anybody else in the group.
Selective: First detector selectively alarms a few other animals of the group.

alarms all, some or none of the other chimps present; for definitions see Table 2.7).

If there were other detectors, i.e. the first detector did not alarm the rest of the group but other animals detected the observer independently of the first detector, E to L were collected for each subsequent detector.

If the detectors reacted while vocalising at the same time, both the reaction and the vocalisation were scored as reaction. However, as the reaction categories were ordered along a scale of increasing degree of habituation, only the less habituated reaction of the two was used in the analysis.

X^2 tests were run to determine possible interactions between the chimpanzees' reactions and independent variables. Independent variables were (1) age/sex class of the detector, (2) distance to the observer at detection, (3) distance to the next chimp at detection, (4) activity before contact, (5) height above ground, (6) number of observers, (7) party size, (8) density of vegetation and (9) location method. For this analysis, categories of variables had to be lumped to avoid empty cells. Expected values in all X^2 tests were calculated from marginal totals.

2.2.2 Chimpanzee follows

Once chimpanzees were located and they were habituated enough not to flee immediately, the observer ascertained the size and composition of the party (definition see above) as far as possible. The observer then chose a focal animal (Altmann, 1974). As females were encountered less frequently than males, females were preferentially chosen as the focal animal if the party contained both sexes. Preferential focal animals were adults; other age classes became focal animals only if no adults were present. The same focal animal was followed for as long as possible.

All activities of the focal animal were recorded continuously. In addition, five-minute instantaneous samples were taken on the focal animal and on its nearest neighbour, recording:

A. Activity (for definitions see Table 2.8)
B. Posture (sitting; lying on back, on front, on the left side, on the right side; standing on all four legs, standing on two legs; hanging by one arm, hanging by both arms, brachiating; sitting but leaning against a support; crouching; in nest)
C. Height above ground
D. Distance of the infant/juvenile (in the case of females with dependent offspring)
E. Identity of the interactant (age/sex class and, if

Table 2.8: Definition of activities during focal animal samples

Feeding: Includes
- feeding plants: foraging, processing, ingesting or chewing plant parts (leaves, fruit, bark, flowers, wood, seeds), including the chewing of fig wadges, which could go on for a considerable length of time after the figs were ingested;
- feeding meat: processing, ingesting or chewing meat;
- spitting juice.

Locomoting: Includes
- moving through the tree or on the ground unless it has the function to procure food;
- traveling on the ground;
- traveling through trees (if the animal does not stop on its way for more than 3 minutes);
- moving from a tree to the ground;
- sitting up (from a lying to a sitting position);
- getting up (from a sitting to a standing position);
- running (on the ground);
- moving out of nest.

Resting: Includes
- sitting or lying with eyes closed or open without doing anything;
- sitting down;
- lying down;
- moving into nest.

Autogrooming: Scratching or grooming self (working through own fur with hands or mouth or both).

Grooming: Includes
- grooming others (working through another chimpanzee's fur with hands or mouth or both);
- reciprocal grooming;
- handclasping: stretching another animal's arm with one's own hand in order to groom it.

Vocalising: Uttering sounds regardless of volume or social context.

Defecating: Producing faeces and/or urine.

Socially positive behaviour: Includes
- playing with another animal (play-chase, play-wrestle, tickle);
- reaching out to another animal with hands or feet without touching it;
- deliberately touching another animal (after having reached out to it);
- following another animal (not chasing it);
- sitting down in front of another animal (within 1 m);
- presenting to another animal (turning the rump toward another animal; Goodall, 1986);
- approaching another animal to within 3 m;
- begging (Goodall, 1968);
- hugging another animal (from the front or the back);

Table 2.8: continued

Socially negative behaviour: Includes
- displaying towards another animal: moving towards another animal in a bipedal swagger (Goodall, 1986);
- charging another animal (running upright toward another animal; Goodall, 1986);
- shaking branches towards another animal;
- fear-grinning towards another animal;
- running away from another animal;
- displacing another animal: sitting down or moving within 3 m of another animal who leaves within 30 seconds;
- chasing another animal (running after it without actually reaching it);
- leaving another animal.

Observer-related behaviour: Includes
- displaying towards the observer;
- hiding from the observer;
- looking at the observer.

Sexual behaviour: Includes
- copulating (mounting or being mounted and thrusting, irrespective of whether intromission is achieved or not);
- G-G rubbing (two animals rub their genital regions against each other);
- having an erection;
- pulling at erect penis;
- presenting (turning the rump toward another animal: Goodall, 1986);
- waving an erect penis at another animal.

Manipulative behaviour: Includes
- shredding leaves (not in a feeding context);
- plucking leaves and then dropping them;
- plucking a leaf, then nibbling at it before dropping it;
- smelling and licking leaves;
- leaf grooming (going through the motions of grooming a leaf; Goodall, 1986);
- wiping swelling with leaves and licking them off;
- touching swelling (or rear) shortly with fingers;
- breaking twigs;
- building nest.

Nursing behaviour: Feeding infant.

Other behaviour: Includes
- sniffing hands or fingers;
- licking hands or fingers;
- yawning;
- rain-dancing.

known, individual identity)

F. Food part eaten and species, if known; specimens collected if unknown)

G. Identity of the nearest neighbour (age/sex class and, if known, individual identity)

H. Distance to the nearest neighbour

I. Party size according to Ghiglieri (number of animals that arrive at or leave a food tree within three minutes; Ghiglieri, 1984)

J. Party size according to Wrangham (all individuals within 50 m (Wrangham *et al.*, 1992), not counting dependent offspring)

K. Diameter at breast height (DBH) of the food tree (estimated)

L. Phenological score of the plant part eaten (on a percentage scale: how much is still left of the original crop)

The data sheet combined both focal animal and instantaneous sampling, including information about the time of the contact, its duration, its location, and the identity of the focal animal.

Only follows that lasted at least 30 minutes were included in the analysis.

At Kanyancu follows started in March 1993, when the chimpanzees were sufficiently habituated not to flee immediately. The aim here was to determine whether the chimpanzees' behaviour changed when more observers were present.

2.3 Identification of chimpanzees

In order to assess the impact of habituation and to obtain useful data on social behaviour, it was important that individual chimpanzees be recognized. During August-September 1991 S. van der Meeren observed the chimpanzees at Ngogo and started an "Identity Kit". With the help of this ID Kit I was able to recognize some individuals from the start of this study, but the ID Kit had to be extended considerably.

When a focal animal was chosen, the observer could usually obtain a good description of it. An ID Sheet was filled in for an animal only if the animal could be described exhaustively or if it had a so-called "killing feature" (a term coined by R. Wrangham). This refers to a feature that makes an individual recognizable beyond doubt, such as a missing limb, a torn ear or a prominent scar. The ID Kit was divided in two sections: the "permanent" list contained descriptions of animals that the author would recognize either on the basis of killing features or on the basis of exhaustive descriptions. The "candidate" list contained descriptions of animals without killing features.

2.4 Census Techniques

2.4.1 Linear transect surveys

Information on chimpanzee population density was gathered as part of general mammal surveys carried out once a month. The line transect survey technique is described in Whitesides *et al.* (1988). The survey route was 4 km in length. Data sheets were filled in, giving details on

A. Time of sighting
B. Location
C. Species of mammal sighted
D. Observer-animal distance
E. Path-animal distance
F. Height of the animal above ground
G. Distance from the observer to the hypothetical centre of the sighted species' group
H. Distance from the path to the hypothetical centre of the sighted species' group (perpendicular distance)
I. Height above ground of the hypothetical centre of the sighted species' group
K. Mode of detection (Sighting, Vocalisations)
L. Number of animals in the group

2.4.2 Chimpanzee nest census

In addition to the above, a nest census was carried out, following a method developed by Plumptre & Reynolds (in prep.). It was assumed that each chimpanzee constructed one nest each night. Day nests were built in such a slip-shod manner that they were easily recognisable as such. They were not included in the analysis. Counts were repeated three times in order to exclude old nests from the analysis. On the first count, all nests were marked, thus it could be assumed on the second count that any unmarked nests had been constructed in the meantime. The census was carried out at Ngogo in the last week of April, in the last week of May and in the penultimate week of June 1993. At Kanyancu censuses were carried out in the first week of May, the first week of June and the last week of June 1993.

Census routes were 40 km in length. The Ngogo study site was divided into a north, south, east and west section and in each section 10 km of trail were selected as a census route. At Kanyancu, all existing trails were censused. Data sheets were filled in, giving details on

A. Location
B. Total number of nests within sight
C. Height above ground
D. Perpendicular distance to mid-path (used in density estimation)

E. Age category of the nest (fresh, recent, intermediate, old, very old; for definitions see Table 2.9)

F. Species of tree used

G. Degree of vegetation cover (complete, intermediate, none; for definitions see Table 2.10)

H. Number of trees used for one nest

I. Day or night nest

2.5 Data Analysis

Statistical procedures were taken from Siegel and Castellan (1988). Paradox^R, version 4.5, served as spreadsheet system, and the statistical package SPSS^R/PC, version 4.0, was used for the analysis wherever possible. Graphs were generated with Quattro-Pro^R, version 5.0.

The census data were analysed using the computer package "DISTANCE" (Buckland *et al.*, 1993). This uses standard line transect techniques to model a decline in observations with increasing distance from the transect. The nest count data were analyzed using the Hazard Rate model, which has been shown to provide the best fit to line transect data of this type by a number of studies (see Plumptre *et al.*, 1994).

All statistical tests are two-tailed unless stated otherwise.

Table 2.9: Definitions of nest age categories

Fresh: Leaves in the building material have not yet wilted.
Recent: Leaves are wilted but not yet brown.
Intermediate: Nest contains some green and some brown leaves.
Old: Nest contains only brown material.
Very old: Nest contains only brown material and has started to fall apart.

Table 2.10: Definitions of degree of vegetation cover

Complete: No sky was visible from underneath the nest.
Intermediate: Some sky was visible from underneath the nest.
None: Unhindered view of the sky from underneath the nest.

Chapter 3

Size and structure of the Ngogo community

3.1 Introduction

Common chimpanzees occur in a variety of habitats, from savanna and dry woodland to medium-altitude tropical forest and low-altitude tropical rain forest. Most data on chimpanzees come from Gombe and Mahale in Tanzania: the habitat at both study sites is wooded savanna (Goodall, 1986; Nishida, 1990). However, studies in other habitats have already indicated considerable variation between populations in community size and structure and in party size and composition (for example, Boesch, 1991; Reynolds & Reynolds, 1965; Sabater-Pi, 1979; Sugiyama, 1981; Tutin *et al*, 1983).

Studies of bonobos *(Pan paniscus)* seem to indicate that this other chimpanzee species is consistently different from common chimpanzees in their grouping patterns and socio-sexual behaviour (for example, Badrian & Badrian, 1984; Kano, 1983, 1987; White, 1988). It is suggested that bonobos represent one extreme end of the scale of variation exhibited by common chimpanzees.

Studies on two communities of common chimpanzees in the medium-altitude tropical forest of Kibale National Park yielded contradictory results concerning population structure: Ghiglieri (1984) observed a mean party size of 2.6, whereas Wrangham recorded 5.0 ± 3.5 (Wrangham *et al.*, 1992). In addition, Ghiglieri's (1984) data suggested that the the degree of female/female association was not different from the degree of male/male affiliation and that females associated with each other more than they associated with males. In contrast, Wrangham *et al.* (1992) found that relationships between sexes at Ngogo were much the same as at Kanyawara and in other chimpanzee communities with females primarily associating with males and a stronger association between males than was found between females. Wrangham *et al.* (1992) suggest that these differences are probably due to differences in methods and definitions. Ghiglieri located chimpanzees mainly through tree vigils (definition see Table 2.3) and defined a party as the number of chimpanzees entering or leaving a feeding tree within three minutes. In contrast, Wrangham *et al.* (1992) used all methods to locate chimpanzees and defined parties as all individual chimpanzees within 50 m. In their study, they indeed find that parties located in tree vigils were significantly smaller than parties located by following vocalisations.

This study employed all methods of locating chimpanzees and both definitions of "party" to determine whether the difference in results between Ghiglieri's (1984) and Wrangham *et al.*'s (1992) study was a real one. It also provides new data on party size and composition for a community of common forest chimpanzees to determine the position of the Kibale chimpanzees on the scale of variance exhibited by common chimpanzees over their various habitats in relation to the position of the bonobos on this scale.

Party composition was determined before a focal animal was chosen and subsequently recorded every five minutes. The composition of parties was monitored whenever it was possible without losing the focal animal and whenever visibility allowed. Only those individuals whose presence could be verified regularly were considered. Therefore the size of large parties was probably underestimated.

Although the Ngogo community had been observed (intermittently from 1976 to 1981) by Ghiglieri (1984) and by Ugandan research assistants from 1989, the chimpanzees' degree of habituation was not very good at the beginning of this study in 1992.

Details of the size and structure of the community emerged slowly over the duration of this study.

3.2 Size and composition of the Ngogo community

Table 3.1 gives an overview of the various age/sex classes. The ID kit was divided into a permanent and a candidate list. The permanent list contains only individuals distinguishable by unique features and their offspring. The candidate list contains individuals from whom a complete description could not be attained or who had no unique features and were therefore not recognizable beyond doubt. From the permanent list it can be concluded that the size of the Ngogo community is no less than 63 animals.

However, as there were at least as many animals again on the candidate list, the Ngogo community is estimated to number more than 100 individuals. This could be confirmed in two ways. First, a cumulative abundance curve of newly-sighted individuals resulted in an estimated number of individuals of over 100 (Figure 3.1). Second, when the number of sightings of identified individuals was plotted against the frequency of sightings, a total number of 129 individuals was estimated (Figure 3.2). It can therefore be concluded that the Ngogo community numbers at least 100, but most likely around 120-130 individuals.

From the composition of the permanent list (Table 3.1), the socioeconomic sex ratio for the Ngogo community is 1.5 (adult males/adult females) and 2.1 respectively

Table 3.1: Representation of various age/sex classes in the Ngogo community.

Age/sex class	Permanent list	Candidate list	Total
Adult males	22	16	38
Subadult males	12	6	18
Juvenile males[a]	2	9	11
Total	36	31	67
Adult females	15	21	36
Subadult females	1	1	2
Juvenile females[a]	1	1	2
Total	17	23	40
Unsexed dependent offspring	10	23	33
Overall total	63	77	140

Note: For definitions of age/sex class see Table 2.4.
[a]Travelling without an adult female.

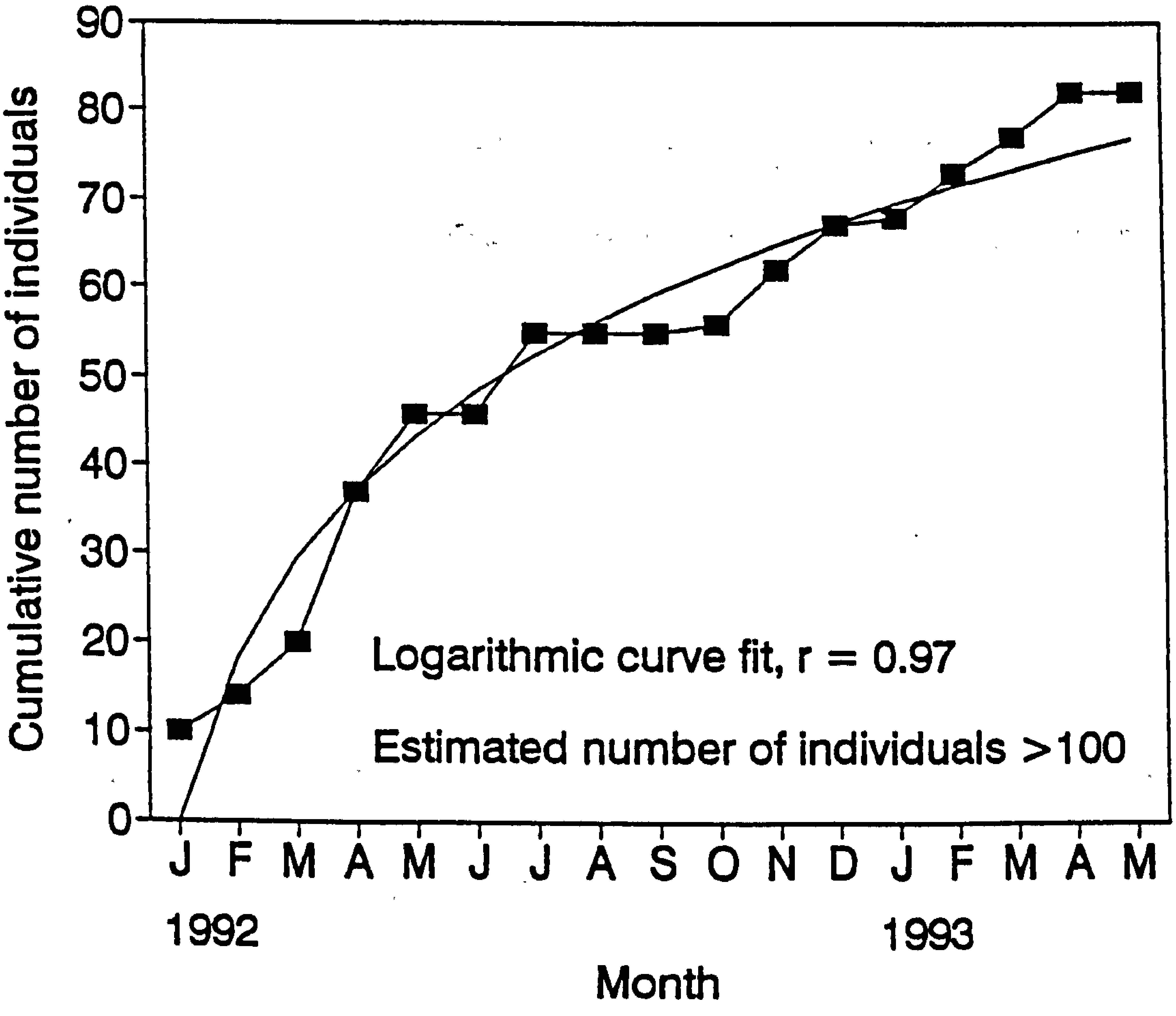


Figure 3.1: Cumulative abundance curve of newly sighted individual chimpanzees at Ngogo.

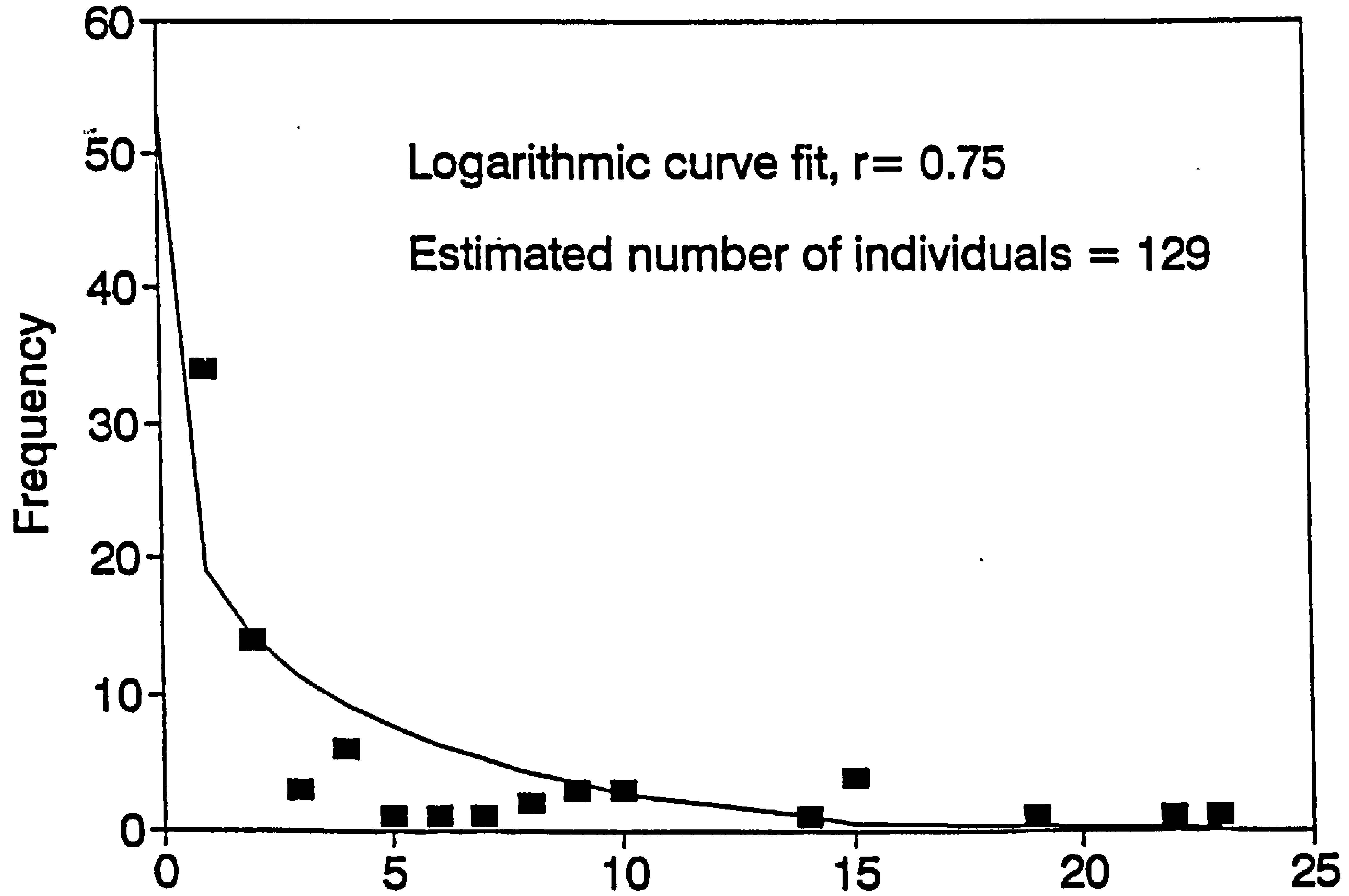


Figure 3.2: Frequency of sightings of identified individual chimpanzees at Ngogo.

(all males/all females excluding dependent offspring). The ratio adults/all others is 1.4.

Table 3.2 gives a break-up of the 36 adult females of the community. Two thirds travelled with an infant or a juvenile or both.

3.3 Party size and composition

3.3.1 Mean party size

When Wrangham *et al.*'s (1992) definition is employed and all location methods used are considered, mean party size at Ngogo was 3.6 ± 0.07 (range 1-17; mode:2; median:2; N=2354) when calculation was based on 15-minute points. When calculation was based on party size on first contact with the observer, mean party size was 4.3 ± 3.7 when dependent offspring were included (range 1-17; mode:2; median:3; N=135) and 3.9 ± 3.4 when dependent offspring were excluded (range: 1-16; mode:1; median: 3; N=152). The result of this study at Kanyancu was a mean party size of 6.0 ± 5.1 (range 1-31; mode:3; median:4; N=437 contacts; calculation based on party size on first contact with observer). The value of 3.6 for Ngogo, which most closely matches Wrangham *et al.*'s (1992) methodology, is significantly different to the value of 6.0 for Kanyancu (t-test for independent samples, $p<0.001$).

Table 3.2: Number of adult females with and without offspring at Ngogo.

	Permanent list	Candidate list	Total
Females without offspring	7	5	12
Females with infants	5	8	13
Females with both an infant and a juvenile	2	7	9
Females with juveniles	1	1	2
Total	15	21	36

Mean party size was greater when chimpanzees were located by following their vocalisations than when they were found through tree vigils (Table 3.3). This difference was significant both at Ngogo and at Kanyancu (t-test for independent samples, Ngogo: $p<0.05$; Kanyancu: $p<0.001$). Hence, these findings corroborate those of Wrangham *et al.* (1992).

When Ghiglieri's definition of "party" was employed, the mean party size at Ngogo was 1.4 (median:1; mode: 1; range: 1-9; N=249 occurrences of animals leaving or entering feeding trees). This is significantly smaller than the mean provided by the definition used by Wrangham *et al.* (1992) (t-test for paired samples, $p<0.001$).

3.3.2 Monthly party size

Tables 3.4 and 3.5 give monthly frequencies of party sizes at Ngogo, derived from counts on first contact with party, while Figure 3.3 gives monthly means of party size from counts at 15-minute intervals. When the former method is employed, monthly means range from 1.2 to 7.5 (N=135; dependent offspring included in count) or from 1.2 to 6.3 (N=152; dependent offspring excluded). When party size is determined at 15-minute intervals, monthly mean party size (dependent offspring excluded) ranges from 1.7 to 5.7 with an overall mean party size of 3.6

Table 3.3: Mean party size at Ngogo and Kanyancu in relation to location method.

Ngogo			Kanyancu			Kanyawara		
All	Vocalizations	Tree vigils	All	Vocalizations	Tree vigils	All	Vocalizations	Tree vigils
4.3	4.9	3.9	6.0	7.8	5.2	6.0[1]	5.1	2.4
N=294	N=136	N=124	N=437	N=146	N=236	N=4142[2]	N=31	N=64

Note: 'Vocalisations' refers to chimpanzees located through following vocalisations; 'Tree vigils' refers to chimpanzees located through tree vigils; for definitions see Table 2.3. N: number of contacts. Data for Kanyawara from Wrangham *et al.* (1992).

[1] Calculated from Wrangham *et al.* (1992) p.85;

[2] N=number of 15-minute points.

Table 3.4: Monthly distribution of party sizes at Ngogo (dependent offspring included in count)[1].

Party	1992												1993						
size	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	All	%
1[2]	0	1	1	6	0	0	2	4	1	0	2	2	0	1	4	2	3	29	21.5
2	0	1	3	0	5	0	3	1	2	0	1	2	2	3	4	2	1	30	22.2
3	0	0	0	1	0	0	2	0	2	0	2	2	1	3	2	1	1	17	12.6
4	1	1	0	0	2	0	2	0	2	0	2	1	0	0	2	0	1	14	10.4
5	2	0	1	0	0	0	2	0	0	0	0	1	0	0	1	2	0	9	6.7
6	0	1	0	1	1	1	2	0	0	1	0	0	1	0	0	1	1	10	7.4
7	0	1	2	0	1	0	1	0	0	0	0	0	0	0	0	1	0	6	4.4
8	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	1.5
9	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	1.5
10	1	0	0	0	2	0	0	0	0	0	0	1	0	1	0	0	0	5	3.7
11	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.7
12	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	0	4	3.0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0.7
15	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	1.5
16	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.7
17	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	2	1.5
N	4	5	7	10	14	2	18	5	7	1	8	12	4	8	14	9	7	135	100
Mean	6.0	4.0	3.7	4.3	6.0	7.5	6.1	1.2	2.7		4.0	4.9	3.3	3.3	3.4	3.6	2.6	4.3	
Median	5.0	4.0	2.0	1.0	5.0	7.5	4.6	1.0	3.0		3.0	3.5	2.5	2.5	2.0	3.0	2.0	3.0	
Mode	5		2	1	2		2	1					2				1	2	

[1] Count on first contact with party.

[2] Only single males or females without offspring included here.

Table 3.5: Monthly distribution of party sizes at Ngogo (dependent offspring excluded; methodology of Wrangham *et al.*, 1992)[1].

Party	1992												1993						
size	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	All	%
1[2]	0	2	2	6	1	0	2	4	1	0	2	2	1	3	5	5	3	39	25.7
2	0	0	2	0	5	0	5	1	2	0	3	2	2	4	5	0	3	34	22.4
3	0	0	1	1	1	1	3	0	2	0	2	2	0	0	3	0	0	16	10.5
4	2	2	2	1	3	1	1	0	2	0	1	3	0	0	2	0	0	20	13.2
5	1	1	0	1	0	0	2	0	0	1	0	0	0	0	1	2	0	9	5.9
6	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	1	2	7	4.0
7	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	0	4	2.6
8	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	5	3.3
9	0	0	0	0	2	0	1	0	0	0	0	1	0	0	0	0	0	4	2.6
10	1	0	0	1	2	1	0	0	0	0	0	1	0	1	0	0	0	7	4.6
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0.7
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	3	2.0
15	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	2	1.3
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0.6
N	4	6	7	13	17	4	18	5	7	1	9	12	4	8	18	11	8	152	100
Mean	5.8	3.8	2.4	4.2	5.0	6.3	5.2	1.2	2.7		3.3	4.3	2.8	2.6	2.6	3.9	2.6	3.9	
Median	4.5	4.0	2.0	3.0	4.0	6.0	3.0	1.0	3.0		2.0	3.5	2.0	2.0	2.0	5.0	2.0	3.0	
Mode	4			1	2		2	1			2	4	2	2		1		1	

[1] Count on first contact with party.

[2] contains single males or females with or without offspring.

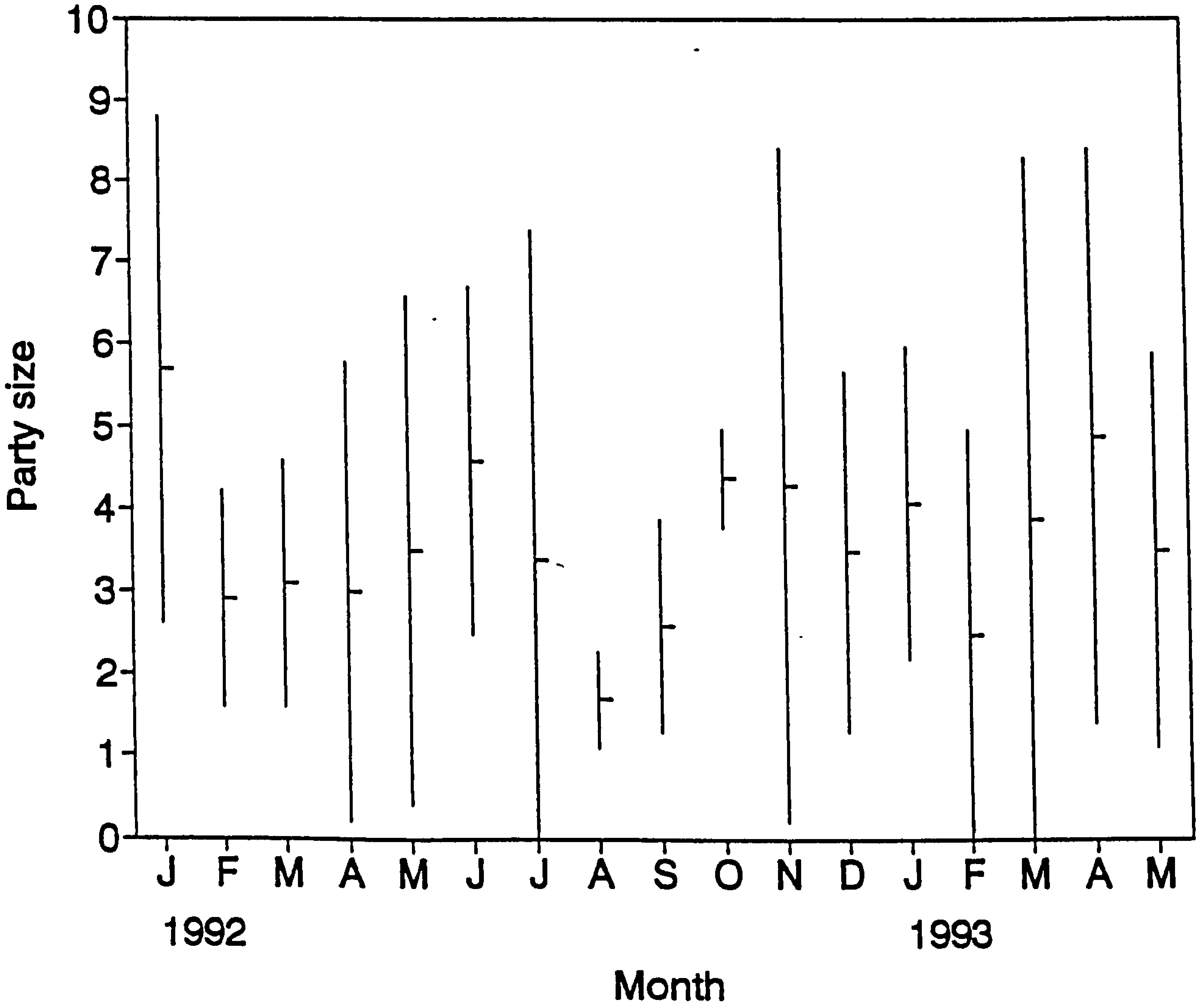


Figure 3.3: Mean monthly party size at Ngogo (N=2354 15-minute intervals).

(N=2354). There is no significant difference between the party sizes arrived at through these different methods (t-test for paired samples, p>0.5).

However, differences between months are not significant (party size arrived at through count on first contact with party; one-way ANOVA, p>0.05 for both counts excluding and including dependent offspring).

At Kanyancu, monthly means of party size range from 3.2 to 9.8 (see Table 3.6a; the only way of determining party size at Kanyancu was the count on first contact with the party, including dependent offspring). Differences between months are significant (one-way ANOVA, p<0.001).

Ghiglieri (1984) showed that the size of feeding aggregations was positively correlated with the crown volume of food trees at Ngogo. Wrangham *et al.* (1992) showed that party size was correlated with a food abundance score at Kanyawara. It is assumed that habitat productivity of the wooded savanna at Gombe (Clutton-Brock & Gillett, 1979; Goodall, 1986) is less than that of the medium altitude tropical forest of Kibale.

In the absence of phenological data for most sites where chimpanzees have been studied, annual precipitation can be used to compare habitat productivity. However, Figure 3.4 shows that in the majority of months, rainfall at

Table 3.6a: Monthly distribution of party sizes at Kanyancu (dependent offspring included in count)[1].

Party size	1992 Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	1993 Jan	Feb	Mar	Apr	May	Jun	All	%
1[2]	1	5	2	6	0	3	4	3	3	4	3	1	3	1	4	4	0	47	10.8
2	1	2	5	0	3	0	3	6	2	8	1	1	4	6	5	3	1	51	11.7
3	0	15	12	2	1	0	7	1	0	3	1	4	3	5	2	4	0	88	20.1
4	0	2	4	2	1	0	7	1	0	3	1	4	3	5	2	4	0	39	8.9
5	1	4	4	1	0	3	1	6	0	0	2	1	1	2	3	6	0	35	8.0
6	0	1	5	0	3	1	2	4	1	4	1	2	1	2	6	6	1	40	9.2
7	1	1	2	0	2	0	1	0	0	1	0	2	1	1	4	1	0	17	3.9
8	0	0	3	1	2	0	0	2	2	0	1	1	2	4	1	0	0	19	4.3
9	3	0	2	0	0	3	2	0	0	1	0	0	0	2	1	2	0	16	3.7
10	2	0	1	3	1	3	1	0	0	3	0	0	0	3	0	2	0	19	4.3
11	1	0	3	0	1	0	0	0	0	1	0	2	0	0	1	1	1	11	2.5
12	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	3	0	7	1.6
13	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	3	0.7
14	0	0	0	0	0	4	0	0	0	0	1	1	0	0	4	0	0	10	2.3
15	1	0	0	0	0	4	0	0	1	0	0	0	0	0	1	0	0	7	1.6
16	0	0	3	0	0	0	0	0	0	0	1	1	0	0	1	1	0	7	1.6
17	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	4	0.9
18	0	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	4	0.9
19	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.2
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	0.7
21	0	0	1	0	0	0	0	0	0	2	0	0	0	2	0	0	0	5	1.1
27	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
30	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0.5
31	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.2
N	12	30	54	15	19	24	24	26	15	40	13	17	17	34	43	49	5	437	100
Mean	9.8	3.2	7.3	4.2	5.8	8.6	4.1	4.4	4.1	7.9	5.3	7.6	3.7	5.9	6.0	6.1	7.8	6.0	
Median	4.5	4.0	2.0	3.0	4.0	6.0	3.0	1.0	3.0	5.0	2.0	3.5	2.0	2.0	2.0	5.0	2.0	4.0	
Mode	9	3	3	1						2	1		2	2	6			3	

[1] Count on first contact with party.

[2] contains males and females without offspring.

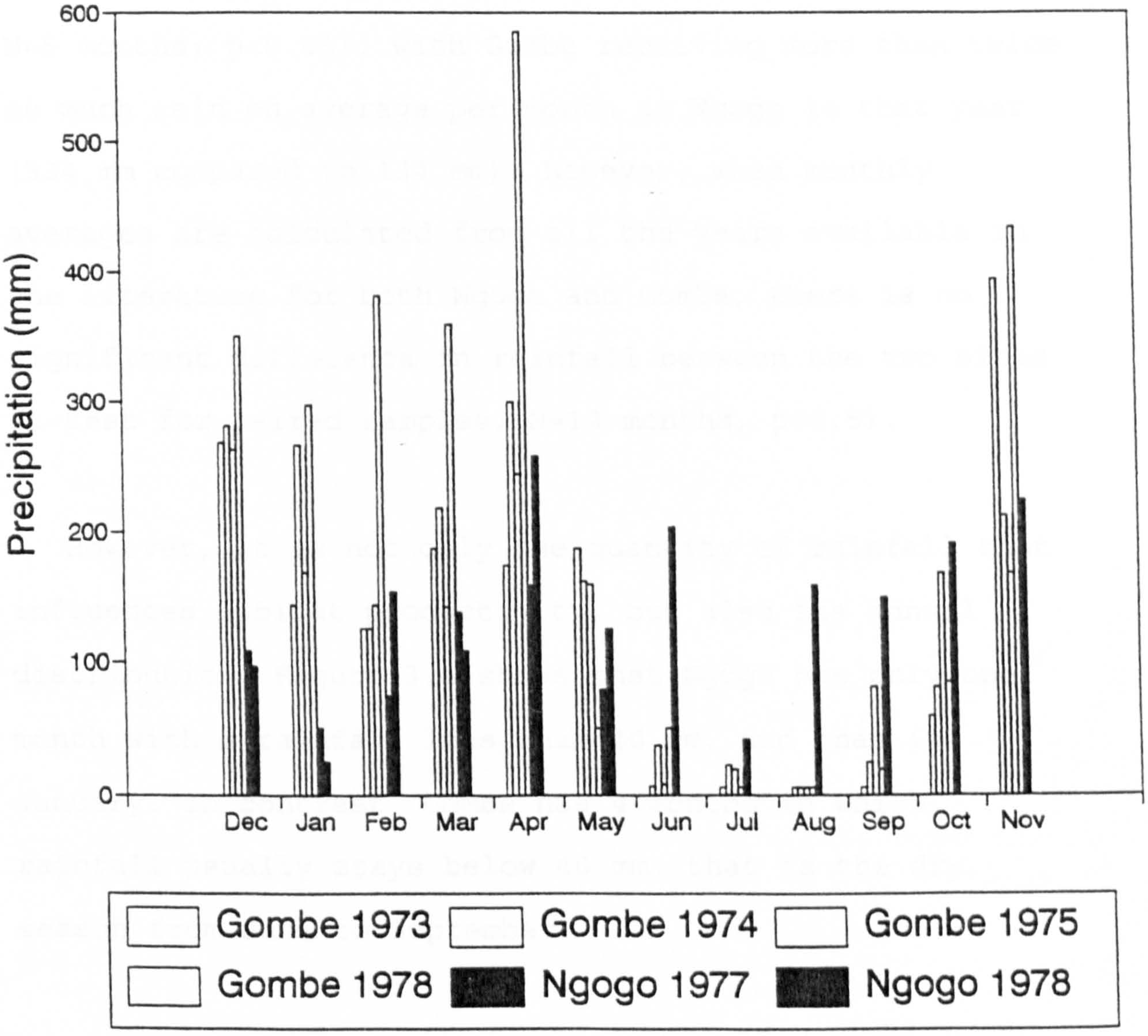


Figure 3.4: Precipitation at Gombe and Ngogo.

Gombe exceeds rainfall at Ngogo (data for Gombe from Figure 3.3, p.48, Goodall, 1986; data for Ngogo from Figure 4, p.19, Ghiglieri, 1984), although only the comparison between the year 1978 at Ngogo and the year 1978 at Gombe is significant (t-test for paired samples, N=5 months; p<0.05), with Gombe receiving more than twice as much rain on average per month as Ngogo in that year (334 mm compared to 134 mm). However, when monthly averages are calculated from all the years available in the literature for both Ngogo and Gombe, there is no significant difference in rainfall between the two sites (t-test for paired samples, N=12 months, p>0.5).

However, it is not only the quantity of rainfall that influences habitat productivity, but also its annual distribution. Figure 3.4 shows that Ngogo has only one month with a rainfall less than 40 mm, and that is January. In contrast, Gombe has 4 months in which rainfall usually stays below 40 mm: that is the dry season from June to September.

Mean monthly party size at Ngogo does not differ significantly from Wrangham's findings at Kanyawara (party size data from 15-minute intervals in both studies; t-test for paired samples, p>0.056) (see Figure 3.5). Neither does monthly mean party size at Kanyancu (t-test for paired samples, p>0.607). However, monthly mean party size (including offspring; determined on first contact with party) is significantly greater at Kanyancu

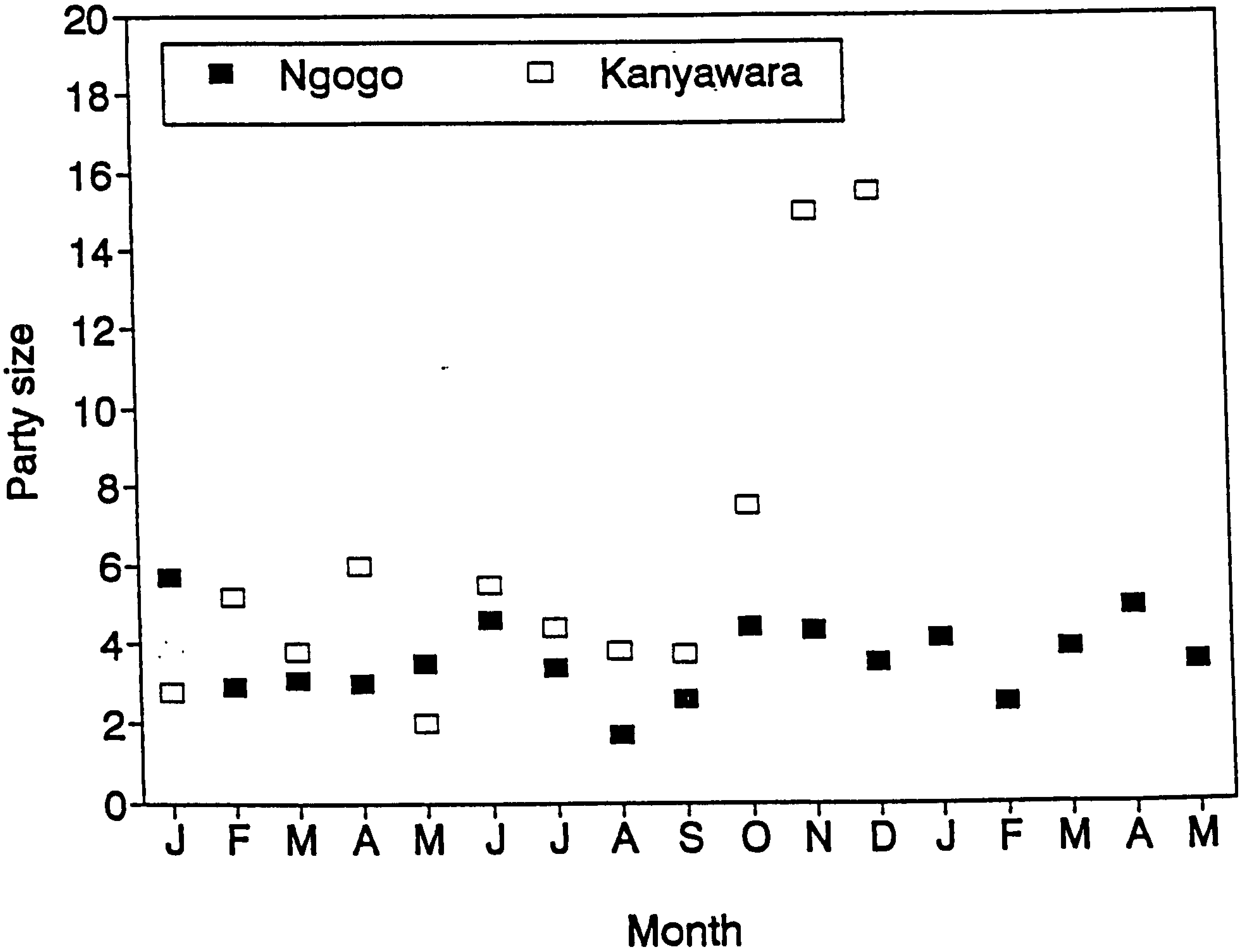


Figure 3.5: Comparison of mean monthly party size at Ngogo in 1992/93 and Kanyawara in 1989.

than at Ngogo (t-test for paired samples, p=0.05; Figure 3.6).

3.3.3 Time spent alone in relation to sex

One way to "measure" female and male sociability is to determine the time spent alone (i.e. without any other adults or subadults). Table 3.6b gives time spent alone for males and females at Ngogo and Kanyancu. Following Wrangham *et al.*'s method , data were used only from the first encounter with the chimpanzee party. Only data from tree vigils were used because parties found by calls bias against small parties (Wrangham *et al.*, 1992).

3.3.4 Comparison of party size with bonobos

One feature quoted as "consistently" distinguishing *P. paniscus* from *P. troglodytes* is their larger party size (Malenky & Stiles, 1991). Table 3.7 gives mean party sizes of a number of *P. troglodytes* and *P. paniscus* communities. Mean party size of all these communities is 5.8 for *P. troglodytes* and 8.9 for *P. paniscus*, which is not significantly different (t-test for independent samples; p>0.05).

3.3.5 Party types

Following Reynolds & Reynolds (1965), parties were classified as mixed, adult, male, maternal and solitary

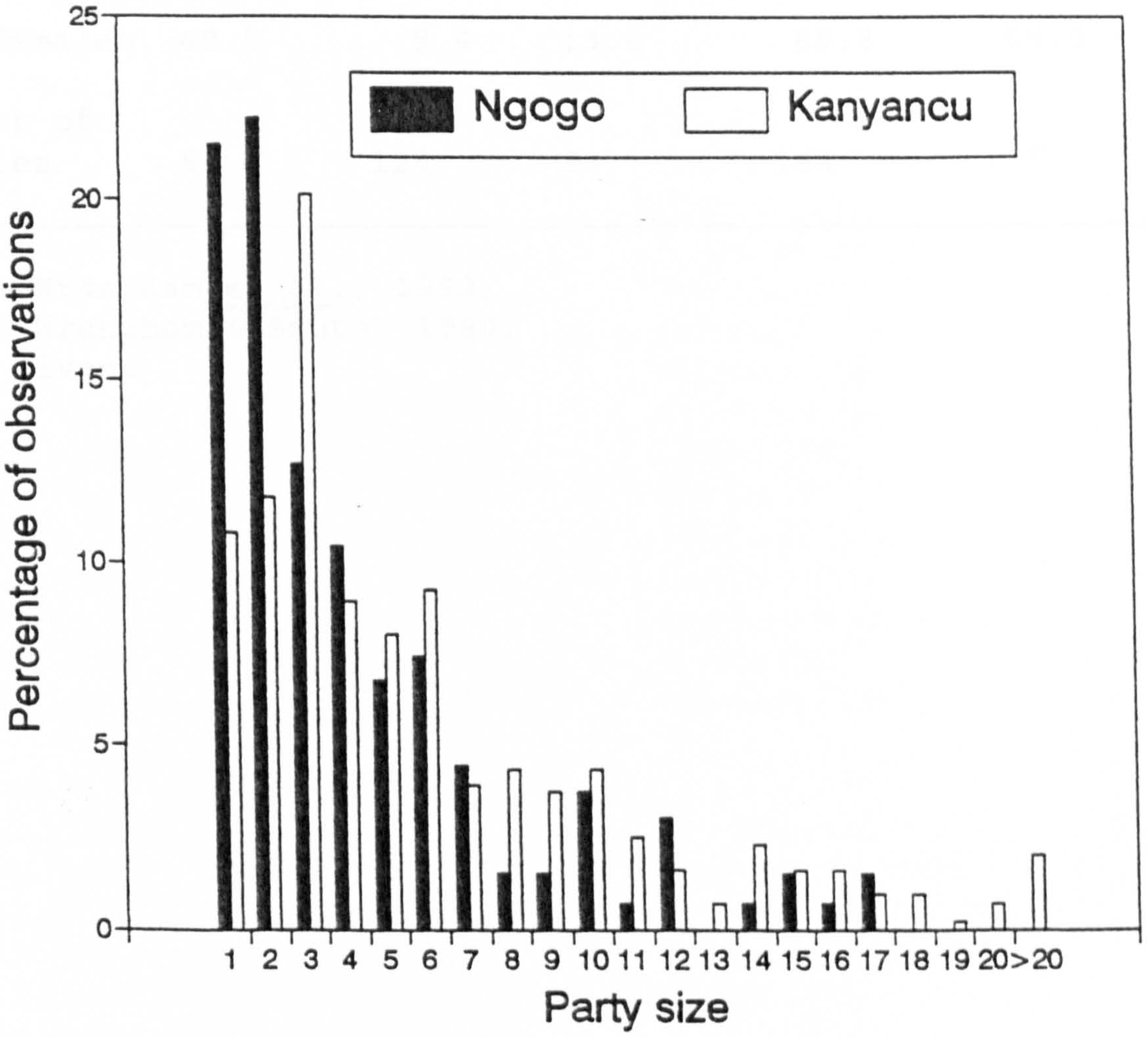


Figure 3.6: Mean monthly party size (including dependent offspring; determined on first contact with party) at Ngogo and Kanyancu.

Table 3.6b: Time spent alone (in percent) by males and females at Ngogo and Kanyancu.

	Ngogo	Kanyancu	Ngogo[a]	Kanyawara[a]	Gombe[b]
Males	20.8	15.5	1.9	20.5	27.0
All females	48.5	9.4	13.8	69.8	65.0
Number of parties	81	124	23	164	c

[a] from Wrangham _et al_., 1992;
[b] from Wrangham & Smuts, 1980;
[c] not given.

Table 3.7: Overview of party sizes of chimpanzees and bonobos.

Site	Mean party size	Source
Chimpanzees		
Kibale (Ngogo), Uganda	3.6[a]	This study
Kibale (Ngogo), Uganda	4.3[b]	This study
Kibale (Ngogo), Uganda	3.9[c]	This study
Kibale (Ngogo), Uganda	5.0	Wrangham *et al.* 1992
Kibale (Ngogo), Uganda	2.6	Ghiglieri 1984
Kibale (Ngogo), Uganda	3.1[g]	Ghiglieri 1984
Kibale (Kanyawara), Uganda	5.2	Chapman *et al.* 1994
Kibale (Kanyawara), Uganda	5.6	Wrangham *et al.* 1992
Kibale (Kanyawara), Uganda	6.1	Wrangham *et al.* 1992
Kibale (Kanyancu), Uganda	6.0[d]	This study
Budongo, Uganda	4.4[e]	Sugiyama 1968
Budongo, Uganda	3.9	Reynolds & Reynolds 1965
Gombe, Tanzania	4.0	Goodall 1986
Mahale, Tanzania	6.2	Nishida 1968
Mt. Assirik, Senegal	5.3[f]	Tutin *et al.* 1983
Bossou, Guinea	5.8	Sugiyama 1981
Bossou, Guinea	8.7	Sugiyama & Koman 1979
Tai, Ivory Coast	10.1	Boesch 1991
Okorobiko Mountains, Rio Muni	9.9	Sabater Pi 1979
Bonobos		
Lomako, Zaire	5.4	Chapman *et al.* 1994
Lomako, Zaire	6.2	Chapman *et al.* 1994
Lomako, Zaire	5.4	Malenky & Stiles 1991
Lomako, Zaire	7.9	Badrian & Badrian 1984
Wamba, Zaire	16.9	Kuroda 1979
Yalosidi, Zaire	8.5	Kano 1983

[a] Calculated from 15-minute points, dependent offspring excluded.
[b] Calculated from first contact, dependent offspring included.
[c] Calculated from first contact, dependent offspring excluded.
[d] Calculated from first contact, dependent offspring excluded.
[e] As calculated from Sugiyama (1968) Tables 2 and 3 (pp. 232-235).
[f] As calculated from Tutin *et al.* (1983) Figure 1 (p. 158).
[g] Feeding and travelling parties combined.

(Table 3.8). In addition, the category "males plus juveniles" was introduced for parties that contained adult and/or subadult males and female juveniles and one other juvenile of unknown sex (N=3) or adult and/or subadult males and juveniles of unknown sex (N=6). This type of party accounted for 5.2 % of all sightings.

In a sample of chimpanzee communities (Table 3.8), the percentage of mixed parties was significantly correlated with party size (r=0.916; p=0.01; N=6).

3.3.6 Comparison of party type frequencies with other chimpanzee communities

The distribution of party types varies significantly between *P. troglodytes* communities with the exception of Budongo and Kasakati, Budongo and Ngogo, Ngogo and Kasakati and Kasakati and Mahale (Tables 3.8 and 3.9). As fifteen comparisons were made, the likelihood of getting a significant result by chance is great. Therefore only results with a probability of p<0.01 were considered significant.

3.3.7 Comparison of party type frequency with bonobos

It has been suggested that another consistent difference between chimpanzees and bonobos is the higher frequency of mixed parties in the latter (Badrian & Badrian, 1984; Kano 1980, 1982, 1987; Malenky & Stiles,

Table 3.8: Composition of parties of *Pan troglodytes* at various sites.

Site	Party composition:					
	Solitary (including females with dependent offspring)	Maternal (several females with offspring)	Males only	Males and juveniles	Bisexual (adults and/ or subadults of both sexes)	Mixed (adults and immatures of both sexes)
Ngogo						
N	39	11	18	7	13	46
%	29.1	8.2	13.4	5.2	9.7	34.3
%[1]	-	11.6	18.9	7.4	13.7	48.4
Source: this study						
Budongo						
N	-	36	34	-	65	80
%	-	16.8	15.8	-	30.2	37.2
Source: Reynolds & Reynolds 1965						
Gombe						
N	63	84	35	-	63	105
%	18.0	24.0	10.0	-	18.0	30.0
%[1]	-	29.3	12.3	-	22.1	36.8
Source: Goodall 1968						

Table 3.8 continued

Site	Party composition:					
	Solitary (including females with dependent offspring)	Maternal (several females with offspring)	Males only	Males and juveniles	Bisexual (adults and/ or subadults of both sexes)	Mixed (adults and immatures of both sexes)
Mahale						
N	91	69	43	-	94	271
%	16.0	12.2	7.6	-	16.5	47.7
%[1]	-	14.5	9.0	-	19.7	56.9
Source: Nishida 1968						
Kasakati Basin						
N	14	3	1	-	5	81
%	13.5	2.8	1.0	-	4.8	77.9
%[1]	-	3.3	1.1	-	5.5	89.1
Source: Suzuki 1969						
Kasakati Basin						
N	-	8	6	-	23	41
%	-	10.3	7.6	-	29.5	52.6
Source: Izawa 1970						

[1] Solitary individuals were excluded from the analysis in order to make the results comparable to the studies at Budongo (Reynolds & Reynolds, 1965)and the Kasakati Basin (Izawa, 1970).

Table 3.9: Results of X^2 tests comparing frequencies of party types between different chimpanzee communities

Comparison	X^2	df	p
Ngogo/Budongo[1]	10.7	3	n.s.
Ngogo/Gombe	24.2	4	<0.001
Ngogo/Mahale	23.9	4	<0.001
Ngogo/Kasakati-Su	42.9	4	<0.001
Ngogo/Kasakati-Iz[1]	8.97	3	n.s.
Budongo/Gombe[1]	12.6	3	<0.01
Budongo/Mahale[1]	25.0	3	<0.001
Budongo/Kasakati-Su[1]	71.0	2	<0.001
Budongo/Kasakati-Iz[1]	7.65	3	n.s.
Gombe/Mahale	37.1	4	<0.001
Gombe/Kasakati-Su	82.1	4	<0.001
Gombe/Kasakati-Iz[1]	15.3	3	<0.01
Mahale/Kasakati-Su	36.8	4	<0.001
Mahale/Kasakati-Iz[1]	4.25	3	n.s.
Kasakati-Su/Kasakati-Iz[1]	29.5	2	<0.001

[1] Reynolds & Reynolds (1965) at Budongo and Izawa (1970) in the Kasakati Basin did not consider solitary individuals. When other sites are compared to these two sites, solitary individuals were disregarded and percentages or party types adjusted accordingly. Degrees of freedom vary because cells had to be collapsed to avoid frequencies below 5.

Sources: Ngogo: this study; Budongo: Reynolds & Reynolds 1965; Gombe: Goodall 1968; Mahale: Nishida 1968; Kasakati-Su: Suzuki 1969; Kasakati-Iz: Izawa 1970.

1991). Tables 3.10 and 3.11 seem to corroborate this. However, X^2 tests show that the distribution of party types at the two bonobo sites is not only significantly different from that of the chimpanzees at almost all sites (with the exception of the Kasakati basin) but also from each other. As thirteen comparisons were made, the likelihood of getting a significant result by chance is great. Therefore only results with a probability of $p<0.01$ were considered significant.

3.3.8 Party composition

At Ngogo, oestrous females occur most frequently in mixed parties and most rarely in maternal parties (Table 3.12). However, anoestrous females also occur most frequently in mixed parties, and so do males. The adult sex classes do not show significant differences in the party type they favour ($X^2=8.88$, df=6, $p>0.18$).

The mean socioeconomic sex ratio of parties is 1.8 (N=64 contacts) when only adults are considered and 1.9 when both adults and subadults are considered (N=70 contacts) (Table 3.13).

3.3.9 Party size in relation to the presence of females

Mean party size was significantly greater when oestrous females were present or when both oestrous and

Table 3.10: Composition of bonobo parties.

Site	Party composition:					
	Solitary (including females with dependent offspring)	Maternal (several females with offspring)	Males only	Males and juveniles	Bisexual (adults and/ or subadults of both sexes)	Mixed (adults and immatures of both sexes)
Wamba						
N	10	8	4	-	4	121
%	6.8	5.4	2.7	-	2.7	82.3
%[1]	-	5.8	2.9		2.9	88.3
Source: Kuroda 1979						
Lomako						
N	36	10	9	-	15	130
%	18.9	5.2	4.7	-	7.9	68.4
%[1]	-	6.1	5.5	-	9.2	79.3
Source: Badrian & Badrian 1984						

[1] Solitary individuals were excluded from the analysis in order to make the results comparable to the studies at Budongo (Reynolds & Reynolds, 1965) and the Kasakati Basin (Izawa, 1970).

Table 3.11: Results of X^2 tests comparing frequencies of party types between bonobo and chimpanzee communities

Comparison	X^2	df	p
Wamba/Ngogo	63.9	4	<0.001
Wamba/Budongo[1]	26.5	1	<0.001
Wamba/Gombe	115.3	4	<0.001
Wamba/Mahale	57.9	4	<0.001
Wamba/Kasakati-Su	4.64	2	n.s.
Wamba/Kasakati-Iz[1]	39.8	2	<0.001
Lomako/Ngogo	28.5	4	<0.001
Lomako/Budongo[1]	66.7	3	<0.001
Lomako/Gombe	78.1	4	<0.001
Lomako/Mahale	26.8	4	<0.001
Lomako/Kasakati-Su	6.57	4	n.s.
Lomako/Kasakati-Iz[1]	20.9	3	<0.001
Wamba/Lomako	15.8	4	<0.01

[1] Reynolds & Reynolds (1965) at Budongo and Izawa (1970) in the Kasakati Basin did not consider solitary individuals. When other sites are compared to these two sites, solitary individuals were disregarded and percentages or party types adjusted accordingly. Degrees of freedom vary because cells had to be collapsed to avoid frequencies below 5.

Sources: Ngogo: this study; Budongo: Reynolds & Reynolds 1965; Gombe: Goodall 1968; Mahale: Nishida 1968; Kasakati-Su: Suzuki 1969; Kasakati-Iz: Izawa 1970; Wamba: Kuroda 1979; Lomako: Badrian & Badrian 1984.

Table 3.12: Representation of males and oestrous and anoestrous females in parties of various types.

Party type	Oestrous females		Anoestrous females		Males	
	N	%	N	%	N	%
Solitary	3	9.4	10	17.5	24	22.2
Maternal	2	6.3	11	19.3	N/A	
Bisexual	5	15.6	9	15.8	15	13.9
Mixed	22	68.8	27	47.4	42	38.9
Males only	N/A		N/A		18	16.7
Males + Juveniles	N/A		N/A		9	8.3
Totals	32	100.0	57	100.0	108	100.0

Table 3.13: Number of adult males and females in all parties.

Number of females	Number of males 0	1	2	3	4	5	6	7	8	9	10	11	Total
0	14	26	7	9	0	2	0	0	-	-	-	-	58
1	19	6	6	7	4	3	1	2	-	-	-	2	50
2	4	1	6	-	-	-	-	-	-	-	-	-	11
3	3	2	-	-	1	1	1	1	-	-	-	-	9
4	-	-	-	-	-	-	2	-	-	-	-	-	2
Total	40	35	19	16	5	6	4	3	--	-	-	2	130

anoestrous females were present than when no adult or subadult female was in the party (Tables 3.14 and 3.15). The difference between parties containing oestrous females only and parties containing oestrous and anoestrous females was not significant when dependent offspring are excluded ($p>0.05$). However, when dependent offspring are included, the difference is significant ($p<0.05$). Females with dependent offspring are more likely to be anoestrous and therefore party size including dependent offspring will be inflated in favour of anoestrous females. Party size excluding dependent offspring is therefore considered to give a more realistic result.

When parties containing oestrous females were compared to those containing anoestrous females, the former are significantly larger. There was no significant difference in party size (excluding dependent offspring) when anoestrous females were present compared to when females were not present in the party.

The socioeconomic sex ratio was almost three times as high in parties which contained only oestrous females (Table 3.14) than in parties containing either anoestrous females or both anoestrous and oestrous females. This difference is significant (t-test for independent samples, $p<0.05$ for oestrous/anoestrous, $p<0.02$ for oestrous/anoestrous and oestrous; Table 3.15). Therefore, with increasing size parties are more likely to contain a

Table 3.14: Mean party size in relation to presence of females

Presence of females	Party size (dependent offspring excluded)	Party size (dependent offspring included)	Adult males/ adult females	All males/ all females[1]
Only anoestrous females present	3.1	4.4	1.3	1.4
Only oestrous females present	5.6	5.6	3.3	3.8
Anoestrous and oestrous females present	7.5	9.6	1.1	1.1
No (adult or subadult) females present	2.3	2.2	-	-
Either anoestrous or oestrous females present or both	4.5	5.7		

Note: [1] adult and subadult males and females

Table 3.15: Results of t-tests for independent samples of mean party sizes with and without anoestrous and oestrous females present.

Presence of females	Party size (dependent offspring excluded)	Party size (dependent offspring included)	Adult males/ adult females	All males/ all females[1]
Anoestrous/none	>0.05	<0.001	-	-
Oestrous/none	<0.01	<0.01	-	-
Both anoestrous and oestrous females in one party/none	<0.001	<0.001	-	-
Oestrous or anoestrous female(s)/none	<0.001	<0.001	-	-
Anoestrous/oestrous	<0.05	>0.05	<0.05	<0.05
Anoestrous/anoestrous	<0.01	<0.001	>0.05	>0.05
Oestrous/anoestrous and oestrous	>0.05	<0.05	<0.02	<0.02

[1] adult and subadult males and females.

higher percentage of males. In fact, party size was correlated significantly with socioeconomic sex ratio (adult males/adult females: $r=0.78$, $p<0.001$; all males/all females: $r=0.74$; $p<0.001$). This was also true when party size included dependent offspring (adult males/adult females: $r= 0.66$; $p<0.001$; all males/all females: $r=0.60$; $p<0.001$).

3.4 Population density

Population density was calculated from general mammal line transect surveys and a chimpanzee nest census (see Chapter 2 for methods. In the general mammal survey, chimpanzees were sighted five times in 48 km of survey; this is equivalent with a population density of 3.03 ± 3.21 as calculated from the DISTANCE programme (Buckland *et al.*, 1993).

In the nest census at Ngogo, 73.64 nests per km^2 were estimated to have been built in the 29 days between the first and the second census and 62.03 in the 25 days between the second and the third census (Table 3.16). This means an estimated 2.539 and 2.481 nests per diem, with a mean of 2.51. Ghiglieri (1984) estimated that 82.6% of a chimpanzee population build nests. If this figure is taken into account, the density of chimpanzees at Ngogo is estimated to be 3.04 per km^2. As the size of

Table 3.16: Result of the nest census at Ngogo.

	First	Second	Third
Number of counted nests	126[1]	98[2]	85[2]
Estimated strip width	15.84 ± 1.444	16.64 ± 1.403	17.13 ± 1.199
Number of nests per km of census	3.15 ± 0.281	2.45 ± 0.248	2.13 ± 0.231
Estimated nest density (number of nests per km^2)	99.41 ±12.67	73.64 ± 9.691	62.03 ± 8.007

[1] Nests estimated to have been built within the last 4 weeks;

[2] Nests built since the previous census.

Figures calculated from the DISTANCE programme.

Table 3.17: Result of nest census at Kanyancu.

	First	Second	Third
Number of counted nests	41[1]	36[1]	4[2]
Estimated strip width	19.30 ± 2.093	25.67 ± 3.239	-
Number of nests per km of census	1.02 ± 0.159	0.89 ± 0.149	0.10 ± 0.050
Estimated nest density (number of nests per km^2)	26.39 ± 5.017	17.42 ± 3.641	1.66

[1] Nests estimated to have been built within the last 4 weeks;
[2] Nests built since the previous census.
Figures calculated from the DISTANCE programme.

the Ngogo community home range is unknown, this figure cannot be compared to the community size data.

At Kanyancu, 17.42 nests per km^2 were estimated to have been built in the 24 days between the first and the second census and 1.66 in the 28 days between the second and the third census (Table 3.17). This means an estimated 0.601 and 0.059 nests per diem with a mean of 0.33. This would mean that the density of chimpanzees at Kanyancu is estimated to be 0.4 per km^2.

3.5 Discussion

3.5.1 Size and composition of the Ngogo community

With an estimated 120-130 individuals, the Ngogo community is 1.1 times larger than any other community of chimpanzees reported to date. The only other community of common chimpanzees that is comparable in size is the M-group at Mahale with 105 members (Hiraiwa-Hasegawa et *al*., 1984; see Table 3.18).

It has been suggested that chimpanzee communities may break up if and when they reach a certain size (R. Wrangham, pers. comm.). The only observed split of a community happened in Gombe when the community numbered 48 individuals (Goodall, 1986). If there is indeed a "critical" size where communities break up, it must be at

Table 3.18: Demographic figures on *P. troglodytes* and *P. paniscus* communities

Name of community	Location	Size of community	Sex ratio (adm/ adf)	Sex ratio (all m/ all f)	Ratio ad/ all others	Community range	Pop. density	Mean party size	Median party size	Modal party size	Range party size	%age mixed parties	Source
Chimpanzees													
K-Group	Mahale, Tanzania	9-37			1.4	10.4^{h}						47.7^{e}	Nishida *et al.*, 1985
M-Group	Mahale, Tanzania	105	0.3	0.5	0.9	14.0	7.5						Hiraiwa-Hasegawa *et al.*, 1984
	Mt Assirik, Senegal	28	1.3	1.0	0.8	228.0	0.1	5.3	4			58	Tutin *et al.*, 1983
Kasakela	Gombe, Tanzania	35-58	1.0	1.2	1.1	26.0^{g}	2.6-3.9^{g}						Goodall, 1983
Reg Pop A	Budongo, Uganda	56	2.0			7.5	6.7						Sugiyama, 1968
Band A	Budongo, Uganda		0.3		2.0								Itani & Suzuki, 1967
	Budongo, Uganda		0.5			–							Nishida, 1967
	Budongo, Uganda	50					3.9					37.2	Reynolds & Reynolds, 1965
Picnic	Budongo, Uganda	85	0.8		2.0								Izawa, 1970
	Budongo, Uganda	85				20.0	4.1						Suzuki, 1977
Ngogo	Kibale, Uganda	130	1.1	1.7	1.1		3.0	3.6/ 4.3	2/3	2/2	1-17/ 1-16		This study
Ngogo	Kibale, Uganda							5.0					Wrangham *et al.*, 1992
Kanyawara	Kibale, Uganda	37					1.0^{d}	5.6/ 6.1					Wrangham *et al.*, 1992
Kanyancu	Kibale, Uganda	>60					0.4	6.0	4	3	1-31		This study
	Tai, Ivory Coast	51-68	<0.3										Boesch, 1991
	Bossou, Guinea	19-21											Sugiyama, 1984
	Okorobiko, Rio Muni							9.9			1-23		Sabater-Pi, 1979
Bonobos													
Bakumba	Lomako, Zaire	50	0.69			22.0	2.0	7.6		2-5	1-50	68	Badrian & Badrian, 1984
Bakumba	Lomako, Zaire							2.1^{a} 5.6^{b}		1-5^{c}			Malenky & Stiles, 1991
E Group	Wamba, Zaire	65^{f}				38.0^{f}	1.7^{f}	16.9			1-54	74.2	Kuroda 1979

Note: a: feeding on THV; b: feeding on fruit; c: feeding on THV; d: R. Wrangham, pers. comm.; e: Nishida, 1968; f: Kano & Mulavwa, 1984; g: Teleki 1983; h: Nishida 1979.

least three times greater at Ngogo than in Gombe. Habitat productivity may be the cause. If the habitat at Ngogo is more productive than the one at Gombe, it can sustain more chimpanzees in their community range.

Although productivity of the wooded savanna habitat at Gombe has not been measured quantitatively, it has been assumed that it is less than the productivity of the medium-altitude tropical forest of Kibale. While the amount of annual rainfall has been shown to be comparable for both sites, its monthly distribution varied strongly between sites. Hence, the habitat at Gombe is more seasonal, which means that the crucial criterion for how many chimpanzees the habitat can sustain is how many it can sustain in the months of low rainfall.

If a chimpanzee community becomes too big to be sustained by the habitat within the community home range in the low rainfall months, the home range will be expanded by individual chimpanzees ranging further in search of food. Depending on pressure from neighbouring communities and the availability of healthy males to patrol and defend the home range boundary (Goodall, 1986), such a home range extension may not be possible and the community has to split instead. However, the Ngogo community does not seem to have reached this stage yet. With a sex ratio skewed in favour of males, there might be sufficient numbers of males to patrol and defend the home range boundaries. It has been shown that groups of colobus monkeys, *Colobus guereza*, also fissioned when they reached a critical size (determined by habitat quality) and could not extend their home range (Dunbar, 1988; Dunbar & Dunbar, 1974).

The socioeconomic sex ratio for the adults of the Ngogo community is slightly biased towards males, but is still well within the range of other chimpanzee communities (see Table 3.18). The fact that the sex ratio derived from party composition is higher than the one derived from the age/sex composition of the community (1.7 compared to 1.5) may indicate that females are more likely to leave a party when the party has been encountered by a human observer. Females are shyer than males and are therefore more easily missed when the composition of the party is established.

The sex ratio derived from party composition was also higher than at any other chimpanzee study site. Again the increased shyness due to a low degree of habituation of the females might be the reason for this, especially at the beginning of the study. In the absence of data on differential mortality rates between sexes, these findings can not be otherwise explained.

The ratio of adults/all others also lies within the range of other chimpanzee communities and indicates that the Ngogo community is a healthy population.

3.5.2 Size and composition of parties at Ngogo

This study's findings corroborate Wranghams's suggestion that the difference in party size between his and Ghiglieri's study (Ghiglieri, 1984; Wrangham *et al*, 1992) is caused by different definitions and methods. However, it might be said that Wrangham *et al*. (1992) only consider travelling parties when they quote a party size (according to Ghiglieri, 1984) of 2.6 (N=667). For "feeding associations", Ghiglieri (1984) gives an average size of 3.6 (N=687). Given that Wrangham *et al*. (1992) do not distinguish between activities in their analysis, I think it is more appropriate to calculate an average party size for both feeding and travelling as a comparative figure. The resulting figure of 3.1 is not so different from what has been found in other studies.

The cause for a significantly greater party size at Kanyancu compared to Ngogo and Kanyawara may be a different dispersion of fruit and especially fig trees. However, as no phenological data are available for Kanyancu, these conclusions need to be tested in the future.

Monthly party sizes vary significantly at Kanyancu whereas they do not at Ngogo. Phenological data from Ngogo and Kanyawara show that the medium basal area of trees and the density of trees is higher at Ngogo than at Kanyawara (Barrett, 1995). This suggests that food resources at Ngogo remain reasonably stable over the months, and so the chimpanzees do not need to split up in smaller parties when foraging. It is suggested that the seasonal variation in food resources is greater at Kanyancu, but in the absence of phenological data from there these suggestions are preliminary.

The fact that females spend less time on their own at Ngogo than they do at Kanyawara (Wrangham *et al.*, 1992) also indicates that feeding conditions are better at Ngogo and they therefore do not suffer as much from feeding competition as females at Kanyawara or at Gombe. From this point of view, females at Kanyancu should suffer even less feeding competition, but the absence of phenological data from Kanyancu again renders this speculative.

Mean party sizes of chimpanzee communities were shown not to be significantly different from mean party sizes for bonobo communities. It can therefore be argued that bonobos and chimps should be arranged on one scale as regards party size, ordered not in relation to being two different species but in relation to some other factor, such as predation pressure, habitat visibility, productivity or seasonality.

The same seems to hold for the apparent difference in party composition between the two species. The variance between common chimpanzee populations turns out to be as large as that between common and pygmy chimpanzees as well as that between pygmy chimpanzee populations. As has been shown, party size and party composition are related: the larger a party is, the higher is the socioeconomic sex ratio. Therefore it can be assumed that whatever factor determines party size in chimpanzees and bonobos will also determine the percentage of mixed parties, i.e. party composition.

The Ngogo community seems to be different from all other chimpanzee communities for which data are available in that parties exist in which males travel not only with male but also with female juveniles. However, the sex of the accompanied juveniles was unknown in six out of nine cases. If they were males, these six cases would have to be included in the *males only* category. In the three cases where one of the accompanying juveniles was known to be female, they might have been orphans.

Party size and socioeconomic sex ratio are largest when at least one oestrous female is present in the party. This suggests that male chimpanzees preferentially join parties with oestrous females.

3.5.3 Population density

Ngogo and Kanyancu are both part of Kibale Forest and separated by approximately 12 km (less if the community boundaries are considered). While Kanyawara is slightly wetter and cooler than Ngogo (Butynski, 1990), differences are not significant. This suggests a comparable habitat productivity. However, it has been shown that Ngogo differed considerably from Kanyawara, the third research site in the Kibale Forest, in tree densities and tree size (Barrett, 1995), probably due to differences in soil quality and the past history of vegetational disturbance. Hence, Ngogo and Kanyancu may also differ in the abundance, density and size of chimpanzee food trees, which may explain the sevenfold difference in chimpanzee population density between the two sites. The forest at Kanyancu contains a high proportion of swamps and may therefore be assumed to be less productive for chimpanzees; on the other hand it contains numerous big trees of various fig species, a preferred food of Kibale chimpanzees (Wrangham *et al.*, 1993). No conclusions can be drawn without phenological data from both sites.

However, the nest census with its three counts was carried out only once in the 18 months study and the results may have been seasonally biased. The size of the chimpanzee community's home range is unknown both at Ngogo and at Kanyancu. In both cases, the communities range beyond the trail system and so it is possible that in the two months in which the census was carried out the majority of the Kanyancu community travelled in another part of their home range whereas the majority of the Ngogo community stayed in the proximity of the Ngogo trail system. If the census had been carried out several times, a more realistic picture of the chimpanzees' population density might have emerged. However, population density figures for other chimpanzee populations (Table 3.18) indicate that the estimate for the Ngogo community might be realistic, whereas the estimate for the Kanyancu community would be the second lowest reported after the savanna habitat on Mt. Assirik in Senegal (Tutin *et al.*, 1983). This suggests that a correction of this value would tend towards the value found at Ngogo.

An alternative explanation for a high population density at Ngogo might be that the Ngogo chimpanzees cannot expand their range because of neighbouring communities or because their community range might already border on the edge of the forest, whereas the Kanyancu community has space to expand. These differences have been used to explain population differences in colobus monkeys in Bole, Ethiopia, and the Budongo Forest, Uganda, respectively (Dunbar, 1988; Dunbar & Dunbar, 1974). However, in this case it is the Ngogo community that is situated in the middle of what used to be the Nature Reserve, far away from the forest edge and no neighbouring communities were ever identified. In contrast, the Kanyancu community inhabits an area bisected by the main road and bordering on the National Park boundary and several villages.

3.6 Summary

- The Ngogo community is estimated to consist of more than 100 chimpanzees.

- The socioeconomic sex ratio for identified individuals was 1.5 (adult males/adult females) and 2.1 (all males/all females).

- Mean party size was 4.3 ± 3.7 for Ngogo and 6.0 ± 5.1 for Kanyancu (calculation based on party size on first contact with observer, dependent offspring included).

- Both at Ngogo and Kanyancu, mean party size was greater when chimpanzees were located by following their vocalisations than when they were found through tree vigils.

- At Ngogo, party size *sensu* Ghiglieri (1984) was significantly smaller than party size *sensu* Wrangham *et al.* (1992).

- Wrangham's *et al.*'s (1992) suggestion that the difference in results between Ghiglieri (1984) and their own study was a consequence of different methods and definitions was therefore confirmed by the present study.

- At Ngogo, monthly means of party size range from 1.2 to 7.5; there are no significant differences in party size between months.

- At Kanyancu, monthly means of party size range from 3.2 to 9.8; differences between months are significant.

- Mean monthly party size at Ngogo is significantly smaller than mean monthly party size at Kanyancu; this may be due to a different dispersion of fruit and especially fig trees.

- Mean party sizes for bonobos on the one hand and chimpanzees on the other are not significnatly different from each other. It is therefore suggested that mean party size is not an appropriate criterion to distinguish between bonobo and chimpanzee social organisation.

- The distribution of party types varies significantly between chimpanzee communities, between bonobo communities and between chimpanzee and bonobo communties. It is therefore suggested that the frequency of party type is not an appropriate criterion to distinguish between bonobo and chimpanzee social organisation.

- At Ngogo, there are no significant differences in favoured party type between adult sex classes.

- The presence of oestrous females resulted in significantly larger parties, whereas the presence of anoestrous females did not.

- With increasing size, parties were more likely to contain a higher percentage of males.

- Population density was estimated to be approximately 3 chimpanzees per km^2 at Ngogo and approximately 0.4 for the Kanyancu community, suggesting that either the habitat at Ngogo is richer or the Ngogo chimpanzees cannot expand their range. The latter seems unlikely.

- A comparison of rainfall data suggests that the wooded-savanna habitat at Gombe is more seasonal than the forest in Kibale.

Chapter 4

Gender Relationships

4.1 Introduction

Although common chimpanzees and bonobos have the so-called fission-fusion social system in common (Badrian & Badrian, 1984; Goodall, 1986; Kano, 1980, 1982, 1983; Kuroda, 1979; Nishida, 1968; Nishida et al., 1990; White, 1988), striking differences in the inter-gender relationships are reported. In chimpanzees, males are always dominant to females (Bygott, 1979; Goodall, 1986), while there seems to be a co-dominance in bonobos (Kano, 1992), or possibly even a female dominance (H. Vervaecke, pers. comm.). Chimpanzee males spend most of their time in male company, and the only time when they interact with females to any great degree is when they court oestrous females. Chimpanzee females tend to spend a great part of their time on their own or accompanied only by their offspring (Goodall, 1968; Halperin, 1979; Muroyama & Sugiyama, 1994; Nishida, 1979; Wrangham & Smuts, 1980). In contrast, bonobo males do not spend that much time together; the bonds between them do not seem to be so strong, and females travel as much in big parties as the males do (Badrian & Badrian, 1984; Kano, 1980; 1982; 1983; Kuroda, 1979; Muroyama & Sugiyama, 1994;

White, 1989). In summary, in common chimpanzees the emphasis is on male relationships (Goodall, 1986; de Waal, 1982), whereas in bonobos it is on male/female relationships (White, 1989).

A difference in the quality of habitat occupied by the two species has been put forward as a possible reason for their differences in social organsiation (for a review, see Chapman *et al.*, 1994). The well-studied populations of common chimpanzees at Gombe and Mahale live in a mosaic of evergreen and semi-deciduous forest, woodland and grassland (Clutton-Brock & Gillett, 1979; Nishida *et al.*, 1979) with annual rainfalls well below 2000 millimetres (Goodall, 1986; Collins & McGrew, 1987; Nishida in McGrew et al., 1981), while bonobos inhabit evergreen tropical rain forests with rainfalls of approximately 2,000 millimetres (White & Lanjouw, 1992). Living in a more productive habitat, bonobos were assumed to suffer less feeding competition than common chimpanzees. The tropical forest is suggested to provide them with more terrestrial herbaceous vegetation (Badrian & Badrian, 1984; Wrangham, 1986) or with bigger food patches (Badrian & Badrian, 1984; White, 1986, quoted in Chapman *et al.*, 1994; White and Wrangham, 1988). They could therefore afford to live in bigger parties which would exhibit social relationships adapted to life in bigger parties.

If this is true, however, common chimpanzees living in habitats more productive than those at Gombe and Mahale should show trends in their social organisations which are similar to bonobos, i.e. they should tend more towards male/female and less towards male/male relationships than other common chimpanzee populations. The Kibale chimpanzees live in a medium altitude moist evergreen and semi-deciduous forest (see Chapter 2) with annual rainfalls between those at Gombe and those at Lomako. If the hypothesis is true that habitat quality influences the details of chimpanzee social organisation, the Kibale chimpanzees should show trends in their social organisation which are more similar to bonobos than to common chimpanzees in poorer habitats.

In his study at Ngogo, Ghiglieri (1984) already suggested that females of the Ngogo chimpanzee community in Kibale Forest followed the "bonobo pattern" in their relationships with other community members rather than the "chimpanzee pattern". However, results from Kanaywara, another study site in the same forest, seemed to contradict this. Wrangham *et al.* (1992) suggested that this apparent difference between the two communities was a result of different methods and definitions. The current study's much more detailed observations of the Ngogo community should enable us to determine conclusively whether this was true or whether there is a real difference between the two communities in the Kibale

Forest and between common chimpanzees from forest and from non-forest habitats.

Due to the poor habituation of the Ngogo chimpanzees and the size of the community (see Chapter 3), individual identities of interactants were most often unknown. Analysis of relationships therefore had to be restricted to an analysis of relationships between age/sex classes. This inevitably raises problems of pseudoreplication (Hurlbert, 1984), which I discuss in detail in later sections.

In order to determine which age/sex class was the preferred partner for social behaviour in adult males and females, proximity relationships, grooming interactions and other types of affinitive behaviour as well as agonistic and submissive behaviour were analysed. For every focal animal sample, all occurrences of approaching, following, leaving, grooming and being groomed by interactants of all age/sex classes were counted. Data were matched for sex class of the focal animal, activity and age/sex class of the interactant. Wilcoxon matched-pairs signed ranks tests were used to compare the frequency of approaching (following, leaving, grooming, being groomed by) with the frequency of being approached (followed, left, groomed by and grooming) by interactants of certain age/sex classes or to compare the frequency of approaching (following, leaving, grooming, being groomed by) interactants of certain age/sex classes with the frequency of approaching (following, leaving, grooming, being groomed by) interactants of other age/sex classes.

4.2 Proximity relationships

The mean nearest neighbour distance for Ngogo chimpanzees was 4.4 m when all adult focal animals were analysed (range 0-25 m, N=1563 five-minute scans) and when males and females were analysed separately (males: range 0-25, N=1074; females: range 0-25 m, N=489).

The distance to the nearest neighbour varied depending on the activity of the focal animal. When feeding, the mean nearest neighbour distance was 5.1 m for all focal animals (range: 0-25 m; N=711) and for males (range: 0-20 m, N=525), while it was only 4.8 m for females (range: 0-25 m, N=186). The mean nearest neighbour distance in all other activities was 3.9 for all focal animals (range: 0-25 m, N=824).

Compared to the chimpanzees at Kanyawara (White & Chapman, 1994), the Ngogo chimpanzees have greater mean nearest neighbour distances except for the females (Table 4.1). Compared to the bonobos at Lomako (White & Chapman, 1994), the Ngogo chimpanzees have identical feeding distances when all data are considered and when the females are analysed separately; however, feeding distances for males are smaller at Ngogo (Table 4.1). When all activities are considered, Ngogo chimpanzees have greater mean nearest neighbour distances than the bonobos at Lomako. The same is true for the Ngogo females, whereas the Ngogo males have smaller mean nearest neighbour distances than the bonobo males.

Adult males were the nearest neighbour of focal adult males more often than any other age/sex class (Table 4.2; only parties with a size of over 2 were included in the analysis). The same was true for focal anoestrous and oestrous females. However, the representation of age/sex classes as nearest neighbours was not significantly different from what would be expected from the representation of each age/sex class in the community (Kolmogorov-Smirnov two-sample test, m=8, n=8; adult males: $D_{m,n}=0.397$, p>0.10; anoestrous females: $D_{m,n}=0.20$, p>0.10; oestrous females: $D_{m,n}=0.555$, p>0.10).

4.3 Proximity interactions

For the following analysis, data were matched for focal animal follow, activity and age/sex class of the interactant. Wilcoxon matched pairs signed ranks tests were used to determine whether differences in the frequency of approaching, leaving and following interactants of a certain age/sex class and approaching,

Table 4.1: Mean nearest neighbour distances (in m) at Kanyawara, Lomako (both White & Chapman, 1994) and Ngogo

	Kanyawara	Lomako[1]	Ngogo
All data, all activities	4.1	4.0	4.4
All data, feeding	4.6	5.1	5.1
All data, all other activities	3.6	2.5	3.9
Males, all activities	3.1	4.8	4.4
Males, feeding	3.3	5.8	5.1
Females, all activities	4.7	3.7	4.4
Females feeding	5.3	4.8	4.8

[1] Distances of over 15 m excluded to make data comparable to the Kibale data; see White & Chapman, 1994.

Table 4.2: Frequencies of nearest neighbours' sex classes.

Age/sex class of nearest neighbour	Focal animal: Adult male		Adult female		Oestrous female	
	N	%	N	%	N	%
Adult male	694	66.8	147	47.1	204	82.6
Adult female	120	11.5	62	19.9	6	2.4
Subadult male	69	6.6	24	7.7	14	5.7
Subadult female	31	3.0	9	2.9	3	1.2
Juvenile male	68	6.5	11	3.5	8	3.2
Juvenile female	0	0.0	47	15.1	5	2.0
Infants	1	.1	5	1.6	3	1.2
Oestrous female	56	5.4	7	2.2	4	1.6
All	1039	99.9[1]	312	100.0	247	99.9[1]

[1] Total percentage of less than 100 due to rounding.

leaving and following interactants of other certain age/sex classes were significant.

Adult males approached other adult males more often than they approached any other age/sex class (Wilcoxon matched-pairs signed ranks test, N=95 focal animal samples, p<0.01 in all comparisons; Table 4.3). They approached infants significantly less often than any other age/sex class (Wilcoxon matched-pairs signed ranks test, N=95; p<0.05 in all comparisons). They approached subadults significantly more often than they approached oestrous females (Wilcoxon matched-pairs signed ranks test, N=95, p<0.05). However, this significance disappears when the data from three all-day follows of the same adult male and subadult female are excluded (Wilcoxon matched-pairs signed ranks test, N=91, p=0.139).

Anoestrous females approached juveniles significantly more than they approached subadults (Wilcoxon matched-pairs signed ranks test, N=43 follow animal samples, p<0.05; Table 4.5), but otherwise there were no significant differences between sex classes.

Oestrous females approached adult males more often than any other age/sex class (Wilcoxon matched-pairs signed ranks test, N=23 focal animal samples, p<0.0001 in all comparisons; Table 4.4). There were no significant

Table 4.3: Occurrences of approaching, following and leaving other animals in samples where the focal animal was an adult male.[1]

Behaviour	Age/sex classes: adult male	adult female	sub-adult male	sub-adult female	sub-adult unknown sex	juvenile male	juvenile female	juvenile unknown sex	infant	oestrous female	N
Approach	43	6	6	39 (1)	0	3	0	4	0	1	102
	0.12	*0.02*	*0.02*	*0.11* (*)	*0*	*0.01*	*0*	*0.01*	*0*	*0.00*	*0.29*
Being approached	51	28	5	69 (4)	0	13	1	11	2	12	192
	0.14	*0.08*	*0.01*	*0.19* (+)	*0*	*0.04*	*0*	*0.03*	*0.01*	*0.03*	*0.54*
Follow	33	0	1	16	0	2	0	0	0	10	62
	0.09	*0*	*0*	*0.04*	*0*	*0.01*	*0*	*0*	*0*	*0.03*	*0.17*
Being followed	10	4	1	29	0	3	0	2	1	7	57
	0.03	*0.01*	*0*	*0.08*	*0*	*0.01*	*0*	*0.01*	*0.00*	*0.02*	*0.16*
Leave	29	6	0	33 (3)	0	6	0	2	0	10	86
	0.08	*0.02*	*0*	*0.09* (+)	*0*	*0.02*	*0*	*0.01*	*0*	*0.03*	*0.24*
Being left	64	18	7	45 (0)	0	8	0	10	0	13	125
	0.18	*0.05*	*0.02*	*0.13* (0)	*0*	*0.02*	*0*	*0.03*	*0*	*0.04*	*0.35*

Note: Numbers in brackets give occurences excluding three all day follows of the same adult male and subadult female. The lower figure in each cell gives rates per focal animal hour. *: 0.00; +: 0.01; [1]N=95 focal animal samples.

Table 4.4: Occurrences of approaching, following and leaving other animals in samples where the focal animal was an oestrous female.[1]

Behaviour	Age/sex classes:										
	adult male	adult female	sub-adult male	sub-adult female	sub-adult unknown sex	juvenile male	juvenile female	juvenile unknown sex	infant	oestrous female	N
Approach	75	0	3	0	0	1	1	1	0	0	81
	0.72	*0*	*0.03*	*0*	*0*	*0.01*	*0.01*	*0.01*	*0*	*0*	*0.78*
Being approached	54	0	1	0	0	7	0	2	0	0	64
	0.52	*0*	*0.01*	*0*	*0*	*0.07*	*0*	*0.02*	*0*	*0*	*0.62*
Follow	37	0	0	0	0	1	0	0	0	0	38
	0.36	*0*	*0*	*0*	*0*	*0.01*	*0*	*0*	*0*	*0*	*0.37*
Being followed	16	0	0	0	0	0	1	0	0	0	17
	0.15	*0*	*0*	*0*	*0*	*0*	*0.01*	*0*	*0*	*0*	*0.16*
Leave	47	0	0	0	0	0	0	0	0	0	47
	0.45	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0*	*0.45*
Being left	67	0	0	0	0	8	0	0	0	0	75
	0.64	*0*	*0*	*0*	*0*	*0.08*	*0*	*0*	*0*	*0*	*0.72*

Note: The lower figure in each cell gives rates per focal animal hour. [1]N=23 focal animal samples.

differences between the frequencies with which other age/sex classes were approached.

Adult males followed other adult males significantly more often than any other age/sex class except subadults (Wilcoxon matched-pairs signed ranks test, N=95 focal animal samples, $p<0.05$ in all comparisons; Table 4.3). When the three-day sample of the same adult male and subadult female is excluded from the data, the comparison between males following males and males following subadults is significant too ($p<0.001$). In addition, adult males follow oestrous female significantly more often than they follow anoestrous females or infants ($p<0.05$).

Anoestrous females followed juveniles more often than subadults (Wilcoxon matched-pairs signed ranks test, N=43 focal animal samples, $p<0.05$; Table 4.5), but otherwise there were no significant differences.

Oestrous females followed adult males almost exclusively: all comparisons involving adult males were significant (Wilcoxon matched-pairs signed ranks test, N=23 focal animal samples; $p<0.001$ in all comparisons; Table 4.4). All other comparisons were not significant.

Adult males left other adult males more often than any other age/sex class (Wilcoxon matched-pairs signed ranks test, N=95 focal animal samples, $p<0.05$ in all

Table 4.5: Occurrences of approaching, following and leaving other animals in samples where the focal animal was an anoestrous adult female.[1]

Behaviour	Age/sex classes:										
	adult male	adult female	sub-adult male	sub-adult female	sub-adult unknown sex	juvenile male	juvenile female	juvenile unknown sex	infant	oestrous female	N
Approach	7 *0.03*	7 *0.03*	0 *0*	1 *0*	0 *0*	1 *0*	1 *0*	5 *0.02*	11 *0.04*	2 *0.01*	35 *0.13*
Being approached	14 *0.05*	10 *0.04*	0 *0*	5 *0.02*	0 *0*	19 *0.07*	14 *0.05*	51 *0.19*	79 *0.30*	1 *0*	193 *0.74*
Follow	3 *0.01*	3 *0.01*	0 *0*	0 *0*	0 *0*	0 *0*	1 *0*	5 *0.02*	1 *0*	1 *0*	14 *0.05*
Being followed	0 *0*	2 *0.01*	0 *0*	2 *0.01*	0 *0*	0 *0*	5 *0.02*	24 *0.09*	15 *0.06*	0 *0*	48 *0.18*
Leave	4 *0.02*	5 *0.02*	0 *0*	1 *0*	0 *0*	1 *0*	3 *0.01*	6 *0.02*	14 *0.05*	3 *0.01*	37 *0.14*
Being left	9 *0.03*	5 *0.02*	0 *0*	4 *0.02*	0 *0*	10 *0.04*	7 *0.03*	26 *0.10*	82 *0.31*	1 *0*	144 *0.55*

Note: The lower figure in each cell gives rates per focal animal hour. [1]N=43 focal animal samples.

comparisons; Table 4.3) except subadults, whom adult males left even more frequently ($p<0.02$). However, when the data on three all-day samples of the same adult male and subadult female are extracted from the datapool, subadults are left more often by males than other males ($p<0.01$).

Anoestrous females leave infants significantly more often than any other age/sex class other than juveniles (Wilcoxon matched-pairs signed ranks test, N=43 focal animal samples, $p<0.05$ in all comparisons; $p=0.398$ in the comparison with juveniles; Table 4.5). Juveniles are left significantly more often than subadults ($p<0.05$).

Oestrous females left adult males signficantly more often than they left any other age/sex class (Wilcoxon matched-pairs signed ranks test, N=23 focal animal samples, $p<0.001$ in all comparisons; Table 4.4). The other differences were not significant.

4.4 Responsibility for maintaining proximity

For the following analysis, data were matched for focal animal follow, activity and age/sex class of the interactant. Wilcoxon matched-pairs signed ranks test was used to determine whether differences in the frequency of approaching, leaving and following an interactant of a certain age/sex class on the one hand and being approached, being left and being followed by interactants of the same age/sex class on the other hand were significant.

In samples where adult males were the focal animal, adult males approached adult females significantly less often than they were approached by them, independent of the females' reproductive state (Table 4.3; Wilcoxon matched-pairs signed ranks test, N=95 focal animal samples; anoestrous females: $p<0.01$, oestrous females: $p=0.0519$). This result holds if subadult females are included in the adult anoestrous category (Wilcoxon matched-pairs signed ranks test, N=95, $p<0.001$). Adult males were never observed to follow anoestrous adult females. They did follow subadult females, although subadult females followed them significantly more often (Wilcoxon matched-pairs signed ranks test, N=95, $p<0.05$). When adult and subadult females are combined, females followed males more often than the other way around (Wilcoxon matched-pairs signed ranks test, N=95, $p<0.05$). They also followed oestrous females, but this did not happen significantly more often than oestrous females following adult males (Wilcoxon matched-pairs signed ranks test, N=95, $p>0.5$). Anoestrous adult females left adult males significantly more often than adult males left them (Wilcoxon matched-pairs signed ranks test, N=95, $p<0.05$); for oestrous females the difference is not significant (Wilcoxon matched-pairs signed ranks test, N=95, $p>0.5$).

These results suggest that the females are mainly responsible for maintaining proximity to the adult males, irrespective of their reproductive state. This is confirmed by the calculation of approach/leave indices (Hinde, 1974): between adult males and anoestrous adult females it is -7.0 (-6.55 if subadult females are included) and between adult males and oestrous adult females it is -35.48.

To test this result, approach/leave indices are calculated from those samples with anoestrous and oestrous females as focal animals (Tables 4.4 and 4.5): the index between oestrous females and adult males is 17.0, i.e. the oestrous female is responsible for maintaining proximity with the adult male. However, the approach/leave index between adult anoestrous females and adult males is only 2.33 (Table 4.5). This is much weaker than what was calculated from the adult male focal samples. Also, Table 4.5 shows that anoestrous adult females are approached by adult males more often than the other way around, although this difference is not significant (Wilcoxon matched-pairs signed ranks test, N=43 focal animal follows, p>0.05).

To increase sample size, rates of approaching, following and leaving per focal animal hour are calculated (Tables 4.3, 4.4, 4.5) which makes it possible to combine all focal animal samples into one table (Table

4.6). A Wilcoxon signed ranks test shows that there is no difference between anoestrous females approaching males and adult males approaching anoestrous females (N=138 focal animal samples, p=0.6373). In contrast, oestrous females approach adult males significantly more often than they are approached by them (Wilcoxon signed ranks test, N=118 focal animal follows, p<0.05).

4.5 Grooming relationships

4.5.1 Frequency of grooming

For the following analysis, data were matched for focal animal follow, activity and age/sex class of the interactant. Wilcoxon matched-pairs signed ranks tests were used to determine whether differences in the frequency of grooming interactants of a certain age/sex class and the frequency of grooming interactants of other age/sex classes were significant.

Adult males groom other adult males significantly more often than they groom any other age/sex class (Tables 4.7, 4.8, 4.9; Wilcoxon matched-pairs signed ranks test, N=95 focal animal follows, all comparisons [adult males as interactants versus anoestrous and oestrous females, subadults, juveniles, and infants]: p<0.001). This holds true even if subadult females are included in the adult female category (Wilcoxon matched-pairs signed ranks

Table 4.6: Mean rates (number of occurrence / focal animal / hour) of adult males approaching, following and leaving anoestrous and oestrous adult females in all focal animal samples.

	Age/sex classes:	
Behaviour	Anoestrous female[1]	Oestrous female[2]
Approach	0.35	0.26
Being approached	0.55	0.38
Follow	0	0.09
Being followed	0.01	0.45
Leave	0.25	0.34
Being left	0.35	0.25

[1] N=138 focal animal samples; [2] N=118 focal animal samples.

Table 4.7: Age/sex classes of interactants in samples with male focal animals.

Behaviour	Adult males	Adult females	Subadults	Juveniles	Infants	Oestrous females	N
Grooming the interactant	194 *90*	17 *84*	65 (16)[1] *48*	33 *57*	1 *52*	23 *2*	333
Being groomed by the interactant	197 *103*	54 *95*	59 (29) *54*	53 *65*	0 *60*	17 *2*	380
Affinitive behaviour	3 *5*	4 *5*	12 (0) *3*	1 *3*	0 *3*	0 *0*	20
Sexual behaviour	15 *8*	0 *8*	11 (0) *4*	0 *5*	0 *5*	5 *0*	31
Agonistic behaviour	5 *11*	0 *11*	32 (4) *6*	3 *7*	0 *7*	2 *0*	42
Submissive behaviour	5 *1*	0 *1*	0 *1*	0 *1*	0 *1*	0 *0*	5
All	495	81	241 (57)	99	1	58	975

Note: For definitions of behaviour types see Chapter 2. [1]Values in brackets give numbers excluding a three-days sample of an adult male and a subadult female. Expected values (according to representation of each age/sex class in the community) in italics. Due to rounding, expected totals may not equal the observed totals.

Table 4.8: Mean rates of grooming: occurrences of grooming per 10 focal animal hours.

Interactant	Focal animal: Adult males	Adult females	Oestrous females
Adult male	5.59	1.64	7.02
Anoestrous female	0.48	0.23	0
Subadult	1.94	0.08	0
Juvenile	0.81	5.31	1.25
Infant	0.03	3.85	0
Oestrous female	0.65	0.19	0
N[1]	95	43	23
Focal animal hours	356	262	104

[1] Number of focal animal follows

Table 4.9: Probabilities in Wilcoxon matched-pairs signed ranks test comparing the frequency of grooming between the focal animal and other age/sex classes.

Comparison of interactants	Focal animal: Adult males[1]	Adult females[2]	Oestrous females[3]
Adult male/adult female	$p<0.0001$	$p<0.05$	$p<0.01$
Adult male/subadult	$p<0.001$ ($p<0.0001$)	$p<0.01$	$p<0.01$
Adult male/juvenile	$p<0.0001$	$p<0.05$	$p<0.05$
Adult male/infant	$p<0.0001$	$p=0.0505$	$p<0.01$
Adult male/oestrous female	$p<0.001$	$p<0.05$	$p<0.01$
Adult female/subadult	$p=0.3627$ ($p=0.9645$)	$p=0.1797$	$p=1.0$
Adult female/juvenile	$p=0.5277$	$p=0.0001$	$p>0.05$
Adult female/infant	$p<0.01$	$p<0.001$	$p=1.0$
Adult female/oestrous female	$p=0.7548$	$p=0.8927$	$p=1.0$
Subadult/juvenile	$p=0.7404$ ($p=0.5509$)	$p<0.0001$	$p>0.05$
Subadult/infant	$p<0.01$ ($p<0.05$)	$p=0.0001$	$p=1.0$
Subadult/oestrous female	$p=0.3464$ ($p=1.0$)	$p=0.4227$	$p=1.0$
Juvenile/infant	$p<0.05$	$p=0.3447$	$p>0.05$
Juvenile/oestrous female	$p=0.6002$	$p=0.0001$	$p>0.05$
Infant/oestrous female	$p<0.0592$	$p=0.0001$	$p=1.0$

Note: Probabilities in brackets from analysis excluding 3 all-day samples of the same adult male and subadult female. [1]N=95 focal anmal samples; [2]N=43 focal animal samples; [3]N=23 focal animal samples.

test, N=95, p<0.001). After other adult males, subadults are adult males' favorite grooming partners. However, the numbers in the subadult column in Table 4.7 are high only when three all-day samples of one adult male, MW, and a subadult female, KW, are included. When these two are excluded from the analysis, subadults are groomed by adult males as little as adult females (Wilcoxon Matched-pairs signed ranks Test, N=95, p=0.96) or oestrous females (N=95; p=1.0).

There is no significant difference in adult males grooming anoestrous or oestrous females, subadults (see above) and juveniles (Table 4.9). Only infants are groomed significantly less by adult males. These results hold even when subadult females are included in the adult category.

However, this distribution of grooming might be due to the fact that different age/sex classes may be represented in the community to different degrees. Adult males represent 27.1% of the Ngogo community, adult females represent 25.7% (see Chapter 3). If grooming is distributed at random, 27.1% should fall on males, 25.7% on females. Similarly, the probability that a female is in oestrus is (30/4 x 365)=0.0205, assuming that the female is in oestrus for 10 days in each of three menstrual cycles before conceiving on each 4-year reproductive cycle (Dunbar, 1988). For the Ngogo community with its 38 adult and subadult females, the expected number of females in oestrus is 0.0205 x 38 = 0.78. This represents 0.56% of the Ngogo community. Hence, 0.56% of grooming should be devoted to oestrous females if grooming is random. This percentage has to be subtracted from the adult anoestrous females.

Table 4.10 shows that grooming is not distributed at random in the Ngogo community. Adult males groom other adult males more than twice as much as would be expected if their grooming was distributed according to the representation of each age/sex class in the community, and they groom oestrous females more than ten times as often (X^2 one-sample test; X^2=393.1, df=2, p<0.001).

The distribution of age/sex classes grooming the focal males is similar to the distribution of age/sex classes being groomed by the focal males: adult males groom focal males significantly more often than any other age/sex class (Tables 4.7 and 4.11) and infants groom focal males significantly less often than any other age/sex class . There are no significant differences in the frequency with which other age/sex classes groom the focal males.

Anoestrous females groom juveniles and infants significantly more often than any other age/sex class and adult males significantly more often than other anoestrous females, subadults or oestrous females (Wilcoxon matched-pairs signed ranks test; p<0.05 when subadult females are included in the adult female

Table 4.10: Expected and observed distribution of grooming

Focal animal	Grooming partner		
	Adult males	Adult females	Oestrous females
Adult male			
Expected	27.1%	25.1%	0.6%
Observed	58.3%	5.1%	6.9%
Adult female			
Expected	27.1%	25.1%	0.6%
Observed	12.3%	1.7%	0.9%
Oestrous female			
Expected	27.1%	25.1%	0.6%
Observed	84.9%	0.0%	0.0%

Table 4.11: Probabilities in Wilcoxon matched-pairs signed ranks test comparing the frequency of the focal animal being groomed by various age/sex classes

Comparison of interactants	Focal animal:		
	Adult males	Anoestrous females	Oestrous females
Adult male/adult female	p<0.01	p=0.505	p<0.001
Adult male/subadult	p<0.01	p=0.110	p<0.001
Adult male/juvenile	p<0.0001	p<0.02	p<0.002
Adult male/infant	p<0.0001	p=0.224	p<0.001
Adult male/oestrous female	p<0.0001	p=0.262	p<0.001
Adult female/subadult	p=0.931	p=0.138	p=1.0
Adult female/juvenile	p=0.498	p<0.02	p=0.1088
Adult female/infant	p<0.01	p=0.799	p=1.0
Adult female/oestrous female	p=0.056	p=0.612	p=1.0
Subadult/juvenile	p=0.528	p<0.01	p=0.109
Subadult/infant	p<0.01	p=0.345	p=1.0
Subadult/oestrous female	p=0.130	p=1.0	p=1.0
Juvenile/infant	p<0.02	p<0.01	p=0.109
Juvenile/oestrous female	p=0.320	p<0.01	p=0.109
Infant/oestrous female	p<0.02	p=0.735	p=1.0

category; Tables 4.8, 4.9, 4.12). However, they groom males less than half as often as their representation in the community would suggest, and they groom other adult females even less frequently ($X^2=105.1$, df=2, $p<0.001$; Table 4.10). The brunt of anoestrous females' grooming goes to juveniles and infants, presumably the females' offspring (Table 4.12).

Anoestrous females were groomed by juveniles more frequently than by any other age/sex class (Tables 4.11 and 4.12). There were no significant differences between the other age/sex classes. It should be mentioned that the difference between anoestrous females grooming focal males and oestrous females grooming focal males almost reaches significance ($p=0.0559$; Tables 4.11).

Oestrous females were observed to groom only males and juveniles in samples with oestrous females as focal animals (N=23 focal animal samples; Tables 4.8 and 4.13). They groom males more than 3 times as much as they should if their grooming was distributed according to the representation of each age/sex class in the community (X^2 one-sample test: $X^2=148.5$, df=2, $p<0.001$; Table 4.10). It should be mentioned that oestrous females were observed to groom anoestrous females, but this happened only in samples where the anoestrous female was the focal animal (see Table 4.12).

Table 4.12: Age/sex classes of interactants in samples where the focal animals were adult anoestrous female.

Behaviour	Adult males	Adult females	Subadults	Juveniles	Infants	Oestrous females	N
Grooming the interactant	43 *95*	6 *88*	2 *50*	176 *60*	120 *55*	3 *2*	350
Being groomed by the interactant	18 *47*	13 *45*	8 *25*	116 *30*	10 *27*	9 *1*	174
Affinitive behaviour	0 *13*	2 *12*	0 *7*	12 *8*	35 *8*	0 *0*	49
Sexual behaviour	1 *1*	1 *1*	0 *0*	0 *0*	0 *0*	0 *0*	2
Agonistic behaviour	0 *0*	0 *0*	0 *0*	0 *0*	0 *0*	0 *0*	0
Submissive behaviour	0 *0*	0 *0*	0 *0*	0 *0*	0 *0*	0 *0*	0
All	72	32	11	317	177	15	624

Note: For definitions of behaviour types see Chapter 2. Expected values (according to representation of each age/sex class in the com̄unity) in italics. Due to rounding, expected totals might not equal the observed totals.

Table 4.13: Age/sex classes of interactants in samples where the focal animals were oestrous females.

Behaviour	Adult Males	Adult Females	Sub-adults	Juveniles	Infants	Oestrous females	N
Grooming the interactant	73	0	0	13	0	0	86
	23	*22*	*12*	*15*	*14*	*1*	
Being groomed by the interactant	135	0	0	13	0	0	148
	40	*37*	*21*	*25*	*23*	*1*	
Affinitive behaviour	6	1	0	0	0	0	7
	2	*2*	*1*	*1*	*1*	*0*	
Sexual behaviour	41	0	5	3	0	0	49
	13	*12*	*7*	*8*	*7.7*	*0*	
Aggressive behaviour	0	0	2	0	0	0	2
	1	*1*	*0*	*0*	*0*	*0*	
Submissive behaviour	7	0	0	0	0	0	7
	2	*2*	*1*	*1*	*1*	*0*	
All	374	1	10	33	0	0	418

For definitions see Chapter 2. Expected values(according to representation of each age/sex class in the community) in italics. Due to rounding, expected totals might not equal the observed totals.

Similarly, only adult males and juveniles were observed to groom oestrous females (Table 4.13) when an oestrous female was the focal animal. Adult males groomed oestrous females significantly more often than any other age/sex class (Tables 4.11 and 4.13). Again, anoestrous females groomed oestrous females on three occasions (Table 4.12), but in these cases the anoestrous female was the focal animal.

4.5.2 Direction of grooming

For the following analysis, data were matched for focal animal follow, activity and age/sex class of the interactant. Wilcoxon matched pairs signed ranks tests were used to determine whether differences in the frequency of grooming an interactant of a certain age/sex class and being groomed by interactants of the same age/sex class were significant.

Adult male chimpanzees were groomed by anoestrous females (with and without offspring) significantly more often than they groomed them (Wilcoxon matched-pairs signed ranks test, N= 95 focal animal follows, $p<0.01$; Tables 4.7, 4.8, 4.14). In contrast, other adult males, subadults and juveniles of either sex and oestrous females groomed focal males approximately as frequently as they were groomed by them (Wilcoxon matched-pairs

Table 4.14: Mean rates of being groomed: occurrences of being groomed per 10 focal animal hours.

Interactant	Focal animal: Adult males	Adult females	Oestrous females
Adult male	5.22	0.69	13.0
Anoestrous female	1.52	0.50	0
Subadult	1.99	0.31	0
Juvenile	1.18	3.21	1.23
Infant	0	0.34	0
Oestrous female	0.48	0.34	0
N[1]	95	43	23
Focal animal hours	356	262	104

[1] Number of focal animal follows

signed ranks test, N=95 focal animal samples; all comparisons: p>0.2; Tables 4.7, 4.8, 4.14).

When anoestrous adult females were focal animals, they groomed adult males significantly more often than they were groomed by them (Wilcoxon matched-pairs signed ranks test, N=43 focal animal follows, p<0.02; Tables 4.8, 4.12, 4.14). They also groomed juveniles and infants more than juveniles and infants groomed anoestrous females (Wilcoxon matched-pairs signed ranks test, N=43, p<0.001 in both comparisons). However, there was no significant difference between grooming and being groomed when the interactants were subadults of either sex, other anoestrous adult females or oestrous females (Wilcoxon matched-pairs signed ranks test, N=43, p>0.2 in all comparisons).

Oestrous females were groomed by adult males significantly more often than they groomed them (Wilcoxon matched-pairs signed ranks test, N=23 focal animal samples; p<0.01; Tables 4.8., 4.13, 4.14). The only other age class observed to groom with oestrous females when they were focal animals was the juvenile class: juveniles groomed oestrous females as often as they were groomed by them (Wilcoxon matched-pairs signed ranks test, N=23, p=1.0).

4.6 Other affinitive types of behaviour

Other affinitive types of behaviour (playing with, reaching out, sitting down in front of, touching, hugging and begging from another animal) were observed in adult males only 20 times, in adult anoestrous females 49 times and in oestrous females 7 times (Tables 4.7, 4.12, 4.13). Play was only observed between adult anoestrous females and juveniles or infants. All other affinitive types of behaviour occurring in anoestrous adult females were also restricted to juveniles and infants.

Adult males touched and reached out to subadult females more than to any other age/sex class. They hardly interacted at all with chimpanzees who had not reached the subadult stage yet.

Oestrous females interacted almost exclusively with adult males. Table 4.15 gives the break down of affinitive types of behaviour.

4.7 Agonistic types of behaviour

Agonistic types of behaviour were observed 197 times in adult males, not at all in anoestrous females and only twice in oestrous females (Tables 4.7, 4.12, 4.13). Subadults received more aggression from adult males than any other age/sex class. However, of 187 agonistic

Table 4.15: Frequencies of affinitive types of behaviour (for definitions see Chapter 2).

Behaviour	Age/sex class of interactant: Adult male	Adult female	Subadult	Juvenile	Infant	Oestrous female	N
Focal animal: adult male[1]							
Reach out	1	0	2 (0)	0	0	0	3
Touch	1	0	11 (0)	1	0	0	12
Reciprocal Touch	1	4	0	0	0	0	5
Play	0	0	0	0	0	0	0
Hug	0	0	0	0	0	0	0
Sitting down in front of	0	0	0	0	0	0	0
All	3	4	13 (0)	1	0	0	20
Focal animal: anoestrous female[2]							
Reach out	0	0	0	2	1	0	3
Touch	0	0	0	1	1	0	2
Reciprocal Touch	0	1	0	0	0	0	1
Play	0	0	0	9	33	0	42
Hug	0	1	0	0	0	0	1
Sitting down in front of	0	0	0	0	0	0	0
All	0	2	0	12	35	0	49
Focal animal: oestrous female[3]							
Reach out	2	0	0	0	0	0	2
Touch	3	1	0	0	0	0	4
Reciprocal Touch	0	0	0	0	0	0	0
Play	0	0	0	0	0	0	0
Hug	0	0	0	0	0	0	0
Sitting down in front of	1	0	0	0	0	0	1
All	6	1	0	0	0	0	7

Note: Numbers in brackets give occurrences excluding three all-day follows of the same adult male and subadult female

[1] N=95 focal animal samples, 365 focal animal hours.

[2] N=43 focal animal samples, 262 focal animal hours.

[3] N=23 focal animal samples, 104 focal animal hours.

incidents against subadults, 183 were against the same subadult female, KW, when she was in a 3-days consortship with MW. The remaining four incidents were against subadult males.

The only two agonistic incidents observed in oestrous females were attacks on subadult males. Table 4.16 gives the break-down.

4.8 Submissive types of behaviour

Anoestrous adult females were observed to behave submissively only twice: once one anoestrous female presented to an adult male and once to another anoestrous adult female. Adult males and oestrous females behaved submissively only towards adult males. (Tables 4.7, 4.12, 4.13, 4.17). Presenting was recorded as submissive behaviour when the actor was either an anoestrous female or an adult male; when the actor was an oestrous female, presenting was recorded as sexual behaviour (Goodall, 1986). The one case where a male presented to a female (Table 4.17) was a solicitation for grooming.

4.9 Sexual types of behaviour

Of 37 observed copulations, 9 happened when the focal animal was an adult male, while 28 happened while the

Table 4.16: Frequencies of agonistic types of behaviour. For definitions see Chapter 2.

Behaviour	Age/sex class of interactant:						
	Adult male	Adult female	Subadult female	Juvenile	Infant	Oestrous female	N
Focal animal: adult male[1]							
Displaying	1	0	17 (1)	0	0	0	9
Charge	1	0	3 (0)	0	0	0	4
Shaking Branches to	0	0	153 (0)	0	0	0	7
Displacing	1	0	2 (2)	1	0	0	4
Chasing	2	0	12 (1)	2	0	2	18
All	5	0	187 (4)	3	0	2	42
Focal animal: oestrous female[2]							
Displaying	0	0	0	0	0	0	0
Charge	0	0	2	0	0	0	2
Shaking Branches to	0	0	0	0	0	0	0
Displacing	0	0	0	0	0	0	0
Chasing	0	0	0	0	0	0	0
All	0	0	2	0	0	0	2

Note. Numbers in brackets give occurences excluding three all-day follows of the same adult male and subadult female.

[1] N=95 focal animal samples, 356 focal animal hours.

[2] N=23 focal animal samples, 104 focal animal hours.

Table 4.17: Frequencies of submissive types of behaviour. For definitions see Chapter 2.

Behaviour	Age/sex class of interactant: Adult male	Adult female	Subadult	Juvenile	Infant	Oestrous	N
Focal animal: adult male[1]							
Fear-grinning to	1	0	0	0	0	0	1
Running away from	1	0	0	0	0	0	1
Move after displacement	3	0	0	0	0	0	3
Presenting	15	0	1	0	0	0	16
All	20	0	1	0	0	0	21
Focal animal: anoestrous female[2]							
Fear-grinning to	0	0	0	0	0	0	0
Running away from	0	0	0	0	0	0	0
Move after displacement	0	0	0	0	0	0	0
Presenting	1	1	0	0	0	0	0
All	1	1	0	0	0	0	2
Focal animal: oestrous female[3]							
Fear-grinning to	1	0	0	0	0	0	1
Running away from	6	0	0	0	0	0	6
Move after displacement	0	0	0	0	0	0	0
All	7	0	0	0	0	0	7

[1] N=95 focal animal samples, 365 focal animal hours.
[2] N=43 focal animal samples, 262 focal animal hours.
[3] N=23 focal animal samples, 104 focal animal hours.

focal animal was an oestrous female (Table 4.18). Oestrous females were observed to present to and copulate with adult, subadult and juvenile males. G-g rubbing (for definition see Table 2.8) occurred only between one pair of animals, adult male MW and subadult female KW.

4.10 The problem of pseudoreplication

The type of analysis conducted in this chapter, i.e. pooling information from a limited number of individual chimpanzees is open to the criticism of pseudoreplication (Hurlbert, 1984). Due to differences in habituation, home ranges and sociability, some individuals contribute more observations than others. These individuals might be odd in some way and therefore influence the data pool in such a way that it reflects their individual peculiarities. The best solution to this problem is to analyse the data on an individual basis. Unfortunately, this was not possible in this study as individuals were not always recognisable and focal animal hours on the same known individuals were few. Under such circumstances, it has to be shown that those individuals contributing most data do not unduely influence the data pool. This is achieved by analysing the data pool when it contains the data from these individuals and analysing it when it does not.

Table 4.18: Frequencies of sexual types of behaviour. For definitions see Chapter 2.

Behaviour	Age/sex class of interactant: Adult male	Adult female	Subadult	Juvenile	Infant	Oestrous female	N
Focal animal: adult male[1]							
Copulating	0	0	5	0	0	4	9
G-G rubbing	0	0	5	0	0	0	5
Waving erect penis at	0	0	0	0	0	1	1
All	0	0	10	0	0	5	15
Focal animal: oestrous female[2]							
Copulating	23	0	4	1	0	0	28
G-G rubbing	0	0	0	0	0	0	0
Presenting	18	0	1	2	0	0	21
All	41	0	5	3	0	0	49

[1] N=95 focal animal samples, 356 focal animal hours.
[2] N=23 focal animal samples, 104 focal animal hours.

4.10.1 Males

The data on the male with the most focal animal hours (50.98), MW, which might be expected to influence the data disproportionately, were taken out and both subsets of grooming data (only the data from MW and all the data except those coming from MW) re-analysed. For the subset of all data other than MW, the results of the Wilcoxon matched pairs signed ranks test in the comparisons made in section 5.4 are almost identical except for a few differences in p values. However, when only those data coming from MW are analysed, the results seem to contradict the results of the general analysis (Tables 4.19 and 4.20): MW apparently grooms all age/sex classes equally frequently and all age/sex classes groom him equally frequently.

4.10.2 Anoestrous females

The dataset for anoestrous females was also divided in two subsets, one for the three females who provided 30.9% of the data, TI, SW and CR, and one for all the other anoestrous females. Tables 4.21 and 4.22 show that the other anoestrous females follow the pattern of all anoestrous females in everything except that there is no significant difference between grooming adult males and grooming juveniles. In contrast, the only significant comparisons in the dataset of TI, SW and CR are those involving juveniles: juveniles are groomed more often by

Table 4.19: Probabilities in Wilcoxon matched-pairs signed ranks test comparing the frequency of grooming between adult males and other age/sex classes based on various data sets.

Comparison of interactants	All adult males (N=95 samples)	MW only (N=15 samples)	All males except MW (N=80 samples)
Adult male/adult female	$p<0.0001$	$p=0.180$	$p<0.0001$
Adult male/subadult	$p<0.001$	$p=0.264$	$p<0.0001$
Adult male/juvenile	$p<0.0001$	$p=0.179$	$p<0.0001$
Adult male/infant	$p<0.0001$	$p=0.180$	$p<0.0001$
Adult male/oestrous female	$p<0.0001$	$p=0.180$	$p=0.0001$
Adult female/subadult	$p=0.363$	$p=0.109$	$p=0.965$
Adult female/juvenile	$p=0.528$	$p=1.0$	$p=0.528$
Adult female/infant	$p<0.01$	$p=1.0$	$p<0.01$
Adult female/oestrous female	$p=0.755$	$p=1.0$	$p=0.755$
Subadult/juvenile	$p=0.740$	$p=0.109$	$p>0.551$
Subadult/infant	$p<0.01$	$p=0.109$	$p<0.5$
Subadult/oestrous female	$p=0.346$	$p=0.109$	$p=1.0$
Juvenile/infant	$p<0.05$	$p=1.0$	$p<0.05$
Juvenile/oestrous female	$p=0.600$	$p=1.0$	$p=0.600$
Infant/oestrous female	$p<0.059$	$p=1.0$	$p=0.059$

Table 4.20: Probabilities in Wilcoxon matched-pairs signed ranks test comparing the frequency of the focal male being groomed by various age/sex classes, based on different datasets

Comparison of interactants	Focal animal:		
	All adult males (N=95 samples)	Mweya only (N=15 samples)	All males except Mweya (N=80 samples)
Adult male/adult female	p<0.01	p=0.655	p<0.01
Adult male/subadult	p<0.01	p=0.201	p<0.001
Adult male/juvenile	p<0.0001	p=0.317	p<0.0001
Adult male/infant	p<0.0001	p=0.317	p<0.0001
Adult male/oestrous female	p<0.0001	p=1.0	p<0.0001
Adult female/subadult	p=0.931	p=0.273	p=0.570
Adult female/juvenile	p=0.498	p=0.317	p=0.563
Adult female/infant	p<0.01	p=0.317	p<0.01
Adult female/oestrous female	p=0.056	p=0.317	p=0.064
Subadult/juvenile	p=0.528	p=0.109	p=0.826
Subadult/infant	p<0.01	p=0.109	p=0.028
Subadult/oestrous female	p=0.130	p=0.201	p=0.367
Juvenile/infant	p<0.02	p=1.0	p=0.012
Juvenile/oestrous female	p=0.320	p=0.317	p=0.272
Infant/oestrous female	p<0.02	p=0.317	p<0.03

Table 4.21: Mean rates of grooming for anoestrous females from different datasets[1]

	Focal animal:		
Interactant	All anoestrous females	TI, SW, CR only	Anoestrous fem. except TI, SW, CR
Adult male	1.64	0.37	2.21
Anoestrous female	0.23	1.48	0.33
Subadult	0.08	0	0.11
Juvenile	5.31	5.06	5.41
Infant	3.85	0.37	5.41
Oestrous female	0.65	0	0.28
N[2]	43	12	31
Focal animal hours	262	81	181

[1] Occurrences of grooming per 10 focal animal hours
[2] Number of focal animal follows

Table 4.22: Probabilities in Wilcoxon Matched-pairs signed ranks Test comparing the frequency of grooming between anoestrous females and other age/sex classes based on various data sets.

Comparison of interactants	Data set: All anoestrous females (N=43 samples)	TI, SW and CR only (N=12 samples)	All other anoestrous females (N=31 samples)
Adult male/adult female	$p<0.05$	$p=0.317$	$p<0.05$
Adult male/subadult	$p<0.01$	$p=0.317$	$p<0.02$
Adult male/juvenile	$p<0.05$	$p<0.05$	$p=0.147$
Adult male/infant	$p=0.0505$	$p=1.0$	$p<0.05$
Adult male/oestrous female	$p=0.05$	$p=0.317$	$p<0.05$
Adult female/subadult	$p=0.180$	$p=1.0$	$p=0.180$
Adult female/juvenile	$p=0.0001$	$p<0.02$	$p<0.003$
Adult female/infant	$p<0.001$	$p=0.180$	$p<0.001$
Adult female/oestrous female	$p=0.893$	$p=1.0$	$p=0.893$
Subadult/juvenile	$p<0.0001$	$p<0.02$	$p=0.001$
Subadult/infant	$p=0.0001$	$p=0.180$	$p=0.001$
Subadult/oestrous female	$p=0.423$	$p=1.0$	$p=0.423$
Juvenile/infant	$p=0.345$	$p<0.02$	$p=0.823$
Juvenile/oestrous female	$p=0.0001$	$p<0.02$	$p<0.002$
Infant/oestrous female	$p=0.0001$	$p=0.180$	$p=0.0002$

focal anoestrous females than any other age/sex class. Compared to other anoestrous females, TI, SW and CR groom adult males less, adult females more, juveniles equally and infants much less often than other anoestrous females (Table 4.21).

When data on TI, SW and CR are excluded from the data pool, anoestrous females continue to be groomed most often by juveniles; however, the differences in frequency between juveniles and adult males and between juveniles and adult females are no longer significant (Tables 4.23 and 4.24). There are no significant differences in being groomed by different age/sex classes in the TI, SW and CR dataset.

4.10.3 Oestrous females

For oestrous females, the dataset was divided into one for Lita, the female who contributed 50.8% of the data on oestrous females (see Chapter 5), and one for all other oestrous females. Tables 4.25 and 4.26 show that the main difference between Lita and the other oestrous females was that Lita did not groom juveniles. The inclusion of Lita's data therefore changed the comparison between oestrous females grooming adult males and oestrous females grooming juveniles from not being significantly different in the other oestrous females to being significantly different in all oestrous females.

Table 4.23: Mean rates of anoestrous females being groomed from different datasets[1]

Interactant	Focal animal:		
	All anoestrous females	TI, SW, CR only	Anoestrous fem. except TI, SW, CR
Adult male	0.69	0	0.99
Anoestrous female	0.50	0	0.72
Subadult	0.31	0	0.44
Juvenile	3.21	2.47	3.54
Infant	0.34	0.49	0.28
Oestrous female	0.34	0	0.50
N[2]	43	12	31
focal animal hours	262	81	181

[1] Occurrences of grooming per 10 focal animal hours
[2] Number of focal animal follows

Table 4.24: Probabilities in Wilcoxon matched-pairs signed ranks test comparing the frequency of the focal anoestrous female being groomed by various age/sex classes, based on different datasets

Comparison of interactants	Data set:		
	All anoestrous females (N=43 samples)	TI, SW and CR only (N=12 samples)	All other anoestrous females (N=31 samples)
Adult male/adult female	$p=0.505$	$p=1.0$	$p=0.505$
Adult male/subadult	$p=0.110$	$p=1.0$	$p=0.110$
Adult male/juvenile	$p<0.02$	$p=0.068$	$p=0.078$
Adult male/infant	$p=0.224$	$p=0.317$	$p=0.062$
Adult male/oestrous female	$p=0.262$	$p=1.0$	$p=0.262$
Adult female/subadult	$p=0.138$	$p=1.0$	$p=0.138$
Adult female/juvenile	$p<0.02$	$p=0.068$	$p=0.060$
Adult female/infant	$p=0.799$	$p=0.317$	$p=0.441$
Adult female/oestrous female	$p=0.612$	$p=1.0$	$p=0.612$
Subadult/juvenile	$p<0.01$	$p=0.068$	$p<0.03$
Subadult/infant	$p=0.345$	$p=0.317$	$p=0.500$
Subadult/oestrous female	$p=1.0$	$p=1.0$	$p=1.0$
Juvenile/infant	$p<0.01$	$p=0.273$	$p<0.01$
Juvenile/oestrous female	$p<0.01$	$p=0.068$	$p<0.05$
Infant/oestrous female	$p=0.735$	$p=0.317$	$p=0.917$

Table 4.25: Mean rates of grooming for oestrous females from different datasets[1]

Interactant	Focal animal: All oestrous females	Lita only	Oestrous females except Lita
adult male	7.02	8.87	5.10
anoestrous female	0	0	0
subadult	0	0	0
juvenile	1.25	0	2.55
infant	0	0	0
oestrous female	0	0	0
N[2]	23	12	11
focal animal hours	104	53	51

[1] Occurrences of grooming per 10 focal animal hours

[2] Number of focal animal follows

Table 4.26: Probabilities in Wilcoxon Matched-pairs signed ranks Test comparing the frequency of grooming between oestrous females and other age/sex classes based on various data sets.

Comparison of interactants	Data set:		
	All oestrous females (N=23 samples)	Lita only (N=12 samples)	All oestrous females except Lita (N=11 samples)
Adult male/adult female	$p<0.01$	$p<0.05$	$p<0.05$
Adult male/subadult	$p<0.01$	$p<0.05$	$p<0.05$
Adult male/juvenile	$p<0.05$	$p<0.05$	$p=0.249$
Adult male/infant	$p<0.01$	$p<0.05$	$p=0.431$
Adult male/oestrous female	$p=0.01$	$p<0.05$	$p=0.431$
Adult female/subadult	$p=1.0$	$p=1.0$	$p=1.0$
Adult female/juvenile	$p>0.05$	$p=1.0$	$p=0.109$
Adult female/infant	$p=1.0$	$p=1.0$	$p=1.0$
Adult female/oestrous female	$p=1.0$	$p=1.0$	$p=1.0$
Subadult/juvenile	$p>0.05$	$p=1.0$	$p=1.0$
Subadult/infant	$p=1.0$	$p=1.0$	$p=1.0$
Subadult/oestrous female	$p=1.0$	$p=1.0$	$p=1.0$
Juvenile/infant	$p>0.05$	$p=1.0$	$p=0.109$
Juvenile/oestrous female	$p>0.05$	$p=1.0$	$p=0.109$
Infant/oestrous female	$p=1.0$	$p=1.0$	$p=1.0$

For all three datasets focal oestrous females were groomed significantly more often by adult males than by any other age/sex class (Tables 4.27 and 4.28).

4.11 Discussion

4.11.1 Intracommunity relationships

The males of the Ngogo chimpanzee community preferred other males as company over any other age/sex class: males approached, followed and groomed other adult males more often than they approached, followed and groomed any other age/sex class. *Leaving* rates are to some extent dependent on approach rates and therefore do not reveal any new information. In contrast to adult males, females did not show special bonds between them: they groomed other females less often than other age/sex classes including males and most of their proximity and other affinitive behaviour was exhibited towards the age/sex classes of their offspring.

These results confirm those from other communities of common chimpanzees where males interact most frequently with other males to form strong intermale bonds for coalitions against other community members (Goodall, 1986, de Waal, 1982) and against members of other communities (Goodall, 1986; Nishida, 1984), while females keep themselves to themselves (Wrangham *et al.*, 1992).

Table 4.27: Mean rates of oestrous females being groomed for different datasets[1]

Interactant	Focal animal: All oestrous females	Lita only	Oestrous females except Lita
Adult male	13.0	13.77	12.16
Anoestrous female	0	0	0
Subadult	0	0	0
Juvenile	1.25	0.38	2.16
Infant	0	0	0
Oestrous female	0	0	0
N[2]	23	12	11
Focal animal hours	104	53	51

[1] Occurrences of grooming per 10 focal animal hours
[2] Number of focal animal follows

Table 4.28: Probabilities in Wilcoxon matched-pairs signed ranks test comparing the frequency of the focal oestrous female being groomed by various age/sex classes, based on different datasets.

Comparison of interactants	Data set: All oestrous females (N=23 samples)	Lita only (N=12 samples)	All oestrous females except Lita (N=11 samples)
Adult male/adult female	p<0.02	p<0.02	
Adult male/subadult	p<0.001	p<0.02	p<0.02
Adult male/juvenile	p<0.002	p<0.02	p<0.05
Adult male/infant	p<0.001	p<0.02	p<0.02
Adult male/oestrous female	p<0.001	p<0.02	p<0.02
Adult female/subadult	p=1.0	p=1.0	p=1.0
Adult female/juvenile	p=0.1088	p=0.317	p=0.180
Adult female/infant	p=1.0	p=1.0	p=1.0
Adult female/oestrous female	p=1.0	p=1.0	p=1.0
Subadult/juvenile	p=0.109	p=0.3173	p=0.180
Subadult/infant	p=1.0	p=1.0	p=1.0
Subadult/oestrous female	p=1.0	p=1.0	p=1.0
Juvenile/infant	p=0.109	p=0.317	p=0.180
Juvenile/oestrous female	p=0.109	p=0.317	p=0.180
Infant/oestrous female	p=1.0	p=1.0	p=1.0

Table 4.29 shows that the Ngogo data with the striking under-representation of female/female grooming, slight under-representation of male/female grooming and over-representation of male/male grooming fits in well with the other data on common chimpanzees from Gombe and Mahale and earlier data from Ngogo, contrasting the grooming relationships of common chimpanzees at Bossou in Guinea, where females were found to groom more frequently than expected, and bonobos at Wamba where not only females groom other females more than expected but more grooming than expected takes place between males and females. It therefore seems that the details of the Ngogo chimpanzees' social organisation resemble more the social organisation of common chimpanzees from other habitats than that of the bonobos, although they also live in a forest habitat with similar ecological conditions such as food distribution and concentration. This result indicates that other factors such as predation pressure or intercommunity relations may have a greater impact than previously thought.

4.11.2 Male/male relationships

Males directed agonistic behaviour most often towards other adult males and towards subadult males (excluding the data on a three-day consortship between an adult male and a subadult female). This confirms results from other sites of common chimpanzees, showing that agonistic interactions occur most often between adult males

Table 4.29: Inter- and intrasexual grooming at various study sites (adapted from Sugiyama, 1988)

Site	Sex ratio	Male/Male	Male/Female	Female/Female	N[a]	X^2	P
Common chimpanzees							
Gombe[1]	15:16	43 (22.1[7]	39 (50.6)	16 (25.3)	98	25.9	<0.001
Mahale[2]	4:11	97 (9.5)	63 (70.0)	7 (87.5)	167	876.2	<0.001
Bossou[3]	2.5:7	21 (15.9)	109 (147.8)	211 (177.3)	341	18.2	<0.001
Ngogo[4]	11:17	28 (11.3)	24 (38.6)	26 (28.1)	78	30.4	<0.001
Ngogo[5]	38:36	391 (208.5)	380 (405.8)	31 (186.9)	802	291.3	<0.001
Bonobos							
Wamba[6]	16:15	27 (45.4)	103 (90.8)	46 (39.8)	176	10.1	<0.01

[a] N=total number of grooming bouts.

[1] Goodall, 1965; [2] Nishida & Tachibana, 1987, quoted in Sugiyama, 1988; [3] Sugiyama, 1988; [4] Ghiglieri, 1984; [5] this study; [6] Kano, 1992. [7] In brackets: expected values calculated from the number of possible combinations of males and females.

(Bygott, 1979; Takahata, 1990b). The fact that males show submissive behaviour almost exclusively towards other males also reinforces findings from other chimpanzee communities, i.e. that males are dominant over all other age/sex classes and, once the dominance hierarchy is established, are not challenged by any sex class other than males (Bygott, 1979; Goodall, 1986; Takahata, 1990a,b).

It should be noted that it is justified to treat the three-day sample of a consortship between an adult male, MW, and a subadult female, KW, separately. There were no alternative interaction partners and interaction rates were much higher than in "normal" samples where focal animals were not engaged in a consortship. Although the subadult female was not in oestrus, the animals showed clear signs of being in a consortship (Goodall, 1986; Tutin, 1979): the male showed a variety of behaviour types to force the female to follow him, including threats, beatings and rapes. Throughout the three days they kept completely quiet and when they heard long-distance calls from other chimpanzees on the third day, they immediately disappeared in complete silence, and therefore unfortunately terminated the sample.

4.11.3 Male/female relationships

Adult males of the Ngogo chimpanzee community did not seek the company of females, irrespective of their reproductive state: oestrous females were responsible for the maintenance of proximity with the adult males. Males' relationships with anoestrous females were restricted to approaching, grooming and leaving, and in grooming and leaving the females took the more active part. Anoestrous chimpanzee females have most contact with adult males when they greet each other after a temporary separation and re-establish the dominance situation between them, or when a female is attacked by a male in his show of dominance, and when she turns to him afterwards for reconciliation or support against others (Goodall, 1986). Hence, while a male has nothing much to gain from the presence of an anoestrous female, it may be in the female's interest to stay near a male and therefore she has to take a more active part in establishing contact.

In contrast, the males may gain a significant reproductive advantage if they succeed in staying close to an oestrous females. Therefore it is difficult to understand why the oestrous female should be mainly responsible for establishing contact with the male and not the other way around. However, there are various possible explanations. One is that the female is coerced by the male into approaching by more or less subtle signals such as staring into the female's direction, shaking of branches and waving of an erect penis (Goodall, 1986) which might be missed by the observer. Another possibility is that the female forestalls the male's approach. Knowing that she may be forced into following by any male, she may choose her suitor by taking the initiative before she can be forced by another male. Once contact is established, males do groom oestrous females more than oestrous females groom them, which does suggest that males are prepared to put a certain amount of effort into forging a bond with the oestrous female.

4.11.4 Individual differences

Males

It has been shown that Mweya's distribution of grooming differed from other males' distribution of grooming. However, it is suggested that this is primarily a problem of sample size as grooming occurred only in 6 out of 15 follows on MW. With N=6 an almost perfect correlation is needed to achieve a significant result in a non-parametric test such as the Wilcoxon matched-pairs signed ranks test. Therefore Mweya's grooming distribution should be regarded as preliminary until more data are collected on this particular animal.

Anoestrous females

It seems that the TI, SW and CR dataset influenced the result of the grooming distribution of all anoestrous females in the comparison between anoestrous females grooming adult males and anoestrous females grooming juveniles. This was probably due to the fact that TI, SW and CR groomed adult males less than other anoestrous females, thereby lowering the frequency of male grooming and widening the gap between male and juvenile grooming. They also groomed infants less than other anoestrous females, although this had no effect on the results of the overall dataset.

Why should these three females behave differently from other anoestrous females? Out of 12 samples in which these three females were the focal animal, males were present for at least part of the time in only 3. This, of course, reduced the females' opportunity to interact with males. However, the basis of a fission-fusion organisation is that animals can join and leave temporary parties as they choose, and it can therefore be assumed that these females chose to be in parties that did not contain males, or, to be in small parties which are less likely to contain males.

SW was in an advanced state of pregnancy (R. Wrangham, pers. comm.) and her activity level was very low (see Chapter 5). She might have avoided big parties and the commotion resulting from big parties in order to save energy in view of her restricted mobility. CR had a very small infant. She might have avoided big parties in order to reduce her infant's risk of being approached and, possibly harmed - it is well-known that chimpanzee infants are at risk from other community members (Goodall, 1986; Hiraiwa-Hasegawa *et al.*, 1984; Nishida, 1989).

The reason for the decreased grooming of infants might simply lie in the fact that only one of these three females, CR, had an infant.

Oestrous females

The female Lita seems to be different from all other oestrous females in that she was not observed to groom juveniles and juveniles groomed her only on two occasions. One reason for this scarcity of interactions between Lita and juveniles might have been that she did not have a juvenile offspring. Lita was seen in oestrus in 10 out of 18 months and it is therefore assumed that she was sterile (see also Chapter 5). Another reason might have been her advanced age. Hasegawa & Hiraiwa-Hasegawa (1992) have found that at Mahale, females' relative copulation rates with immature males decreased significantly with the females' age. Lita was estimated to be past prime, i.e. more than 33 years old (Goodall, 1986) and she might therefore not have been very interested in juveniles in general. Nonetheless, she was almost always in big groups with many males, who were very interested in her. Therefore, another reason for her not having been observed to groom juveniles might have been that she was such a popular mating partner with adult males, that she had no time to spend with anybody else.

In summary, re-analysis of the data indicates that generalisations from individuals to whole age/sex classes might be affected by those animals who contribute most data. This effect can be estimated by analysing the dataset in two ways: once including data from those animals who contribute most data and once excluding those data and comparing the results of the two analyses. In this study, the degree of this effect seemed to be slight.

4.12 Summary

- The mean nearest neighbour distance for Ngogo chimpanzees was 4.4m.

- Mean nearest neighbour distances varied with activity.

- Adult males approached, followed and left other adult males more than any other age/sex class.

- Anoestrous females approached, followed and left all age/sex classes equally rarely with the exception of juveniles and infants.

- Oestrous females approached, followed and left adult males more than any other age/sex class.

- Oestrous females were mainly responsible for maintaining proximity to the adult males.

- Adult males were adult males' preferred grooming partners.

- Although adult males did not groom oestrous females more often than they groomed other age/sex classes, they groomed them about ten times as often as their representation in the community would have suggested.

- Anoestrous females groomed primarily juveniles and infants.

- Oestrous females groomed adult males significantly more often than they groomed any other age/sex class.

- The distribution of age/sex classes grooming the focal animals reflected the distribution of age/sex classes being groomed by the focal animal.

- Adult males were groomed by anoestrous females significantly more often than they groomed them.

- Oestrous females were groomed significantly more often by adult males than they groomed them.

- Other affinitive types of behaviour occurred mainly between anoestrous females and their offspring.

- Agonistic types of behaviour were observed almost exclusively in males.

- Submissive behaviour was directed almost exclusively towards adult males.

- Analysis based on datasets excluding those individuals who contributed most data yielded only slightly changed results compared to analysis of the complete datasets, although the individuals concerned were rather different from all other representatives of their sex. A problem of sample size and different individual circumstances were put forward as possible explanations for these individual differences.

- The Ngogo community of chimpanzees exhibited the same pattern of social relationships as found in most other studies of common chimpanzees. In common chimpanzees, forest habitats are therefore not necessarily associated with social relationships which are more typical of bonobos.

Chapter 5

Time budgets

5.1 Introduction

Animals are constrained by their own physiology and the environment in which they live: only limited amounts of energy are available to conduct subsistence activities within limited time frames. Therefore the relative costs and benefits of activities will have an impact on whether these activities are carried out and how frequently (Dunbar, 1988).

In general, primate females have higher energetic demands than males because of the costs of gestation and lactation (Dunbar 1988). This is regarded as a possible reason for females spending more time feeding than males in many primate species (Chivers, 1977; Clutton-Brock, 1974; Dunbar, 1977; Pollock, 1977; Smith, 1977; Waser, 1977). There is no reason why the argument of higher energetic costs for females should not apply to apes, and yet it has been shown that adult male orang-utans (*Pongo pygmaeus*) and silverbacked male gorilla (*Gorilla* sp.) spend more time feeding than adult females (Rodman, 1977; Fossey & Harcourt, 1977). It has been suggested that the extreme sexual dimorphism in these species could be responsible: adult males have to feed more than females because they are feeding on the same things but are so much larger (Clutton-Brock, 1977; Clutton-Brock and Harvey, 1977). Chimpanzees do show sexual dimorphism, but not as pronounced as in orang-utans and gorillas: females weigh about three quarters of what males weigh (Napier & Napier, 1985; Uehara & Nishida, 1987; Wrangham & Smuts, 1980). If the size difference is of overriding importance, then chimpanzee males should spend more time feeding than females; if the higher energetic costs incurred by females because of reproduction cancels this out, both sex classes should spend similar amounts of time feeding. This study's data on time budgets in males and females should enable us to distinguish between these two predictions and hypotheses.

An examination of time budgets may also help us to determine whether the chimpanzees of the Kibale Forest behave in a way more similar to the savanna chimpanzees of Western Africa or to the bonobos of tropical rainforests. The two crucial points are time spent feeding and time spent socialising. If bonobos really live in a more productive environment, they should spend less time feeding than common chimpanzees. In general, data from the literature support this. Bonobos at Lomako indeed spend less time feeding (40.4%; White, 1992) than common chimpanzee populations at Gombe (55.7%), Ngogo (57.3%) and Kanyawara (59.7%) (Wrangham, 1977; Ghiglieri, 1984; Wrangham *et al.*, 1991). In contrast, they spend approximately the same time feeding as the chimpanzees in Rio Muni (40.4%) (Sabater-Pi, 1979) and more than the chimpanzees at Mahale (29.7%; Huffman, 1990). Bonobos at Wamba spend even less time feeding than those at Lomako (18.0%; Kano & Mulavva, 1984).

Bonobo females are reported to be more sociable than common chimpanzees (Kano, 1980, 1987; Thompson-Handler *et al.*, 1984; White, 1988). If this is true, bonobo females should spend more time socialising than chimpanzee females. Unfortunately, as time spent socialising is often amalgamated into time spent resting, the only published data on time spent socialising in common chimpanzees come from Gombe (6.2%; Wrangham, 1977) and Mahale (12.0%; Huffman, 1990). However, the Gombe data were collected from males only, while the Mahale data were pooled for males and females. The only published data on percentage of time spent socialising in bonobos come from Lomako (White, 1992) and the percentage of 6.3 again refers to males and females. It is obvious that the reputed greater sociability of bonobo females cannot be determined from data which combine males and females.

In view of this lack of data, we have to assume that bonobo females spend more time socialising than chimpanzee females. If the forest chimpanzees are more like bonobos, forest chimpanzee females should spend as much time engaged in social activities as bonobo females and they should spend at least as much time socialising as forest chimpanzee males.

Time budgets were calculated from the number of 5-minute scans spent feeding, moving, resting, socialising and engaged in other activities. "Feeding" included foraging; "moving" included travelling and moving within a tree if the movement did not take the chimpanzee into or out of a feeding tree. Resting was defined as being inactive (but including auto-groom and scratch); socialising included all social behaviours, whether affinitive, agonistic, submissive or sexual. "Other" included all activities not covered by these definitions, such as coughing, building nests, manipulating swellings etc.

It was not possible to sample all hours of the day evenly. As it is likely that activities undergo diurnal rhythms, an uneven representation of certain hours in the dataset would result in a time budget skewed in favour of activities taking place mainly at times better represented in the dataset. Therefore, data were matched for the hours of the day between07.00 and 13.00h. For example, in the comparison of time budgets between males and females, time spent feeding by males was compared by the hour with time spent feeding by females. In each case, all the samples from the same hour time-block were averaged to give an hourly time budget. The other activity categories were compared in the same way.

This procedure also helped to circumvent another sampling problem. Although only follows longer than half an hour were included in the analysis, there was still a considerable variation in sample duration. Ideally, time budget data should come from all-day follows. Unfortunately, due to the chimpanzees' poor habituation, all-day follows were infrequent during this study. If samples had been compared with each other individually, there would have been the danger that shorter samples would have resulted in skewed time budgets, simply because samples might not have been long enough to sample all activities. However, as samples were compared only within pools of data, e.g. for males or females, and then only at the time of day when they actually occurred, the problem of different sample durations was alleviated.

5.2 Overall time budgets

The Ngogo chimpanzees spent most of their time resting and feeding (Figure 5.1). Adult males tended to spend more time feeding than resting, while adult females spent more time resting than feeding.

A separate analysis for anoestrous and oestrous females (Figure 5.2) shows that anoestrous females follow the female pattern (Wilcoxon matched-pairs signed ranks test, all comparisons $p<0.01$ except for move/social:

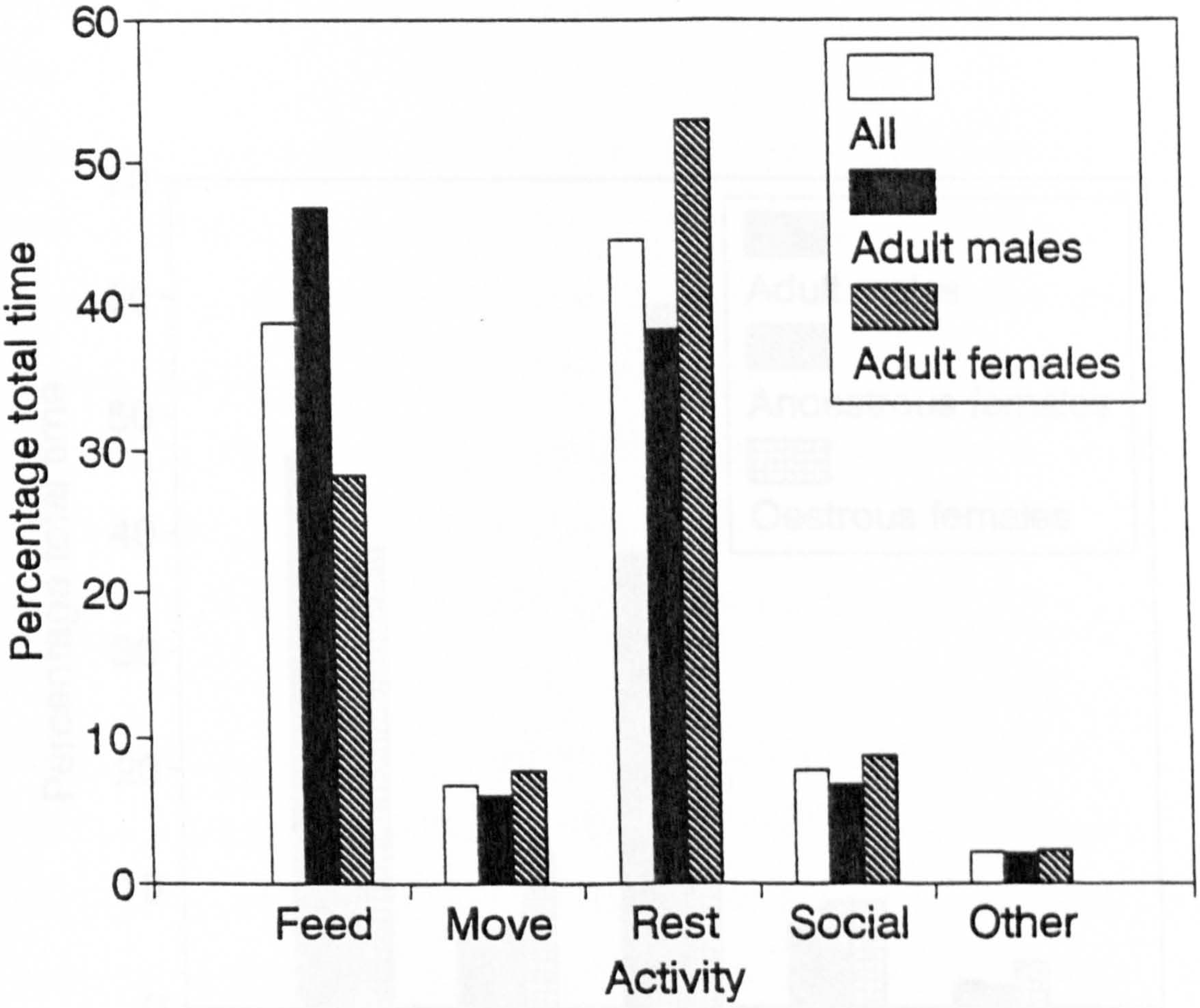


Figure 5.1: Overall time budgets of the Ngogo chimpanzees.

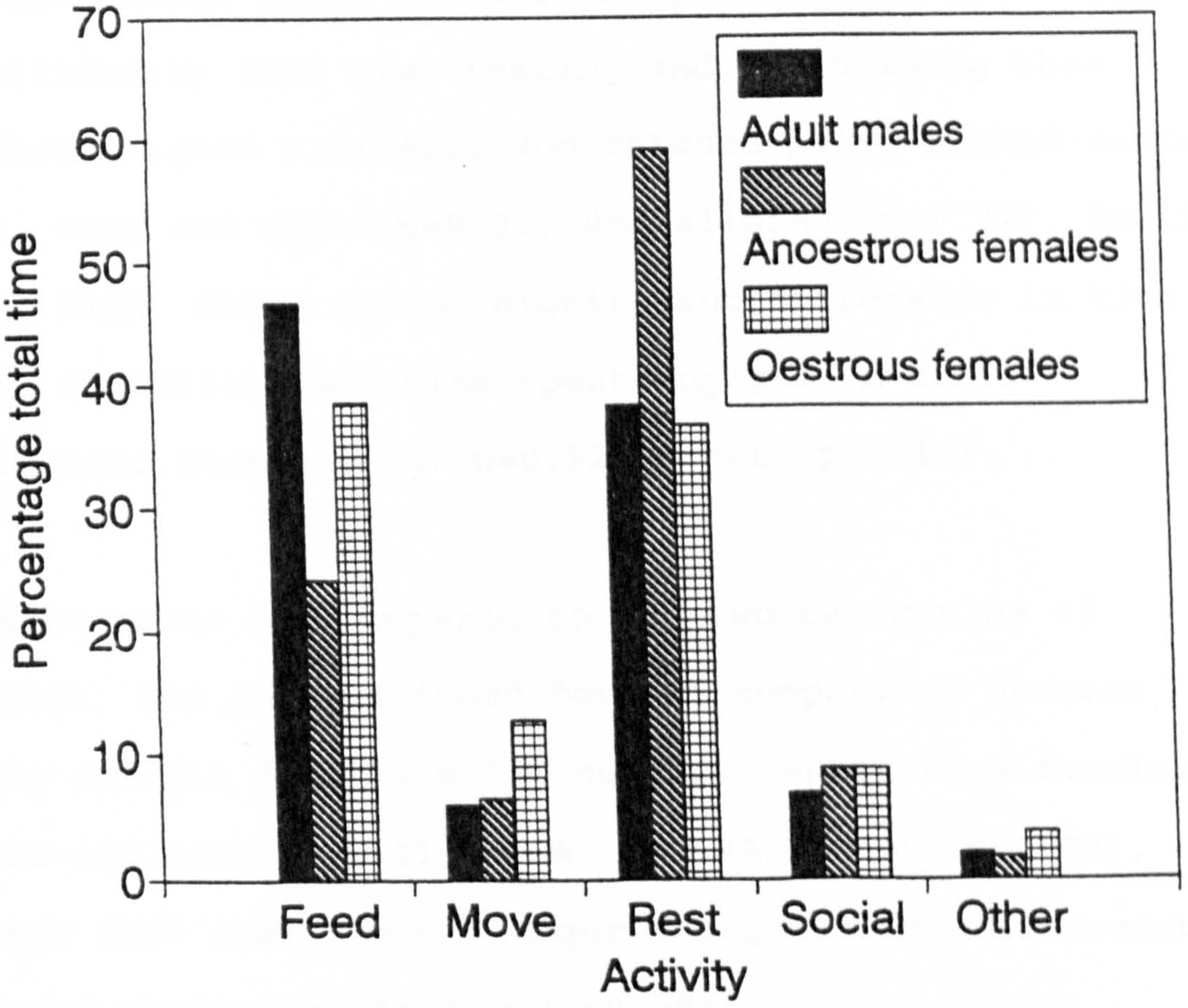


Figure 5.2: Male time budget in comparison to anoestrous and oestrous female time budgets.

p=0.15), while there is no significant difference between time spent feeding and resting in oestrous females (Wilcoxon matched-pairs signed ranks test, all comparisons p<0.01 except for social/other: p<0.05, feed/rest: p=0.88 and move/social: p=0.72).

5.3 Comparisons between genders

Adult males spent significantly more time feeding and significantly less time resting and socialising than females (Figure 5.1; Wilcoxon matched-pairs signed ranks test, feed and rest: p<0.01, socialising: p<0.02). On the other hand, there was no significant difference in time spent travelling and time spent engaged in other activities (travelling: p=0.12, other: p=0.48).

When males are compared to the two categories of females, the results found for the comparison between males and all females still hold for anoestrous females (feed and rest: p<0.01, move: p=0.89, other: p=0.78), except that there is no longer a significant difference in time spent socialising (p=0.084).

In the comparison of time budgets of males and oestrous females the only significant difference is that oestrous females spend less time feeding (p<0.02; all other comparisons: p>0.05).

When the time budgets of anoestrous and oestrous females are compared, oestrous females spent more time feeding and less time resting than anoestrous females (Wilcoxon matched-pairs signed ranks test, feed and rest: $p<0.01$, move: $p=0.060$, social: $p=0.58$, other: $p=0.11$; Figure 5.2).

In order to determine whether the difference in time spent socialising between males and females is a real one, time spent socialising was broken down by age/sex class of the interactant. Table 5.1 shows that over half of females' interactants were juveniles and infants, i.e. most probably the females' offspring. In contrast, males spent less than a fifth of the time they spent interacting overall with members of this young age class. This difference is significant ($X^2=123.3$, df=1, $p<0.0001$).

When time spent socialising is restricted to socialising with adults and subadults, males spent an average of 5.6% of their time socialising, whereas females spent an average of 3.0% of their time engaged in social activities. This difference is significant (Wilcoxon matched-pairs signed ranks test, $p<0.01$).

Table 5.1: Age classes of adult males' and females' interactants.

Age class of interactants	Adult males N	Adult males %	Adult females N	Adult females %
Adult and subadults	278	82.2	134	40.5
Juveniles and infants	60	17.8	197	59.5
All	338	100.0	331	100.0

5.4 The problem of pseudoreplication

In order to test whether the results were unduly influenced by those individuals with the most focal animal hours (see Chapter 4), the data were divided into subsets of those individuals and all the others.

5.4.1 Males

Figure 5.3 shows the time budgets of Mweya, the male who contributed 14.3% of the data, and all the other males (35 identified and 57 unidentified). Mweya spent significantly less time feeding than resting (Wilcoxon matched-pairs signed ranks test, $p<0.01$; all other comparisons between activity categories $p<0.01$ except for move/other: $p<0.05$ and move/social: $p=0.51$). The opposite was true for the other adult males (Wilcoxon matched-pairs signed ranks test, $p<0.05$; $p<0.01$ in all other comparisons except social/other: $p<0.05$ and move/social: $p=0.94$).

When time budgets are compared between Mweya and all the other males, Mweya spent significantly less time feeding and significantly more time resting than all the other males (Wilcoxon matched-pairs signed ranks test, feed and rest: $p<0.01$, other comparisons: $p>0.05$).

Given that Mweya's time budget is significantly different from that of all the other adult males, it has

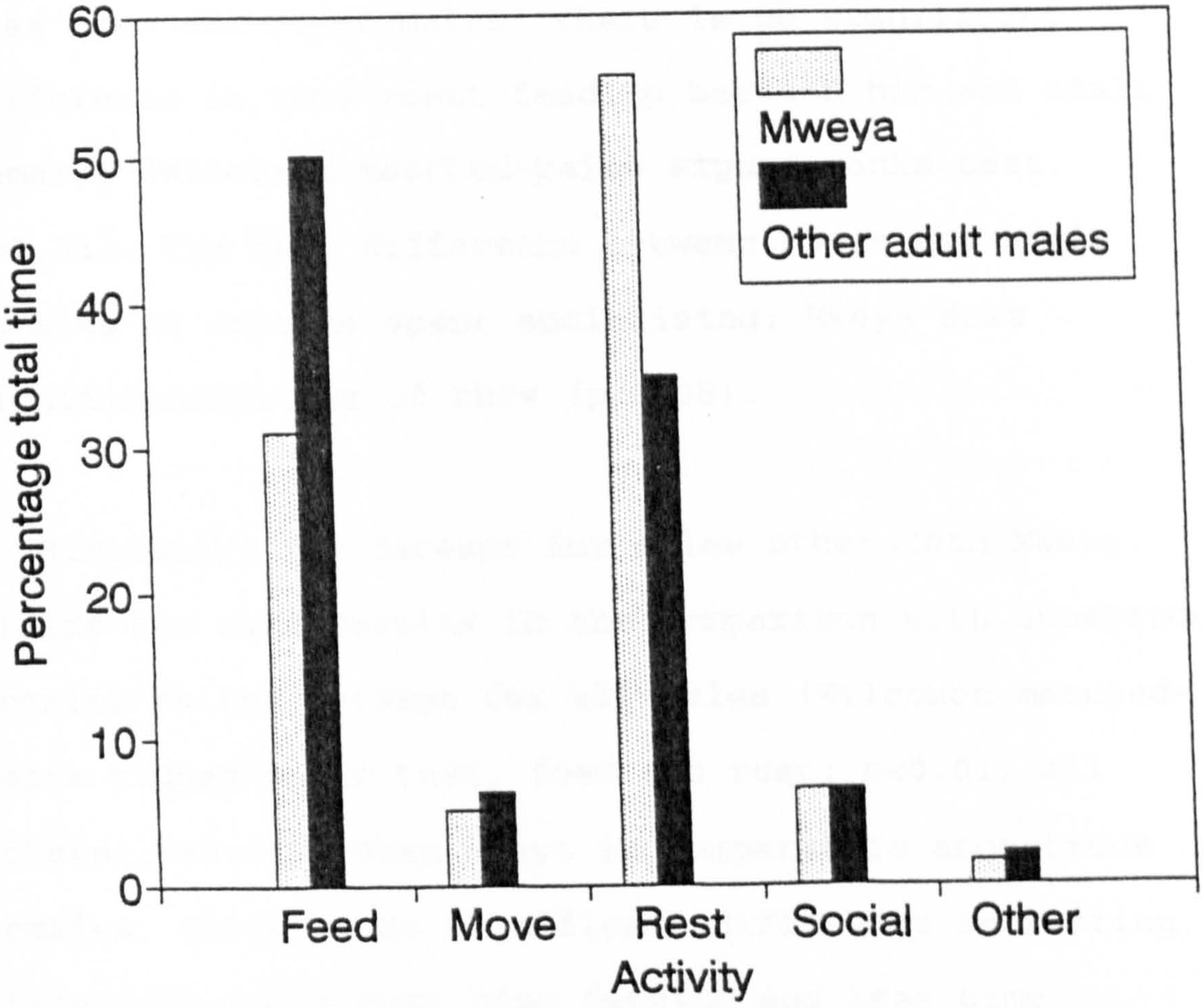


Figure 5.3: Mweya's time budget in comparison to other males' time budget.

to be shown that the inclusion of Mweya's data has no adverse effect on the comparisons between adult males and other sex classes. In fact, the results of the comparison between adult males and adult females hold when Mweya's data are omitted and the data for all females are compared to the data for all other males (Wilcoxon matched-pairs signed ranks test: feed and rest: $p<0.01$, social: $p<0.02$, move: $p=0.31$, other: $p=0.96$). However, the data for Mweya do not follow this pattern. As he fed less than all other males, there is no significant difference in time spent feeding between him and adult females (Wilcoxon matched-pairs signed ranks test, $p=0.31$). The only difference between Mweya and adult females is in time spent socialising: Mweya does significantly less of this ($p<0.05$).

Similarly, the dataset for males other than Mweya yields the same results in the comparison with anoestrous females as the dataset for all males (Wilcoxon matched-pairs signed ranks test, feed and rest: $p<0.01$, all others: $p>0.05$). When Mweya is compared to anoestrous females, there is no significant difference in resting, whereas he spent more time feeding and less time socialising (Wilcoxon matched-pairs signed ranks test, feed and social: $p<0.05$, others: $p>0.05$).

When males other than Mweya are compared to oestrous females only, they show the same pattern as all adult males: they spend significantly more time feeding

(Wilcoxon matched-pairs signed ranks test, $p<0.01$), but they also spend signficantly less time socialising ($p<0.05$; all other comparisons: $p>0.05$). The difference in time spent feeding disappears when only Mweya is compared to oestrous females ($p=0.084$). He also spends more time resting ($p<0.01$) than oestrous females.

These findings suggest that while Mweya is different from all the other males, the inclusion of his data has no effect on the overall results.

The obvious feature that distinguishes Mweya's sample from the samples of all other males is the fact that it includes 3 days (35.1 hours) of consortship with a subadult female. If these three days are excluded from Mweya's sample, there are no significant differences between him and all the other males (Wilcoxon matched-pairs signed ranks test, N=11 hours of the day, feed, rest, move, social: $p>0.213$).

5.4.2 Anoestrous females

The dataset for anoestrous females was also divided into two subsets, one for the three females who contributed 30.9% of the data, TI, SW and CH, and one for all the other anoestrous females (12 identified and 29 unidentified). Both groups spent significantly more time resting than feeding as was also indicated in the dataset for all anoestrous females (Wilcoxon matched-pairs signed ranks test, $p<0.01$; Figure 5.4). While the other anoestrous females also followed the female pattern in the other categories ($p<0.01$ in all comparisons except for move/social: $p=0.24$), TI, SW and CH spent approximately the same amount of time on other activities and moving ($p=0.067$) and on other activities and social activities ($p=0.069$; other comparisons: $p<0.01$ except move/social: $p=0.39$).

However, when time budgets are compared between the two groups, TI, SW and CR spent significantly less time feeding, moving and socialising and significantly more time resting than all other anoestrous females (Wilcoxon matched-pairs signed ranks test, feed, move and rest: $p<0.01$, social: $p<0.02$, other: $p=0.72$).

To determine whether the fact of TI, SW and CR being rather different from all the other anoestrous females has an effect on overall comparisons involving anoestrous females, both subsets of data are compared to that of the adult males. While adult males still spend significantly more time feeding and less time resting than the females in either dataset (Wilcoxon matched-pairs signed ranks test, $p<0.01$ in all comparisons), TI, SW and CR spent significantly less time moving than adult males and all other anoestrous females spent significantly more ($p<0.05$ in both comparisons). In addition, there was no significant difference in time spent socialising between adult males and all anoestrous females, and between adult

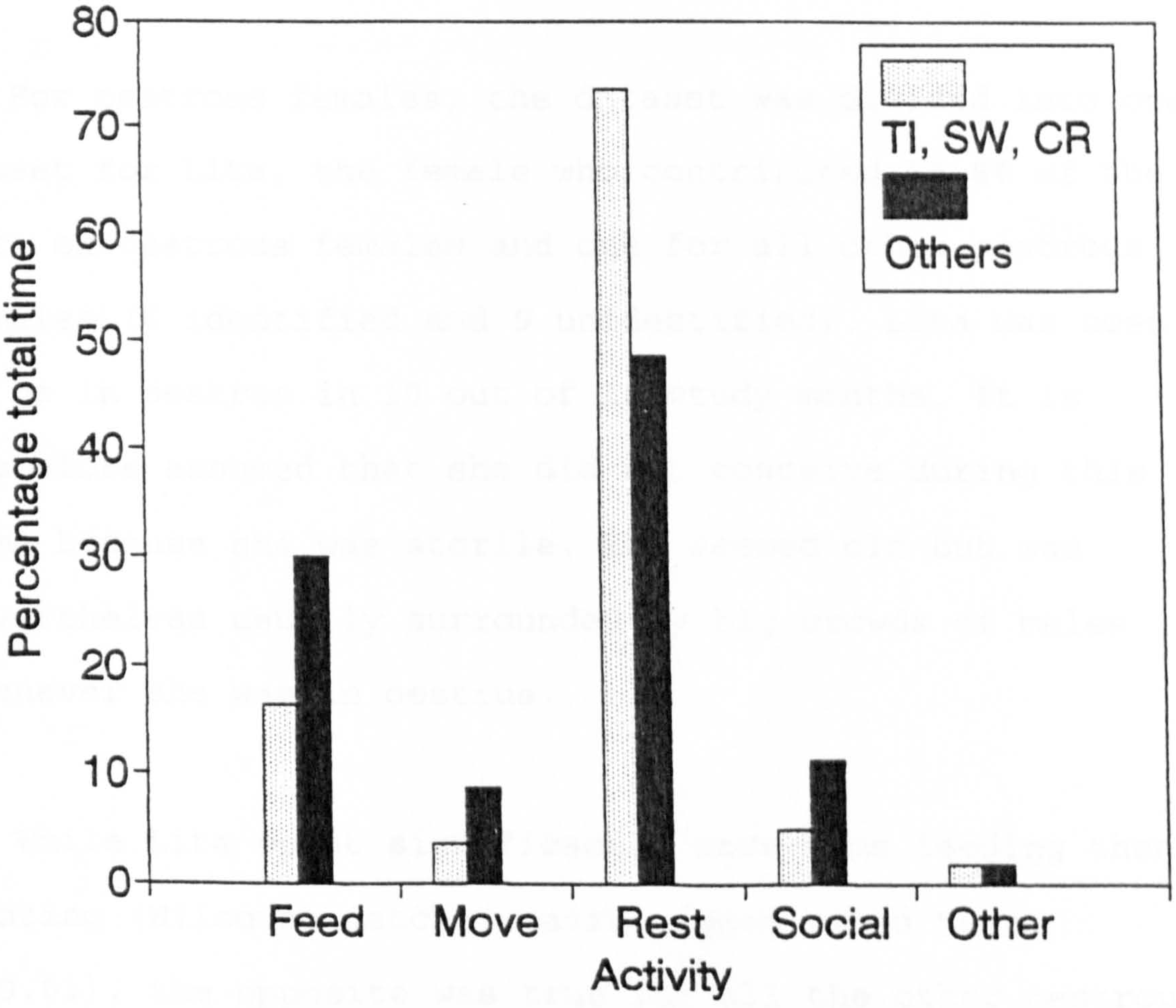


Figure 5.4: **Time budgets of those anoestrous females who contributed most data compared to other anoestrous females' time budgets.**

males and TI, SW and CR, whereas anoestrous females spent more time socialising than adult males when data on TI, SW and CR were excluded (p<0.01).

It must therefore be concluded that the inclusion of the data from TI, SW and CR has an effect on the results of overall comparisons.

5.4.3 Oestrous females

For oestrous females, the dataset was divided into one subset for Lita, the female who contributed 50.8% of the data on oestrous females and one for all other oestrous females (6 identified and 9 unidentified). Lita was seen to be in oestrus in 10 out of 18 study months. It is therefore assumed that she did not conceive during this time because she was sterile. She seemed old but was nevertheless usually surrounded by big crowds of males whenever she was in oestrus.

While Lita spent significantly more time feeding than resting (Wilcoxon matched-pairs signed ranks test, p<0.01), the opposite was true for all the other oestrous females (Wilcoxon matched-pairs signed ranks test, p<0.01; Figure 5.5).

Otherwise, Lita's time budget shows the same tendency as the time budget gained from data on all oestrous females: she spent significantly more time feeding than

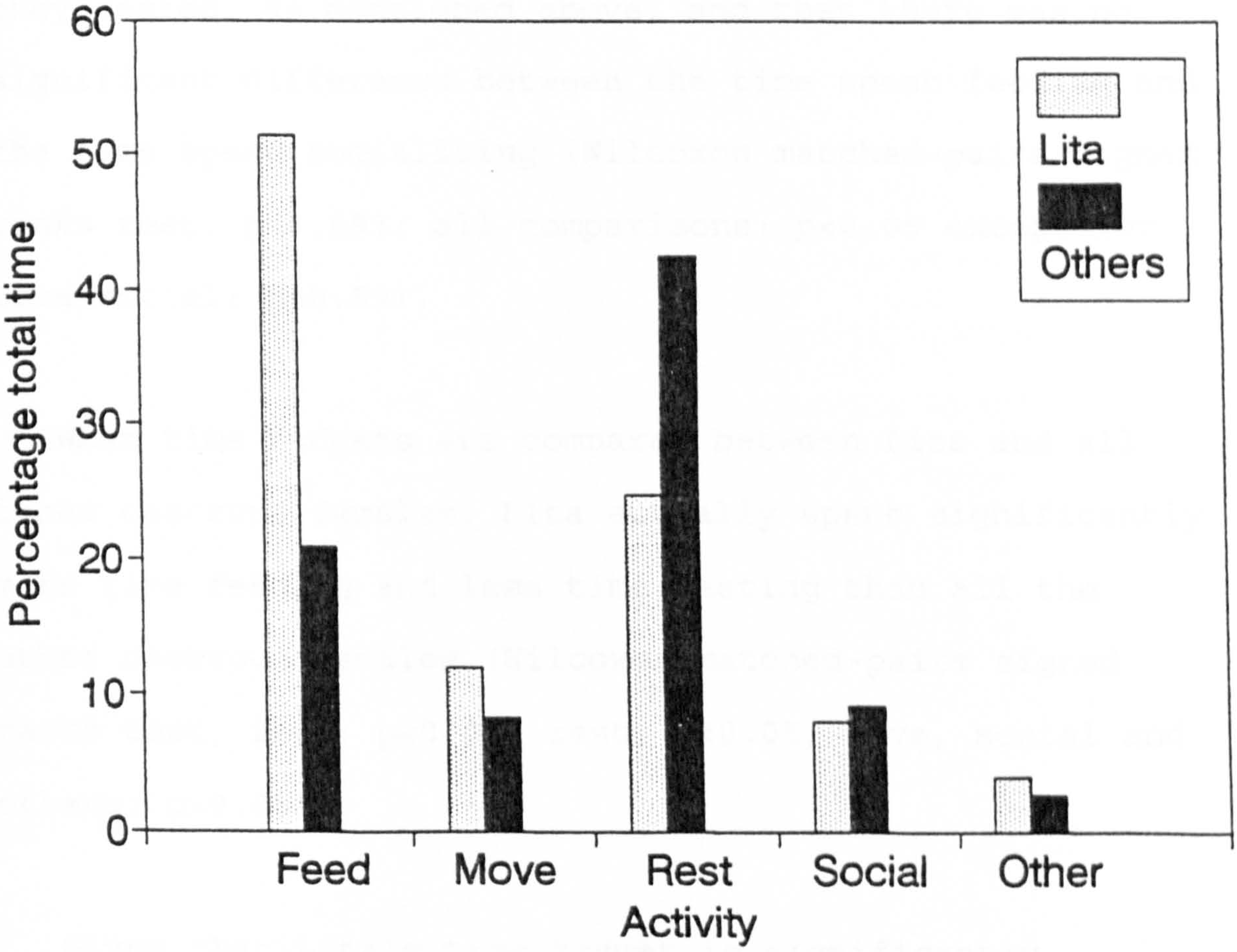


Figure 5.5: Lita's time budget in comparison to other oestrous females' time budgets.

doing anything else (Wilcoxon matched-pairs signed ranks test, all comparisons $p<0.01$). Her next most frequent activity was resting (all comparisons $p<0.01$). Similar to results in all the other sex classes, there was no difference between time spent moving and time spent engaged in social behaviour ($p=0.64$).

Other oestrous females follow the pattern of all oestrous females combined except that they fed less than they rested, as mentioned above, and that there was no significant difference between the time spent feeding and the time spent socialising (Wilcoxon matched-pairs signed ranks test, $p=0.093$; all comparisons: $p<0.05$ except for move/social: $p=0.59$).

When time budgets are compared between Lita and all other oestrous females, Lita actually spent significantly more time feeding and less time resting than all the other oestrous females (Wilcoxon matched-pairs signed ranks test, feed: $p<0.01$, rest: $p<0.05$, move, social and others: $p>0.05$).

Given that Lita's time budget is significantly different from the time budget of the other oestrous females, it has to be shown what effect the inclusion of Lita's data has on the comparisons with other sex classes. In the comparison between oestrous and anoestrous females, the significant difference in time spent feeding disappears when Lita's data are excluded

(Wilcoxon matched-pairs signed ranks test, $p=0.33$), although anoestrous females still rest more than oestrous females ($p<0.05$). When anoestrous females are compared to those samples that come exclusively from Lita, the results are the same as in the comparison between all anoestrous and all oestrous females.

This suggests that the inclusion of Lita's data does have an effect on the overall results.

5.4.4 Adjusted time budgets

As it was shown that those individuals who had contributed most data had an effect on the results of overall comparisons, data were re-analysed without those for Mweya, TI, SW, CR and Lita. Figures 5.6 and 5.7 show these revised time budgets. In the overall comparison between males and females, males spent significantly more time feeding and significantly less time resting, moving and socialising (Wilcoxon matched-pairs signed ranks test, feed, rest and social: $p<0.01$, move: $p<0.02$; other: $p=0.88$). In the comparison between males and anoestrous females, males spent more time feeding and less time resting and socialising than anoestrous females (Wilcoxon matched-pairs signed ranks test, feed, rest and social: $p<0.01$, move: $p=0.071$, other: $p=0.29$). In the comparison between males and oestrous females, the only significant difference is in males spending more time feeding (Wilcoxon matched-pairs signed ranks test, $p<0.01$; all

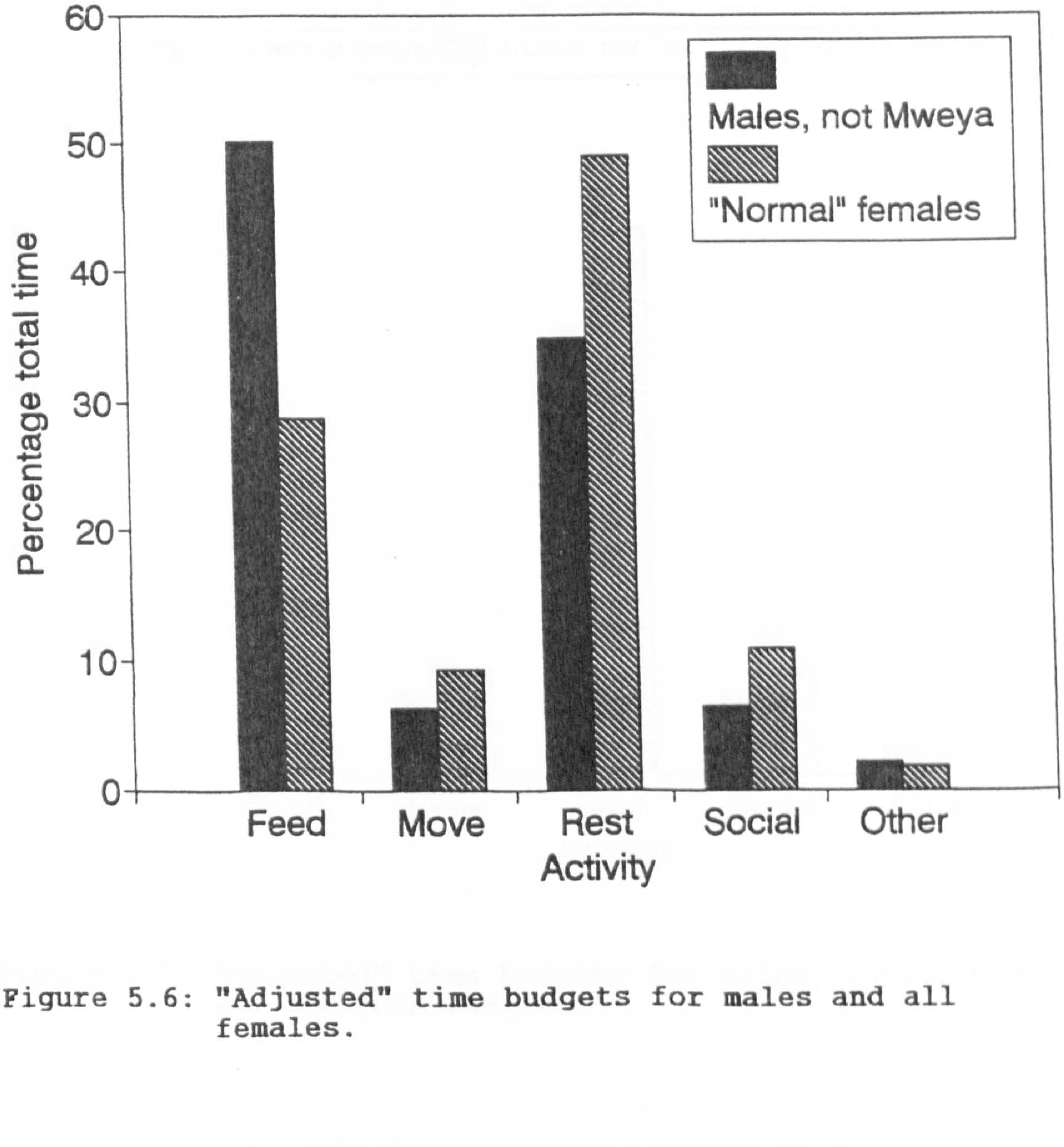


Figure 5.6: "Adjusted" time budgets for males and all females.

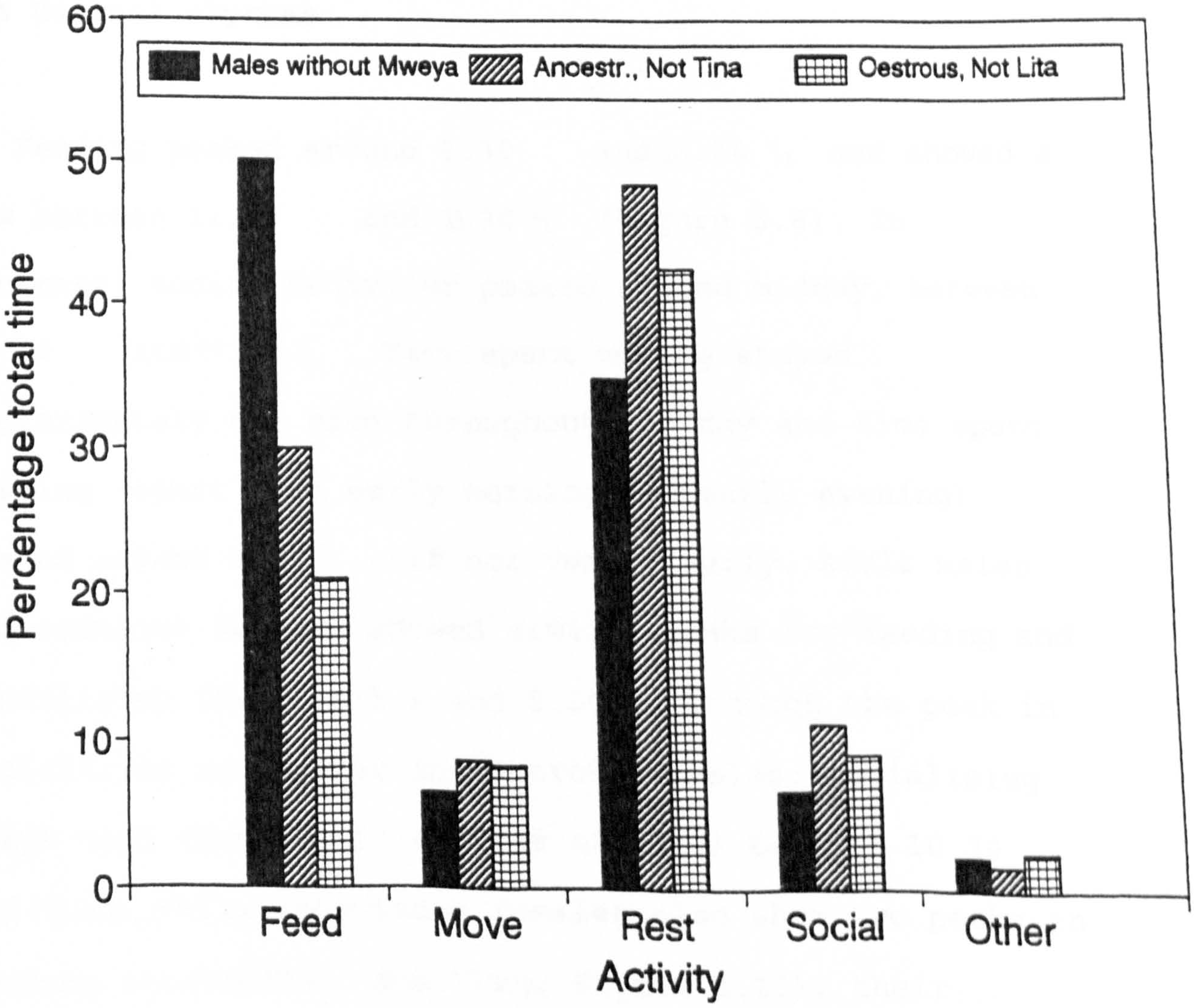


Figure 5.7: "Adjusted" time budgets for males, anoestrous and oestrous females.

other comparisons: p>0.05). Without the data on TI, SW, CR and Lita, there are no significant differences in time budgets between anoestrous and oestrous chimpanzee females.

5.5 Diurnal rhythms

Feeding peaked around 8.30 and 18.30 h and showed a low between 11.30 and 13.30 h (Figure 5.8). In contrast, social behaviour peaked around midday, between 11.30 and 14.30 h. Time spent moving stayed approximately the same throughout the day and time spent resting (apart from early morning and early evening) peaked around 13.30 h, if not very clearly. Adult males and oestrous females showed similar peaks for feeding and socialising (Figures 5.9 and 5.10), although the peak in socialising is broader in oestrous females: socialising stays high (between 10 and 25% of time) between 10.30 and 15.00h. While anoestrous females also show two peaks in feeding (around 07.00 and 17.00h; Figure 5.11), their socialising has a more irregular distribution during the day.

To test whether adult males, anoestrous and oestrous females have similar activity patterns, correlation coefficients between sex classes were calculated for each category of activity (unit of analysis: hour of the day). Only time spent socialising was significantly correlated

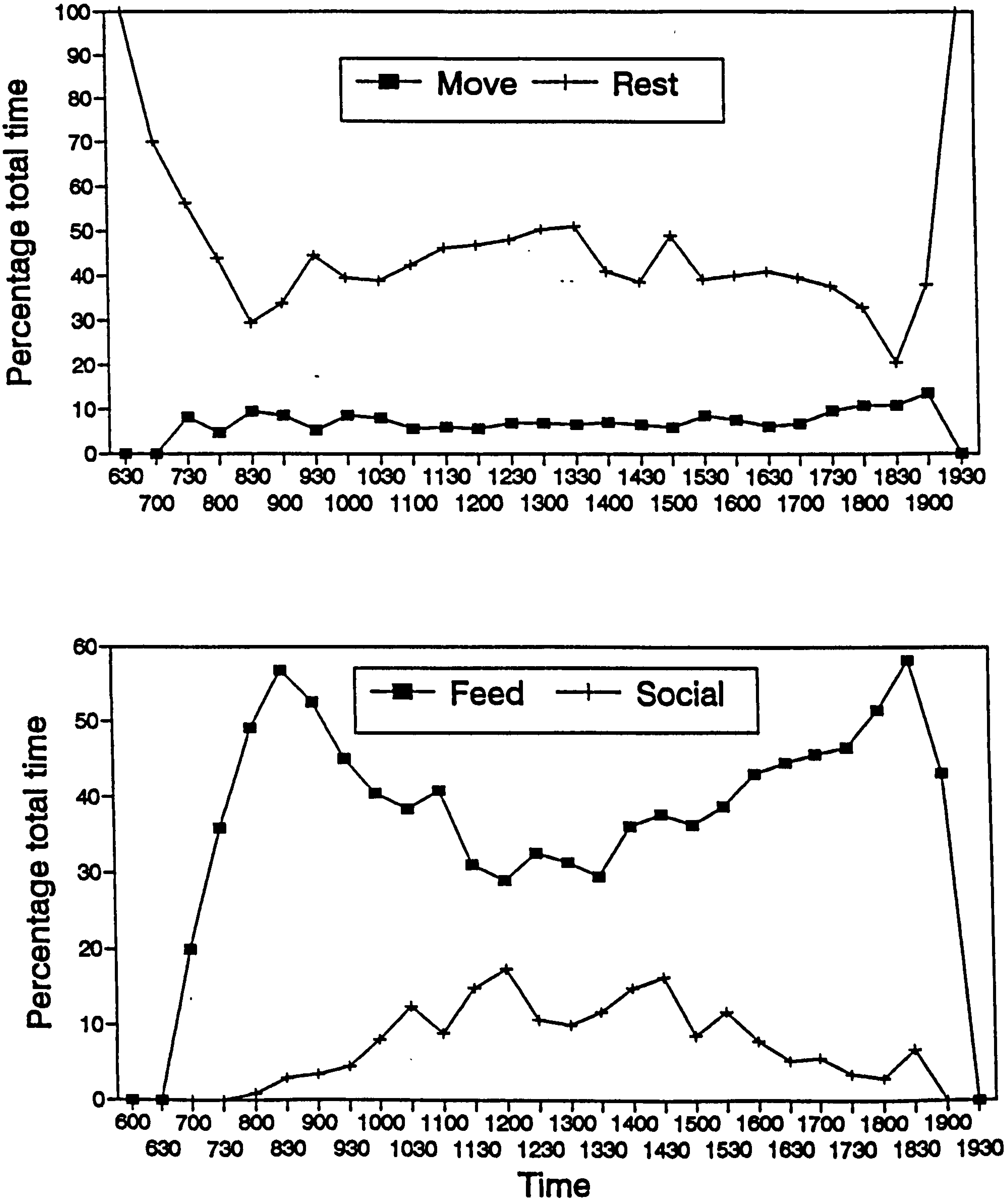


Figure 5.8: Diurnal rhythms of the Ngogo chimpanzees.

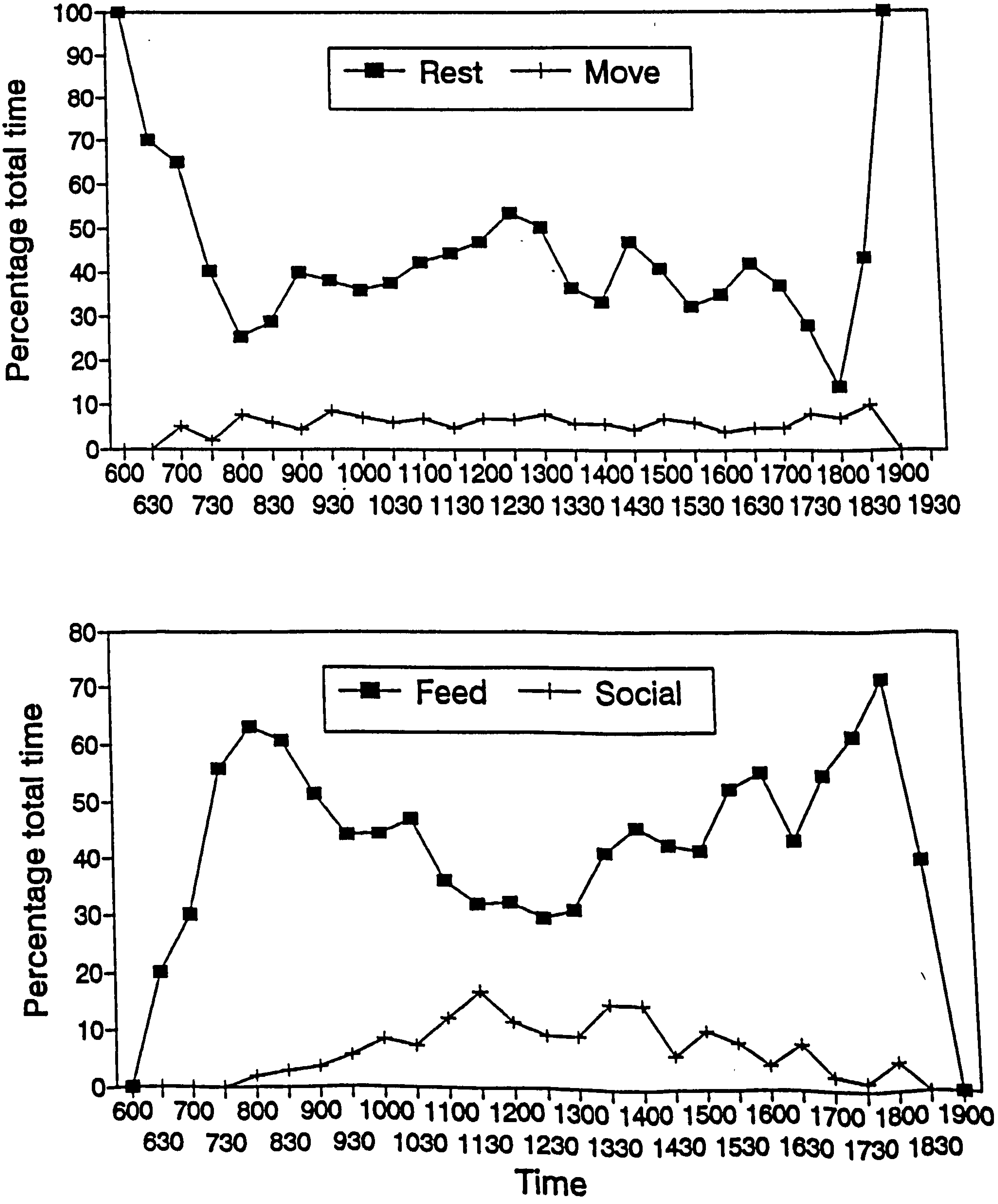


Figure 5.9: Diurnal rhythms of adult males.

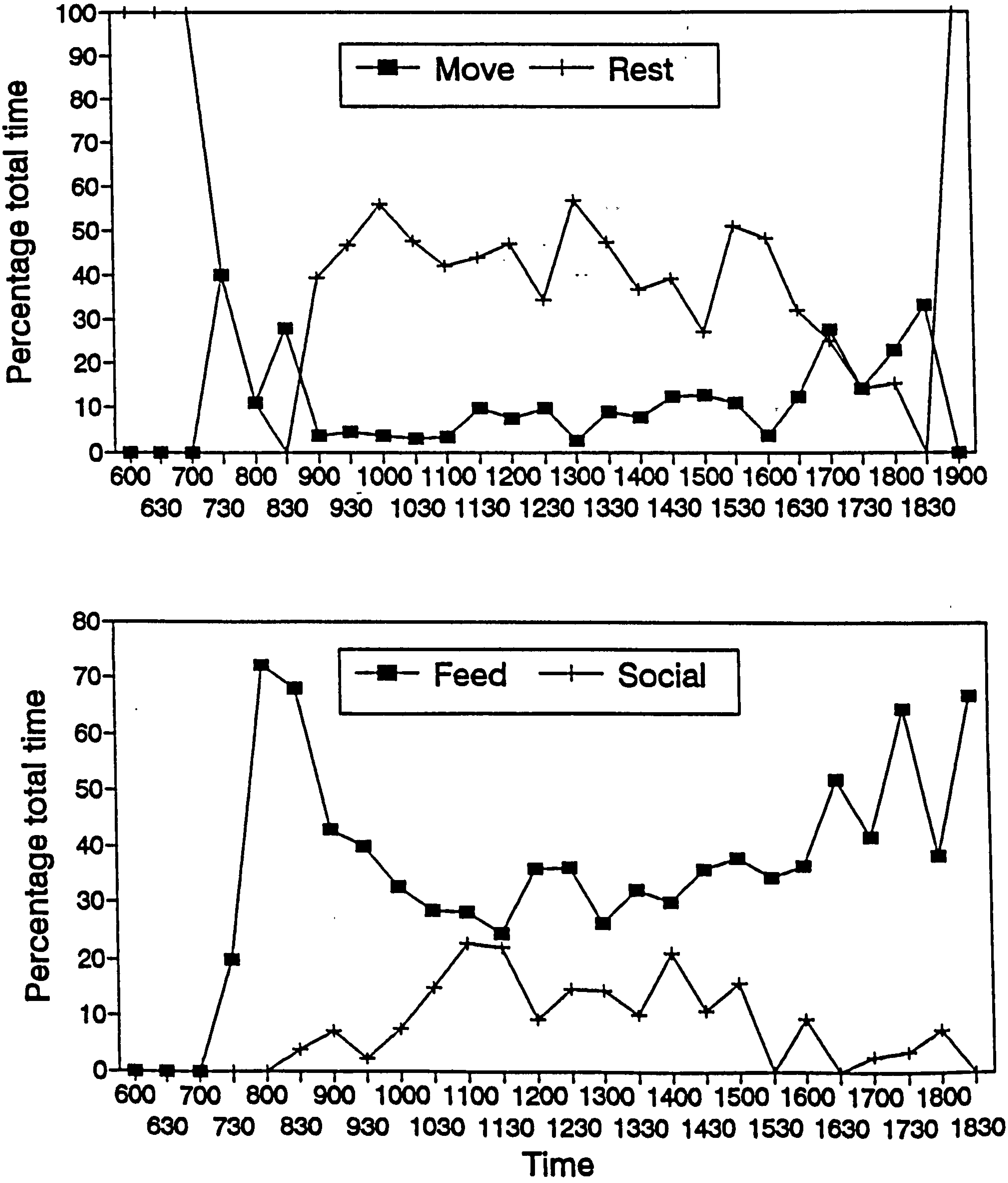
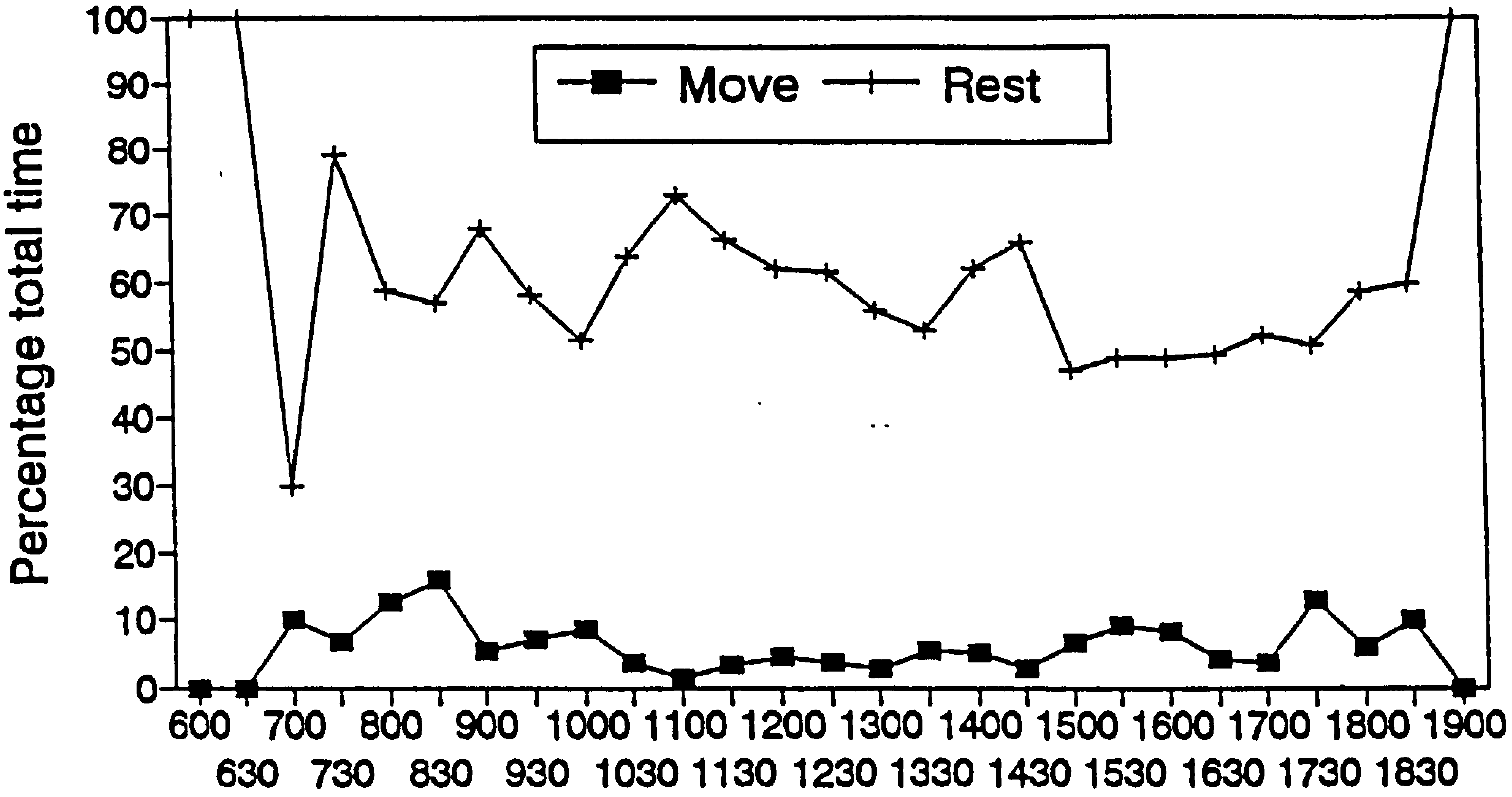


Figure 5.10: Diurnal rhythms of oestrous females.



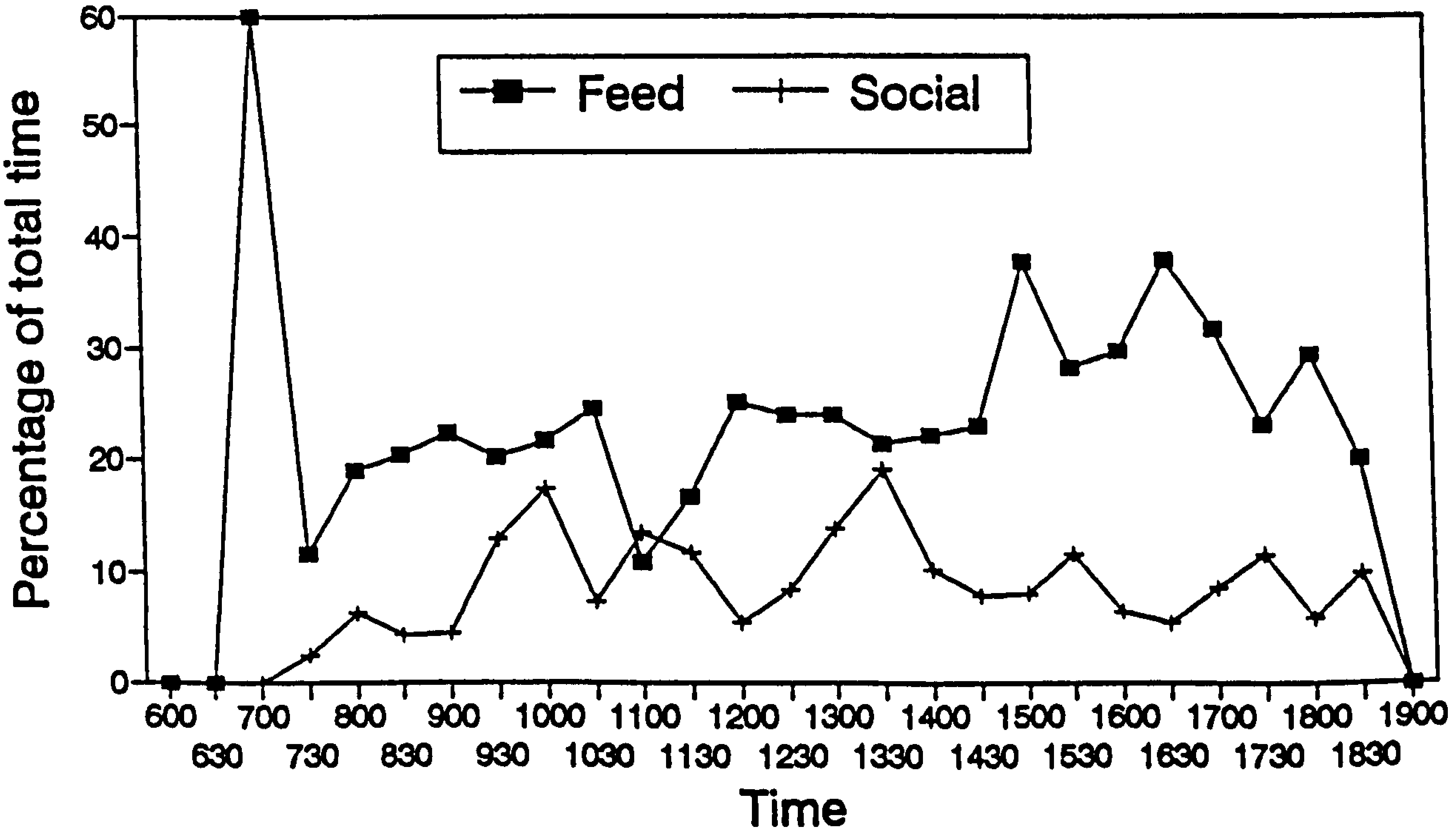


Figure 5.11: Diurnal rhythms of anoestrous females.

between adult males and oestrous females (r=0.918, p<0.001, N=12 hours of the day).

5.6 Impact of location method

Ghiglieri (1984) suggested that his time budget data underestimated time spent travelling because half of his observations were made after the chimpanzees had been located in tree vigils. In order to determine whether the method with which the chimpanzees are located has an impact on resulting time budgets, time budgets were analysed in relation to location method. Table 5.2 shows that chimpanzees located in tree vigils spent more time feeding than chimpanzees located by following vocalisations. This difference was significant (Mann-Whitney U test, N=240, p<0.001), but there were no significant differences in the other activities. This suggests that Ghiglieri's feeding time is an overestimate, whereas his travelling time seems to be unaffected by location method.

5.7 Comparison to other study sites

The adjusted time budget of the Ngogo chimpanzees is compared to chimpanzees' time budgets from other study sites. Data were matched to hour of the day. Wilcoxon matched-pairs signed ranks tests were used to determine

Table 5.2: Time budgets in relation to location method.

Activity	Tree vigils N=99	Following vocalisations N=141
Feed	44.5	33.9
Travel	5.0	8.1
Rest	41.2	44.5
Social	7.1	11.2
Other	2.1	2.3

whether differences in time spent on various activities were significant between sites.

According to the pooled data for males and females, the chimpanzees at Ngogo spent less time feeding and moving and more time resting and socialising than chimpanzees at Gombe (Wrangham, 1977; Table 5.3), Okorobiko in Rio Muni (Sabater-Pi, 1979) and at Ngogo as described by Ghiglieri (1984). They also spent less time feeding than the chimpanzees of the neighbouring Kanyawara community (feeding time: 59.7% according to Wrangham *et al.*, 1991). The differences between the results of this study and Ghiglieri's results (as taken from his Figure 5, p.67 in Ghiglieri 1984) were significant (Wilcoxon matched-pairs signed ranks test, $N=12$, $T^+=78$, $p=0.0002$ for each category, *rest*, *social* and *other* combined; Table 5.4), as were the differences between Ngogo and Rio Muni. As the data for Gombe represent only adult males, it is more adequate to make the comparison with adult males (without Mweya) at Ngogo. In this comparison, the difference in feeding is not significant (Table 5.4), but the difference in time spent socialising (Table 5.4) is. Comparisons in the other activity categories are not possible, because detailed data on resting and travelling were not given by Wrangham (1977).

In contrast, the chimpanzees at Mahale seemed to spend less time feeding and more time socialising than the

Table 5.3: Time budgets in various chimpanzee and bonobo communities.

Activity	Gombe[1] (Wrangham 1977)	Ngogo[2] (Ghiglieri 1984)	Ngogo[3] (This study)	Rio Muni (Sabater-Pi 1979)	Mahale (Huffman 1990)	Wamba (Kano & Mulavva 1984)	Lomako (White 1992)
Feed	55.7	57.3	38.8	40.8	29.7	18.0	40.4
Travel	13.8	11.1	6.8	27.5	19.5	13.0	16.1
Rest	24.1	31.78	44.5	31.7[4]	38.6	43.08	31.9
Social	6.2		7.7		12.0[5]	6.3	
Other	1.2[6]		2.2		33.0[7]		

[1] Percentages at Gombe from Table V in Wrangham, 1977 (adult males only).

[2] Adult males and females.

[3] Adult males and females. Figures for all chimpanzees were used in the comparison because other studies did not take the possible effect of idiosyncratic individuals into account.

[4] Includes social and others.

[5] "Social" includes only grooming here.

[6] Instead of an "other" category, Wrangham had a "not observed" category.

[7] This number is made up of 13.0% of "other" activities and 20.0% of "terrestrial activities". See text for explanation.

Table 5.4: Results of Wilcoxon matched-pairs signed ranks test in the comparisons of time budgets between this and other studies

Site	Feed	Rest	Move	Social
Common chimpanzees				
Gombe[1,2]	0.480	-	-	0.0505
Ngogo[3]	0.0002	0.0002[4]	0.0002	-
Rio Muni[5]	0.008	0.003	0.006	-
Bonobos				
Lomako[6]	1.0	0.754	0.023	-
Wamba[7]	0.002	0.071	0.367	-

Note: N=12 hours of the day, from 07.00 to 19.00h, except in the comparison with Rio Muni, where N=11 (07.00 to 18.00h). Dashes indicate which comparisons were not possible because on some activity categories no detailed data were available in the literature.

[1] Wrangham, 1977; [2] only adult males used in both samples; [3] Ghiglieri, 1984; [4] includes rest, social and other; [5] Sabater-Pi, 1977; [6] White, 1977; [7] Kano & Mulavva, 1984.

chimpanzees in this study (Huffman, 1990). Unfortunately, no detailed data on chimpanzee time budgets at Mahale are available in the literature. A Kolmogorov-Smirnov test determines that the differences between Mahale and Ngogo are not significant ($m=5$, $n=5$, $D_{m,n}=2.33$, $p>0.1$).

Compared to bonobos, the Ngogo chimpanzees spent more time feeding than the bonobos at Wamba and less time travelling than the bonobos at Lomako; all other possible comparisons were not significant (Tables 5.3 and 5.4).

Separate data for time budgets of male and female chimpanzees exist in the literature only for Gombe (Wrangham, 1977, only males), Ngogo (Ghiglieri, 1984) and Mahale (Huffman, 1990). When male and female chimpanzees are analysed separately, males spent significantly less time feeding and travelling and more time resting and socialising in this study than in Ghiglieri's (Wilcoxon matched-pairs signed ranks test, $N=12$, feed: $p<0.02$; travel: $p<0.01$, rest [including social and others]: $p=0.0005$). Similarly, the females in this study spent less time feeding and more time resting and socialising than the females in Ghiglieri's study (Wilcoxon matched-pairs signed ranks test, $N=12$, feed: $p<0.01$; rest [including social and others]: $p=0.0002$). The difference between time spent travelling was not significant ($p=0.084$; Table 5.5).

Table 5.5: Time budgets of males and females in various chimpanzee communities.

Activity	Gombe (Wrangham 1977)	Ngogo (Ghiglieri 1984)		Ngogo[1] (This study)		Mahale (Huffman 1990)	
	Males	Males	Females	Males	Females	Males	Females
Feed	55.7	62.1	52.4	46.8	28.2	30.7	29.4
Travel	13.8	12.1	10.0	6.0	7.8	18.3	19.9
Rest	24.1	25.85	37.6[2]	38.3	53.0	33.7	40.1
Social	6.2			6.8	8.7	17.0[3]	10.5[4]
Other	1.27	2.0	2.3				

[1] Figures for all chimpanzees were used in the comparison because other studies did not take the possible effect of idiosyncratic individuals into account.

[2] Includes social and others.

[3] "Social" restricted to "grooming".

[4] Wrangham had a "not observed" category rather than a "other" category.

There was no significant difference in time spent feeding by males in this study and the study at Gombe (see above), but males at Ngogo spent significantly more time socialising. Males at Ngogo spent less time travelling and more time resting than males at Gombe (Table 5.5), but as no detailed data on these activity categories are available from the literature, no statistical analysis is possible.

Wrangham & Smuts (1980) indicate that Gombe females spent more time feeding than males in the period 1972-1975, but not significantly so. However, Goodall (1986) gives monthly means of time spent feeding for males and females for 1978, and a Wilcoxon matched-pairs signed ranks test determines that females spent significantly more time feeding than males in that year (matched for month, N=12 months, $p<0.05$).

Male chimpanzees at Mahale spent less time feeding but more time travelling and socialising than the males in this study, whereas time spent resting is approximately the same. The females of these two communities spent approximately the same time feeding, but the Mahale females spent more time travelling and less time resting. As no detailed data were given by Huffman (1992), a Wilcoxon matched-pairs signed ranks test is not possible. A Kolmogorov-Smirnov test determines that there are no significant differences between the males of Ngogo and the males of Mahale ($m=5$, $n=5$, $D_{m,n}=4.9$; $p>0.1$) and none between the females of the two sites ($m=5$, $n=5$, $D_{m,n}=2.8$; $p>0.1$).

5.8 Discussion

5.8.1 General time budgets in comparison with results from other studies

Ghiglieri (1984) suggested that the method with which chimpanzees were located had an effect on time budgets, meaning that he underestimated travelling time because approximately half of his data came from tree vigils. This study showed that location method had indeed an effect on the chimpanzee time budget, but not in time spent travelling. There was, however, a marked effect on time spent feeding: chimpanzees spent more time feeding when they had been located during tree vigils than when they had been located by following vocalisations. As approximately half of Ghiglieri's data came from tree vigils and the other half from following vocalisations (Ghiglieri, 1984), it can be assumed that his feeding time is an overestimate. Samples on chimpanzees located by following their vocalisations give a better picture of feeding time as chimpanzees vocalise both when they travel and when they are in feeding trees (Goodall, 1986) and therefore both activities are more likely to be sampled in proportion to their occurrence. As 36.9% of follows originated during tree vigils in this study, it is suggested that the feeding time derived from this study's data gives a more realistic picture of chimpanzees' time budgets at Ngogo.

However, as this study's data do partly stem from tree vigils, feeding time might still be overestimated compared to a feeding time arrived at by means of all-day follows, as was the case at Gombe (Wrangham, 1977). In all-day follows chimpanzees are followed from when they get up from their nests in the morning to when they settle down again for the next night. Time budgets from data representing the whole day can be assumed to give the best representation of the real chimpanzee time budget. In addition, Ngogo chimpanzees spent approximately the same amount of time feeding as resting, whereas Gombe chimpanzees spent more time feeding than resting. Both these facts suggest that Ngogo chimpanzees obtain their required nutrients in a shorter time than the chimpanzees at Gombe and therefore spend more time in other activities such as resting. This may be because food at Ngogo is more nutritious. Another reason may be a more even distribution of food patches. This would mean that the chimpanzees at Ngogo would not have to travel as far to fulfill their nutrient requirements and therefore would not incur such high energy demands. The fact that Ngogo chimpanzees spent less than half the time travelling compared to Gombe chimpanzees, indicates that this might be true.

If the percentage of time spent feeding by chimpanzees is an indicator of habitat quality, Mahale should rank at least as high as Ngogo with Okorobiko only slightly lower. However, it is doubtful whether the data for these sites are representative. In Mahale, the data were part of a study on the manifestations of old age and came from only 2 males (72.5 hours) and 7 females (289.2 hours), one male and two females being described as old and 2 females as nulliparous. Although no significant differences were found in the activity patterns between old individuals and younger ones, it was recognised that this might be due to the small sample size and that there was a general decline in activity in the old individuals. It is therefore suggested that the decreased percentage of time spent feeding reflects the fact that the sample was not representative of a whole chimpanzee community. As research has been going on in Mahale for 30 years, data on time budgets must exist. It is hoped that someone will pull them out of Mahale's big data pool and publish the results, so that realistic comparisons can be made with other chimpanzee communities.

The data from Rio Muni stem from only 119 hours of observation on what seem to be unhabituated chimpanzees. Therefore the estimate of time spent travelling can be questioned. If the chimpanzees were poorly habituated, 27.5% may have been an overestimate resulting from the fact that they fled whenever they detected the observers. If they were partially habituated, 27.5% may have been an underestimate for the same reasons as given for the present study (see below). If the estimate of percentage of time travelling is not a good one, obviously the percentage of time spent in other activity categories must be doubted as well. More research on the chimpanzees in Rio Muni is desirable to shed light on their time budgets.

An alternative explanation for lower travelling times at Ngogo, compared to those found at other study sites and by Ghiglieri at Ngogo, might be that the chimpanzees of this study were not very well habituated. They were habituated sufficiently to tolerate observers on the ground as long as the chimpanzees themselves were up in the trees, but when they came down from the trees, more often than not they travelled at such a speed that the observer lost the focal animal and the follow had to be terminated. For example, no boundary patrols (Goodall *et al.*, 1979; Goodall, 1986), which require most travelling, were ever witnessed. However, it is difficult to see why Ghiglieri shouldn't have had this problem as well, because the chimpanzees were completely unhabituated when he started his study. As in this study, he also suggested that the chimpanzees at Ngogo travel less than those at Gombe, although it is not clear whether this is a significant difference.

Data from Lomako on bonobo time budgets would suggest that the chimpanzees at Ngogo live in an environment of similar distribution and quality. The Ngogo chimpanzees seem to be even more social than bonobos at Lomako, judging by the time spent socialising. However, given that time spent travelling at Ngogo may be underestimated, time spent on another activity would have to decrease if travelling increases. Further research must show which category this would be. Time budget data on Wamba seem to confirm these conclusions. As a provisioned population (Kano & Mulavva, 1984), these bonobos can be said to have the best environment in terms of nutrient availability, and this is reflected in the exceptionally low time spent feeding (if one takes the figure of 18% [Kano & Mulavva, 1984] at its face value). However, I think that these data should be treated with caution. Apart from the fact that the percentages given add up to 107%, Kano & Mulavva (1984) introduce a category of "terrestrial" activities, consisting of, one is forced to assume, all that the observers weren't able to observe on the ground. "Because resting was an important factor in terrestrial activities, it may be inferred that the total feeding time (arboreal and terrestrial) does not exceed 30%." (Kano & Mulavva, 1984, p.263). As research at Lomako continues, it is hoped that more reliable data on time budgets will be made available.

5.8.2 Gender differences

Male chimpanzees spent more time feeding than either anoestrous or oestrous females at Ngogo. Ghiglieri (1984) also found that males spent significantly more time feeding than females. He suggests that this may be because the males also spent significantly more time travelling. Therefore the males' "metabolic demands are increased by increased travel" (Ghiglieri, 1984, p.68) so that they have to feed more to meet those demands. However, a re-analysis of Ghiglieri's time budget data did reveal a significant difference in time spent feeding and time spent resting between the sexes, but not in time spent travelling (Wilcoxon matched-pairs signed ranks test, matching hours of the day, feeding: $N=12$ hours of the day, $p<0.05$; resting: $N=12$, $p<0.001$; moving: $N=12$, $p=0.21$). Hence, Ghiglieri's data do, in fact, not support the hypothesis that males' greater amount of travelling causes them to spend more time feeding.

As the data on travelling in this study remain inconclusive, the possibility that males do spend more time travelling than females cannot be excluded, especially as data for Gombe and Mahale show that males there travel indeed further than females (Hasegawa, 1990; Wrangham, 1979; Wrangham & Smuts, 1980). Assuming that this is also true for Ngogo, males would need more nutrients to fuel the higher physical demands made on them (Taylor *et al.*, 1970). On the other hand, females were shown to spend more time resting. This might mean that females follow a different strategy from males: rather than incur higher energetic costs which they have to fuel by feeding, they conserve energy by resting more than males. The fact that they also spend more time moving than males seems to contradict such a strategy. However, an alternative explanation for this distribution of travelling might again lie in different degrees of habituation. Females are reportedly shyer than males (Goodall, 1986; R. Wrangham, pers. communication), and this study was no exception. It is possible that while habituated sufficiently not to flee, females might have been more nervous than males in the presence of an observer and therefore spent more time moving about, perhaps to keep the observer in view or at a distance.

However, at Gombe females spent more time feeding than males. In the absence of weight data from Kibale, it is assumed that the weight differences between males and females are approximately the same at both sites. This might mean that Ngogo males have to spend more time travelling than Gombe males, and they therefore need to spend relatively more time feeding than Ngogo females to fuel their (in comparison to Gombe males) increased physical activity. In absence of reliable travelling data from Ngogo, this remains speculation. However, home range size may indicate whether this explanation might be true. The community range of Gombe was estimated at 24 km^2 at its maximum (Goodall, 1986). Taking a population density of 3 chimpanzees per km^2 and a community size of 130 individuals as the basis for an estimate of community range size at Ngogo (see Chapter 3), this would yield a community range of 43.3 km^2, which is almost twice that of Gombe at its maximum. Clearly, it would take more travelling to patrol the border of such a community range.

From differences in their time budgets, it would also seem that adult male chimpanzees at Ngogo were less sociable than adult female chimpanzees. However, most of the females' social behaviour was spent on presumed offspring. Once this "maternal" behaviour has been partialled out, male chimpanzees at Ngogo spent more time engaged in social behaviour than females, and they therefore follow the same pattern as other common chimpanzee populations, where males are more sociable than females (Goodall, 1986; Huffman, 1990; Wrangham *et al.*, 1994).

While concerns as to the representativeness of Mahale time budget data make comparisons with data on males and females from other study sites questionable, it seems worth pointing out that the males at Mahale seem to spend approximately three times as much time socialising as the males at Ngogo or those at Gombe or the bonobo males at Lomako. On the other hand, if time spent travelling by females at Ngogo was an underestimate and it turned out to be higher, and if time resting decreased to compensate for this, then the females at Ngogo and those at Mahale would have nearly identical time budgets, which might suggest that Mahale and Ngogo habitats are not dissimilar from a nutritional point of view. Clearly, more data on time budgets at Mahale are needed as well as data from better habituated chimpanzees at Ngogo.

5.8.3 Individual differences

It has been shown that the data from all those individuals that had contributed most, could influence the results of comparisons to a considerable degree. It is therefore always advisable to omit those data and determine if the results still hold. Especially in studies of only partly habituated animals, we need to ask whether the fact that some individuals show less fear of the observer than other individuals is an indication that they may also be "peculiar" in other ways. Hence their data should be treated with particular caution.

In this study, it could be said that Mweya behaved more like a female and Lita behaved more like a male than average representatives of their sex would. In Mweya's case, however, it seems that he is only different from other males when a three-day consortship is included in the data. Goodall points out that time spent feeding may be depressed by "tensions occurring on the first day of a consortship" (Goodall, 1986, p.241). In fact, 156 agonistic interactions happened during the first day of this consortship, whereas 21 happened on the second day and only 6 on the third. It is therefore suggested that the reason why Mweya fed significantly less than other males was the fact that more than half of his data came from a consortship.

In Lita's case, she behaved very much like a sterile female at Gombe, Gigi (Goodall *at al.*, 1979; Goodall, 1986). Goodall stresses that Gigi behaved very much like a male. For example, she often goes on boundary patrols with the males, displays and hunts more often than other females. Although Lita was not observed to display or hunt during this study, her time budget resembled more that of an average male than that of an average female in that she spent more time feeding and less time resting.

TI, SW and CR contributed most individual data because in contrast to most other anoestrous females at Ngogo they did not try to escape from the observer and therefore permitted several whole day follows. However, SW was suspected to be in an advanced state of pregnancy (Wrangham, personal communication) and CR had a very small infant that needed constant support. This might have been the reasons why these females spent so much time resting and so little time doing anything else, compared to other members of their sex class.

5.9 Summary

- The Ngogo chimpanzees spent most of their time resting and feeding.

- Adult males spent more time feeding and less time resting and socialising than anoestrous females. Most of the females' socialising was directed towards their offspring. When these data were omitted, males spent significantly more time socialising than anoestrous females, following the pattern of other common chimpanzee communities.

- Adult males spent more time feeding than oestrous females.

- There are no significant differences in time budgets between oestrous and anoestrous females.

- Those individuals who contributed most data were shown to be different from all the other members of their sex class and to influence the time budgets accordingly.

- Time spent feeding showed two peaks, one in the morning and one in the evening.

- Social behaviour peaked around midday.

- The diurnal rhythms of adult males, anoestrous and oestrous females were not correlated with each other except for socialising which was correlated between males and oestrous females.

- The method with which chimpanzees are located has an impact on the estimate of time spent feeding.

- Chimpanzees at Ngogo spent less time feeding and moving and more time resting and socialising than chimpanzees in Rio Muni.

- There was no difference between time spent feeding by chimpanzee males at Ngogo and the males in Gombe.

- Compared to bonobos, the Ngogo chimpanzees spent more time feeding than the bonobos at Wamba and less time travelling than the bonobos at Lomako.

- It is suggested that the differences between chimpanzee time budgets at Gombe and at Ngogo are a consequence of differences in habitat productivity.

- In conclusion, the time budget of the Ngogo chimpanzees resembles more closely a bonobo time budget than the time budget of a common chimpanzee community from a non-forest habitat.

Chapter 6

Habituation

6.1 Introduction

Different species of animals become habituated to humans to different degrees (Schaller, 1963; Geist, 1971; Nishida, 1979; Fossey, 1983; Goodall, 1986; Tutin & Fernandez, 1991). There may even be differences within one species. The mountain gorilla habituated to observers quite well in a relatively short time (Schaller, 1963; Fossey, 1986), whereas the western lowland gorillas *Gorilla gorilla gorilla* at Lopé in Gabon have not habituated well to humans in over 4 years (Tutin & Fernandez, 1991). Chimpanzees habituated completely and relatively quickly to the presence of humans (Goodall, 1986; Nishida 1979) when they were provisioned with food. However, when Ghiglieri (1984) tried to habituate chimpanzees without provisioning in the Kibale Forest in Uganda, he achieved only partial success. Similarly, bonobos habituated better when they were provisioned with sugar cane at Wamba (Kano, 1980), although they were successfully habituated eventually at Lomako without provisioning (Badrian & Badrian, 1984). The distinct disadvantage of provisioning is that it might alter the species' natural behaviour. Wrangham (1974) found that the chimpanzees at Gombe had a higher rate of aggressive interactions in the artificial feeding area and they were more likely to hunt baboons after they had been feeding at the artificial feeding area.

The impact of observers on the behaviour of gorillas (*Gorilla gorilla beringei*) has been investigated to some degree (Schaller, 1963; Aveling & Harcourt, 1984; Aveling & Aveling, 1989). However, Schaller's (1963) findings cannot be generalised to visits by tourist groups, because most of his encounters with gorillas involved only one or two observers. The only previous data on chimpanzee habituation is also from a non-tourist site (Tutin & Fernandez, 1991).

Habituation is usually a means to an end, i.e. to get the animals sufficiently used to one or several observers for the sake of research or conservation in the form of tourism. With ecotourism (e.g. Boo, 1990; Burnie, 1994; Giannecchini, 1993) on the rise, the questions of whether the animals are actually disturbed in their behaviour through the process of habituation and the presence of people and to what degree become ever more important. Monitoring programmes fulfill two vital functions. First, they enable us to evaluate the progress of habituation with time. Second, they enable us to determine whether changes in the animals' behaviour take place over time and what causes these changes. Only in such a way is it possible to detect potential problem areas at an early stage so that countermeasures can be taken.

This study monitored chimpanzees' initial reactions to observers over a period of 18 months whenever they were encountered in the forest at Ngogo and Kanyancu. The categories of reactions are ordered in increasing degree of habituation. While the exact position of each category may be arguable, it is assumed that the flight and charge categories together represent "unhabituated" reactions, whereas *curiosity* and *ignore* are at the other end of the scale and together represent "habituated" reactions. The remaining categories, *approach and wait*, *stealthy retreat*, *loud vocalisations*, *soft vocalisations* and *hide* together represent the intermediate state between "unhabituated" and "habituated".

Observers were the author, field guides and research assistants. As reaction categories are self-explanatory and consist mostly of rather obvious activities (for definitions see Table 2.5), the problem of inter-observer reliability was considered negligible after the guides and assistants received initial training (but see Discussion, 4.6.3). A variety of factors which might have an effect on the chimpanzees' reactions were monitored at the same time. In addition, focal animal samples were conducted at Kanyancu with different numbers of observers (including tourists) present to allow for comparisons of behaviour under these conditions.

Assuming that any community of chimpanzees will eventually habituate to the presence of non-threatening humans, the predictions were as follows:

- The percentage of *unhabituated* reactions would decrease with time.

- The percentage of *habituated* reactions would increase with time. (Since no predictions can be made about *intermediate* reactions, two-tailed probabilities are applied in statistical tests in this case).

- Percentage of time spent locomoting would increase with more observers present.

- Percentage of time spent resting and feeding would decrease with more observers present.

- Vocalising rates would increase with more observers present, as would behaviours such as hiding or displaying towards the observers.

Intersite comparisons were made both within Kibale and with Lopé in Gabon (Tutin & Fernandez, 1991) in order to determine whether differences in habitat might have an impact on chimpanzee habituation.

6.2. Changes in reactions to observers over time

The relative frequency of chimpanzees' reactions to contact with observers is presented for both Kanyancu and Ngogo as summed totals (Table 6.1a and b) and monthly percentages (Table 6.2a and b). Spearman's rank correlation coefficients between monthly percentages of reaction categories and time were calculated (Table 6.3). Both at Kanyancu and Ngogo, charge reactions decrease significantly over the study period, whereas ignore reactions increase at Kanyancu and curiosity reactions increase with time at Ngogo. In addition, stealthy retreat reactions decrease at Ngogo.

When reaction categories are lumped to *unhabituated* (flight and charge), *intermediate* (approach/wait, stealthy retreat, loud vocalisation, soft vocalisation, and hide) and *habituated* (curiosity and ignore), the percentage of unhabituated reactions decreases significantly over time at both study sites, whereas the percentage of habituated reactions increases (Table 6.4, Figures 6.1 and 6.2). The percentage of intermediate reactions does not change over time.

Table 6.1a: Relative frequencies of individual chimpanzees' reactions to observers (all categories of detectors) at Kanyancu.

	All age/sex classes		Adult male		Adult female	
	N	Percent	N	Percent	N	Percent
Flight	111	25.5	37	19.6	52	31.0
Charge	57	13.1	46	24.3	10	6.0
Approach/wait	2	0.5	0	0	0	0
Stealthy retreat	42	9.6	10	5.3	18	10.7
Loud vocalisation	31	7.1	15	7.9	13	7.7
Soft vocalisation	21	4.8	7	3.7	13	7.7
Hide	30	6.9	5	2.6	14	8.3
Curiosity	29	6.7	16	8.5	6	3.6
Ignore	113	25.9	53	28.1	42	25.0
All	436	100.0	189	100.0	168	100.0

Table 6.1b: Relative frequencies of individual chimpanzees' reactions to observers (all categories of detectors) at Ngogo.

	All age/sex classes		Adult male		Adult female	
	N	Percent	N	Percent	N	Percent
Flight	72	23.5	11	8.8	15	24.6
Charge	7	2.3	6	4.8	1	1.6
Approach/wait	5	1.6	4	3.2	0	0
Stealthy retreat	17	5.6	4	3.2	4	6.6
Loud vocalisation	27	8.8	10	8.0	6	9.8
Soft vocalisation	16	5.2	7	5.6	5	8.2
Hide	21	6.9	6	4.8	9	14.8
Curiosity	20	6.5	6	4.8	2	3.3
Ignore	121	39.5	71	56.8	19	31.1
All	306	100.0	125	100.0	61	100.0

Table 6.2a: Monthly percentages of reactions at Kanyancu. All detector categories.

Month of study	Flight	Charge	Approach/ wait	Stealthy retreat	Loud vocal.	Soft vocal.	Hide	Curiosity	Ignore	N[1]
0292	20.0	46.7	0	0	20.0	0	0	0	13.3	15
0392	25.8	6.5	0	16.1	3.2	12.9	0	9.7	25.8	31
0492	31.1	26.2	0	8.2	4.9	11.5	0	6.6	11.5	61
0592	25.0	25.0	0	12.5	18.8	0	12.5	6.3	0	16
0692	31.6	26.3	0	10.5	10.5	0	5.3	0	15.8	19
0792	27.3	0.0	0	4.5	9.1	4.5	18.2	22.7	13.6	22
0892	34.8	13.0	4.3	8.7	0	8.7	0	13.0	17.4	23
0992	17.4	17.4	0	0	8.7	0	8.7	0	47.8	23
1092	26.7	0.0	0	13.3	0.0	0	26.7	0	33.3	15
1192	21.6	18.9	0	16.2	0.0	5.4	10.8	0	27.0	37
1292	27.3	9.1	0	27.3	18.2	0	0	0	18.2	11
0193	35.7	7.1	0	7.1	7.1	7.1	14.3	0	21.4	14
0293	12.5	6.3	0	0	0	6.3	6.3	6.3	62.5	16
0393	19.4	5.6	0	11.1	11.1	5.6	8.3	2.8	36.1	36
0493	36.6	0.0	0	7.3	9.8	0	4.9	9.8	31.7	41
0593	12.2	8.2	2.0	10.2	8.2	0	10.2	12.2	36.7	49
0693	42.9	0.0	0	14.3	0	14.3	0	14.3	14.3	7

[1] Occurrences of behaviour pooled from several individuals.
For definitions see Table 2.3.

Table 6.2b: Monthly percentages of reactions at Ngogo. All detector categories.

Month of study	Flight	Charge	Approach/ wait	Stealthy retreat	Loud vocal.	Soft vocal.	Hide	Curiosity	Ignore	N[1]
0192	30.0	0	0	20.0	10.0	0	0	0	40.0	10
0292	16.7	5.6	0	11.1	11.1	11.1	11.1	0	33.3	18
0392	23.5	5.9	5.9	23.5	5.9	11.8	5.9	0	17.6	17
0492	44.4	5.6	0	5.6	5.6	11.1	5.6	0	22.2	18
0592	0	20.0	0	20.0	10.0	0	0	0	50.0	10
0692	66.7	0	0	0	0	33.3	0	0	0	3
0792	20.0	0	0	20.0	0	20.0	0	0	40.0	5
0892	0	0	0	0	0	0	0	0	0	0
0992	10.0	10.0	0	0	20.0	20.0	10.0	0	30.0	10
1092	42.9	0	0	0	0	0	0	14.3	42.9	7
1192	18.5	3.7	0	0	11.1	3.7	7.4	18.5	37.0	27
1292	22.2	0	11.1	5.6	0	0	5.6	5.6	50.0	18
0193	49.1	0	5.9	5.9	11.8	0	0	5.9	23.5	17
0293	37.0	0	0	7.4	11.5	3.7	3.7	7.4	29.6	27
0393	10.6	0	2.1	0	2.1	2.1	6.4	6.4	70.2	47
0493	22.2	0	0	2.8	5.6	0	13.9	11.1	44.4	36
0593	19.4	0	0	0	22.2	8.3	11.1	8.3	30.6	37
0693	0	0	0	0	40.0	0	13.3	0	46.7	15

[1] Occurrences of behaviour pooled from several individuals.
For definitions see Table 2.3.

Table 6.3: Changes of reaction categories over time.

Reaction	rs Kanyancu	rs Ngogo
Flight	0.058	- 0.207
Charge	- 0.615**	- 0.551*
Approach/wait	-	-
Stealthy retreat	0.114	- 0.598$^+$
Loud vocalisation	- 0.262	0.280
Soft vocalisation	0.045	- 0.354
Hide	0.159	0.445
Curiosity	0.192	0.610**
Ignore	0.593**	0.337

rs: Spearman's rank correlation coefficient.
* significant at level $p<0.025$ (one-tailed)
** significant at level $p<0.01$ (one-tailed)
$^+$ significant at level $p<0.02$

Table 6.4: Changes of combined reaction categories over time.

Reaction	rs Kanyancu	rs Ngogo
Flight & Charge	- 0.510**	- 0.461*
Approach/wait & Stealthy retreat & Loud vocalisation & Soft vocalisation & Hide	0.042	- 0.103
Curiosity & Ignore	0.551**	0.426*

* significant at level $p<0.05$ (one-tailed)

** significant at level $p<0.025$ (one-tailed)

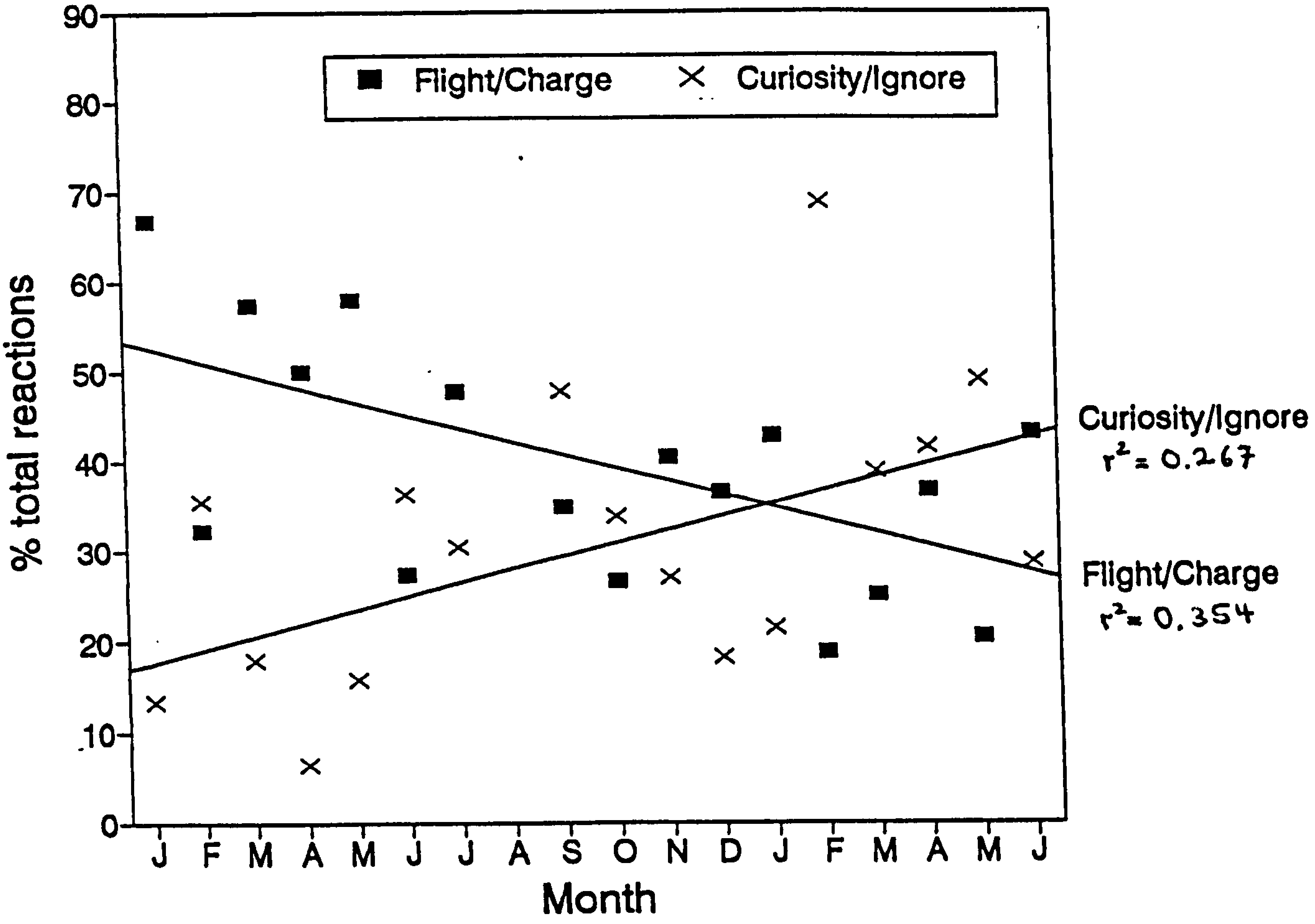


Figure 6.1: Change of percentage of reaction categories over time at Kanyancu.

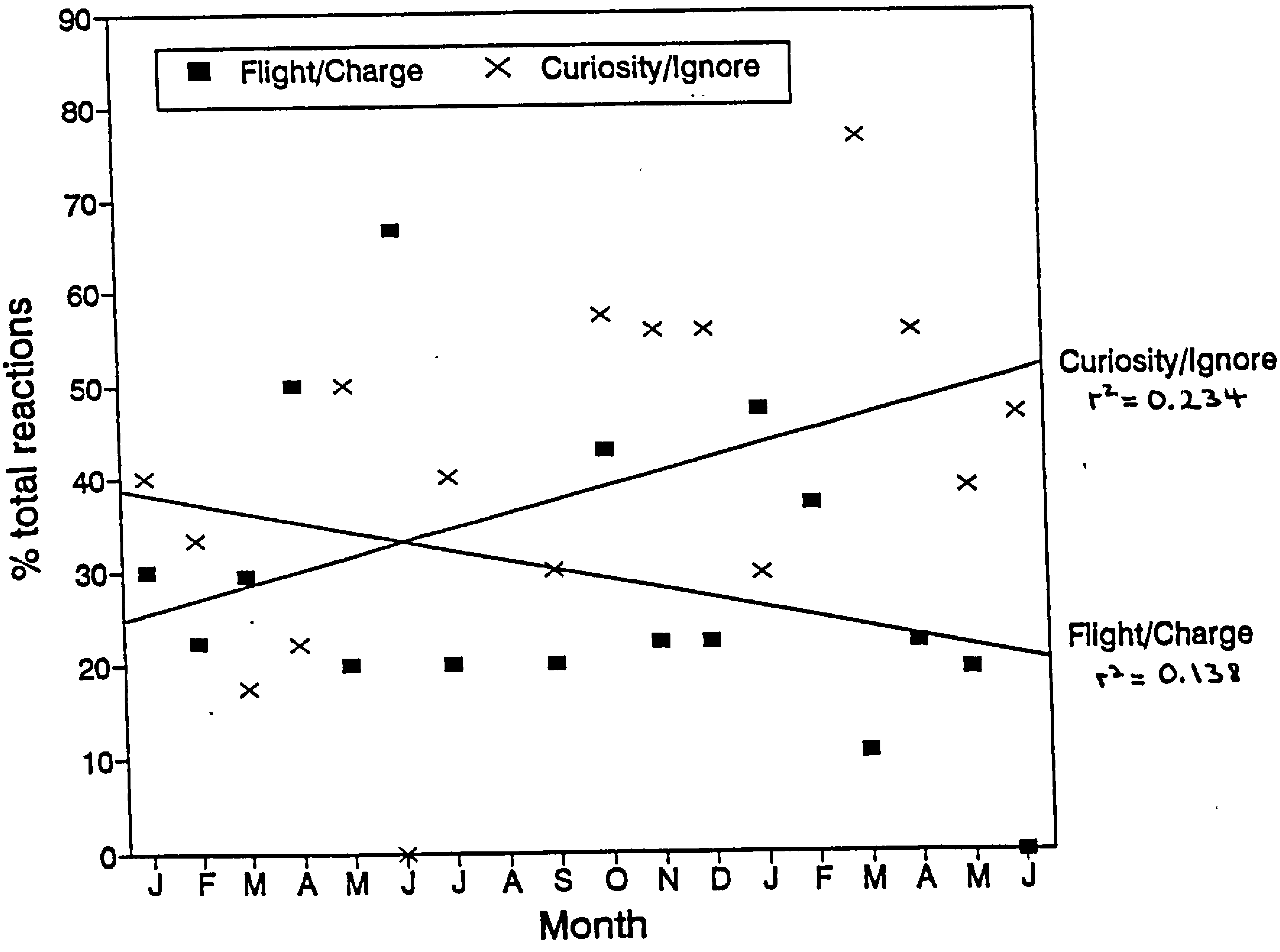


Figure 6.2: Change of percentage of reaction categories over time at Ngogo.

6.3. Comparison of habituation rates at Kanyancu and Ngogo

There is a significant difference between the frequencies of chimpanzees' reactions to the observer at Kanyancu and at Ngogo (for summed totals: $X^2=42.2$; df=8; $p<0.001$). A partitioned X^2 test reveals that the difference lies in two reaction categories: the chimpanzees at Kanyancu charge more often than those at Ngogo (partitioned $X^2=19.2$; df=1; $p<0.001$) and ignore less often than at Ngogo (partitioned $X^2=15.5$; df=1; $p<0.001$) (Table 6.5).

The fact that the regression lines for *unhabituated* and *habituated* reactions intersect later in time at Kanyancu than at Ngogo also suggests that chimpanzees at Kanyancu were less habituated than those at Ngogo (Figures 6.1 and 6.2).

6.4 Factors influencing reactions

Findings at Lopé suggested that various factors influenced the chimpanzees' reactions (Tutin & Fernandez, 1991). These were the age/sex class of the detector, the distance to the observer at detection, the distance to the next chimpanzee, the activity the chimpanzee was engaged in before it detected the observer, the detector's height above ground and the density of

Table 6.5: Additive partitions of X^2 test of differences in reaction categories between Kanyancu and Ngogo (all detector categories). Expected values (in brackets) calculated from marginal totals.

Reaction	Kanyancu	Ngogo	Combined
Loud vocalisation	31 (34)	27 (24)	58
Soft vocalisation	21 (22)	16 (15)	37
Total	436	306	N=742

(1): X^2=0.102; critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Kanyancu	Ngogo	Combined
Loud and soft vocalisation	52 (56)	43 (39)	95
Hide	30 (30)	21 (21)	51
Total	436	306	N=742

(2): X^2=0.229; critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Kanyancu	Ngogo	Combined
Loud and soft vocalisation and hide	82 (86)	64 (60)	146
Curiosity	29 (29)	20 (20)	49
Total	436	306	N=742

(3): X^2=0.138; critical value for X^2 (p=0.05, df=1): 3.84

Table 6.5 continued

Reaction	Kanyancu	Ngogo	Combined
Loud and soft vocalisation and hide and curiosity	111 (115)	84 (80)	195
Approach/wait	2 (4)	5 (3)	7
Total	436	306	N=742

(4): X^2=2.2; critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Kanyancu	Ngogo	Combined
Loud and soft vocalisation and hide and curiosity and approach/wait	113 (119)	89 (83)	202
Flight	111 (108)	72 (76)	183
Total	436	306	N=742

(5): X^2=0.837, critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Kanyancu	Ngogo	Combined
Loud and soft vocalisation and hide and curiosity and approach/wait and flight	224(226)	161 (159)	385
Stealthy retreat	42 (35)	17 (24)	59
Total	436	306	N=742

(6): X^2=3.57; critical value for X^2 (p=0.05, df=1): 3.84

Table 6.5 continued

Reaction	Kanyancu	Ngogo	Combined
Loud and soft vocalisation and hide and curiosity and approach/wait and flight and stealthy retreat	266 (261)	178 (183)	444
Charge	57 (38)	7 (26)	64
Total	436	306	N=472

(7): X^2=19.2; critical value for X^2 (p=0.001, df=1): 10.83

Reaction	Kanyancu	Ngogo	Combined
Loud and soft vocalisation and hide and curiosity and approach/wait and flight and stealthy retreat and charge	323 (299)	185 (209)	508
Ignore	113 (138)	121 (97)	234
Total	436	306	N=472

(8): X^2=15.5; critical value for X^2 (p=0.001, df=1): 10.83

vegetation. In addition, this study also considered the chimpanzees' party size, the way chimpanzees were located (*location method*) and the numbers of observers present. X^2 tests were conducted on these factors with reaction as the dependent variable. Table 6.6 gives an overview of the results.

6.4.1 Age/sex classes

When results for the entire study period are pooled, adult males and females differ significantly in their reactions to observers. This was the case both at Kanyancu ($X^2=38.9$, df=7, $p<0.001$: to avoid empty cells in the X^2 test, approach/wait had to be dropped from the analysis) and Ngogo ($X^2=12.4$, df=2, $p<0.002$; for the χ^2 test reaction categories were combined to *unhabituated*, *intermediate* and *habituated*) (see Tables 6.1a, b and 6.9a, b).

At Kanyancu, males and females were encountered at approximately the same rate ($N_m=189$, $N_f=168$). Males and females differ mainly in *charge*, *flight* and *hide*: males charge more often than females (partitioned $X^2= 16.7$, df=1, $p<0.001$), but flee and hide less often than females (*flight*: partitioned $X^2=6.32$, df=1, $p<0.02$; *hide*: partitioned $X^2= 6.59$, df=1, $P<0.02$) (Table 6.7). The sample sizes for males and females of the younger age classes were not sufficiently large to test for sex differences.

Table 6.6: Results of X^2 tests with reaction as dependent variable.

Independent variable	Kanyancu: df	X^2	p	Ngogo: df	X^2	p
Age/sex class of detector	4	19.1	<0.001	2	12.4	<0.002
Distance to the observer at detection	9	35.4	<0.001	2	32.7	<0.001
Distance to the next chimp at detection	4	14.5	<0.01	2	3.1	0.214
Activity before contact	6	13.7	<0.05	2	3.1	0.214
Height above ground	4	11.2	<0.05	4	28.0	<0.001
Number of observers	9	13.4	>0.05	3	7.7	0.056
Party size	4	4.1	>0.05	4	4.1	>0.05
Density of vegetation	2	1.3	>0.05	2	0.9	>0.05
Location method	4	29.9	<0.001	4	9.2	0.056

Degrees of freedom vary because categories had to be lumped to avoid empty cells; Pearson X^2 was used.

Table 6.7: Additive partitions of X^2 test of differences in reaction categories between adult males and females (all detector categories) at Kanyancu. Expected values (in brackets) calculated from marginal totals.

Reaction	Males	Females	Combined
Ignore	53 (50)	42 (45)	95
Curiosity	16 (12)	6 (10)	22
Total	189	168	N=357

(1): X^2=2.06; critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Males	Females	Combined
Ignore and Curiosity	69 (62)	48 (55)	117
Hide	5 (10)	14 (9)	19
Total	189	168	N=357

(2): X^2=6.998; critical value for X^2 (p=0.02, df=1): 5.41

Reaction	Males	Females	Combined
Ignore or Curiosity or Hide	74 (72)	62 (64)	136
Soft vocalisations	7 (11)	13 (9)	20
Total	189	168	N=357

(3): X^2=2.64; critical value for X^2 (p=0.05, df=1): 3.84

Table 6.7 continued

Reaction	Males	Females	Combined
Ignore or Curiosity or Hide or Soft vocalisations	81 (83)	75 (73)	156
Loud vocalisations	15 (15)	13 (13)	28
Total	189	168	N=357

(4): X^2=0.026; critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Males	Females	Combined
Ignore or Curiosity or Hide or Soft vocalisations or Loud vocalisations	96 (97)	88 (87)	184
Stealthy retreat	10 (15)	18 (13)	28
Total	189	168	N=357

(5): X^2=2.64, critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Males	Females	Combined
Ignore or Curiosity or Hide or Soft vocalisations or Loud vocalisations or Stealthy retreat	106 (112)	106 (100)	212
Charge	46 (30)	10 (26)	56
Total	189	168	N=357

(6): X^2=18.4; critical value for X^2 (p=0.001, df=1): 10.83

Table 6.7 continued

Reaction	Males	Females	Combined
Ignore or Curiosity or Hide or Soft vocalisations or Loud vocalisations or Stealthy retreat or Charge	152 (142)	116 (126)	268
Flight	37 (47)	52 (42)	89
Total	189	168	N=357

(7): X^2=6.15; critical value for X^2 (p=0.02, df=1): 5.41

Table 6.8: Additive partitions of X^2 test of differences in reaction categories between adult males and females (all detector categories) at Ngogo. Expected values (in brackets) calculated from marginal totals.

Reaction	Males	Females	Combined
Habituated	77 (66)	21 (32)	98
Intermediate	31 (37)	24 (18)	55
Total	125	61	N=186

(1): X^2=7.88; critical value for X^2 (p=0.02, df=1): 5.41

Reaction	Males	Females	Combined
Habituated and Intermediate	108 (103)	45 (50)	153
Unhabituated	17 (22)	16 (11)	33
Total	125	61	N=186

(2): X^2=4.48; critical value for X^2 (p=0.05, df=1): 3.84

Note: Habituated includes ignore and curiosity; intermediate includes stealthy retreat, loud vocalisations, soft vocalisations and hide; unhabituated includes flight and charge.

Table 6.9a: Monthly percentages of reactions at kanyancu. Adult males only, all detector categories.

Month of study	Flight	Charge	Approach/ wait	Stealthy retreat	Loud vocal.	Soft vocal.	Hide	Curiosity	Ignore	N[1]
0292	9.1	63.6	0	0	9.1	0	0	0	18.2	11
0392	20.0	13.3	0	13.2	6.7	6.7	13.3	0	26.7	15
0492	16.7	44.4	0	2.8	8.3	2.8	0	8.3	16.7	36
0592	14.3	57.1	0	0	14.3	0	0	14.3	0	7
0692	9.1	45.5	0	18.2	18.2	0	0	0	9.1	11
0792	36.4	0	0	9.1	0	0	18.2	36.4	0	11
0892	33.3	16.7	0	16.7	0	16.7	0	16.7	0	6
0992	25.0	37.5	0	0	12.5	0	0	0	25.0	8
1092	14.3	0	0	14.3	0	0	14.3	0	57.1	7
1192	25.0	25.0	0	8.3	0	8.3	0	0	33.3	12
1292	25.0	25.0	0	25.0	0	0	0	0	25.0	4
0193	66.7	0	0	0	0	16.7	0	0	16.7	6
0293	11.1	0	0	0	0	0	11.1	0	77.8	9
0393	20.0	10.0	0	0	5.0	10.0	5.0	5.0	45.0	20
0493	18.2	0	0	0	18.2	0	0	27.3	36.4	11
0593	0	14.3	0	0	21.4	0	0	7.1	57.1	14
0693	100.0	0	0	0	0	0	0	0	0	1

[1] Occurrences of behaviour pooled from several individuals.
For definitions see Table 2.3.

Table 6.9b: Monthly percentages of reactions at Kanyancu. Adult females only, all detector categories.

Month of study	Flight	Charge	Approach/ wait	Stealthy retreat	Loud vocal.	Soft vocal.	Hide	Curiosity	Ignore	N[1]
0292	50.0	0	0	0	50.0	0	0	0	0	4
0392	33.3	0	0	16.7	0	25.0	0	8.3	16.7	12
0492	45.0	0	0	20.0	0	25.0	0	5.0	5.0	20
0592	16.7	0	0	16.7	33.3	0	33.3	0	0	6
0692	57.1	0	0	0	0	0	14.3	0	28.6	7
0792	20.0	0	0	0	20.0	10.0	20.0	10.0	20.0	10
0892	30.0	20.0	0	0	0	10.0	0	10.0	30.0	10
0992	16.7	8.3	0	0	8.3	0	8.3	0	58.3	12
1092	40.0	0	0	20.0	0	0	20.0	0	20.0	5
1192	33.3	26.7	0	6.7	0	6.7	13.3	0	13.3	15
1292	33.3	0	0	33.3	0	0	0	0	33.3	3
0193	33.3	33.3	0	0	33.3	0	0	0	0	3
0293	0	33.3	0	0	0	33.3	0	0	33.3	3
0393	25.0	0	0	0	37.5	0	12.5	0	25.0	8
0493	40.0	0	0	13.3	6.7	0	6.7	0	33.3	15
0593	22.2	5.6	0	16.7	5.6	0	11.1	5.6	33.3	18
0693	33.3	0	0	16.7	0	16.7	0	16.7	16.7	6

[1] Occurrences of behaviour pooled from several individuals.
For definitions see Table 2.3.

At Ngogo, males were encountered twice as often as females (Nm=125; Nf=61). Here, males reacted in an unhabituated way less often than females (partitioned $X^2=4.48$, df=1, $p<0.05$) and more often in a habituated way (partitioned $X^2=7.83$, df=1, $p<0.02$) (Table 6.8).

As there was a difference between adult males and adult females in their reactions to observers, a comparison of the pooled data with other age classes would not be appropriate. A comparison by sex was not possible, as the sample size for the other age classes was too small (subadult: N=19; juveniles and infants: N=32).

6.4.2 Number of observers

Analysis of contacts

Number of observers did not have an impact on the chimpanzees' reactions at either study site (Kanyancu: $X^2=13.4$, df=9, $p>0.05$; Ngogo: $X^2=7.7$, df=3, $p>0.05$; Tables 6.10a, b).

As another means of testing for a possible correlation between numbers of observers and *reaction*, correlation coefficients between numbers of observers and percentage of reaction categories were calculated (Table 6.10a). The only reaction category that changed significantly with higher number of observers (range 1-5,

Table 6.10a: Reactions (%) for different numbers of observers present at Kanyancu. All categories of detectors.

No. observ.	Flight	Charge	Approach/ Wait	Stealthy retreat	Loud vocal.	Soft vocal.	Hide	Curiosity	Ignore	N[1]
1	22.9	5.7	0	8.6	8.6	8.6	0	8.6	37.1	35
2	24.1	13.4	0.4	10.3	7.6	5.4	8.5	8.0	22.3	224
3	35.1	9.6	0	10.6	6.4	2.1	5.3	3.2	27.7	94
4	21.1	23.7	0	13.2	7.9	0	2.6	5.3	26.3	38
5	27.3	9.1	0	0	0	0	9.1	18.2	36.4	11

[1] Occurrences of behaviour pooled from several individuals.
For definitions see Table 2.3.

Table 6.10b: Reactions (%) for different numbers of observers present at Ngogo. All categories of detectors.

No. observ. present	Flight	Charge	Approach/ wait	Stealthy retreat	Loud vocal.	Soft vocal.	Hide	Curiosity	Ignore	N[1]
1	24.0	3.3	2.2	8.2	5.5	6.6	7.7	8.2	34.4	183
2	22.5	1.4	1.4	2.8	9.9	2.8	1.4	5.6	52.1	71
3	18.8	0	0	0	25.0	12.5	12.5	0	31.3	16
4	30.0	0	0	0	30.0	0	10.0	0	30.0	10
9	0	0	0	0	100.0	0	0	0	0	1

[1] Occurrences of behaviour pooled from several individuals.
For definitions see Table 2.3.

mean 2.41) at Kanyancu was *soft vocalisations* (r= -0.9577; p=0.01, two-tailed).

At Ngogo, when single reaction categories are analysed, the percentage of *loud vocalisations* increased significantly with higher numbers of observers (r=0.9927; p=0.001), whereas *ignore* reactions decreased significantly (r=-0.8946; p=0.04). If reaction categories are lumped to a habituated category including *curiosity* and *ignore* and an unhabituated category including all other reaction categories, the percentage of habituated reactions decreased significantly with higher numbers of observers (r=-0.9162, p=0.03), whereas the percentage of unhabituated reactions increased (r=0.9147; p<0.03) (Table 6.10b).

Analysis of follows at Kanyancu

Fourteen follows were conducted (involving four female and six male chimpanzees) during which the number of observers changed. A Wilcoxon signed ranks test was used to determine whether there were significant differences in activities with different numbers of observers present. The test matched the situation before the tourist group arrived ("before": with only 2 to 3 observers present) to the situation when the tourist group was present ("present": with 4 to 15 observers present). Also, where possible, the situation "present" was compared with that after the tourists had left ("after": with 1 to 4 observers present) (Table 6.11).

Table 6.11: Changes of numbers of observers during follows.

Case[a]	Number of observers: Before tourist group arrived[1]	While tourist group was present[2]	After tourist group had left[3]
Kfre2503	3	11	3
Kfrf3103	3	11	3
Kfrf0104		7, 9, 15	3
Kfrf0704		5	2
Kfgf1204	2	6	2
Kfgf1704		6	2
Kfrm2603	3	7, 12, 7	3
Kfrm2903		6, 7	2
Kfrm3003		10	2
Kfrm3103	3	9	3
Kfrm0604	3	7	
Kfrm1904		8	2
Kfrm2604		4	1
Kfrm2804		7	4

[1] Usually one research assistant and two habituators;
[2] Including research assistants, habituators and guides;
[3] Usually one research assistant with habituators.
[a] explanation see p.258

There were no significant differences in time spent feeding, locomoting or resting, no matter how many observers there were (Table 6.12). However, overall vocalising rates increased when there were more observers, i.e. when "present" was compared with "before" and "after".

An alternative cause for changing vocalisation rates may be the number of chimpanzees present: the more chimpanzees are in a party, the more vocalising might occur. If this is the case and chimpanzee party size changes during a follow, this might be a sufficient explanation for changing vocalisation rates. However, there is no significant correlation between party size and rate of vocalisation ($r=-0.1485$, $p=0.149$) (Figures 6.3 and 6.4).

There are suggestive differences between the sexes. Significance was only reached among males in a comparison of vocalising rates which combines before and after ($p=0.055$; Table 6.12).

In order to determine whether vocalisation rates could be used as indicators as to how long observers should stay, rates of vocalising were compared between the first half hour of the visit and afterwards. There was no significant change (Wilcoxon signed ranks test; $p=0.438$).

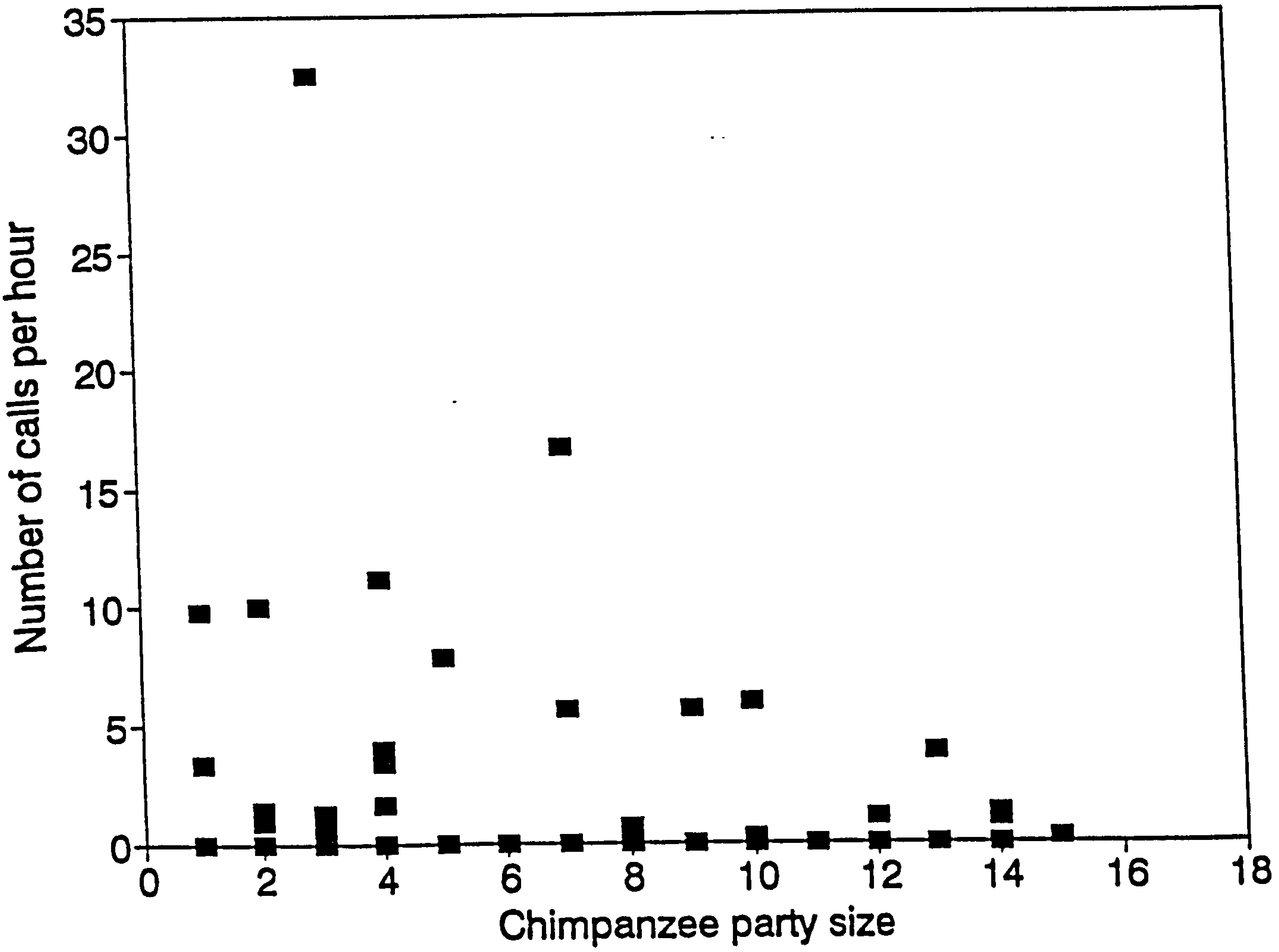


Figure 6.3: Male call rate in relation to party size at Ngogo.

Party size according to Wrangham *et al.*, (1992). Call rate: Number of vocalisations (soft and loud) per hour. Separate vocalisation rates were calculated for the same follow when party size changed during a follow.

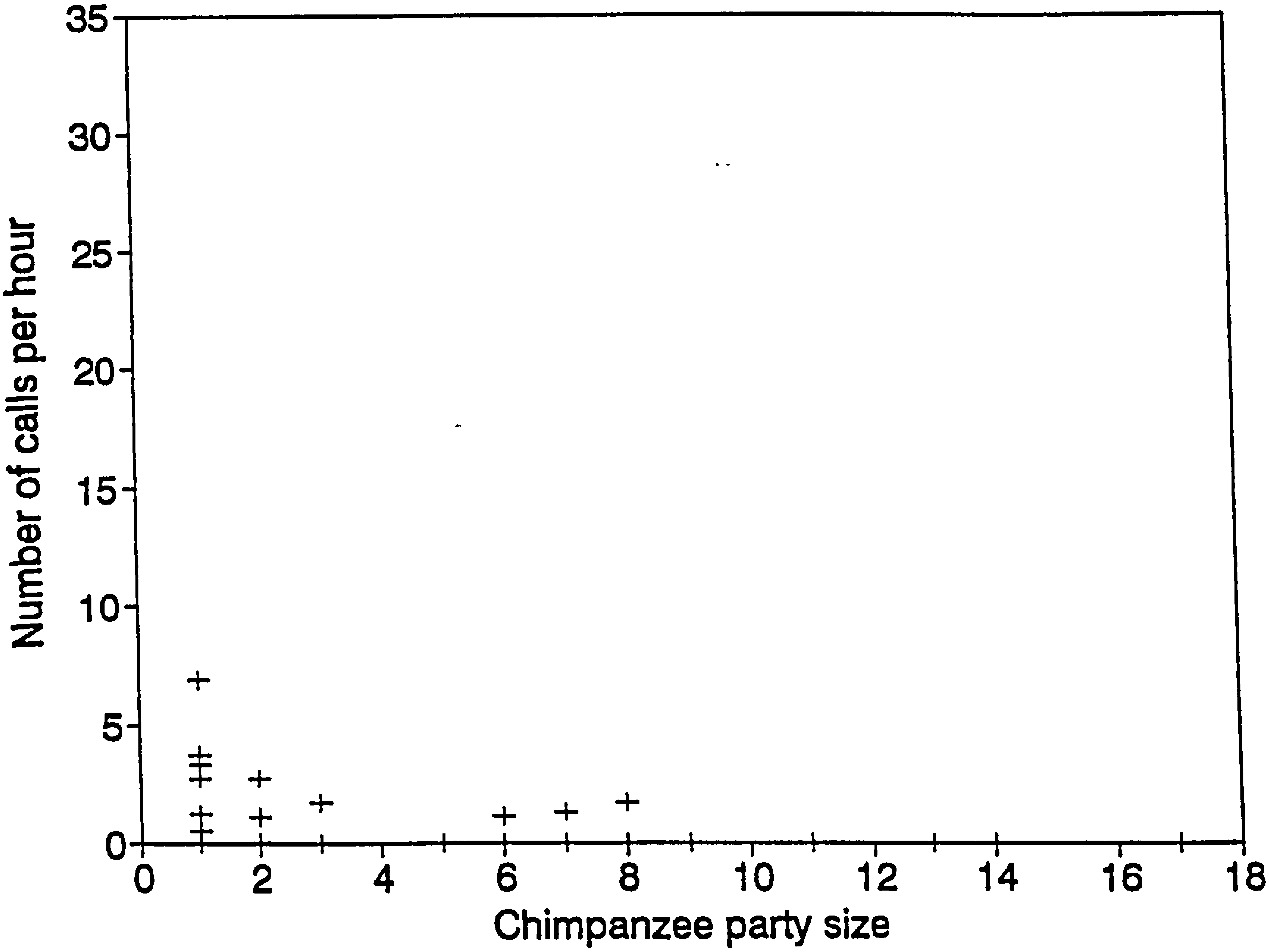


Figure 6.4: Female call rate in relation to party size.

Party size according to Wrangham *et al.*, (1992). Call rate: Number of vocalisations (soft and loud) per hour. Separate vocalisation rates were calculated for the same follow when party size changed during a follow.

Table 6.12: Wilcoxon signed ranks tests comparing percentage of time spent feeding, locomoting and resting, and on vocalizing rates before, during and after observers were present.

Activity	Before/Present	Present/After	Combined
Feeding	p>0.563 (4)	p>0.260 (11)	p=0.511 (15)
Males	-	p>0.406 (5)	p=0.531 (7)
Females	-	p>0.344 (6)	p=0.527 (8)
Locomotion	p=0.625 (3)	p>0.500 (13)	p=0.209 (16)
Males	-	p>0.531 (7)	p=0.527 (8)
Females	-	p>0.500 (6)	p>0.527 (8)
Resting	p=0.500 (5)	p>0.515 (13)	p=0.423 (18)
Males	-	p>0.527 (8)	p>0.500 (10)
Females	p=0.375 (3)	p>0.500 (5)	p>0.527 (8)
Vocalizing	p=0.063 (4)	p>0.148 (7)	p=0.034 (11)
Males	-	p=0.156 (5)	p=0.055 (7)
Females	-	-	p=0.313 (4)

Note: (n) = number of follows used in comparison. Where no probability is given, n was too small (2 or less). Comparisons were based on percentage of time spent feeding, locomoting and resting. For vocalising, occurrences per hour were used to avoid an underestimate (Altman 1974).

As the sample size of cases where the number of people present exceeded 10 was small (n=4; Table 6.11), any application of these findings has to be regarded as preliminary.

In 40 follows the number of observers stayed the same throughout (range 1-8, median 2, mean 2.85) (Table 6.13). Nine known and eight unidentified males were focal animals, with three known and nine unidentified females. Correlation coefficients were calculated to determine whether there was a significant relationship between percentage of time spent in certain activities or activity rates and numbers of observers present.

Neither the percentage of time spent feeding, locomoting or resting changed significantly (feeding: r= -0.245, P=0.127; locomoting: r= -0.051, P=0.754; resting: r= 0.251, P=0.118) (Tables 6.14 and 6.16). Rates of autogrooming, grooming, vocalising and defecating did not change either (autogrooming: r=-0.115, p=0.487; grooming: r=-0.16, p=0.925; vocalising: r=0.071, p=0.669; defecating: r=-0.195, p=0.234; Tables 6.15 and 6.16). Reanalysis for each sex separately revealed no significant within-sex correlations either (Table 6.16). Observer-related activities such as displaying towards the observer or hiding from the observer could not be tested statistically because they occurred too rarely.

Table 6.13: Sample sizes of follows with unchanging number of observers.

Number of observers	Number of follows
1	1
2	20
3	12
4	4
6	1
7	1
8	1

[a] "Case" refers to the focal animal sample. The "case number" codes each sample as in the following example. Case k5rf2603 is derived from: Kanyancu (k), 5-minute sample type (5), observer (r), sex of focal animal (f), date 26/03.

Table 6.14: Percentage of time spent in certain activities during follows.

Case[a]	Sex	No observers present	Feeding	Locomoting	Resting	Auto-grooming	Grooming	Vocalising	Defecating
k5rf2603	2	3	0	0	50.0	0	50.0	0	0
k5rf0504	2	3	40.8	5.3	36.8	5.3	7.9	0	0
k5rf0406	2	2	75.9	10.3	3.4	3.4	3.4	0	3.4
k5rf1504	2	1	60.0	10.0	0	0	10.0	0	20.0
k5gf1804	2	3	65.7	14.3	11.4	0	0	0	8.6
k5gf2904	2	2	20.0	5.0	55.0	5.0	0	15.0	0
k5gf3004	2	8	25.0	12.5	37.5	0	0	12.5	0
k5gf1005	2	2	42.9	0	28.6	0	0	0	0
k5gf1105	2	2	35.7	7.1	42.9	0	7.1	0	7.1
k5gf115	2	2	87.0	8.7	0	4.3	0	0	0
k5gf1705	2	4	42.5	17.5	27.5	12.5	0	0	0
k5gf1905	2	2	95.8	4.2	0	0	0	0	0
k5ge2005	2	2	55.9	0	29.4	8.8	0	0	5.9
k5gf2105	2	2	37.5	8.3	50.0	0	0	4.2	0
k5gf2205	2	3	43.8	0	31.3	6.3	0	6.3	6.3
k5gf225	2	2	33.3	8.3	58.3	0	0	0	0
k5gf2505	2	3	30.8	11.5	42.3	7.7	0	0	3.8
k5gf2106	2	3	24.1	3.4	58.6	10.3	0	0	3.4
k5rm2303	1	6	38.3	8.5	44.7	8.5	0	0	0
k5rm2403	1	2	68.4	7.9	18.4	5.3	0	0	0
k5rm2503	1	3	70.3	5.4	18.9	2.7	2.7	0	0
k5rm0204	1	2	19.5	7.3	61.0	9.8	0	2.4	0

Table 6.14: continued

Case	Sex	No observers present	Feeding	Locomoting	Resting	Auto-grooming	Grooming	Vocalising	Defecating
k5rm0704	1	4	38.5	15.4	46.2	0	0	0	0
k5rm194	1	2	77.8	11.1	11.1	0	0	0	0
k5rm2104	1	2	47.1	7.8	27.5	15.7	0	0	2.0
k5rm0705	1	3	46.2	0	46.2	0	0	7.7	0
k5rm1105	1	4	71.4	9.5	19.0	0	0	0	0
k5rm1205	1	3	55.0	10.0	15.0	5.0	0	10.0	0
k5rm1305	1	3	63.6	0	18.2	0	0	9.1	9.1
k5rm135	1	3	28.6	0	57.1	14.3	0	0	0
k5gm0104	1	2	45.1	4.2	40.8	2.8	0	2.8	2.8
k5gm0604	1	2	82.4	17.6	0	0	0	0	0
k5gm1504	1	2	61.5	15.4	23.1	0	0	0	0
k5gm1704	1	2	54.5	18.2	18.2	0	0	9.1	0
k5gm2604	1	2	87.5	12.5	0	0	0	0	0
k5gm0105	1	2	54.5	45.5	0	0	0	0	0
k5gm1005	1	2	20.0	50.0	30.0	0	0	0	0
k5gm1105	1	4	69.2	7.7	23.1	0	0	0	0
k5gm2005	1	2	47.4	0	26.3	26.3	0	0	0

Note: Sex: 1=male, 2=female.
Definitions see Table 2.5.

Table 6.15: Activity rates (number of occurrences per hour) during follows.

Case	Sex	No observers present	Auto-grooming	Grooming	Socially positive behav.	Vocalising (loud and soft)	Defecating	Socially negative behav.	Observer-related behav.
kfrf2603	2	3	0	10.3	0	0	0.5	0.5	0
kfrf0504	2	3	1.4	3.6	1.8	0.4	3.9	0	0
kfrf0406	2	2	0.8	1.2	1.2	1.2	2.1	0.4	0.8
kfgf1804	2	3	0	0	0	0.4	1.8	0	0
kfgf2904	2	2	1.3	0	0	2.7	1.3	0.7	1.3
kfgf3004	2	8	0	0	0	3.3	0	0	0.0
kfgf1005	2	2	1.9	0	0	3.7	0	1.9	3.7
kfgf1105	2	2	3.6	1.8	0	0	2.7	0.9	0
kfgf115	2	2	6.8	0	0	0.5	2.1	0	0
kfgf1705	2	4	5.3	0.7	0.4	0	1.4	0	0
kfgf1905	2	2	0.5	0	0.5	0	1.1	0	0
kfge2005	2	2	2.0	0	0	0.8	3.1	0.4	0
kfgf2105	2	2	1.1	0	0	2.7	4.3	0	0
kfgf2205	2	3	1.3	0.7	0	0.7	2.0	0.7	0
kfgf225	2	2	1.1	0	0	1.1	3.2	0	0
kfgf2505	2	3	5.5	0.5	0	0	3.0	0.5	0
kfgf2106	2	3	4.3	1.1	0.5	0.5	2.1	0	0.5
kfgf1504	2	1	0.0	1.3	0	0	2.6	1.3	0
kfrm135	1	3	1.7	0	0	3.4	1.7	0	1.7
kfgm0104	1	2	1.9	0	0.2	0.9	1.5	0	0
kfgm0604	1	2	0	0	0	0	0.7	0	0
kfgm1504	1	2	2.1	0	0	1.1	0	0	0

Table 6.15: continued

Case	Sex	No observers present	Auto-grooming	Grooming	Socially positive behav.	Vocalising (loud and soft)	Defecating	Socially negative behav.	Observer-related behav.
kfgm2604	1	2	0	0	0	1.6	0.8	0	0
kfgm1005	1	2	1.3	0	0	5.1	3.8	3.8	0
kfgm1105	1	4	2.0	0	0	0.7	1.3	0	0
kfgm2005	1	2	3.3	0	0	0.7	4.7	0	0
kfrm2303	1	6	1.2	0	0	0	1.9	0.2	0
kfrm2403	1	2	0.8	3.7	0	0	1.4	0	0
kfrm2503	1	3	0.7	0.7	0.4	0.4	0.4	0.4	0
kfrm0204	1	2	1.2	0	0	0.9	3.0	0	0.3
kfrm64	1	3	0	2.6	0	0	1.3	0	0
kfrm0704	1	4	0	0	0	1.9	4.9	0	0
kfrm194	1	2	0	0	0	0	1.4	0	0
kfrm2104	1	2	3.4	0	0	3.4	3.9	0	0
kfrm0705	1	3	0	0	0	9.8	3.3	0	3.3
kfrm1105	1	4	0.6	0	0	1.8	1.8	0	0
kfrm1205	1	3	0.7	0	0.7	5.4	0	0	0.7
kfrm1305	1	3	0	0	0	6.3	1.1	0	0

Note: Sex: 1=males, 2=females.
Definitions see Table 2.6.

Table 6.16: Correlation coefficients, number of cases and associated probabilities in the correlation analysis of activity rates and numbers of observers present.

		Feeding	Locomoting	Resting	Auto-grooming	Grooming	Vocalising	Defecating
All categories of detector	r	-0.245	-0.051	0.251	-0.115	-0.157	0.071	-0.1953
	N	40	40	40	39	39	39	39
	p	0.127	0.754	0.118	0.487	0.925	0.669	0.234
Adult males only	r	-0.117	-0.247	0.330	-0.216	-0.101	-0.369	0.328
	N	22	22	22	21	21	21	21
	p	0.605	0.268	0.133	0.348	0.663	0.874	0.888
Adult females only	r	-0.341	0.327	0.200	-0.070	0.016	0.283	-0.433
	N	18	18	18	18	18	18	18
	p	0.167	0.185	0.427	0.782	0.950	0.256	0.072
Animals followed more than once	r	-0.345	0.178	0.318	-0.254	-0.142	0.473	-0.190
	N	17	17	17	17	17	17	17
	p	0.175	0.494	0.214	0.325	0.586	0.055	0.466
Animals followed only once	r	-0.040	-0.164	0.094	0.212	0.248	0.040	-0.230
	N	23	23	23	22	22	22	22
	p	0.857	0.455	0.668	0.343	0.267	0.861	0.303

Pearson's correlation coefficient.
Feeding, locomoting, resting: analysis based on percentage of time spent on the activity; **auto-grooming, grooming, vocalising, defecating:**analysis based on number of occurrences per hour.

In order to determine whether the data were biased towards more habituated animals, the correlation analysis was conducted on two subsets of data: first on those animals that were followed at least twice and therefore could be assumed to be more habituated and for those who were followed at most once, including all unidentified individuals. There is no difference between these two groups (Table 6.16).

6.4.3 Distance to the observer

The distance to the observer when the chimpanzee detected the observer had an impact on the animal's reaction (Kanyancu: X^2=35.4; df=9; p<0.001; Ngogo: X^2=32.7; df=2; p<0.001; Tables 6.17a and b). At Kanyancu, of those animals encountered at a distance of less than 20 m (N=130), almost half (49.2%) either fled or charged. In contrast, only 9.1% of those animals encountered at a distance of over 40 m (N=22) showed this reaction. At Ngogo, of those animals encountered at a distance of less than 20m (N=101), 45.5% reacted in an unhabituated way. Of those animals encountered at distances of more than 20m (N=144), 58.3% reacted in a habituated way.

6.4.4 Distance to the next chimpanzee

The distance to the next chimp affected the reaction of the detector at Kanyancu (X^2=14.48; df=4; p<0.006; Table 6.18a), but not at Ngogo (X^2=3.08; df=2; p=0.214; Table

Table 6.17a: Frequency of reactions at Kanyancu in relation to distance to the observer.

Reaction	Observer at: 10m<x<20 N	 %	 20m<x<30m N	 %	 30m<x<40m N	 %	 >40m N	 %
Unhabituated	64	49.2[1]	83	36.4	17	33.3	2	9.1
Approach/wait, stealthy retreat, loud vocalizations	20	15.4	34	14.9	10	19.6	11	50.0
Soft vocalizations, hide	15	11.5	22	9.6	8	15.7	5	22.7
Habituated	31	23.8	89	39.0	16	31.4	4	18.2
All	130		228		51		22	

Note: *Unhabituated* includes *flight* and *charge; Habituated* includes *ignore* and *curiosity*.

[1] Due to rounding, percentages may not add up to 100.

Table 6.17b: Frequency of reactions at Ngogo in relation to distance to the observer.

Reaction	Observer at: below 20m N	%	above 20m N	%
Unhabituated	46	45.5[1]	20	13.9
Intermediate	25	24.8	40	27.8
Habituated	30	29.7	84	58.3
All	101		144	

Note: **Unhabituated** includes flight and charge;
Intermediate includes approach and wait, stealthy retreat, loud vocalisations, soft vocalisations, hide;
Habituated includes ignore and curiosity.

[1] Due to rounding, percentages may not add up to 100.

Table 6.18a: Frequency of reactions at Kanyancu in relation to distance to the nearest neighbour

Reaction	Nearest neighbour: Under 5m N	%	Between 5m and 10m N	%	Over 10m N	%
Unhabituated	42	31.1	13	26.5	20	58.8
Intermediate	38	28.1	10	20.4	8	23.5
Habituated	55	40.7	26	53.1	6	17.6
All contacts	135		49		34	

Note: **Unhabituated** includes flight and charge; **Habituated** includes ignore and curiosity; **Intermediate** includes stealthy retreat, loud vocalisations, soft vocalisations and hide.
Due to rounding, percentages may not add up to 100.

Table 6.18b: Frequency of reactions at Ngogo in relation to distance to the nearest neighbour.

Reaction	Nearest neighbour: Under 5m N	%	Over 5m N	%
Unhabituated	11	19.6	2	6.1
Intermediate	18	32.1	12	36.4
Habituated	27	48.2	19	57.6
All contacts	56		33	

Note: **Unhabituated** includes flight and charge; **Habituated** includes ignore and curiosity; **Intermediate** includes stealthy retreat, loud vocalisations, soft vocalisations and hide.
Due to rounding, percentages may not add up to 100.

6.18b). If the next chimpanzee was more than 10 m distant at Kanyancu, the detector was more likely to flee or charge (58.8% of 34 cases) than when the next chimpanzee was within 5 m (31.1% of 135 cases).

6.4.5 Activity before contact

The activity the chimpanzee was engaged in before detecting the observer made a difference to the animal's reaction at Kanyancu (X^2=10.43; df=3; p<0.02; Table 6.19a), but not at Ngogo (X^2=3.10; df=6; p=0.796; Table 6.19b). When the animals fed on plants at Kanyancu, they were more likely to react with *flight* or *charge* (40.4%, N=319) than when they were resting (26.2%, N=61). When they were engaged in social activities, they more frequently ignored the observer (62.5%, N=8).

6.4.6 Height above ground

Both at Kanyancu and at Ngogo, the chimpanzee's vertical location has an impact on its reaction to the observer (Kanyancu: X2=11.18, df=4, p<0.05; Ngogo: X^2=27.98, df=4, p<0.001; Tables 6.20a and b). Both at Kanyancu and at Ngogo, the majority of reactions below 15m are unhabituated reactions (58.0% and 41.7%, respectively). The percentage of unhabituated reactions decreases with increasing height at both sites, whereas the opposite trend is true for habituated reactions. Spearman ranks correlation coefficients between percentage of

Table 6.19a: Frequency of reactions at Kanyancu in relation to activity before contact.

Reaction	Activity: feed plants N	%	rest N	%	travel N	%	others N	%
Unhabituated	215	67.4[1]	36	59.0	33	84.6	3	37.5
Habituated	104	32.6	25	41.0	6	15.4	5	62.5
All	319		61		39		8	

Note: **Unhabituated** includes flight, charge, approach and wait, stealthy retreat, loud vocalisations, soft vocalisations, and hide;

Habituated includes ignore and curiosity.

[1] Due to rounding, percentages may not add up to 100.

Table 6.19b: Frequency of reactions at Ngogo in relation to activity before contact.

Reaction	Activity: Feed		Rest		Travel		Others	
	N	%	N	%	N	%	N	%
Unhabituated	23	22.3[1]	9	23.1	21	28.8	1	7.1
Intermediate	26	25.2	10	25.6	30	29.7	6	42.9
Habituated	54	52.4	20	51.3	50	49.5	7	50.0
All	103		39		101		14	

Note: **Unhabituated** includes flight and charge;
Intermediate includes approach and wait, stealthy retreat, loud vocalisations, soft vocalisations and hide;
Habituated includes ignore and curiosity.

[1] Due to rounding, percentages may not add up to 100.

Table 6.20a: Frequency of reactions at Kanyancu in relation to height above ground

Reaction	Height: Below 15m[1] N	%	Between 15m and 30m N	%	Above 30m N	%
Unhabituated	29	58.0	89	37.6	37	33.9
Intermediate	14	28.0	70	29.5	33	30.3
Habituated	7	14.0	78	32.9	39	35.8
All	50		237		109	

Note: **Unhabituated** includes flight and charge; **Intermediate** includes approach and wait, stealthy retreat, loud vocalisations, soft vocalisations and hide; **Habituated** includes ignore and curiosity.

Due to rounding, percentages may not add up to 100.

[1] Including the ground.

Table 6.20b: Frequency of reactions at Ngogo in relation to height above ground

Reaction	Height: Below 15m[1] N	%	Between 15m and 30m N	%	Above 30m N	%
Unhabituated	50	41.7	16	14.0	3	15.0
Intermediate	29	24.2	29	25.4	8	40.0
Habituated	41	34.2	69	60.5	9	45.0
All	120		114		20	

Note: **Unhabituated** includes flight and charge; **Intermediate** includes approach and wait, stealthy retreat, loud vocalisations, soft vocalisations and hide; **Habituated** includes ignore and curiosity.

Due to rounding, percentages may not add up to 100.

[1] Including the ground.

unhabituated reactions and height categories were calculated for both sites and were found to be significant (Kanyancu: r_S=-0.701, N=12, p<0.02; Ngogo: r_S=-0.892, N=8, p<0.05). However, the Spearman ranks correlation coefficient between percentage of habituated reactions and height categories was significant only at Kanyancu (r_S=0.657, N=11, p<0.05; Ngogo: r^S=0.179, N=7, p>0.05).

6.4.7 Location method

The way the chimpanzees are located had an effect on their reaction at Kanyancu (X^2=29.87, df=4, p<0.001; Table 6.21a). Of 242 animals contacted in tree vigils, 43 % reacted as if habituated (*curiosity* or *ignore* reactions). This compared with 16.8% of animals that were found by following vocalisations (N=137) and 25.5% of animals that were contacted by other methods (N=51). Put differently, 74.3% of habituated reactions (N=140) came from animals that were contacted in tree vigils.

At Ngogo, the effect of location method was not quite so clear-cut (X^2=9.21; df=4; p=0.056; Table 6.21b). Of 127 animals contacted in tree vigils, 53.5% showed habituated reactions. However, habituated reactions (N=141) were distributed fairly evenly between those animals contacted through vocalisations (44.0%) and those contacted in tree vigils (48.2%).

Table 6.21a: Frequency of reactions at Kanyancu in relation to location method

Reaction	Location method: Vocalisations		Tree vigils		Others	
	N	%	N	%	N	%
Unhabituated	68	49.6	79	32.6	19	37.3
Intermediate	46	33.6	59	24.4	19	37.3
Habituated	23	16.8	104	32.2	13	25.5
All	137		242		51	

Note: **Unhabituated** includes flight and charge; **Intermediate** includes approach and wait, stealthy retreat, loud vocalisations, soft vocalisations and hide; **Habituated** includes ignore and curiosity.
Due to rounding, percentages may not add up to 100.

Table 6.21b: Frequency of reactions at Ngogo in relation to location method

Reaction	Location method: Vocalisations		Tree vigils		Others	
	N	%	N	%	N	%
Unhabituated	43	30.5	23	18.1	11	31.4
Intermediate	36	25.5	36	28.3	13	37.1
Habituated	62	44.0	68	53.5	11	31.4
All	141		127		35	

Note: **Unhabituated** includes flight and charge; **Intermediate** includes approach and wait, stealthy retreat, loud vocalisations, soft vocalisations and hide; **Habituated** includes ignore and curiosity.
Due to rounding, percentages may not add up to 100.

6.4.8 Other factors

The chimpanzees' party size and the density of vegetation did not have an impact on the chimpanzees' reaction at either study site (Tables *6.6; 6.22a, b;* 6.2 a, b).

6.5 Comparison between chimpanzee habituation at Kibale and Lopé, Gabon.

Table 6.24 gives the relative frequencies of chimpanzees' reactions to human observers at Lopé in Gabon (after Table 10.3 from Tutin & Fernandez, 1991). Table 6.25 gives the frequency of the first detectors' reactions at Kanyancu and Ngogo compared to those at Lopé. There is a significant difference between Lopé and Kanyancu (overall X^2=127.0, df=7, p<0.001: *curiosity* and *ignore* were combined) and between Lopé and Ngogo (overall X^2=100.5, df=7, p<0.001). Fewer animals charge in Gabon than in Kanyancu (partitioned X^2=16.02, df=1, p<0.001). In Gabon, there is a well represented component of *approach/wait* that hardly exists in Kanyancu (partitioned X^2=81.1, df=1, p<0.001) (Table 6.26) or at Ngogo (partitioned X^2=27.2, df=1, p<0.001) (Table 6.27). At Kanyancu it was observed in only 2 cases by a juvenile male and female, and at Ngogo four times by adult males and once by a subadult female, whereas in Gabon this reaction accounted for 43.3% of cases in adult females.

Table 6.22a: Frequency of reactions at Kanyancu in relation to chimpanzee party size

Reaction	Chimpanzee party size: Below 5 N	%	Between 5 and 10 N	%	Above 10 N	%
Unhabituated	90	35.7	46	44.2	21	33.9
Intermediate	72	28.6	31	29.8	20	32.3
Habituated	90	35.7	27	26.0	21	33.9
All	252		104		62	

Note: **Unhabituated** includes flight and charge; **Intermediate** includes approach and wait, stealthy retreat, loud vocalisations, soft vocalisations and hide; **Habituated** includes ignore and curiosity.
Due to rounding, percentages may not add up to 100.

Table 6.22b: Frequency of reactions at Ngogo in relation to chimpanzee party size

Reaction	Chimpanzee party size: Below 5 N	%	Between 5 and 10 N	%	Above 10 N	%
Unhabituated	60	28.2	15	23.1	1	6.7
Intermediate	56	26.3	20	30.8	6	40.0
Habituated	97	45.5	30	46.2	8	53.3
All	213		65		15	

Note: **Unhabituated** includes flight and charge; **Intermediate** includes approach and wait, stealthy retreat, loud vocalisations, soft vocalisations and hide; **Habituated** includes ignore and curiosity.
Due to rounding, percentages may not add up to 100.

Table 6.23a: Frequency of reactions at Kanyancu in relation to vegetation density

Reaction	Vegetation density: Dense forest		Open forest		Other	
	N	%	N	%	N	%
Unhabituated	29	54.7	135	59.2	3	27.3
Habituated	24	45.3	93	40.8	8	72.7
All	53		228		11	

Note: **Unhabituated** includes flight, charge, approach and wait, stealthy retreat, loud vocalisations, soft vocalisations, and hide; **habituated** includes ignore and curiosity.
Due to rounding, percentages may not add up to 100.

Table 6.23b: Frequency of reactions at Ngogo in relation to vegetation density

Reaction	Vegetation density: Dense forest		Other	
	N	%	N	%
Unhabituated	44	23.0	27	28.1
Intermediate	54	28.3	26	27.1
Habituated	93	48.7	43	44.8
All	191		96	

Note: **Unhabituated** includes flight and charge; **Intermediate** includes approach and wait, stealthy retreat, loud vocalisations, soft vocalisations and hide; **Habituated** includes ignore and curiosity.
Due to rounding, percentages may not add up to 100.

Table 6.24: Relative frequencies of chimpanzees' reactions to observers in Gabon.

Reaction	All age/sex classes N	All age/sex classes %	Adult male %	Adult female %
Flight	59	38.6	49.1	38.3
Charge	2	1.3	1.8	1.7
Approach/wait	39	25.5	9.1	43.3
Stealthy retreat	16	10.5	21.8	5.0
Loud vocalisation	12	7.8	10.9	0.0
Soft vocalisation	12	7.8	0.0	3.3
Hide	7	4.6	3.6	5.0
Curiosity	2	1.3	1.8	0
Ignore	4	2.6	1.8	3.3
All	153	100.0	100.0	100.0

Note: Only first detectors were used in analysis.

Table 6.25a: Number of occurrence of reaction categories over the whole study period at Kanyancu (first detectors only) and in Gabon. Expected values (in brackets) calculated from marginal totals.

Reaction	Kanyancu	Gabon	All
Flight	100 (109)	59 (50)	159
Charge	41 (30)	2 (13)	43
Approach/Wait	2 (28)	39 (13)	41
Stealthy Retreat	33 (34)	16 (15)	49
Loud vocalisation	23 (24)	12 (11)	35
Soft vocalisation	19 (21)	12 (10)	31
Hide	23 (21)	7 (9)	30
Curiosity/Ignore	96 (70)	6 (32)	102
All	337	153	490

Table 6.25b: Number of occurrence of reaction categories over the whole study period at Ngogo (first detectors only) and in Gabon. Expected values (in brackets) calculated from marginal totals.

Reaction	Ngogo	Gabon	All
Flight	53 (63)	59 (49)	112
Charge	6 (5)	2 (4)	8
Approach/Wait	3 (24)	39 (18)	42
Stealthy Retreat	11 (15)	16 (12)	27
Loud vocalisation	18 (17)	12 (13)	30
Soft vocalisation	12 (14)	12 (10)	24
Hide	11 (10)	7 (8)	18
Curiosity/Ignore	85 (51)	6 (40)	91
All	199	153	352

Table 6.26: Additive partitions of X^2 test of differences in reaction categories between Kanyancu and Gabon. Expected values (in brackets) calculated from marginal totals.

Reaction	Kanyancu	Gabon	Combined
Stealthy retreat	33 (34)	16 (15)	49
Loud vocalisation	23 (24)	12 (11)	35
Total	337	153	N=490

(1): X^2=0.025; critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Kanyancu	Gabon	Combined
Stealthy retreat or Loud vocalisation	56 (58)	28 (26)	84
Soft vocalisation	19 (21)	12 (10)	31
Total	337	153	N=490

(2): X^2=0.305; critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Kanyancu	Gabon	Combined
Stealthy retreat or Loud vocalisation or Soft vocalisation	75 (79)	40 (36)	115
Hide	23 (21)	7 (9)	30
Total	337	153	N=490

(3): X^2=1.45; critical value for X^2 (p=0.05, df=1): 3.84

Table 6.26 continued

Reaction	Kanyancu	Gabon	Combined
Stealthy retreat or Loud vocalisation or Soft vocalisation or Hide	98 (100)	47 (45)	145
Flight	100 (109)	59 (50)	159
Total	337	153	N=490

(4): $X^2=0.747$; critical value for X^2 ($p=0.05$, df=1): 3.84

Reaction	Kanyancu	Gabon	Combined
Stealthy retreat or Loud vocalisation or Soft vocalisation or Hide or Flight	198 (209)	106 (95)	304
Charge	41 (30)	2 (13)	43
Total	337	153	N=490

(5): $X^2=16.02$, critical value for X^2 ($p=0.001$, df=1): 10.83

Reaction	Kanyancu	Gabon	Combined
Stealthy retreat or Loud vocalisation or Soft vocalisation or Hide or Flight or Charge	239 (239)	108 (108)	347
Curiosity/Ignore	96 (70)	6 (32)	102
Total	337	153	N=490

(6): $X^2=23.4$; critical value for X^2 ($p=0.001$, df=1): 10.83

Table 6.26 continued

Reaction	Kanyancu	Gabon	Combined
Stealthy retreat or Loud vocalisation or Soft vocalisation or Hide or Flight or Charge or Curiosity/ Ignore	335 (309)	114 (140)	449
Approach/Wait	2 (28)	39 (13)	41
Total	337	153	N=490

(7): X^2=85.1; critical value for X^2 (p=0.001, df=1): 10.83

Table 6.27: Additive partitions of X^2 test of differences in reaction categories between Ngogo and Gabon. Expected values (in brackets) calculated from marginal totals. First detectors only.

Reaction	Ngogo	Gabon	Combined
Stealthy retreat	11 (15)	16 (12)	27
Loud vocalisation	18 (17)	12 (13)	30
Total	199	153	N=352

(1): X^2=2.1; critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Ngogo	Gabon	Combined
Stealthy retreat or Loud vocalisation	29 (32)	28 (25)	57
Soft vocalisation	12 (14)	12 (10)	24
Total	199	153	N=352

(2): X^2=0.005; critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Ngogo	Gabon	Combined
Stealthy retreat or Loud vocalisation or Soft vocalisation	41 (46)	40 (35)	81
Hide	11 (10)	7 (8)	18
Total	199	153	N=352

(3): X^2=0.660; critical value for X^2 (p=0.05, df=1): 3.84

Table 6.27 continued

Reaction	Ngogo	Gabon	Combined
Stealthy retreat or Loud vocalisation or Soft vocalisation or Hide	52 (56)	47 (43)	99
Charge	6 (5)	2 (3)	8
Total	199	153	N=352

(4): $X^2=1.52$; critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Ngogo	Gabon	Combined
Stealthy retreat or Loud vocalisation or Soft vocalisation or Hide or Charge	58 (60)	49 (47)	107
Flight	53 (63)	59 (49)	112
Total	199	153	N=352

(5): $X^2=1.06$, critical value for X^2 (p=0.05, df=1): 3.84

Reaction	Ngogo	Gabon	Combined
Stealthy retreat or Loud vocalisation or Soft vocalisation or Hide or Charge or Flight	111 (124)	108 (95)	219
Approach/Wait	3 (24)	39 (18)	42
Total	199	153	N=352

(6): $X^2=27.2$; critical value for X^2 (p=0.001, df=1): 10.83

Table 6.27 continued

Reaction	Ngogo	Gabon	Combined
Stealthy retreat or Loud vocalisation or Soft vocalisation or Hide or Charge or Flight or Approach/ Wait	114 (148)	147 (113)	261
Curiosity/Ignore	85 (51)	6 (40)	91
Total	199	153	N=352

(7): X^2=67.9; critical value for X^2 (p=0.001, df=1): 10.83

Stealthy retreat, loud and soft vocalisations and hide are comparable at the three sites, but curiosity and ignore score much higher in Kibale (Kanyancu: partitioned $X^2=23.4$, df=1, $p<0.001$; Ngogo: partitioned $X^2=67.9$, df=1, $p<0.001$) (Tables 6.26 and 6.27).

Tutin and Fernandez (1991) draw attention to the difference in the "approach/wait" category between females and males. However, when statistics are applied to their data, there is no overall difference in adult males' and females' reactions at Lopé ($X^2=1.46$, df=2, $p>0.05$; as the frequency in many cells was below 5, categories had to be combined to flight/charge, curiosity/ignore and other) (Table 6.28). No other age classes could be tested for sex differences as sample sizes were too small.

There is no difference in reactions between adults and juveniles/infants ($X^2=2.85$, df=2, $p>0.05$) (Table 6.29). The sample size for subadults is too small to test them against the other age classes.

6.6 Discussion

6.6.1 Success of habituation

The significant overall decrease of *unhabituated* reactions and increase of *habituated* reactions over the

Table 6.28: Number of occurrence of reaction categories of adult males and females at Lope[1].

Reaction	Males	Females
Unhabituated	28 (25)	24 (27)
Intermediate	25 (28)	34 (31)
Habituated	2 (2)	2 (2)
All	55	60

Note: **Unhabituated** contains flight and charge; **Intermediate** contains stealthy retreat, approach/wait, loud vocalisation, soft vocalisation and hide; **Habituated** contains curiosity and ignore.

[1] Calculated from Table 16.3 in Tutin and Fernandez 1991. Expected values (in brackets) calculated from marginal totals.

Table 6.29: Number of occurrence of reaction categories of adults and juveniles/infants at Lope[1].

Reaction	Adults	Juveniles/Infants
Unhabituated	52 (49)	5 (8)
Intermediate	59 (62)	14 (11)
Habituated	4 (4)	1 (1)
All	115	20

Note: **Unhabituated** contains flight and charge; **Intermediate** contains stealthy retreat, approach/wait, loud vocalisation, soft vocalisation and hide; **Habituated** contains curiosity and ignore.

[1] Calculated from table 10.3 in Tutin and Fernandez 1991. Expected values (in brackets) calculated from marginal totals.

study period suggests that the chimpanzees both at Kanyancu and Ngogo were becoming more habituated to observers. The reason that the reaction category of *flight* did not decrease on its own may be that the effect of habituation is reduced by the number of different chimpanzees that are encountered: by early 1994, 60 animals were identified in the Kanyancu community and 130 animals in the Ngogo community. If the same individual is encountered frequently, it will become used to the presence of humans more quickly. On the other hand, many individuals will be encountered only relatively rarely. Therefore most contacts will include some animals that ignore the observer and many that still flee. As individual chimpanzees show different tendencies to react it is not possible to detect an overall trend for the whole community.

The difference in reaction categories between Kanyancu and Ngogo suggests that overall, the Ngogo chimpanzees were better habituated than those at Kanyancu.

6.6.2 Factors influencing reactions to observers

Age/sex classes

The only age class that could be tested for gender differences was the adult class. The difference between adult male and female chimpanzees' reactions that was found at Kanyancu and at Ngogo reflected gender differences in this species' general behaviour (Goodall

1986). Females are shyer than males and are therefore expected to flee more easily in an unfamiliar situation. They are shyer than males even if they are becoming more habituated, which means that fleeing will be superceded by hiding reactions while males would probably ignore the observer. Males are generally more aggressive than females and are therefore expected to charge more often. They also often use charging as an intimidation display (Goodall 1986). Thus the higher occurrence of charging in adult males can be accounted for in several ways. The fact that the data from Lopé do not show these sex differences, may be due to the relatively small sample size.

Numbers of observers

Initial reactions

Up to 5 observers did not influence the chimpanzees' initial reactions at Kanyancu apart from causing a decrease in soft vocalisations. Soft vocalisations may be directed at the observer or other chimpanzees. When more people are present, the chimpanzees may concentrate more on the observers than on conspecifics and therefore communicate less with conspecifics. Alternatively, the more observers are present, the more noise they make, and the easier it is to miss a chimpanzee's soft vocalisation.

Ngogo differs in that here the number of observers does have an effect. This may be due to the fact that observers were usually on their own at Ngogo, while at Kanyancu observers were normally in groups of at least two. Thus, although the Ngogo community had a higher degree of habituation overall (i.e. to one observer), the animals reacted more strongly to higher numbers of observers.

Long-term impact

For chimpanzees who are habituated sufficiently not to flee from humans immediately, activity rates do not change significantly when numbers of observers (or tourists) increase. Vocalising rates are the only exception to this and may be an indicator of nervousness of the animals. They also indicate that the comparison between when the tourists are present and after they have left is less viable than the comparison between before the tourists have arrived and when they are present, because the animals may take a while to calm down after the tourists have left. As there is no correlation between chimp party size and vocalising rate, chimp party size can be ruled out as an alternative cause for changing vocalisation rates.

It could be argued that these data are biased towards better habituated animals because the observer will always follow the animals that are easiest to follow, i.e. the best habituated ones. Unfortunately, this is a problem inherent to this type of research. However, Table 6.16 shows that there was no difference between those animals that were contacted only once and those that were contacted more than once.

However, the data may still be biased towards better habituated animals. 51 out of 54 follows originated during tree vigils. As the data on initial reactions have shown, chimpanzees contacted through tree vigils are more likely to be habituated to some degree. An alternative explanation for this phenomenon might be that chimpanzees approaching a stationary observer doing a tree vigil have time to adjust to the observer at their own pace, whereas the observer seems to actively harass the chimpanzees when he finds them by following calls. This was corroborated by an analysis of the distance to the observer at detection: When a chimpanzee detects an observer at a smaller distance, it feels more threatened and it is more likely that it will react in an unhabituated way. This also coincides with results from Lopé.

Distance to the next chimpanzee

At Kanyancu and at Lopé, the close proximity of a conspecific appears to have a soothing effect on chimpanzees. They are less likely to react in an unhabituated way when they are close to another chimpanzee. As there is no such effect at Ngogo, it is suggested that the large Ngogo community may not be as closely knit as the smaller communities at Kanyancu and Lopé. Alternatively, the effect of this factor may not be as pronounced as in the other two communities, because the Ngogo community is better habituated.

Activity before contact

The data from Kanyancu are corroborated by those from Lopé which show that the activity the chimpanzees were engaged in on contact had an impact on the chimpanzees' reaction. Again, the fact that activity before contact had no such effect at Ngogo indicates that this community was better habituated and therefore not as easily deterred from whatever the chimpanzees were doing when they came in contact with an observer.

Height above ground

According to Tutin & Fernandez (1991), chimpanzees at Lopé were more alarmed when in trees. In contrast, Kibale chimpanzees always seemed more nervous on or close to the ground and the data confirm that below 15m most reactions to the observer were unhabituated ones. This can be explained easily: when encountered on or close to the ground, the chimpanzees are naturally closer to the observer, and it has already been shown that the closer the chimpanzees are to the observer, the more unhabituated they will react. There is no obvious reason why the Lopé chimpanzees should differ from this pattern. As no actual data are offered by Tutin & Fernandez (1991) their conclusion remains open to doubt.

Leopard predation is unlikely to have an impact, because Tutin & Fernandez themselves (1991) state that in the one leopard incident they witnessed, the chimpanzees climbed high in trees on discovering a leopard. It can be assumed that they climb into trees in such a situation because they feel more secure there. This is confirmed by Boesch & Boesch (1991) who mention that female chimpanzees climbed into trees during a leopard attack while the males went in search for the leopard (p.225).

Location method

When a fig tree was in fruit, both observers and chimps were drawn to it over a number of days. The same individual chimpanzee would visit it on several days and so they would get used to the presence of humans. An observer conducting a tree vigil was more likely to get habituated responses than when following vocalisations or locating chimps by any other method. As the Ngogo community was better habituated than the one at Kanyancu, this effect was diminished at Ngogo. Tutin and Fernandez (1990) did not consider location method in their study at Lopé.

Other factors

The fact that density of vegetation had no effect on the chimpanzees' reactions could be ascribed to a more open and more homogeneous forest in Kibale compared to the one at Lopé. However, this remains a speculation as density of vegetation was not measured quantitatively.

The party size of the chimpanzees had no effect on the chimpanzees' reaction. This implies that the chimpanzees in Kibale do not feel more secure when there are more of them in the group. The chimpanzees' social system, described as a fission-fusion system (Goodall, 1986) may account for this. Although they do seek each other's company sometimes, they spend a considerable amount of their time on their own (Wrangham *et al.*, 1992) and can therefore not rely on others for help. In contrast, Cowlishaw (1994) found that baboons' reactions to the observer depended on the baboons' group size. Baboons occur in much more closely knit social groups (Dunbar, 1988) than chimpanzees and can therefore rely on the presence of other group members for support. Similarly, groups of bonobos at Lomako and Yalosidi showed different reactions depending on the size of the group they were in (Badrian & Badrian, 1984; Kano, 1983). This might mean that bonobo groups are more cohesive than chimpanzee groups.

6.6.3 An explanation of differences in habituation rate between Kibale and Lopé

The fact that chimpanzees at Lopé ignore humans far less often than their conspecifics in Kibale indicates that they are less well habituated.

A higher frequency of charging at Kanyancu can also be explained by a higher degree of habituation compared to Lopé. Charging was put on the ordinate scale of reactions after flight, because it is more likely to happen when the animals are already habituated to some degree. Given that charging is an intimidation display (Goodall 1986) the charging animal must feel confident enough not to run away immediately but stay and try to intimidate the opponent (i.e. the observer). The charging animal may well be more habituated to the observer than the fleeing one.

The enormous difference in the category of *approach and wait* reactions between Kibale and Gabon needs to be explained. It is possible that the current age structure of the community influences the occurrence of this reaction. If most of the infants in Kanyancu were younger than the ones in Gabon, they were more likely to be carried by their mothers at all times, and so the mothers were less likely to have to fetch them before they fled or charged or whatever. Alternatively, the Kibale mothers may be more restrictive than the Lopé mothers which, again, would mean that they would not have to fetch them as often. On the other hand, this difference may be due to a difference in observer reliability. "Approach and Wait" is rather a subtle behaviour, for which the observer needs to see the other chimp. Reactions like flight and charge are much more obvious, so it is possible that a chimp is scored as having fled because the observer missed seeing the female picking up her infant first. This opens up the discussion as to whether it makes sense at all to include "approach and wait" as a category of reaction to the observer, because the final outcome is the same as in "flight" and "stealthy retreat": The chimpanzee is driven to stop whatever it was doing before and leave. The only difference is one of speed and whether the chimpanzee does it on his own or not.

Various reasons could account for a difference in degree of habituation: a) different population densities and therefore different rates of encounters with the same individual chimps; b) duration of the habituation process; c) number of people working in the forest and searching time per day, d) different site histories.

The population density of chimpanzees at Lopé is given by Tutin and Fernandez (1991) as about 1 per km^2, whereas the population density at Kanyancu is 0.4 per km^2 and at Ngogo 3.0 per km^2, as estimated from a nest census (see Chapter 3) The Gabon project had been underway for 6 years in 1990, whereas habituation had been underway for only 2 years at Kanyancu by the end of this study, and for 6 years at Ngogo. Tutin and Fernandez (1991) give no information on the number of people and hours spent working in the forest, therefore these factors cannot be compared between the two sites.

From the above factors, the chimpanzees at Lopé might be expected to be better habituated than those at Kanyancu and at least as well as those at Ngogo. Site history may be a crucial factor. Hunting pressure from humans is negligable at Lopé as it has been a Game Reserve since 1946 and it is considered unlikely that chimpanzees there have ever been hunted by poachers (Tutin and Fernandez 1991). Although Kibale has been a forest reserve since 1932, many chimpanzees still suffer injuries caused by snares set for duikers by local poachers. Lopé is isolated from human influence except for the research station and some logging operations (Tutin & Fernandez 1991), whereas the chimps at Kanyancu are close enough to human settlements to regularly experience people walking through the forest in order to collect firewood, plants and other forest products. The chimps also raid certain of the villagers' crops. The fact that the Kanyancu chimps have always been more exposed to humans, even in adverse circumstances, may account for their easier and faster habituation.

The community of the chimpanzees at Ngogo is situated centrally in the former Nature Reserve and they are therefore more removed from people. However, Ngogo has been a subsidiary study site since 1977 (Struhsaker, 1977), and they had therefore regularly encountered people walking through the forest for 15 years by the start of this study.

It should also be taken into consideration that two different subspecies of chimpanzees are represented in Gabon and in Kibale: The central chimpanzee (*Pan troglodytes troglodytes*) occurs at Lopé whereas the eastern chimpanzee (*Pan troglodytes schweinfurthi*) populates Uganda (Lee *et al.*, 1988). Tutin and Fernandez (1991) have drawn attention to the fact that different subspecies of gorillas react differently to humans. Perhaps adaptability to new environmental conditions also varies between chimpanzee subspecies.

6.7 Summary

- A significant decrease of unhabituated reactions to the observer and increase of habituated reactions suggest that chimpanzees in both study communities became better habituated in the course of the study.

- Chimpanzees at Kanyancu charged the observer more and ignored the observer less often than those at Ngogo, suggesting that the Kanyancu community was less habituated than the Ngogo community.

- At Ngogo, adult females reacted in an unhabituated way more often than males; at Kanyancu, adult females fled and hid more often than adult males while males charged more often.

- At Kanyancu, the number of observers (up to 5) did not have an impact on the chimpanzees' initial reaction except for *soft vocalisations* which decreased. At Ngogo, unhabituated reactions increased and habituated reactions decreased with higher numbers of observers.

- In focal animal samples during which numbers of observers changed, the number of observers (up to 12) did not have an impact on time spent feeding, locomoting or resting during focal animal samples, whereas vocalising rates increased with more observers present.

- Call rate was not correlated with chimpanzee party size at Kanyancu.

- There was no difference between call rates in the first half hour of the visit and afterwards.

- At Kanyancu, the chimpanzees' reaction to the observer was influenced by the distance to the observer, the distance to the next chimpanzee, the activity before contact, the vertical position of the chimpanzee, and the way the chimpanzees were located.

- At Ngogo, only distance to the observer, vertical position of the chimpanzee and location method had an impact on the chimpanzees' reaction to the observer.

- The chimpanzees' party size and the density of the vegetation did not have an impact on the chimpanzees' reaction to the observer at either study site.

- The comparison with an habituation study in Gabon suggests that there are significant differences between the community in Gabon and the two communities studied in Kibale, indicating that the latter are better habituated.

- From several factors, site history seems to be the one mainly responsible for this difference.

Chapter 7

Discussion

In the preceding chapters, data were presented to test a prediction of the hypothesis that a more productive habitat is the main factor responsible for the differences in the details of social organisation between bonobos and common chimpanzees. If this hypothesis is true, forest-living chimpanzees should exhibit traits in their social organisation closer to bonobos than to chimpanzees living in non-forested habitats.

Existing data come mainly from wooded-savanna habitats such as Gombe and Mahale Mountains in Tanzania (e.g. Goodall, 1986; Nishida, 1990). The few studies on forest-living chimpanzees suggested that these chimpanzees might show traits in their social behaviour which were similar to bonobos in some ways, but the sites were either isolated (Bossou in Guinea; Sugiyama & Koman, 1987) or had a high predator pressure (the Tai Forest in the Ivory Coast; Boesch, 1991) and could therefore not be considered representative of forest-living chimpanzees. Another forest-living community at Budongo, Uganda showed social behaviour typical of savanna-living chimpanzees (Sugiyama, 1969). To supply new data to investigate the hypothesis, the Ngogo community in the Kibale Forest was studied as a representative of forest-living chimpanzees.

A number of characteristics such as party size and composition, relationship within and between the sexes and activity budgets have been described to differ between bonobos and chimpanzees (e.g. Badrian & Badrian, 1984; Ghiglieri, 1984; Kano, 1980, 1987; 1992; Kano & Mulavva, 1984; White, 1989, 1992, 1996; White & Chapman, 1994; Wrangham, 1977; Wrangham & Smuts, 1980). They were therefore investigated in this study of the Ngogo community. This chapter will explore and expand on the possible links between these traits with particular attention to habitat quality as the one factor to whom differences between the two species may be attributed.

7.1 Structure of the community

The Ngogo community is estimated to number more than 100 individuals which would make it one of the biggest communities ever studied. There are two posssible reasons for such a big community not undergoing a split. Firstly, that they do not have any neighbouring communities who would resist them expanding their home range; secondly, the habitat they live in is sufficiently productive to sustain a high number of individuals. While neighbouring communities exist, the extent to which their ranges abut those of the Ngogo community could not be determined in the present study. Thus the two causes cannot be distinguished conclusively.

In terms of community structure, mean party size and the distribution of party types have always been quoted as consistently different between common chimpanzees and bonobos (e.g. Badrian & Badrian, 1984; Kano, 1980, 1982, 1987; Kuroda, 1979; Malenky & Stiles, 1991; White & Wrangham, 1988). Mean party size both at Ngogo and at Kanyancu, the other chimpanzee community in the Kibale Forest investigated in this study, was well within the range of other common chimpanzee communities, even those in non-forested habitats. However, statistical tests on data from the literature revealed that intraspecific variance in these two characteristics in both chimpanzees and bonobos is equal to interspecific variance. Mean party size and the distribution of party types therefore give no indication of where the Ngogo chimpanzees stand in relation to other chimpanzee communities and bonobos.

This study confirmed Wrangham *et al.*'s (1992) suggestion that differences in mean party size between their and Ghiglieri's study at Ngogo were due to differences in definitions and methods.

7.2 Inter- and intrasexual relationships

Bonobos and chimpanzees differ mainly in their inter- and intrasexual relationships. Bonobo females are more sociable in general, but especially more sociable with each other, than are chimpanzees. The hub of bonobo relationships are those between females and males. In contrast, among chimpanzees, males form the central relationships in a community, with females being very asocial with each other.

The Ngogo chimpanzees were shown to follow the same pattern as other chimpanzee communities: females hardly ever groomed with each other, males associated mainly with males, and the relationships between males and females were almost restricted to those between males and oestrous females. The conclusion is that the Ngogo chimpanzees do not resemble the bonobos in their inter- and intrasexual relationships.

7.3 Activity budgets

If bonobos live in a more productive habitat than chimpanzees, as is always assumed, they should spend less time feeding. The data from the literature bear this out if data from chimpanzees at Rio Muni (Sabater-Pi, 1979) and Mahale (Huffman, 1990) are disregarded for reasons given in Chapter 6. The Ngogo chimpanzees spent approximately as much time feeding as the bonobos at Lomako. It can be concluded that, in this variable, the Ngogo chimpanzees resemble the bonobos more than other common chimpanzee communities.

If bonobo females are more intrasexually sociable than males, females should spend more time socialising. Unfortunately, the literature does not contain data to test this hypothesis. However, if the Ngogo chimpanzees resemble bonobos more than other chimpanzee communities, the same should apply to them. The results of this study have shown that, once the time spent on presumed offspring is subtracted from the time the females spend socialising, males spend more time socialising than females. The conclusion is that at Ngogo, males are more social than females , as is the case in other common chimpanzee communities.

7.4 Quality of habitat

Unfortunately, phenological data are available for only a few sites where chimpanzees have been studied. The rainfall data for various chimpanzee study sites have shown that differences in social organisation between bonobos and chimpanzees are not simply correlated with rainfall (as an index of habitat productiviy; Dunbar, 1988). The comparison between rainfall data for Ngogo and Gombe has shown that the answer may rather lie in the

Both chimpanzees and bonobos occupy a frugivorous ecological niche, although they also eat terrestrial herbaceous vegetation (THV) as a fall-back food. The difference in the quantity of THV consumption between the two species is one factor that has been considered responsible for the difference in party size and stability between the two species. Recently, emphasis has been placed more on a difference in THV quality, where bonobos are assumed to consume more THV of high quality than chimpanzees. So far, this has been confirmed only for the chimpanzees at Kanyawara, where no high-quality THV exists (Wrangham *et al.*, 1996). It remains to be seen whether the same is true for Ngogo.

seasonality of habitat, a theory also put forward by Malenky (1990, as quoted in Chapman *et al.*, 1994) and White (1996).

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7.5 Habituation

The study has shown that it is possible to monitor the chimpanzees' reactions to one characteristic of their habitat, the presence of humans. The process of habituation can be monitored and made quantifiable so that it can be compared with results from other sites. The significant differences in habituation between the Lopé community in Gabon and the two communities which were investigated in this study are striking. They naturally lead to the question as to how bonobos react when they are habituated. Obviously they do habituate, otherwise it would not have been possible to study them at the various sites. Like chimpanzees, they habituate better and faster when they are provisioned, and it may therefore be assumed that they react in similar ways to chimpanzees in other respects as well. However, as no data on this have been published to date, whether bonobos are affected in their habituation by the same factors as chimpanzees is a matter of speculation. This may become important when bonobos are opened up to ecotourism. Being so similar to chimpanzees, they will be equally attractive to tourists, and suffer similar risks from humans as chimpanzees. It is therefore suggested that guidelines for the habituation of chimpanzees might be helpful in the habituation of bonobos as well, when this becomes necessary.

Applied aspects

The results of this study can serve as a basis for habituation and chimpanzee tourism guidelines. Results suggest the following method . Site maps showing the fruit trees that are visited by chimpanzees should first be drawn up. These trees have to be monitored on a regular basis to record when they bear fruit. Once they are in fruit, tree vigils will lead to contacts with chimpanzees. Trails can be established linking fruit trees, thus decreasing the potential damage to the vegetation. In order to enlarge the population of habituated chimpanzees and therefore increase the chance of the visitors seeing them, habituation needs to employ methods other than tree vigils.

In order to avoid data biased towards better habituated animals, various location methods should be used in equal frequency both at early and later stages of habituation. Since different age/sex classes may react differently to observers, as many as possible should be targeted during habituation. In studies of impact assessment, vocalising rates could be used as indicators of how strongly the animals are disturbed. However, since vocalising rates may depend on other factors, such as party size, adequate data have to be collected to control for these factors in the analysis.

When decisions have to be made as to how many people should be in one group when visiting chimpanzees, several factors have to be taken into consideration. Although the data of this study indicate that neither the chimpanzees' initial reactions nor time spent feeding, locomoting and resting are significantly correlated with number of observers present, it must be kept in mind that the sample size of cases with high numbers of observers (from 8 to 15) was limited and so these results should be regarded as preliminary. In addition, the data came almost exclusively from chimpanzees that were contacted in tree vigils, which is when they are most likely to react in an "habituated" way. Although these data seem to show that only two categories of chimpanzees exist - completely unhabituated ones and completely habituated ones - there must be an interim period when the unhabituated chimpanzee turns into an habituated one. As these animals are more difficult to follow, they are targeted only rarely by the observer. In most cases there will be a few animals in the party that are going through this interim phase and therefore will react according to the number of people present, even if the great majority of animals in the party do not.

To maximise visitor enjoyment and minimise damage to the vegetation, it is suggested that a maximum number of

10 people in a viewing party (including guides) is appropriate. They should only be allowed to go straight to known fruit trees as groups of visitors of this size will inevitably make more noise than smaller groups and therefore cause a greater disturbance to the forest in general as well as to chimpanzees that are not in fruiting trees. Therefore only smaller groups of visitors should be allowed to move off trails through the forest in search of chimpanzees.

If tree vigils are used, several groups of visitors a day can be allowed, because relatively few chimpanzees will spend the whole day in the same fruit tree and so they will not be exposed to humans more than once.

There is no current information on visitor group size at Gombe or at Mahale. In Tongo and at Kanyancu, groups of six visitors at a time are taken into the forest and allowed to stay with chimpanzees for 1 hour. This level of visitation lies within the recommendations derived from this study. However, these recommendations are not merely of academic interest. The authorities responsible for established sites might be tempted to increase the size of visitor groups when more tourists arrive, as has happened in the Galapagos (Burnie, 1994), and new sites are being set up all the time.

It needs to be pointed out that the results of this study need not necessarily apply to other primate species. For example, black macaques were found to react according to tourist group size (Kinnaird and O'Brien, 1994). The degree of disturbance caused has to be assessed in each case and decisions made accordingly. It may not even be possible to generalise between sites for the same species. As the comparison between Kanyancu and Lopé in Gabon has shown, site history may affect the animals' tolerance of human observers considerably. The length of time required for studies to determine the success of habituation and to identify maximum visitor numbers will thus vary between sites.

7.6 Conclusions

In all social criteria, the Ngogo chimpanzees are closer to chimpanzees elsewhere than to bonobos. In contrast, their time budget seems to resemble more the time budget of a bonobo community. Time budgets may be described best as a compromise between the animals' needs and what the habitat has to offer and are therefore quite adaptable. However, social behaviour may be more genetically determined and therefore less adaptable.

If, as this study suggests, forest-living and savanna-living chimpanzees show the same social behaviour, this could mean either of two things. Either it means that habitat does not determine the social differences between bonobos and chimpanzees and it is more a question of species-specific, hard-wired behaviour, or it means that the difference between forested and non-forested chimpanzee habitats is not as great as the difference between bonobo and chimpanzee habitats, including forested chimpanzee habitats. With very restricted phenological data available, it is not possible at the moment to test the second hypothesis and so the two hypotheses cannot be distinguished.

7.7 Future work

It is hoped that future research will corroborate the results of this study. In particular, phenological data for all chimpanzee and bonobo study sites are desirable, such that habitat quality can be assessed directly and comparisons made between sites. Future research on the community at Ngogo should reveal its exact size and why these chimpanzees spend less time feeding than any other chimpanzee community. More work on the Kanyancu community will hopefully reveal why there is such a large difference in population density between Kanyancu and Ngogo and whether it is permanent or seasonal. Finally, more research on other forest-living chimpanzee communities is necessary to determine that they do not resemble bonobos, either, so that it can be finally determined whether different habitat productivity is the cause for differences in social behaviour between bonobos and chimpanzees.

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