# TACTICAL BEHAVIOUR AND DECISION MAKING IN WILD CHIMPANZEES

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# Preface

The text of this dissertation does not exceed 80,000 words (or 350 pages). The material herein has not been submitted for a degree, diploma or other qualification to this or any other university. This dissertation is the result of my own work and includes nothing which is the outcome of the work done in collaboration. All photographs included were taken by the author during the course of this work.

# Acknowledgements

First and foremost I must thank my supervisor, Dr. P. C. Lee (Pili), without whose support and encouragement this project would not have even been possible. For constantly believing I could complete this research, for the whiskey, and the holiday in Amboseli (for which I am also indebted to C. Moss), I owe an immense debt of gratitude. Prof. V. Reynolds I must thank for allowing me to study chimpanzees in Budongo, and for making me part of the Budongo Forest Project. In Budongo, Dr. A. J. Plumptre selflessly shared his house and meals, and his paraffin-fuelled fridge made life in the forest more than bearable. Without the work put in by A. Plumptre and C. Bakuneeta to establish the Budongo Forest Project, my work would have been far more difficult. I would also like to thank Dr. C.G.N. Mascie-Taylor, for offering statistical advice on the most obscure of behavioural questions, and for running a relaxed and friendly department.

In Budongo, my first thanks must go to my field assistant, Geresomu Muhumuza, who kept me company during long days in the forest, and worked willingly and without complaint. Without Geresomu's help, the scope of this project would have been far more limited. Without the efforts made by Zephyr T. Kwede and other field assistants to habituate the chimpanzees, no-one would be following chimpanzees through Budongo today. To Zephyr, the other field assistants, and staff of the Budongo Forest Project, I am indebted. Without the permission of the Uganda Council for Science and Technology, The President's Office, and the Forest Department, to live and work in Budongo, and without the funds supplied by the L.S.B. Leakey Foundation, the Leakey Trust (UK), the Boise Fund, and Churchill College, Cambridge, I would have been unable to pursue this research. For constructive comments and criticism on parts of this dissertation I must thank Dr. D. Chivers, and Prof. A. Harcourt.

Without the love and support of my family, especially my parents, over the last twenty-seven years, nothing I have achieved would have been possible. By encouraging a love of learning, and understanding a small child's interests in Africa and its apes, they allowed a dream to come true. Sarah's love and support kept me sane during the writing of this dissertation.

For giving me a glimpse of their world, and for their tolerance, I must thank the chimpanzees of Budongo.

Finally, I want to thank E.R. Burroughs, and Jane for starting it all.

# ABSTRACT

## TACTICAL BEHAVIOUR AND DECISION MAKING IN WILD CHIMPANZEES

Nicholas Edward Newton-Fisher

The mind of the chimpanzee poses something of a paradox. In captivity, chimpanzees show cognitive abilities which seem only rarely used in the wild. The contention of this thesis is that the added complexity which a fission-fusion social system imposes on a Machiavellian primate requires complex decision-making, and that it is in making these decisions that wild chimpanzees use their cognitive abilities.

The extent of social complexity in the relationships between male chimpanzees was investigated in an unprovisioned community in the Budongo Forest, Uganda. Statistical modelling and the construction of mutually exclusive hypotheses were used to determine the extent of tactical behaviour and decision-making in the social lives of these animals.

Male chimpanzees were found to live in a highly dynamic social milieu, showing complex patterns of associations which appeared to be tactical. Chimpanzee males changed their associates frequently every day, and it is argued that each change represents a decision. In pursuit of association strategies, each decision is tactical, and requires cognitive representations of strategic goals and the relationships between individuals. Individual males appeared to deliberately select their association partners. Over time, the tendency a dyad had to associate changed, as individuals sought to alter their relationships, in pursuit of association, and broader social, strategies. Two such association strategies were distinguished; one in which individuals maintained an even level of association with other males, another where males concentrated on associating with only a few others. Individuals switched from one strategy to another as their social status changed, although both strategies could lead to increased status. A preference for higher status males as nearest neighbours lead to competition for proximity partners, and individuals, particularly the middle to high status males, appeared to use proximity tactically. In choosing between grooming partners, male chimpanzees appeared to to select the individual with whom they had the stronger association relationship. This implied a cognitive comparison of the value of each relationship. Male ranging patterns were examined, and the majority of time was spent within small core areas which were both partially overlapping and distinct. Each male’s core area had a similar habitat composition, and overlap between core areas was positively related to dyadic association tendencies. It is hypothesised that these core areas function to enable the location of individuals to be predicted by other members of the community.

The cognitive demands of decision-making by wild chimpanzees is discussed in relation to the demonstrated abilities of captive individuals, as are the implications for an understanding of the evolution of the chimpanzee mind.

*To my parents*

*Brian and Jennifer*

# TACTICAL BEHAVIOUR AND DECISION MAKING IN WILD CHIMPANZEES

# CONTENTS

# Chapter 1

# INTRODUCTION

> *“knowledge of man’s position in the animate world is an indispensable preliminary to the proper understanding of his relations to the universe—and this resolves into an inquiry into the nature and closeness of the ties which connect him with those singular creatures [the great apes]”*
>
> *T. H. Huxley, On the Relations of Man to the Lower Animals, 1906*

The social system of a group of animals is the product of the relationships between individuals; relationships which are themselves the product of repeated interactions (Hinde, 1976). These relationships, and the social structure they create, are the means by which the animals solve ecological problems presented by their environment (Dunbar, 1989). Where the nature of these problems is such that alternative solutions are possible, these alternatives further diversify the types of relationships between individuals, and increase the complexity of their social system. Navigating though social complexity requires individuals to make decisions concerning their trajectories, their social strategies, and the tactics necessary to continue pursuit of these strategies.

For much of this century, attempts to understand the behaviour of animals have been dominated by the spirit of B. F. Skinner and the behavourist tradition founded by J. B. Watson (McFarland, 1985). Increasingly, it has become apparent this school of thought provides inadequate explanations of any but the simplest forms of behaviour (Crook, 1980; McFarland, 1985). In examining the complex interactions between individual animals in a social group, and between those animals and the environments in which they live, more satisfying answers have been obtained by considering the intentions of the animals themselves, and the goals towards which they aim (reviewed by: Byrne & Whiten, 1988; Cheney & Seyfarth, 1990; Krebs & Davies, 1991).

Such an approach need make no claims about the mechanisms by which these intentions are enacted, however. Modern behavioural ecology (Krebs & Davies, 1987) seeks to identify the evolutionary function, or adaptive value, of each facet of an animal’s behaviour, and such investigations answer different questions to those concerning mechanisms (Tinbergen, 1963). A functional explanation postulates that the ultimate goal of an animal’s behaviour is to maximise its Darwinian fitness; activities which achieve this persist, whilst others are eliminated by natural selection. To maximise fitness, an animal has to overcome a variety of problems, from finding sufficient food to finding an ideal mate, often simultaneously (Dunbar, 1989). Over evolutionary time, success in finding an optimal compromise between these different sub-goals becomes correlated with maximising fitness.

Using the language of intentionality as a short-hand for heritable genetic differences between individuals, animals *intend* to achieve *goals*, such as avoiding a predator or finding high quality food, and make *choices* concerning the best way to reach these goals. Those that do, will, on average, leave more surviving offspring over a lifetime than those who are less successful. Animals clearly ‘make decisions’ all the time, from selecting potential mates (for example, Smuts, 1987; Clutton-Brock et al., 1982; McClintock & Uetz, 1996) to finding food (for example, Goss-Custard, 1977; Oates, 1987). Calling such events ‘decisions’ merely indicates that a non-random selection from a range of options is being made, whether by the mechanism of cognitive choice or, for example, mere sensory bias.

The way an animal pursues its goals can be termed a *strategy*, particularly where two or more routes to maximising fitness are possible; two or more compromise solutions are equally valid. This idea can be applied to the pursuit of each sub-goal, such that individuals may have different foraging strategies which lead to the same total energy balance, or different strategies for acquiring mates which, on average, lead to the same number of offspring being born. The strategy pursued is therefore the result of a choice between two or more alternate means of achieving the same goal. Within each strategy are a number of tactics, further decisions an animal has to make, choosing between different means of pursuing the same strategy. At each level of analysis, a strategy is the more general, while a tactic is the more specific. Tactics at one level become strategies when considered at the level below (Dunbar, 1988a).

The behaviourist tradition persists in the assumption that the most parsimonious position is to consider animals as mere mechanisms, without thought or feeling. Growing lines of evidence suggest this may not be the case for many higher animals, especially primates (Griffin, 1976, 1984; deWaal, 1982; Whiten & Byrne, 1988a; Cheney & Seyfarth, 1990; Savage-Rumbaugh & Lewin, 1994; Matsuzawa, 1996). Highly complex and extremely flexible behaviour shown in response to complex ecological and social environments may be more simply explained by postulating cognitive information processing—thought—by the animals concerned, than by assuming a convoluted pathway of learned contingencies (Griffin, 1976; Crook, 1980). The principle of parsimony, made explicit by Morgan’s canon (Morgan, 1894, cited by McFarland, 1985), was constructed to avoid imbuing animals with cognitive powers for which there was no evidence. It was not intended to deny such abilities to those animals which demonstrably possess them (see Whiten & Perner, 1991).

Primates live in complex social groups, made more complicated than those of non-primates by the formations of alliances and coalitions (Harcourt, 1989). Alliance partners become social resources to be competed for, and individuals become “consummate social tacticians” (Harcourt, *ibid*) in their attempts to deal with the social environment. Such social complexity argues strongly for rapid cognitive decision-making by the animals concerned. The ability to use abstract criteria to describe relationships is a more parsimonious method of assessing the relationships between other individuals (Kummer, 1982; Dasser, 1985), and so predicting their behaviour (Humphrey, 1976; Whiten & Byrne, 1988b,c), than memorising every interaction. Vervet monkeys (*Cercopithecus aethiops*) selectively use referential signals as alarm calls dependent on their social environment. They, and other monkeys, seem able to represent social relationships and classify members of their social group using these abstract criteria (Dasser, 1988; Cheney & Seyfarth, 1990). They do not, however, appear to be aware of these abstractions, nor are they able to make use of them in other areas.

In seeking to understand the nature and evolution of the human mind it is necessary to search for the origins of the mechanism which governs much of human decision-making, self awareness. This is the ability to access cognitive processes, to think about thinking. (Crook, 1980). For this we must, as Thomas Huxley wrote, look to our closest living evolutionary relatives, the great apes.

Evidence strongly suggests that chimpanzees (*Pan troglodytes*) are self aware (Gallup, 1970; Menzel et al., 1985; Povinelli et al., 1997), and supports the idea that they are aware of the minds of others, that they have a theory of mind (Premack & Woodruff, 1978). They appear to attribute intentions to other individuals (Povinelli, unpubl., cited in Byrne, 1995a), and to be able to cooperate and exchange roles when solving problems (Menzel, 1973; deWaal, 1982; Povinelli et al., 1992). If they do possess such cognitive abilities, a far richer interpretation of chimpanzee social behaviour becomes possible. Unfortunately much of the available evidence comes from studies of captive individuals, who have had long exposure to humans and, according to critics, have become ‘enculturated’. As such they are said to show a cognitive dexterity absent in their wild counterparts.

Evidence of cognitive skills in wild apes has been looked for in both social and ecological spheres. Evidence for tactical deception (Whiten and Byrne, 1988) is predominantly confined to primates, with only the great apes showing evidence for cognitively intentional deception (Byrne, 1995a). In wild chimpanzees, intelligence is most clearly demonstrated in the manufacture of tools such as termite-fishing wands, and leaf sponges (McGrew, 1992). Construction implies a cognitive representation of the finished item, and an understanding of the cause-and-effect relationship between the tool and the problem it is designed to solve (Byrne, 1995a). Other evidence of cognitive skill amongst the great apes comes from food processing techniques in mountain gorillas (*Gorilla gorilla beringei*: Byrne & Byrne, 1993), and in chimpanzees, apparent teaching (Boesch, 1991a), anticipation (Goodall, 1986; Byrne, 1988, 1995a; Matsuzawa, 1991), gestural communication and the concealment of vocalisations (Tomasello & Call, 1994).

Such tantalising evidence is, unfortunately, weakened by its rarity. As Byrne (1995a) says “if cognitive abilities are so useful...why aren’t [they] much more common and obvious”. The abilities shown by captive chimpanzees seem to be latent in their wild counterparts; that they are unnecessary in the pursuit of their day to day lives (Humphrey, 1976**)**. Likewise, the demands of a subsistence level existence amongst humans do not appear to require the intellectual skills developed through education (Crook, 1980). The demands of a complex society may account for the apparent differences in cognitive skills between anthropoid primates and other animals (Jolly, 1966; Humphrey, 1976; Whiten & Byrne, 1988a,b**)**, while Dennett (1987) has argued that humans and possibly chimpanzees are more complex still in their cognition because the web of their social interactions is far more entangled, and thus demanding, than it is for other primates.

This thesis builds on Dennett’s suggestion, and contends that chimpanzees use advanced cognitive abilities far more frequently than has been heretofore supposed. I take as demonstrated that chimpanzees are, at least in captivity, capable of thought, and that there are strong indications that they have at least a rudimentary theory of mind, equalling at least Dennett’s level 2 intentionality (Dennett, 1988; see Chapter 7). While I do not seek to demonstrate that chimpanzees have a theory of mind, I aim to provide evidence that the mundane day-to-day lives of chimpanzees are cognitively demanding with the cognitive skills demonstrated in captivity required on an almost continual basis. I further suggest that this cognitive demand may be responsible for the evolution of the ape mind.

The fission-fusion (Kummer, 1968) social system of chimpanzees has been much described elsewhere (see Goodall, 1986). At its most basic, a fission-fusion social system is the extreme example of a foraging pattern seen in some primates (for example, *Papio* baboons: Dunbar, 1988a; *G. g. gorilla*: Goldsmith, 1996), whereby a fairly coherent social group fragments into semi-autonomous sub-groups. Such a system may be a natural consequence of the foraging costs associated with group living in these animals, permitting each individual to make more efficient use of its habitat.

In chimpanzee society, individuals have considerable freedom to move between sub-groups, and to associate and interact with whomsoever they choose. As a result, the processes of alliance formation and social competition are complicated. In keeping track of relationships, individuals are unlikely to be able to observe all, or even most, of the interactions between other individuals. Individuals pursuing social strategies would be expected to develop tactics to deal with the fluidity of the social environment, in order to exert some degree of control over the identities of their associates. Without controlling their associations, individuals would be at the mercy of stochastic factors, or strategies pursued by other individuals. Such tactics would be implemented on a regular basis, and require cognitive assessments of possibilities; intentional choice.

This thesis thus has two linked objectives: to show that, in chimpanzees, the combination of machiavellian social politics typical of Old World monkeys with a fission-fusion social systems produces a society the nature of which is more complex than has yet been realised, and that this complexity requires chimpanzees to use advanced cognitive abilities in their day to day social behaviour. The cognitive demands of processing alliance strategies in a fluid social environment will be advanced as a possible selective pressure responsible for the evolution of the minds of the great apes.

This will require the use of varied statistical techniques, bringing methods from other areas of zoological research to bear on these most singular of creatures. The following chapter provides a detailed introduction to the study site and animals, explaining the peculiarities of the site and the rational for a study of forest living chimpanzees, and Chapter 3 covers the general methods applicable to the rest of the volume, including general field methods, data collection techniques, and the terminology and definitions used.

Chapters 4 - 7 present results of different analyses, each addressing a different aspect of chimpanzee sociality. Each chapter begins with a review of relevant theory and past work. In Chapter 4 new ideas on the issues of dominance and social status are addressed, developing a new measure of social status, investigating the dynamics of social status, and the relationship between social status and affiliative interactions. Chapter 5 is the core of the thesis, and looks at association patterns, testing the idea that these are the result of conscious, tactical, decisions, requiring an almost continual cognitive processing. Chapter 6 looks at the ecology of social behaviour, looking in depth at ranging patterns, the spatial associations of individuals, testing ideas about the very nature of chimpanzee society. In Chapter 7 decision-making and the selection of dyadic partners are investigated, examining the internal structure of chimpanzee groups, and investigating the factors predicting the choice of grooming partners by means of naturally occurring choice experiments. Chapter 8 summarises the main findings and discusses their implications for an understanding of the evolution of hominoid sociality and cognition.

# Chapter 2

# STUDY SITE AND POPULATION

> *"In these great wastes of forest, life...struggles ever upward towards the light. Every plant...to the green surface, twining itself round its stronger and taller brethren. Of animal life there was no movement amid the majestic vaulted aisles...but far above our heads...that multitudinous world of snake and monkey...looked down in wonder at...the obscure depths...below them"*
>
> *A. Conan Doyle, The Lost World, 1912.*

## INTRODUCTION

Within their tropical niche, chimpanzees are catholic in their choice of habitat, living almost anywhere from tropical forest through seasonal forest and woodland, to savannah and bush country. They remain, however, dependent on tropical forest, requiring a minimum of 1% by area of their range (Kortlandt, 1983; Wrangham, 1986). Despite the variation in habitat, most of what is known about chimpanzee social behaviour and ecology is based on chimpanzees living in savannah-woodland mosaics, specifically Gombe and Mahale National Parks in Tanzania. At around the same time that the studies began in the woodlands of Gombe and Mahale, forest living chimpanzees were being studied by Adriaan Kortlandt (1962) in what is now the Peoples Republic of Congo (Zaire), and by Vernon and Frankie Reynolds in the Budongo Forest, Uganda (Reynolds and Reynolds, 1965). These studies did not develop into long-term investigations, although in Budongo there were brief studies by Y. Sugiyama (1968) and A. Suzuki (1969, 1971). Civil unrest and war during the 1970s and 1980s put an end to studies in Budongo, while data continued to flow from the Tanzanian sites.

From these studies a consistent picture of chimpanzee socioecology has emerged. Chimpanzees are large bodied, predominantly frugivorous, African apes. Average body weights are 30kg for females and 40kg for males (Reynolds, 1967; Parker, 1990). Highly social, chimpanzees live in multi-male, multi-female groups (communities: Goodall, 1973) numbering from 15 to 105 (Nishida & Hiraiwa-Hasegawa, 1987). The members of each community share a common home range, varying in size from 5-50km$^2$ in forest (Reynolds & Reynolds, 1965; Wrangham, 1986; Chapman & Wrangham, 1993; Yamagiwa et al., 1996), to over 300km$^2$ in open savannah habitats (Tutin et al., 1983). This range is defended cooperatively by the males of the community, against similar coalitions of males in neighbouring communities (Goodall et al., 1979; Nishida &

Hiraiwa-Hasegawa, 1987).

Within a community, females are generally solitary, spending 50%-80% of their time alone or with dependent dependent offspring (Halperin, 1979). Females mature 2-3 years earlier than males, and transfer from their natal communities as adolescents; some leave only temporarily, returning after becoming pregnant (Pusey, 1979). Females spend the majority of their time in small core areas, which are thought to provide access to food resources (Wrangham & Smuts, 1980; Pusey et al., 1997).

Males are more social, spending 2%-54% of their time alone (Halperin, 1979), and form the core of the society; they do not transfer, except perhaps as infants in the company of their mothers. As a result females are generally unrelated to one another, whilst males are more closely related (Morin et al., 1993; but see Gagneux et al., 1996). Males are thought to range fairly evenly across the shared home range, defending its boundaries by means of vocal advertising and boundary patrols, behaviour which is conducted as a group (Wrangham, 1979; Goodall, 1986). Hostile relationships between neighbouring communities can escalate into ‘warfare’, leading to the extermination of communities (Goodall et al., 1979).

Foraging is thought to be opportunistic, and the number of species consumed is large (Wrangham, 1977). Diets are highly variable from one populations to the next, but in all cases are dominated by ripe fruit (Reynolds & Reynolds, 1965; Hladik, 1977; Wrangham, 1977; Wrangham et al., 1996). Leaves are also an important component of the diet. Up to 5% of foraging time is spent collecting invertebrate and vertebrate prey. Hunting of monkeys and other small mammals has been observed at both East African and West African sites (Goodall, 1965; Boesch & Boesch, 1989). Some chimpanzee communities show evidence of cooperative hunting (Boesch, 1994), and predation by chimpanzees can be a major source of mortality for prey species (Stanford, 1995). 45%-60% of the day is spent feeding, usually in the early morning and late afternoon (Wrangham, 1975); during the middle of the day chimpanzees rest, either on the ground, or in simple nests constructed in trees. More elaborate nests which function as sleeping platforms are constructed at dusk (Goodall, 1986; see also Plumptre & Reynolds, in press).

Chimpanzees live in a fission-fusion social system; individuals associate with one another in temporary parties (Sugiyama, 1968), the size and composition of which is highly variable. Most parties are small and members of a single community rarely, if ever, associate as a single group (Goodall, 1986). A loose dominance hierarchy is pronounced in males (Bygott, 1979), and present but less obvious in females (Pusey et al., 1997). Male chimpanzees appear to be highly motivated to acquire high status (Goodall, 1986). Alpha status gives definite reproductive advantages, at least in terms of access to females (Nishida, 1979, 1983).

The female's menstrual cycle has an average length of 34 days, and is characterised by the waxing and waning of a large anogenital swelling (Tutin & McGinnis, 1981; Hasegawa & Hiraiwa-Hasegawa, 1983). This swelling is at its maximum size for 6-7 days, during which females are highly attractive to males. After ovulation, the swelling decreases rapidly (Goodall, 1986). Mating is usually promiscuous, with males showing a high degree of tolerance of one another, although towards the end of the period for which the female is 'swollen', competition between males becomes more intense and the alpha male may show possessive behaviour in an attempt to gain exclusive access to the female (Tutin, 1979). Other males may attempt to sneak copulations under these conditions (personal observation). An alternate strategy is for a male and female to form a 'consortship', during which they range apart from other members of the community. Such behaviour is more likely to provide exclusive access to the female for non-alpha males (Tutin & McGinnis, 1981).

The sociability of males is shown in their strong relationships; all studies report high levels of affiliative, primarily grooming, interactions. Males form coalitions and alliances with one another as a competitive strategy (Wrangham, 1986), and such alliances are important in determining and maintaining social status (Nishida, 1983; Goodall, 1986; Uehara et al., 1994). As a result, opportunities exist for individuals to manipulate relationships to their own ends. Alliance partners sometimes show "allegiance fickleness" (Nishida, 1983), switching support from one competitor to another. Such a strategy can allow the supporting individual to achieve a higher level of mating success than would otherwise be the case (Nishida & Hiraiwa-Hasegawa, 1987).

Chimpanzees use and manufacture a variety of tools. Stems are cut to length and stripped of leaves to form tools designed to extract termites (primarily *Macrotermes* spp.), or to feed on aggressive driver ants (*Dorylus spp.*) (McGrew, 1974, 1992). Leaves are crushed and crumpled to form a sponge to retrieve otherwise inaccessible water (Goodall, 1986; McGrew, 1992). Branches are used as weapons (Kortlandt, 1980), and in West Africa, chimpanzees use stones as hammer and anvil in the cracking of nuts (Sugiyama & Koman, 1979; Boesch & Boesch, 1983; Matsuzawa, 1996).

Details of chimpanzee evolution are at best only sketchily known, although it must have occurred during the last five to eight million years in tropical Africa. This period was characterised by a drying of the climate in Africa, and the resultant fragmentation of the forests of the Middle Miocene. It has been suggested that chimpanzees evolved in a mosaic habitat of semi-deciduous forest, woodland, bush and savannah (Kortlandt, 1972), a suggestion supported by analysis of morphological trends in hominoid evolution (Andrews & Martin, 1991). Increasing habitat diversity will have led to increased competition for forest habitat and the resources therein.

In populations located in areas where food availability dropped, with both decreasing food patch size, and increasing distance between patches, females (primarily) will have been forced, by virtue of large body size and general dietary dependence on fruit (Dunbar 1988a), to forage in smaller and smaller groups (Wrangham, 1979, 1986), and this led to a State Shift (*sensu* Foley & Lee, 1989) in their social system, producing that seen amongst extant chimpanzees. Consideration of competition with other ape and early hominid species would suggest that chimpanzees evolved to exploit a generalist forest-frugivore niche.

To fully understand the evolution of the chimpanzee social system, and the links with those of early hominids, it is thus necessary to gather data on chimpanzees in a range of habitats, representative of the late Miocene and Plio-Pleistocene. Present day tropical forests vary enormously from place to place and time to time, in structure, species composition and food abundance, and this variation is likely have to been as true in the past. Thus what are needed are data on the ways in which habitat variation and socioecology are interlinked.

To this end studies were started in the Taï Forest, Côte D’Ivoire by Boesch & Boesch (1983) and by Tutin and Fernandez (1985) in the Lópe Reserve, Gabon. More directly comparable data with that produced from the woodland sites was made available when studies of the chimpanzees in the Kibale Forest were initiated by Ghiglieri (1984), and later Isabyre-Basuta (1988) and Wrangham (Wrangham et al., 1992). This remained an isolated and in some ways, atypical site (Wrangham et al., 1996), until studies in Budongo were restarted by the return of Professor Vernon Reynolds to the Forest. When considered in isolation, Budongo is perhaps no less atypical than Kibale, but it provides the opportunity to collect comparative data on chimpanzees who are geographically close to those in Kibale, and until fairly recently likely to have been linked by limited gene flow. It also provides the opportunity to investigate some of the claims of earlier studies. With work on the chimpanzees conducted as part of an integrated study of forest ecology, the effects of ecological variation on chimpanzee socioecology can be more clearly elucidated.

## THE STUDY SITE

### The Budongo Forest Reserve

#### *Description*

The Budongo Forest Reserve covers an area of 793km² of grassland and forest on the

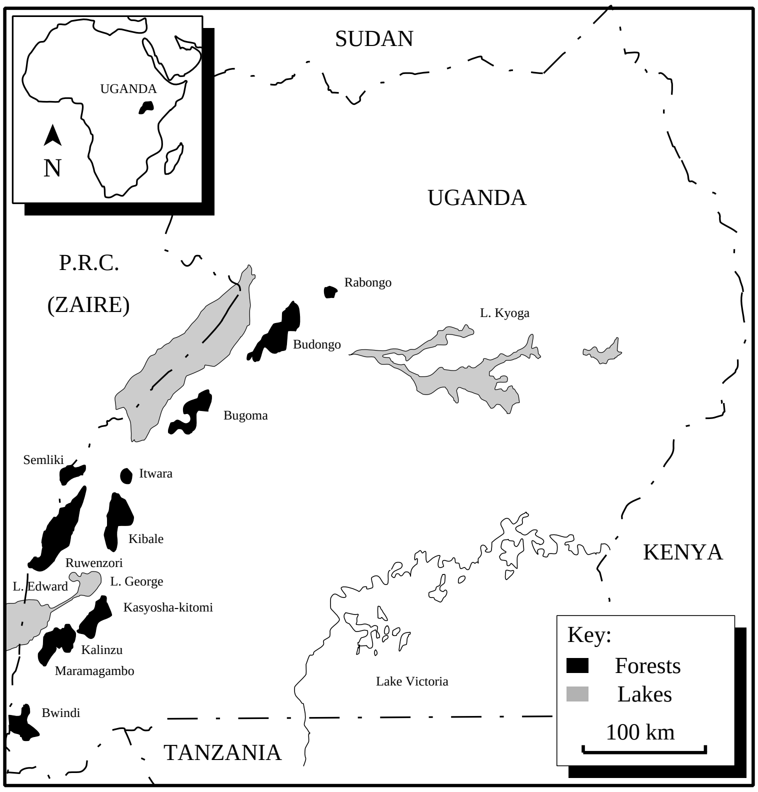

**Figure 2.1.** Map of Uganda showing forests containing populations of chimpanzees. Lakes (other than L. Victoria) are shaded. Murchison Falls National Park lies immediately to the north of Budongo forest, and encompasses Rabongo forest.

*(figure not included in this PDF version)*

**Figure 2.2.** Map of Budongo Forest, showing primary forest types as determined by aerial photography in 1990. From Plumptre & Reynolds (1994), with permission.

edge of the Western rift valley, near Lake Albert in Western Uganda (Fig. 2.1). 428km² of the reserve is forested (Fig. 2.2), classified as moist, medium altitude, semi-deciduous tropical forest (Eggeling, 1947; Howard, 1991). The forest is situated between latitudes 1°35´ and 1°55´ North, and longitudes 31°18´ and 31°42´ East, with an average altitude of 1100m (3600ft.) (Eggeling, 1947). To the north and west of the forest, bush and grassland stretch to the edge of the rift. In the north, the grassland is contiguous with the Kabalega game reserve and Murchison Falls National Park, the largest national park in Uganda.

Rainfall is fairly predictable, heavy and plentiful throughout most of the year, with the exception of a three month dry season from mid December to mid March. Suitably, “budongo” translates from Lunyoro, the local language, as “mud”. A ‘short dry season’ of around 4 weeks duration occurs in the middle of the year, although perhaps more accurately described as an ‘inter-rains’, a period of reduced rainfall between two definite wet seasons. Precisely when, and even if, it occurs, varies from year to year. No ecological changes are noticeable during this period, in contrast to the true dry season when the forest dries noticeably, many trees drop their leaves, the forest becomes more open, and flooded areas of swamp forest dry as river levels drop considerably (personal observation).

The perhumidity index, or PI (Walsh, 1992), summarises rainfall seasonality data into a single index in an attempt to measure the “continuity of wetness” (Walsh, 1996). It gives different weights to different levels of rainfall and differing lengths of dry season, to allow for varying levels of soil moisture. The index can range from -24 (all monthly means less than 50mm) to +24 (all monthly means greater than 200 mm). Rain forest is associated with values ranging from 5 to 24 (Walsh, *ibid*). For the years 1994 and 1995 Budongo forest has PI values of 3 and 4 respectively, and thus is at the very boundary between (wet) seasonal forest and true rain forest. As way of comparison, annual rainfall data for the 1930’s and 1940’s (Eggeling 1947) appear in Table 2.1. Although at first glance it might seem that the climate is becoming drier, it should be noted that Eggeling presents data showing no trend in rainfall patterns despite considerable yearly variation over the first 40 years of this century.

It is possible to calculate PI values for each of the years 1934 to 1942 (Table 2.2). These show no clear trend and vary from -½ to +9. Calculating a value for the entire period, using monthly means over 10 years, gives a PI of 4. Walsh (1996) notes that when the PI is calculated over years, as in this instance, it tends to fall a few points lower than when calculated on a yearly basis.

Figure 2.3 shows daily minimum and maximum temperatures, recorded over three years at the Budongo Forest Project field station, plotted on a monthly basis. Minimum daily temperature varies less than maximum temperature across the year, though this variation is statistically significant (Kruskal-Wallis analysis of variance: minimum temperature: $H$ = 104.05, $df$ = 11, $p < 0.0001$; maximum temperature: $H$ = 529.87, $df$ = 11, $p < 0.0001$**)**. Lowest minimum daily temperatures occur in January/February, and July-September. The difference between maximum and minimum temperatures is greatest between December and March. Together these data give clear evidence for a single relatively arid dry season, falling between December and March, where daily temperature variation is greater than for the rest of the year.

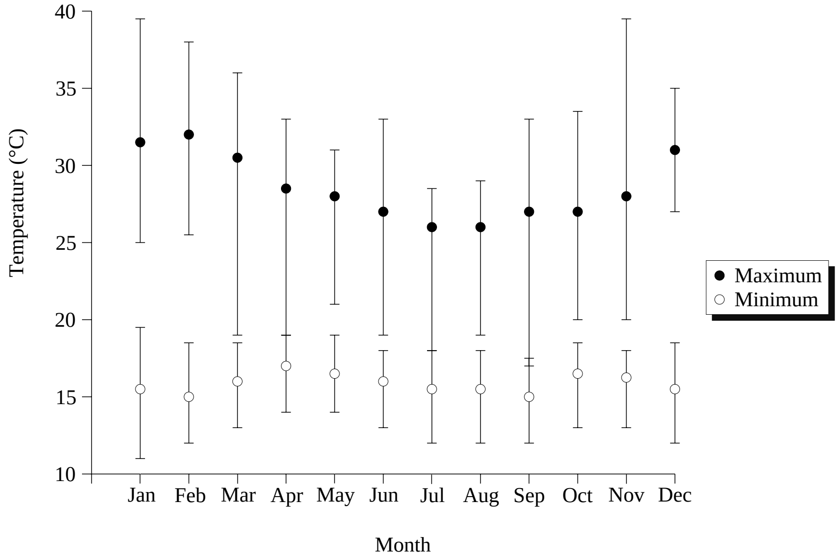

**Figure 2.3.** Maximum and minimum (shade) temperatures for the Sonso region of the Budongo Forest Reserve, plotted on a monthly basis from daily records collected over three years, 1993-1995. Maximum temperatures show greater variation than do minimum temperatures.

**Table 2.1**. Mean annual rainfall records for Budongo Forest Reserve. By geographical location, the Sonso data are most comparable to the 1945 'centre of forest' record. Eggeling (1947), the source for the earlier data, suggested average annual rainfall was between 1780 and 1900 mm over the forest. In comparison to the 1940's, the early 1990's seem a relatively dry period. Rainfall was consistently high in 1994, with no 'short dry season' (inter-rains). Eggeling's Busingiro data were recorded *outside* the forest, although close to the edge.

| Collection site (date) | Annual Rainfall (mm) |
|---|---|
| Sonso (BFP) Research Station (1995) | 1460 |
| Sonso (BFP) Research Station (1994) | 1601 |
| Sonso (BFP) Research Station (1993) | 1241 |
| Busingiro (1945) | 1414 |
| Centre of Forest (1945) | 1842 |
| Busingiro (mean, 1933-1943) | 1495 ± 186 |

**Table 2.2.** Annual rainfall and perhumidity values for the period 1934 to 1942. Rainfall data for 1934-1942 collected at Busingiro (from Eggeling, 1947), with perhumidity indices calculated from monthly data, following Walsh (1996). The perhumidity index measures the 'continuity of wetness', with more continually wet habitats having higher PI scores.

| Year (1934-1942) | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 |
|---|---|---|---|---|---|---|---|---|---|
| Annual Rainfall (mm) | 1083 | 1728 | 1739 | 1602 | 1449 | 1429 | 1484 | 1411 | 1476 |
| Perhumidity index | -½ | +6½ | +9 | +7½ | +1½ | +2 | +7 | +1 | +1½ |

A climate diagram (see Walter, 1985), combines rainfall and temperature data to distinguish 'wet', 'drought' and 'intermediate' months, and so determine the location and extent of different seasons. 'Wet' months are defined as those with more than 100 mm precipitation, 'intermediate' months as those with less than 100 mm precipitation, and 'drought' months as those where the rainfall plot falls below the temperature plot. Temperature is plotted in degrees celsius and rainfall in millimetres, with the rainfall scale half that of temperature scale. Such a diagram constructed for the Sonso region, using average values for the period 1993-1995 (Fig. 2.4), shows seven 'wet' months, one 'intermediate' month, and 3 'drought' months. The presence of a single dry season is clearly demonstrated. Figure 2.5 shows similar profiles for 1994 and 1995. The short dry season is clearly then only an inter-rains of varying aridity, and only a single true dry season occurs, centred on January and February. In some years December is dry and March wet, in others the opposite situation occurs.

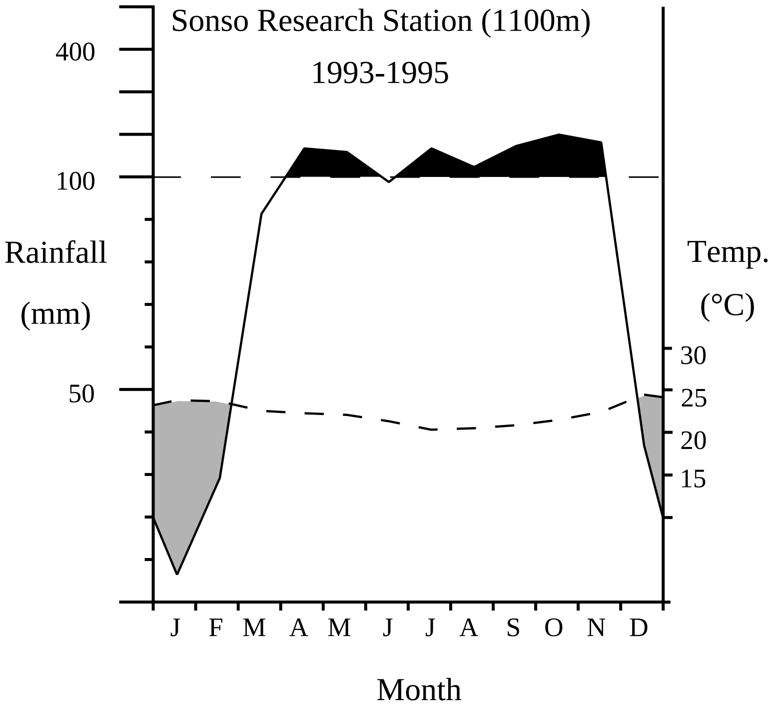

**Figure 2.4.** A Climate diagram constructed using monthly averages for the period 1993 - 1995. Temperature and rainfall data were collected at the Budongo Forest Project research station. Months exceeding 100mm of rain are classified as 'wet', and are shaded black. Months where the rainfall plot falls below the temperature plot are classified as dry, and are shaded grey.

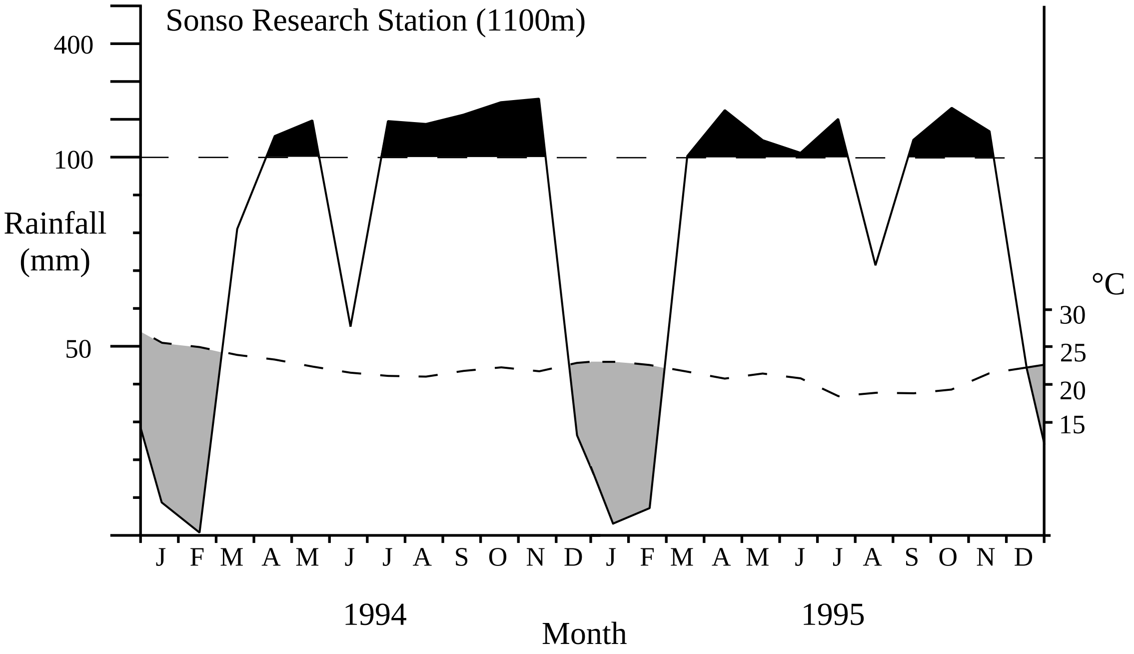

**Figure 2.5.** Climate diagram for the years 1994 and 1995, covering the period of this study. Dry season months are shaded grey, wet season months shaded black.

## *Forest Structure*

The forest is a mosaic of vegetation types, each with its characteristic mix of species. This is the result of both natural processes and logging practices (see below). Terrain within the forest itself is gently undulating, with generally low broad hills separated by wide shallow valleys, though some of the smaller valleys are steep sided. W. J. Eggeling, in his classic study of forest ecology which has formed the basis of all subsequent work in Budongo (Eggeling, 1947), proposed a classification of four main forest types, emphasising what he distinguished as natural succession and deliberately excluding secondary forest.

Forest ecology is, however, a highly dynamic process (Terborgh, 1992; Richards, 1996), with a continuing turnover of species. Large old trees fall to create gaps in which the process of succession can occur, increasing the mosaic nature of the forest. Thus secondary forest and the process of succession are natural, internal, features of a living forest (Richards, *ibid*). In addition, until the mid 1970’s the forest was home to a small but significant number (1000-1500 in the late 1960s; Laws et al., 1975) of African elephants (*Loxodonta africana*) which had a modifying influence on the structure of the forest. These animals were part of a larger population of around 10,000 animals living in Northern Bunyoro. These figures may well have been underestimates (Laws et. al., *ibid*). The majority of the forest has also been exploited at some time or other for timber and other forest products, and could today be described as consisting largely of areas of ‘secondary’ forest.

### *Forest types*

Eggeling's (1947) classification provides a convenient starting point in the description of the structure of the forest, and works well at the level of coarse grained or large scaled (for example forest-wide) comparisons (for example Plumptre et al., 1994; Howard, 1991).

The four basic forest types, defined by Eggeling, are:

1. Swamp Forest, a possible edaphic climax (Eggeling, 1947), found along the permanent and seasonal streams. It is the least common forest type (Plumptre & Reynolds, 1994). Dominant species include *Raphia farinifera*, *Mitragyna stipulosa*, and *Pseudospondias microcarpa* (Synnott, 1985). Woody lianas are highly abundant in swamp forest. Swamp forest is seasonally inundated, and differs depending on whether or not water is permanently present (personal observation). It invariably contains islands of slightly higher ground, upon which species more typical of other forest types are found.

2. Colonising Forest. This is dominated by *Maesopsis eminii*, *Cordia millenii*, and *Diospyros abyssinica*. Eggeling describes two forms, *Maesopsis* forest, and Woodland, where *M. eminii* is absent or scarce. Found in large blocks only around the edge of the forest, the dynamics of forest succession result in small patches of *M. eminii* or *C. millenii* dominated (colonising) forest deep within the heart of the forest. Small herbaceous climbers, and taller non-woody climbers are common, though woody lianas are rare (*Maesopsis* forest) or absent (woodland).

3. Mixed Forest. The single most common forest type (Eggeling, 1947; Plumptre & Reynolds, 1994), it is also the least clearly differentiated. It is dominated by *Celtis mildbraedii*, *Celtis zenkeri*, *Khaya anthotheca*, *Chrysophyllum albidium*, and *Funtumia elastica*. Woody lianas are most abundant in mixed forest, with other types of climbers less common.

4. Ironwood (*Cynometra*) Forest. Eggeling suggests this represents the climatic climax, with *Cynometra alexandrii* dominating, forming over 75% of the canopy (Eggeling 1947). *Lasiodiscus mildbraedii* is the dominant understorey tree. Fewer tree species are found in this forest type than in others. Climbers of all types are less abundant in the climax forest than elsewhere, though some tall non-woody climbers are present, and some woody lianas do occur, usually clustered about the oldest ironwoods.

Diversity within a forest type varies across the forest, decreasing from west to east, with more *C. alexandrii* towards the east of the forest (Plumptre, 1996). Eggeling (1947) also records ecotones between colonising and mixed forest, and between mixed and ironwood forest, these three forest types and two ecotones being the stages of natural forest succession.

### Management (Logging) History

Budongo Forest serves as the primary timber production forest in Uganda. It was gazetted between 1932 and 1939 by the British colonial administration (Howard, 1991), and produced timber on a sustainable basis from the mid 1920's until the 1970's. Today the sawmills are largely defunct but illegal timber extraction (pit-sawing) continues and is a major problem—both economically and ecologically—in many areas of the forest.

The Ugandan Forest Department's intention was to manage the forest to produce a sustainable yield of timber, to which end various techniques were used. Favoured timber species included *E. angolense*, *E. cyclindricum*, *E. utile*, *K. anthotheca*, *Looa trichiliodes*, and *Milicia excellsa*, and it was thought that these were excluded by the monodominant climax species, *C. alexandrii*. The prime focus of management policy was therefore to reduce the area of climax forest in favour of the timber-rich mixed forest, which could then be sustainably logged.

Initially all old timber trees were removed, with the aim of subsequently harvesting after 80 years, and thereafter every forty years. However, by the 1950's it was realised that growth rates, combined with damage caused by logging operations made this scheme impractical, and modifications were introduced.

To encourage regeneration of mahogonies (*Khaya anthotheca* & *Entandrophragma spp*.) replanting was attempted. Arboricide was used to poison non marketable "weed" species, particularly the ironwood *Cynometra*, to open up the canopy, favouring the regenerating mahogonies, and encouraging the development of mixed forest. Planting of mahogonies ceased when it was found natural regeneration was as effective at replacing felled trees (Plumptre et al., 1994). Despite the continued slaughter of elephants in Bunyoro from the nineteenth century onward, a scheme to eliminate large numbers of elephant was instigated in the 1950's (Laws et al., 1975), as they were suspected of damaging valuable timber trees, and favouring the development of ironwood (*Cynometra*) forest.

#### *Compartments*

The Uganda Forest Department divided the forest into 47 compartments, many of which have been logged at least once. Selective logging was conducted on a compartment by compartment basis and as each compartment was treated as a unit, each has a unique logging history. At least two compartments were never logged, one of which was set aside as a nature reserve. Records were kept detailing logging dates, treatments used and quantities of timber extracted for each compartment. Many of these survived Uganda's civil wars, and are summarised in Plumptre (1996).

### *Current situation*

Analysis of present day species composition (Plumptre et al., 1994; Plumptre, 1996) indicates that arboricide treatment failed to have the desired effect, and although there has been a significant increase in the area of mixed forest, the change in species composition has not been predictable. The main effect of the logging was to alter the structure of the forest, with unlogged areas having larger trees and more contiguous canopy. Logged compartments, which differed initially in their species composition, were logged at different times with varying quantities of timber extracted and different arboricide treatments used. This has resulted in a complicated mosaic of habitat types (Reynolds, 1992; Plumptre et al., 1994).

The elimination of the migratory elephant herds is likely to have had an impact on forest ecology, but Plumptre et al. (1994) found no evidence that elephants had encouraged the formation of the climax *Cynometra* forest. Aside from damage to regenerating saplings, it is likely that the elephants posed no significant threat to timber exploitation; certainly less than the illegal and uncontrolled pit-sawing.

As the timber mills have fallen into a state of disrepair, unable to compete economically with pit-sawing, attempts have been made to control the pit-sawing. Logging concessions have been issued but it remains difficult to enforce regulations, and given the immense returns from even a single mature mahogany, the future for sustainable logging looks bleak indeed. The intense pressure on the forest for mahogany threatens to strip all the valuable timber from the forest, with the concomitant damage to forest ecology. With no enforced minimum diameter limit to trees felled, or protection of large seed trees, illegal timber extraction threatens to destroy the value of Budongo as an economic—and ecological—resource. This squandering of mahogany reserves is damaging to the Ugandan economy, and threatens one of the key reasons for the forest's continued protection.

Only the presence of the Budongo Forest Project (see below) with its designated study areas, has discouraged the illegal loggers (personal observation). For the remainder of the forest, only a massive investment of men, time and money by the forest department, will help protect the timber stocks for future utilisation. An alternative would be for the forest to be put under the auspices of the new Uganda Wildlife Authority, merging it with the contiguous areas of the Kabalega Game Reserve and Murchison Falls National Park which stretch from the Northern edge of the forest to beyond the Albert Nile. This option would create an enormous protected area to rival those in other areas of Africa, large enough to support a combination of uses, such as tourism, logging and low-level (traditional) hunting. This would be possible without moving any local people, and could directly involve those living around the reserve in the running of associated projects, as is currently being implemented at two chimpanzee tourist sites established within Budongo.

### *Fauna*

The forest is rich in fauna as well as flora, much of which remains uncatalogued and unstudied. Five species of diurnal primate share the forest with an unknown number of nocturnal species: chimpanzees, olive baboons (*Papio cynocephalus anubis*), black and white colobus (*Colobus guereza*), red-tailed monkeys (*Cercopithecus ascanius*) and blue monkeys (*C. mitis*). Unlike Kibale forest there are no red colobus (*Colobus badius*) or mangabeys (*Cercocebus albigena*). Other large mammals include bushbuck (*Tragelaphus scriptus*), red duiker (*Cephalophus natalensis*), blue duiker (*C. monticola*) and bushpig (*Potamochoerus porcus*).

Buffalo (*Synceros caffer*) still wander south through the forest from the grasslands to the North as the dry season approaches, although there are no longer any elephants; the fraction that survived the civil wars are now confined to Murchison Falls National Park. Lions (*Panthera leo*) continue to be sighted in the northern most parts of the forest, and it seems likely that leopards (*P. pardus*) are also present. Both are known to be chimpanzee predators (Tsukahara, 1993; Boesch, 1991b) although no evidence of either was found within the study community’s range. Genets (*Genetta genetta*) and civets (*Civettictis civetta*) were present, and among the smaller mammals at least six species of squirrel, flying squirrels (*Anomalurus sp.*) and numerous rodents, including giant elephant shrews (*Rhynchocyon curnei*).

The forest is home to huge diversity of bird species including the long-crested hawk eagle (*Lophaetus occipitalis),* and the crowned hawk eagle (*Stephanoaetus coronatus*) which preys almost exclusively on guenons. A multitude of lizards, skinks and geckos live in and around the forest, as do many snakes, including some of the most poisonous species in Africa: Gaboon viper, puff adder, rhinoceros viper, and Jameson’s mamba, as well as enormous pythons (*Python sebae*). Invertebrate life is ubiquitous, ranging from beautiful butterflies, to the unpleasant biting flies and mosquitos.

## The Sonso Region

The Sonso region of Budongo was chosen as the study site, as it was here that the Budongo Forest Project had been established, and habituation of chimpanzees initiated (see Chapter 3). The Budongo Forest Project research station is situated atop a small hill in the large clearing surrounding the largely defunct Sonso sawmill. This is close to the centre of compartment N(Nyakafunjo)3, selectively logged between 1947 and 1952. The forest immediately surrounding the camp is classified as Mixed-Exploited (Uganda Forest Department, unpublished), after Eggeling (1947). In comparison with the nearby compartment N15, set aside as a nature reserve and never logged, N3 could be described as secondary forest although, as discussed above, this label is somewhat misleading.

### *The Budongo Forest Project*

Initiated by Dr. V. Reynolds, and starting in 1990 with Jane Goodall Institute (JGI) funding for Chris Bakuneeta to study the impact of logging on chimpanzee ecology, the Budongo Forest Project formally began in 1991 with the award of National Geographic Society funding for the continued habituation and study of the chimpanzees, and Overseas Development Administration (ODA) funding to assess both the effects of logging practice on forest ecology, and the importance of frugivorous primates to forest regeneration (Reynolds, 1992), this work being orchestrated by Dr. A. J. Plumptre, co-director of the project from 1992-1997, who developed detailed ecological studies.

With money from USAID, the Budongo Forest Project established the research station within the forest, and has deliberately attempted to provide training and research opportunities for both Ugandan and foreign researchers. In addition, it has provided a source of secure employment for around thirty local Ugandans, primarily as transect cutters and field assistants. A stringent requirement of the project is that all prospective field assistants be educated to a minimum of ‘O’ level standard, and this has ensured a generally high quality of staff, who are trained to a high level of competency in a variety of skills, including the identification of forest trees and observational techniques for collecting data on forest primates. The Project has also aided in the implementation of chimpanzee-focused tourism within the forest, providing training for the tourist guides.

The Budongo Forest Project has provided a foundation for the integrated study of many aspects of forest ecology, with A. J. Plumptre’s studies forming a core linking the more disparate studies undertaken by both Master’s and Doctoral students.

### *The Trail System*

In each of eight compartments, including N3 and N15, five transects of at least two kilometers in length were cut for census work (Plumptre et al., 1994), and these have become the framework for trail systems which now exist in four of the eight compartments, cut to provide rapid access through the forest, and to enable researchers to know their own position in relation to the research camp. In addition, the system of trails aids in systematic study of ranging and habitat use. In two of the compartments, Kaniyo-Pabidi [an agglomeration of three forest department compartments, KP(11-13)], and Busingiro [Biiso (B4)], the trail systems have been established to aid habituation of chimpanzees for viewing by tourists. In N3 and N15 the trail systems serve primarily research interests, and are connected by two of the original transects.

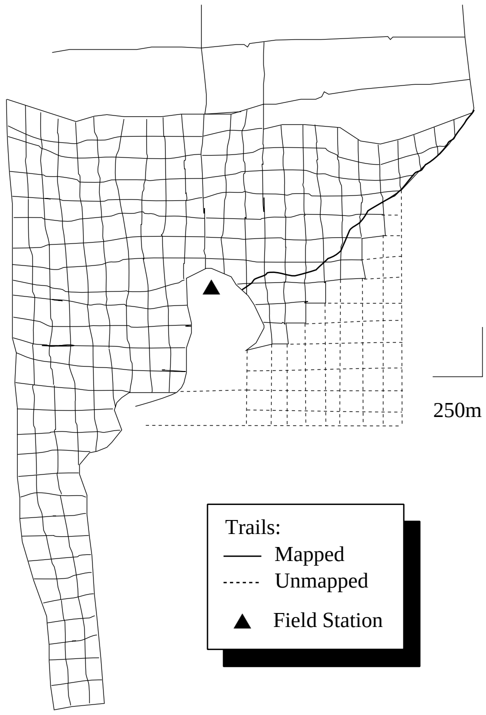

**Figure 2.6.** Trail system in the Sonso region of the Budongo Forest. Additional trails ran to the west, connecting this system with one in compartment N15. Trails were mapped by pacing on compass bearing. Mapping was conducted primarily by C. Fairgreave and G. Muhumuza. Unmapped trails are shown in their estimated positions.

The trail system in N3 consists of north-south and east-west trails which intersect to give ‘blocks’, ideally measuring 100m by 100m (Fig. 2.6). Practical difficulties, such as encountering a small *korongo* (valley), or a patch of dense thorn-rich or swamp forest, when cutting trails, led to deviations from the true compass bearing, and somewhat less than straight trails. Deficiencies in compass use, particularly the following of east-west bearings, amongst the transect cutters, further complicated the issue. As a result, block areas vary fairly widely (Fig. 2.6). To the east, the trail system is bisected by the Waibira road, a logging road which runs the width of the forest, linking to several other such dirt tracks within the body of the forest. Numerous other minor trails also run through the forest, maintained only by repeated use. Many of these are temporary trails used by pit-sawyers when removing mahogany, cut into planks *in situ*, from the forest. Other well worn trails meandering through the forest are ‘game’ trails, forming an unmapped network used extensively by the chimpanzees.

## ***Levels of Disturbance***

The area immediately adjacent to the sawmill clearing was used by people scavenging for firewood, although few people ventured deeper into the forest. Exceptions were Budongo Forest Project employees and poachers. The latter would venture deep into the forest to set wire snares of varying degrees of elaboration, aimed at catching (illegally) duiker and bushpig. Unfortunately, the snares would occasionally catch, maim, and possibly kill chimpanzees.

### *Pit-Sawing*

A further source of disturbance were the aforementioned pit-sawyers. Pit-sawing is a technique for extracting timber from a forest which produces cut planks at the site of tree felling. As such it does not require a large investment in milling equipment or the construction of logging roads, and avoids the damage associated with the dragging of entire trees from the forest. It is highly intensive in terms of man-power, and because of the minimal capital investment and the low wage levels, produces far larger profits than would milling the timber, despite the fact it is highly wasteful. A far higher proportion of timber is rejected, or simply not used: trees are felled above the buttresses, and knotted timber interferes with the sawing into planks. As a result, it is a form of timber extraction with which the sawmills cannot compete.

Once the tree has been felled, a long shallow pit is excavated, and over it, a frame erected. The trunk, cut into long sections, is then rolled onto the frame, and marked for sawing. Two-man, hand held saws are used to slice the trunk into planks, one man standing in the pit beneath the trunk, the other on the trunk itself (personal observation). Pit-Sawing has been illegal in Uganda, although recently efforts have been made to license certain pit-sawyers, and so generally uncontrolled. Any valuable timber tree is liable to be felled, without thought to management for the future, and thus pit-sawing responsible for widespread ecological damage.

### *Forestry Training*

Occasional disturbance to the day to day life of the forest would be caused by Forest Department officials checking on research plots, and trainee Forest Officers on field courses; although neither seemed to seriously disturb the chimpanzees, they could conceivably have affected their range use patterns.

In the main, the only human a chimpanzee would encounter in the forest, particularly when more than 200-300 metres from the clearing, would be a researcher or field assistant.

## CHIMPANZEES OF BUDONGO

The chimpanzees of the Budongo Forest are members of the subspecies of Eastern or long-haired chimpanzees (*P. t. schweinfurthii*), the same as found in Kibale Forest National Park, Uganda, and in the Gombe and Mahale Mountains National Parks, Tanzania. Budongo's chimpanzees were first studied in the 1960s (Reynolds and Reynolds, 1965; Sugiyama, 1968; Suzuki, 1971).

### Study Community

The study community consisted of 38 known, named, and individually recognisable individuals at the beginning of the study, a female and her infant being the most recent of a handful of individuals to disappear since the Budongo Forest Project began, most of whom were old and presumably died. The community is generally referred to as the Sonso community, named after the river which flows through part of their range. Table 2.3 gives a breakdown of the study community by age and sex. Table 2.4 gives a detailed breakdown providing names and identity codes for each individual.

**Table 2.3.** Age/sex classification of the Sonso community of chimpanzees. * Three infants were born during the course of the study, one of which remained unsexed and is not included here.

| | Numbers (by sex) | | | |
|---|---|---|---|---|
| | Initial (8.94) | | Final (12.95) | |
| Age class | Male | Female | Male | Female |
| Adult | 12 | 10 | 12 | 14 |
| Adolescent | 3 | 4 | 4 | 2 |
| Juvenile | 2 | 1 | 2 | 4 |
| Infant* | 4 | 3 | 5 | 2 |

Community size rose to 46, including infants, by the end of the study. Three infants (*Kwezi, Bahati* & *Kalu*) were born to named females (*Kwera, Kalema & Zana*, respectively), and an adolescent, or young adult, female (*Mukwano*) returned to the community after an absence of over a year. Two other females of similar age (*Sara* & *Jane*) joined the community, and a mature female (*Mama*), who may have been ranging more peripherally was recognised and named, together with her juvenile daughter (*Mhara*). In addition, a previously unknown juvenile male (*Nik*) was recognised and named; possibly he was the newly independent son of an unhabituated peripheral female.

At least two very poorly habituated adult females, a dependent juvenile, and an infant, were seen feeding deep within the study community's range, and associating peaceably

**Table 2.4.** Community breakdown for habituated chimpanzees of the Sonso community, August 1994 to December 1995. *= female with one or more known offspring. †= dependent individuals

| Name (mother) | ID code | Name (mother) | ID code |
|---|---|---|---|
| *Adult males* | | *Adult females* | |
| Magosi | MG | Kutu* | KU |
| Kikunku | KK | Kigere* | KG |
| Maani | MA | Zana* | ZA |
| Bwoya | BY | Ruda* | RD |
| Muga | MU | Ruhara* | RH |
| Nkojo | NJ | Zimba* | ZM |
| Tinka | TK | Nambi* | NB |
| Duane | DN | Banura* | BN |
| Vernon | VN | Kalema* | KL |
| Jambo | JM | Kwera* | KW |
| Black | BK | Mama* | MM |
| Chris | CH | Jane | JN |
| | | Mukwano | MK |
| | | Sara | SR |
| *Adolescent males* | | *Adolescent females* | |
| *Late* | | | |
| Zesta | ZT | Kewaya | KY |
| *Early* | | Salama | SL |
| Andy | AY | | |
| Zefa | ZF | | |
| Nik | NK | | |
| *Juvenile males* | | *Juvenile females* | |
| Gashom | GS | Vita | VT |
| Bwoba (ZA) | BB | Gonza (ZM)† | GZ |
| Jake | JK | Shida (BN)† | SH |
| | | Muhara (MM)† | MH |
| *Infant males* | | *Infant females* | |
| Kadogo (KG)† | KD | Grinta (RH)† | GT |
| Kato (KU)† | KT | Bahati (KL)† | BH |
| Musa (NB)† | MS | | |
| Bob (RD)† | BO | *Unsexed infant* | |
| Kwezi (KW)† | KZ | Zalu (ZA)† | ZL |

with known community members. These I consider to be members of the study community, although until they are recognised and named, they are not included in the figure for community size. A single juvenile male (*Jake*) appeared after the study started, but then disappeared. Whether the victim of a predator or snare, or whether he returned to his mother, is unknown.

### *Sampled Individuals*

The study focused on all twelve of the adult males, each of whom were subjects for the entire duration of the study, and three adolescent males—one late adolescent, and two young adolescent males—who were incorporated into particular aspects of the study. These adolescents could not be consistently followed, tending to be nervous when alone, and thus were excluded from the list of potential focal subjects.

Although none of the individuals reached a level of habituation to rival that found in Gombe National Park, all subject animals were sufficiently tolerant of humans to permit 30 minute focal samples (see Chapter 3) during 1995, and all save Tinka (TK) during the last quarter of 1994. Two of the lowest ranking individuals [TK and Muga (MU)] remained nervous when alone, particularly when compared to the other males.

## Other Communities

Current estimates of the number of chimpanzees in the Budongo Forest Reserve range from 675 to 2046, depending on the method used (Plumptre & Reynolds, 1996). Estimates based on nest counts vary from 675 to 890. The larger figures come from visual sightings along transects, which gave a mean number of 1066, but with very poor confidence limits, from 556 to 2046 individuals. When corrected for the proportion of individuals who do not construct nests (17.5%), and for proportion of nests reused, estimates based on 'standing crop' nest counts give figures of 906 or 950 individuals (Plumptre & Reynolds, *ibid*).

Thus it seems the total population is close to 1000 individuals, although probably not more. Interestingly, this is close to the mean estimate given by Plumptre and Reynolds (*ibid*) for visual sightings.

Assuming an average community size of fifty, a population of a thousand individuals would divide into twenty distinct communities. At present there is no information on whether the population is expanding, stable or contracting. Likewise there is no evidence as to whether the forest is inhabited uniformly by chimpanzees, or how density varies from area to area. With the mosaic nature of the forest, it seems likely that densities vary, with productive areas supporting more chimpanzees.

At least two communities of unhabituated chimpanzees are thought to inhabit forest adjacent to the range used by the study community, and there may be as many as four. Two that have been tentatively identified are the Nature Reserve (N15) community, and the Kasenene Hill (Waibira) community. Unhabituated chimpanzees have been both seen and heard in these areas, and the locations of sightings mesh fairly well with observed ‘patrolling’ behaviour by the study community’s males.

N15 lies to the west of the Sonso communities range, and may in fact be utilised by two distinct communities of chimpanzees. Consisting of *Cynometra* and *Cynometra*-mixed forest, food supply is thought to be more seasonal than in true mixed forest, and it seems likely that chimpanzees occupying this area would have to range more widely into other parts of the forest. Kasenene hill lies to the north-east, in the Waibira section of the forest. Unhabituated chimpanzees have been observed in the extreme north-east of the trail system, and so have been tentatively labelled as the Kasenene Hill community.

Two more distant communities have been identified, and some of their members individually recognised. In each case this is being done primarily to facilitate (eco) tourism, although as the chimpanzees become more habituated, opportunities will arise for research. Both communities live in a different mix of forest types than does the Sonso community, and the possibilities of ecological comparison between members of the same population are exciting.

These two areas are Kaniyo-Pabidi, and Busingiro. The Busingiro community lives in the area in which the early studies of Budongo chimpanzees were conducted (Reynolds & Reynolds, 1965; Sugiyama, 1968; Suzuki, 1969), further to the west than the Nature Reserve community. There may only be one community between the Busingiro and Sonso communities, and so there is potential for gene flow between them. Early evidence from dung analysis indicates that the Busingiro may be more carnivorous that the Sonso chimpanzees (A. J. Plumptre, personal communication), at least at present.

The Kaniyo-Pabidi community live in the extreme northeast of the forest, in an unlogged outlier of forest, although they also range into the main body of Budongo. This area is frequented by lions, who have elsewhere been shown to be predators of chimpanzees (Tsukahara, 1993). In addition there are reports that the chimpanzees make more elaborate use of leaves as tools than in Sonso.

## *Early Studies of Budongo Chimpanzees*

Early work on forest living chimpanzees suggested that differences existed in behaviour when compared to the woodland populations of Gombe and Mahale. Most notably, these included a less pronounced territoriality, and generally more relaxed social relationships.

Much of this early work was conducted in Budongo Forest, Uganda. Latterly, long-term projects in the Taï (Boesch, 1991, 1996) and Kibale Forests (Wrangham et al., 1996) have cast doubt upon some of the earlier conclusions concerning forest chimpanzees, although confirming differences with other habitats did exist, as chimpanzees coped with different food sources and differing habitat structures. To date, however, no direct re-evaluation has been made of the early claims for the chimpanzees of Budongo.

Neither the study by Reynolds and Reynolds (*ibid*) nor those by Sugiyama (1968) and Suzuki (1971), found any evidence of the termite fishing reported by Goodall (1965), or tool use other than two instances of a twig with leaves used to fan away flies, and branches thrown from the trees as a threat to human observers (Sugiyama, 1969). In addition, only Suzuki (1971) found evidence of predation by chimpanzees on other primates, at a much lower rate than at other sites. As a result, the importance of a savannah-woodland environment for the evolution of tool-use and hunting has been emphasised.

Reynolds and Reynolds (1965) failed to find any evidence of a dominance hierarchy in Budongo chimpanzees, and emphasised the flexibility of chimpanzee associations. The generally peaceful nature of chimpanzees in Budongo reported by Reynolds and Reynolds (*ibid*) has been used to argue that provisioning of study animals at other sites distorted their behaviour (Power, 1991). This seems unlikely, however, as provisioning is thought to have had little effect on the behaviour of the chimpanzees, particularly away from the feeding area (Wrangham & Smuts, 1980). In addition, the first evidence of infanticidal behaviour by male chimpanzees, a behaviour argued by Power (1991) to be produced by artificial provisioning, came from the Budongo Forest (Suzuki, 1971).

Observations made during this study, however, suggest that hunting is more common in Budongo than suggested by these early studies, and that infanticide also continues, with two instances observed within a period of six months.

Tool use is also a fairly regular occurrence. The most commonly seen tool-use by male chimpanzees of the Sonso community was the leaf-sponge, used to extract water from otherwise inaccessible cavities in tree boles. Amongst tools that were not deliberately constructed, branches were often used to enhance the impact of male displays, and males would frequently shake branches ‘at’ females with whom they wished to copulate. The chimpanzees do not need to use tools to extract the *Cubitermes* termites on which they feed, as the mounds are easily broken by chimpanzee hands. On one occasion a female was observed to incorporate a leaf into play with her infant.

In contrast to prevailing ideas of chimpanzee social organisation, Reynolds and Reynolds (1965) did make the perceptive comment that the ‘instability’ of chimpanzee groups had been exaggerated, suggesting instead that the social organisation possessed by chimpanzees was “so highly developed that it can persist in the absence of immediate visual confirmation”. Reynolds & Reynolds (*ibid*) also noted that females habitually occupied smaller areas than males, and that ranging patterns were influenced by spatial distribution of fruiting trees.

One of the most exceptional observations made by Reynolds and Reynolds (*ibid*) was of the prolonged bouts of hooting and drumming, which they termed ‘carnivals’. They suggest these may be related to the meeting of “bands that may have been relatively unfamiliar with each other”.

These have not been reported in other studies, and may have been the result of unique ecological circumstances. Reynolds and Reynolds (*ibid*) conducted their study at time when intensive logging operations were underway elsewhere in the forest which may have forced chimpanzees out of these areas. An increase in local population density is likely to have been the result, explaining the Reynolds’ relatively high estimate for population density. Under these circumstances individuals from neighbouring communities were forced into using some of the same food resources.

These ‘carnivals’ may in fact have been encounters between large parties from different communities, converging independently on the same food source. In the depths of Budongo, two ‘bands’ of quietly moving individuals would each be unaware of the other’s presence until very close, and the result would be an immediate contest over the resource in question, and the range-space in which it occurred. Such a contest would be highly vocal and involve many displays and associated buttress drumming.

# Chapter 3

# GENERAL METHODOLOGY

> *"the natural habitat...where observing, recording and analysing take the place of contrived testing...where the only experiments are nature's own, and only time—eventually—may replicate them".*
>
> *J. Goodall, The Chimpanzees of Gombe, 1986.*

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## INTRODUCTION

This chapter provides an introduction to the methods used during fieldwork. Specific methodologies and analysis techniques are detailed in the appropriate chapters. Fieldwork was conducted from August 1994 until December 1996, during which period I spent a total of 14 months in the field. The first two months were spent *habituating* (see below) the study group, and refining methodology. Data collection began in October 1994, and continued through to December 1995, with my field assistant collecting data while I was absent from the site. The chimpanzees were observed for more than 1400 hours, with systematic data collection accounting for 1365 hours of observation.

### Habituation

In classical learning theory, *habituation* is the process of non-associative learning by which a response to a repeatedly presented stimulus declines over time until the response is extinguished (McFarland, 1985). The subject can be said to be fully habituated when further presentation of the stimulus evokes no response. The animal learns that it need not respond to the stimulus, since it is not followed by any reinforcement.

In naturalistic behavioural studies, the term is used to refer to the response of the subject animal(s) to the observer. Initially the subjects are generally fearful and flee, but after continued exposure to the observer this response diminishes until the subjects generally ignore the presence of the observer, and engage in 'normal' behaviour. A critical assumption of all observational studies is that the presence of the observer exerts only a minimal influence on the behaviour of the subjects, such that, given a state of complete habituation, behaviour performed in the presence of the observer is that which would occur in identical situations with the observer absent. It would be extremely difficult, if not impossible, to test this assumption, and so it remains a primarily philosophical issue. The observer must rely on subjective impressions to minimise any influence their presence has on the subject's behaviour.

### *Initial Stages*

Work to habituate the chimpanzees in the Sonso region of the Budongo Forest Reserve began in 1990. This was conducted by Mr. C. Bakuneeta, and others, most notably Zephyr T. Kwede and Geresomu Muhumuza, and was done by searching through the forest for chimpanzees, primarily by listening for calls—the loud ‘pant-hoots’ (Goodall, 1968)—and secondarily by visiting fruiting trees which the chimpanzees were suspected or known to frequent. No effort was made to hide from the chimpanzees and the field assistants would talk amongst themselves, habituating the chimpanzees to the sounds of their voices. This process continued with the founding of the Budongo Forest Project in 1991.

Initially attempts were made to habituate chimpanzees suspected to be members of two communities, one inhabiting logged,  the other unlogged, forest. Progress with the later group was very slow and eventually abandoned. The chimpanzees in the logged area proved more amenable, and habituation proceeded rapidly, perhaps due to the high density of food trees in this particular area. By August of 1994 the chimpanzees were partially habituated, to the extent that they would tolerate human observers while in the trees, but would rapidly seek to avoid contact when on the ground. It was thus possible to observe chimpanzees in trees, but not on the ground. Attempts to follow chimpanzees along the ground were generally fruitless, lasting a matter of minutes at best.

### *Later Work*

Arriving in August 1994, I decided to intensify the efforts to habituate the chimpanzees which ranged in the area around the research camp. After more than four years the field assistants had become accustomed to watching the chimpanzees in the trees, and had not been encouraged to pursue them on the ground. I gave them that encouragement.

Together with my field assistant, Geresomu Muhumuza, I attempted to follow the chimpanzees wherever they went, rather than using only the system of cut trails, and not to ‘back off’ should the chimpanzees appear nervous of being followed. I reasoned that the only way to habituate the chimpanzees to observers following them on the ground was to do just that, and to continually push the limits of the chimpanzees’ tolerance. Any chimpanzee seriously worried by these efforts was able to escape in a matter of seconds with a sharp burst of speed, and initially, many did so. We did not, therefore, place the animals in a position from which they could not escape. They were continually presented with a choice: tolerate the presence of observers or depart, with only the minimum of effort.

This strategy very rapidly began to pay dividends, with first the larger males, and later the smaller males ceasing in their attempts to avoid pursuit. After only two months of this regime, I concluded all adult males to be sufficiently habituated to permit the recording of data. Habituation to human observers continued throughout the study period, and so data collected later in the study is more reliable than that collected earlier. For this reason, certain analyses use only data collected during 1995. For much of the study period it remained very difficult to follow lone females, although they remained relaxed when arboreal, or when in the company of males.

## DATA COLLECTION

### Observation Methods

Chimpanzees were located by a combination of methods. Searching for chimpanzees would begin soon after dawn, and continue for a variable number of hours. If no chimpanzees were found in the morning (after around four hours searching), or if chimpanzees had been sighted but lost, a second search would be instigated in the afternoon. Listening for calls was a prime method for locating chimpanzees, but this would be carried out while walking around the system of trails, checking known fruiting trees and areas in which chimpanzees had recently been sited, and also searching at random. Random searches tended to be a method of last resort, but efforts were taken to reduce the biases associated with locating chimpanzees by calls alone. Groups of chimpanzees located in this manner would be likely to be larger than average, and often feeding. Wandering the trail system increased the chances of locating lone individuals and small groups.

Following the chimpanzees as they travelled from one area to another was done by myself and my field assistant, moving along the same route taken by the chimpanzees, wherever possible. However, the thick forest slowed bipedal humans more than quadrapedal chimpanzees; particularly problematic were thin non-woody climbers, colloquially known as ‘vines’, which would snare passing limbs. In situations where we could predict the chimpanzee’s destination, either my field assistant or I would attempt to circle ahead of the chimpanzee, using the trail system, and ‘pick up’ the chimpanzee further along its line of travel. In this way we aimed to have at least one observer in visual contact with the chimpanzees at all times. Observations were made unaided, and with binoculars (8 x 30 in my case, 10 x 50 for my field assistant).

#### *The Role of the Field Assistant*

I was assigned Geresomu Muhumuza to be my field assistant by the co-directors of the Budongo Forest Project. One of the project’s senior field assistants, he was trained in the identification of tree species, and had previously worked as a field assistant to a PhD student, who instructed him in the collection of data through scan sampling. Although he had only minimal experience with chimpanzees, he and I rapidly learned to identify individuals under the instruction of Zephyr T. Kwede, senior chimpanzee field assistant.

Initially Geresomu worked as a guide and identifier of trees; we identified chimpanzees by consensus. During the collection of preliminary data, used to develop precise methodology, I realised I would need assistance with the simultaneous collection of scan sample, and focal sample, data. Geresomu worked diligently and accurately, and so I used him to collect much of the scan sample data whilst I collected focal samples. This made Geresomu part of the study, and more than just an employee. Working as a team we were able to monitor an entire chimpanzee party, something impossible for a single observer confined to a single location.

## Sampling Methodology

In order to collect reliable data, an unbiased sampling regime is required, as it is impossible to record every moment of a single subject's life, let alone that of a dozen or more individuals. I used four methods of data collection, after Altmann (1974): Focal scan sampling (instantaneous), focal animal sampling (continuous), focal behaviour sampling (continuous) and *ad libitum* sampling. These are described in more detail below. The mixture of sampling regimes allows for a more comprehensive coverage of the phenomena being studied. Data on the habitat used were collected together with other aspects of the subject's behaviour; sampling of available habitat was carried out separately, and is dealt with in the next section.

### ***Recording Methods***

#### *Data Sheets*

Data were recorded on custom-designed data sheets, the design of which was finalised during the first two months of fieldwork once the possibilities for research became clear. They were fully field tested before data collection began. The two designs used for data collection are presented in Appendix 1.

For the collection of scan sample data a rigid 'box-like' design was used, with each cell having a limited number of possible entries. This design is clear and easy to use, and convenient for computer data entry, while allowing more data to be collected than would a classical check-sheet of similar size. Continuous data (focal animal and focal behaviour sampling) were recorded on a second type of data sheet, using a short-hand notation developed during the preparatory phase of field-work. Maximum flexibility in what was recorded was thus retained, accommodating the complex nature of the chimpanzees' behaviour.

Initially, data sheets were A4 sized paper, carried on a clip-board, and protected from the rain by plastic sheets. Later, these were supplemented by home-made ‘wipe clean’ sheets carried in a personal organiser, the data being recorded by OHP marker pens, and later transcribed to A4 sheets. These two methods permitted the division of labour between myself and my field assistant.

### *Tape Recording*

During periods of heavy rain, and when the subjects were moving rapidly from one location to another, it proved impossible to make written notes. A ‘dictaphone’ was used to record continuous focal data in these situations, and on occasion, instantaneous scan data. Recordings were later transcribed to the standard A4 data sheets.

### *Note Taking*

Additional notes were made at the bottom and on the reverse of data sheets, and in notebooks to clarify data collected by systematic sampling. These were in the form of sketch maps, short notes, descriptive passages, and, in the case of particular behaviour patterns, *ad libitum* observations (detailed below).

### *Photography*

Efforts were made to take photographs to illustrate aspects of chimpanzee behaviour and habitat. Low light levels within the forest made this a difficult undertaking. I used a 35mm Ricoh XR-X camera body, with Ricoh 35-70mm zoom and Sigma 75-300 zoom lenses. Light levels dictated primarily ISO 400 Kodak and Fuji film. ISO 200 film was also used. Faster films would have many more photographs possible, but the loss of quality was judged unacceptable. Faster lenses and an auto-focus camera would have permitted recording of dynamic behaviour, such as male displays. Flashguns tended to disturb the chimpanzees and so were little used. Photography proved to be a full time occupation, and could not be carried out together with data collection. As a result, many of the most interesting aspects of chimpanzee behaviour were not recorded on film.

## ***Definitions and Terminology***

### *Groupings of Chimpanzees:*

| | |
|---|---|
| Community: | A ‘semi-closed’ network of male and female chimpanzees sharing a common range area, showing mutual tolerance and often affiliative interactions. Members of different communities generally have hostile relationships. After Goodall (1973). The same as the Unit-group (Nishida, 1968). |
| Party: | A fragment of a community, of variable membership and temporary |

| | |
|---|---|
| | duration; a collection of individuals showing coordination in behaviour. An upper limit of around 35 metres was set operationally; individuals moving beyond this were clearly moving away from other party members, and thus considered to be leaving the party. Participation in group behaviour, specifically ‘pant-hoot’ choruses, was used to confirm party membership, as such vocalisation is an active demonstration by the chimpanzees of coordination. Individuals within one party would call together in response to a similar chorus from another party. Only *independent* individuals were included in calculations of party size. After Sugiyama (1968). |
| Independent individual: | Any individual who ranged apart from its mother; showing freedom of choice as to association partners. Weaned and independently locomoting individuals were not classed as ‘independent’ if they were found only in parties with their mothers. Infants were likewise excluded. This is the same definition as is used by researchers in Kibale forest (R. W. Wrangham, personal communication). |
| Association: | The presence of independent individuals within the same party. |

## *Behaviour Patterns:*

| | |
|---|---|
| *Foraging behaviours:* | Searching for food items within a food patch and ingesting them. |
| Food item: | Any plant part, animal, or other item placed in the mouth and ingested. |
| Feed: | The process of picking (with hand, foot, or mouth) and ingesting food items. |
| Forage: | A combination of feeding and moving, such that each behaviour alternates in short succession, with breaks in movement sufficient only to ingest a few items, and each *feed* occurs at a different feeding site from that previously used. |
| Wadge: | A feeding technique used by chimpanzees to separate and reject fibrous parts of fig fruit (*figs*). A number of figs are picked and then repeatedly compressed between the inner surface of the lower lip and the teeth. Could be continued whilst otherwise resting, in a |

| | |
|---|---|
| | manner superficially analogous to cud-chewing in bovids. |
| *Locomotor behaviour:* | The movement of the chimpanzee under its own power from one place to another. |
| Move: | General translocation which is entirely arboreal, and neither directly up or down. |
| Climb (up): | Vertical or near vertical arboreal movement, with an increase in height. |
| Climb (down): | As above, but height decreases. Often used to descend from trees to the ground. |
| Leap: | Rapid aerial movement from one substrate to another. |
| Travel: | Translocative behaviour which is entirely terrestrial. Generally quadrapedal, with speed variable. |
| *Resting behaviour:* | The ‘default’ behaviour; no other behaviour being exhibited. No energy expenditure, above that needed to maintain posture and for basic metabolic processes. |
| Rest (sitting): | Resting in a posture with the weight supported by the sides and back of the legs, with the trunk more or less upright. Additional support occasionally provided by leaning against a trunk or fallen log, or by clutching a branch with hand or foot. |
| Rest (lying): | Resting in a prone position; the trunk is in contact with the substrate. |
| Rest (vigilant): | Resting, but showing signs of alertness; specifically, visual scanning of the environment. |
| Rest (nest): | Resting within a nest. |
| Build (nest): | The construction of a night or day nest. |
| *Grooming behaviour:* | Combing through hair with the fingers, ostensibly to remove dirt and ectoparasites. |

Groom (self): An individual performs grooming movements on its own body, often giving the impression of simply being something to do.

Groom (other): One individual performs grooming movements on another’s body. The identity of the ‘other’ is specified [for example: Groom (DN)]

Groom (receive): One individual is groomed by another whilst otherwise resting. The ‘groomee’ may or may not relax as it is groomed.

*Proximity behaviour:* Behaviour patterns which serve to alter spatial distance between any two individuals, and involve no other behaviour patterns other than *Locomotor* patterns. The distance of each individual from the focal animal was recorded quantitatively (see below).

Approach: One individual reduces the spatial distance between itself and other.

Join: One individual approaches another, usually stationary, and settles at a short distance (less than 2 metres).

Leave: One individual increases the spatial distance between itself and another.

*Other social behaviour:*

Display: A charging display. The individual charges at a fast or slow run, invariably showing piloerection. Other details after Goodall (1968, 1986)

Rain dance: A prolonged display, often performed very slowly. Temporal coincidence with rain or thunder.

Threaten: After Goodall (1986). One of the following directed towards another individual: *head tip, arm-raise, hit-towards, flapping, swaying branches, flailing, cough-threat, waa-bark.*

Attack: An assault, involving physical contact, of one individual upon another.

Reassure: Affiliative gestures which serve to calm an excited or nervous individual. Often a touch of outspread hands. Other patterns after Goodall (1986).

*Vocal behaviour:*

| | |
|---|---|
| Vocalise: | The chimpanzee gives any otherwise undefined call. |
| Pant-hoot: | Classic chimpanzee distance call, after Goodall (1986). Pant-hoots were not subdivided into particular types. |
| Pant-grunt: | A ‘voiced’ pant, after Goodall (1986). Grades into pant-barks and pant-screams (here subsumed into this one category) as the vocaliser becomes more fearful. |
| Food-grunt: | Soft grunts given in rapid succession at the start of feeding, and intermittently through the feeding bout, after Goodall (1986). |
| Scream: | High pitched, loud vocalisation generally given in response to aggression (Goodall, 1986). Subdivisions were not distinguished, although the context of the call was recorded. |

## *Focal Scan Sampling*

Scan sampling is defined by Altmann (1974) as instantaneous sampling of all members of a particular group. Instantaneous sampling is:

> *“a technique in which the observer records an individual’s current activity at preselected moments in time...it is a sample of states, not events.”*

Here I refer to it as *focal* scan sampling, as the selection of the group to be sampled was determined by the presence of a particular individual, the current *focal* animal. The integrated nature of the sampling regime meant this individual was actually or potentially the subject of a continuous focal animal sample. As detailed below, each instantaneous sample recorded a number of variables, some pertaining to the group as a whole, some to each individual within the group, and others to the focal animal alone.

The scan samples form the core of this study, and provide a framework linking the focal animal and focal behaviour samples. Initially I sampled at intervals of fifteen minutes, starting from the time of first contact with a chimpanzee party, but changed to sampling on the hour and at fifteen minute intervals thereafter as this proved a more manageable approach. The interval of fifteen minutes was chosen for practical considerations, being long enough to allow other activities, such as identifying of tree species, or pacing distances, to be carried out between samples, but being intuitively short enough to avoid missing behaviour of moderate duration.

The degree of temporal dependence, or auto-correlation, between successive records is likely to differ between behaviour patterns, such that short duration behaviour patterns are less likely than long duration patterns to show dependence at any given sampling interval. In order to maximise the amount of data collected while minimising the degree of temporal dependence between successive records when sampling a range of behaviour patterns at the same time, it is important therefore to use a time interval which optimises both. Although this relatively short interval may result in the collection of temporally auto-correlated data for some of the variables sampled, the possibility of extracting independent data points from the resultant data set during analysis is retained. Sampling at fifteen minute intervals may result in collection of data dependent at fifteen minute intervals, but not at perhaps 30 or 60 minutes. Sampling at one of these intervals would, however, significantly reduce the amount of data collected for behaviour which was not auto-correlated at a shorter time interval.

Fifteen minutes was the chosen interval, appropriate given the 30 minute duration of the focal samples (see below), with a scan sample falling at either end of the focal, and midway through. 15 minute intervals have been used in other studies of chimpanzees (Wrangham, 1975; Wrangham & Smuts, 1980; Chapman et al., 1994; C. J. Uhlenbroek, personal communication), and its use is the first step in ensuring a similarity in methods such that results of different studies can be compared.

**Table 3.1.** Scan samples containing one or more adult or adolescent males, by month, over the fifteen month study period.

| Month (Oct 1994 - Dec 1995) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| O | N | D | J | F | M | A | M | J | J | A | S | O | N | D |
| 162 | 433 | 165 | 378 | 395 | 302 | 371 | 524 | 261 | 374 | 407 | 406 | 391 | 387 | 202 |

$x$ = 343.87 ± 104.05
CV = 30.26

## *Selection of Focals*

The selection of the focal animal, and thus the group, to be scanned, is described in more detail below. A randomised list of subjects was followed, with efforts made to achieve an equal sampling of subjects *as focals*. Focal scan sampling, and the selection and rotation of focals, continued independently of continuous focal animal sampling, although when both were conducted simultaneously, the same focal animal would be used.

## *Data Collected*

Each scan sample was indexed by date, time of day, and focal animal.

Grid Location: The grid square within the trail system occupied by the group. In situations where individuals were spread over more than one square (for example, when the group was near a trail or trail intersection), this was the square which contained the focal animal (but see below).

Weather: Current weather conditions: *Sunny* (bright sunlight); *Fine* (clear skies); *Overcast* (uniform cloud cover); *Cloudy* (large rain-threatening clouds); *Rain: Light*, & *Heavy* (sufficient to prevent normal data collection). *Storm* was recorded if thunder was heard. An occasional cold mist was recorded as *Misty*.

Group Activity: Summary of overall group behaviour: the behaviour of the majority of group members. When the majority of members are evenly split into two groups, each with a different behaviour, Group Activity was defined as a combination of these two dominant behaviours (for example: *Forage/Rest*). If no clear summary of group activity could be recorded, for example if all individuals showed different behaviours, Group Activity was simply coded as *Mixed*. The following behaviour patterns were distinguished‡:

- Forage: Majority of individuals are feeding or searching for food (*moving* and *feeding*) within a food patch.
- Move: Majority of individuals are moving arboreally from one location to another. No accompanying *feeding*, although *wadging* of food, or carrying of food items may occur.
- Travel: Majority of individuals are moving terrestrially from one location to another. No accompanying *feeding*, although *wadging* of food, or carrying of food items may occur.
- Rest: Majority of individuals are sitting or lying, engaging in no other behaviour (the default).
- Groom: Majority of individuals are grooming themselves, or engaged in grooming interactions with others.
- Vocalise (call): Majority of individuals vocalising - either a ‘*pant-hoot*’ chorus or collective ‘*pant-grunting*’.
- Aggression: Majority of individuals involved in aggressive

interaction (fighting, or *displaying*/avoiding *display*).*

- Hunt: Individuals showing interest in monkeys, and moving to pursue or intercept. Success not a criterion.
- Patrol: Generally silent travel with frequent breaks during which members of the party show vigilant behaviour. Occurs only at or beyond current range boundaries. Parties mostly or wholly composed of males.
- Nest: Majority of individuals constructing nests.
- Copulate: Majority of individuals copulating.*

*These are likely to occur as group activities only when party size is small.

‡ see Definitions and Terminology for definitions of individual activities.

Dispersal: The estimated distance (in metres) between the two most widely spread individuals within the party. For a lone individual, this variable was not applicable.

Height: Distance above ground for the focal; estimated in metres. An indicator of vertical habitat use. When the focal was on the ground, a value of zero was recorded.

Food Type: Species and specific food item, recorded whenever one or more members of the party were feeding, using species codes devised by A.J. Plumptre (Appendix 2). Very occasionally members of a party would feed on more than item, almost invariable either on single items from two species or two items from the same species. If situations arose where more than two species were being eaten (which hardly ever occurred), an *a priori* decision was made to record only the two most common items (determined by number of individuals feeding).

Habitat Type (7 variables):

Trees: The tree species in which the chimpanzees were located, together with the nearest 4 species within a 10 metre radius having a “diameter at breast height” (DBH) of 10 cm or greater. This size category included small trees capable of supporting adult chimpanzees. Where the party were spread over more than one tree, the tree holding the focal animal was taken as the first of the five trees. When the chimpanzees were on the ground, the nearest tree to the focal, and the four nearest to that, were taken as indicators of habitat type. There were four conditions in which no trees were present:

- Closed canopy, low stem density; the forest was fairly open. The variables were simply recorded as ‘no tree’
- Broken canopy, high density of climbers or rattan canes (*Calamus deeratus*); species coded and recorded.
- Broken canopy, clearing dominated by terrestrial herbaceous vegetation. Any trees were recorded, otherwise ‘no tree’ recorded.
- Broken canopy, clearing dominated by grasses. Habitat coded as ‘grassland’.

Slope: An estimate of topography, coded using a four point scale: 0 (flat); 1 (slight); 2 (medium); 3 (steep).

Visibility: The distance (in metres) at which a chimpanzee would be visible, estimated from a position 1 metre above ground level.

By individual:

Presence: Each *independent* individual (see Definitions and Terminology) present in the party at the instant of the sample was recorded with a tick. If individuals were suspected to be present, but could not be seen at the instant of the sample, a question mark was used to indicate probable presence. To record only those individuals clearly visible would have led to serious under-estimates of party size. When behaviour could be observed, this was recorded instead of simple presence.

Behaviour: When visible, the behaviour of each individual was recorded using a series of two letter codes, each representing a behaviour category (see Definitions and Terminology). More categories were used than for group activity, the majority of which were defined prior to data collection. New categories were defined when none of the existing categories described the behaviour.

| | |
|---|---|
| Location: | The position of each individual in relation to the trail system was recorded by pacing along compass bearings; within the trail system this was to two perpendicular cardinal points, giving east-west and north-south distances to the nearest trail intersection. The paced distances were converted into coordinates relating the position to the Grid Location (above), and were recorded as 25 meter bands: 0 (on a trail); 1 (1-25m); 2 (26-50m); 3 (51-75m); 4 (76-100). The coordinate system was extended, such that positions to the west or south of the trail intersection were given negative coordinates, and positions further to the north and east (for example where the party was distributed in two trail system blocks), by the use of a code 5. |

Additionally, for every female present, the cycle state and/or the presence of a dependent (infant or juvenile) was recorded. Initially a five point scale was used to describe the anogenital swelling as an index of stage within menstrual cycle, but was replaced by a simpler three point scale: 0 (flat); 1 (partly swollen); 2 (fully swollen).

## *Focal Animal Sampling*

Focal animal sampling is defined by Altmann (1974) as having two key characteristics:

> *"(i) all occurrences of specified interactions of an individual [and] (ii) A record...of the length of each sample period and...the amount of time that [the focal] is actually in view."*

Focal animal sampling has the advantage of recording duration and sequencing of behaviours, data missed by instantaneous sampling.

Continuous data were collected for a period of 30 minutes, before switching to a new focal animal. An interval of at least 15 minutes was left between each consecutive sample to reduce dependence within the data set. The half-hour duration proved to be the most consistent period for which a single individual could be followed, at least at the beginning of data collection. Once problems of poor habituation had been overcome, the thick habitat continued to pose problems both for keeping a focal in sight, and for following a focal animal along the ground. Even by the end of the study, attempted 12 hour follows of selected individuals (conducted mainly by Budongo Forest Project field assistants under the direction of A.J. Plumptre) failed more often than not.

The short duration of focal samples was beneficial, in that it permitted a number of individuals to be sampled each day, and the frequent switching of focal animals meant that losing sight of a particular focal animal wasted only a limited amount of time. In addition, the 30 minute period was short enough to permit highly intensive continuous collection of data with good time resolution.

Collecting data in this way meant, however, that data would be lost if an interaction continued beyond the end of the thirty minute period, and that a complete picture of daily activities could only be inferred from a number of different samples collected over a number of days. A changing social and ecological environment inevitably results in a loss of resolution when examining such patterns. As daily changes in behaviour were not the focus of this study, this becomes an acceptable problem. Some patterns of behaviour, such as the ‘day-range’ cannot be recorded using this system of short duration, rotating focal samples.

The use of this type of sampling also results in the collection of large quantities of data not germane to the primary aims of the study, such as data on foraging and resting patterns. Time spent recording such data is time unavailable for the recording of social behaviour between other, non-focal, individuals.

### *Data Collected*

The focal samples were designed to collect the maximum amount of data within the time period, and were specifically concerned with social behaviour. This design bias did not preclude the collection of data relating to other aspects of behaviour, such as foraging, although this was inevitably less detailed.

The primary objective of each 30 minute sampling session was to record, to the second, a continuous account of the behaviour of the focal animal. A secondary objective was to do the same for the focal’s nearest neighbour, although this was not always possible, at least not to the same degree of accuracy. However, recording direct social interactions involving the focal would automatically record the behaviour of the nearest neighbour. The identity of the nearest neighbour could change a number of times during the sample period, as the animals within the focal’s group changed their relative positions.

A further objective was to record proximity relationships; the relative positions of individuals, and the changes in these. This was done continuously throughout the 30 minute focal, by recording graphically (to the nearest metre) the positions and movements of individuals within a five metre radius of the focal, with an extra band to include individuals beyond 5m and within 10m of the focal.

Recording of behaviour was by means of two, and three, letter codes, using the same behaviour codes as for scan sampling, and arrows to indicate directionality of behaviour.

For example:

| *min:sec* | *Focal* |  | *Nearest Neighbour* |  |
|---|---|---|---|---|
| 14:53 | MG *Rs* |  | BY *Rl* | [Adult male MG resting (sitting), Adult male BY resting (lying)] |
| 15:10 |  |  | BY *Mv* | [BY ceases to rest and moves (arboreally)] |
| 15:15 | MG | ⇐ | BY $G_{MG}$ | [Reaching MG, BY begins to groom MG] |

A notable addition was the recording of important social interactions (potentially) observed *by the focal*. Specifically, agonistic interactions, pant-grunts, and copulations were recorded.

## *Selection of Focals*

Focals were selected according to a randomised list, drawn up early in the study. Sampling would begin with the first individual observed, and proceed from individual to individual according to their position on the list. However, because members of the same party were rarely consecutive on the list, all subjects present (the adult males described in the previous chapter) would be sampled once before attempts were made to find other subjects.

The difficulties in finding chimpanzees in the forest, particularly when they were silent, meant that contact with chimpanzees would not be deliberately broken unless I considered the possibility of finding other subject to be fairly high. Efforts were made, however, to maintain a fairly balanced sampling regime by deliberately switching to a new subject who was not the next on the list when the number of focal samples on that individual were low.

The fluid fission-fusion social system meant that party composition often changed while conducting focal samples, thus providing ‘new’ individuals to sample. Many times however, individuals would join and leave a party (come into temporary association with the focal) before the current sample (plus non-sample interval) had passed. This, combined with the unpredictability of encountering particular individuals, led to uneven (focal) sampling of individuals on a month by month basis. The variation in number of samples per individual appears to be random; that is, there were no consistent sampling biases. Over the entire study period, the number of focal samples was similar for ten of the 12 males (median = 86.5, range 72 - 94). One of the 12 was more heavily sampled (DN, n = 131), though not excessively so, and one considerably under-sampled (JM, n = 44). This male was difficult to find, both on his own and in parties, although he was fairly well habituated when located. A total of 1,023 focal samples were collected between October 1994 and September 1995, after which they were replaced by focal behaviour sampling.

**Table 3.2.** Number of completed focal animal samples, by individual, by month. Focal animal samples were conducted from October 1994 to September 1995, after which they were replaced by focal behaviour sampling.

| | Focal Animal | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH | Totals |
| Oct | 8 | 3 | 2 | 2 | 3 | 3 | 4 | 5 | 2 | 0 | 4 | 1 | 37 |
| Nov | 10 | 14 | 7 | 11 | 14 | 7 | 6 | 14 | 13 | 10 | 16 | 5 | 127 |
| Dec | 5 | 3 | 6 | 5 | 6 | 7 | 5 | 10 | 4 | 2 | 5 | 2 | 60 |
| Jan | 15 | 11 | 9 | 10 | 4 | 14 | 15 | 15 | 11 | 4 | 7 | 11 | 126 |
| Feb | 11 | 13 | 11 | 13 | 7 | 8 | 15 | 17 | 9 | 11 | 13 | 5 | 133 |
| Mar | 5 | 2 | 6 | 4 | 2 | 0 | 1 | 6 | 4 | 2 | 3 | 3 | 38 |
| Apr | 2 | 5 | 11 | 2 | 10 | 12 | 11 | 10 | 6 | 0 | 2 | 12 | 83 |
| May | 3 | 11 | 11 | 7 | 16 | 7 | 19 | 23 | 8 | 1 | 10 | 11 | 127 |
| Jun | 4 | 1 | 5 | 7 | 3 | 0 | 5 | 13 | 2 | 1 | 3 | 5 | 49 |
| Jul | 5 | 11 | 10 | 7 | 5 | 3 | 5 | 3 | 12 | 5 | 3 | 2 | 71 |
| Aug | 10 | 7 | 12 | 8 | 5 | 7 | 6 | 14 | 7 | 5 | 3 | 7 | 91 |
| Sep | 12 | 5 | 4 | 7 | 11 | 6 | 1 | 1 | 11 | 3 | 12 | 8 | 81 |
| Totals | 90 | 86 | 94 | 83 | 86 | 74 | 93 | 131 | 89 | 44 | 81 | 72 | 1023 |

## *Focal Behaviour Sampling*

Referred to as "Sequence Sampling" by Altmann (1974):

> *"The focus of observation is an interaction sequence, rather than any particular individual(s)"*

This technique was used during the last three months of the study to collect detailed data on social interactions (see for example, Lee, 1987). Altmann (*ibid.*) identifies two key problems with this method: (i) identifying beginning and end, and (ii) selecting sequences. Determining beginning and end was not a problem here, as I confined myself to collecting data on specific behaviours whose initiation and termination was clear and unambiguous (see below). This methodology was used to record complete bouts of behaviour, and not to be constrained by a fixed time period focused on a single individual. As a result the first of Altmann's problems is avoided. The second potential problem was circumvented by following a sampling rule applied across all individuals. This rule stated that all observed occurrences of the specified behaviour pattern, involving at least one of the subject animals, for which initiation was observed, would be recorded. This ensured that comparable data would be recorded for all subjects.

### *Data Collected*

Grooming:

- Identities of participants.
- Initiation: time; identity (responsibility for proximity); identity (groom request); identity (first groom).
- Roles: Identity of groomer/groomee; body part groomed; time of switch to new body part.
- Change in behaviour state (each participant): groom, receive grooming, pause, rest, depart, join. — time of each change.

Aggression:

- Type: Threat; Display; Attack.
- Identities of participants.
- Initiation: time, responsibility.
- Termination: time, responsibility.
- Duration.

Copulating:

- Identities of participants.
- Initiation: time of initiation, responsibility for proximity.
- Duration: time of intromission.
- Female behaviour (during): vocal/silent; (after): leap away/remain with male.
- Male behaviour (after): rest; groom female; move away.

## *Ad Libitum Sampling*

*Ad lib.* sampling is the collection of unsystematic observations. This was used to supplement more systematic methods of data collection to aid the qualitative interpretation of results, and to record rare behaviours. An example would be the behaviour of individuals other than the focal and nearest neighbour during rare events such as infanticide, or pant-grunts between males of otherwise similar status. As described above, clarifying notes were made in conjunction with systematic data collection. Technically, all such notes are *ad lib.* data. However, I prefer to reserve the term to cover the unsystematic collection of data which would otherwise be collected through systematic sampling, making use of the same terms and definitions, rather than general notes.

One of the greatest drawbacks associated with *ad lib.* sampling is that it is biased towards observable phenomena and observable individuals, producing biased estimates of relative rates of behaviour, and distorting differences between individuals in the performance of behaviour patterns. There is no obvious way to determine whether apparent differences are real, or simply the result of these biases (Altmann, 1974). A third source of bias is observer preference. There are no systematic rules for the selection of behaviour patterns, and where two or more patterns occur simultaneously, the observer merely picks—if only subconsciously—which to record. Over any period of time it is impossible to determine whether such a bias remains constant, or even the extent and direction of the bias.

*Ad libitum* sampling, however, often remains the only method available for the collection of infrequently occurring behaviour. If the behaviour patterns to be recorded are specified *a priori* the problem of observer preference is overcome, although other sources of bias remain. The data provided are useful for determining the direction of interactions and partners for these interactions. For each individual the rate of interaction with each partner cannot be determined from *ad lib.* data, but the relative direction of interactions can be determined. Considering only a single behaviour, the problem of differential observability between behaviour patterns is removed, and when considering interactions between any particular dyad, the individuals observed are held constant, thus eliminating the problem of differential observability of individuals.

### *Contrasts with Focal Behaviour Sampling*

In some respects focal behaviour sampling can be thought to resemble *ad libitum* sampling. However, there are key differences.

- Focal behaviour sampling specifies which behaviours will be recorded, and how these will be selected. *Ad lib*. sampling does not have this systematic character.

- A requirement of focal behaviour sampling is that start and end points for data collection must be predetermined, as must the initiation and termination conditions for the behaviour sequence under consideration. These systematic rules remain constant for focal behaviour sampling; neither condition applies to *ad lib.* sampling.

- *Ad libitum* sampling simply records the elements judged important by the observer at the time; Focal behaviour sampling requires *a priori* decisions as to which elements will be recorded, and these remain constant from one sample to the next.

## Habitat Survey

In order to understand the social nature of chimpanzee behaviour, it is necessary to understand the environment in which they live. To integrate this study with others conducted under the auspices of the Budongo Forest Project, and to enable comparison with other studies of chimpanzees, various ecological data were collected.

The habitat used by the chimpanzees was recorded during instantaneous scan sampling, as described above. In this section I introduce methods used to collect independent data on the availability of different habitat types. Details concerning the implementation of these methods can be found in Chapter 6.

### *Methods*

Two standard techniques were used to asses habitat availability, point sampling and line transect sampling. Point sampling is the methodology of choice here, although it has the serious drawback of requiring that large number of points be sampled, with the points sampled specified entirely at random. Point sampling most closely replicates the sampling of habitat used, collected during the systematic scan samples.

In order to check the validity of the results produced by any one method, an alternate method of sampling aimed at answering the same question can be used. With forest wide sampling of available habitat using the line transect method (Plumptre and Reynolds, 1994), the second technique chosen was line transect sampling, a systematic method of sampling which involves sampling at intervals along a line, the transect. If care is taken with the placement of transect lines, this approach becomes equivalent to *systematic* point sampling. It has the advantage that it is much quicker than random point sampling, and in addition it is much easier to revisit precise locations should this prove desirable (for example to confirm the identification of a particular species, or for phenological studies).

To classify habitat type, variables thought likely to be important to chimpanzees were recorded: forest type, topography (slope) and visibility at ‘chimp height’ (standardised to 1m). Forest type was determined by the presence/absence of particular tree species, and their relative abundance within the sample. Details are given in Chapter 6.

## Other Sources of Data

Ancillary data were provided by A. J. Plumptre, and by the Budongo Forest Project. Rainfall data were collected at dawn each day in the center of the research camp clearing. Daily minimum and maximum (shade) temperatures were also collected at the research camp. Detailed forest ecology studies were conducted by A. J. Plumptre; his coding of plant species is used here with permission. Chimpanzee sightings collected by Budongo Forest Project field assistants were to a limited extent incorporated into ranging data sets, although in general these location data were not sufficiently precise to allow their inclusion. In addition, data on female menstrual cycles were combined to get a clearer picture of the availability of potential mates.

## STATISTICAL DATA ANALYSIS

Details of specific statistical techniques can be found in the relevant chapters. Both parametric and non-parametric techniques are used. All statistical tests were two-tailed, with $\alpha = 0.05$, except were stated otherwise. Observed frequencies of interactions are appended to the body of the thesis.

Before using parametric techniques the degree to which the sample approximated a normal distribution was assessed by visual inspection of histograms and probability plots, and by the use of a test for skewness presented by Snedecor & Cochran (1980). This test divides skew by the standard error of the skew to determine the degree to which the tested distribution is skewed from normal. Values of 1.96 or less are considered to come from approximately normal distributions if at least 150 samples are included. This is the Cox test described by Mascie-Taylor (1994). For smaller samples, the table of values in Snedecor & Cochran (1980) was used. Parametric techniques were only used where the necessary assumptions be met—if necessary by using transformed data. Averages of normally distributed data are presented as ‘mean ± standard deviation’.

Non-parametric techniques were used where such assumptions could not be met. Average values of skewed data distributions are presented as median and (total) range, except when inter-quartile range is stated.

The majority of the analyses were conducted using SPSS for Windows™ version 6.0. Microsoft Excel™ version 5.0 was used for limited data analysis, as were computer programs presented in Neave & Worthington (1988) and Siegel & Castellan (1988). Other general statistical texts used were Sokal & Rohlf (1981) and Snedecor and Cochran (1980). Ranging patterns (Chapter 6) were analysed using the Ranges V suite of programs (Kenward and Hodder, 1996). Matrix permutation tests, introduced in Chapter 4, were computed using a program written by Hemelrijk (1990). This program was limited in that it would not accept decimal numbers; data had to be scaled to circumvent this problem. This did not influence the outcome of the tests, but did result in absolutely large values of the Z & R statistics (see Chapter 4). Regressions using the Mantel statistic were calculated using the Excel spreadsheet.

# Chapter 4

# SOCIAL STATUS

> *"Oldcastle quickly hatched a plot to overthrow the government, and instructed his followers...The plan was to kidnap the king and his brothers at Eltham on Twelfth Night, seize the capital, and, apparently, to depose the existing hierarchy of king, magnates, and prelates. The rising, of course, failed miserably."*
>
> *E. Powell, The Restoration of Law and Order, 1985.*

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## INTRODUCTION

Group living, whether for reasons of resource defence, predation, mating or infant care, either singly or in combination, imposes costs. Competition for access to resources, such as food and mates, can lead to increased levels of aggression between members of the group, and favour the evolution of mechanisms, or strategies, to reduce the costs incurred by each individual of such competition. Where competition is predominantly 'contest' or 'interference' competition (Milinski & Parker, 1991), one 'cost-reducing' mechanism is social dominance: a series of relationships which enable each individual to predict the outcome of contests with each of the others within the group, and thus resolve contests without resorting to energetically expensive or risky agonistic interactions.

Social dominance is essentially a series of dyadic relationships, in which the individual with the higher probability of winning any contest (the *dominant* individual) is able to acquire the contested resource with only a minimum expenditure of time and energy, while the individual with the lower probability of winning (the *subordinate* individual), avoids wasting both time and energy in a contest it is likely to loose. Both members of the dyad avoid the risk of injury, which is likely to be greater for the subordinate.

The extent to which a dominant-subordinate relationship is respected depends on the difference in the probabilities of winning a contest, which in turn depends on the value of the resource in question to each individual, and also the inherent power, or resource holding potential ('RHP': Parker, 1974), of each. A dominant individual need not win every interaction; the degree to which the relationship is expressed will depend on the value of the resource (Dunbar, 1988a).

Classically, dominance thus defined refers to 'agonistic dominance' (Maslow, 1937; Bernstein, 1981; Walters & Seyfarth, 1987; Mason, 1993), and the emphasis is very much on strength and fighting ability. What is key, however, is the relative probability of winning, *regardless of the means used.* Behavioural strategies are at least as important as physical strength, and the best course may well depend on what everyone else is doing (Milinski & Parker, 1991): investing time and energy in affiliative interactions may also secure the desired resource.

From a multitude of studies (reviewed by: Bernstein, 1981; Walters & Seyfarth, 1987) it seems that as a general principle the dominance relationships between all members of a group tend to resolve into a dominance hierarchy of some kind, with individuals ranked relative to one another. The position of an individual within a dominance hierarchy is often referred to as its ‘dominance rank’ or ‘dominance status’.

Dominance, however, is a property of inter-individual, dyadic, relationships (Hinde, 1976, 1978), while social position is an element of group-level structure. Describing an animal’s relative position within a group, its status or rank, as ‘dominance’ confuses two distinct phenomena. In effect it makes the *a priori* decision that social position is simply the sum of all (agonistic) dominance relationships (Dunbar, 1988a). While this may indeed prove to be the case, it precludes other possibilities. In complex social systems, it is likely that more than simply an individual’s relative agonistic ability determines social position.

Rowell (1966, 1974) has suggested that dominance hierarchies are maintained largely by the behaviour of subordinates, an idea deWaal (1982) has applied to female chimpanzees, stating the hierarchy was maintained by “respect from below”. Rowell’s (1966) argument is that while high ranking animals initiate interactions, it is the response of subordinates (primarily, avoiding the other’s approach) which determines their outcome.

A relationship emerges through a series of interactions (Hinde, 1976**)**, and, as a dyadic phenomenon, is a result of the behaviour of both partners, whether that be active or passive. Ascribing the structure which emerges from these relationships as the result of the behaviour of only half of each dyad is meaningless. Rowell’s (1974) “subordinance hierarchy” explanation also implies a categorical, static, social structure, and while it may be adequate during periods of social stability, is unable to explain behaviour of individuals during periods of change. When individuals show evidence of striving for social position, as seem the case in male chimpanzees, the “subordinate hierarchy” explanation is insufficient. While it may be adequate for established female chimpanzee hierarchies, its relevance for their formation has been questioned (Goodall, 1986).

The terms ‘rank’ and ‘status’ are not themselves synonymous, although ‘rank’ has been used, sometimes interchangeably with ‘status’, to describe social position, for example: ‘low’ ranking (Bygott, 1979; Nishida, 1983; Goodall, 1986), ‘high’ status (Simpson, 1973; Coelho et al., 1983).

Status is an individual’s position in relation to others within the social group, a description of an individual’s location within ‘social space’. Any particular status is, at least potentially, not unique: while each individual will occupy a unique position in ‘social space’, these locations may be close enough to ascribe functionally equivalent status to each individual. Status is thus determined multidimensionally, by more than one independent criterion. Rank is a unique position in relation to other members of the social group determined by a single criterion. It is thus possible to rank animals using the combination of factors determining their status (see, for example, Richards, 1974). What often happens, however, is that only a single factor, such as agonistic ability, is used to rank animals, with rank then simply substituting for ‘the sum of agonistic dominance’ as a descriptor.

If a number of animals have functionally similar social positions—they are very similar in status—then it becomes meaningful to talk about status levels. An individual’s precise status, measured multidimensionally, may fluctuate over time within a particular status level, without necessarily altering that individual’s functional status. Such fluctuations are unlikely to affect the status of any other individual within the group. It is also possible for an individual to move between status levels, which may or may not alter other individuals’ status. In either case, however, were the animals to be ranked, a change which leads to an individual shifting to a new rank will alter the ranks of all those either below or above the new rank, depending on the direction of the change, regardless of whether the animal actually occupies a new social position. Only in relatively small, stable groups, where ‘position in society’ is determined, as opposed to being measured, by a single criterion, will rank and status be indistinguishable.

This use of rank to describe social position has led to questions concerning the meaning of a particular rank position to an individual (Bernstein, 1981). What is the real difference between being ranked 13th or 14th in a group of thirty individuals? The problem here lies in the use of only a single criterion to describe social position, and particularly the use of ordinal measures of rank.

Ordinal ranking has the unavoidable consequence of creating a rank order which suggests the difference between each pair of adjacent ranks is similar, whether individuals are ranked 2nd and 3rd, or 21st and 22nd. It also conflates the ideas of transitivity and linearity. Transitivity exists if there are no circular relationships. Thus if individual A is dominant to individual B, and B dominates C, then A will dominate C. More crucially, this result is predictable without the need for a contest. Linearity is only present if the distance between ranks is equal for each adjacent pair of individuals.

Linearity requires transitivity, but the reverse does not apply. The use of cardinal ranks (Boyd and Silk, 1983) circumvents these problems, retaining information about the degree of difference between different ranks. With such information it becomes possible to determine whether all rank differences are equal, or whether ranks ‘group’, such that it is the gaps between ranks which are meaningful.

There is, as Rowell (1966) realised, a very real sense in which the individual’s position within its social group is determined as much by its own behaviour towards those to whom it is subordinate as by the behaviour of dominant individuals. It may be that the subordinate’s behaviour is elicited by the agonistic dominance of others, and thus cannot be regarded as a separate descriptor of status. This may be the case in many groups of social mammals (Ungulates: Clutton-Brock et al., 1982; Eccles & Shackleton, 1986; Fournier & Festa-Bianchet, 1995; Pinnipeds: Haley et al., 1994; Rodents: Herrera & Macdonald, 1993), although the issue is more complicated where there is assessment of agonistic ability and active subordinate behaviour without challenge (for example Canids: Fox & Bekoff, 1975; Bradshaw & Nott, 1995).

Where subordinates actively ‘confirm’ another’s higher status, perhaps by initiating subordinance-dominance interactions, it is meaningful to view status as conferred by others as well as the individual’s own ability to dominate. This additional component, for want of a better term, can be called ‘conferred respect’. This term is appropriate, as ‘respect’ is a component of an individual’s status, determined by the *behaviour* of others in the social group. It leaves open the issue of whether the relationship is represented cognitively, such that individuals perceive others to have particular social positions.

Respect in chimpanzees differs from the “avoidance” shown by Rowell’s baboons, in that it is an active behaviour directed *towards* superiors, and is demonstrably *not* the result of individuals being cautious or misinterpreting the behaviour of dominant animals. Status relationships are determined by the behaviour of both individuals in each dyad, with ‘respect’ a component contributed by subordinates. It seems likely, given the evidence of cognitive ability demonstrated by wild and captive chimpanzees (see Savage-Rumbaugh & Lewin, 1994; Byrne, 1995a, for reviews), that they are in fact *attributing* particular levels of status to members of their social group. They may in fact be attaching a ‘status label’ to a mental representation of each group member, and using this mental representation to guide the expression of their subordinate behaviour, rather than responding to some cue from the more ‘dominant’ animal.

In chimpanzees, it is both possible and practical to rank individuals by agonistic dominance criteria, and by ‘conferred respect’, as the data required for each are distinct. The ‘pant-grunt/pant-bark’ graded vocalisation (Goodall, 1986), referred to as the ‘rapid oh-oh’ vocalisation by those working at Arnhem (deWaal, 1982; Hemelrijk, 1990), is described as a strictly unidirectional behaviour, given by 'inferior' animals to their 'superiors' (Goodall, 1986; van Hooff, 1974). Inferior animals are defined as those that acknowledge, through their behaviour, another's higher social position. Conversely, superiors are those whose position is acknowledged by others. As with dominance, superior-inferior classifications are properties of inter-individual relationships.

Pant-grunting has been referred to as a greeting (deWaal, 1982; Goodall, 1986), and amongst wild chimpanzees, individuals will give pant-grunt vocalisations spontaneously to others (personal observation) apparently as a means of expressing subordinate status, or 'showing respect' (Goodall, 1986). Pant-grunts do not appear to be submissive vocalisations given as direct response to threats or other agonistic behaviour, with 'squeaks' and 'screams' being given in these circumstances (Bygott, 1979; Goodall, 1986). The majority of pant-grunt vocalisations are given by females and young males to adult males, and pant-grunt vocalisations between adult males, although rare, have been used to determine which male is the undisputed alpha (Bygott, 1979; Goodall, 1986; Takahata, 1990), a position which carries reproductive advantages (Tutin, 1979, 1980; Hasegawa & Hiraiwa-Hasegawa, 1983; Nishida, 1983; Nishida & Hosaka, 1996).

It would appear that chimpanzees are conferring a higher status upon those to whom they pant-grunt. A cardinal ranking of individuals can therefore be constructed for the conferred respect component, or dimension, of status using the direction and frequency of pant-grunts. Agonistic dominance rank can be determined by the direction and number of agonistic interactions. Other studies of male chimpanzees have invariably found 'dominance' hierarchies, although these have only proved to be linear where the number of adult males was small (Nishida & Hosaka, 1996).

Chimpanzee males seem highly motivated to acquire high status (Goodall, 1973, 1986; Nishida, 1983). With resource holding potential determining one component of status, it becomes interesting to assess the relationships between status, size, and age. For status-striving behaviour to have arisen and be maintained through natural selection, it must confer some fitness benefit. Two of the most fundamental aspects of an animal's biology are access to food and access to mates. As a preliminary step in assessing the functional benefits associated with striving for high status, I shall test the following hypotheses:

| | |
|---|---|
| Hypothesis 1: | Status is a means of acquiring a greater proportion of copulations, a proximate correlate to fitness. |
| *Prediction*: | A positive correlation between status and number of copulations |
| Hypothesis 2: | Status is a means of gaining access to food resources. Assuming food requirements are relatively equal between adult males, |

preferential access to foods should result in less time being needed for foraging. Adolescent males are likely to differ from adult males in their nutritional demands (Pusey, 1990) and this needs to be controlled for.

*Prediction*: A negative correlation between status and proportion of time spent foraging.

Dominance is only one component of the total relationship between two individuals (Hinde, 1978; Dunbar, 1988a), and while dominance has been found to be important in chimpanzee society (Nishida, 1983; Uehara et al., 1994; Bygott, 1979; Goodall, 1986), relationships as a whole are clearly far more complex. Male chimpanzees within a single community have both affiliative and agonistic relationships with each other, and it is conceivable that both influence social status. Alternatively, affiliative relations and relative status may be independent components of a dyadic relationship. It is therefore important to investigate the interaction between status and affiliative behaviour (see Hill & van Hooff, 1994).

Seyfarth (1977) proposed a model of grooming in female monkeys in which grooming is directed from lower to higher ranking individuals, with the majority of grooming occurring between monkeys of adjacent ranks (see also Hemelrijk, 1996). At least some male monkeys also preferentially groom higher ranking individuals (Silk, 1994).

Simpson (1973) found that for male chimpanzees in the feeding area of Gombe National Park, higher-ranking individuals were groomed more frequently, and, when the anomalous individual ‘Goliath’ was excluded, for longer. Bygott (1979), however, studying the same population, concluded that individuals preferentially groomed older males “at least as much as dominant males”. This leads to the first hypothesis regarding the way affiliative interactions are distributed in relation to dominance or status interactions:

Hypothesis 1: Affiliative behaviour is closely tied to relative status, such that high status males are more attractive social partners, and so attract more affiliative behaviour.

*Prediction*: A positive correlation between status and receipt of affiliative behaviour.

Simpson (1973) also found that high ranking males were more affiliative, in that they groomed more frequently. In light of contrary observations concerning the direction of grooming, it is of interest to examine whether higher status Sonso chimpanzees are more affiliative, using both grooming and ‘joining’ as indicators of an affiliative relationship:

Hypothesis 2: Status determines the frequency at which affiliative behaviour patterns are performed, with higher status males being more affiliative.

*Prediction*: A positive correlation between status and performance of affiliative behaviours.

Chimpanzees are often described as having preferred partners for affiliative interactions, and grooming in particular has been singled out as a behaviour often used tactically (for example, deWaal, 1982; Nishida, 1983; Koyama & Dunbar, 1996). Some affiliative behaviour may be directed towards older or higher ranking individual, while some is towards other potential allies or long standing friends. In light of this, the distribution of affiliative behaviours within a group would not be expected to be directly related to dominance:

Hypothesis 3: As a separate component of relationships, affiliative behaviour is reciprocated between particular dyads in a manner unrelated to social status.

*Prediction*: A positive correlation between affiliative interactions received and affiliative interactions performed.

Hypothesis 4: Grooming (the largest component of affiliative behaviour) between males is reciprocated.

*Prediction*: A positive correlation between grooming received and performed.

# METHODS

## Data Collection

Details of the study site and population are to be found in Chapter 2. All 12 adult males and three adolescents were included in these analyses. General methodological details are given in Chapter 3. For the analyses presented here I used primarily data from focal animal samples, together with some *ad libitum* observations. During focal samples, agonistic behaviours, pant-grunt vocalisations, and affiliative behaviours performed or received by the focal or his nearest neighbour were recorded, as were those of other individuals in the vicinity of the focal—those that he could potentially have observed. *Ad libitum* observations, of occurrence and directionality, contributed to each of these categories, although primarily to observations of pant-grunts.

Five behaviours were lumped together as ‘agonistic’:

- threats
- displacements/supplants
- displays
- attacks
- chases

Two were lumped as ‘affiliative’:

- grooming
- joining

For each behaviour the total number of interactions between each individual and each of the 14 potential partners was recorded.

For most agonistic interactions, a winner and looser were clear, in that the interaction was unidirectional. Usually one individual would perform an agonistic act, and the recipient would back away displaying a fear grin, scream or run. Very few cases of retaliation were observed, although if retaliation did occur the interaction would snowball as more individuals became involved.

For many, perhaps the majority, of such escalating agonistic interactions, limited visibility made it impossible to keep track of the interactions and to identify a winner. The outcomes of a number of agonistic interactions were thus missed because of dense vegetation. For the purposes of this study, the agonist was defined as the winner (see Samuels et al., 1984), except in instances where retaliation occurred and the winner, either agonist or retaliator, could be clearly confirmed.

Affiliative interactions were grooming and ‘joining’. A single grooming bout was any episode of grooming in which interruptions were less than one minute. Interruptions or breaks, of one minute or greater, marked the end of each bout. Each grooming bout in which an individual groomed was classified as a single interaction. ‘Joining’ was the affiliative equivalent of a supplant; one individual moved to within two metres of another, who did not move away.

## Data Analysis

The inclusion of *ad lib.* records prevented the use of individuals’ ‘focal time’ to correct interaction data for different amounts of observation. Total time for which individuals were observed, the number of 15 minute scan samples in which each individual was present, was used to take into account differing degrees of observation.

Frequencies of interactions were corrected for observation time in two ways: ‘actor correction’ and ‘dyad correction’. In the former, the sum of each dyadic interaction was divided by the total number of scan samples for which the actor was present. In the latter, each was divided by the number of samples for which the respective dyad existed. These corrected figures were multiplied by a constant to produce an integer. For actor correction, this constant was the total number of scans for which the most heavily sampled individual was observed (DN: 2134 scans). The dyad corrected data were multiplied by the number of scan samples for which the most common dyad existed (DN-VN: 1195 scans).

The resulting scores became, in effect, predicted values for frequency of interaction. That is, the correction provided a prediction of the number of interactions the actor would have had with each partner, *if* he been sampled as much as the most commonly observed individual, or dyad. The dyadic correction is the more preferable, as it corrects for differential sightings of both actor and recipient. In the following analysis, observed frequencies transformed by the dyadic correction method are used unless stated otherwise. Data were summed over the entire 15 month period of data collection, and also analysed separately by three and six month blocks for 1995 to investigate changes over time.

Although a variety of methods exist for ranking individuals, I followed the method used by Fournier and Festa-Bianchet (1995), and calculated ratios based on win/loss or received/given criteria, depending on which behaviour formed the basis of the ranking. The use of a ratio allows rank to be based on behaviour both given and received. For agonistic dominance, the ratio used was: Rank = (wins+1) / (losses+1). For conferred respect the ratio became: Rank = (pant-grunts received+1) / (pant-grunts given+1).

To check the validity of the agonistic interactions and pant-grunts for the assigning of social ranks, I used matrix correlation tests (see Dietz, 1983) presented by Hemelrijk (1990). These tests compare an ‘actor’ matrix, in which the acts performed by each individual occupy a separate row, with a ‘receiver’ matrix, in which the acts received by each individual occupy a separate row. For both matrices, the columns represent the individuals to whom (actor matrix), and from whom (receiver matrix), acts are directed or received, respectively. To achieve a meaningful ranking of social status the behavioural criteria should be generally unidirectional—if acts are reciprocated then the *direction* of those acts cannot be used to rank one individual over another, although *quantitative* measures may still be used.

The issue of interest is whether the behaviour pattern is unidirectional: this occurs when a behaviour pattern is not reciprocated. The appropriate test is for ‘qualitative reciprocation’, unidirectionality being demonstrated by a significant *negative* correlation. A modified Mantel $Z$ test, referred to as the $R_r$ test by Hemelrijk (*ibid*.), or Hemelrijk’s own $K_r$ test, both of which test for correlations within rows of the matrices can be used, correlating an actor matrix with interactions scored as either 1 or 0 (i.e. present or absent) with a receiver matrix similarly coded. The $K_r$ test is analogous in the way it describes associations to Kendall’s $\tau$ (Dietz, 1983), and to interpret the strength of the correlation the $K_r$ statistic can be converted to a $\tau$ value by correcting for sample size and tied values (Hemelrijk, 1990).

These tests are appropriate because they are ‘distribution free’, and as such do not assume independence of data; an assumption not met by data within interaction matrices. Testing within rows allows for individual variation, such that individuals with particularly high or low propensities to perform a particular behaviour do not bias the results. Using the ‘quadratic assignment method’ random permutations of the matrices are generated, and for each permutation the test statistic generated. With sufficient numbers of permutations this produces a distribution of the test statistic, against which the significance of the statistic calculated for the original matrices can be judged (Adams & Anthony, 1996).

Such permutation tests are becoming more popular in biological studies (for example: Dietz 1983; Schnell et al., 1985; White & Burgman, 1990; Cole, 1996; Hemelrijk, 1996) The randomly generated distribution approximates to the population distribution, assuming the sample is in some way representative of the population (Manly, 1991), and thus testing against it is legitimate (Adams & Anthony, 1996). The tests presented by Hemelrijk (1990) are designed to test hypotheses about the interchange or reciprocation of behaviours, and probabilities are one-tailed. The right-hand tail of the distribution gives the probability of a significant positive correlation, while the left-hand tail represents a negative relationship the opposite of reciprocation—unidirectionality (Hemelrijk, 1990). Following the recommendation of Adams & Anthony (1996), 5000 permutations were used for each of these tests. When using these tests to investigate two-tailed hypotheses with $\alpha = 0.05$, results were considered significant if the one-tailed probability was less than or equal to 0.025.

A second method of determining social rank is based on the proportion of individuals dominated. Dominance value (DV) is the square root, arcsine transformation of this proportion: $DV = \text{arcsine}(\sqrt{x})$ (Fournier & Festna-Bianchet, 1995; Beilharz & Mylrea, 1963). This second method was used to provide comparable ranking to two biologically meaningful ways of classifying ‘respect’: the number of individuals pant-grunting *to* the subject (the number conferring respect), and the number of individuals *to whom* the subject pant-grunts (the number whose superiority the subject acknowledges). These two measures of dominance rank were compared using a Spearman's rank correlation test.

The agreement between the two conceptually distinct components of status was tested by correlating agonistic dominance ranks and conferred respect ranks, to assess the validity of combining the measures. One way to produce a combined 'status' interaction matrix is to sum uncorrected frequencies for both agonistic and pant-grunt interactions for each dyad, and then transform this matrix using the dyadic correction method. Interactions are combined such that pant-grunts received are combined with agonistic behaviours performed. This has the potential to produce distorted results, however, as it rates pant-grunts and agonistic interactions as equal in determining status, and crucially, rates an agonistic act by a normally subordinate animal to a normally more dominant animal equal to a reversal in the direction of pant-grunting. To circumvent this problem, a status ratio, termed the 'status score', was calculated by adding the two component ratios (for agonistic dominance and conferred respect) together. This assumes that neither component carries more weight than the other.

I used tests devised by Appleby (1983) to test the assumption that the rank orders constituted a generally transitive hierarchy. Particular ordering of the data can impose hierarchies where these do not naturally exist. Kendall's test derives a $\chi^2$ value to asses whether the observed transitivity is statistically significant—that is, occurs more often than would be expected by chance—by counting the number of circular (intransitive) triads within a group of known size. The test can be performed with incomplete data sets, although this has the effect of increasing the number of possible circular triads and thus decreasing the likelihood of finding statistically significant transitivity.

The degree of transitivity, which for an ordinal ranking is equivalent to the degree of linearity, is indicated by $K$, Kendall's 'coefficient of concordance'. This can vary from 1 (complete transitivity) to 0 (complete intransitivity). Incomplete data will produce lower values of $K$. Use of these procedures has shown it is impossible to produce a statistically significant transitive hierarchy for groups with fewer than 6 individuals; the probability of any particular hierarchy arising by chance is too great (Appleby, 1983).

The use of ordinal ranks discards a large amount of available data, and in itself imposes a linear structure onto a dominance hierarchy. The alternative is to use cardinal ranks which preserve information about the relative differences in status between individuals, and ideally, permit the use of parametric statistical tests (Boyd & Silk, 1983). A method for deriving normally distributed cardinal ranks is presented by Boyd & Silk (*ibid*), but they state this method is likely to be inappropriate for data with few reversals, such as those analysed here. An alternative is to use the values of the ratios derived from agonistic and pant-grunt interactions as ranks themselves. This has the disadvantage that the data are highly skewed from normal. This problem can be overcome by searching for a transformation of the data which reduces the skew and brings the distribution closer to normal. A second alternative is to use randomisation procedures (Adams & Anthony, 1996) such as the matrix correlation techniques described above on the corrected interaction data to examine relationships between behaviour patterns.

To investigate the question of the relative value of each status rank I used both approaches. A dual transformation of the data proved to be the most effective: natural logarithms of square-rooted data. I repeated the correlation between agonistic dominance and conferred respect for transformed data (cardinal ranks) using Pearson's correlation. To see whether the differently ranked individuals fell naturally into groups corresponding to general levels of status (*sensu* Bygott, 1979) I plotted, for each male, the difference between his status and that of the alpha male, to achieve a graphical representation of relative status. The number of males who recognise, by pant-grunting, an individual's status (subordinates), and the number whose status an individual recognises (superiors), are both good indicators of the view each chimpanzee has of the social structure of its community. Thus I examined the correlations between these measures, recalculated as dominance values, and social status (cardinal ranks), using Pearson's correlations.

To see if the relationship between pant-grunts and agonistic behaviour was one of direct interchange, I used the $K_r$ matrix correlation test with 5000 permutations, correlating the performance of agonistic acts with the receipt of pant-grunts. The $K_r$ correlation tests for 'relative' interchange of behaviour patterns. Relative interchange implies each individual ranks the other members of its social group according to the frequency with which it receives acts from them, and distributes its behaviour according to this ordinal ranking; individuals interact relatively more frequently with those with those who more frequently interact with them (Hemelrijk, 1990). Separate rankings may exist for each behaviour pattern. There is no assumption that the individuals keep track of the absolute level (frequency, duration) of interactions. The test can also be used to examine 'qualitative' interchange, looking simply at occurrence and non-occurrence of interchange, without regard to the number of interactions (Hemelrijk, *ibid*).

In this case, if direct interchange occurs at a relative level, individuals receive more pant-grunts from those they are more agonistic toward, which implies respect is the product of agonistic dominance. If interchange occurs at a qualitative level, individuals receive pant-grunts from those to whom they are agonistic, but there is no correlation between the frequency of agonistic behaviour and the frequency of receipt of pant-grunts. The implication is that individuals respect (i.e. pant-grunt to) individuals who tend to be agonistic. If so, treating pant-grunting and agonistic dominance as separate components of status would seem justifiable.

Testing the four hypotheses concerning the interaction between affiliative and dominance aspects of individual relationships was done using the same test, together with the Mantel $Z$ and $R$ tests. If a hypothesis of relative interchange is supported by the $K_r$ test, it is possible to test whether a significant degree of ‘absolute’ interchange occurs. Absolute reciprocity (interchange of the same behaviour: Bertram, 1982) occurs when each individual returns the same frequency of behaviour it receives from each of interaction partners. Absolute interchange occurs when either the same frequency or, where the behaviour patterns ‘exchanged’ differ in either their value or cost, a multiple of frequency, is returned.

Absolute levels of interchange can be tested for using the Mantel $Z$ test, which is essentially a generalised regression technique (Schnell et al., 1985). Regressing a matrix against its transposed form assesses the probability of significant symmetry in the matrix; a symmetrical matrix is one which is identical to its transposed form. If the actor matrix is symmetrical with the receiver matrix then interchange is absolute. A Mantel $Z$ test uses the values of each cell within each matrix, and as such is sensitive to the presence of outliers. It is also dependent on the scale of measurement (Dietz, 1983). The Mantel $R$ test is a non-parametric version of the $Z$ tests, in which cell values are replaced by within-matrix ranks (Dietz, *ibid*). Hemelrijk (1990) suggests that the $Z$ test be used to test for absolute interchange, supplemented by the $R$ test to overcome the deficiencies in the $Z$ test. Absolute interchange does not necessarily imply a directly proportional relationship between performance and receipt of directed behaviour.

Data on status interactions were sparse for the first three months of data collection, and so only data collected during 1995, divided into time blocks, were used to examine status changes over time. Data for agonistic interactions and pant-grunting were divided into two six-month, and four three-month blocks, and then corrected using the dyad correction method, accounting for the number of times each dyad was seen in that block. The scaling factor was chosen to permit comparisons between the two half-year blocks, and between the four three-month blocks. The appropriate fraction ($^2/_5$ & $^1/_5$ respectively) of the 15 month scaling factor (1195) was used (i.e. 478 for the six month blocks, 239 for the 3 month blocks). Agonistic dominance and conferred respect values were then generated in an identical manner to that used for the full data set, and summed to give status scores. These scores were then transformed to approximate normality, using the same transformation, to yield cardinal status ranks.

For the three and six-month time blocks there were many missing values in each of the interaction matrices, and so Appleby’s (1983) tests were not used. For each of the three month blocks a few individuals were not observed to interact over status and so it was impossible to determine status for those individuals that block. Status scores calculated for each of the three month, and six month, blocks were therefore used for descriptive purposes only.

Both size and age are potential determinates of agonistic rank and/or status and so I examined their influence on each. With only rough estimates for size and age, I performed limited correlational analyses. I classified males into four age categories (adult/old; adult/mature; adult/young; and adolescent) and five size categories (large; medium/large; medium; medium/small; small), and correlated these with agonistic dominance and social status. Size and age categories were assigned subjectively during fieldwork.

To investigate the possible benefits of high status, I examined the relationship between social status (cardinal ranks) and number of copulations (transformed for observation time using the dyadic correction), and between status (cardinal ranks) and proportion of time spent feeding. Proportion of time spent feeding was calculated for each of the fifteen males, lumping all feeding and foraging behaviour patterns (see Chapter 3 for definitions) within each individual, from behaviour recorded during scan sampling. Where an individual was recorded as being present, but no behaviour was recorded, the 'group activity' behaviour was substituted. As adults and adolescent males fall into two distinct age groups with their characteristic nutritional and social demands (Pusey, 1990), partial correlations, controlling for age group, were calculated.

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# RESULTS

## Dominance Hierarchy

In common with chimpanzees elsewhere, the Budongo chimpanzees showed clear dominance components to their relationships. Over the 15 month period for which data were collected, clear hierarchies existed for both agonistic dominance and conferred respect. Pant-grunting was demonstrably unidirectional (Matrix correlation: $K_r = -95$, $\tau = -0.35$, $p_l = 0.002$, n = 15). A similar analysis for agonistic interactions also demonstrated significant unidirectionality ($K_r = -75$, $\tau = -0.19$, $p_l = 0.016$, n = 15).

Hierarchies constructed using transformed interaction rates for agonistic encounters and pant-grunts (Figs. 4.1, 4.2) with individuals arranged according to the derived ratios were significantly non-random, and somewhat linear (transitive). For agonistic interactions, there were many missing values. Including all fifteen males, with the assumption that missing values could be replaced by an equal probability of either individual in each missing dyad being dominant, yielded a non-significant ($\chi^2 = 34.28$, *df*

= 23, $0.05 < p < 0.1$), non-linear (Kendall’s coefficient: $K = 0.299$) hierarchy.

| | VN | DN | BK | CH | MA | MG | JM | BY | KK | MU | NJ | ZF | TK | AY | ZT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| VN | X | | 2.50 | 2.52 | 7.41 | 8.88 | 11.09 | 9.93 | 9.35 | | 2.33 | | | 5.99 | |
| DN | 2.00 | X | 5.74 | 2.16 | 3.47 | 6.79 | 2.73 | 5.67 | 11.73 | 17.94 | | | | 6.39 | 11.60 |
| BK | | | X | 17.73 | 6.68 | 7.76 | | 7.91 | 8.20 | 4.98 | 9.68 | | | 4.30 | |
| CH | | 2.16 | | X | | | 9.45 | 2.69 | 2.92 | 4.67 | 5.38 | | 6.71 | | 6.42 |
| MA | 1.24 | | | | X | 1.69 | 3.39 | 1.59 | 3.29 | 4.54 | 2.54 | | | | |
| MG | | 2.72 | | | | X | 3.48 | | 3.96 | 6.32 | | 5.53 | | | |
| JM | | | | | | | X | | | 6.53 | | 6.04 | | 2.91 | |
| BY | | 1.42 | 5.28 | | | | | X | | | | | 8.85 | | |
| KK | | | | | | | 6.32 | | X | 3.50 | | | | | 4.76 |
| MU | | | | | | | | 7.29 | | X | | | | 2.91 | |
| NJ | | | | | | | | | 3.27 | | X | | | | |
| ZF | | | | | | | | | | | | X | | | |
| TK | | | | | | | | | | | | | X | | |
| AY | | | | | | | | | | | | | | X | |
| ZT | | | | | | | | | | | | | | | X |

**Figure 4.1**. Matrix of agonistic interactions. Individuals in rows are agonistic towards those in columns. The numbers are the dyad-corrected frequencies of interactions.

| | DN | VN | MG | BK | MA | JM | CH | BY | KK | NJ | MU | TK | ZT | AY | ZF |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DN | X | | 5.43 | 5.74 | 5.79 | 5.47 | 4.33 | 9.92 | 17.60 | 13.48 | 49.32 | | 19.34 | 31.95 | 15.32 |
| VN | | X | 3.55 | | 3.71 | 5.55 | 4.84 | 9.93 | 9.35 | 14.00 | 22.25 | 4.65 | 9.41 | 20.96 | 25.34 |
| MG | | | X | | | 3.48 | 3.14 | | 11.89 | 3.61 | 3.16 | 4.05 | 4.65 | 16.89 | 5.53 |
| BK | | | | X | 4.45 | 5.24 | 3.55 | 2.64 | | | 4.98 | 5.24 | | 4.30 | |
| MA | | | | | X | | 2.60 | 3.17 | | | 6.80 | 7.29 | 4.08 | 2.84 | 13.18 |
| JM | | | | | | X | | | | | | 8.07 | | 7.76 | 9.96 |
| CH | | | | | | | X | | | | 4.27 | | 6.42 | | |
| BY | | | | | | | | X | 1.92 | | | 4.43 | | | |
| KK | | | | | | | | | X | | 3.50 | 4.48 | | | |
| NJ | | | | | | | | | | X | 3.82 | | | | |
| MU | | | | | | | | | | | X | | | 2.91 | |
| TK | | | | | | | | | | | | X | | | |
| ZT | | | | | | | | | | | | | X | | |
| AY | | | | | | | | | | | | | | X | |
| ZF | | | | | | | | | | | | | | | X |

**Figure 4.2**. Matrix of pant-grunt interactions. Individuals in rows receive pant-grunts from those in columns. The numbers are the dyad-corrected frequencies of interactions.

The assumption that all missing values can be replaced thus is somewhat questionable. Adult male chimpanzees are normally capable of dominating all younger males and all females (Goodall, 1986), and Figure 4.1 shows no indication of agonistic dominance by these individuals over the adult males. Making the assumption that the adolescent males, together with the single adult male (TK) showing a similar lack of agonistic dominance and known to have ambiguous dominance relationships with adult females, are subordinate to all other adult males, is perhaps more realistic. This produced a highly significant ($\chi^2 = 90.11$, $df = 23$, $p << 0.0001$) and fairly linear hierarchy ($K = 0.85$). An alternative method for dealing with the problem of adolescent males and missing data, is to confine the analysis to the adult males only, which yielded similar, although less strongly significant, results ($K = 0.83$, $\chi^2 = 45.75$, $df = 21$, $0.001 < p << 0.01$).

Ranking males by pant-grunts produced a hierarchy of 'respect', and yielded a significantly non-random ($\chi^2 = 59.11$, $df = 23$, $p < 0.0001$) but not particularly linear ($K = 0.54$) hierarchy. This was likely to be due to a treatment of missing values, similar to that used above. Under the assumption that adolescent males are subordinate to all adult males, the hierarchy was both significantly non-random ($\chi^2 = 84.02$, $df = 23$, $p << 0.0001$), and fairly linear ($K = 0.79$). Examining only the adult males showed the hierarchy to be significant ($\chi^2 = 45.89$, $df = 21$, $0.001 < p << 0.01$), but not strongly linear ($K = 0.61$). The lack of transitivity is interesting, given that pant-grunting was significantly unidirectional (reversals in rank, in addition to missing values, reduce the value of Kendall's coefficient). This indicates that individuals were not acknowledging as superiors all of those to whom they would have been expected to pant-grunt, given that they pant-grunted to others of similar status. Some of an individual's acknowledged superiors may in fact pant-grunt to a male to whom the individual does not pant-grunt. Pant-grunts were seen in 58 of 210 male dyads (28%). Agonistic interactions were observed in 60 of 210 male dyads (29%).

Ordinal rankings for agonistic dominance and conferred respect were highly significantly correlated ($r_s = 0.97$, n = 15, $p < 0.001$; Fig. 4.3), as was the agreement between rank determined by win/loss ratios and by 'dominance value' (supordinates: $r_s = 0.94$, n = 15, $p < 0.001$; superiors: $r_s = 0.82$, n = 15, $p < 0.001$). Table 4.1 gives the combined status ranking for the 15 males, together with agonistic and respect ratios, rank by dominance value and by numbers of acknowledged 'superiors' and 'inferiors'.

Categorisation of individuals by age and size was only approximate. Within the adult males age and size are uncorrelated (adult males only: $r_s = 0.53$, n = 12, $p = 0.086$, ns.), although with the adolescents included the association between size and age categories is significant (all fifteen males: $r_s = 0.72$, n = 15, $p = 0.002$). Rank by status score is positively correlated with body size ($r_s = 0.80$, n = 15, $p = 0.001$), but not with age. This effect may have been due to adolescents being both small and subordinate. Removing them from the analysis reduces the strength and significance of the correlation (adult males only: $r_s = 0.64$, n = 12, $p = 0.01$). Size also correlates significantly with agonistic dominance (adult males only: $r_s = 0.63$, n = 12, $p = 0.03$).

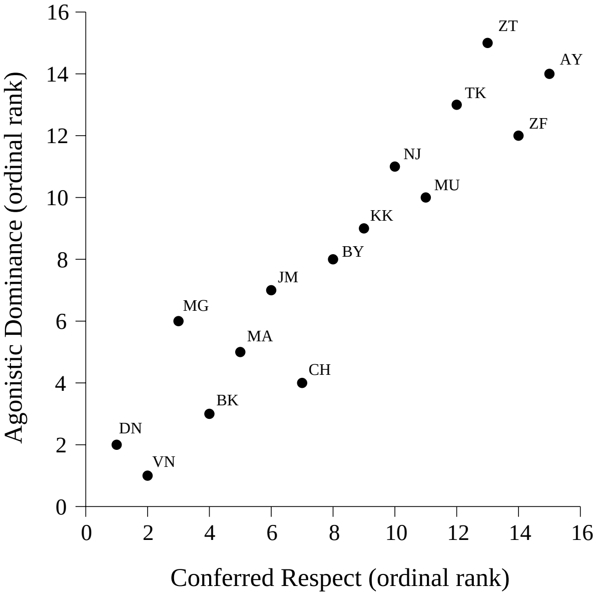

**Figure 4.3.** Relationship between ordinal rankings of agonistic dominance and conferred respect (pant-grunts). Low ranks are given high numbers. Letters indicate individual identity.

**Table 4.1.** Social status: Ordinal and cardinal rankings, with criteria used to define status.

| | Status Score | Status 'rank' | | Agonistic Dominance | Conferred Respect | Subordinates | | Superiors | |
|---|---|---|---|---|---|---|---|---|---|
| | | Ordinal | Cardinal | | | Number | DV | Number | DV |
| DN | 195.24 | 1 | 2.64 | 10.58 | 184.66 | 12 | 1.18 | 0 | 1.57 |
| VN | 147.90 | 2 | 2.50 | 14.36 | 133.54 | 12 | 1.18 | 0 | 1.57 |
| BK | 9.36 | 3 | 1.12 | 4.70 | 4.66 | 7 | 0.79 | 1 | 1.30 |
| MG | 6.54 | 4 | 0.94 | 0.83 | 5.71 | 9 | 0.93 | 2 | 1.18 |
| MA | 3.78 | 5 | 0.66 | 1.04 | 1.04 | 7 | 0.79 | 3 | 1.09 |
| CH | 2.38 | 6 | 0.43 | 1.78 | 0.60 | 2 | 0.39 | 5 | 0.93 |
| JM | 1.73 | 7 | 0.27 | 0.44 | 1.29 | 3 | 0.48 | 4 | 1.01 |
| BY | 0.70 | 8 | -0.18 | 0.42 | 0.28 | 2 | 0.39 | 4 | 1.01 |
| KK | 0.58 | 9 | -0.27 | 0.36 | 0.22 | 2 | 0.39 | 4 | 1.01 |
| NJ | 0.33 | 10 | -0.55 | 0.18 | 0.15 | 1 | 0.27 | 3 | 0.71 |
| MU | 0.27 | 11 | -0.65 | 0.23 | 0.04 | 1 | 0.27 | 8 | 1.09 |
| ZF | 0.09 | 12 | -1.20 | 0.08 | 0.01 | 0 | 0.00 | 5 | 0.93 |
| TK | 0.09 | 12 | -1.20 | 0.06 | 0.03 | 0 | 0.00 | 7 | 0.79 |
| ZT | 0.06 | 14 | -1.41 | 0.04 | 0.02 | 0 | 0.00 | 5 | 0.93 |
| AY | 0.05 | 15 | -1.47 | 0.04 | 0.01 | 0 | 0.00 | 7 | 0.78 |

**Agonistic Dominance** = { [ n(Ag. Int. won) × DC] + 1 } / { [ n(Ag. Int. lost) × DC] + 1 }

**Conferred Respect** = { [ n(Pgs. recieved) × DC ] + 1} / { [ n(Pgs. performed) × DC] + 1}

**Subordinates:** **Number** = n (individuals from whom pant grunts are recieved)
**DV** = Arcsine √ [ (*number of subordinates*) / ($N_i$-1) ]
**Superiors:** **Number** = n (individuals to whom pant grunts are given)
**DV** = Arcsine √ { [ ($N_i$-1) - (*number of superiors*) ] / ($N_i$-1) }

**Status:** **Score** = *Agonistic Dominance* + *Conferred Respect*
**Cardinal rank** = ln √ (*Status Score*)

*where: **Ag. Int.** = agonistic interaction, **Pgs.** = pant-grunts, **DC** = dyad correction (1195, see page 4.9), and* $\mathbf{N}_i$ *= total number of individuals in hierarchy (15, see page 4.8).*

## Relative Status

Ordinal and cardinal ranks for each male are shown in Table 4.1. The cardinal ranks were approximately normally distributed, as judged from histograms and the test for skewness (see Chapter 3). Correlating agonistic dominance and conferred respect using cardinal ranks showed again the highly significant, positive relationship (Pearson's correlation: $r = 0.95$, n = 15, $p < 0.001$; Fig. 4.4), with the males divided into four status groups (cf. Fig. 4.3).

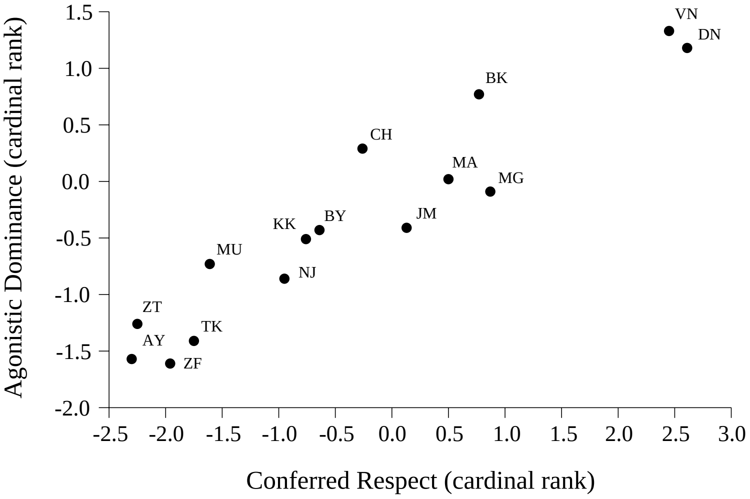

**Figure 4.4**. Relationship between cardinal rankings of agonistic dominance and conferred respect. Low ranks are given low numbers. Letters indicate individual identity.

A plot of differences in status (cardinal ranks: Fig. 4.5), showed clear division into three, and possibly four groups, the most obvious of which was that containing the two highest ranked males, DN and VN. On status scores they could be labelled alpha and beta respectively. However, the nominally beta male (VN) was *never* observed to pant-grunt to DN, despite this dyad having been the most heavily sampled. DN was able to displace/ supplant VN; however the reverse was not observed. The second obvious grouping lay at the other extreme of the status scale—the four most subordinate males. This group contained the three adolescent males, and also one of the oldest males, TK.

The remaining males fell into two groups. The first, of high to mid-ranking males, were distributed almost linearly, suggesting that it was among these five males that precise rank position—at least in relation to one another—was important. The fourth group contained four mid to low ranking males.

Number of subordinates, and number of superiors, transformed to approximately normal distributions, were highly significantly correlated both with each other, as one would expect ($r = 0.89$, n = 15, $p < 0.001$), and also with agonistic dominance (subordinates: $r = 0.78$, n = 15, $p = 0.001$; superiors: $r = 0.87$, n = 15, $p < 0.001$), conferred respect (subordinates: $r = 0.71$, n = 15, $p = 0.003$; superiors: $r = 0.81$, n = 15, $p < 0.001$), and the combined measure of social status (cardinal ranks: subordinates: $r =$

0.98, n = 15, $p < 0.001$; superiors: $r = 0.91$, n = 15, $p < 0.001$).

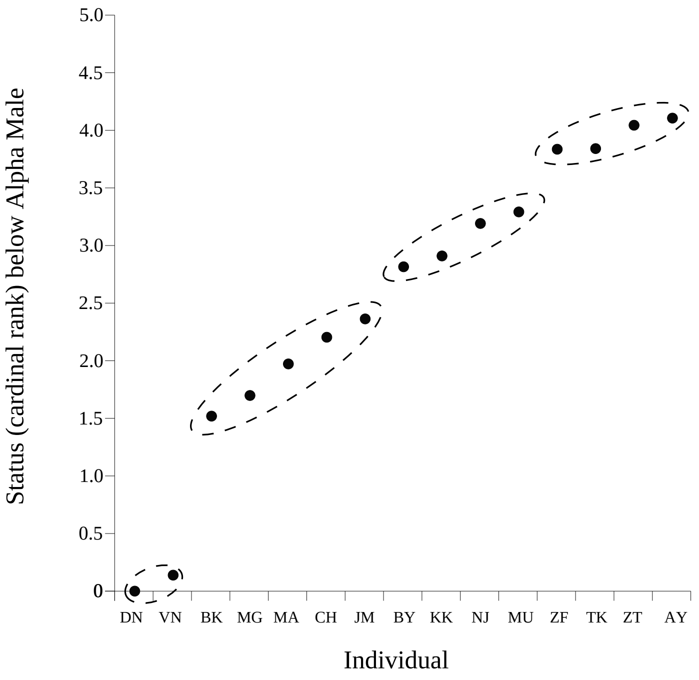

**Figure 4.5**. Plot of differences in status (cardinal ranks). Vertical distance betwen each pair of individuals represents the difference between them in status. Individuals fall into 4 status levels; within-level status differences are less than those between levels.

Plotting the number of subordinates (or the transformed value) against status, either as cardinal or ordinal rankings, revealed the same pattern (Fig. 4.6a): the five high to mid ranking males fell in two groups. This division was even clearer with the transformed data (dominance values: Fig 4.6b).

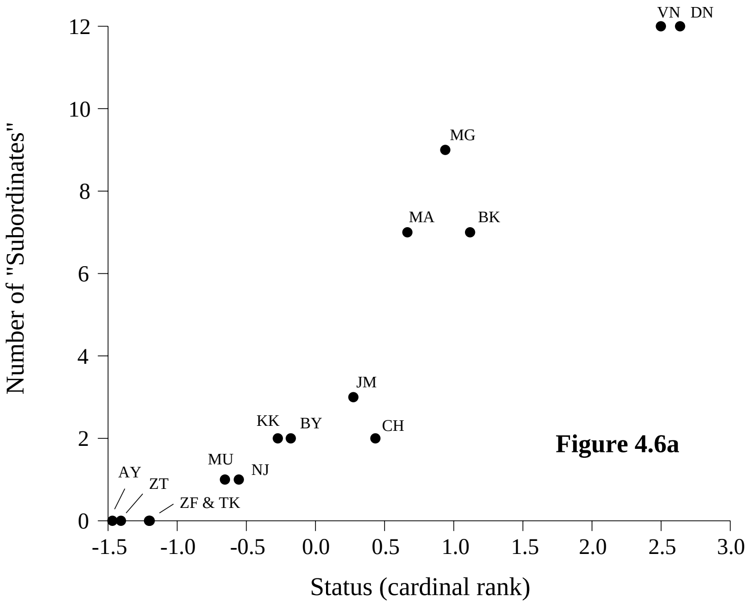

**Figure 4.6a**. Plot of number of subordinates, individuals to whom the male pant grunts, against status (cardinal rank). Males are separated into 4 groups.

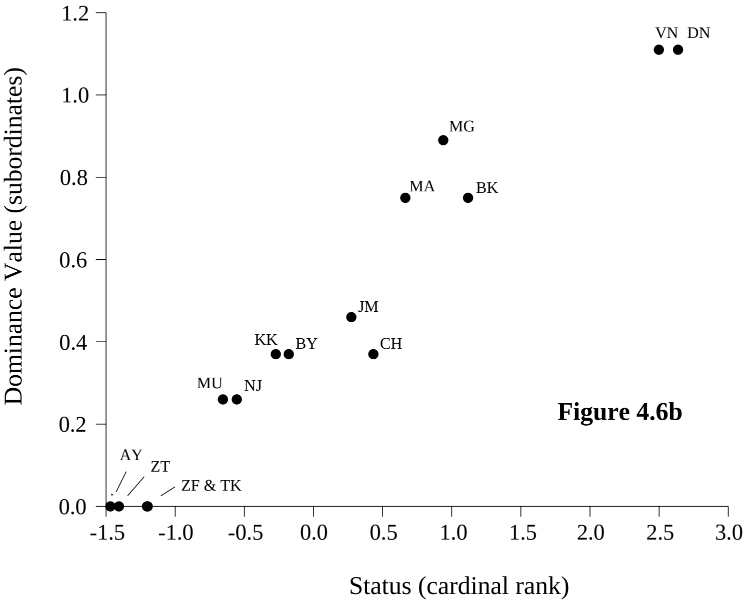

**Figure 4.6b**. Plot of number of subordinates, given as a dominance value, against status (cardinal rank). The four status groups are more clearly defined than in Fig 4.6a.

Looking at the number of superiors (Fig. 4.7) the division of the group of five males was again apparent; BY & KK 'regarded' their own status to be similar, while NJ 'refused' to acknowledge low status, pant-grunting to only three other individuals. BK acknowledged only DN as his superior, while MA acknowledged DN, VN, & BK. MG acknowledged only DN & VN, although agonistically subordinate to both MA & BK.

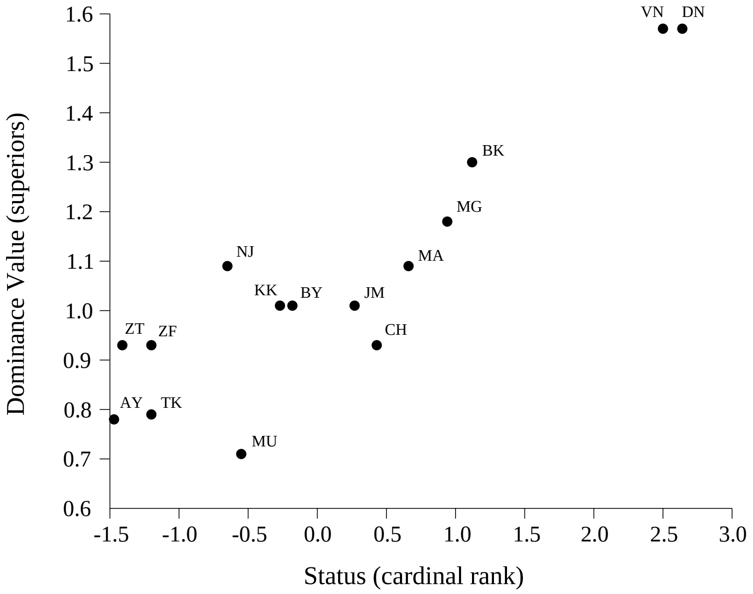

**Figure 4.7**. Plot of number of superiors, the individuals to whom each male pant-grunts, against status (cardinal rank).

Individuals who pant-grunted frequently tended to receive proportionally more agonistic acts (adult males only: $K_r$ = 121, $\tau$ = 0.36, n = 12, $p_r$ = 0.003), but individuals who were agonistic did not tend to receive respect (adult males only: $K_r$ = 40, $\tau$ = 0.16, n = 11, $p_r$ = 0.07). Adolescent males were excluded, as they have high frequencies of pant-grunting but perform no agonistic acts. The more general 'qualitative' interchange was also not significant (adult males only: $K_r$ = 28, $\tau$ = 0.20, n = 11, $p_r$ = 0.05, ns: Bonferroni correction, α = 0.025). Clearly some interchange did occur, as some males used a strategy of agonistic interaction to force respect from others (e.g. CH & BK in Fig. 4.4). The significance levels of the $K_r$ tests indicate it this was not a general strategy, however.

Scaling the cardinal ranks from Table 4.1 so that the lowest ranked individual was ranked ‘1’, with higher numbers indicating higher status, and correcting to one significant figure, yielded a number which described the individual’s status level. BK stood out as the lone member of status level 4 (Table 4.2).

**Table 4.2.** Relationship between ordinal and cardinal ranks, and possible status levels. Levels are calculated from cardinal ranks by scaling to remove negative values, and rounding to one significant figure. In the first column, high numbers equal high status; in the second, low numbers equal high status. BK’s status as gamma male is only clear by the fourth quarter of 1995 (see Fig. 4.10d).

| | Ordinal rank | Cardinal rank | Status level | Status description |
|---|---|---|---|---|
| DN | 1 | 2.64 | 5 | Alpha status |
| VN | 2 | 2.50 | 5 | Beta status |
| BK | 3 | 1.12 | 4 | Gamma / High status |
| MG | 4 | 0.94 | 3 | Mid status (high) |
| MA | 5 | 0.66 | 3 | Mid status (high) |
| CH | 6 | 0.43 | 3 | Mid status (low) |
| JM | 7 | 0.27 | 3 | Mid status (low) |
| BY | 8 | -0.18 | 2 | Low status (high) |
| KK | 9 | -0.27 | 2 | Low status (high) |
| NJ | 10 | -0.55 | 2 | Low status (low) |
| MU | 11 | -0.65 | 2 | Low status (low) |
| ZF | 12 | -1.20 | 1 | Very low status |
| TK | 12 | -1.20 | 1 | Very low status |
| ZT | 14 | -1.41 | 1 | Very low status |
| AY | 15 | -1.47 | 1 | Very low status |

## Changes Over Time

The status positions in Table 4.2 are summaries over a fifteen month period, and thus obscure changes during that time. Although the status levels seemed fairly robust, individuals moved from one status level to another with the result that it was difficult to ascribe meaningful status descriptions to at least some individuals. Status values (cardinal ranks) calculated for three and six month blocks showed status to be highly dynamic (Fig. 4.8). Within each block the number of status interactions observed is low, despite high sampling effort (see Chapter 3). As noted elsewhere (Hayaki et al., 1989) adult males seldom interact over status, possibly to maintain ambiguity in their status relationships (Hayaki et al. *ibid*). Dynamic trends are shown in Figure 4.8, with status values given in Table 4.3; for reasons given above, no statistics were calculated.

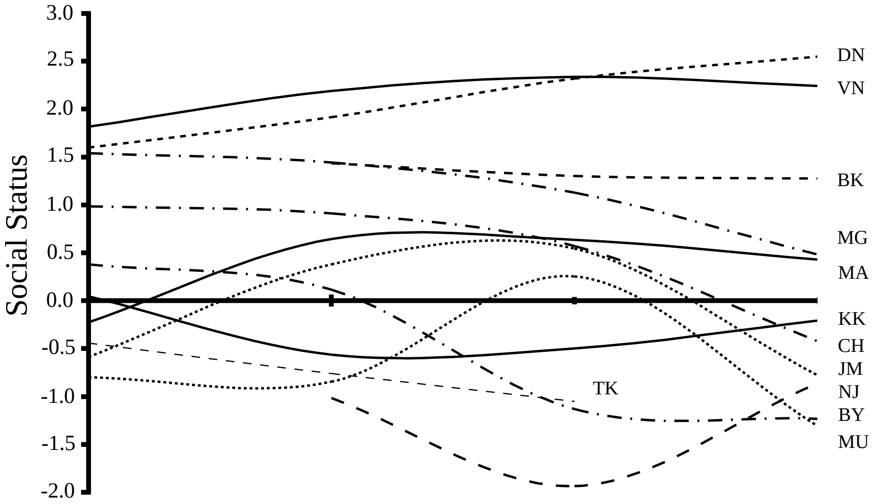

**Figure 4.8.** Smoothed plot of individual status trajectories over 1995. Plotted from values in Table 4.3, smoothed using Excel software.

**Table 4.3.** Changes in status over time. Status (cardinal ranks) for six and three month blocks, with data from 1995. Figures are corrected to three decimal places, and ordered according to cardinal ranks for the first half year. Status values are comparable between blocks of equal duration only.

| ID | Jan-Jun | Jul-Dec | Jan-Mar | Apr-Jun | Jul-Sep | Oct-Dec |
|---|---|---|---|---|---|---|
| DN | 2.153 | 2.798 | 1.597 | 1.916 | 2.319 | 2.547 |
| VN | 2.147 | 2.619 | 1.816 | 2.190 | 2.335 | 2.243 |
| MG | 1.129 | 0.870 | 1.540 | 1.444 | 1.130 | 0.482 |
| MA | 0.622 | 0.375 | -0.225 | 0.644 | 0.637 | 0.429 |
| CH | 0.340 | 0.232 | 0.984 | 0.912 | 0.570 | -0.424 |
| BK | 0.332 | 1.267 | no value | 1.435 | 1.302 | 1.275 |
| BY | 0.220 | -1.284 | 0.379 | 0.115 | -1.130 | -1.234 |
| KK | -0.164 | -0.363 | 0.044 | -0.563 | -0.499 | -0.207 |
| JM | -0.323 | 0.329 | -0.586 | 0.379 | 0.545 | -0.777 |
| NJ | -0.919 | -1.074 | no value | -1.017 | -1.936 | -0.862 |
| TK | -0.923 | -1.180 | -0.444 | -0.759 | -1.051 | no value |
| MU | -1.228 | -0.109 | -0.798 | -0.845 | 0.252 | -1.307 |
| ZT | -1.405 | -1.019 | -1.894 | -1.138 | -1.011 | -0.839 |
| AY | -1.922 | -1.564 | -1.112 | no value | -1.300 | -1.068 |
| ZF | no value | -1.248 | no value | -2.137 | -1.171 | -1.533 |

From one six month block to another, seven of the males fell in status and eight, including the three adolescents, rose. If functionally important status differences were those between status levels, the most interesting issue was the extent to which individuals move from one level to another. To examine this, differences in status (cardinal ranks) were plotted for each of the six month blocks (Fig. 4.9a,b) and each of the three month blocks (Fig. 4.10a-d). The most obvious change between the six month blocks was the strengthening of the alpha male position, reflected in the relative increase in status ‘distance’ between the alpha and other males. The other key events were the change in status of BK, from a mid to high status male, and the fall in status of BY, from mid to low status. Also falling in status were NJ and TK. The two young adolescents AY & ZF moved from a status level below the adult males, to the lowest status group incorporating the adults.

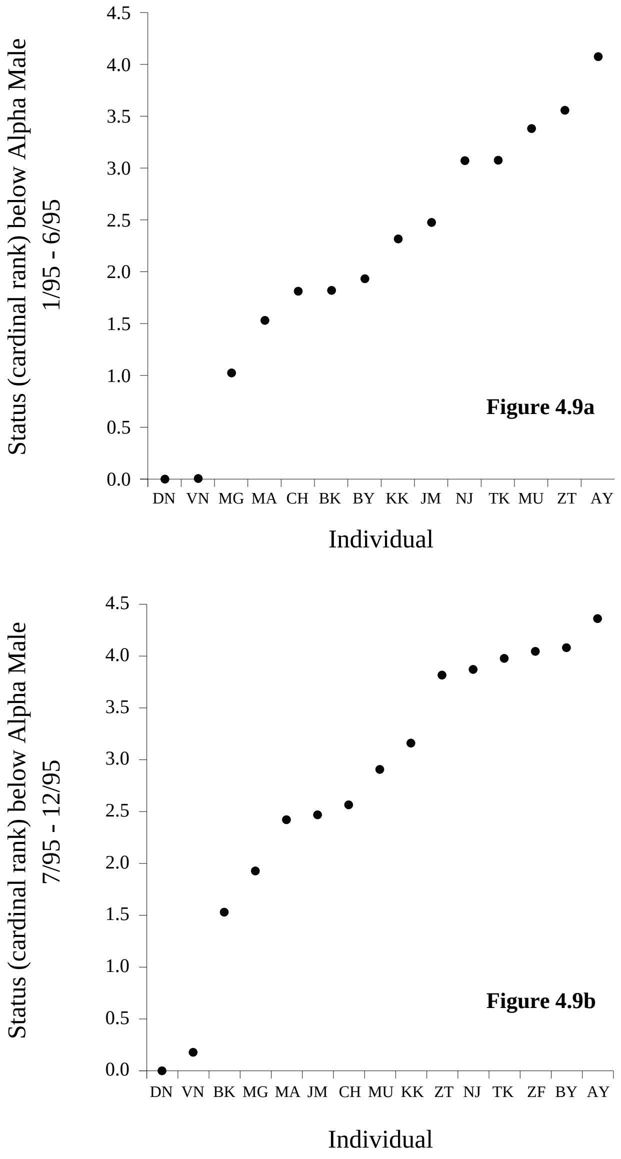

**Figure 4.9.** Plots of differences in status (cardinal ranks) for each half of 1995. Vertical separation represents the difference in status between individuals.

Plots of differences in status (cardinal ranks) for three month blocks revealed an interesting picture of complex status shifts. Caution was required in interpreting the figures, however, as the data from which they were calculated was sparse. In the first quarter (Fig 4.9a) the majority of males were relatively undifferentiated, and formed an approximately linear ranking. This may be an artifact, the result of sparse data, a particular problem for this time-block. More importantly, VN appeared as the nominal alpha male, although he, DN and MG shared the same status level, and no clear alpha could be distinguished. CH and BY were the closest in status to this group, with CH clearly of high status.

This changed in the second quarter as BY and CH began to drop in status. Three levels of status were clearly distinguishable: high, medium and low. CH and BY were in the mid-status group, BK joined VN, DN and MG in the high status group. VN began to strengthen his nominal alpha position, and MG began to fall away. By the third quarter, VN and DN were clearly established as an alpha and beta pair, with no clear status distance between them. BK surpassed MG in the high status grouping, and BY dropped considerably to join the low status males.

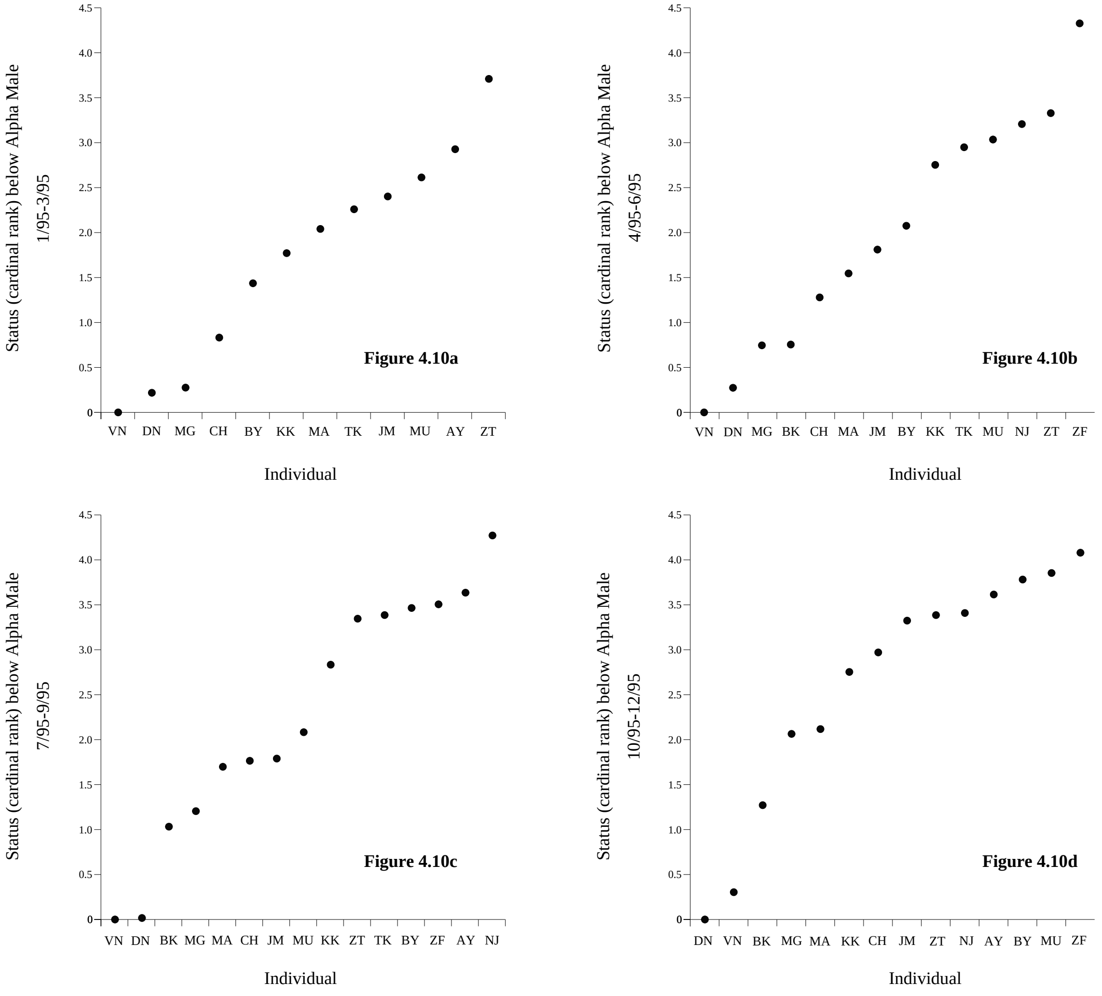

**Figure 4.10a-d.** Plots of differences in status (cardinal ranks) for each of the four quarters of 1995. a) no clear alpha male, and individuals fairly linearly arranged, b) & c) individuals within a level differ little in status, while status differences between levels are larger, d) a clear alpha male emerges, and differences in status between other individuals are suppressed.

In the final quarter, DN was clearly alpha and VN, beta. BK was clearly the gamma male, the only high status male, while MG had dropped to a mid status level shared with MA. CH was lowest of the mid status males, and BY very low ranking. It was not possible to calculate a status score for TK for this period, but from behavioural evidence (TK lost a fight with the female MM), it seemed he would fall below ZF.

## Status and Affiliative Behaviour

A highly significant positive correlation existed between status (as the giving of agonistic behaviour and receipt of pant-grunts) and the 'giving' of affiliative behaviour ($K_r = 544$, $n = 15$, $\tau = 0.44$, $p_r = 0.0002$). Higher status males tended, therefore, to engage in affiliative behaviour more frequently than did those of low status. Status and the receipt of affiliative behaviour were also significantly correlated, although not as strongly ($K_r = 271$, $\tau = 0.23$, $n = 15$, $p_r = 0.02$). Affiliative interactions appeared to be directed 'up the dominance hierarchy', although not strongly so, and higher status males tended to be responsible for more frequent affiliative interactions.

Affiliative behaviours were reciprocated at both the 'relative' ($K_r = 673$, $\tau = 0.60$, $n = 15$, $p_r = 0.0002$), and at the 'absolute' levels (Mantel tests: $Z = 45904$, $n = 15$, $p_r = 0.0002$; $R = 2897724.5$, $n = 15$, $p_r = 0.0002$). Not only were male chimpanzees more affiliative towards those who were more affiliative towards them, but the hypothesis that male chimpanzees reciprocated affiliative behaviours in proportion to the frequency with which they were received is supported by the significant degree of symmetry between the matrices of performed and received affiliative behaviours. The implication was that the chimpanzees must have been keeping track of the absolute frequencies with which they performed and received affiliative acts.

Much of this affiliative interaction was through grooming, and taken alone, grooming too was reciprocated ($K_r = 694$, $\tau = 0.61$, $n = 15$, $p_r = 0.0002$) in the same 'absolute' manner ($Z = 39554$, $n = 15$, $p_r = 0.0002$; $R = 2897075$, $n = 15$; $p_r = 0.0002$), which implied a 'record keeping' by individuals of the frequency at which they groomed and received grooming, and a proportional relationship between the receipt and performance of grooming. As with affiliative interactions generally, the frequency of grooming was significantly correlated with status ($K_r = 533$, $\tau = 0.43$, $n = 15$, $p_r = 0.0002$), as was the frequency at which it was received ($K_r = 251$, $\tau = 0.21$, $n = 15$, $p_r = 0.031$). The pattern was consistent with Seyfarth's model of grooming (Seyfarth, 1977).

A quadratic relationship accounted for the greatest proportion of the variance (Curve fitting: $r^2 = 0.71$; $F_{2,12} = 18.23$, $p = 0.0002$) in the relationship between status (cardinal ranks) and the amount of grooming received (both of which were approximately normally distributed); it was the mid-high status males who received most grooming

(Fig 4.11a). A quadratic relationship also provided the best fit between status (cardinal ranks) and (log-transformed) grooming performed **(**$r^2 = 0.51$, $F_{2,12} = 8.15$, $p = 0.006$**),** with the same mid-high status males performing the most grooming, as would expected from the absolute levels of reciprocation (Fig 4.11b).

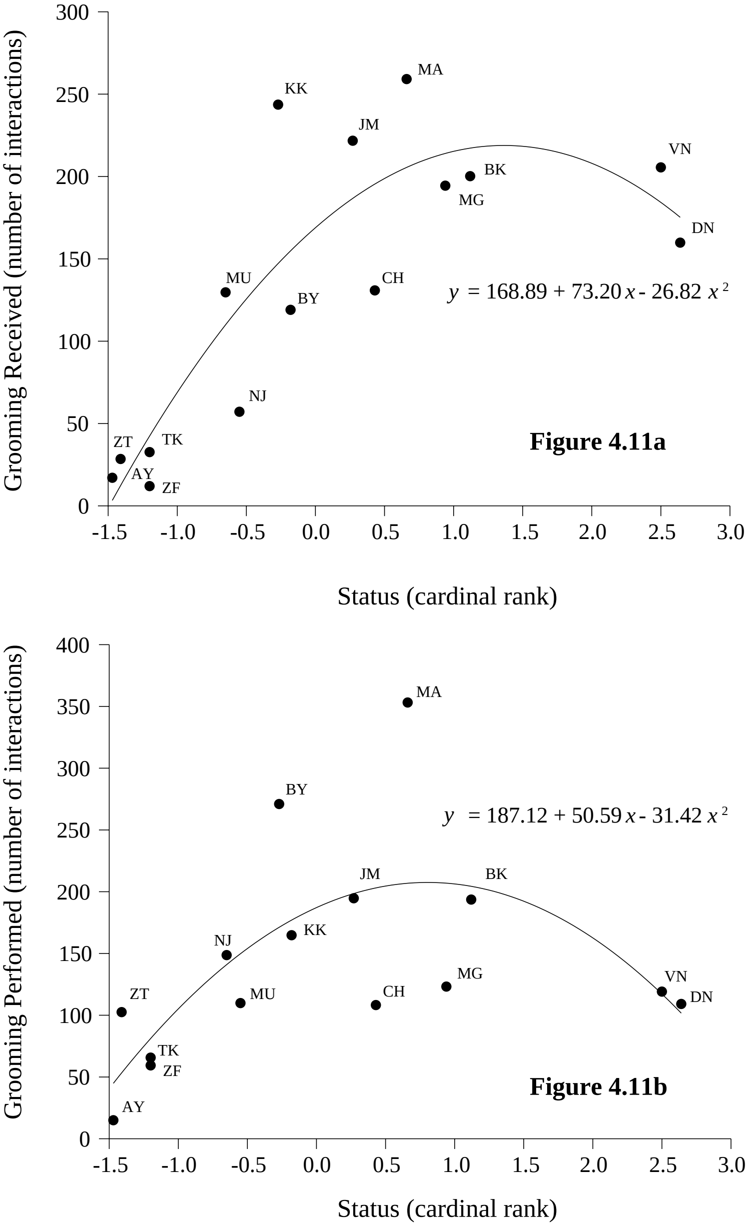

**Figure 4.11a,b.** Relationships between grooming and status. Grooming performed and received are the dyad-corrected number of interactions. The middle and high status males, those below the beta male, perform and receive the most grooming.

## Benefits of High Status

### *Mating Success*

Number of copulations were not significantly skewed from normal ($^{\text{skew}}/_{\text{s.e. skew}}$ = 1.72), despite the presence of a single outlier. A slightly significant correlation existed between status and number of copulations (Pearson's $r$ = 0.53, n = 15, $p$ = 0.042; for copulation frequencies see Appendix 5.3**)**, although this was due entirely to the extreme number of copulations achieved by the alpha male, a number significantly greater than that achieved by other males (Student's $t$ = 3.60, $df$ = 13, $p$ = 0.003). The alpha male also showed possessive behaviour towards 'receptive' females, maintaining close proximity and actively preventing other males from copulating. This occurred after a period of time during which the female had been 'swollen' and mated promiscuously.

### *Access to Food*

Adolescent males feed for a significantly greater proportion of their time than do adult males ($t_s$ = 3.05, $df$ = 13, $p$ = 0.009). They are also significantly lower in status. Controlling for this effect, there is no significant relationship between status and proportion of time spent feeding ($r$ = -0.37, n = 12, $p$ = 0.194).

## DISCUSSION

Male chimpanzees of the Sonso community in the Budongo Forest show a complex pattern of dominance and affiliative interactions. They can be ranked according to a status hierarchy, but this is neither completely linear nor fully transitive. The use of cardinal rankings allows all but one pair of males to be assigned unique ranks, which cluster into different status levels.

Status positions are dynamic, with individuals shifting within status levels, and moving from one status level to the next. The status determined for each individual varies from one three-month block to another, and over the course of twelve months individuals move between status levels. The status an individual holds is related to his body size, and so his physical power, but not to his age.

Status brings no benefit in terms of access to food resources, as measured by time spent feeding. There is no mating advantage associated with status, other than alpha status which confers significant mating advantages. Affiliative behaviours are reciprocated in proportion to the frequency with which they are received, in a manner which does not appear to be linked to the status hierarchy. Affiliative and status interactions thus appear to be separate dimensions of inter-individual relationships.

## Status Hierarchies

Adult male chimpanzees were only rarely observed to engage in status interactions, and did not always pant-grunt to individuals who occupied higher status levels. As a result, there was variation in the number of recognised superiors. BK, for example, was throughout the study of lower status than VN, but was never observed to acknowledge this fact. This reticence may have been part of a deliberate strategy to maintain ambiguity about relationships between males (Hayaki et al., 1989). The status hierarchy cannot therefore be described as fully linear.

Both pant-grunting and agonistic interactions were significantly unidirectional, as has been found elsewhere (Bygott, 1979; Noë et al., 1980; Hayaki et al., 1989), although a number of agonistic reversals, where a normally subordinate individual threatens or attacks an individual of higher status, occurred. This is known to be a feature of chimpanzee social interactions:

> *"A chimpanzee, during intense social excitement...may display towards or hit a superior (to whom he would normally pant-grunt); but the latter will not pant-grunt to him" J. Goodall, 1986.*

The relationship between agonistic behaviour and pant-grunting supports the observation that pant-grunts are not submissive, but subordinate, vocalisations, conferring respect and acknowledging superior status. Although agonistic individuals seem in general to receive more respect, there was no direct causal relationship.

At least four status levels were distinguished from an examination of the data-set as a whole: the alpha and beta pair, high, mid and low status. On the finer time scale of three month blocks, the number of distinct levels varied.

Absolute status differences were large. The alpha and beta males had by far the highest ratios of agonistic and pant-grunting interactions, and were very much 'in a class of their own', primarily because neither was observed to pant-grunt, and both received large numbers of pant-grunts from 12 of the 15 males (54% of all pant grunts from males over 15 months). Differences between other dyads were numerically not so large, but important relative to each other. The number of superiors and subordinates each individual has may demonstrate a difference between a male's perception of his status, and the status which others ascribe to him. NJ, for instance, only recognises MG, VN and DN as superiors, whereas only MU is prepared to acknowledge NJ as his superior.

Some studies have found linear rankings amongst adult male chimpanzees (Takahata, 1990; Hayaki, 1989, 1990), whilst others have found only general levels of status (Simpson, 1973; Bygott, 1979). It seems that in small groups (i.e. few males) it is possible to rank each male in relation to each other, but in large groups the relationships become ambiguous (Nishida & Hosaka, 1996).

In chimpanzees at least, the model of linear, ordinal hierarchies seems insufficient, and to further understand social structure cardinal rankings and non-linear hierarchies need to be used. Using a method of cardinal ranking, it becomes possible to rank males in large groups, and in addition to examine what those ranks mean to the individuals concerned, by showing the degrees of difference between dyads. It may be that levels of status, revealed by cardinal ranking, are biologically more meaningful than relative position on an ordinal ranking.

An approximation to linear ranking was only approached *within* status levels. Judged by the differences in number of acknowledged superiors, and the values of conferred respect it can be argued that the concept of status levels is one recognised by the chimpanzees themselves. Chimpanzees have the ability to categorise objects using abstract criteria (Savage-Rumbaugh & Lewin, 1994; Matsuzawa, 1990), and it would seem this ability could be used to assign status levels to other members of the community, and thus categorise the relative positions of third parties. Keeping track of the status level to which each male can be assigned would be cognitively less demanding than continually computing a precise status score for each individual.

Apparent knowledge of the relative positions of third parties was demonstrated by the changes seen when a new alpha male became established, and in the ambiguity of many status relationships, particularly the tendency of some individuals to ‘treat as equals’ those immediately above them in the status hierarchy, and to be selective in their recognition of superiors. BK, for example, moved from the mid-status level to a clear, high status gamma position during the study; one of his strategies was to withhold pant-grunting from four out of five of those animals that initially held higher status. Despite BK recognising only one superior, only half of the adult and adolescent males acknowledged him as a superior by the end of 1995.

It has been found that winning and loosing fights are positively reinforcing, so that winners tend to win (Chase et al., 1994). Amongst adult male chimpanzees, body size seemed to explain less than half of the variance in status, although size was assessed only subjectively. Other factors, such as the timing and location of agonistic interactions and the gradual accumulation of respect from other individuals, must have played a role in determining an individual’s status. Two of the most agonistic individuals (BK and CH) changed status, in opposite directions, during 1995. BK’s agonistic behaviour appeared to force an increase in status, despite a lack of ‘support from below’, while CH was unable to avoid falling in status. One could ask: Had he lost the ‘respect’ of the other males?

The ‘winners tend to win’ effect may apply to status in general. Increased acknowledgement of an individual’s status by others may increase that individual’s perception of its own status (if only because as more animals recognise the individual’s superiority there are fewer available for the individual himself to recognise as superiors). Acknowledging, or refusing to acknowledge another’s superior status, could alter the perceptions of third parties regarding both relative status, and absolute social position.

## Changes Over Time

Cardinal rankings can be used to show the degree of change over time. When analysed by time blocks, social position was seen to be highly dynamic, at least for some individuals. At times no clear alpha existed; at others, apparent differentiation within the mid-status level was observed as individuals shifted relative to each other. When a clear alpha male was established, status differences between all individuals became more pronounced.

Caution is required when interpreting the quarterly scores, however, as they rely on fairly limited quantities of data. For instance, JM’s status scores are possibly anomalous, in that he was fairly asocial, but received many pant-grunts from the adolescents AY and ZF, and these boosted his status score to a level higher than perhaps it should have been; JM was rarely in association with other males and did not appear to engage in direct status challenges.

During the first half of the year there was an apparent contest for alpha status, with the eventual replacement of the old (presumed) alpha, MG, by an alliance between DN and VN. VN was nominally alpha male during this first period, because of his greater agonistic dominance. He was also the largest male in the community. However, neither DN nor VN pant-grunted to one another, even once DN was established as the new alpha male. There was thus no acknowledgement from VN of a subordinate position. Although DN received the greater respect, VN did not receive any agonistic behaviour from those lower in the hierarchy, unlike DN. VN and DN performed joint displays, and perhaps a continued alliance was necessary for DN to remain alpha; DN was once defeated by a BY-MG coalition when VN was absent. If DN continued to need VN’s help, VN would have been expected to gain some advantage from the arrangement.

Unlike many beta males (deWaal, 1982; Nishida, 1983; Uehara et al., 1994), VN showed no evidence of challenging DN. He did not appear to be exploiting his status, however, achieving only a very low number of observed copulations. Towards the end of 1995, while DN maintained exclusive proximity, and thus access, to ‘swollen’ females, VN continued to harass the other males. A possibility was that VN was DN’s older brother, and aided DN much in the same way that Faben helped Figan in the Kasakela

(Gombe) community (Goodall, 1986). However, the low number of observed copulations remains puzzling.

MA's increase in status may have been the result of pursuing a strategy of affiliating with DN and VN. BK's rise to gamma male status appeared opportunistic, temporarily allying with DN; BK was able to dominate both of MG's allies, the initially high status CH, and high/mid-status BY, who fell considerably in status following MG's defeat.

Had these chimpanzees been studied during a less socially turbulent period, their status relations may have been found to be more stable. When such a period would occur is questionable, as demographic factors should lead to a continuing, if episodic, supply of maturing adolescent males challenging for status. From the changes seen here, the existence of a strong, established alpha male appears to 'clamp down' on attempts to change status, possibly by supporting lower status animals in contests (deWaal, 1982). Jostling for position may continue amongst the low and mid-status males, however, if there are benefits to increasing status (see below).

The choice of allies is crucial, not only for support in attempts to increase status, but because supporting the 'wrong' side appears to have disastrous consequences for one's own status. Sonso males showed a variety of tactics in their attempts to increase status. DN and VN performed joint displays, often aimed directly at MG. On occasion, they would begin the display out of sight of the others, appearing in the middle of the party in full display. DN in particular used bipedal elements in his displays. MG also performed impressive displays. MA rarely displayed, but spent many hours grooming, and both gave and received grooming more frequently than any other male. By becoming a close associate of VN and DN, he seems to have been able to increase his status, at least temporarily. If chimpanzees make judgements as to the nature of others' relationships by, in part, observing their association patterns, then one tactic to increase status may be to influence others' perception of status by associating with high status individuals, a tactic perhaps best described as 'basking in reflected glory'.

BK and CH seemed to be using a more direct tactic of overt aggression, and BK would often be found in small groups apart from the males contesting alpha status. Despite a relatively small body size, he also displayed impressively, with pronounced piloerection, often using the same tactic as DN & VN, displaying from a position out of sight of the others, and thereby adding surprise to the impact of the display.

## Status and Affiliative Behaviour

Male chimpanzees of the Sonso community groom, and are generally affiliative towards, those from whom they receive the most affiliative behaviour. In this they are similar to chimpanzees in Gombe National Park (Simpson, 1973), and the results lend themselves to interpretation by Seyfarth's (1977) grooming model. However, as Seyfarth (*ibid.*) notes, grooming in chimpanzees is more complex than that shown by female monkeys. Males in the upper middle of the hierarchy most frequently engage in affiliative interactions, leading to the appearance of a correlation between status and affiliative interactions. Grooming is not simply directed up-the-hierarchy.

The similarity in results to Simpson's (1973), despite using different methodologies in data collection and analysis, and studying different populations in radically different habitats, increases confidence in the general validity of the pattern seen here.

Much of this study covered a period of significant change, as the old, possibly long standing, alpha male was replaced, and other individuals moved from one status level to another. Alliances appeared well established at the beginning of 1995, and no "allegiance fickleness" (Nishida, 1983) was observed. It seems clear, however, that grooming was being used to cement and subtly modify relationships amongst males best placed socially to take advantage of the period of instability. The results are consistent with the interpretation that grooming was being used tactically, as part of political strategies. MA, for instance, was the most frequent individual in grooming interactions, often with the alpha-beta pair, and increased in status over the study period.

## The Function of Status

Why should males compete for status? The argument is usually that high status confers reproductive advantages, in that it allows preferential access to females, resulting in a higher number of copulations and, potentially, greater mating success. This is presumed to translate into greater lifetime reproductive success, with competition for high status being an adaptive trait (reviewed by: Silk, 1987).

On balance, this relationship appears to hold, both for mammals generally (Dewsbury, 1982), and for some primates (Altmann et al., 1996). In studies which show this, there is usually a correlation between rank (often measured ordinally) and some measure of mating success. In at least some of these studies however, it seems the correlation is due primarily to a singularly successful beta (Hausfater, 1975), or alpha (Samuels et al., 1984; Dixson et al., 1993) male, as is the case for chimpanzees.

The lack of any relationship between status and number of copulations for Sonso male chimpanzees, other than the distinct advantage of alpha status, agrees with results from other studies (Bygott, 1979; Takahata, 1990; Nishida, 1979, 1983; Tutin, 1979, 1980). The advantages associated with high, non-alpha, status remain unclear. Bygott (1979) suggested that there was no benefit to high status per se, but that it was in the interests of all individuals to minimise agonistic interactions, and that a series of dominant-subordinate relationships develop to reduce the incidence of fights as a result of individual differences in strength and aggressiveness. However, if advantages exist for the alpha male, these should drive competition for status and Bygott's argument looses much of its force.

The question then still remains. If only the top ranking male is benefiting from high status, why should other males strive for high status? Why not simply adopt a two-tier 'despot' system (Lott, 1991), in which a single individual is 'dominant' to all the others who are of equally low rank (for example, Coelho et al., 1983)?

Other than increased mating chances, high ranking males may benefit by increased access to desired resources, particularly protein—or more likely essential amino acids—in the form of meat and/or insects. In this study, VN was observed to share meat (an infant chimpanzee) with DN, although the original possessor of the carcass was not observed. Given later events, when DN was observed to kill a second chimpanzee infant, it seems plausible that DN was sharing with VN. On a separate occasion, VN and MA 'shared' half the carcass of a red-tailed monkey. MA joined VN's party carrying the meat, presumably having already eaten some, and was then forced to 'yield' the meat to VN, who consumed all but the tail. DN was not present, and may have been in the party from which MA came. MG was observed to share termites with KK, dividing a large lump of termite-ridden clay, and handing part to the younger male.

Another possible explanation for status striving behaviour, based on the fragmentation of groups rather than reunions between separated individuals, is that there is some advantage to being the most dominant individual within whichever party the individual finds himself. If a mid to high status male, in the company of those of lower status, can locate an 'oestrus' female before higher status males, he may be able to monopolise the female through possessive behaviour, or by initiating a consortship (Tutin, 1979). Such a strategy would be obscured by group level analysis of status. Study of females' interactions with males would be the best way to establish whether such a behaviour occurred, although an indirect method of testing this idea would be to look at party size selection by males (see Chapter 5).

If males are attempting to follow such a status-dependent strategy there should be an indication of tactical choices to be the highest status individual, or at least the highest ranked on agonistic dominance, within a party. This strategy is likely to become more effective when the number of females in the community is high. With more females, the number of simultaneously cycling females should increase, although no evidence has been found for reproductive synchrony between females (Mahale: Takahata et al., 1996). While a powerful alpha male may be able to intimidate a number of rivals to such an extent he can monopolise a number of females simultaneously (Nishida & Hosaka, 1996), the effectiveness of this will depend on the distribution patterns of the females, and the general level of visibility in the habitat. The most likely situation is that the alpha male will be able to monopolise only one female at a time, and when a number of females are cycling simultaneously, other high status males are potentially at an advantage.

Consideration of lifetime status ‘trajectories’ (Bygott, 1979; Goodall, 1986; Dunbar, 1988a) suggests an explanation of the apparent desire for high status in male chimpanzees. It may be that over the course of a lifespan the average status of each male, and any benefits attributed to that status, will be equal, but only if they pursue a strategy of questing for high status. In a manner analogous to van Valen’s (1973) ‘red queen’ hypothesis, males are trapped into a power struggle, simply to maintain equality over a lifetime. Any male who opts out of this struggle, or is forced to through injury or disease, achieves a lower lifetime average status, which should correlate with lower fitness, and thus lower lifetime reproductive success.

Such a situation would not preclude, and may indeed even favour, the development of alternate strategies to achieve the average lifetime status, and thus average fitness. Conceivably, a male could aim to achieve and hold a mid to high status position and hold it for a long time. This would, of course, depend on being able to gain sufficient fitness benefits at this status, which in turn would favour the development of alternate mating strategies, such as the searching in small parties for oestrus females, and forming consortships.

Status, however, may not function to increase fitness over the short term, and have little to do directly with mating success. It may be that fitness benefits accrue to different status levels through a physiological mechanism mediated by corticosteroid or other stress hormones. Research conducted on baboons (*Papio cynocephalus*), talapoin monkeys (*Miopithecus talapoin*) and other primates (Keverne et al., 1982; Sapolsky, 1993, 1996) has shown that levels of stress hormones are elevated in lower ranking animals. Sapolsky (1996) points out that it is not merely the animal’s rank, but its personality and experience of both rank and the society within which it dwells that determine the extent to which the animal develops the physiological symptoms of chronic stress.

Should chronic stress, through impaired immune responses or other factors, lead to reduced reproductive lifespan, selection would favour the evolution of mechanisms to reduce chronic stress, and possibly to reduce chronic stress at the expense of others within the social group, depressing their expected LRS while raising that of the less stressed individual. Status may be one such mechanism, with mid to high status individuals having the lowest levels of chronic stress. Although under stable social conditions levels of chronic stress are negatively correlated with status, when conditions are unstable, levels of stress hormones are high in both low and high ranking individuals, and lowest in mid ranking animals (Sapolsky, 1993). Among chimpanzees, the alpha male tends to maintain a level of arousal sufficient to maintain partial piloerection to emphasise his status (Goodall, 1986), and has to be ready for potential challenges. In addition, he has to coordinate territorial defence of the community's territory (Nishida & Hiraiwa-Hasegawa, 1987). Under such conditions, one would predict elevated hormones characteristic of chronic stress. Personality differences have been noted as being important for tenure of alpha males (Takahata, 1990; Murray, 1995; Nishida & Hosaka, 1996), and, insofar as personality is reflected in behavioural 'style', appear to mediate the effects of chronic stress (Ray & Sapolsky, 1992; Virgin & Sapolsky, 1997**)**. During a period of alpha-male turnover, males directly involved are likely to show a disproportionate increase in levels of stress hormones. With such situations continuing for a number of months, the highest status males may be paying a physiological cost in their gamble for the often short-term mating advantages of alpha status.

Excluding the alpha male, there are no significant differences in the number of copulations achieved by males of different status. If the function of high status is to minimise chronic stress, and chronic stress were to reduce the probability of achieving fertilization, then individuals with higher status, and so lower stress levels, would have potentially higher lifetime reproductive success. Status striving behaviour should thus be favoured by selection. The system may be capped by the elevated stress levels associated with highest status (Packer et al., 1995; Sapolsky, 1996) during period of social instability.

It seems that while all of the above may be benefits associated with increased status, some are likely to have been more important than others in the evolution of 'status striving' behaviour. Given the widespread nature of the link between physiology and status in primates, and the importance of reproductive success over a lifetime, I would suggest that physiological 'health', leading to a longer reproductive lifespan, perhaps in combination with the impact of fertility related effects, was a major factor. In addition, once 'status striving' evolved, the 'red queen' factor would come into play.

# Chapter 5

# TACTICAL ASSOCIATION

*"First Witch: When shall we three meet again, In thunder, lightning, or in rain?*

*Second Witch: When the hurleyburley's done, When the battle's lost and won."*

*Macbeth*

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## INTRODUCTION

To understand the dynamics of the chimpanzee social system, it is vital to determine not only why chimpanzees form parties but why they form the parties they do. Much past research has centred on the impact of feeding competition on the sizes of the temporary sub-groups, or parties, in an attempt to elucidate the ecological factors responsible for the fragmentary nature of chimpanzee communities. However, while relative food abundance constrains party size (Wrangham et al., 1992), other factors are clearly important in determining party size and composition (Boesch, 1996).

In chimpanzees, and some other species (for example, spider monkeys, *Ateles geoffroyi;* Janson, 1984; Strier, 1994), there is no coherent single grouping, and the composition of the small 'foraging' sub-groups is fairly fluid. The existence of a larger social group, in the sense of a "closed social network" (Wrangham, 1986), can be demonstrated by examining association patterns. That a concept of 'own social group' may exist in the minds of individual animals is indicated by the extemely xenophobic behaviour of chimpanzees, and the contrasting behaviour towards group members, as the group rarely, if ever, assembles to form a single cohesive unit.

Mean party size has been found to correlate closely with food abundance (Kibale Forest: Wrangham et al., 1992) and while there is some indication that mean party size may be smaller in harsher habitats [for example, 4.0 (Mount Assirik**)** vs. 10.1 (Taï Forest): Table 5, Chapman et al., 1994], there is no clear trend. Indeed, Dunbar (1988a) has suggested that large parties are the result of either limited, highly clumped sources, or high predation pressure. Recently it has been suggested that average party size is an inappropriate measure, and that variance in party size provides a better indicator of feeding competition (Chapman et al., 1994; Malenky et al., 1994). These analyses assume that feeding competition is likely to determine female grouping patterns, with males mapping themselves to the female distribution (Wrangham, 1980).

Food abundance and distribution (Wrangham, 1986; Dunbar, 1988a) can facilitate or constrain particular grouping patterns, and as such should be less of a constraint on males than females. Under a fission-fusion social system, foraging parties distribute themselves between a number of food patches, each of which may contain insufficient resources for the entire community to forage together. Increasing food abundance can be realised as an increase in the number of resource patches, an increase in the value of each of a few patches, or a combination of these. Where resources are available in only a few, large patches, the community is likely to be more cohesive, and form larger parties. If such patches are widely distributed, travel costs and subsequent loss of interaction opportunities between separated individuals should reinforce this trend toward large parties.

If resources become more abundant through an increase in the number of available patches, feeding competition is likely to result in a more fragmentary group structure, with small parties formed at each patch. Where a number of patches are located in fairly close proximity, it becomes easier, and less costly, for individuals to move between parties, enhancing the fluidity of these parties. As a result, association patterns should become more dynamic.

With the absence of any surface structure (Hinde, 1976) greater than the temporary party, these parties form a shifting milieu for all social interactions, and become more than a means to enhance foraging efficiency. Assessing the costs and benefits of joining, or leaving, a party of particular size and composition becomes increasingly complex. In order to gain a fuller understanding of the evolution of great ape societies, it is necessary to determine the factors which bring individuals together, as well as the factors limiting their aggregation (Lee, 1994).

Reproductive opportunities for male chimpanzees are potentially influenced by social factors, primarily the nature of their relationships with the other males within their community, and to a lesser extent their relationships with particular females (Goodall, 1986). High social status has been shown to lead to increased mating opportunities (Nishida, 1983), particularly when the operational sex ratio shifts towards 1:1; the *alpha* male cannot monopolise access to more than one receptive female at any one time (personal observation). Status itself is highly dependent on coalitional support from other males (deWaal, 1982; Nishida & Hosaka, 1996).

### *A Model of Chimpanzee Association Patterns*

The chimpanzee social system is likely to have evolved via a number of state shifts (Foley & Lee, 1989; Lee, 1994), possibly passing through a solitary or semi-solitary state prior to the development of the fission-fusion system.

With females essentially solitary, or becoming so if shifting from a more cohesive system, the increasingly wide spatial distribution of females would have made it more profitable for males to travel in search of receptive females than to remain with them permanently (Dunbar, 1988a). These (semi-) solitary males would encounter one another at feeding sites, and more critically around receptive females. Travel costs, together with the benefits of local knowledge, would ensure the same males met repeatedly, and competed for access to the same females.

Selection would favour the formation of dominance relationships, as these would reduce the time and energy costs of each bout of competition, and the formation of coalitions between pairs of males, as these would improve dominance status for one or both partners, reduce competition costs, and increase mating success. Such a process would be faster in a system diverging from a cohesive group than in one where the males were initially solitary, but would be favoured in both cases.

These male-male relationships would bring greatest benefits when formed before crucial competitive events, and so selection should favour active association between males, resulting in the formation of parties. Given a limited number of locally resident males, the establishment of relationships would be accompanied by an identification of individuals belonging to the same social system. Defending access to females from non-members would increase the costs of solitary behaviour, and accelerate the formation of closed xenophobic communities. As each male potentially attaches a different value to each of the other males, as possible alliance partners, the parties formed are likely to originate around a number of separate cores, and to be unstable.

The selection of coalition and alliance partners on the basis of their potential value as allies is characteristic of primates (Harcourt, 1989). This selection is complicated in fluid fission-fusion societies, where potential partners are not necessarily available, and further complicated when the value of potential allies is dependent on the alliances of these individuals. Male chimpanzees need to interact with each other in order to form alliances, and to interact they need to be in the same party; before a male chimpanzee can select an alliance partner, he must of necessity select his association partners. This decision is likely to be influenced by the need to associate, and subsequently interact, with other members of the community. Each male's 'ideal' association group may rarely if ever exist, as other males are simultaneously making similar decisions, with party compositions reflecting a compromise between the decisions made by each male.

In pursuit of a particular alliance strategy, males will need to pursue association strategies, which balance the need to form alliances with the need to associate with other community members. The association decisions are thus tactical, in the sense that a male chooses from a variety of party compositions which *at that moment* best match the goals of his association and alliance strategies.

The decision is further complicated by the fact that a male can only know the present composition of the party of which he is a member, and has to predict the composition of other parties, based perhaps on hearing recent vocalisations, or by associating particular males with particular areas. The fluidity of chimpanzee parties means that association decisions must be made frequently, with a new set of options assessed each time. The degree of flexibility and amount of information processed strongly suggests cognitive decision-making. The making of short term decisions in pursuit of long term goals is strongly suggestive of *intentional* decision-making.

Under this model, chimpanzees would be predicted to actively associate with all males within their community, in order to remain recognised as a member, but otherwise they should attempt to associate with particular individuals with whom they can interact to increase their own status, and ultimately, reproductive success. The ability of high ranking individuals to monopolise access to receptive females will ensure that males associate only in small groups, as lower ranking individuals should attempt to discover receptive females before their superiors. In addition the need to form and maintain coalitions and alliances will aid in the formation of small parties, as the interactions necessary to establish such relationships are less likely to be disrupted by the behaviour of other individuals.

Here I attempt to show that the association patterns of the male chimpanzees of the Budongo Forest are best explained by this reasoning. Their associations are tactical, in the sense that the choice of association partners is deliberate, and aimed at achieving particular social goals. These tactics are the moment to moment decisions about with whom to associate. When considered over time, these tactics resolve into consistent social strategies appropriate to each individual's social status, and that, as circumstances change, strategy shifts occur.

## METHODS

### Data Collection

Details of the study site and population are given in Chapter 2. All adult (12) and adolescent (three) males were included in these analyses. General methodological details are given in Chapter 3. Association data were collected by focal scan sampling, with a total of 5171 scan samples collected on parties containing at least one of the 12 adult and 3 adolescent males (median number of scans per male = 1138) over the 15 month period. Visibility was often less than 10 metres on the ground, and accurate monitoring of the composition of the party necessitated changing location between scan samples, and the use of a second observer.

## Data Analysis

In analyses of associations between individuals, consecutive samples often lack statistical independence: if two individuals are present in the first sample, and the duration of their association greater than the time interval between samples, successive samples will overestimate the strength of their association. Classically, problems such as this are resolved by using a technique to determine the characteristic ‘bout length’ of the behaviour in question. Log survivorship curves for changes in intervals of association can be constructed, with discontinuities in the curves used to identify the appropriate time interval required to ensure independence (Slater, 1974).

This technique was used on a sub-sample of the scan sample data set, consisting of data collected during November 1995. This month was chosen at random from those known to contain a large quantity of high quality data. Association bout length was assessed for all parties in which adult males were present, other than those containing cycling females. These parties were deliberately excluded from analysis of bout length as the aim was to determine typical male-male association bout length and the presence of such females may introduce unquantified bias.

No tendency for a change in slope was detected, with a smooth decline in probabilities of association with increasing sample interval. It was not possible to determine a point at which samples could be considered independent as no characteristic ‘bout length’ could be determined. In part this may be due to the nature of the sampling methodology; scan samples were co-coordinated with focal samples and thus may reflect search intensity (moving to another party after completing the focal) when party sizes were small. Continual samples of a single party in excess of two hours were rare. Alternatively, it may reflect more about the stability of parties and the nature of social decisions among chimpanzees, who can join and leave associations at will. Long durations of association may indicate strength of inter-individual relationships, or simply a propensity for an individual to be ‘social’ after a period of being alone.

An alternative method (for example, White, 1986) is to use the first sighting of association between individuals. Since party composition is highly variable, however, this may underestimate common associations, while accurately reflecting rare associations. Simply scoring all new associates on a single day as one sighting fails to record dynamic shifts in associations, ignores persisting associations, and masks inter-individual differences.

With no effective means to ensure rigorous sample independence, I decided to make use of the behaviour of the animals themselves to determine ‘independent’ records. I made the assumption that each observed change in party composition represents a ‘decision event’ when each individual has a choice to end or continue their current associations. This in fact leads to a conservative measure of association, which scores only instances where a change was observed, and not instances where two or more individuals decide to remain in association.

Therefore, to minimise dependency between successive sightings of the same combination of individuals, I analysed records only where a change in party composition occurred. That is, one or more individuals either joined or left the party between consecutive records, with a minimum 15 minute interval between the data points. After passing through this ‘filter’, 3164 scan samples remained for use in analysis. This method of measuring party size is similar to that used in other studies (initial party size, plus a count with every change in composition: White & Burgman, 1990; Boesch, 1991b; Chapman et al., 1994), but with the addition of a minimum time interval between successive counts which should decrease the dependence between successive records.

Comparisons of party size data between studies are complicated by differing sampling regimes, different degrees of subject habituation, and even different definitions of what precisely constitutes a party (Chapman et al., 1993, 1994). Differences between sites in factors, such as the level of predation pressure, which are difficult to assess, mean that caution is required even when comparing results from studies at superficially similar sites.

In the majority of studies of common chimpanzees, data on party sizes are male biased, whether by design or accident, because males tend to become habituated more rapidly than females, and are more obvious in their behaviour. Long-term studies are more likely to provide comparable data for females, and so provide a better estimate of average party size, although males will remain easier to locate, and personal preferences among male field assistants may continue to bias estimates. Figures for ‘average party size’ may thus differ between sites simply as a result of stage of habituation and sampling effort. Where such a sex bias is explicitly recognised, useful comparisons may still be made.

Average party sizes were calculated from this data set for the study period as a whole, and for individual months. I investigated possible seasonal variation in party size using the non-parametric Mann-Whitney, and Kruskal-Wallis, tests. Coefficients of variation were calculated to compare monthly mean party sizes for the Sonso chimpanzees with similar data for Kibale chimpanzees from the Kanyawara community. Kibale data were taken from Wrangham (1986). Dry and wet season months were established by means of a climate diagram (Chapter 2). Variation in party size with group activity was investigated by means of a Kruskal-Wallis one-way analysis of variance, and *post hoc* multiple comparisons using Dunn’s procedure (Dunn, 1964, presented in Neave & Worthington, 1988). Group activity records (Chapter 3), were grouped into five categories: *forage* (including hunting), *rest*, *groom*, *travel*/*move* (including patrolling) & *other*. Each of these categories accounted for at least 1% of scan samples.

Two ‘dual’ group activity categories (see Chapter 3), ‘groom/rest’ and ‘rest/groom’, also exceeded the 1% level. Each accounted for 1.4%, and the scans were distributed equally between *rest* and *groom*. Two further categories, ‘forage/rest’ and ‘rest/forage’ accounted for 1.8% and 1.3% of scan samples. The former were assigned to *forage*, the latter to *rest*; the first behaviour in each pair was the observer’s subjective impression of group activity. No other group activity reached the 1% level, and all were lumped as *other*.

Reproductively active females, showing full or partial anogenital swellings (hereafter, ‘cycling females’) are thought to influence the size of temporary parties, increasing the number of males present (Goodall, 1986; Boesch, 1996). To investigate whether party sizes of Sonso chimpanzees were influenced by the number of reproductively ‘available’ females, I calculated the number of cycling females present in each party, and used a Kruskal-Wallis analysis of variance, with Dunn’s *post hoc* multiple comparisons procedure, to test the following hypotheses:

| | |
|---|---|
| Hypothesis 1: | Cycling females are attractive social partners, and thus become the nucleus of large parties. Party size increases as more females cycle simultaneously. |
| Hypothesis 2: | Cycling females specifically attract adult males, with the result that increasing numbers of cycling females lead to increasing numbers of adult males present in the party. |

In order to examine association patterns, a measure of the tendency of each pair of males to associate was calculated, termed dyadic association strength. The calculation of this statistic is a two stage process, and controls for biases introduced by differential sampling of both individuals and dyads.

Step one was to calculate a ‘twice-weight’ association index for each dyad:

$$I_{AB} = \#AB / (\#A + \#B - \#AB)$$

Where ‘#AB’ is the number of scans with individuals A & B both present, ‘#A’ the total number of scans in which A is present, and ‘#B’ the total number of scans in which

B is present. This is the least biased index in situations where the sampling bias is toward finding individuals together (Cairns & Schwager, 1987) and is commonly used in studies of chimpanzees (Nishida, 1968; White & Burgman, 1990; Wrangham et al., 1992).

Step two converts this index into a relative measure of association, expressing dyadic association strength as its deviation from the mean level of association across all adult and adolescent males:

$$Z_{AB} = (I_{AB} - I) / s$$

Where ‘$I_{AB}$’ is the association index, ‘I’ the mean index across all males, and ‘s’ the sample standard deviation. Party sizes were determined from the same data set, and are the sum of all independent individuals present in each scan sample.

In an attempt to explain association patterns, three mutually exclusive hypotheses were constructed, each giving different predictions concerning the relationship between the dyadic association strength and party size:

| | |
|---|---|
| Hypothesis 1: | Male chimpanzees associate at random with respect to one another. |
| *Prediction*: | No relationship between association strength and party size. |
| Hypothesis 2: | Male chimpanzees show a non-random pattern of association, but are only ‘passively’ associating. The observed associations are caused by males being drawn independently to the same location, for example, food resources or cycling females. |
| *Prediction*: | A positive relationship between the two variables. With males being drawn independently to the same location, the probability of any two males being in the same party increase as the size of the party increases. |
| Hypothesis 3: | Male chimpanzees show non-random, tactical association. They show preferential but flexible association which is responsive to changes in their status and social goals. |
| *Prediction*: | A negative relationship exists between the two variables. Males in dyads with high tendency to associate prefer each other’s company, and thus will seek each other out. Conversely, individuals in dyads with a low tendency to associate will be more likely to find themselves together in large parties. |

Hypothesis 3 makes two further predictions. The first is that association patterns should be dynamic, and second, that they should resolve into distinct association strategies. The changes in association patterns and strategies should also be ‘adaptive’, although this is difficult to demonstrate in such long-lived animals.

To test these hypotheses I examined the relationship between dyadic association strength and mean dyadic party size: for each dyad, the mean size of parties containing both individuals. Each dyad thus has an association strength and a mean party size. Logarithmic transformations were used to normalise the distributions of both measures, to permit the investigation to use parametric tests.

I fitted curves to these normalised data in an effort to establish the nature of the relationship between the two variables, and used regression analysis to investigate the variation in party size accounted for by association strength. I assumed that the association strength of a particular dyad was an inherent property of the relationship between the individuals at any particular moment, determined by the relative value of the relationship to each individual. Under this assumption, party size can be a function of association strength, while the reverse cannot.

The hypothesis that there is a minimum association requirement for all adult males, regardless of their sociability, was investigated by calculating proportion of time spent alone, and proportion of time spent as the only adult male within a party. This second measure may be a more reliable measure of whether a minimum association requirement for community membership exists. These calculations were made using all 5117 scans, as to do otherwise would introduce further bias against lone individuals.

Cluster analysis of the dyadic association strength matrix, calculated over the entire 15 month period, was carried out to achieve a graphic representation of the relationships between individuals. I used the ‘unweighted pair group method using arithmetic averages’ (UPGMA) or ‘average linkage’ method. The data were then separated into 5 blocks, each covering a three month period, and matrices of dyadic association strengths calculated for each block. The first of these blocks (October to December, 1994) was excluded from further analysis, as during the first three months the subjects were less habituated, and the nature of their relationships unclear. I used the same method of cluster analysis on each of the four remaining matrices to investigate changes over the twelve month period.

Multidimensional scaling (Schiffman et al., 1981) was used to display individuals in two-dimensional space. As for cluster analysis, a scaling plot was derived for the matrix of dyadic association strengths, and subsequently for each of the three-month time blocks. The ALSCAL algorithm, implemented by SPSS, was used to calculate squared euclidian distances between individuals, the same measure used in the cluster analysis.

The resultant plots give a more immediate impression of the clustering of individuals than do the results of cluster analysis.

# RESULTS

## Party Size and Composition

Mean party size for Budongo chimpanzees calculated across all party types was 5.70 ± 3.48 (median 5.0, range 1.0-19.0). This is within the range reported by other studies, at Budongo and elsewhere (Chapman et al., 1994: Table 5). In comparison, the Kanyawara community in Kibale formed parties averaging 5.6 ± 2.6 individuals for the period 1984 to 1985, 6.1 ± 4.5 for 1988 to 1989 (Wrangham et al., 1992) and 5.11 (range 1.22-12.26) for 1988 to 1991 (Chapman et al., 1994). Inter-annual within-site variation in mean party size can thus be greater than that found between study sites. Seasonal variation in mean party size (Fig. 5.1) at Kibale (Kanyawara: CV = 70.02) is more pronounced than in Budongo (Sonso: CV = 18.31), although there is no significant difference between mean party sizes, taken over the year for the two periods compared (Wilcoxon signed ranks test: $Z = -0.31$, n.s.). For much of the two periods, both communities showed the same monthly mean *relative* party sizes. Modal party size was the same for both communities: 2 individuals.

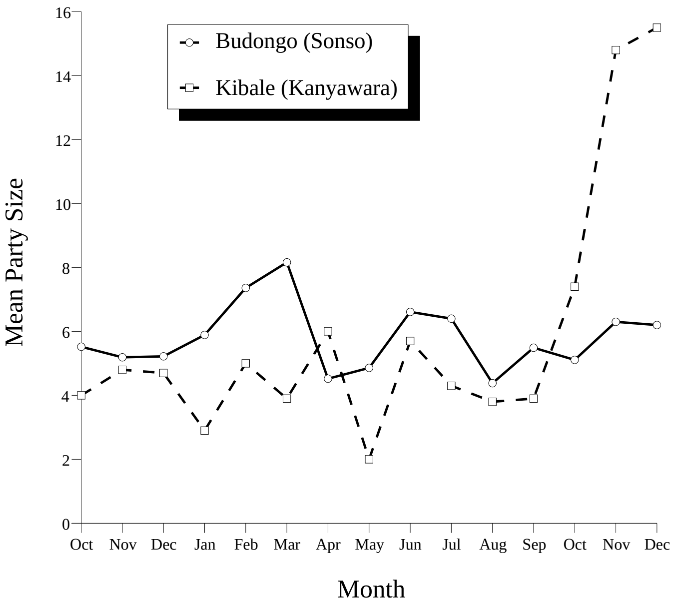

**Figure 5.1**. A comparison of month by month mean party sizes for two forested study sites. Budongo data are from this study, and run from 10/94 to 12/95. Kibale data are taken from Wrangham et al. (1992), and run from 10/88 to 12/89.

Within the Sonso community, there were significant differences in average (median) party size from month to month (Kruskal-Wallis one-way anova: $H = 218.85$, $df = 11$, $p < 0.0001$), although no trend in monthly averages was apparent (Runs test: $Z = -0.83$, runs = 5, $p = 0.40$ n.s.). Median party size during the dry season months (January, February, March) was however significantly greater than the median for all other months

(Mann-Whitney $U = 719215.5$, $n_{dry} = 679$, $n_{wet} = 2479$, $p < 0.0001$). There may therefore be some seasonal effect, although not particularly strong; average party size in some wet season months exceeds that in dry season months.

Party size varied significantly with group activity (Fig. 5.2: Kruskal-Wallis one-way anova $H = 83.00$, $df = 4$, $p < 0.0001$). *Post hoc* analysis (Dunn's procedure) indicated that median party size associated with travelling and moving was significantly lower than that associated with foraging, resting, grooming, or other activities, and that foraging parties were slightly, but significantly, smaller than resting parties.

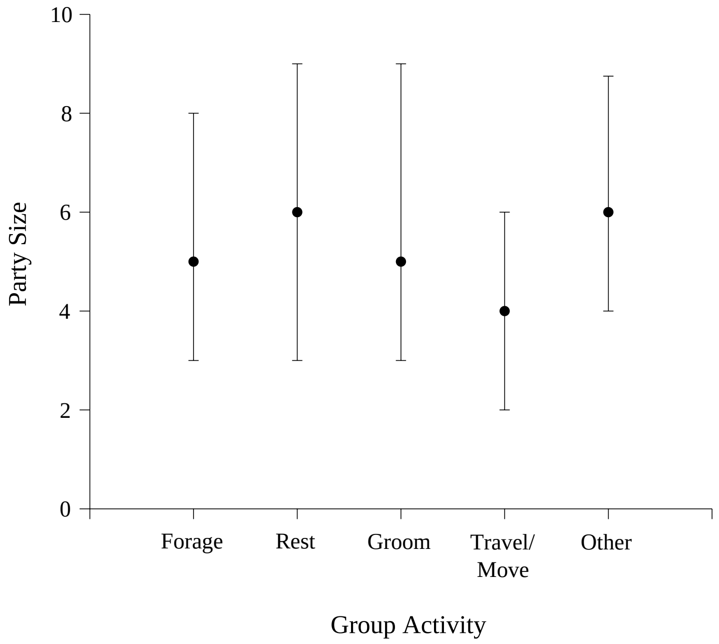

**Figure 5.2**. Median party size (with inter-quartile range) associated with each category of group activity.

Since this study was concerned with adult and adolescent males, the size of parties in which males found themselves were examined in detail. Males spent 74.3% of their time in mixed sex parties, and 25.7% of their time in male-only parties (n = 3005 scans), including time spent alone. The mean size of parties containing at least one adult or adolescent male was 5.88 ± 3.45 (median = 5). When males were not solitary, time in mixed-sex parties was 80.6%, with 19.4% of time in male-only parties. Mean party size for non-solitary males was 6.3 ± 3.27 (median = 6). In both cases the modal party size was 4 individuals. No evidence of core party formation (parties containing most or all adult males) was found over the course of the study.

Just over half of all parties contained one or more cycling females (50.16%, n = 1587; Fig. 5.3). One cycling female was present in 35.37% of parties (n = 1119), two cycling females in 11.21% of parties (n = 355), three cycling females in 3.12% of parties (n = 99), and four cycling females present in 0.44% of parties (n = 14).

The size of parties was influenced by the number of cycling females (Kruskal-Wallis

*H* = 1067.8, *df* = 4. *p* < 0.0001); median party size increasing with the number of cycling females present (Figure 5.4). Parties containing a single cycling female were significantly larger than those containing no cycling females, and parties containing two cycling females were significantly larger than those containing a single cycling female. The size of parties containing more than two cycling females was not significantly different to those containing two cycling females (Dunn's *post hoc* multiple comparison procedure, with $\alpha = 0.05$ across all tests).

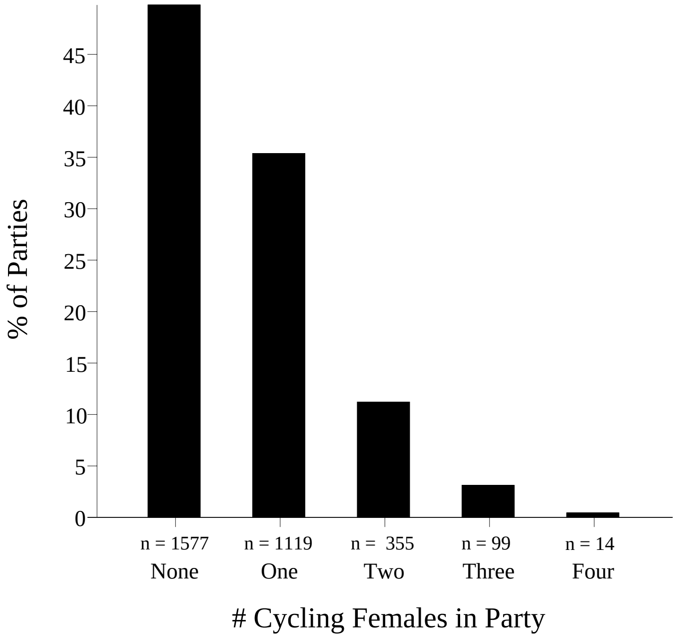

**Figure 5.3**. Percentage of parties containing both males and cycling females. 49.8%, of parties had no cycling females present. One cycling female was present in 35.37%, two cycling females in 11.21%, three cycling females in 3.12% of parties and four cycling females present in 0.44% of parties.

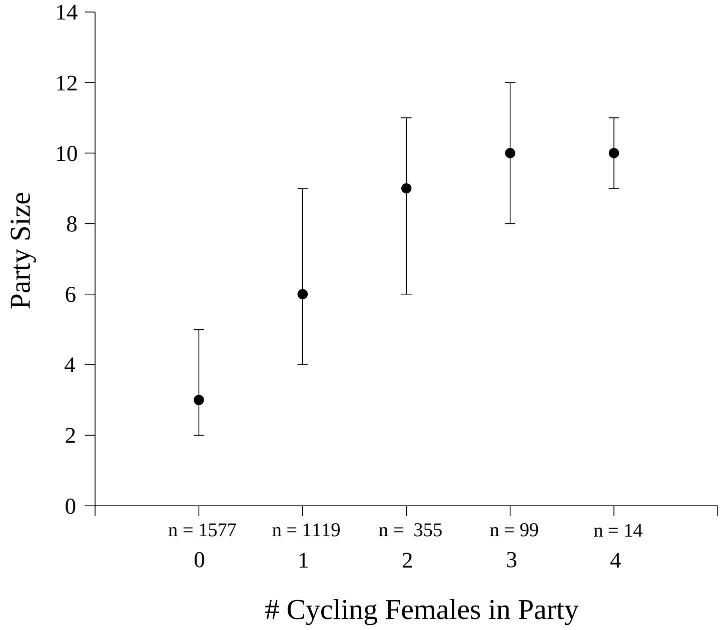

**Figure 5.4**. Median party size (with inter-quartile range) associated with the number of cycling females present. The presence of cycling females appears to be linked to larger party sizes, although parties with three or four cycling females are not larger than those with two cycling females.

The average (median) number of males present in a party increased significantly with the presence of cycling females (Kruskal-Wallis *H* = 492.11, *df* = 4, *p* < 0.0001). The number of males associated with a single cycling female was significantly greater than that associated with non-cycling and no females, and the median number of males associated with more than one cycling female was significantly greater still (Fig. 5.5). There were no significant differences in the number of males in parties containing two, three or four females. Furthermore, there was no difference between the number of males in parties contain one, and four, cycling females, perhaps due to the small sample of parties including four cycling females (Dunn's *post hoc* multiple comparison procedure, with $\alpha = 0.05$ across all tests).

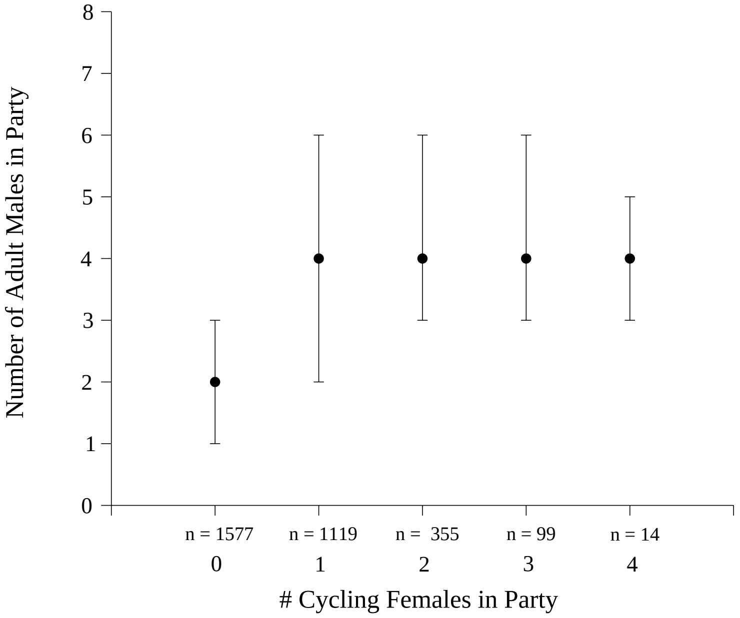

**Figure 5.5**. The number of adult males (median and inter-quartile range) in parties with from zero to four cycling females.

## Association Patterns

Budongo male chimpanzees varied in their tendency to associate, with association strength ranging from -0.88 to +3.87 (15 individuals, 105 dyads). That is, some pairs of individuals were found together more often than other pairs, as has been found in other studies of chimpanzees (for example, Goodall, 1986).

### *Time Alone*

Mean percentage time alone across all 15 subjects was only 2.49 ± 2.07% (median = 2.29). This ranged from 0.16% for ZF, the youngest adolescent, to 8.66% for TK, one of the older males. Time as the only male in the party was calculated only for the adult males, and averaged 7.89 ± 4.44% (median = 7.41). Time alone and time as the only male in a party were significantly correlated (Spearman rank correlation: $r_s = 0.76$, n = 12, $p = 0.005$). Neither measure showed a significant correlation with association strategy (see below), nor with social status (see Chapter 4). All adult males spent similar amounts of time associating with other males, apart from TK, who spent at least 18% of his time apart from other adult males. TK was significantly more asocial than the other males (time alone: $t_s = 5.28$, $df = 13$, $p < 0.001$; time as only male in a party: $t_s = 3.30$, $df = 10$, $p = 0.008$).

### *Association Strength and Party Size*

The relationship between mean (dyadic) party size and dyadic association strength, once normalised by logarithmic transformations, was best explained by a linear model. For all parties (Fig. 5.6), dyadic association strength accounted for 31% of the variation in party size ($F_{1,103} = 45.68$, $p < 0.0001$); for parties containing males only (Fig. 5.7), 24% ($F_{1,103} = 31.70$, $p < 0.0001$). As predicted by the hypothesis of tactical association, this relationship was significantly negative (significance test of gradient: all parties: $t_s = -6.76$, $df = 103$, $p < 0.0001$; male-only parties: $t_s = -5.63$, $df = 103$, $p < 0.0001$). These results were contrary to the predictions of the alternate hypotheses. Neither the hypothesis of random association, or that of independent attraction, were supported by these data.

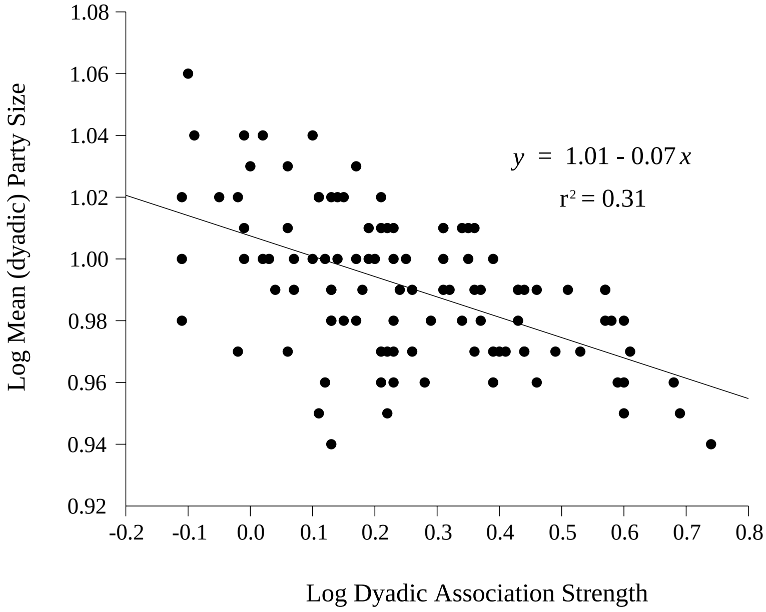

**Figure 5.6**. Mean dyadic party size (the mean size of parties containing each dyad) as a function of dyadic association strength. Data from ***all*** parties containing adult and adolescent males.

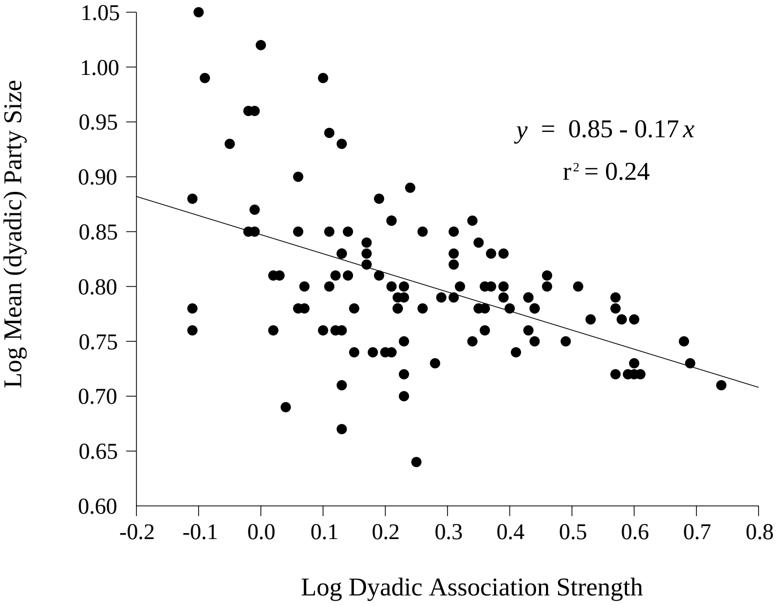

**Figure 5.7**. Mean dyadic party size (the mean size of parties containing each dyad) as a function of dyadic association strength. Data from parties containing ***only*** adult and adolescent males.

Residuals for the regression of male-only parties revealed a transition in the impact of association strength on party size. It appeared to be more important in determining the size of male-only parties containing 6 or fewer individuals (Fig. 5.8). Furthermore, the dyads with positive association strengths were those which appeared to be attempting to come together in small parties [dyads with association strengths > 0 only (male-only parties): $r^2 = 0.50$, $F_{1,40} = 39.95$, $p < 0.0001$].

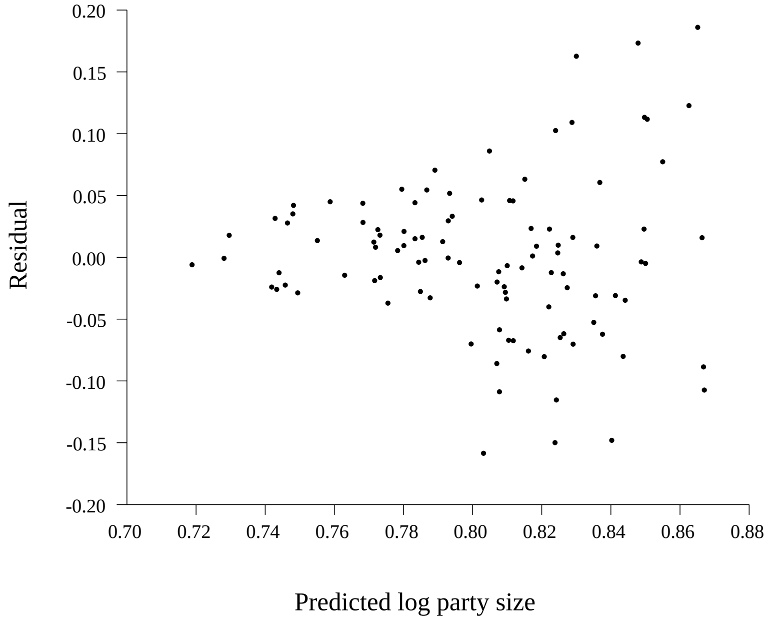

**Figure 5.8**. Plot of residuals from the regression of mean dyadic party size with male-only parties (Fig. 5.7).

## *Association Strategies*

The dendrogram for the full, 15 months, data set separated the males into four ‘association’ groups (Fig. 5.9): three clusters with high to medium levels of association, and a fourth group of outliers showing low levels of association. The outlying group contained a single adult male and two adolescent males. The pattern was strongly suggestive of at least two distinct social strategies.

The first, and tightest, cluster contained three males, DN, VN, and MA. The second, three different males (KK, BY, & MG). These two groups of highly associating individuals were labelled ‘intense’ strategists, as each was a member of a few dyads with high dyadic association strength. These males appeared to be following a high investment strategy whereby they ‘spent’ their association time on the formation of few, strong, relationships. DN and VN were known to have a strong social relationship, and to be alliance partners, as were MG and BY for at least part of the study.

The other adult males, aside from TK, were much less tightly clustered, dividing their time amongst most or all the other males, a strategy described as ‘gregarious’. Association strengths for dyads containing these males were lower and more evenly distributed than was the case for ‘intense’ strategy males. The gregarious strategy permitted much greater flexibility in social relationships, and the monitoring of the relationships between others.

For the second group of ‘intense’ strategists, the clustering was not as tight as for the first. This may have been due to the individuals in the second cluster following either a mixed strategy, or simply be the result of changes between the two strategies within the 15 month period summarised here.

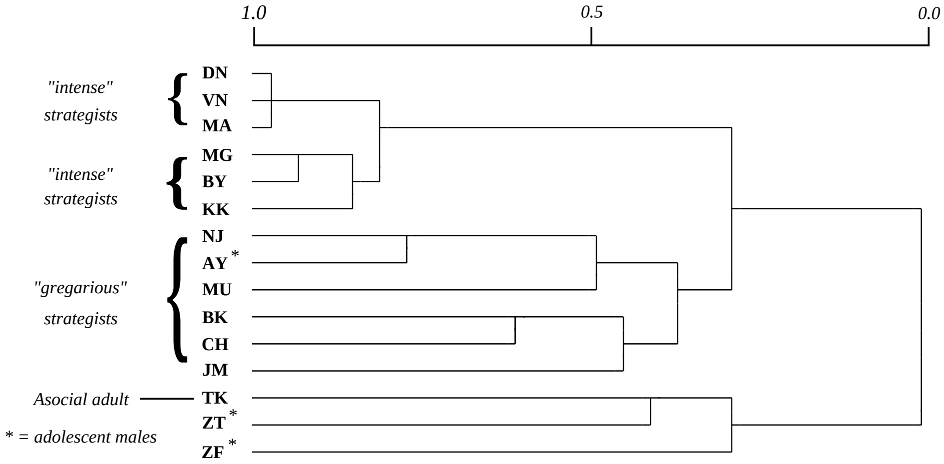

**Figure 5.9.** Dendrogram showing the results of cluster analysis of dyadic association strengths. Individuals cluster into three main groups: outlying asocial males, ‘gregarious’ association strategists, and ‘intense’ association strategists.

Similar trends were apparent in the two-dimensional scaling plot (Fig. 5.10).

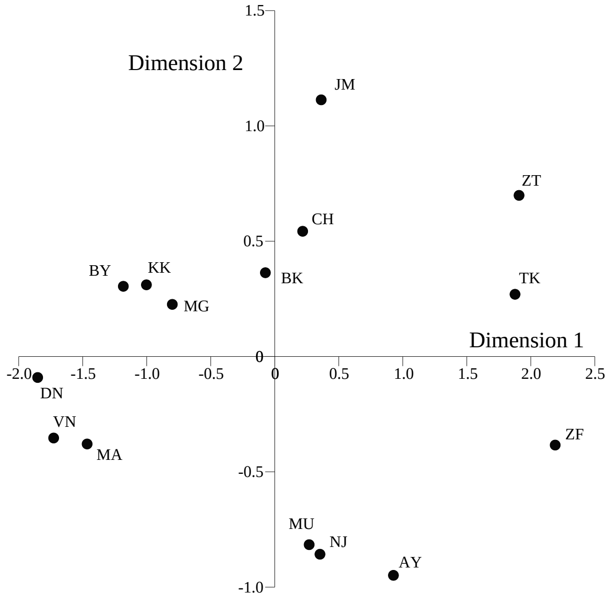

**Fig 5.10**. Two dimensional plot of the cluster analysis results, showing the division of individuals into different association groups.

Dimension 1 separated the ‘intense’, ‘gregarious’ and asocial males, while dimension 2 separates the two groups of ‘intense’ strategists. Furthermore the second dimension separated the gregarious males. This dimension may describe some aspect of flexibility in strategy. Males with negative values on this dimension were more consistent in association strategy than those with positive values. Alternatively, this dimension may represent social stability; males who had stable social status fell below the axis, males with unstable social status fell above the axis.

### *Dynamic Associations*

Association strength, the tendency of a dyad to associate, varied considerably from month to month within a particular dyad. Figures 5.11a-d, line plots smoothed using Microsoft Excel™, illustrate this. Changes in association strength appeared to be non random and to respond to changes in inter-individual relationships. This can be seen in Figure 5.11a, where DN's associations with each of three key males are plotted. MA became a close association partner as DN attained alpha status, while MG's association with DN varied inversely with VN's association with DN. This implies either avoidance, or exclusion, such that the DN-VN dyad existed at the 'expense' of the MG-DN dyad.

These changes in associations were reflected in the changes in association strategy. The dynamic nature of individual association strategies became apparent in the analysis of the three month time blocks. The results of the cluster analysis (Fig. 5.12) were interpreted using the same line of reasoning as used before. DN pursued an intense strategy throughout 1995, maintaining his alliance with VN, although not until the second quarter was his superior status acknowledged by MG. Only in the second half of the year was DN the undisputed alpha male. MG, in contrast, changed his association strategy at least twice. Having acknowledged the loss of his high, possibly alpha, status he switched to a gregarious strategy, only to return to an intense strategy, forming an alliance with BY, to challenge for high rank. BY was injured, possibly during a challenge, and subsequently MG appeared to relinquish his challenge, and pursued a more mixed strategy. Similar patterns were seen in the two-dimensional scaling plots (Fig. 5.13).

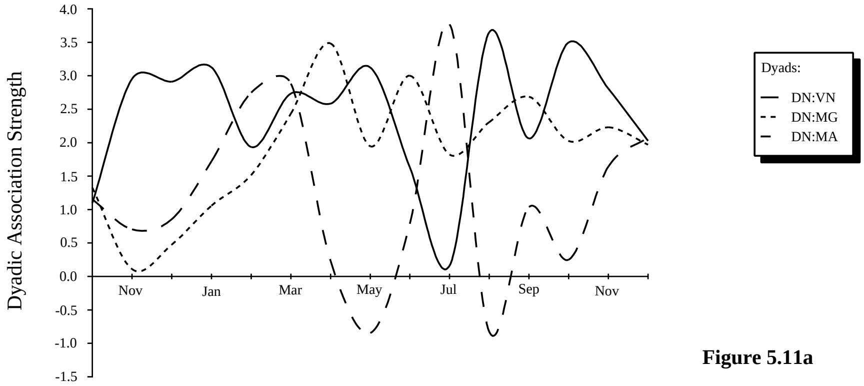

**Figure 5.11a**

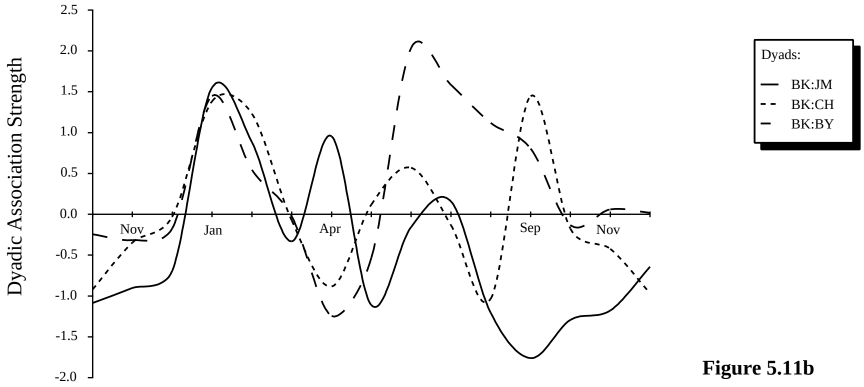

**Figure 5.11b**

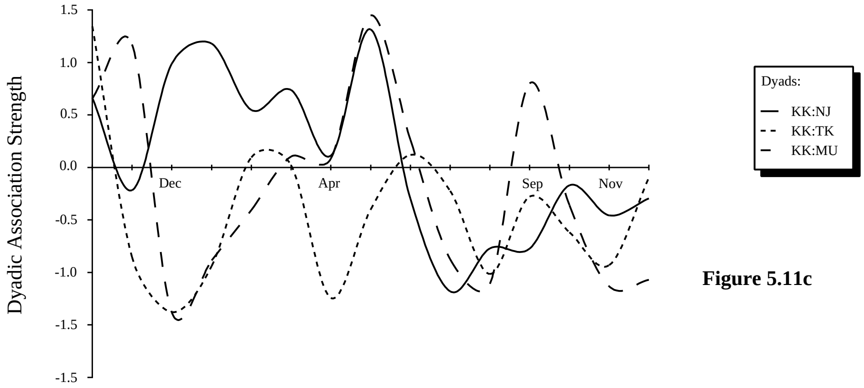

**Figure 5.11c**

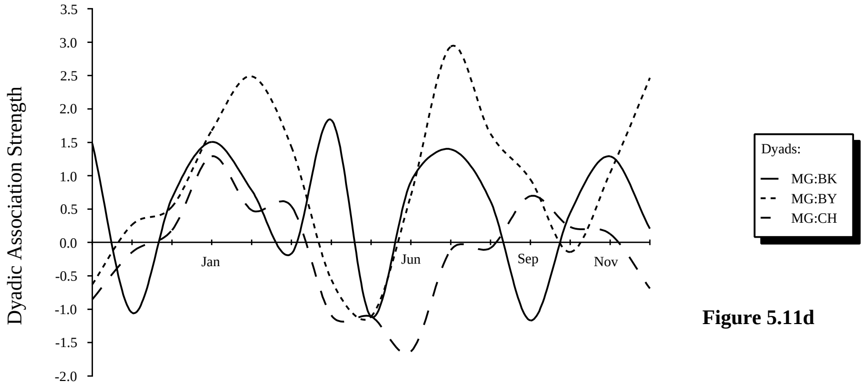

**Figure 5.11d**

**Figure 5.11**. Smoothed plots of monthly dyadic association strengths for males of the Sonso community, illustrating the dynamic nature of individual associations.

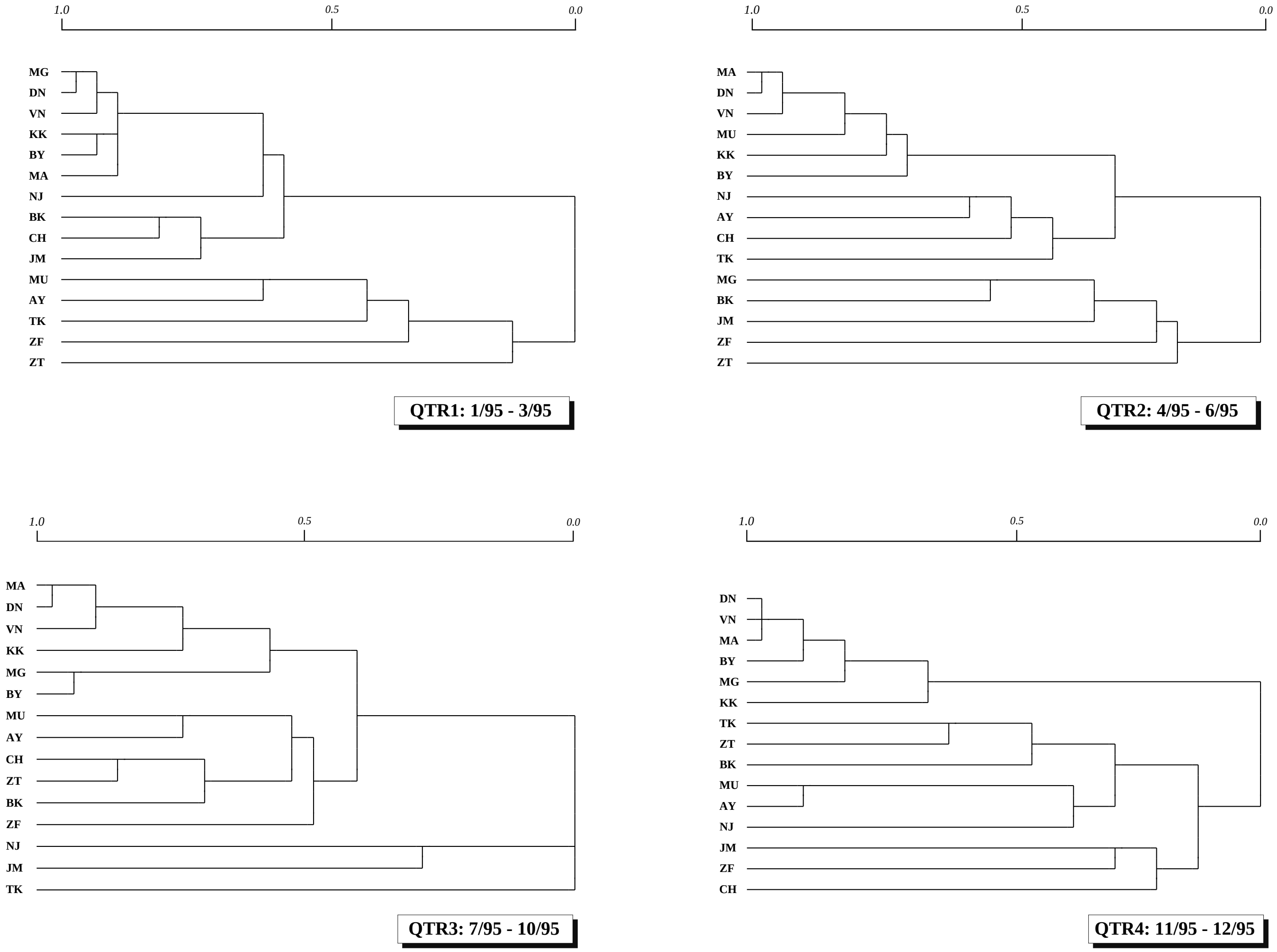

**Figure 5.12.** Dendrograms showing the results of cluster analysis of dyadic associations for each quarter of 1995

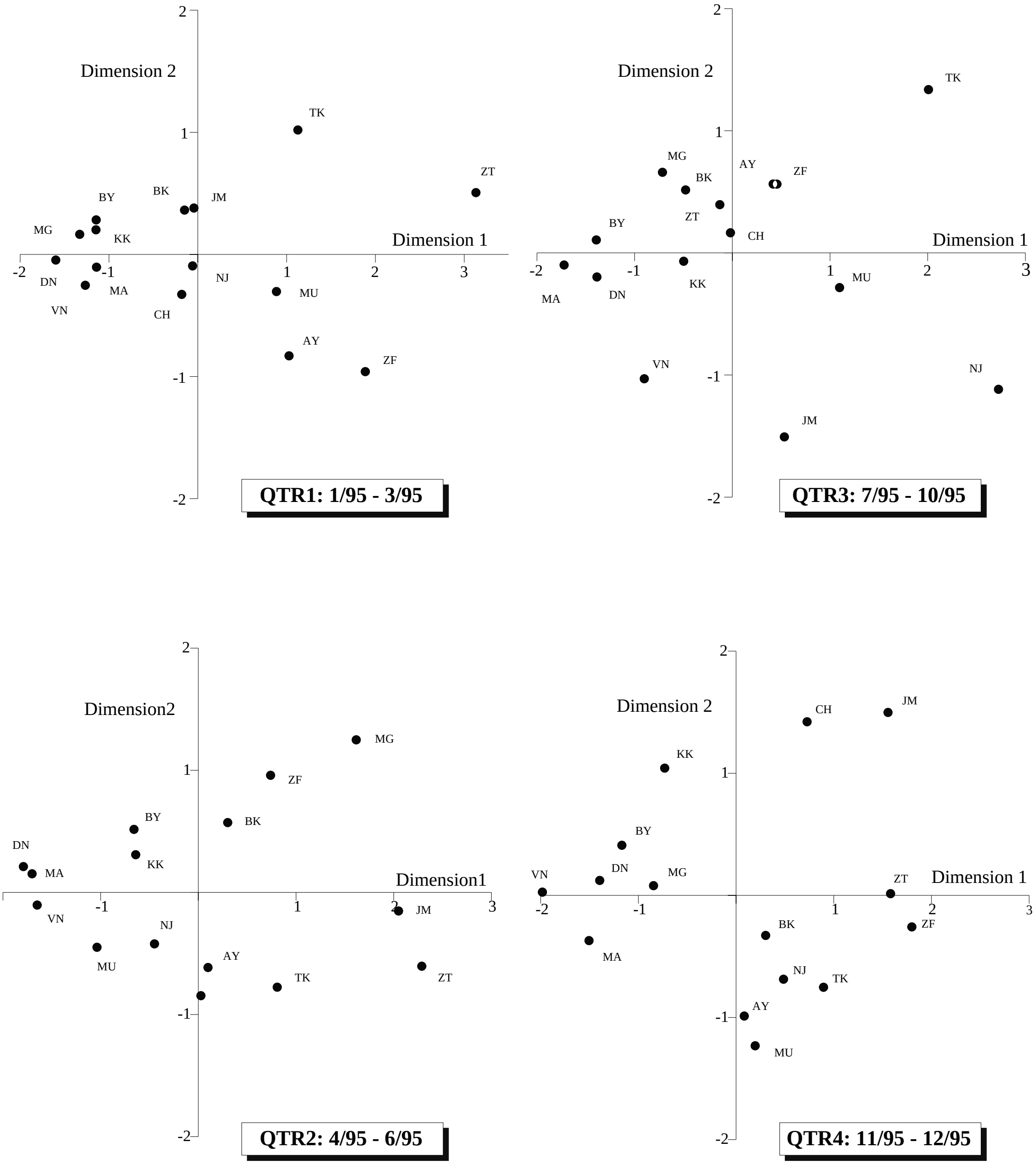

**Figure 5.13**. Two dimensional scaling plots of dyadic associations for each of the quarters of 1995. The distances between the individual represent the degree of similarity in their association patterns.

## DISCUSSION

The association patterns of male chimpanzees of the Budongo Forest are best explained by the hypothesis of non-random, tactical association. Different association strategies, responsive to changes in social circumstances, are indicated by cluster analysis. The dyadic association patterns through which these strategies are expressed can be highly dynamic, and most crucially, there is a highly significant negative relationship between the tendency to associate and party size, an effect more prominent in small parties.

Chimpanzee associations are generally considered to be constrained, through feeding competition, by food supply (Wrangham, 1977, 1986; Chapman et al., 1994), such that larger party sizes occur at times of abundance. In the Sonso region of Budongo, however, average party size varies little in relation to behaviour, and shows no clear seasonal pattern. Furthermore, Plumptre and Reynolds (personal communication) have found that as food abundance increases, party size for Sonso chimpanzees decreases significantly, assessed on a monthly basis.

This suggests that food resources may be more abundant in the Sonso region than in some other areas (Gombe: Wrangham, 1977; Kibale: Wrangham, 1986; Chapman & Wrangham, 1996), and that such resources are fairly evenly dispersed. Observations suggest that abundant food resources do not occur in patches small enough to excessively constrain the size of foraging parties. Foraging constraints on Sonso chimpanzees seem to be fairly constant, and absolutely lower, than those faced by some other populations (for example, the Kanyawara population: Chapman & Wrangham, *ibid*). As a result, variation in party size and the composition of parties are likely to be due more to social than ecological factors, as concluded by Plumptre and Reynolds (personal communication).

### *Strategic Association*

The idea that chimpanzees behave politically, showing flexible behavioural strategies, was presented by deWaal (1982), based on his study of captive individuals. A key difference between captive and wild chimpanzees is the ability of wild chimpanzees to change their associates and it has been suggested that captive animals show complex social strategies as a response to their inability to spend time apart from their companions (Goodall, 1986). While examples of tactical behaviour have been noted in wild chimpanzees (Goodall, 1986; Nishida, 1983; Uehara et al., 1994) they have often been described by critics as mere ‘anecdotes’, although it is now clear that wild chimpanzees do pursue social strategies (Nishida & Hosaka, 1996). In searching for examples of tactical behaviour, the emphasis has remained with highly observable social interactions.

Here I have attempted to step back from the level of interactions, and to examine in detail the choice of association partners. Individuals' association priorities are likely to differ, and as a result a compromise between these priorities determines observed patterns of association, and so provides the foundation for elaborate social interactions. The most fundamental strategic behaviour should therefore exist, together with the most frequent use of tactical decisions, in inter-individual associations. The cognitive capacities seen in captive chimpanzees are unlikely to remain dormant in the natural habitat (Humphrey, 1976); cognitive abilities will have evolved only if used to some advantage. If chimpanzees are changing their association partners in order either to interact with other individuals, or simply to monitor both their own and others' relationships, they will be required to continually make decisions about their association partners and thus whether to join, leave, or remain in a party. The decision should be based on the presence and absence of particular individuals already in the party, as well as party size. Such a process would require the continuing use of immense cognitive power (see Whiten & Byrne, 1988a), and provides a possible explanation for its evolution.

The percentages for time spent alone given here are much lower than have been reported previously (Wrangham & Smuts, 1980; Wrangham et al., 1992), almost certainly because the data were unavoidably biased towards parties. This bias was introduced by using vocalisations to locate chimpanzees, and even when searching at random the probability of locating a party is greater than finding a lone individual. Nevertheless, the data do permit comparisons between males, even though absolute levels may be an underestimate.

The amount of time adult males spend apart from all other adult males is indicative of their sociability, and the bias against lone individuals is reduced by including associations between a single adult male and females and juveniles. All the adult males, aside from TK spend only a small and similar proportion of their time apart from other males. The lack of a correlation between time apart from other males and association strategy implies that the two strategies are true alternatives, at least as far as time allocation is concerned. The pursuit of a particular strategy is not related in any obvious way to age or size differences, although TK's asocial 'strategy' may be an example of a making the 'best of a bad job' (Krebs & Davies, 1987). Old and crippled in both hands, TK has extremely low social status.

In the absence of data on lifetime reproductive success, it is impossible to establish whether the association strategies are true evolutionary alternatives, although this possibility exists. In a very real sense these strategies are only components—tactics within tactics—of the chimpanzees' mating strategies, and to attribute reproductive benefits to one or another association pattern would be immensely difficult.

### Party Size

Parties formed by Sonso chimpanzees appear to reflect a compromise between the tactics pursued by each male, together with the availability of receptive females. The results presented here suggest that chimpanzee males selectively attempt to form small parties, rather than being forced into small parties by resource availability.

Smaller party sizes may provide an easier social environment for the development of relationships, with less chance of interference by other males, and a more advantageous competitive environment when encountering receptive females. It may be that high status males are less likely to monopolise females when vital allies are potential competitors. Alternatively, or additionally, if a small party of males coalesces with a female-only party containing more than one receptive female, then each male has a greater likelihood of copulating, and possibly achieving fertilisation. In effect, each male ‘wins by default’ against the absent males, at least in terms of immediate access.

The optimal party size for an individual chimpanzee may in fact be smaller than those in which he finds himself, and while free to leave a party this choice is constrained by the behaviour of each of the other males; if all desired partners are in the current party, then the individual has to endure the large party in order to associate with them. If a small number of individuals do leave, others may follow in an attempt to remain in association, preventing the formation of a party of optimal size. Alternatively, the individual may be unable to find others with whom to associate and forced to spend time alone, in what is, in effect, a sub-optimal sized party.

From an individual chimpanzee’s perspective, the average number of companions may be less critical than the identities of those associates, particularly when costs of feeding competition are reduced by multiple patches of abundant food. The composition of a party may be more important in determining an individual’s behaviour than the size of that party.

### Core Parties

At Budongo, there was no evidence for the formation of ‘core parties’ containing most or all of the adult males, a feature common to other long-term study sites (Mahale: Nishida, 1968; Gombe: Goodall, 1986; Taï: Boesch & Boesch, 1989; Kibale: Wrangham et al., 1992). The function of core parties has yet to be determined, and three plausible explanations as to their non-occurrence in Budongo come to mind.

Core parties, where they are found, often occur only seasonally. At Kibale, they are associated with a large overall party size and high food abundance. Kibale chimpanzees have been found to feed only on a few preferred food items (Wrangham et al., 1996), which often occur in large groves (C. A. Chapman, personal communication; Wrangham et al., 1996). Highly abundant food may therefore be highly clumped, incidentally resulting in the formation of core parties. During the course of this study, food resources in the Sonso region of Budongo were widespread with a number of patches of the same food available at the same time (personal observation). A fairly even spatio-temporal distribution of food patches may enable male chimpanzees to continue the pursuit of their association strategies, forming small to medium sized parties, freed from the restrictions of highly clumped resources.

However, core parties may serve a defensive function in inter-community relations. Should patches of highly desirable food items lie near community borders, or in border zones between territories, the possibility of encountering males from other communities may precipitate the formation of large parties, containing most or all males, by foraging chimpanzees. This would both protect party members from attack, and deter inter-community competition over food resources. Core parties would thus be predicted not only to occur more frequently during periods where food patches are highly dispersed, particularly if the value of each patch is high (as occurs in Kibale), but also to occur more frequently at the edges of a range. They also would be predicted to be more frequent in communities with fewer adult males than neighbouring communities, particularly in proportion to overall community size and the relative resource value of the home range.

An increase in territorial pressure from neighbouring communities resulting in a reduction in community range (see for example, Goodall et al., 1979) should increase the frequency of core-party formation. The absence of core parties in Budongo may indicate a lack of such pressure, perhaps due to the relatively large number of adult males in the Sonso community.

The formation of core parties may only be possible under relatively stable conditions when cooperation between the males will be more likely. Intensified competition during periods of social instability may mitigate against their formation. The period of this study was one of some social instability for the Sonso community, with a change in alpha male, and this provides a plausible proximate explanation for the absence of core parties in this community. If core parties form in response to threats from neighbouring communities, periods of within-community instability may be particularly hazardous to resident males. As a result, instability within one community, may, if a neighbouring community is both strong and stable, lead to inter-community instability, and the expansion of one community's range at the expense of the other's.

This process, and the ensuing hazards, can be seen in the long term records of the chimpanzees of the Gombe National Park. In 1971, during a two year period of social instability, the KK study community split into Kasakela and Kahama communities. The instability in the Kasakela community ended when Figan attained alpha status (Goodall, 1986). With Figan at the start of a six year period as alpha male, the Kasekala community expanded its range to the north, before beginning the annihilation of the Kahama community to the south (Goodall, et al., 1979). Another two year period of social instability ensued after Figan lost his alpha status, during which the Kasakela community's range contracted in the face of pressure from communities from the north and south, culminating in 1982 with males from the southern Kalande community travelling into the core of the Kasakela community's home range (A. E. Pusey, personal communication; Goodall, 1986).

The flexibility each male has in his associations is constrained by ecological factors, particularly the degree of clumping in food resources, both directly and via the impact on female distribution, and territorial threats of neighbouring communities. However, chimpanzees do not need to feed continually, and unless the community is relatively small or contains relatively few adult males, threats are likely to be a problem only at range boundaries. Time and space thus remain available for males to associate tactically in small parties. Social pressures mediating reproductive success may have been at least as important as ecological pressures in shaping chimpanzee sociality, with the development of the fission-fusion system requiring high cognitive ability and tactical behaviour.

# Chapter 6

# RANGING PATTERNS

> *"They traveled for the most part upon the ground...[and] roamed a tract...almost continually, often cover[ing] the territory in a very few days. Much depended on food supply, climatic conditions and the prevalence of animals of the more dangerous species...though...often...for no other reason than that...[they] had tired of remaining in the same place."*
>
> *E. R. Burroughs, Tarzan of the Apes, 1912*

## INTRODUCTION

Detailing ranging behaviour is fundamental to an understanding of association patterns and ensuing interactions, revealing the opportunities individuals have to interact, and the degree to which one individual may be able to predict the location of others. However, ranging behaviour of male chimpanzees has received less attention than that of females, and remains poorly understood.

Female chimpanzees have been found to spend the majority of their time within a relatively restricted 'core area' while males range more widely, patrolling the boundaries of a shared home range (Wrangham, 1977, 1979; Wrangham & Smuts, 1980). These observations have been interpreted in the light of theoretical considerations of the factors limiting reproductive success. The result is a model of chimpanzee sociality in which female core areas function as dispersed foraging areas, whilst males range fairly evenly (Wrangham, 1975, 1986) over an area containing a number of female core areas. Males are regarded as cooperating to defend access to these females from males in other groups, a single male being unable to defend access to one or more females because of the sheer size of female core areas (Wrangham, 1979; Mitani & Rodman, 1979; Dunbar, 1988a). Relationships between neighbouring groups of males are thus competitive, and often intensely hostile (Goodall et al., 1979; Nishida, 1979).

Models of male reproductive strategies (Dunbar, 1988a) support the notion that males search for reproductively active, or cycling, females at random throughout their shared range, in the process foraging and defending the community territory. An alternative strategy, remaining with a group of females, becomes a better option only when females form relatively large, somewhat stable, groups, or when the distance at which males can detect females is very short.

Further observations suggest, however, that the currently accepted model (Wrangham, 1975, 1979) is an incomplete explanation of male chimpanzee ranging patterns, and thus their reproductive strategies. Chimpanzee males spend much of their time associating, and interacting, with other males, forming the relationships which appear to be critical in determining their reproductive success (Wrangham, 1986; Nishida & Hiraiwa-Hasegawa, 1987). Such interactions occur in small parties, which rarely contain more than a fraction of the community's males. Pursuit of particular relationships requires non-random association patterns (see Chapter 5) and by implication, non-random ranging strategies.

Male chimpanzees of the Kasakela community in the Gombe National Park spend 80% of their time in relatively restricted parts (40-60%: Wrangham & Smuts, 1980) of the community range, occupying core areas which are on average larger than female core areas, but otherwise similar; evenly distributed over the community range and almost completely overlapping (Wrangham, 1977; Wrangham & Smuts, 1980). No evidence of a sex difference in patterns of range use was found for the Kanyawara community of Kibale National Park, other than more frequent sightings of males towards the edge of the trail system (Chapman & Wrangham, 1993).

Wrangham's original model (1975) does not preclude the existence of male core areas, although it does not predict them either. In the absence of detailed data on individual ranging patterns (Wrangham, 1977), his model, for convenience, assumed no differences between males in their ranging patterns (Wrangham, 1979). As a result, subsequent thinking has ignored a potentially important facet of male chimpanzee behaviour. Male core areas have not been assessed, no functional explanation for their existence has yet been made, and no attempt has been made to explain why male ranging patterns might deviate from the expectations of the currently accepted model of chimpanzee sociality. Furthermore, the implications of restricted ranging for male mating strategies have yet to be examined.

The behaviour of females appears also to cast doubt on the assumed mating patterns of chimpanzees. Females do not appear to remain in their core areas when sexually receptive, but may seek out and associate with adult males. When cycling and showing full or partial anogenital swelling, females are known to range more widely than at other times, associating with adult males and travelling throughout the community home range (Tutin, 1979; Nishida, 1979). Observations at Mahale suggest that females search actively for mating partners. They are described as approaching adult males, copulating, and departing (Takahata et al., 1996).

Given the importance of inter-male relationships for chimpanzees, consistently finding appropriate individuals, whether allies or competitors, is likely to be of crucial importance. The ability to predict the location of these males would clearly aid in this and so be of adaptive advantage.

If males spend the majority of their time in relatively restricted cores areas, and this is known to other community members, any individual should be able to locate that male with a fair degree of predictability, at least to within vocal communication range. Chimpanzee long distance calls, pant-hoots, are given primarily by males, and are thought to summon, or at least notify, the caller's allies of his location (Mitani & Nishida, 1993; Clark, 1993; Clark & Wrangham, 1993, 1994).

While the call may carry information regarding the caller's identity, and his approximate direction, less information regarding the distance between caller and receiver, is likely to be conveyed. Attenuation of calls in thick forest is likely to be fairly rapid, and, through a mosaic of vegetation, unpredictable. The existence of core areas, particularly if highly structured, should aid in predicting the location of the caller. In thick forest pant-hoot vocalisations may travel less than 800 metres, while in more open forest they can travel well over a kilometre (personal observation; Z. T. Kwede, personal communication). Where the habitat covers rough terrain**,** vocalisations may be restricted in range to a single valley. Any male would be at an advantage if his allies knew where to find him, and were likely to be relatively close *before* any call is made. Males' core areas may therefore function to increase the probability that males can be located by any individual searching for them. This hypothesis yields the following predictions:

*Prediction 1*: Core areas are small relative to total range areas, such that most time is spent in a small fraction of the home range.

*Prediction 2*: Individual males' core areas should be recognisably distinct, as determined by the degree to which they overlap, with overlaps significantly less than the near complete overlap (95-100%) assumed in the Wrangham model. The risks associated with range boundaries, together with competition for access to the same females should, however, mitigate against completely dispersed, distinct and non-overlapping, male core areas.

*Prediction 3*: With core areas serving a social rather than ecological function, there should be no systematic difference between male core areas in relation to habitat. Any habitat differences should be random with respect to age, status, and social strategy.

If the size and location of male core areas are produced by patterns of association and avoidance, then the *degree* of overlap, which can be interpreted as the probability of two animals using the same area, should be proportional to the tendency to associate derived from observed composition of parties. Pressure to occupy the same space may result in the creation of multinuclear ranges, with each core a number of discontinuous areas. The overlap between these 'fragmented' cores should be relatively low, as each male becomes identified with particular locations.

*Prediction 4*: Core area overlap should correlate positively with association strength.

A further crucial assumption of Wrangham's model is that males 'share' a community range and cooperate in its defence (Wrangham, 1979). Data presented in Chapter 4, and elsewhere (Tutin, 1979; Nishida, 1983) suggests that the alpha male benefits disproportionately from group defence of female core areas, and lower status males may withhold cooperation in range defence (Bygott, 1979). Nishida & Hiraiwa-Hasegawa (1987) point out that both allying with the alpha male in range defence, and usurping alpha status, are likely to be adaptive strategies, and that low status males may support an alpha male only so long as he remains strong. Lower status males would thus support, in effect, the male most able to maintain group defence of the community's territory. Whether or not males cooperate in range defence is likely to be determined by the stake they have in community survival. If subordinate males pursue the strategy of 'controlling' the alpha male by withholding support, they will participate less frequently in 'border patrols', and should have significantly smaller estimates of range area size than estimated for the community range. Males who pursue a strategy of supporting the alpha male should have range area estimates which do not differ significantly in size from that estimated for the community range.

The ranging behaviour of individual male chimpanzees may influence their availability as association partners. If chimpanzees are using the same areas at the same time, this provides them with the opportunity to associate and interact, but says nothing about whether they do so. The technique of "dynamic interaction analysis" (Macdonald et al., 1980; Kenward et al., 1993**)** assesses the tendency of individuals to be in the same places at the same time by comparing the distances between 'same-time' locations recorded for members of a dyad with the average distance between all possible locations of each of the two individuals. Assessing dynamic interaction as the tendency to use the same area on the same day, a positive relationship between the index of dynamic interaction, and dyadic association strength would suggest that association partners are selected from those ranging nearby, or recently encountered. No relationship would indicate that other factors are responsible for the choice of association partners, and suggest that individuals seek desired association partners.

Current estimates of the sizes of the home ranges for different chimpanzee communities vary inversely with perceived habitat quality (Table 6.1). The limited data so far available indicate that habitat quality, rather than group size, is the major factor affecting the size of community ranges, and thus individual home ranges. This implies that the flexibility inherent in a fission-fusion social system offsets the effects of increasing group size. High quality habitat, in relation to food supply, should result in small home ranges and high local population density. Range area therefore provides a crude index of the habitat quality experienced by the animals themselves.

If chimpanzee ranging behaviour is influenced by resource distribution, there should be good evidence of habitat preferences. The relative frequency with which different habitat types are used should differ from that predicted by an assessment of habitat availability. Habitat types are here defined by species composition, to reflect forest types containing important chimpanzee food species. Such a definition is likely to define habitat types important to chimpanzees.

**Table 6.1.** Relationship between community home range, community size, and rainfall (as a indicator of habitat quality). Modified from Wrangham (1986) & Dunbar (1988a). Data from: (1) Tutin et al., 1983 (2) Ghiglieri, 1984 (3) Chapman & Wrangham, 1993 (4) Goodall, 1965 (5) Sugiyama, 1968 (6) Nishida, 1968. Sizes for two study communities are given for sites (4) and (6). For methodological reasons discussed below, range sizes are likely to be overestimates.

| | Study Site | | | | | |
|---|---|---|---|---|---|---|
| | Mt. Assirik[1] | Kibale[2] | Kibale[3] | Gombe[4] | Budongo[5] | Mahale[6] |
| Community range (km$^2$) | ~300 | 23-30 | 9-15 | 10-13 | 19 | 10-17 |
| Community size | ~25 | >44 | >41 | 19;36 | >80 | 27;106 |
| Rainfall (mm) | 955 | 1360 | 1360 | 1495 | 1570 | 1760 |

Resource abundance is a consideration in any study of social behaviour. Smaller ranges should increase the probability of encountering other individuals by chance alone, and in habitats where resources are both abundant and dispersed, opportunities exist for individuals to vary their social environment without incurring foraging costs. In small rich habitats, deliberate searching for other individuals becomes a viable strategy and smaller ranges increase the probability of encountering other parties of community members.

Habitat-specific constraints on visibility may also impinge on chimpanzee grouping patterns. Large cohesive parties are a common response to predation pressure (Krebs & Davies, 1987), and this may be the case in chimpanzees (see Tutin et al., 1983). Low levels of visibility may impede efforts to maintain party cohesion. If chimpanzees are at greater risk of predation in more open habitats, both party size and the degree to which individuals bunch together should increase with increasing visibility. Differences should also be apparent in group activity. If individuals feel threatened in conditions of either poor or good visibility then they would be expected to spend less time resting, when they are likely to be at their most vulnerable, than predicted on the basis of habitat availability.

Analyses of ranging behaviour have been hampered by problems with both defining and measuring an animal’s range. Range is most easily defined as the total area used over a specified time period. Home range is that fraction of the total range ‘habitually used’. This definition is a succinct summary of Burt’s (1943) generally accepted (Seaman & Powell, 1996) definition, “...that area traversed by the individual in its normal activities...Occasional sallies outside the area, should not be considered as part of the home range”. This definition has the advantage of contrasting ‘home’ and ‘total’ range.

The lack of an objective method of defining ‘habitual’ has led some authors (eg Clutton-Brock, 1975) to suggest that the term be avoided, using instead only quantitative measures of the proportion of time spent within each fraction of the range. For many species, measuring the range over any extended period of time is impossible, and the range can only be estimated. To analyse ranging behaviour properly, and estimate sizes of range areas, statistical techniques, and thus quantitative data, are required. Such methods permit an objective definition of home range, based on the probability of an animal being within a particular area (Seaman & Powell, 1996).

A ‘utilisation distribution’, the “two dimensional relative frequency distribution for the points of location of an animal over a period of time” (van Winkle, 1975), describes the relative amounts of time an animal spends in any place. The home range is thus defined as “the smallest sub-region which accounts for a specified proportion of its total utilisation” (Jenrich & Turner, 1969). The total ‘utilisation distribution’ can be estimated from the observed distribution of locations, producing a probabilistic model of home range.

A valid estimate requires minimal temporal autocorrelation between locations; that the location of an animal at time Y is independent of its location at time X. The time interval between successive fixes must therefore be sufficient for an animal to move from any location within the range to any other. A large enough sample size is needed to ensure that the model is a good estimate. When sufficient samples have been taken, a cumulative plot of observed locations against estimated home range area reaches an asymptote (Harris et al., 1990), such that further sampling does not significantly alter the estimate.

A range thus defined will be that habitually used by the animal, as occasional forays beyond the defined range boundaries will not influence the position of those boundaries, so long as the forays are only of short duration. Should an animal be transient, or dispersing, and thus have no *home* range, an asymptote will not be produced (Bowen, 1982; Harris et al., 1990).

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# METHODS

## Data Collection

### *Ranging Data*

Location data were collected during 15 minute interval scan sampling for all independent individuals present in the party. The distance of the focal animal from a known reference point on the trail system was paced on east-west and north-south compass bearings. This ‘known location’ was most often the nearest intersection of trails. The location of other individuals was paced, or occasionally visually estimated, from the location determined for the focal male. When chimpanzees were arboreal, this pacing was done from a point immediately below the subject. When subjects were on the ground, visual estimation would be used for distances up to 10 metres, in conjunction with pacing along a parallel bearing, to minimise disturbance to the animals. On many occasions when the chimpanzees were resting on the ground, and when subjects were travelling, the location would be marked, and returned to later. The majority of pacing was conducted by my field assistant while I conducted focal samples. Visual estimation and short distance pacing were conducted by both observers, with trials indicating a high degree of accuracy and inter-observer agreement (Appendix 3).

The paced distances were converted into a score ranging from -1 to 5, reflecting 25m increments from the trail intersection acting as origin for the grid square coordinates (see Chapter 2): 1 (1-25m), 2 (26-50m), 3 (51-75m), 4 (76-100m), 5 (first 25m beyond the next trail). Zero (0) was used for locations on trails, and -1 for the first 25m before the appropriate trail—the subject was in an adjacent block. This situation arose when the party was distributed around a trail intersection, and individuals were in blocks other than that containing the focal.

Trails were not completely regular, and so not all blocks were 100m x 100m. This was overcome somewhat by pacing to the nearest corner, although occasionally, when the chimpanzees were deep within a block, and the observers were unaware of the closest trail, pacing was not to the nearest corner. Pacing was the fastest method of determining distances, other than visual estimation which itself was severely limited in range. ‘Range finders’ with a limit of 30 metres were available, but poor light and low levels of visibility, combined with the limited maximum range, precluded their use. A tape only gave accurate readings when taut, and not tangled over vegetation. Collapsing the paced distances to 25m$^2$ blocks is a conservative approach to the accuracy limits of the methods used to define location; in many cases the location of individual chimpanzees was accurate to within 10, and possibly to within 5 metres. Such accuracy is likely to have fallen away when recording locations away from the trail system, and I judged 25m blocks to give a sufficient degree of accuracy, across all samples, similar to many radio-tracking studies of medium sized mammals (Forde, 1989; Harris et al., 1990).

## *Habitat Data*

### *Point Sampling*

The habitat used by the chimpanzees was assessed as part of 15 minute instantaneous sampling. With each scan, data on seven habitat variables (nearest 5 trees within 10 metres, slope, visibility) were recorded (see Chapter 3). A comparable method was used to determine the availability of habitat types, the same data being collected for 1000 randomly determined points. These points were generated using a simple BASIC program written to produce series of coordinates related to a 25m x 25m grid superimposed upon a map of the trail system. This grid extended beyond the limits of the trail system to cover more completely the area used by the chimpanzees. Points were visited in the most efficient manner possible, sampling points close to one another during the same sampling period. Five of the 1000 points overlapped with previously sampled points, and as a result only 995 random point samples were collected.

At each point, the seven habitat variables described above were sampled. Collection of data was primarily done by my field assistant—this method of sampling was only made possible by his extensive knowledge of trees and very rapid, and precise, identification. For unknown species, a sample was taken, which I identified later with the aid of botanic keys (Hamilton, 1981; Hawthorne, 1990), and the combined experience of project staff.

### *Line Transect Sampling*

Systematic line transect sampling is an alternate method of assessing available habitat. Seven transects were used, five which ran east-west, and two which ran north-south. The east-west transects were the five transects used by the Budongo Forest Project habitat survey (Plumptre & Reynolds, 1994), although three were extended to the east to sample areas of forest known to fall within the chimpanzees’ range. Use of existing transect lines provides the opportunity for a direct comparison of results. Each of these five transects was located in a stratified random manner (Plumptre & Reynolds, *ibid*). The north-south transects were selected from existing trails as the two furthest apart, to sample areas not covered by the original lines. Habitat changed more noticeably along north-south gradients within the study area, and it seems unlikely that the non-random placement of these lines would lead to anomalous results. The N-S transects were 4500 metres and

3250 m in length, and 1km apart in an east-west direction. The E-W transects were (from north to south) 2100 m, 2225 m, 2200 m, 2375 m and 3325 m in length.

Sampling was conducted at 25 m intervals; at each interval, identical data to those collected by random point sampling were recorded. Identification of trees was conducted by my field assistant.

## Data Analysis

### *Ranging Data*

In order to use many of the sophisticated techniques developed to analyse ranging data, a minimal level of temporal autocorrelation between data points is necessary to ensure data points are independent (Swihart & Slade, 1985; Harris et al., 1990). In addition, dependence between individuals should be minimal, to enable valid comparisons of range area and overlap. The estimate of an individual’s range must be freed from any bias introduced by association decisions made by the animal if it is to be used to test for such decisions.

To minimise temporal autocorrelation, I calculated a maximum range area for two wide ranging males, and, following Rodman & McHenry (1980**),** calculated an average travel speed for chimpanzees. This is not simply a theoretical straight-line speed of travel (see Harris et al., 1990) but takes account of the meandering which is characteristic of chimpanzee travel. It was not possible to calculate average speed for Budongo chimpanzees, as the methods used here precluded the calculation of day range length and so I used data presented in Wrangham (1977). The figure was in close agreement with that calculated by K. Hunt (personal communication).

Numerous dawn-dusk follows of single individuals were conducted by Budongo Forest Project field assistants, but these were heavily biased in favour of short day ranges—where the chimpanzees had been followed away from the trail system, no effort was made to record location until they re-entered the trail system, and thus these records were not useful for calculating day range length. Comparison of range dimensions and travel speed indicated an interval of 2-4 hours between successive locations would provide sufficient time for an individual chimpanzee to move from any one location within the range to any other. I used a four hour time interval.

For each adult male, a data-set of locations separated by at least 4 hours was extracted from scan sample records. These data sets contained records only when the subject was focal, first sighted after an interval of over four hours, and, where an individual was in a party for more than four hours continually without being the subject of a focal sample, a single record of location separated by more than four hours from the preceding record.

A regular grid of north-south and east-west lines, each 25m apart, was superimposed upon an enlarged map of the study area. For each record in each male's location data set, the grid square and the 1-4 coordinate system was converted to a location within this grid. Records which lay outside the trail system were in the form of a number of paces along a compass bearing. These were converted directly into east and north coordinates.

Location data recorded by Budongo Forest Project field assistants was generally not of sufficient accuracy to allow its inclusion in these data sets. Three such points, which had been visited by myself and my field assistant, were of sufficient accuracy to allow their inclusion.

### *Analysis Techniques*

Various methods have been developed for the analysis of home range data. The simplest are the 'non-statistical' empirical techniques, minimum convex polygons and grid cell analysis, the former being the most widely used technique in home range studies (Harris et al., 1990). Both techniques have been used in studies of chimpanzee ranging patterns (Wrangham, 1975; Wrangham & Smuts, 1980; Chapman & Wrangham, 1993).

A minimum convex polygon (MCP) is the smallest area polygon to encompass all of the animal's locations, or 'fixes'. As such, this method is heavily biased by the presence of outlying, peripheral fixes, and thus fails to exclude "occasional sallies outside the area" (Burt, 1943). It also fails to provide any information about the internal 'structure' of the range. It is, however, the only method directly comparable between studies, and for this reason alone Harris et al. (1990) recommend its use in all studies.

Grid cell analysis is a good method for the examination of habitat usage and conspecific interactions, although less useful for determining range area (Harris et al. *ibid*). Grid cell analysis is highly sensitive to the size of the grids used (Clutton-Brock, 1975), requiring small grid cells to provide accurate results. It thus requires a large data set, which may be prohibitive for large range areas. For these reasons, this method was not used in this study.

Statistical techniques for the analysis of ranging data are more complex, and model the animal's ranging behaviour based on a sample of fixes. The models attempt to construct a 'utilisation distribution' for each animal. Simple probabilistic models, such as bivariate normal ellipses (Jenrich & Turner, 1969), assume the pattern of an animal's use of space conforms to a specific distribution, usually some version of the normal distribution. They can thus be described as parametric. This assumption is unlikely to hold (Seaman & Powell, 1996; Kenward & Hodder, 1996), and these methods are not used here.

Non parametric techniques include harmonic mean and kernel methods, together with cluster analysis and Dirichlet's tessellations (Worton, 1989: Dixon & Chapman, 1980; Kenward, 1987; Wray et al., 1992).

The harmonic mean method provides details concerning both range area and structure. It is not particularly sensitive to departures from normality, and has been described as "elegant" (Harris et al., 1990). The technique models the utilisation distribution using the distribution of fixes, but is unfortunately very sensitive to differences in the accuracy of locating fixes ('tracking resolution'), and to the grid size used during analysis (Kenward & Hodder, 1996). Different implementations of the techniques are thus likely to give different results (Kenward & Hodder, *ibid*). Although Boulanger and White (1990) found this to be the best method of home range estimation, the technique is not used here since it has been surpassed by developments in the 'kernel' method of analysis (Worton, 1989), which currently appears to be the most accurate technique available (Seaman & Powell, 1996).

Kernel analysis uses the kernel density estimator, a non-parametric statistical technique for estimating probability densities (Silverman, 1986), to model the utilisation distribution. The kernel density estimator is not influenced by grid size effects (unlike the harmonic mean method), and can potentially estimate densities which are non-normal (Seaman & Powell, 1996). The width of the kernel, or probability distribution, is known as the 'smoothing parameter'. The density (at any one location) is the amount of time spent at that location. During data analysis, each observation point, or fix, is replaced by a kernel with a density corresponding to the amount of time spent at that location. A regular rectangular grid (unrelated to that used to record the observations) is superimposed, and for each grid intersection an estimate of density (time spent) is obtained. This estimate is based on information from all observation points, with those close to the intersection contributing more to the estimate than those far away. In essence, the density estimate at an intersection is a weighted average of the densities of all kernels which overlap that intersection (Seaman & Powell, *ibid*).

High values of the smoothing parameter produce wide kernels, emphasising the general shape of the distribution, and 'smoothing out' the resultant range. Low values produce narrow kernels, and emphasise details in the data structure (Seaman & Powell, 1996; Kenward & Hodder, 1996). Different values for the smoothing parameter can have significant effects on range size, one of the primary drawbacks of this method (Harris et al., 1990). The smoothing parameter can be determined objectively by a method known as 'least squares cross validation' (LSCV: Silverman, 1986). This method sub-samples the data set in the manner of a 'jackknife estimator', and searches for the smoothing parameter which gives the lowest error (the "mean integrated square error": Silverman *ibid*; Worton, 1989) associated with the density estimate. Non-normal utilisation distributions can thus be modelled, with the kernel being tailored to the animal’s use of space.

Kernel analysis can be conducted (Worton, 1989; Seaman & Powell, 1996; Kenward & Hodder, 1996) as fixed (smoothing is the same for all areas), adaptive (more smoothing for low density areas, less for high density areas), or inverse adaptive. Adaptive kernel analysis adds emphasis to areas where only few observations were observed, and was initially thought to provide more accurate results (Worton, 1989). More recently, fixed kernels have been found to give better results (Seaman & Powell, 1996). Data structure can however influence the results of kernel analysis, and for this reason it was decided to use both fixed and adaptive kernel analysis here. Kernel analysis is, unlike harmonic mean analysis, little influenced by outliers, but for a modelling technique requires a relatively large number of fixes (50 - 150, Seaman & Powell, *ibid)*. For LSCV to find optimal smoothing parameters, the error in locating animals must be small in relation to range size.

Other techniques, such as Dirichlet’s tessellations (Wray et al., 1992) and cluster analysis (Kenward, 1987), are particularly useful in identifying core areas. These techniques produce similar results (Kenward & Hodder, 1996). They are non-parametric, but require relatively high numbers of fixes to provide accurate results. Cluster analysis is a step-wise process in which the two nearest fixes are joined to form a single cluster, the fix nearest to this cluster is added next, unless it is closer to a fourth fix in which case a second cluster is formed. This process continues, with clusters being joined when the nearest fix to a cluster is already within a cluster, until the required percentage of fixes are included (Kenward, 1987).

Two methods of determining the distance between fixes were available, ‘nearest neighbour’, and ‘centroid’ (mean distance of fix to all other fixes in the cluster). The ‘nearest neighbour’ method is suggested to provide best results when the animal makes a series of forays from a ‘home base’ (Kenward & Hodder, 1996). This is not typical of chimpanzee behaviour, and so the centroid method was used to determine distances.

To summarise, minimum convex polygons were used to provide an initial estimate of range area, comparable across studies. Kernel analyses, both fixed and adaptive methods implementing least squares cross validation, were used to provide more accurate estimates of range area and details of range structure. Cluster analysis was used similarly, but especially to provide detail of range cores.

### *Analysis Conducted*

Home ranges were calculated for each of the adult males, for the period 10/94 - 12/95. Once data were selected to ensure independence between sequential locations and between individuals, the number of data points for each male was judged insufficient to warrant analysis by time blocks. Individual male's data sets were merged, excluding same time, same location records, and the resultant file analysed using the same techniques to produce estimates of community home range.

Although it is usual (Cresswell & Harris, 1988; Harris et al., 1990) to specify the area enclosing 95% of fixes as the home range, thereby excluding Burt's (1943) "occasional forays", I decided to use 100% inclusion to define home range. This was because study animals were occasionally sighted beyond the area they were systematically sampled, and occasionally followed on such short duration forays. These locations did not appear in the data set used for ranging analysis.

The ranges presented here are thus not total ranges over the study period, but estimates of habitually used areas, or home ranges. Incremental area analysis (Kenward & Hodder, 1996) was used to determine whether range areas reached asymptotes, and were thus good estimates of home range. Spearman rank correlations were used to determine whether estimated range area was independent of the number of locations for each male.

The same data sets were also used to calculate the size of core areas, defined, following Wrangham (1979), as 80% of the utilisation distribution; the areas where there was an 80% probability of locating the individual at any particular time. For both home range and core areas, agreements between the different analysis methodologies were assessed using Spearman rank correlations, and to determine whether range and core areas were related to status and association strategy. Range characteristics of the asocial male TK were compared to that of social males using Student's t-test, comparing a single observation to a sample. The fraction of each male's range which accounted for his core area was calculated as a percentage.

The degree to which two individuals use the same area can be determined by measuring the overlap between ranges, with each overlap considered as a percentage of the range 'shared' with another individual. As range areas differ, the percentage of A's range overlapped by B can be different from the percentage of B's range overlapped by A. Assessing all dyadic overlaps produces an asymmetrical matrix, in which areas in rows are overlapped by areas in columns.

The degree of overlap between individual male core areas was investigated using Kruskal-Wallis one way analyses of variance, and Mann-Whitney U tests, comparing identity, status, and association strategy with the degree of overlap between core areas.

Mann-Whitney U tests were also used to compare the median degree of core area overlap determined by both cluster and kernel analysis with a set of randomly determined overlaps falling between 95 and 100%, to test whether males conformed to one of the assumptions made about their ranging behaviour in Wrangham's (1975) model. The range 95-100% was chosen to represent an 'almost complete' overlap. To determine the tendency of individuals to be in the same part of the forest on the same day, dynamic interaction analysis was used.

Dynamic interaction analysis compares observed, and possible, distances between pairs of animals. The average distance between all same time (here, same day) fixes for each pair is calculated, and compared to the same measure calculated for a number of possible distances equal to the square of the number of same time fixes (with a maximum of 5000 possible distances). Possible distances are those between any of the observed locations of each of the animals irrespective of the temporal relationship between the fixes. The difference between the observed and predicted locations is expressed as an index (Kenward & Hoddar, 1996). Here indices were calculated using median, and geometric mean distances.

Matrix correlation permutation tests (see Chapter 4) were used to examine the relationship of dyadic association strengths (Chapter 5) with core area overlaps, both static (percentage of core area overlap) and dynamic (dynamic interaction index) overlap.

### Habitat data

For each sampled point, during scan, and vegetation point, sampling, the five recorded species of tree were allocated to a single forest type. To identify forest types with possible relevance to chimpanzees, scan sample records were analysed to establish which species of tree contributed most to the chimpanzee diet, as measured by feeding time. In addition, the relative contributions of fruit and leaves to the diet, and 'major' and 'minor' fruit species (*sensu* Wrangham et al., 1996) were established. Food items consumed, and percentages of time spent feeding on each species are given in Appendix 4.

The forest types presented by Eggeling (1947; see Chapter 2) and those used by the Ugandan forest department (A. J. Plumptre, personal communication) were elaborated upon to distinguish a 'chimp-orientated' forest type classification. *Mixed forest* was subdivided into mixed forest types dominated by the top five food plant genera, and other forest types not recognised by Eggeling (1947) were distinguished. Estimates of available habitat produced by random point sampling and systematic line sampling were compared using a chi-squared test. Visibility estimates were grouped into four categories: *low* (0-5m), *medium-low* (6-10m), *medium-high* (11-15m), and *high* (16m +).

To investigate habitat selection, a one sample chi-squared test was used to compare the observed use of habitat with that predicted by line transect sampling, for both forest types and level of visibility. For each forest type, Ivlev's electivity index (Krebs, 1989) was calculated to indicate degree of preference:

Ivlev's index = %used - % available / % used + % available

This index ranges from -1 to +1, with zero indicating no preference, -1 complete avoidance, and +1 complete preference.

A habitat map was constructed using both randomly sampled and scan sampled point data, and used to determine the habitat composition of each male's home range. The number of habitat points for each forest type within home range and core boundaries were counted for each male. and transformed into percentages of habitat samples within the range. Differences in habitat proportions for male core areas were investigated using the non-parametric Friedman's two-way analysis of variance by ranks, with Dunn's *post hoc* multiple comparisons.

The relationship between visibility limits and party size and dispersion was assessed using the party size data set (Chapter 5), selecting parties which were terrestrial, or no more than two metres above the ground. Kruskal-Wallis analysis of variance, with Dunn's *post hoc* multiple comparisons, was used to determine the influence of visibility on party size and group dispersion. Differences in the relative frequencies of behaviour between visibility categories were investigated using chi-squared tests, for chimpanzees on the ground only, and for those on, and within two metres of, the ground. For this analysis visibility categories were redefined to avoid expected frequencies of less than one, and to reduce the number of expected frequencies under five to fewer than 20%. The categories used were: *low* (0-5m), *medium* (6-10m), and *high* (11m+).

# RESULTS

## Habitat

### *Diet*

Sonso chimpanzees were observed feeding on more than 55 species of plant, five animal (four vertebrate, and one invertebrate) species, consuming at least 114 plant food items (see Appendix 4). Fruit accounted for 64.5% of feeding time, and leaves 19.7%. 3.2% of feeding time was spent eating terrestrial herbaceous vegetation (THV) pith. Eight tree species (from 6 genera) accounted for 81.2% of feeding time. Four species were distinguished as major fruit species: *Ficus sur*, *Ficus mucuso, Maesopsis eminii* and *Celtis durandii*. While these four species accounted for more than 75% of time eating fruit, they only accounted for 49.2% of feeding time.

## *Forest Types*

A total of 13 forest types, arranged in five groups, were distinguished (see Appendix 2 for species codes):

### *Ironwood forest*

| | |
|---|---|
| Cynometra mixed: | *Cynometra* (ironwood) dominated mixed forest. Two or more of the following species present in the sample: *Cya*, *Lm*, *Ri*. No other species more highly represented. No *Bpy* or *Me*. |

### *Mixed forest*

| | |
|---|---|
| Khaya mixed: | *Khaya* (mahogany) dominated forest. At least one *Ka* present in the sample. No more than two other type defining species present. No *Bpy* or *Me*. |
| Celtis mixed: | *Celtis* dominated mixed forest. Two or more *Celtis* trees present in sample. No other species more strongly represented. No *Bpy* or *Me*. |
| Ficus mixed: | *Ficus* dominated mixed forest. Two or more *Ficus* trees present in sample. No other species more strongly represented. No *Bpy* or *Me*. |
| Mixed forest: | No type-defining species, or no single species, dominating sample. |

### *Swamp*

| | |
|---|---|
| Swamp forest: | At least one *Rf* or *Mst* present in the sample. Permanently or seasonally inundated. 'Open' swamp forest is also characterised by spiked non-woody vegetation, with waterlogged soil throughout most or all of the year. |

### *Colonising forest (woodland)*

| | |
|---|---|
| Maesopsis: | *Me* dominated woodland. At least one *Me* present in the sample. No more than two of any other type defining species present. |
| Maesopsis-celtis: | *Me* woodland with two or more *Celtis* trees present in sample. |
| Maesopsis-ficus: | *Me* woodland with two or more *Ficus* trees present in sample. |

| | |
|---|---|
| Broussonetia: | Broussonetia dominated woodland. All trees in sample *Bpy*. |
| Broussonetia-mixed: | At least one *Bpy*, and one other species, present in the sample. No *Me* present. |

### *Open areas:*

| | |
|---|---|
| Climber thicket: | Open area dominated by woody climbers. Sample consists of unspecified climber species. |
| Other: | Open area covered by grass or other low level vegetation, village gardens, village and sawmill buildings. Heterogeneous habitat type. |

Certain forest types were abundant in the Sonso region, whilst others were rare (Table 6.2). Point, and line transect, sampling produced significantly different estimates of the 'availability' of different forest types ($\chi^2 = 67.06$, $df = 12$, $p < 0.001$; Table 6.2), and also areas of different visibility ($\chi^2 = 42.65$, $df = 3$, $p < 0.001$). Partitioning the degrees of freedom within the contingency table showed significant differences were due only to rare, and presumably localised, forest types. Point sampling produced significantly greater estimates of the abundance of Maesopsis woodland ($\chi^2 = 7.81$, $df = 1$, $p < 0.01$) and Broussonetia woodland ($\chi^2 = 3.89$, $df = 1$, $p < 0.05$). Line transect sampling produced significantly greater estimates of the abundance of Maesopsis-celtis woodland ($\chi^2 = 7.30$, $df = 1$, $p < 0.01$), climber thickets ($\chi^2 = 21.76$, $df = 1$, $p < 0.001$) and open areas ($\chi^2 = 23.47$, $df = 1$, $p < 0.001$).

Point sampling was carried out intensively within a restricted area, in and around the trail system. Line transects passed through this region, but extended far beyond the limits of the trail system. Point sampling was thus more appropriate for habitat analysis of individual ranges and core areas, whilst line transect sampling of habitat was more appropriate for community range-wide analysis, specifically the question of habitat selection by chimpanzees.

## *Habitat Selection*

Chimpanzees showed clear evidence of selecting particular habitat types, being found significantly more or less often in certain habitat types than predicted on the basis of habitat availability ($\chi^2 = 23112.76$, $df = 12$, $p < 0.0001$; Table 6.3). This effect was primarily due to strong preference for Broussonetia, and Broussonetia-mixed, woodland, a strong preference for Ficus-mixed forest, and avoidance of Cynometra-mixed forest. *Broussonetia papyrifera*, and *Ficus* spp. were major chimpanzee food items. Cynometra-mixed forest is thought to be low in food abundance (A. J. Plumptre, personal communication), except for a short period during which *Cynometra alexandrii* fruits.

**Table 6.2.** Habitat composition of the Sonso region, assessed by both random point sampling, and systematic line transect sampling.

| | Point sampling | | Line transect sampling | |
|---|---|---|---|---|
| Forest Type | n (=995) | % habitat | n (=856) | % habitat |
| Cynometra-mixed | 177 | 17.8 | 147 | 17.2 |
| Khaya-mixed | 127 | 12.8 | 93 | 10.9 |
| Celtis-mixed | 236 | 23.8 | 192 | 22.4 |
| Ficus-mixed | 97 | 9.8 | 84 | 9.8 |
| Mixed forest | 242 | 24.3 | 215 | 25.1 |
| Swamp | 40 | 4.0 | 30 | 3.5 |
| Maesopsis woodland | 38 | 3.8 | 13 | 1.5 |
| Maesopsis-celtis | 5 | 0.5 | 15 | 1.8 |
| Maesopsis-ficus | 2 | 0.2 | 4 | 0.5 |
| Broussonetia woodland | 10 | 1.0 | 2 | 0.2 |
| Broussonetia-mixed | 16 | 1.6 | 12 | 1.4 |
| Climber thicket | 0 | 0.0 | 18 | 2.1 |
| Other | 5 | 0.5 | 31 | 3.6 |

**Table 6.3.** Habitat selection, comparing habitat used from all range analysis locations with habitat available determined by line transect sampling. Habitat preference is measured by Ivlev's electivity index = (%used - %available)/(%used + %available), from Krebs (1989).

| | Available | | Used | | Electivity |
|---|---|---|---|---|---|
| Forest Type | n (=856) | % habitat | n (=2226) | % habitat | index |
| Cynometra-mixed | 147 | 17.2 | 110 | 4.9 | -0.56 |
| Khaya-mixed | 93 | 10.9 | 82 | 3.7 | -0.49 |
| Celtis-mixed | 192 | 22.4 | 465 | 20.9 | -0.03 |
| Ficus-mixed | 84 | 9.8 | 492 | 22.1 | +0.39 |
| Mixed forest | 215 | 25.1 | 420 | 18.9 | -0.14 |
| Swamp | 30 | 3.5 | 21 | 0.9 | -0.59 |
| Maesopsis woodland | 13 | 1.5 | 65 | 2.9 | +0.48 |
| Maesopsis-celtis | 15 | 1.8 | 69 | 3.1 | +0.27 |
| Maesopsis-ficus | 4 | 0.5 | 8 | 0.4 | -0.11 |
| Broussonetia woodland | 2 | 0.2 | 315 | 14.1 | +0.97 |
| Broussonetia-mixed | 12 | 1.4 | 164 | 7.4 | +0.68 |
| Climber thicket | 18 | 2.1 | 11 | 0.5 | -0.62 |
| Other | 31 | 3.6 | 4 | 0.2 | -0.90 |
| Visibility Category | n (=856) | % | n (=1836) | % | E.I. |
| Low (0-5m) | 219 | 25.6 | 438 | 23.9 | -0.03 |
| Med.-low (6-10m) | 399 | 46.6 | 992 | 54.0 | +0.07 |
| Med.-high (11-15m) | 192 | 22.4 | 341 | 18.6 | -0.09 |
| High (16m+) | 46 | 2.6 | 65 | 3.5 | +0.15 |

Chimpanzees also showed significance preference with regard to visibility constraints ($\chi^2 = 16.08$, $df = 3$, $p < 0.01$; Table 6.3). The low values for the preference indices suggest that the degree of preference is not strong, however, with only the index for areas of high visibility exceeding 0.10. No clear pattern was present in visibility preferences. Slight preferences for medium-low (6-10m) and high (16m+) visibility areas, and a slight avoidance of areas of medium-high (11-15m) visibility, suggest that within the majority of forest types, chimpanzees may prefer an intermediate level of visibility, whilst other factors influence the preference for high visibility areas. *Bpy*-woodland, for example, is often more open than other forest types.

## Ranging

The four analysis techniques produced differing results for home range area, as was expected. With no method available to determine which was the 'best' estimate, all figures are presented in Table 6.4.

### *Home Range*

Estimates of home range areas produced by both kernel methods were highly correlated ($r_s = 0.88$, n = 12, $p < 0.001$). MCP and cluster routines use the same algorithm for 100% range areas, and so produce identical total home range area estimates. Kernel estimates were not significantly correlated with cluster or MCP estimates (adaptive: $r_s = 0.29$, ns; fixed $r_s = 0.31$, ns).

Community range area approached an asymptote (Fig. 6.1) after around 350 fixes. The differences between sequentially and randomly plotted fixes may be the result of a seasonal expansion of the range. Individual ranges likewise reach asymptotes between 110 and 160 fixes (Fig. 6.2). Range estimates for two males, NJ and JM, failed to show evidence of an asymptote and the existence of an asymptote is questionable for the male CH. The community range area (Fig. 6.3), and the areas for nine or ten of the twelve males can therefore be regarded as good estimates of the habitually used areas for the time period October 1994 and December 1995. Range areas were not correlated with sample size (MCP/cluster: $r_s = 0.21$, n = 12, $p > 0.20$; fixed kernel: $r_s = 0.29$, n = 12, $p > 0.50$; adaptive kernel: $r_s = 0.24$, n = 12, $p > 0.50$).

The ranges of individual males varied in size. Kernel estimates of range size were not correlated with status (adaptive: $r_s = 0.61$, $p > 0.50$; fixed: $r_s = 0.38$, $p > 0.50$), while size estimated by either MCP or cluster analysis was correlated with status ($r_s = 0.74$, n = 12, $p = 0.006$). Minimum area polygon estimates are heavily influenced by outlying points, and the significant correlation may indicate that high status males ranged, albeit infrequently, more widely than those of lower status.

**Table 6.4.** Estimates of community (all males considered together) and individual male home ranges, using four analysis techniques: Minimum convex polygons (MCP); Fixed kernels with least squares cross validation (KNF); Adaptive kernels with least squares cross validation (KNA); Cluster analysis (CST). Range estimates based on 100% fix inclusion.

| | | Home Range Areas: Size (km$^2$) & Percentage of total (%) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | MCP | | KNF | | KNA | | CST | |
| Individual | n | km$^2$ | % | km$^2$ | % | km$^2$ | % | km$^2$ | % |
| All Males | 836 | 6.78 | *100.0* | 6.89 | *100.0* | 14.51 | *100.0* | 6.78 | *100.0* |
| MG | 204 | 4.57 | *67.4* | 4.29 | *62.2* | 10.87 | *74.9* | 4.57 | *67.4* |
| KK | 198 | 4.23 | *62.4* | 3.04 | *44.1* | 8.76 | *60.4* | 4.23 | *62.4* |
| MA | 238 | 4.87 | *71.8* | 4.36 | *63.3* | 8.54 | *58.9* | 4.87 | *71.8* |
| BY | 182 | 4.90 | *72.3* | 4.89 | *71.1* | 13.16 | *90.7* | 4.90 | *72.3* |
| MU | 211 | 3.83 | *56.5* | 3.51 | *51.0* | 8.27 | *57.0* | 3.83 | *56.5* |
| NJ | 173 | 5.41 | *79.8* | 3.45 | *50.1* | 7.29 | *50.2* | 5.41 | *79.8* |
| TK | 160 | 3.17 | *46.8* | 1.07 | *15.5* | 5.02 | *34.6* | 3.17 | *46.8* |
| DN | 250 | 5.89 | *86.9* | 4.27 | *62.0* | 9.17 | *63.2* | 5.89 | *86.9* |
| VN | 242 | 5.63 | *83.0* | 4.52 | *65.6* | 12.85 | *88.6* | 5.63 | *83.0* |
| JM | 111 | 5.16 | *76.1* | 4.70 | *68.2* | 10.95 | *75.5* | 5.16 | *76.1* |
| BK | 161 | 5.40 | *79.6* | 1.84 | *26.7* | 5.69 | *39.2* | 5.40 | *79.6* |
| CH | 171 | 5.03 | *74.2* | 3.92 | *56.9* | 10.69 | *73.7* | 5.03 | *74.2* |

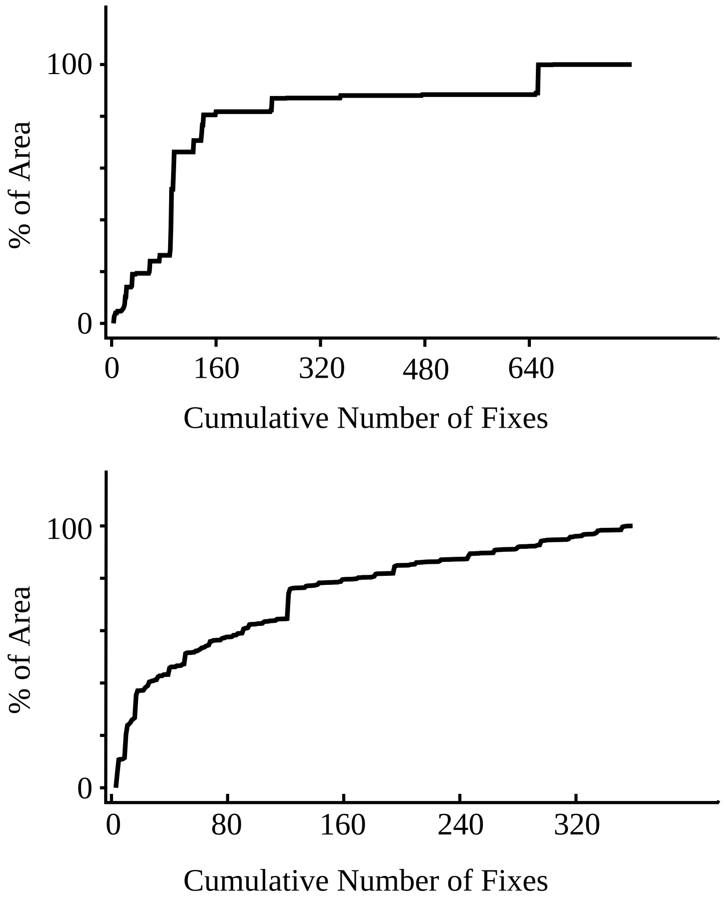

**Figure 6.1**. Incremental area plots for community range, with fixes entered in the order of collection (above) and randomly (below).

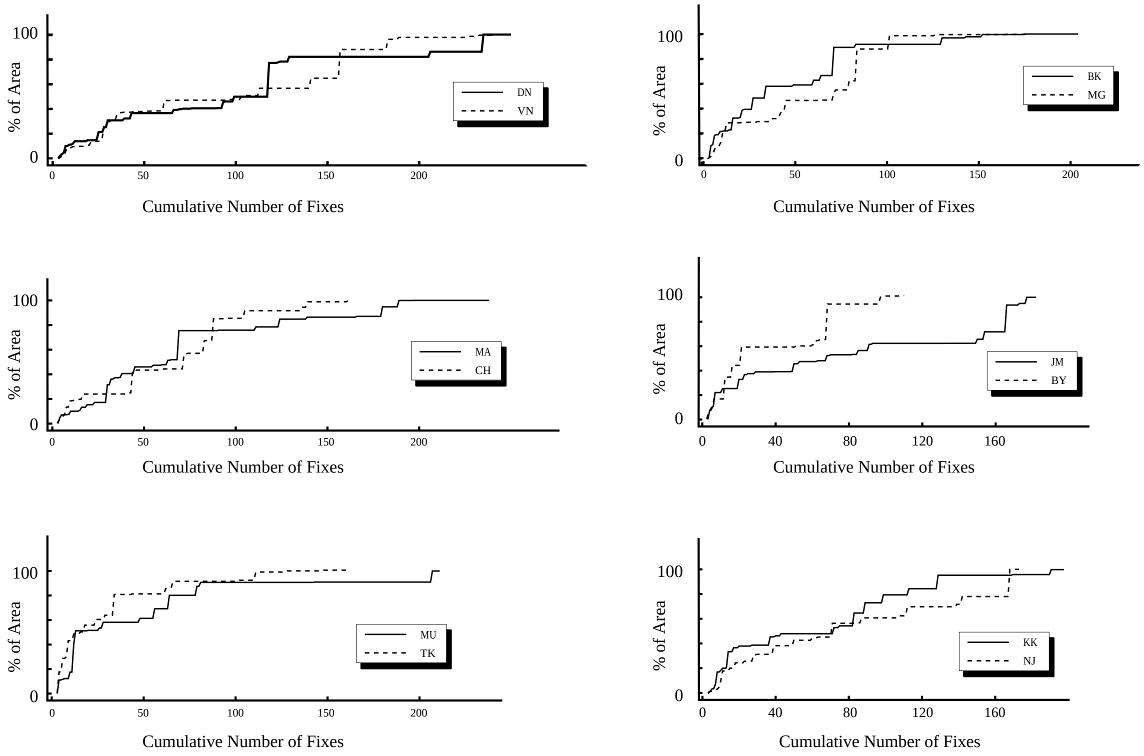

**Figure 6.2.** Incremental area plots for the home range of each adult male. Males are arranged by rows in order of decreasing social status; consecutive pairs are plotted on the same axes.

## *Core Areas*

Little evidence was found for distinct core areas, indicated by discontinuities in utilisation plots. Slight discontinuities were apparent between 70% and 95% of fixes included; the precise value varied with individual and analysis method. These discontinuities were not distinct enough to confidently distinguish core areas. What was clear, however, was that chimpanzee males did not range evenly over the community range, but spent the majority of their time within a relatively small area (Table 6.4; Fig 6.4). Core areas, in the sense of subregions of the home range used disproportionately, did clearly exist, as was found by Wrangham and Smuts (1980) for the Gombe chimpanzees.

Estimates of core area size produced by both kernel methods were highly correlated ($r_s$ = 0.80, n = 12, $p$ = 0.002), although neither adaptive ($r_s$ = 0.23, ns) nor fixed ($r_s$ = 0.33, ns) kernel estimates were correlated with the cluster estimates of the size of core area. Cluster analysis emphases fine grain multi-nuclear cores, whereas kernel methods tend to produce more unified, mono-nuclear core areas. These correlations were thus expected—the methods were deliberately chosen to reveal different aspects of the range structure. MCP estimates were not correlated with estimates produced by any other method, and were not analysed further.

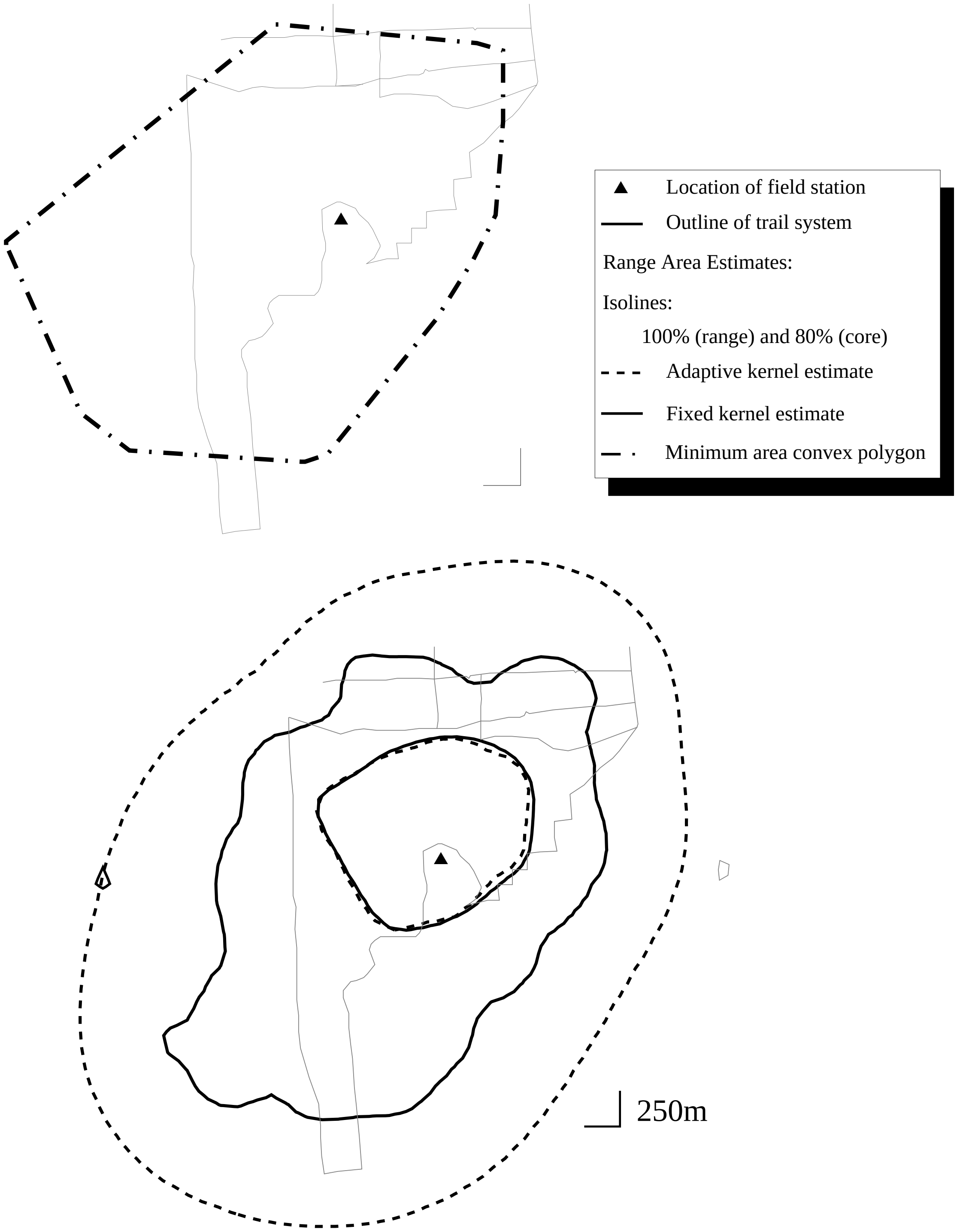

**Figure 6.3**. Community range outlines, as determined by the minimum convex polygon, adaptive kernel, and fixed kernel analysis methods. The location of the Budongo Forest Project field station and an outline of the trail system are shown for reference.

**Table 6.5.** Estimates of 80% core areas; community (all males) and individual males, using four analysis techniques: Minimum convex polygons (MCP); Fixed kernels (KNF) and adaptive kernels (KNA), both with least squares cross validation; Cluster analysis (CST). Size in km$^2$, and core as a percentage of both the respective home range ($\%_{HR}$), and of the total (community) range ($\%_{CR}$).

| | Core Areas: size, % of individual's home range ($\%_{HR}$) & of community range ($\%_{CR}$) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MCP | | | KNF | | | KNA | | | CST | | |
| | km² | $\%_{HR}$ | $\%_{CR}$ | km² | $\%_{HR}$ | $\%_{CR}$ | km² | $\%_{HR}$ | $\%_{CR}$ | km² | $\%_{HR}$ | $\%_{CR}$ |
| All | 1.23 | *18.1* | *18.1* | 1.48 | *21.5* | *21.5* | 1.39 | *9.6* | *9.6* | 1.36 | *20.1* | *20.1* |
| MG | 1.01 | *22.1* | *14.9* | 1.18 | *27.5* | *17.1* | 1.13 | *10.4* | *7.8* | 0.33 | *7.2* | *4.9* |
| KK | 0.96 | *22.7* | *14.2* | 0.99 | *32.6* | *14.4* | 1.02 | *11.6* | *7.0* | 0.24 | *5.7* | *3.5* |
| MA | 1.15 | *23.6* | *17.0* | 1.19 | *27.3* | *17.3* | 1.12 | *13.1* | *7.7* | 0.31 | *6.4* | *4.6* |
| BY | 1.02 | *20.8* | *15.0* | 1.18 | *24.1* | *17.1* | 1.23 | *9.3* | *8.5* | 0.34 | *6.9* | *5.0* |
| MU | 1.12 | *29.2* | *16.5* | 1.06 | *30.2* | *15.4* | 1.05 | *12.7* | *7.2* | 0.34 | *8.8* | *5.0* |
| NJ | 1.00 | *18.5* | *14.7* | 1.25 | *36.2* | *18.1* | 1.20 | *16.5* | *8.3* | 0.31 | *5.7* | *4.6* |
| TK | 0.82 | *25.9* | *12.1* | 0.48 | *44.9* | *7.0* | 0.96 | *19.1* | *6.6* | 0.26 | *8.2* | *3.8* |
| DN | 1.27 | *21.6* | *18.7* | 1.19 | *27.9* | *17.3* | 1.22 | *13.3* | *8.4* | 0.44 | *7.5* | *6.5* |
| VN | 1.41 | *25.0* | *21.0* | 1.07 | *23.7* | *15.5* | 1.12 | *8.7* | *7.7* | 0.31 | *5.5* | *4.6* |
| JM | 1.06 | *20.5* | *15.6* | 1.41 | *30.0* | *20.5* | 1.59 | *14.5* | *11.0* | 0.23 | *4.6* | *3.4* |
| BK | 1.02 | *18.9* | *15.0* | 0.85 | *46.2* | *12.3* | 1.02 | *17.9* | *7.0* | 0.27 | *5.0* | *4.0* |
| CH | 0.98 | 19.5 | 14.5 | 1.12 | 28.6 | 16.3 | 1.23 | 11.5 | 8.5 | 0.29 | 5.8 | 4.3 |

The size of male cores areas were not significantly correlated with status (fixed kernel cores: $r_s = 0.22$, n = 12, $p = 0.50$; adaptive kernel cores: $r_s = 0.24$, n = 12, $p = 0.45$; cluster cores: $r_s = 0.26$, n = 12, $p = 0.41$). Males pursuing either 'intense' or 'gregarious' association strategies (see Chapter 4) did not differ significantly in the sizes of home range and core areas (Table 6.6).

**Table 6.6.** Results of Mann-Whitney U tests, comparing home range and core area sizes for males pursuing different association strategies. Range sizes determined by three methods: Fixed kernels (KFL), adaptive kernels (KAL), cluster analysis (CST). No comparisons are significant.

| | Mann-Whitney U tests ($n_{intense} = 6$, $n_{gregarious} = 5$) | | |
|---|---|---|---|
| | KFL | KAL | CST |
| Home range size | $U = 8$, $p = 0.20$ | $U = 7$, $p = 0.14$ | $U = 14$, $p = 0.86$ |
| Core area size | $U = 15$, $p = 1.00$ | $U = 13$, $p = 0.71$ | $U = 8.5$, $p = 0.23$ |

The asocial male TK did have a significantly smaller home range than other males as determined by MCP or cluster analysis (MCP: $t_s = 2.86$, $df = 10$, $p = 0.017$; cluster: $t_s = 1.94$, $df = 10$, $p = 0.038$), although not by kernel analysis (adaptive: $t_s = 1.94$, $df = 10$, $p = 0.085$; fixed: skewed data). TK's core area did not differ significantly from other males' core areas in size (MCP: $t_s = 1.86$, $df = 10$, $p = 0.092$; cluster: $t_s = 0.84$, $df = 10$, $p = 0.42$; kernel analysis: skewed data). These results suggest that TK ranged less widely.

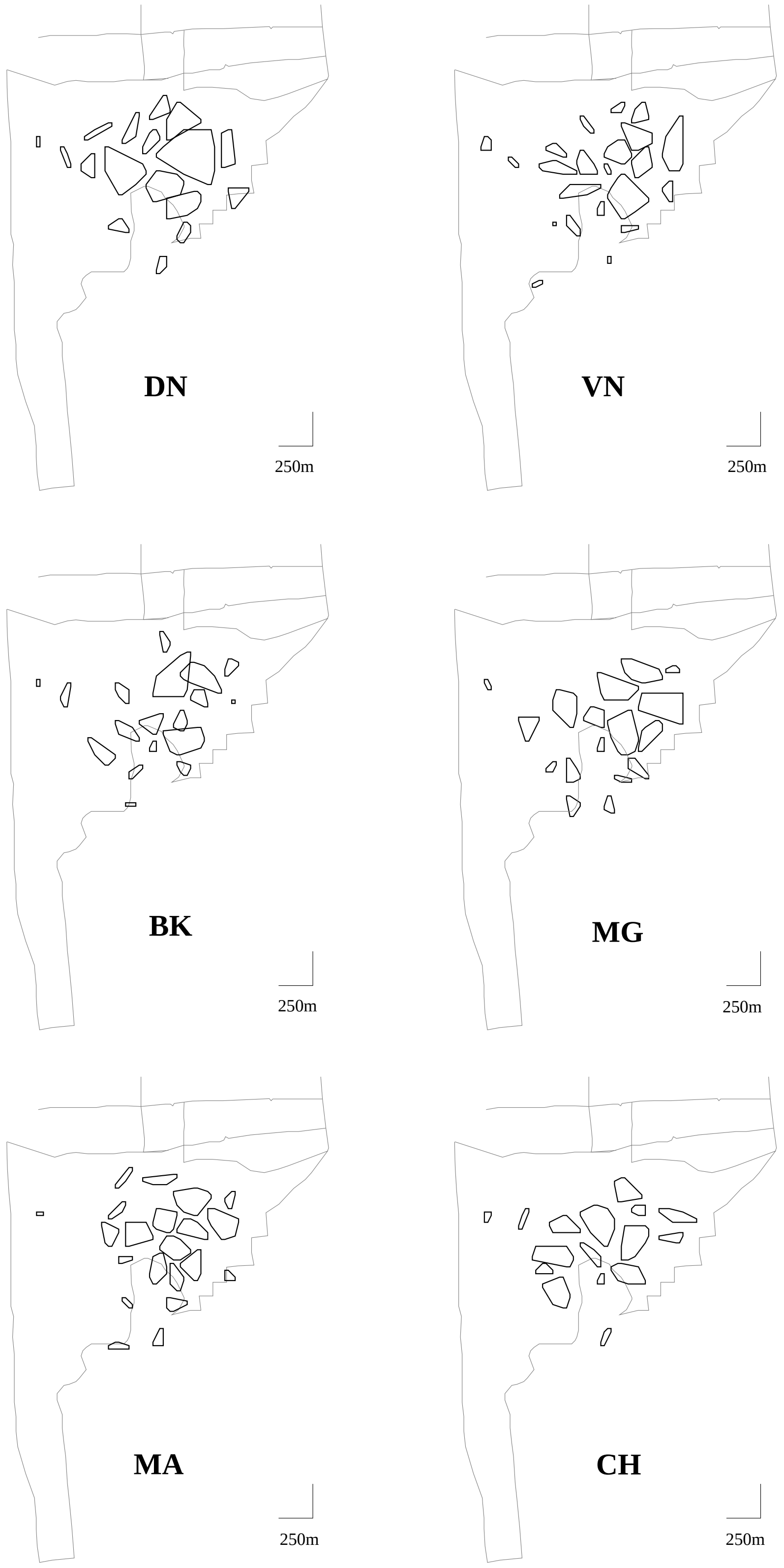

**Figure 6.4a**. Core areas, as determined by cluster analysis, for the six highest status adult males of the Sonso community. An outline of the trail system is provided to permit comparison. Males are ordered in rows by decreasing social status.

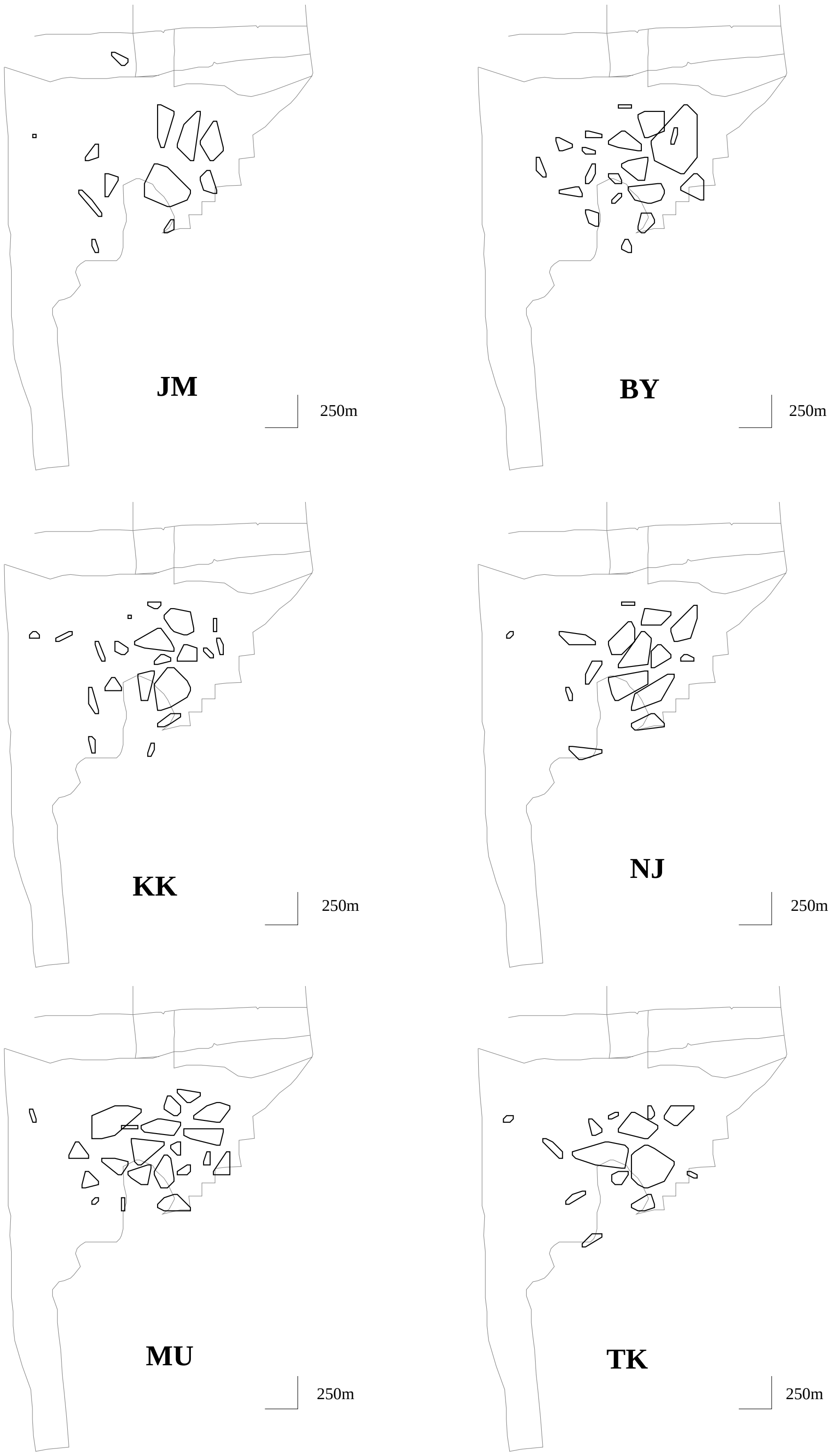

**Figure 6.4b**. Core areas, as determined by cluster analysis, for the six lowest status adult males of the Sonso community. An outline of the trail system is provided to permit comparison. Males are ordered in rows by decreasing social status.

### *Core Area Overlaps*

Males had geographically distinct core areas, as demonstrated by the degree of overlap of each pair of core areas. Percentage overlaps between core areas varied widely between dyads (kernel analysis: range = 32% to 100%, median = 87.5; cluster analysis: range = 31% to 72%, median = 49.8; Fig. 6.5). This suggests that the ranging behaviour of these males did not appear to fit the assumptions of Wrangham's (1975, 1979) model. The median degree of overlap between male core areas was significantly lower than 95-100%, whether cores were determined by kernel analysis (Mann-Whitney $U = 1584.5$, $n_1 = 132$, $n_2 = 132$, $p < 0.0001$) or cluster analysis ($U = 0.0$, $n_1 = 132$, $n_2 = 132$, $p < 0.0001$). Cluster analysis produces core areas which overlap significantly less than those determined by kernel analysis ($U = 1298.5$, $n_1 = 132$, $n_2 = 132$, $p < 0.0001$).

There were significant differences between dyads in the proportion of shared core areas (Kruskal-Wallis anova: cluster: $H = 73.19$, $df = 11$, $p < 0.0001$; fixed kernel: $H = 42.68$, $df = 11$, $p < 0.0001$). Association strategy had no influence on the extent of overlap between core areas determined by kernel analysis (Mann-Whitney U test: $U = 1686.0$, ns). Association strategy did, however, influence the extent of overlap of core areas determined by cluster analysis. Males pursuing an 'intense' association strategy had core areas which overlapped a larger percentage of other males' core areas than did the core areas of males pursuing a 'gregarious' strategy ($U = 853.0$, $n_{\text{intense}} = 66$, $n_{\text{gregarious}} = 55$, $p < 0.0001$; 11 core area overlaps per male).

Cluster analysis emphasises the internal structure of ranges more than does kernel analysis, and thus these results suggest that association strategy does have an influence on the structure of core areas. One possible explanation is that the core areas of males pursuing intense strategies are more localised than those pursuing gregarious strategies. These cores are multi-nuclear, and so gregarious males may spend the majority of their time in a number of dispersed areas. This may be demonstrated in the extreme by the asocial male, TK. The percentage of this male's core area which overlapped the core areas of other males was significantly less than the average percentage (cluster: $U = 338.5$, $n_{\text{TK}} = 11$, $n_{\text{Other Males}} = 121$, $p = 0.0071$; kernel: $U = 0.0$, $n_{\text{TK}} = 11$, $n_{\text{Other Males}} = 121$, $p < 0.0001$).

Overlaps between core areas determined by cluster analysis were significantly and positively correlated with dyadic association strength ($K_r = 315$, $\tau = 0.49$, $n = 12$, $p_r = 0.001$), as predicted by the 'social core' hypothesis. This was not the case for core areas determined by kernel analysis ($K_r = 101$, $\tau = 0.16$, $n = 12$, $p_r = 0.18$).

The degree to which each dyad shares a core area seems to be related to the strength of the association between them, although this relationship was masked by the smoothing used in kernel analysis. Alliance partners are likely, therefore, to be nearby when required, and within range of pant-hoot vocalisations. Social status, however, did not appear to significantly influence the overlap of core areas (cluster cores: $K_r = 165$, $\tau = 0.25$, n = 12, $p_r = 0.11$; $K_r = 53$, $\tau = 0.08$, n = 12, $p_r = 0.35$).

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | 100.00 | 82.19 | 88.56 | 90.82 | 85.34 | 93.21 | 37.78 | 84.88 | 81.69 | 98.87 | 71.69 | 83.94 |
| KK | 97.69 | 100.00 | 98.97 | 99.77 | 91.65 | 98.78 | 43.03 | 96.89 | 95.48 | 99.69 | 79.56 | 91.34 |
| MA | 87.41 | 82.21 | 100.00 | 94.27 | 82.99 | 96.47 | 37.00 | 90.94 | 85.62 | 93.28 | 68.66 | 82.57 |
| BY | 91.14 | 84.12 | 95.48 | 100.00 | 85.13 | 97.84 | 37.13 | 90.41 | 86.09 | 96.47 | 70.72 | 84.34 |
| MU | 95.28 | 85.80 | 93.73 | 94.64 | 100.00 | 97.13 | 41.24 | 92.13 | 92.28 | 95.42 | 78.09 | 96.64 |
| NJ | 87.52 | 77.90 | 91.68 | 91.69 | 81.69 | 100.00 | 36.25 | 89.54 | 83.56 | 92.25 | 67.56 | 83.30 |
| TK | 86.32 | 82.03 | 86.07 | 84.81 | 84.56 | 87.67 | 100.00 | 87.50 | 86.58 | 86.66 | 81.85 | 84.72 |
| DN | 83.91 | 80.12 | 90.61 | 88.97 | 81.66 | 94.03 | 38.53 | 100.00 | 87.63 | 86.44 | 66.84 | 87.09 |
| VN | 89.79 | 88.17 | 95.09 | 94.47 | 90.75 | 97.44 | 42.30 | 97.47 | 100.00 | 91.72 | 75.84 | 93.88 |
| JM | 82.59 | 70.00 | 79.06 | 80.44 | 71.29 | 82.15 | 31.79 | 73.44 | 69.97 | 100.00 | 60.17 | 70.66 |
| BK | 98.19 | 91.97 | 95.31 | 96.78 | 95.56 | 98.47 | 49.12 | 92.72 | 94.84 | 98.84 | 100.00 | 96.03 |
| CH | 87.70 | 80.16 | 87.43 | 87.98 | 90.96 | 92.93 | 39.16 | 92.43 | 89.59 | 88.38 | 73.44 | 100.00 |

**Figure 6.5a**

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | 100.00 | 44.26 | 50.83 | 55.49 | 49.52 | 48.61 | 47.50 | 66.06 | 50.23 | 34.65 | 45.62 | 40.72 |
| KK | 62.41 | 100.00 | 68.64 | 59.88 | 56.39 | 65.81 | 47.62 | 71.54 | 61.44 | 50.73 | 61.89 | 50.22 |
| MA | 53.01 | 51.17 | 100.00 | 55.40 | 50.67 | 53.62 | 42.48 | 65.09 | 55.57 | 41.09 | 45.20 | 39.87 |
| BY | 53.40 | 42.29 | 52.81 | 100.00 | 51.07 | 49.64 | 35.64 | 65.69 | 50.79 | 41.84 | 44.42 | 38.09 |
| MU | 46.97 | 39.61 | 47.63 | 49.86 | 100.00 | 47.95 | 43.15 | 54.17 | 46.75 | 33.01 | 41.08 | 39.39 |
| NJ | 52.50 | 50.69 | 54.59 | 54.20 | 55.02 | 100.00 | 50.95 | 59.58 | 49.42 | 35.75 | 47.83 | 43.93 |
| TK | 59.88 | 43.15 | 52.96 | 44.76 | 57.12 | 59.41 | 100.00 | 64.44 | 50.20 | 36.63 | 52.28 | 44.22 |
| DN | 50.87 | 40.89 | 49.13 | 51.51 | 43.04 | 44.55 | 39.65 | 100.00 | 50.78 | 36.58 | 40.57 | 39.38 |
| VN | 53.26 | 48.27 | 57.90 | 54.28 | 51.39 | 48.78 | 42.48 | 69.00 | 100.00 | 45.27 | 46.56 | 41.25 |
| JM | 49.44 | 51.52 | 57.62 | 59.95 | 49.12 | 49.52 | 40.21 | 66.77 | 59.79 | 100.00 | 52.25 | 38.28 |
| BK | 59.40 | 56.70 | 55.75 | 57.24 | 54.13 | 57.58 | 52.84 | 67.92 | 54.59 | 47.50 | 100.00 | 45.13 |
| CH | 46.03 | 40.98 | 43.68 | 44.89 | 47.18 | 46.84 | 40.39 | 56.99 | 43.15 | 30.85 | 40.79 | 100.00 |

**Figure 6.5b**

**Figure 6.5.** Percentages of core area overlaps, determined by fixed kernel analysis (Fig. 6.5a) and cluster analysis (Fig. 6.5b). Figures are the percentage of row core area overlapped by column core area.

### *Dynamic Interactions*

Male chimpanzees of the Sonso community were usually found in the same parts of the community range on the same day, although the degree to which this was so varied between dyads. Figure 6.6 shows the results of dynamic interaction analysis.

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | X | 0.88 | 0.96 | 0.87 | 0.89 | 1.00 | 0.34 | 0.00 | 0.00 | | | |
| KK | | X | 0.95 | 0.98 | 0.68 | 0.79 | 0.61 | 0.11 | 0.00 | | | |
| MA | | | X | 0.97 | 0.90 | 0.96 | 0.96 | 0.76 | 0.99 | 0.90 | 0.00 | |
| BY | | | | X | 0.89 | 0.98 | 0.93 | 0.82 | -0.13 | | | |
| MU | | | | | X | 0.81 | 0.88 | 0.89 | 0.91 | 0.00 | | |
| NJ | | | | | | X | 0.89 | 0.89 | 0.96 | 0.81 | 1.00 | |
| TK | | | | | | | X | 0.88 | 0.92 | 0.96 | 0.71 | 0.00 |
| DN | | | | | | | | X | 0.97 | 0.91 | 0.95 | 0.84 |
| VN | | | | | | | | | X | 0.97 | 0.87 | 0.98 |
| JM | | | | | | | | | | X | 0.88 | 0.98 |
| BK | | | | | | | | | | | X | 0.97 |
| CH | | | | | | | | | | | | X |

**Figure 6.6a**

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | X | 0.64 | 0.99 | 0.97 | 0.99 | 1.00 | 0.05 | 0.00 | 0.00 | | | |
| KK | | X | 0.67 | 0.68 | 0.88 | 0.91 | 0.40 | 0.73 | 0.00 | | | |
| MA | | | X | 0.53 | 0.95 | 0.98 | 0.91 | 0.96 | 0.98 | 0.00 | | |
| BY | | | | X | 0.66 | 0.99 | 0.98 | 0.88 | -0.99 | | | |
| MU | | | | | X | 0.74 | 0.93 | 0.95 | 0.88 | 0.00 | | |
| NJ | | | | | | X | 0.91 | 0.96 | 0.98 | 0.97 | 1.00 | |
| TK | | | | | | | X | 0.62 | 0.96 | 0.96 | 0.93 | 0.00 |
| DN | | | | | | | | X | 0.47 | 0.98 | 0.96 | 0.87 |
| VN | | | | | | | | | X | 0.93 | 0.88 | 0.98 |
| JM | | | | | | | | | | X | 0.91 | 0.99 |
| BK | | | | | | | | | | | X | 0.89 |
| CH | | | | | | | | | | | | X |

**Figure 6.6b**

**Figure 6.6.** Dynamic interaction indices, assessed by median (Fig. 6.6a) and geometric mean (Fig 6.6b) distances. High positive values indicate that individuals tend to be in the same areas on the same days.

For fourteen of the sixty-six dyads, no observations of both members of the dyad on the same day were present in the ranging data set, and so it was impossible to make a comparison of observed and possible positions. For a further six dyads (those with indices equalling zero) only a single ‘same day’ observation remained in the data set. As a result, this analysis must be regarded as preliminary.

Nevertheless, for the remaining dyads the indices can be interpreted as the tendency of the members of the dyad to be in the same part of the forest on the same day, regardless of whether they were in association (in the same party). With all but one of the values positive, there was a strong positive tendency for males to range in the same areas at the same time. My subjective impression was that at different times, different parts of the range would be used more heavily, with travelling parties consistently heading for the same areas over a period of days or weeks. Two or three parties within a few hundred metres of one another would remain in contact through pant-hoot choruses.

Indices of dynamic interaction are not correlated with dyadic association strength (indices based on median distances: $K_r = 37$, $\tau = 0.06$, n = 12, $p_r = 0.24$; indices based on geometric mean distances: $K_r = -8$, $\tau = -0.01$, n = 12, $p_l = 0.44$). If other parties, and possibly solitary individuals are nearby, more information is available for chimpanzees to make strategic decisions concerning their association patterns. A lack of correlation with dyadic association strength, the tendency for each pair of males to associate, suggests that partner selection is occurring; male chimpanzees are not simply associating with those whose ranging behaviour makes them available as potential partners, but are seeking out association partners.

### *Habitat Within Ranges*

Significant differences were found between male ranges in their habitat composition (100% kernel range: $F_r = 20.71$, $df = 11$, $p < 0.05$; 100% cluster range: $F_r = 22.72$, $df = 11$, $p < 0.02$). *Post hoc* tests, with $\alpha = 0.05$ overall, revealed significant differences between DN and JM’s ranges (cluster analysis), and between BK and JM’s ranges (kernel analysis). The estimates of JM’s range are based on an insufficient sample size and are thus unlikely to be accurate. The biological significance of these statistical differences should therefore be questioned.

Male core areas, however, did not differ significantly in habitat composition; no differences existed between males in the proportion of each habitat type (80% kernel cores: $F_r = 5.86$, ns.; 80% cluster cores: $F_r = 5.65$, ns.). The habitat composition of core areas does not therefore vary with either status or association strategy.

#### *Visibility*

The dispersal of party members was significantly affected by visibility (Kruskal-Wallis $H = 14.54$, $df = 3$, $p = 0.002$). There appeared to be a trend towards greater cohesion under conditions of higher visibility (Dunn’s *post hoc* comparisons). Parties found in conditions of low visibility were significantly more dispersed than those under medium-low visibility conditions with $\alpha = 0.05$. However, Dunn's procedure is conservative, and a higher significance level may be justified here (see Neave & Worthington, 1988). With $\alpha$ set to 0.15, parties under high visibility conditions were significantly more clumped than those in low visibility areas of forest. No other pairwise comparisons were significant at $\alpha = 0.15$. Party size was also affected by visibility ($H = 13.17$, $df = 3$, $p = 0.0043$), with significantly larger parties parties associated with medium-high visibility than with medium-low conditions of visibility. Other pairwise comparisons were not significant.

Visibility constraints did not appear to affect the relative frequencies of chimpanzee behaviour, using the relatively coarse measure of group activity (parties terrestrial or no more than 2 metres from the ground: $\chi^2 = 10.75$, $df = 8$, ns; parties terrestrial only: $\chi^2 = 6.95$, $df = 8$, ns; Table 6.7).

**Table 6.7.** Frequencies of different group activities by visibility, for terrestrial parties, and those no more than 2 metres from the ground. Visibility categories were *low* (0-5m), *medium* (6-10m) and *high* (11m+).

| | Visibility | | | | | |
|---|---|---|---|---|---|---|
| | Terrestrial parties | | | ≤2m from the ground | | |
| Activity | Low | Med | High | Low | Med | High |
| Forage | 26 | 34 | 18 | 35 | 52 | 25 |
| Rest | 56 | 127 | 63 | 62 | 135 | 67 |
| Groom | 16 | 32 | 18 | 16 | 32 | 20 |
| Travel/move | 14 | 43 | 22 | 15 | 46 | 22 |
| Other | 3 | 5 | 5 | 3 | 8 | 10 |

## DISCUSSION

The Sonso community lives in an area of secondary forest which is a mosaic of different forest types. As a community, and as individuals, male chimpanzees show clear evidence of preferring particular forest types. These forest types are distributed across the Sonso region, and the chimpanzees range widely from day to day. Despite ranging widely, male Sonso chimpanzees spend the majority of their time within a relatively restricted area, each male has a ‘core area’ which, while not exclusive, only partially overlaps with the core areas of each other individual. The size of cores area is not related to either status or association strategy, although it does seem that the asocial male TK is less wide ranging. These core areas do not differ between males in their habitat composition, and this, together with the lack of any status influence, indicates that core areas do not function to allow priority of access to food resources as seems to be the case for female chimpanzees (Wrangham & Smuts, 1980). Overlaps between core areas are significantly influenced by association strategy. although not apparently by status. There is strong evidence that males are more likely to be in the same area on the same day than would be expected on the basis of their ranging behaviour alone.

That males spend the majority of their time in small partially overlapping core areas, which do not appear to differ in their habitat composition, lends weight to the idea that male core areas have a social function. These core areas are probabilistic and, given that chimpanzees appear to be able to predict the behaviour of others and future events (Menzel, 1974; Goodall, 1986; Savage-Rumbaugh & Lewin, 1994; Koyama & Dunbar, 1996), it is at least conceivable that they are able to use this information. These core areas should not, however, be regarded as ‘purely’ social. No evidence exists to support the idea that chimpanzees go to ‘waiting areas’ simply to ensure others can find them. Instead, core areas are locations where particular individuals tend to be as they pursue the mundane business of eating and sleeping, and participating in the social life of the community.

## *Ranging analysis*

Home range estimates for the Sonso community fall at the low end of estimates for chimpanzee home ranges (see Table 6.1), with all but the adaptive kernel method estimating a community home range of around 7 km². This is less than half that estimated for the Kanyawara community in Kibale using the minimum convex polygon method, although close to the 8.5 km² calculated by summing grid squares (Chapman & Wrangham, 1993). Different methods of data collection mean that only the minimum convex polygon is strictly comparable between studies (Harris et al., 1990), and thus it would appear the Sonso community home range is no more than half that estimated for the Kanyawara, particularly in light of recent indications that the Kanyawara community range may in fact be much larger (A. J. Plumptre, personal communication).

The range area of the Kasakela (Gombe) chimpanzees was estimated at 13 km² (Wrangham & Smuts, 1980), based on 500 x 500 metre grid squares. Kanyawara range estimates, based on sightings in a 200 x 200 metre grid, are between 8 and 9 km². Clutton-Brock (1975) found that a reduction in grid size led to a reduction in range area estimates, which implies range areas for the Kasakela and Kanyawara communities are actually fairly similar, and that habitat quality as perceived by the chimpanzees is also similar. In Kibale, an appearance of good health and maintenance of body weight suggest that the severe seasonal stress experienced by the Gombe chimpanzees may be lacking (Wrangham et al., 1996), although the long inter-birth interval may be indicative of a poor quality habitat (Wrangham et al., *ibid*), or possibly some form of ‘social stress’.

Community range area estimates for the Sonso community, based on far more accurate locations are smaller, and imply a richer habitat. As yet, no data on inter-birth intervals are available for Budongo.

These differences have implications for comparisons of chimpanzee ecology and behaviour between the study sites, and demonstrate that chimpanzees respond to the detailed structure of their environment; forest living communities are no more similar to each other than are savannah living groups. The different range areas suggest that the resource base in the Sonso region is different from that in Kanyawara, with resources more abundant and more evenly distributed in the former, and highly spatially and temporarily dispersed, occasionally superabundant, in the later (Chapman & Wrangham, 1996).

Home range size estimates are only as good as the methods used in their determination. Observations of patrolling behaviour gives confidence to the positions determined for the northeast and southwest boundaries, as do observations of unhabituated chimpanzees to the northeast. Focal subjects were lost when travelling through forest beyond the trail system, and thus the results of ranging analysis are likely to underestimate the ‘true’ home range.

This was particularly true for movements to the south-east, which occurred more frequently than was recorded during systematic sampling. The south-east of the Sonso region is separated from the rest by thick swamp forest and the Sonso river. No trails ran into this area, which made it difficult to search, or to follow fast moving chimpanzees. On occasions when chimpanzees were followed through this region it proved possible only to follow their calls; visual contact was impossible. My impression was that the chimpanzees seemed more nervous in this area, possibly because they were unaware of who was trailing them; they remained wary of strangers throughout the study. Without visual contact, and a means of obtaining location data (there being no reference points), it was not possible to record ranging in this area. Forest cover proved too thick to permit the use of global positioning systems (GPS).

The estimates clearly do not reflect the full range of the Sonso chimpanzees over the study period, but the asymptotes found for the majority of males suggest the estimates of *home range* size are fairly accurate. With estimates of individual range areas uncorrelated with sample size, it seems reasonable to assume differences between males are not an artifact of sampling.

Simulation studies (Seaman & Powell, 1996) have shown range area estimates calculated using the fixed kernel method to be the most accurate, although somewhat sensitive to data structure. The agreement found here between estimates produced by fixed kernel, minimum convex polygon, and cluster analyses, which are very different methods of estimating range area, increase confidence that the figures reflect good estimates of home range area.

The method used to collect data (sampling started with the first male contacted on each day) may have led to bias in the data set, such that more points lay close to the research station than far away, despite efforts being made to minimise this effect by searching widely through the forest (see Chapter 3). The adaptive kernel method, which gives more weight to areas of low fix density, may counteract some of this bias, and the higher estimates suggest that perhaps these are closer to the *total range* than the home range.

### *Core Areas*

Males of the Sonso community spend the majority of their time in only a fraction of the total community range, but defining these core areas is subjective. Any figure greater than 50% of fixes could be used to define an area where the majority of time is spent. This is a problem of quantitative ranging analysis generally, as no precise technique for defining core areas has been developed (Kenward & Hodder, 1996). Inspection of utilisation plots for discontinuities in slope is a widely used method, and here discontinuities were found at a proportion of fixes which varied from individual to individual. These discontinuities were not, however, particularly strong.

It may be inappropriate to use this method of determining distinct core areas when investigating chimpanzee home ranges, as the conceptual model of a home range with a distinct core does not necessarily reflect the nomadic nature of chimpanzees. There are no permanent, continually reused nests, lying up sites, or dens, to which the animals return after each foraging trip. While chimpanzees do revisit areas, and may have preferred nesting sites, they are able to construct nests wherever they happen to be at the end of each day. The core areas may thus be truly statistical, representing ‘preferred’ areas of activity, but having no physical centre. Under these conditions the multi-nuclear cores generated by cluster analysis may be more accurate, in terms of defining these preferred areas, than are the perhaps excessively smoothed kernel estimated cores.

For the Gombe Kasakela community, male core areas were significantly larger than female core areas, and females in Kibale Forest have been found to occupy smaller ranges than do males (Chapman & Wrangham, 1993). Although Kasakela males had core areas generally around twice the size of female core areas, the overlap in size was considerable—sizes of female core areas fell within the range of the sizes of male core areas (Wrangham & Smuts, 1980). For both males and females, core areas represented the same fraction (40-60%) of each individual’s total range. Core areas for male Sonso chimpanzees cover a smaller proportion of the total range, averaging 32% (kernel analysis) or 7% (cluster analysis), which may be the result of absolutely greater levels of food abundance.

### *Habitat and Visibility*

Chimpanzees feed on a wide variety of food items (Appendix 4; Wrangham 1977), and it has been suggested that they follow a strategy of maximising nutrient, rather than energy, intake (Hladik, 1977). The diet of the Sonso chimpanzees appears more similar to the Gombe chimpanzees than it does to the Kibale chimpanzees (see Wrangham 1977; Wrangham et al., 1996), at least as measured by proportions of different food types. Despite this variety in diet, feeding time is concentrated on food items from a few preferred species. The distribution of these preferred items, together with the distribution of any ‘fallback’ foods consumed when more desired food items are unavailable, is likely to influence ranging patterns.

Terrestrial herbaceous vegetation (THV) has been suggested as a fallback food, when arboreal fruit are scarce, for some chimpanzee populations (Malenky et al., 1994; Wrangham, et al., 1996). In comparison to the Gombe and Budongo chimpanzees, THV appears to replace arboreal leaves in the diet of the Kanyawara chimpanzees. Although THV is four times as common in Kibale than it is in Budongo (A. J. Plumptre, personal communication), this is insufficient to account for the observed differences in reliance on THV.

It may be that the Sonso chimpanzees have alternate foods to buffer them against periods of food shortage. *Cynometra alexandrii* fruits only for a restricted period each year, and its seeds have elsewhere been described as an important food for chimpanzees in Budongo (Sugiyama, 1968), specifically during the relatively short dry season. The Sonso chimpanzees have access to *Broussonetia papyrifera* planted close to the largely defunct sawmill, and this is slowly colonising forest gaps. This provides an almost year-round food supply, with the chimpanzees consuming young and mature leaves, flowers and fruit. The availability of this food may be the reason for the relatively small home range estimated for the Sonso community, and the locally high population density. The presence of the *B. papyrifera* means that the Sonso community should not be regarded as typical of Budongo chimpanzees, although the mosaic nature of the forest is likely to ensure that each chimpanzee community within the forest encounters a different mix of habitats and food distribution.

The lack of any difference in habitat composition between male core areas is further evidence that forest types, and the food resources they contain, are equally accessible to each male, and unlikely to lead to differences in individual behaviour. Similarly, no difference in the habitat composition of male home ranges, other than a difference between the ranges of two males, was found. Constraints on association patterns imposed by food supply are unlikely to be strong, with alternate, if perhaps less preferred, choices of food items being available. The lack of any obvious ecological difference between male core areas is strongly suggestive that these cores are social in their function.

Visibility appears primarily to affect party cohesion. Under low levels of visibility, parties are more dispersed, and thus individuals are out of sight of one another. With visibility between six and fifteen metres, party size increases with increasing visibility, while dispersion remains unchanged; more chimpanzees are aggregating in the same area. These results suggest that the ability to see other party members is important in keeping track of party composition.

When visibility exceeds fifteen metres, parties become significantly more clumped than under low visibility conditions, which may be a functional response to predation pressure.

### *The Chimpanzee Social System*

Evidence from the Sonso chimpanzees supports the predictions of the ‘social cores’ hypothesis, and fails to support an ecological explanation of males core areas. Male home ranges have core areas, and males do not therefore range evenly over the community range. These core areas, where the probability of finding each male is 80%, represent on average only a third of each male’s home range. They are distinct, and overlap significantly less than would be the case if males used the community range more or less equally. There are no significant differences in the habitat composition of male core areas. These cores may therefore function to increase the predictability of being located by other males, and enable males to make choices as to social partners.

Both males and females (Wrangham & Smuts, 1980) appear to spend the majority of their lives in relatively small core areas. Males were thought to range widely in order to defend access to a number of female core areas, and to search for reproductively active females. Observations suggest that female core areas are important to ensure access to food resources for females with infants. However, cycling females do not remain in their core areas, but associate more with males (Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1987). If males occupy core areas to facilitate location by allies, then females may take advantage of this behaviour to predict the location of a preferred male, or to ensure that all males are aware of her cycle state. The female benefits by increasing the probability of a successful consortship, or monopolisation and fertilisation by the alpha male.

Furthermore, it seems that community boundaries are hazardous for males (Goodall, et al., 1979; Nishida, 1979). Males caught alone on a boundary risk serious injury or death. Nevertheless, the need to defend boundaries requires a system of range defence which minimises the amount of time each male spends near a boundary and so the probability of encountering males from other communities. Selection should thus favour the evolution of territorial behaviour which puts individuals at low risk. Range defence should be infrequent, unpredictable, and conducted in powerful groups, characteristics typical of chimpanzee boundary patrols and the loud vocal advertisements of male presence (Goodall, 1986; personal observation).

If the risks associated with trespassing into a neighbouring community's range are sufficiently high, and the possibility of encountering other community males is unpredictable, then range defence may be maintained by 'mutual respect' (Frank, 1995). So long as boundaries are 'defended' occasionally, and unpredictably, range boundaries should be respected. Males of each community would be expected to test range boundaries, making incursion patrols in strong groups, and the mutual respect system would break down if one community was too weak, in the sense of having too few adult males, to maintain range defence.

In thick forest with no strong topographic features to define community range boundaries unambiguously, boundary *zones* may develop to reduce the chances of males from different communities encountering one another at short range. Core areas for Kasakela males cover around half of the community range (Wrangham & Smuts, 1980), in a habitat where frequent ridges provide obvious markers of community boundaries. The same may apply to the chimpanzees of the Kibale Forest, where valleys and ridges are pronounced. Core areas for Sonso males cover no more than a third of the community range. In this forest, there are few clear markers for range boundaries, and it appears that difficulties in identifying clear range boundaries favour small core areas situated well away from range edges.

# Chapter 7

# DECISION MAKING
## PROXIMITY AND GROOMING

> *"Social primates are required by the very nature of the systems they create and maintain to be calculating beings"*
>
> *N. K. Humphrey, The Social Function of Intellect, 1976*

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## INTRODUCTION

Behaviour, by its very nature, requires the making of decisions. Whether an animal is selecting a single behaviour from its repertoire, or a target for that behaviour, whenever it makes a choice from a range of alternatives, be it behaviour patterns, habitat, prey, social partners or potential mates, it makes a decision. The flexibility an individual animal has in making decisions is determined by the particular mechanism responsible for that choice. The more complex the environment to which the animal has to respond, the more decisions the animal will be required to make. The more variable the environment, the greater the flexibility in decision-making an animal will need. It is therefore in the most complex behaviour that the clearest examples of decision-making are likely to be found.

Decision-making by animals has been investigated both from a functional perspective and from a mechanistic perspective (reviewed by McFarland, 1985; Krebs & Kacelnik, 1991). Functional studies have looked primarily at the behaviour of animals in their natural environment, whereas mechanistic studies have concentrated on a few species held in highly controlled, and artificial, conditions.

From a functional perspective, an animal's decisions are considered in terms of costs and benefits to its Darwinian fitness, pursuing the idea that natural selection optimises choices, such that on average individuals make those choices which provide a maximum fitness benefit, given various constraints (Dawkins, 1986; Krebs & Davies, 1987). Functional analysis treats animals as if they make decisions based on a rational consideration of the different costs and benefits of the options available but assumes simply that natural selection has produced animals which behave *as if* they can make such decisions, without investigating the mechanisms responsible. Decision-making is thus very much a metaphor, but potentially explains much about the natural behaviour of animals (Krebs & Kacelnik, 1991).

Mechanistic analysis instead attempts to identify how an animal makes, what functional analysis would identify as, the optimal choice. Although apparent decision-making can occur when an animal takes behavioural alternatives at random (McFarland, 1985), the term ‘decision’ should be avoided when describing random alteration of behaviour to distinguish this from alterations which are the result of some stimulus.

The most basic form of stimulus-based decision-making is the simple and inflexible response, such as the apparent preference for damp habitat shown by common woodlice (*Porcellio scaber*). Preference is only ‘apparent’ in this case as the animals are not selecting the humid habitat, but simply ending up there as a result of increased activity in conditions of low humidity (McFarland, 1985). Active selection requires some degree of information processing in relation to the available options.

Much of the work investigating mechanisms of decision-making has been concerned with motivation, concentrating on basic behaviour patterns such as feeding. An animal switches from one behaviour to another as the motivation to perform the current behaviour drops, perhaps as a result of performance, below that for another behaviour. Feedback and delay loops may exist to prevent the animal simply oscillating between activities, but ultimately a motivation model becomes incredibly complex if it tries to explain all but the simplest of decision-making processes in simple animals (McFarland, 1985; Dawkins, 1986). Although apparently a parsimonious means of explaining the mechanisms of decision-making, the motivational model does not necessarily reflect the processes occurring inside the animal, and, in postulating complex process, ceases to be a simple description of decision-making (Crook, 1980; Dunbar, 1988b)

An alternative explanation for decision-making is that of cognitive information processing. Alternative options are compared to an internal referent, and the option which most closely matches, or brings the animal’s state closer to the ‘ideal’, is selected. Thus the animal can be said to select, at a mechanistic level, one of the options—its decision is a choice. The cognitive decision, however, need be not ‘conscious’; the animal need not be aware of the decision-making process.

This cognitive mechanism is evident even in motivational studies investigating the balance between tendencies to drink and feed (McFarland, 1969). Doves **(***Streptopelia sp.*). for example, appear to make the decision whether to eat of drink on the basis of ‘motivation’, but when a barrier is placed between food and water, they appear to take into account the difficulty, or cost, of changing between behaviours (McFarland, 1985). They are, it seems, making a decision based on a cognitive combination of environmental information.

To say that individuals are making choices, rather than simply responding in some fixed way to a range of options, inevitably implies a degree of intentionality in the decision. Intentionality (Dennett, 1971, 1988) means that animals have mental representations of the goals they are attempting to reach, that, in essence, they think before acting. Dennett's system ascribes desires and beliefs to animals by a number of levels, each of increasing complexity. Creatures capable of only 'zero order' intentionality are automata. They respond inflexibly, and so do not 'think'.

Animals capable of first order intentionality have desires, or beliefs, but no beliefs about those beliefs. They can be said to think, but not to think about what they think; their thought processes are inaccessible to them. The behaviour of such animals can be said to be voluntary (Cheney & Seyfarth, 1990). Second order intentionality is 'thinking about thinking', with higher orders describing further recursions of thinking about thinking (Dennett, 1988). Second, and higher, levels of intentionality imply that the animal is capable of reflecting on its own thoughts, and attributing thoughts to others. They know what they know, and are therefore 'self-aware'. Animals with second and higher orders of intentionality possess some form of consciousness (see Chapter 8).

Although Byrne (1995a) concludes that there are no observable differences between the behaviour of animals with zero order and first order intentionality, Cheney & Seyfarth (1990) suggest that alarm calling in vervet monkeys is voluntary, as it can be performed or withheld depending on circumstances, and that this is evidence that vervet monkeys are at least capable of first order intentionality. The same appears to be the case for a range of birds and mammals (Cheney & Seyfarth, *ibid*).

Decision-making in chimpanzees has been little investigated outside the laboratory. That chimpanzees are capable of rational choice is shown in their ability to choose from an array of inherently meaningless symbols to describe objects, request items, and apparently announce future actions (see: Savage-Rumbaugh & Lewin, 1994; Matsuzawa, 1996). They appear to be capable of making decisions based on assessment of the mental states of other individuals, both of humans (Premack & Woodruff, 1978; Povinelli, 1992), and other chimpanzees (deWaal, 1982; Menzel, 1973; Savage-Rumbaugh & Lewin, 1994). They are clearly capable, therefore, of thinking (first order intentionality), and may well be capable of 'thinking about thinking' (second order intentionality). Decision-making in chimpanzees can therefore be regarded as intentional.

Chimpanzees, unlike monkeys, appear capable of understanding the properties of tools (Visalberghi & Limongelli, 1994; Byrne, 1995a) and make appropriate tools in the wild (McGrew, 1992). Matsuzawa (1996) describes individual chimpanzees as having favourite stone tools, but the factors which determine the preference are not known. Determining the factors which influence the choice of tool, or raw material, should illuminate the mental processes involved in the choice. Since social partners can be regarded, potentially, as 'social tools' (see reviews by Whiten & Byrne, 1988c; Cheney

& Seyfarth 1990; Byrne 1995a), a fruitful line of investigation may be to examine the choice of social partners. The range of alternatives is fairly easily specified, and the choice is likely to be a common event. The cognitive demands of such social decisions should be evident in the factors predicting the choice.

Studies of chimpanzees commonly assume that the spatial organisation of a set of individuals reflects the underlying nature of the relationships between those individuals (Sugiyama, 1988; Kawanaka, 1993; White & Chapman, 1994; Furuichi & Ihobe, 1994); a reasonable assumption supported by available data. The *composition* of chimpanzee parties is thought to be the result of decisions made by individuals concerning the identities of their associates (see Chapter 5), while the structure of these parties, the relative positions of party members, is thought to result from decisions concerning the identities of those individuals nearest to them, their ‘nearest neighbours’, and the intervening distances (White and Chapman, 1994). Individual chimpanzees thus have opportunities to make decisions regarding their social partners on two levels: party composition, the identities of associates, and party structure, the relative positions of individuals. If chimpanzees are pursuing social strategies, they are likely to make tactical choices which reflect their strategic goals.

Under the hypothesis of tactical association, individuals associating in order to interact would be expected to position themselves in close proximity to association partners, while those associating purely to observe the behaviour and relationships of others should show no strong tendency to maintain close proximity to other individuals. The tendency of any two individuals to be nearest neighbours should therefore mirror the tendency of that dyad to associate in the same parties; the fundamental decision is that of party membership (Chapter 5).

However, the social environment may be more complex still, as individuals associating with one another have only limited control over the associations of other individuals; association between two or more individuals does not preclude their association with a third. This raises the possibility that the tendencies individuals have to be in close proximity will not closely mirror their association tendencies; their choice of proximity partners is constrained by the composition of the party, and the strategies of the other individuals present. High association strength may reflect a highly competitive relationship, or one where one individual ‘follows’ a second. In either case, there is no reason to expect a equally high tendency to be in close proximity. Differences between the proximity tendency predicted by association strength, and the observed proximity tendency, together with the absolute values of each, reflect details of the relationships between members of each dyad.

Furthermore, the existence of partner preferences which are explicable in terms of social strategies suggests that chimpanzees are required to use cognitive information processing to select their proximity partners from the highly variable social environment, balancing the available options with those available should they change parties. The requirement for a cognitive mechanism can be investigated further by looking directly at decision events, when individual chimpanzees select, or choose, grooming partners. This decision involves both a choice of proximity partner, and a decision to groom. The individual is clearly *motivated* to groom, but the decision of interest is who is chosen as the grooming partner. Factors which predict the choice should suggest the mechanism involved; the more abstract the factors, the more necessary is a cognitive mechanism.

## METHODS

### Data Collection

Data on party structure were collected during 30 minute focal sampling of twelve adult males. The positions of all individuals within 10 metres of the focal animal were recorded on a continuous basis throughout the sample, to the nearest half metre. Male chimpanzees almost invariably held higher social status than females (see Chapter 4), and so should have had the ability to displace a female from a position in proximity to another male. As a result, an investigation of the relationships between males and the factors influencing their decisions need consider only the spatial organisation of males within a party, and can ignore the spatial position of females.

Data concerning the choice of grooming partners, in the form of natural ‘choice experiments’, were extracted from the focal samples. In all instances where one individual approached and then groomed a second, when a third individual was also present within 10 metres, the identities of the three individuals were recorded. The identities of other males within 10 metres were also recorded, as were the initial distances between the ‘choosing’ individual and each of the possible grooming partners. The time delay between initial approach and grooming initiation (‘latency to groom’) was recorded, as was the duration of grooming before a response was obtained from the partner. When no response was obtained, the duration of grooming was recorded until the bout was terminated.

### Data Analysis

#### *Proximity*

Proximity data are by their very nature autocorrelated (White and Chapman, 1994), as an animal’s position at any one time determines its location at a subsequent time. To minimise the effects of such dependency, only a single point sample of spatial proximity was taken from the continuous record of each focal sample; the initial proximity record in each sample. Each proximity sample was thus separated by a minimum of 45 minutes. Records where no male was within 10 metres of the focal were discarded for this analysis.

Three indices of proximity were derived, reflecting (1) the frequency of each dyad existing as ‘focal-nearest male’, (2) the frequency of each dyad existing as ‘focal-nearest male’, weighted by the distance separating the members of the dyad and (3) the frequency of being ‘nearby’, where members of the dyad were either ‘focal-nearest male’, or ‘focal-second nearest male’.

A similar methodology to that used in Chapter 5 for constructing association indices was used here. The first step was to convert frequencies of proximity into an index of proximity to control for the effects of differential focal sampling. Observations of both members of each dyad were combined using the index:

$$P_{AB} = (N_{AB}+N_{BA})/(F_A+F_B)$$

where $N_{AB}$ is the number of observations of B as the nearest male to focal A, $N_{BA}$ is the number of observations of A as the nearest male to focal B, $F_A$ is the number of focal samples of individual A, and $F_B$ is the number of focal samples of individual B.

This index is that used by White and Burgman (1990) in their study of party structure in bonobos (*Pan paniscus*). The second step was to control for differential observation of dyads, by converting these indices into internal Z scores:

$$Z_{AB} = (P_{AB} - P) / s$$

where ‘$P_{AB}$’ is the proximity index, ‘P’ the mean index across all males, and ‘s’ the sample standard deviation.

Weighting the frequency of proximity was done by multiplying the frequency of proximity by the median reciprocal distance between the members of the dyad. More importance is thus attached to close, than to distant, proximity, with the difference attached to each unit change in distance decreasing as the distance from the focal increases. To give the greatest importance to individuals in contact with the focal, the distance between the individuals was set to one half metre.

The first of these three measures of proximity, expressed as internal Z scores, was interpreted as the tendency of each dyad to be in close proximity, such that they were nearest neighbours. The second measure was interpreted similarly, but the weighted frequencies reflected more of the strength of the dyadic proximity relationship. The measures were thus termed ‘unweighted’, and ‘weighted’, dyadic proximity strengths. The third measure reflected the tendency individuals had to be in close proximity without necessarily being nearest neighbours, and so described the tendency of individuals to form clusters within parties. This measure was termed ‘clustering tendency’.

Proximity measures such as ‘nearest neighbour’ produce data which show dependency between dyads, as when A is B’s nearest neighbour, C cannot be B’s nearest neighbour. Unlike association data, where any number of individuals can be in association at any time, only a single nearest neighbour can exist at each time point. Appropriate statistical tests in these circumstances are the distribution free permutation tests based on Mantel matrix correlation procedures (see Chapter 4). $K_r$ correlation tests, which allow for individual differences and are not subject to the undue influence of outliers, were used to test the hypothesis that the three methods of assessing proximity strength measure the same phenomenon, and that differences between the indices reflect peculiarities of particular dyadic relationships.

Individual males differ in the nature of their associations with other males. Some tend to form dyads which strongly associate, while others form dyads which tend to associate only infrequently. In all cases the association tendencies vary from dyad to dyad (dyadic association strengths, see Chapter 5). To investigate the variation in proximity relations, dyadic proximity strength, both weighted and unweighted, was plotted for each dyad. Plots were organised to show proximity relationships of each individual with each of his potential nearest neighbours, and any difference between weighted and unweighted dyadic proximity strengths.

To examine further the nature of each individual’s proximity relationships multidimensional scaling (the ALSCAL algorithm: Schiffman et al., 1981) was used to calculate and plot graphical representations of proximity tendencies. Squared euclidian distances between individuals were calculated from the matrix of dyadic proximity strengths, for both weighted and unweighted indices. Individuals were then plotted in two dimensions, such that the distances between individuals in these plots reflect their similarity in proximity tendencies.

High status males have been proposed as attractive social partners (see Chapter 4). To investigate this, matrix correlations were conducted, using each of the three proximity measures, to test the relationship between proximity and social status.

Hypothesis: The tendency of male chimpanzees to be in close proximity is a function of their status, such that high status males have greater proximity strength values than do lower status males.

*Prediction* A positive correlation between status and dyadic proximity strength.

To determine whether the proximity relationships between individuals are produced by a preference for individuals of a particular relative status, an hypothesis matrix was constructed for each of the following four hypotheses, in which each cell conforming to the hypothetical relationship was filled with a 1, all other cells by a zero. These mutually exclusive hypotheses are one tailed, as each specifies the direction of the predicted relationship.

| | |
|---|---|
| Hypothesis 1: | Proximity relationships are produced by a preference for individuals of a similar status level (Chapter 4). |
| Hypothesis 2: | Proximity relationships are produced by a preference for individuals of higher status. |
| Hypothesis 3: | Proximity relationships are produced by a preference for individuals of lower status. |
| Hypothesis 4: | Proximity relationships are produced by a preference for individuals of a different status level. |

The hypothesis of tactical association predicts that the tendency of individuals to be in close proximity should reflect the tendency of individuals to associate in the same parties. This was investigated by regressing measures of proximity against association tendency. The possible interdependency of proximity data meant that the significance of such relationships could not be tested using standard parametric or non-parametric techniques, and so the Mantel test, a generalised regression method (Schnell et al., 1985) which models a simple linear relationship (Smouse et al., 1986), was used. The significance of the Mantel Z statistic was assessed by means by means of a random permutation procedure, using 5000 permutations (see Chapter 4).

Differences between dyadic association strength and dyadic proximity strength may indicate characteristics of the relationship between members of a dyad. Dyads with high dyadic association strength, but low dyadic proximity strength may be found together because one individual wishes to associate whereas the other does not, whereas if both dyadic association strength and dyadic proximity strength are high the indication is that the association is the result of a mutual decision. The position of the dyad in relation to the regression line potentially indicates the affiliative or antagonistic nature of the social relationship between the members of the dyad.

Both measures of dyadic proximity strength, and clustering tendency, were regressed against dyadic association strength using the Mantel procedure, and the residuals for each dyad were calculated. These residuals were examined to ascertain the suitability of the regression model, and analysed further to investigate the nature of the proximity relationship between members of each dyad.

### *Grooming Decisions*

Subjective impressions suggested that grooming partners were being chosen intentionally. To determine whether a choice was in fact being made, and if so, to establish the factors important to any decision, three hypothesis were constructed to explain the apparent choice. To test between these hypotheses, it was necessary to determine the predictability of choice:

| | |
|---|---|
| Hypothesis 1: | No choice occurs. Selection of grooming partners is random. |
| *Prediction*: | No factors predict the identity of selected partner. No partner preference. |
| Hypothesis 2: | Grooming is the result of a grooming ‘drive’. When an individual wishes to groom, it ‘selects’ the nearest individual. |
| *Prediction*: | Relative distance between potential choices completely predicts the selected individual. |
| Hypothesis 3: | Choice is the result of a cognitive assessment of the relative value of each potential partner. |
| *Prediction*: | The nature of relationship between choosing individual and potential choices predicts the selected individual. |

Grooming partner choice was investigated by comparing the frequency of partner selection with the frequency with which the individuals were available as choices, initially by the construction of preference indices, using Ivlev’s index (see Table 6.1). Sample sizes were small, and so indices were constructed only for males observed making eight or more choices. Other individuals made no more than four selections. As a measure of preference, Ivlev’s index is weakest when sample sizes are small. If an individual is available, but not selected, the index suggests extreme avoidance. When only a few selections are made in total, however, low preference individuals are likely to be ignored, whereas when more choices are made, they may be selected, albeit at a low level. The index was used therefore simply to examine whether any preference was shown, and how this varied between individuals.

To investigate the effect of distance, the frequency at which individuals selected either the nearest, or ‘not nearest’ potential partner was determined, and the average (median) distance of the selected partner compared to the median distance for rejected potential partners by means of a Mann-Whitney test. For cases where the number of potential partners was two, and thus each individual was either selected or rejected, the distance from the selecting individual to each potential partner was compared using a Wilcoxon matched pairs signed ranks test.

The delay between initiating an approach and initiating grooming, the ‘latency to groom’ is potentially indicative of decision-making. Spearman rank correlations were used to examine the relationships between latency to groom and the number of individuals present, the mean status of potential grooming partners, the status of the partner eventually selected, and the status of the choosing individual. Similar correlations were also used to examine the associations between latency to groom and the dyadic measures of association strength and proximity strength.

If partners are deliberately chosen, aspects of the nature of the relationship between individuals should predict the choice. Descriptors of different aspects of the dyadic relationship used here were the relative status of each of the individuals, dyadic association strength, and dyadic proximity strength. Each is a potential predictor of grooming partner choice. Their relative importance as predictors should show which aspects of dyadic relationship influence the choice of grooming partner. If grooming is used tactically, individuals should choose to groom those individuals with whom they choose, tactically, to associate.

With the possibility of multiple factors acting simultaneously, and potentially interacting with one another, multivariate rather than univariate analysis is more appropriate. In the ‘natural choice experiments’ investigated here, the number of individuals available as potential grooming partners varied from two to six. Where there are three or more potential choices analysis is complicated, and analysis of all observations together is more complex still, since the probability of random choice varies as the number of potential choices changes. As a first step in such an investigation, the choice of one of two potential partners was analysed. Each potential choice was classified by a number of categorical variables, and chi-squared tests were used to examine the degree of association between these variables. A logistic regression was then used to build a statistical model from a list of potential predictor variables (Table 7.1) to determine which, if any, of these predicted the choice of grooming partner. The variables were entered into the logistic regression using a forward stepwise method.

Forward stepwise logistic regression is a method which assesses the significance of each independent variable’s influence on the dependent variable alone, and then, starting with a model containing none of the independent variables adds the most significant independent variable, recalculates the significance of the influence of each of the remaining excluded variables, and adds the most significant of these. After the addition of each variable, the significance of the explanatory value of the model is reassessed, and variables continue to be added until no further significant improvement in the model is achieved.

**Table 7.1.** Potential predictor variables used in logistic regression to determine factors influencing the choice of grooming partners. *Weighted* dyadic proximity strength was used. A is the individual performing the selection, B the individual chosen, and C the individual rejected. Coding of categorical variables is indicated.

| Type of variable | Potential predictor variable |
|---|---|
| *Continuous* | |
| | Status of choosing individual (A) |
| | Status of potential choice (B, C) |
| *Categorical* (coding) | |
| (nearer/further) | Relative distance; A to B, A to C |
| (higher/lower) | Relative status between A & B, A & C |
| (higher/lower) | Relative status between B & C |
| (stronger/weaker) | Relative dyadic association strength; AB vs AC |
| (stronger/weaker) | Relative dyadic proximity strength; AB vs AC |

Once grooming is initiated, the nature of the relationship between the individuals may influence the nature of the groomed individual’s response. Kruskal-Wallis analysis of variance was used to determine whether the type of response (defined below) was related to the status of both the selecting and responding individual, the duration of grooming preceding the response, and to the initial latency to groom. In addition, the length of time an individual has to groom before grooming is reciprocated, the ‘latency to response’ may itself reveal something of the nature of the relationship between individuals. Spearman rank correlations were used to investigate the association between latency to response and (1) the status of each grooming individual (2) the difference in their status (3) dyadic association strength and (4) dyadic proximity strength.

## RESULTS

### Proximity

The average (median) distance between nearest males was 1m (inter-quartile range 0.5-3m, n = 72), considering distances no greater than 10m because of frequent, habitat imposed, visibility constraints (see Chapter 6). Measures of proximity were significantly interrelated. Unweighted dyadic proximity strength was significantly correlated with weighted dyadic proximity strength ($K_r$ = 256, $\tau$ = 0.39, n = 12, $p_r$ = 0.0002), and with cluster tendency ($K_r$ = 455, $\tau$ = 0.69, n = 12, $p_r$ = 0.0002). Weighted dyadic proximity strength was also correlated ($K_r$ = 223, $\tau$ = 0.34, n = 12, $p_r$ = 0.0006) with cluster tendency.

Individuals showed a large degree of variation in the frequency with which they were in proximity with others (Fig. 7.1a,b), and for some dyads weighting frequencies changed the respective dyadic proximity strengths. Some dyads (for example, CH-VN, KK-DN) were in proximity frequently, but rarely in close proximity, whilst others (for example, DN-JM, MA-NJ, MG-BK) were infrequently in proximity, but when in proximity, inter-individual distances were short.

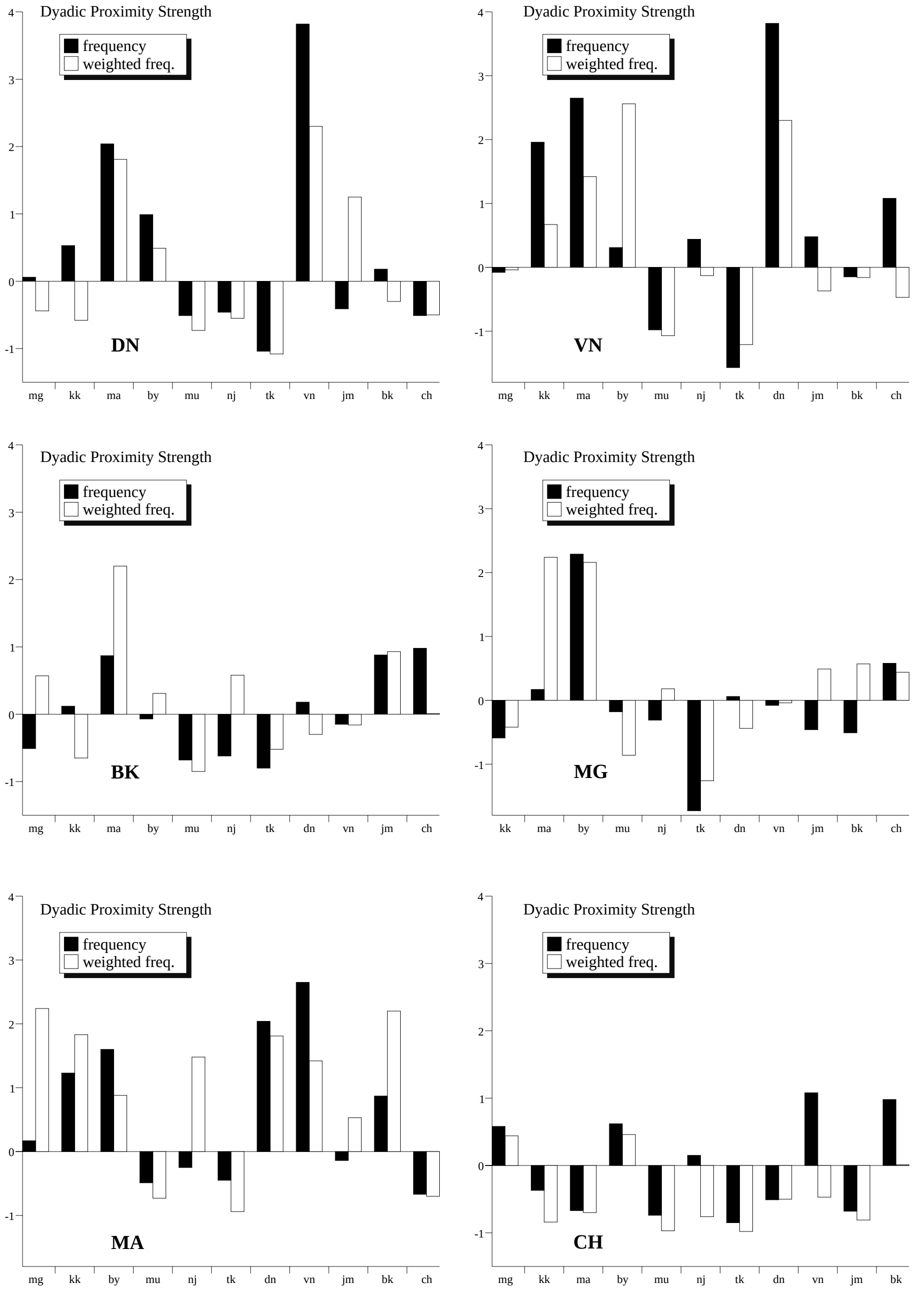

**Figure 7.1a.** Dyadic proximity strengths for high and mid-status focal males, assessed both by frequency and frequency weighted by reciprocal distance. Males are arranged according to social status by rows: DN to CH.

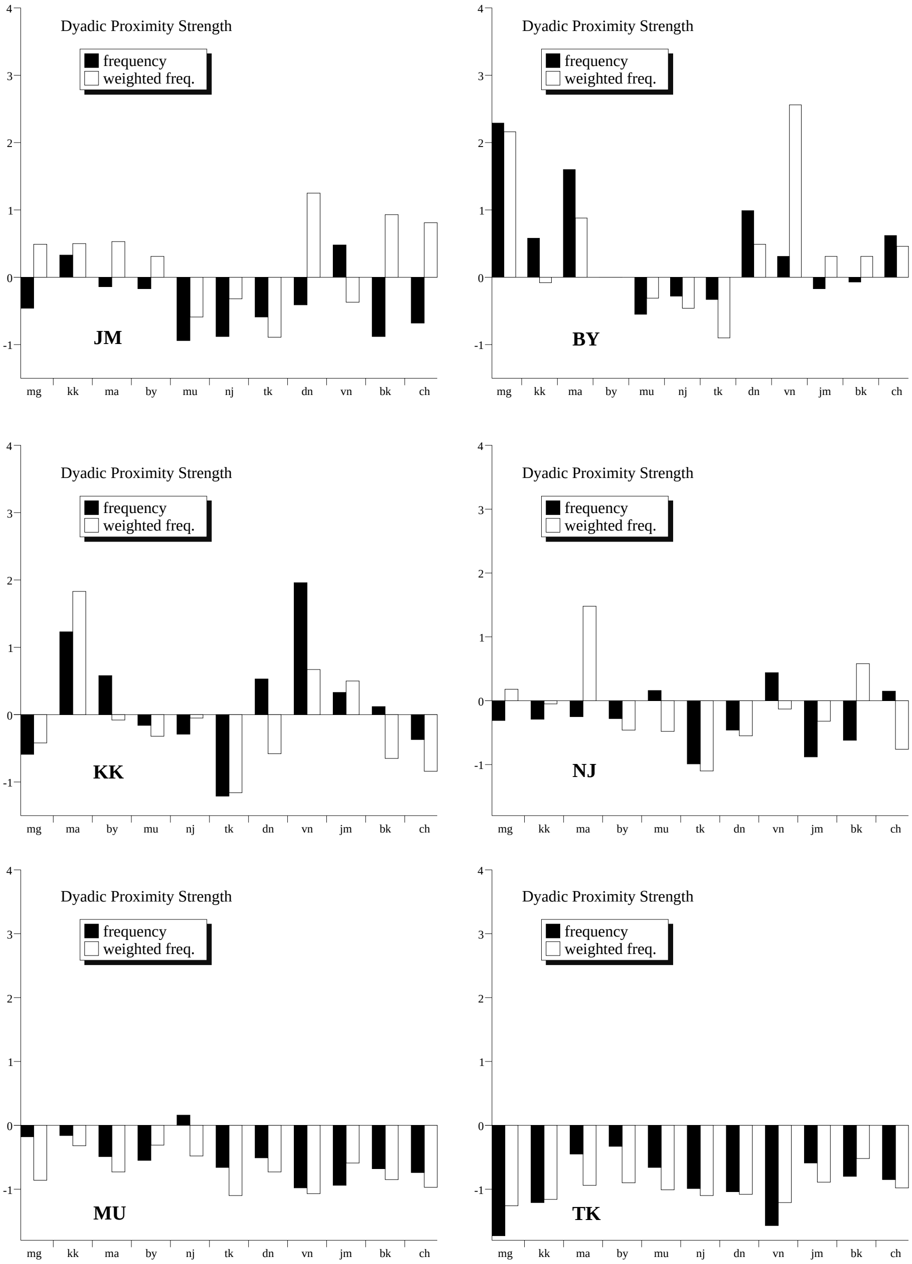

**Figure 7.1b.** Dyadic proximity strengths for mid and low status focal males, assessed both by frequency and frequency weighted by reciprocal distance. Males are arranged according to social status by rows: JM to TK.

Two dimensional scaling plots of the similarity between individuals in their proximity tendencies are shown in Figure 7.2. The distances between individuals accounted for a large proportion of the variance in the matrix of dyadic proximity strengths (frequency only: 90%; weighted frequencies: 87%).

Although no strong clustering was apparent, the majority of individuals were close to the centre of the diagram. This suggested that there was large degree of individual variation in proximity behaviour. TK, and to a lesser extent MU, were to the left of the the plot, which indicated a generally negative tendency to be in proximity with other males. This was unaffected by weighting frequencies (cf. Fig. 7.1). VN and MA were consistently to the right of the plot, and many of their dyadic proximity strengths were strongly positive. It seemed that the first dimension reflected the strength of proximity tendencies. The interpretation of the second dimension was less clear.

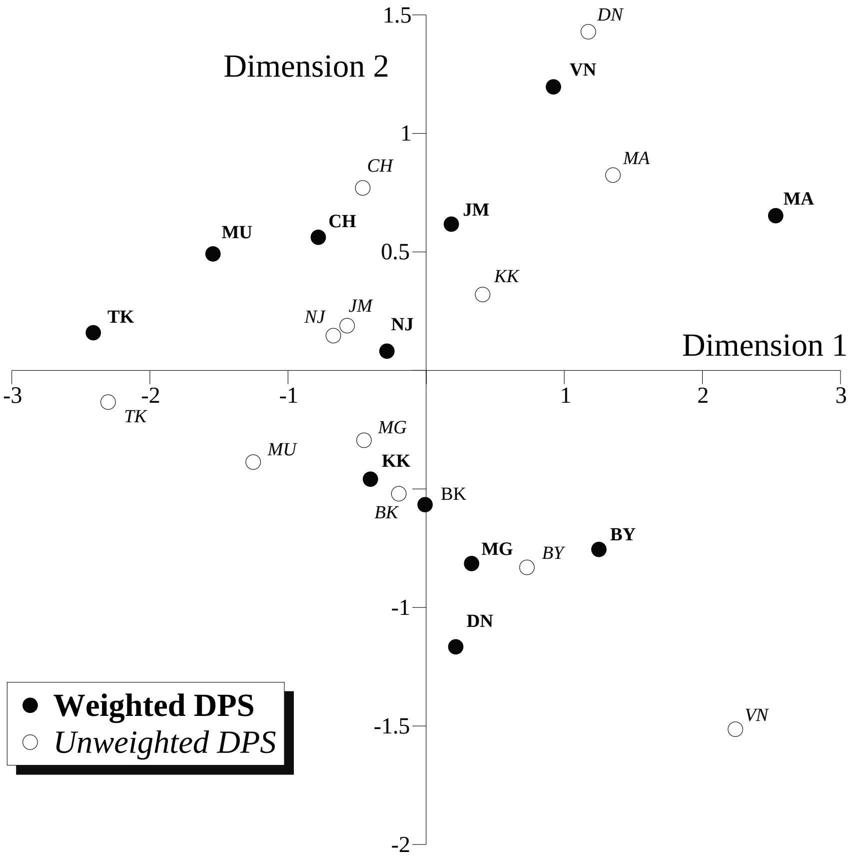

**Figure 7.2**. Two-dimensional scaling plots of weighted, and unweighted dyadic proximity strengths.

Figure 7.3 shows the relationship between dyadic proximity and association strength. Dyads falling below the line had lower dyadic proximity strength than predicted by their dyadic association strength. Those falling above the line had higher dyadic proximity strength than expected. The antagonistic nature of the relationships between DN and MG, and between VN and MG, was demonstrated by the position of these dyads below the regression line together with the absolute values. The affiliative relationships or alliances between DN and VN and between MG and BY are reflected by these dyads falling above the regression line. The relationship between DN and KK may be an example of a uni-directional relationship; the proximity relationship is less than would be predicted by their positive dyadic association strength, suggesting that low status KK maintains a positive association with the alpha male, DN, but DN does not reciprocate. As alpha male, DN is able to exert control over the identities of his nearest neighbours. That most dyads cluster within one standard deviation of the origin suggests that these relationships are not dominated by strong preferences.

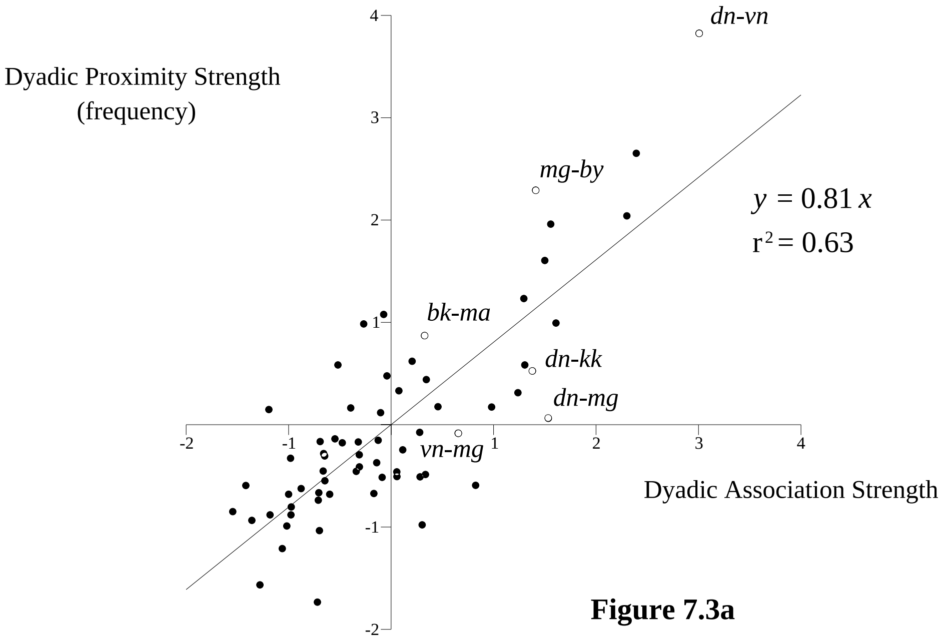

**Figure 7.3a**

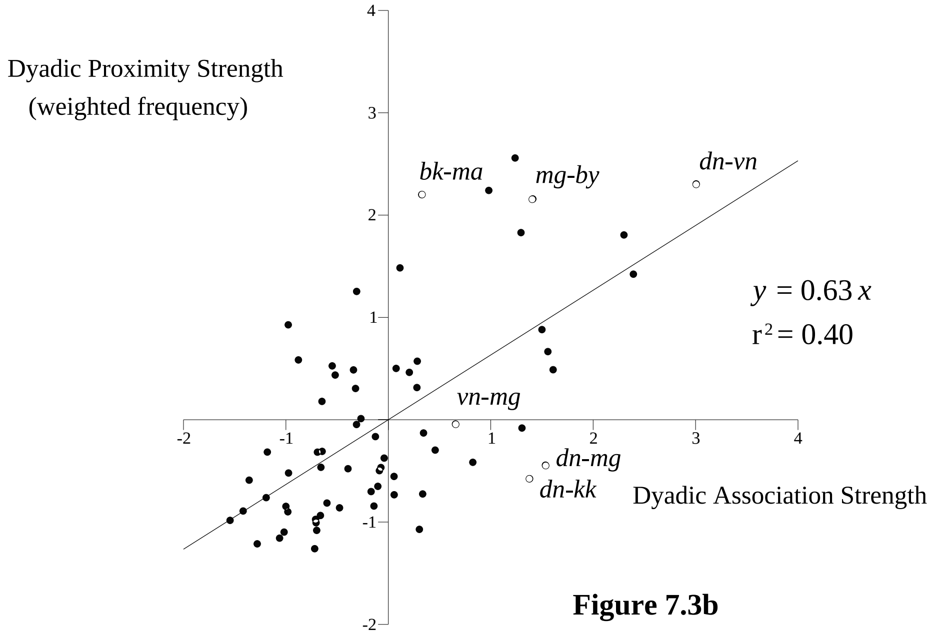

**Figure 7.3b**

**Fig 7.3a,b**. Dyadic proximity strength as a function of association strength, for both weighted and unweighted measures of proximity. Dyads discussed in the text are highlighted and labelled. Regression lines calculated by the Mantel regression procedure indicate the predicted proximity relationship on the basis of association strength.

Regression analysis showed a linear model to fit the relationship between dyadic proximity strength and dyadic association strength, with no trends apparent in the residual plots. Dyadic association strength explains significant proportions of the variance in both clustering tendency and dyadic proximity strength [unweighted dyadic proximity strength ($Z = 105$, $t = 4.07$, $p_r = 0.0002$; $r^2 = 0.65$); weighted dyadic proximity strength ($Z = 82$, $t = 3.01$, $p_r = 0.001$; $r^2 = 0.40$)]. Dyadic association strength explained most variance in clustering tendency ($Z = 110$, $t = 4.09$, $p_r = 0.0002$; $r^2 = 0.72$). This was not surprising as clustering tendency includes two of each male's nearest neighbours, and so comes closer to simply measuring association than do either of the other measures.

The results of these regressions suggested that proximity choices were in part a result of the more fundamental association decisions, but that other factors influenced the choice of nearest neighbours. One of these factors may have been relative status (see Table 7.2). Cluster tendency was significantly related to a preference for higher status individuals, and an avoidance of lower status individuals; within a party, males appear to position themselves away from those below them in status, and cluster around those with higher status. As a result, proximity relationships are likely to reflect the outcome of competition for spatial position within a party. Higher status males are therefore likely to have greater control over their proximity relationships. This is unlikely to be possible for all individuals, and males would be expected to compete for position with a party. Weighted dyadic proximity strength was significantly related to a preference for higher status males, a trend that was apparent for unweighted dyadic proximity strength as well. Other proposed influences of relative status were not significant.

**Table 7.2**. Results of matrix correlations ($K_r$ tests), presented as $\tau$ values. * = Result significant at $\alpha$ = 0.05. # = apparent trend (i.e. just not significant at $\alpha$ = 0.05).

| | Proximity measured by: | | |
|---|---|---|---|
| | Nearest male | | Nearest/second nearest |
| Hypothesis | Frequency | Weighted frequency | Frequency |
| Preference for: | | | |
| same status level | 0.06 | 0.09 | 0.03 |
| other status level | -0.04 | -0.09 | -0.01 |
| higher status level | *0.16*$^{\#}$ | **0.27*** | **0.23*** |
| lower status level | -0.17 | -0.19 | **-0.25*** |

Differences between the results of the proximity strength regressions suggested that frequency of proximity and the distance between nearest neighbours mean different things for the relationship between two chimpanzees. The residuals which seemed to differ most between the unweighted (Fig. 7.3a) and weighted (Fig. 7.3b) proximity strength regressions were those for dyads with low positive, or slightly negative association strengths. BK and MA, for example, had a fairly ambivalent 'association' relationship, but showed a positive 'proximity' relationship, particularly when proximity frequencies were weighted by distance, suggesting that *when* these males are together, they are often close, probably grooming. These males were both members of the group of middle and high status males who performed, and received, the most grooming (Chapter 4). These males potentially have the most complex political lives, and would be expected to be the most frequent users of grooming as a social tactic.

To investigate this, each dyad was categorised by the number of middle and high status males (BK, MG, MA, CH, JM; see Table 4.2) in that dyad. The highest status males, DN and VN, were not included in this group as they were an alpha-beta alliance and potentially less in need of political tactics in their social interactions. Mean values of dyadic residuals were negative for dyads without any of these males, close to zero for those containing only one of the five, and positive for dyads composed of two of these five males (Table 7.3). There were no significant differences between dyads classified in this way for residuals computed from the regression of unweighted proximity strengths ($F_{2,63} = 0.83$, $p = 0.44$). For the residuals from the weighted proximity strength regression however, dyads composed of two of the five middle and high status males had significantly stronger proximity relationships than did dyads containing one or none of these males ($F_{2,63} = 6.86$, $p = 0.002$; *post hoc* Scheffé test), supporting the idea that these males may be using proximity tactically. Despite there being no general preference for individuals of similar status (see Table 7.2), and close to average frequencies of association and proximity, *when* in proximity these males tend to be close to one another.

**Table 7.3**. Mean residuals (± standard deviation) from regressions of unweighted and weighted dyadic proximity strength against dyadic association strength, grouped by the number of middle to high status males comprising the dyad.

| Number | Mean residual | |
|---|---|---|
| of males | Unweighted | Weighted |
| None | -0.085 ± 0.51 | -0.304 ± 0.67 |
| One | -0.024 ± 0.60 | -0.076 ± 0.72 |
| Two | 0.183 ± 0.69 | 0.626 ± 0.76 |

## Grooming Decisions

Individual chimpanzees were observed to select a grooming partner from two or more potential partners on 81 occasions during focal sampling. In 41 cases the choice was between two males, in 20 cases between three males and in 15 cases between 4 males. Only two cases involved a choice between five males, and three cases between six males. The number of occasions on which a single individual chose a grooming partner from two or more possibilities varied from two to 15. Five individuals were observed choosing grooming partners on eight or more occasions, and these males show clear preferences for particular individuals (Table 7.4). These results must be treated with caution given the small sample sizes.

**Table 7.4**. Preference for grooming partners as shown by naturally occurring 'choice experiments', with degree of preference indicated by Ivlev's index (Krebs, 1989). "+" indicates degree of preference, " - " indicates degree of avoidance.

| BY (15 choices) | # occasions | | % occasions | | Ivlev's | |
|---|---|---|---|---|---|---|
| Partner | selected | available | selected | available | index | Preference |
| AY | 0 | 1 | 0.00 | 2.33 | -1.00 | - - - |
| BK | 1 | 2 | 6.67 | 4.65 | 0.18 | + |
| CH | 4 | 8 | 26.67 | 18.60 | 0.18 | + |
| DN | 0 | 4 | 9.30 | 0.00 | -1.00 | - - - |
| GS | 0 | 1 | 0.00 | 2.33 | -1.00 | - - - |
| JM | 2 | 2 | 13.33 | 4.65 | 0.48 | ++ |
| KK | 0 | 1 | 0.00 | 2.33 | -1.00 | - - - |
| MA | 0 | 1 | 0.00 | 2.33 | -1.00 | - - - |
| MG | 5 | 11 | 33.33 | 25.58 | 0.13 | + |
| MU | 0 | 1 | 0.00 | 2.33 | -1.00 | - - - |
| NJ | 1 | 1 | 6.67 | 2.33 | 0.48 | ++ |
| VN | 1 | 8 | 6.67 | 18.60 | -0.47 | - - |
| ZT | 1 | 2 | 6.67 | 4.65 | 0.18 | + |

| KK (14 choices) | # occasions | | % occasions | | Ivlev's | |
|---|---|---|---|---|---|---|
| Partner | selected | available | selected | available | index | Preference |
| AY | 0 | 2 | 0.00 | 5.88 | -1.00 | - - - |
| BK | 0 | 1 | 0.00 | 2.94 | -1.00 | - - - |
| BY | 4 | 6 | 28.57 | 17.65 | 0.24 | + |
| CH | 1 | 3 | 7.14 | 8.82 | -0.11 | - |
| DN | 2 | 5 | 14.29 | 14.71 | -0.01 | *none* |
| JM | 1 | 2 | 7.14 | 5.88 | 0.10 | + |
| MA | 3 | 6 | 21.43 | 17.65 | 0.10 | + |
| MG | 1 | 2 | 7.14 | 5.88 | 0.10 | + |
| MU | 1 | 2 | 7.14 | 5.88 | 0.10 | + |
| VN | 1 | 5 | 7.14 | 14.71 | -0.35 | - - |
| ZT | 0 | 2 | 0.00 | 5.88 | -1.00 | - - - |

| DN (12 choices) | # occasions | | % occasions | | Ivlev's | |
|---|---|---|---|---|---|---|
| Partner | selected | available | selected | available | index | Preference |
| BK | 0 | 1 | 0.00 | 2.70 | -1.00 | - - - |
| BY | 1 | 6 | 8.33 | 16.22 | -0.32 | - |
| JK | 0 | 1 | 0.00 | 2.70 | -1.00 | - - - |
| JM | 0 | 1 | 0.00 | 2.70 | -1.00 | - - - |
| KK | 0 | 3 | 0.00 | 8.11 | -1.00 | - - - |
| MA | 3 | 9 | 25.00 | 24.32 | 0.01 | *none* |
| MG | 3 | 5 | 25.00 | 13.51 | 0.30 | + |
| MU | 1 | 2 | 8.33 | 5.41 | 0.21 | + |
| NJ | 0 | 1 | 0.00 | 2.70 | -1.00 | - - - |
| TK | 0 | 1 | 0.00 | 2.70 | -1.00 | - - - |
| VN | 4 | 6 | 33.33 | 16.22 | 0.35 | + |
| ZT | 0 | 1 | 0.00 | 2.70 | -1.00 | - - - |

(**Table 7.4.** *Cont*.)

| MA (9 choices) | # occasions | | % occasions | | Ivlev's | |
|---|---|---|---|---|---|---|
| Partner | selected | available | selected | available | index | Preference |
| BK | 1 | 1 | 11.11 | 3.70 | 0.50 | ++ |
| BY | 2 | 4 | 22.22 | 14.81 | 0.20 | + |
| CH | 0 | 2 | 0.00 | 7.41 | -1.00 | - - - |
| DN | 2 | 5 | 22.22 | 18.52 | 0.09 | + |
| JM | 1 | 1 | 11.11 | 3.70 | 0.50 | ++ |
| KK | 0 | 1 | 0.00 | 3.70 | -1.00 | - - - |
| MG | 1 | 2 | 11.11 | 7.41 | 0.20 | + |
| MU | 0 | 2 | 0.00 | 7.41 | -1.00 | - - - |
| NJ | 1 | 3 | 11.11 | 11.11 | 0.00 | *none* |
| VN | 1 | 4 | 11.11 | 14.81 | -0.14 | - |
| ZT | 0 | 1 | 0.00 | 3.70 | -1.00 | - - - |
| ZF | 0 | 1 | 0.00 | 3.70 | -1.00 | - - - |

| VN (8 choices) | # occasions | | % occasions | | Ivlev's | |
|---|---|---|---|---|---|---|
| Partner | selected | available | selected | available | index | Preference |
| BY | 4 | 6 | 50.00 | 25.00 | 0.33 | + |
| CH | 0 | 2 | 0.00 | 8.33 | -1.00 | - - - |
| DN | 1 | 5 | 12.50 | 20.83 | -0.25 | - |
| JM | 1 | 1 | 12.50 | 4.17 | 0.50 | ++ |
| KK | 0 | 2 | 0.00 | 8.33 | -1.00 | - - - |
| MA | 1 | 2 | 12.50 | 8.33 | 0.20 | + |
| MG | 1 | 1 | 12.50 | 4.17 | 0.50 | ++ |
| MU | 0 | 2 | 0.00 | 8.33 | -1.00 | - - - |
| NJ | 0 | 3 | 0.00 | 12.50 | -1.00 | - - - |

In 74 cases (90.2%) the selecting individual initiated grooming with his selected partner. In 7 cases (8.5%) the selecting individual moved to the selected grooming partner, but did not initiate grooming; grooming was initiated instead by the chosen individual.

In 31 cases (38%) at least one rejected individual was as close to the selecting individual as was the selected grooming partner. Of the remaining 51 cases, the nearest individual was selected in 24 cases, a more distant individual selected in 26 cases. Together, these results suggest distance alone did not influence selection. The median distance to the selected partner was, however, significantly less than that to rejected potential partners (selected: 2m, inter-quartile range 0.75-4m; rejected: 3m, inter-quartile range 1-5m; Mann-Whitney U test: $U = 5235.5$, $z = -2.11$, $n_{\text{selected}} = 81$, $n_{\text{rejected}} = 155$, $p = 0.03$), although when choice was between two possible partners, there were no significant differences in the distances between the selecting individual and the selected and rejected partners (selected: 1.5m, inter-quartile range 0.5-2.75m; rejected: 1m, inter-quartile range 0.5-3.25m; Wilcoxon sign ranks test: $z = -0.99$, $p = 0.32$).

The number of individuals available as potential grooming partners was significantly, though not strongly, correlated with the status of the individual performing the selection ($r_s$ = 0.25, n = 79, $p$ = 0.026). Higher status males therefore had a slightly wider range of potential grooming partners from whom to make a choice, than did lower status males. This was likely to have been the result of the preference for higher status proximity partners.

Latency to groom was negatively correlated with the status of the selected individual (Pearson's correlation: $r$ = -0.26, n = 60, $p$ = 0.043); individuals approach and begin grooming more rapidly when selecting a high status individual. There were no significant correlations between latency to groom and other status measures, or between latency to groom and measures of association or proximity (Table 7.5), although there was a trend towards a negative relationship between latency to groom and mean status of potential partners.

**Table 7.5**. Results of Spearman rank correlations with latency to groom. No correlations are significant at $\alpha$ = 0.05.

| Variables | n | $r_s$ | $p$ = |
|---|---|---|---|
| Status of choosing individual | 60 | -0.18 | 0.16 |
| Mean status of potential choices | 59 | *-0.25* | *0.06* |
| Variance in status of potential choices | 59 | 0.16 | 0.22 |
| Number of individuals in party | 60 | 0.14 | 0.30 |
| Dyadic association strength | 60 | -0.19 | 0.16 |
| Dyadic proximity strength | 56 | 0.10 | 0.49 |

When choosing one of two possible grooming partners, a decision to select or reject was significantly associated with the relative strength of the dyadic associations ($\chi^2$ = 8.00, $df$ = 1, $p$ = 0.005) and dyadic proximities ($\chi^2$ = 5.23, $df$ = 1, $p$ = 0.022). The median status of selected individuals was higher than that of those rejected (selected: 3.41, inter-quartile range 3.01-4.28m; rejected: 2.9, inter-quartile range 2.2-3.5; $U$ = 464, $n_{selected}$ = 36, $n_{rejected}$ = 36, $p$ = 0.04). The other categorical variables in Table 7.1 showed no significant association with the choice of grooming partner (relative status (A&B, A&C): $\chi^2$ = 3.29, $df$ = 2, $p$ = 0.19; relative status (B&C): $\chi^2$ = 3.63, $df$ = 2, $p$ = 0.16; relative distance (A&B, A&C): $\chi^2$ = 2.63, $df$ = 2, $p$ = 0.27).

Logistic regression produced a significant model of grooming choice ($\chi^2$ = 7.98, $df$ = 1, $p$ = 0.005; see Table 7.6), identifying only dyadic association strength as a significant predictor of choice. Other variables, including absolute measures of status, and relative measures of both status and distance, were not significant in the model. The model predicted that individuals selected as grooming partners those individuals with whom they had the greater dyadic association strength, with a probability of 68%. Although other variables were excluded as non-significant predictors, the partial correlation of dyadic association strength with selection was fairly low ($R = 0.252$).

Together, these results suggest that other variables, not entered into the regression, may be important predictors of grooming choices. The most obvious possible predictors not investigated here are the length of time since the selecting individual groomed each of the potential partners, and the current activity of each of the potential partners. The first of these can only be included if continual (all day) focal sampling of the selecting individual is conducted, a method which was not practical in this study (see Chapter 3).

To include the activity of potential partners as a potential predictor variable in the regression model would have required data for both individuals for each record included. Activity of individuals other than the focal animal was only recorded for the focal's nearest neighbour, and so the necessary data were missing for most cases of grooming partner selection. When the selecting individual was not the focal animal, only cases where the focal and his nearest neighbour had been potential grooming partners could have been included. When the selecting individual was the focal animal, only cases where the potential partners included the nearest neighbour, and the two potential partners were interacting with one another, could have been included.

**Table 7.6.** Results of logistic regression used to determine factors predicting selection of grooming partners. Relative dyadic association strength was coded 1 = relatively weaker, 0 = relatively stronger.

| *Variable* | *B* | *Wald* | *P* | *R* |
|---|---|---|---|---|
| Dyadic assoc. strength (weak/strong) | -1.4839 | 7.458 | 0.006 | -0.252 |
| Constant | 0.7419 | 3.729 | 0.05 | |

$\chi^2 = 7.979$; $df = 1$; $p = 0.0047$

Probability (event) = 1 / (1 + $e^{-z}$), where $z = B_0 + B_1X_1 + B_2X_2$...
z = 0.7419 + (-1.4839 x relative dyadic association strength)
For relative dyadic association strength = strong (coded 0)
Probability = 0.68
For relative dyadic association strength = weak (coded 1)
Probability = 0.32

In 63 of the 81 instances of grooming partner selection (78%) the immediate outcome of the groomer's efforts was recorded. Four different responses were recorded:

- Initiator continues to groom, while partner returns grooming; both grooming simultaneously (*ABgroom*). 24 cases (29.2%).

- Initiator terminates grooming bout, without getting a response from his partner (*Aterm*). 23 cases (28%).
- The partner terminates the grooming bout, without returning the grooming he received (*Bterm*). 4 cases (4.9%).
- The partner returns the grooming, while the initiator stops grooming (*BgroomA*). 12 cases (14.6%).

Responses did not appear to be related to the status difference between individuals (Kruskal-Wallis one way anova: $H = 5.6$, $df = 3$, $p = 0.13$), or the status of the selecting individual ($H = 1.52$, $df = 3$, $p = 0.68$). There was a trend for higher status individuals to terminate grooming bouts without reciprocating grooming, and for lower status individuals to respond by reciprocating the grooming ($H = 7.21$, $df = 3$, $p = 0.065$). The nature of the response was not related to the duration for which the initiating individual groomed ($H = 2.26$, $df = 3$, $p = 0.52$), or to the delay between approach and grooming ($H = 3.95$, $df = 3$, $p = 0.27$).

The duration of grooming before the groomed individual responded was only weakly related to the initiator's status ($r_s = -0.22$, n = 63, $p = 0.081$) suggesting that a response of some kind tended to be more rapid when the groomer was of higher, rather than lower, status. Latency of response was not significantly correlated with the status of the selected partner ($r_s = -0.004$, n = 63, $p = 0.98$), the difference in status between the individuals ($r_s = -0.12$, n = 63, $p = 0.35$), dyadic association strength ($r_s = -0.04$, n = 63, $p = 0.73$) or (weighted) dyadic proximity strength ($r_s = -0.04$, n = 59, $p = 0.76$).

## DISCUSSION

Although work in captive chimpanzees suggests that they are capable of intentional decision-making (Boysen, 1994; Rumbaugh et al., 1994; Povinelli, 1994), this capacity has been little investigated in wild chimpanzees. Stanford et al. (1994) examined the decision to hunt in free-living chimpanzees. They found that while the number of adult males present and the size of the party were both positively correlated with a decision to hunt, for all but the smallest parties it was the number of 'oestrus' females which significantly predicted the occurrence of a hunt. While that investigation was aimed at identifying the evolutionary function of hunting, and not at providing evidence for the mechanism of decision-making, its identification of social factors as the primary determinants of hunting decisions suggests that male chimpanzees make complex assessments of their current social environment. The results presented here strongly support the hypothesis that chimpanzees consider social factors before making decisions.

Individual chimpanzees generally have considerable freedom to associate with other individuals, but are less able to alter the association patterns of other individuals. It is difficult for male chimpanzees to exclude individuals from a party without resorting to overt aggression, which is often insufficient to force an individual to depart (personal observation). An individual leaving a party himself suffers obvious social costs. The distance between individuals is potentially far easier for those individuals to modify, and so should be more sensitive to individual preference.

Male Sonso chimpanzees demonstrate clear preferences with regard to the identities of those with whom they associate within parties, their proximity partners. Association preferences and status appear to interact to produce the spatial structure of parties; within a party, males position themselves close to those individuals with whom they prefer to associate, clustering away from lower status individuals and towards higher status animals. Proximity may therefore reflect social tactics, as close associates are likely to be potential allies, or important competitors, and higher status males more useful as either allies, or as maintainers of social harmony (Harcourt, 1989; deWaal, 1982).

It is unlikely that any single configuration of individuals would be the optimal arrangement for each individual, and as a result, an ongoing process of assessment and shifting of relative distances is likely to ensue. Any decision to alter spatial position is likely, therefore, to depend on an assessment of the social environment; the nature of association relationships, and relative status. In addition, animals are likely to move from one feeding site to another, increasing the complexity of any assessment of relative position. Juvenile males often form an attachment to a particular adult male (Goodall, 1986; Pusey 1990; personal observation), and move to maintain a fairly constant distance to the relevant male, compensating for his movements (personal observation). When feeding, individuals sometimes move frequently from one feeding site to another, apparently without exhausting the available food at each site. At other times individuals move very little between apparently equivalent feeding sites (personal observation). Such movement may be more related to social considerations of inter-individual distances than to foraging strategies.

Proximity may be used tactically; by being close to a particular individual, others are potentially deterred from coming into close proximity. Close proximity may enhance the probability of interacting with the nearby individuals, or disrupting their interactions with others. Middle and high status males, in particular, show an apparent tactical use of proximity. They tend not to have strong association relationships with one another, nor do they tend to be in close proximity more frequently than would be predicted on the basis of their associations. When nearest neighbours, however, they are often close, and as the results presented in Chapter 4 suggest, often grooming. These males are close in status and probably similar in competitive ability. They are likely, therefore, to be both the most useful allies, and the most likely competitors. If, as is suggested in Chapter 4, status benefits accrue to high status males and not just to the alpha male, it becomes important to defend high status. Competing with one another for status, and defending their status from challenges from below, may result in these males having the most political social lives of all community members. To defend their positions, they are likely to have to form coalitions against individuals climbing the social hierarchy from below, and to push for higher status, to form coalitions against one another. During this study two of these males, BK and MA, both improved their social status, and two, MG and CH, fell in status.

Although factors such as the current activity of potential grooming partners may influence the choice of grooming partners, the choice appears to be related to the status of the potential partners, relative differences in association relationships, and relative differences in proximity relationships. Proximity preference and grooming are therefore closely linked. Grooming, however, may not be used as a social tactic, but simply as a means of calming the grooming individual, possibly rewarding the groomer through endogenous opiates (Keverne et al., 1989; Hemelrijk, 1996). If this explanation was true, the nearest available ‘stress relieving mechanism’ should be selected, as there would be no reason for the selection of preferred grooming partners. That chimpanzees do not select partners on the basis of distance alone, however, casts doubt on the validity of a simplistic ‘stress relieving’ hypothesis.

A second possibility is that grooming is used as a means of maintaining group cohesion (Dunbar 1988a). Under this hypothesis, chimpanzees would be expected to choose as grooming patterns those with whom they associate only occasionally; when associating with an infrequently encountered individual, the opportunity to confirm the relationship through grooming should be taken. This, however, was not seen. These chimpanzee males are neither selecting at random their grooming partners, nor are they simply selecting the nearest male when they wish to groom. They are choosing to groom those individuals with whom they also choose to associate relatively more often, supporting the idea that grooming may be used tactically, perhaps as part of a ‘package’ of social tactics.

The mechanism of the choice of grooming partner may be cognitive. The only significant predictor of the chosen grooming partner of those tested here is the relationship between the selecting individual and each potential partner, as measured by relative association strengths of the dyads, suggesting that the selecting individual compares the value of his relationship with each of the potential partners. Each relationship is an abstract concept, and this decision apparently requires the ‘magnitude’ of two or more such concepts to be evaluated.

Alternatively, chimpanzees may simply select the individual with whom they last associated. On average, they would tend to groom their most common associates. This would be more complex than it first appears, however. Chimpanzee parties usually consist of more than two individuals, and the same individual may associate repeatedly. Each male would be required to remember the members of the previous party of which he was a member. Furthermore, parties are not discrete entities. Their composition is highly fluid, and changes in composition are unpredictable. As a result, the record of 'last associates' would need frequent updating.

It is also difficult to see how the 'last associate' mechanism of choice could work without an historical record of association. If the available grooming partners are members of group of individuals who remain in association despite other changes in composition, the relative order in which they came into association must be recalled to determine which of the potential grooming partners was the 'last associate'. Such a mechanism seems less parsimonious than one in which each relationship is maintained as an abstraction, the image of the relationship only being updated after particular interactions. Chimpanzees are capable of simple numeracy (Perusse & Rumbaugh, 1990; Boysen & Berntson, 1990), and so it seems a simple extension for a number representing the relative value of each relationship to be added to the representation of that relationship. Relationships could then be ordered, and selection of grooming partner based on the position of the dyad in the 'list'.

Evidence has been presented elsewhere (Goodall, 1986; Koyama & Dunbar, 1996) which suggests chimpanzees are capable of anticipating future events, and planning their behaviour accordingly (see Whiten & Byrne 1988c), an activity which requires cognitive representations of events. Such behaviour is also reported for macaques (*Macaca arctoides*: Mayagoitia et al., 1993). In order to respond adaptively to a highly dynamic social system it seems unlikely that simple decision rules would be adequate, and that instead a cognitive system to process the information would be necessary. These results support the idea that grooming and proximity may be used as social tactics, and further support the idea that dyadic associations are also tactical. If grooming partners are selected by cognitive choice, then it seems reasonable to regard the choice as intentional. Similar processes may be responsible for the choice of proximity and association partners, particularly given the dynamic nature of association tendencies, and with the potential dynamics in proximity relationships.

# Chapter 8

# THE MIND OF THE ALMOST MAN

> *"It is just like man's vanity and impertinence to call an animal dumb because it is dumb to his dull perceptions"*
>
> *M. Twain, What is Man?, 1906*

The great ape clade is distinguished from other primates by large body size, male-centered social systems, and a high degree of intelligence. These apes, and particularly the chimpanzee, appear to have cognitive abilities qualitatively greater than those shown by other primates, showing evidence of insight, self awareness, and an understanding of the intentions of others; a theory of mind (Köhler, 1925; Premack & Woodruff, 1978; Menzel et al., 1985; Povinelli et al., 1997).

## *Intelligence and Social Complexity*

Social complexity is a possible selective factor in the evolution of advanced cognitive abilities, and is thought to be responsible for the differences in mental ability between primates and other mammals (Humphrey, 1976; Whiten & Byrne, 1988a; Byrne 1995b). Ecological complexity seems unlikely as an explanation for the evolution of primate minds; primates do not necessarily face more demanding environmental problems than other mammals (Byrne, 1995b), and primate neocortex size, assumed to be an index of cognitive capacity and measured as the ratio of neocortex volume to brain volume, appears to be unrelated to ecological variables (Dunbar, 1992). Neocortex size is, however, related to group size, although not linearly, suggesting that it is not absolute group size, the number of relationships an individual has, which demands advanced cognitive skills, but either the quality of an individual's different relationships or the number of third party relationships an individual has to track (Dunbar, *ibid*).

The social lives of many primates are dominated by the need to form coalitions and alliances in order to compete effectively. Individuals differ in their value as allies, and for alliance formation to be an effective competitive strategy, it is important that individuals select the most valuable allies. This is thought to be why they need to track relationships and their interactions with others (Harcourt, 1989). Alliances increase an animal's competitive ability, and so temporarily increase an individual's effective dominance rank. When high social status brings reproductive benefits (see Silk, 1987), individuals are likely to compete for alliance partners, in order to achieve high social rank.

The idea that the monitoring and manipulation of social relationships has been the driving force in the evolution of primates intelligence has been called the Machiavellian Intelligence hypothesis (Whiten & Byrne, 1988a,c). Numerous examples of tactical deception in Old World primates (Whiten & Byrne, 1988c; Byrne & Whiten, 1991) suggest that Machiavellian intelligence is an adaptation common to all catarrhines, and the term seems an apt description; social manipulation is commonplace, with individuals using other members of the social group as “tools”, and redirecting aggression against the kin of previous opponents (Cheney & Seyfarth, 1990).

If a ‘Machiavellian mind’ is an adaptation characteristic of catarrhines, it can be seen as forming part of the phylogenetic inheritance of the great apes. Apes, it seems, do possess mental abilities greater than monkeys (see Whiten, 1996). In particular, they appear to show the capacity for greater insight. While the ‘Machiavellian Intelligence’ (Whiten & Byrne, 1988a,c) hypothesis can account for the differences between primates and non primates, it does not seem sufficient to explain the greater cognitive skills of the great apes, who in the wild at least, do not appear to engage in social manipulation more elaborate than that shown by monkeys (Byrne, 1995b).

In this thesis I have endeavoured to examine the complexity of chimpanzee society, in particular focusing on the relationships between the adult males who form the core of the social system. My aim has been to investigate the paradox of the apparent absence in wild chimpanzees of the complex cognitive abilities shown in captivity: are the lives of male chimpanzees more complex than has been heretofore realised, such that the cognitive ability they show in captivity is an adaptation to deal with that very complexity?

In both space and time, chimpanzee society is especially fluid. Over time, individuals fluctuate in their social status, change their association patterns, and alter their alliance partners. As they move through the social hierarchy, individuals change in their value to others as friends and allies. Furthermore, their own aims, goals, and perceptions of those around them may also change. Alliance changes alter the range of potential allies for each of the other males. At any moment in time, an individual chimpanzee may be alone or surrounded by a number of others; spatially, chimpanzees have no single coherent grouping. The identities of these others, the precise composition of the temporary grouping, will also vary from one occasion to another. The result is an intricate and ever changing social environment.

Like other primates, chimpanzees are seemingly capable of noticing and judging fine social distinctions (Byrne, 1995b), and engage in shifting patterns of coalition and alliance formation, assessing the value of potential partners and selecting appropriately (Harcourt, 1989). Male chimpanzees show status striving behaviour (Goodall, 1986), forming alliances to improve their own social status. However, among chimpanzees, unlike other primates, the patterns of alliance formation are complicated by the extreme fluidity of the social system. All primates are likely to face occasional and unpredictable group splintering, but none, other than perhaps ateline monkeys, have group fluidity as an integral part of their social system. Baboon (*Papio* spp.) groups, and those of many monkey species, commonly splinter into semi-autonomous sub-groups (Dunbar, 1988a) whilst foraging for food, but communication is maintained between sub-groups such that the entire group travels *en masse* in a coordinated fashion around its home range.

Evidence of complex cognitive skills in chimpanzees comes primarily from captive subjects (see Chapter 7), and other than in the making of tools (McGrew, 1992), demonstrations of such skills seem rare in the natural habitat. This has raised something of a paradox; chimpanzees have cognitive abilities in captivity which, presumably, have evolved through natural selection, and yet they appear not to use them in their natural habitat. Such a view, however, overlooks the demands of the fluctuating social environment; the apparently mundane behaviour of moving from one temporary party to another. The observed behaviour of male chimpanzees supports the idea that they make intentional decisions concerning their association partners, and that such decisions require the use of the cognitive abilities demonstrated in captivity.

Each chimpanzee is presented with a changing social environment, with the identities of its current associates in a state of constant flux. To remain in contact with allies, or to form new alliances, each male chimpanzee must decide which mix of association partners best matches his goals; if a desired ally is in the same party, but an existing ally and a competitor are in another, should the individual change parties? The decision whether to remain with current associates or to leave can potentially be made every time the available information changes; every time one or more individuals leave or join, every time a vocalisation from an individual in another party is heard.

Combining the problems of alliance formation with the demands of a fluid society may pose an additional demand on the cognitive capacities of the animals sufficient to require the development of the ability to consciously access knowledge. The merits of remaining with current social companions have to be balanced with those to be gained by changing companions, with the further complication that competitive or affiliative interactions between individuals in other parties may lead to changes in status or alliances, particularly given male chimpanzees' penchant for "allegiance fickleness" (Nishida, 1983). To be able to represent possible combinations of associates cognitively, and to compare this to the available information on current associates, would clearly be advantageous.

Information on the composition of other parties comes through the occasional pant-hoot choruses; chimpanzees are thought to be able to identify individuals from their pant-hoot vocalisations alone (Bauer & Philip, 1983; Goodall, 1986). To do this, and to identify individuals as members of one community or another, requires a mental representation of the vocalising animal. To have access to this representation allows any response to be conditional on current associates, and the cognitive implementation of strategic behaviour. The added complexity of alliance formation in a fission-fusion society requires, this thesis contends, intentional decision-making by individual chimpanzees, evidenced by a complex layering of social tactics and strategies.

Male chimpanzees pursue strategies aimed at improving social status, which should ultimately relate to reproductive success, strategies which revolve around the formation of alliances. The interactions which lead to these relationships occur in the the small parties in which chimpanzees spend their lives, and in order to interact with particular individuals, male chimpanzees appear to select their social partners in an attempt to achieve the optimum social environment for alliance formation and social competition. The decisions made in pursuit of these optimal environments can thus be regarded as tactical decisions.

The complexity of the social environment and the frequent need for re-evaluation of association decisions strongly suggests that these decisions are both cognitive and intentional, and that alternate proximate explanations for decision-making in chimpanzees are less parsimonious. This complexity has, it is suggested, selected for self awareness and a theory of mind; it is in the social problems faced by chimpanzees on a day to day basis that their cognitive skills are required.

Experimental studies suggest that chimpanzees are capable of self-awareness, and the testing of albeit limited numbers of chimpanzees suggest they have mental abilities similar to those of a two or three year old human (Povinelli, 1994, 1997). Premack and Woodruff (1978) showed an adult chimpanzee capable of recognising the intentions of humans. The behaviour of chimpanzees suggests that they are conscious, in the sense that they “know what they know” (Cheney & Seyfarth, 1990). If this is true then they have an ability to create an inner analogue of the world, which can be used to assess the impact of new information, reviewing past scenarios and comparing them to the current situation. It is not necessary that words be used to construct this inner analogue (Crook, 1980). This inner analogue would enable individuals to mentally rehearse the results of possible association decisions, weighing the advantages and disadvantages of changing companions.

Although it is common to compare the mental abilities of chimpanzees with small children (for example, Whiten & Byrne, 1991; Povinelli, 1994) it is important to remember that chimpanzees are unlikely to have the same mentality as juvenile humans;

chimpanzee intellect may have evolved in a different direction from that of humans (Povinelli, 1994). The chimpanzee view of the world would be expected to differ enormously from that of a human, even a two year old. Chimpanzees seem to share with small children a very egocentric view of the world, but are far more concerned with power and sex. While it seems chimpanzees are capable of creating internal analogues of the world, it is likely that these place the individual at the centre, and that while the ability exists to understand the intentions of others (Premack, 1988; Povinelli et al., 1990; Povinelli et al., 1992) this understanding is likely to be weighted strongly by the individual's own desires.

If the demands of social politics in a fission-fusion society are responsible for the evolution of chimpanzee cognition, then the possibility exists that such demands are responsible for the evolution of intelligence in all great apes. Problems remain with the idea that the differences between apes and monkeys in their cognitive skills can be explained in this manner, however, not the least of which is the lack of any such social complexity in gorillas and orang-utans (*Pongo pygmaeus*).

Studies of captive or feral orang-utans and gorillas (see Russon et al., 1995) suggest that their intelligence is similar to that of chimpanzees, although the evidence is not as strong (Byrne, 1995a). In particular, they appear to make even less use of complex cognitive abilities in the natural habitat than do chimpanzees. It may be that, rather than the demands of complex society selecting for high intelligence, the cognitive skills of the chimpanzee (and by implication the bonobo) *permit* such a complex social system, with cognitive abilities, particularly self-awareness, evolving perhaps to deal with the problems faced by a large bodied animal in a relatively fragile arboreal environment (Povinelli & Cant, 1995)

Povinelli (1993) has suggested that gorillas were subject to selection for rapid maturation and large body size, incidentally resulting in a secondary reversal of cognitive skills. In comparison to chimpanzees, gorillas do reach a larger body size at a younger age of sexual maturity than chimpanzees, and as a result have a smaller brain relative to body size (Parker, 1990). However brain size remains absolutely large. Many gorillas fail the 'mirror-recognition' test (Gallup 1970), although the language-trained gorilla Koko does show evidence of self-awareness (Patterson & Cohn, 1994). Gorillas also show evidence of intention, and of understanding that others have minds (Gomez, 1991). In the wild, gorillas show complex food processing skills, argued to require complex cognition (Byrne & Byrne, 1993).

Furthermore, understanding of great ape social systems is far from complete. The nature of the orang-utan social system is still far from clear, and may be more complex than their apparently solitary nature suggests (Dunbar, 1992; van Schaik & van Hooff, 1996). Orang-utans may in fact live in a community system, containing one or more adult males, with foraging constraints forcing individuals to remain apart most of the time (van Schaik & van Hooff, *ibid*). Evidence seems to suggest that each ‘population’ of orang-utans consists of a stable core of 6-15 individuals resident in a given area (Dunbar, 1992). Orang-utans are likely to have similar neocortex size in proportion to total brain size as chimpanzees, supporting the idea that either orang-utans were more social in the recent evolutionary past than they currently appear to be, or that they are currently more social than has been realised (Dunbar, *ibid*). Much of what is known about the gorilla social system comes from studies of mountain gorillas, which are adapted to an extreme environment and unlikely to be representative of gorillas in general. Recent research (Goldsmith, 1996) suggests that social groups of lowland gorillas (*Gorilla g. gorilla*) may contain a number of males and females, which separate to forage during the day, with each sub-group containing a single adult male and a few females.

It has been proposed that the social system of the ancestor of African apes, if not all great apes, resembled most closely that of modern day gorillas (Foley, 1989; Isbell & Young, 1996). However, early hominids (*Australopithecus afarensis*) are thought to have been similar in body size and diet to modern chimpanzees (Andrews & Martin, 1991), and to have lived in social groups containing multiple males and females (Isbell & Young, 1996). It seems likely that the social systems of early hominids were constrained by that of the common ancestor with extant apes, and only a limited range of social states, defined by the association patterns within and between sexes, seem possible for hominoids (Foley & Lee, 1989). Possible routes by which one social ‘state’ can evolve into another are constrained; some changes are more ecologically viable than others, with certain routes being ‘blocked’ by immediate fitness drops (Foley & Lee, *ibid*).

The implication is that the common ancestor of gorillas, chimpanzees, and humans was more like a chimpanzee than other extant apes, physically, perhaps mentally, and with some form of ‘male-bonded’ social system (Foley, 1987, 1989). The possible similarities between the social systems of extant great apes suggest further that this social system was a more flexible, fission-fusion, system than is seen in present day gorillas.

If both lowland gorillas and orang-utans do live in such fluid social systems, and this was also characteristic of early hominids, it becomes much easier to see all great ape social systems as variations on a theme. Machiavellian intelligence can be seen as a fundamental characteristic of catarrhine primates, present in both old world monkeys and apes. Male-bonded fission-fusion social systems may have evolved only in the apes, perhaps as recently as the common ancestor of African apes and orang-utans. The additional intricacy this imposed on the machiavellian social politics already present may then have been a major selective force for the evolution of the cognitive abilities seen in extant great apes.

If fission-fusion is characteristic of the ‘original’ great ape social system then the added dimension it gives to alliance formation may be responsible for the evolution of great ape mental capabilities. At first sight this reasoning would predict similar abilities in spider monkeys. These monkeys seem very similar in their social behaviour to chimpanzees (Symington, 1990; Chapman et al., 1995), with strong affiliative bonds and agonistic dominance between males, and a fission-fusion social system. While these monkeys form coalitions, what is less clear is the extent of *political* behaviour. Grooming rates, a key component to male chimpanzee social strategies, are very much lower in spider monkeys than in chimpanzees, suggesting that intricate social strategies may not be present.

Other ateline monkeys, such as the woolly spider monkey or muriqui (*Brachyteles arachnoides*), have very egalitarian societies (Strier, 1990, 1994), suggesting this may have been an ancestral state for spider monkeys, whereas the widespread nature of hierarchical societies in Old World primates suggests that hierarchical structures may be an adaptation of catarrhine primates alone, not shared with the platyrrhines of the New World. The suggestion is that Machiavellian-type social strategies, and the cognitive structures necessary for their implementation, were present in the social system of ancestral ape species. If the common ancestor of great apes were forced, by virtue of large body size in an increasingly patchy environment, to shift to a fission-fusion social system, the increasing fluidity of the social system may then have led to increasing complexity in status competition and alliance formation. The need to maintain alliance structures may have selected for increased intelligence. Social dominance in spider monkeys may have evolved without a Machiavellian heritage, with the result that the cognitive demands of their fission-fusion society may not be as great as those in great ape societies.

Alternatively, complex cognition may emerge simply as the result of an absolutely large brain size (Byrne, 1993). The large neocortex ratios of chimpanzees (and presumably orang-utans) support the idea that social complexity has been important in the evolution of intelligence, but the neocortex ratios of gorillas are no larger than those of *Papio* baboons (Dunbar, 1992; Byrne, 1995a). The key difference between gorilla and baboon brains is one of absolute size. However, brain tissue is energetically expensive (Parker, 1990) and a functional explanation of *why* such a large brain evolved is still required. Povinelli & Cant (1995) have suggested that the sense of self may have evolved for another purpose, such as navigating through an unstable environment, and been subsequently sequestered to aid in prediction and understanding of others behaviour, leading to an escalating of the complexity of social relationships.

## *A Strategic Social System*

The fission-fusion characteristic of chimpanzee society is seen here as the result of individual social strategies, constrained by the interaction between large body size and a frugivorous diet. The conventional explanation of the evolution of chimpanzee society, Wrangham's (1975, 1979) model, is that females were forced, by virtue of large body size and dispersed food sources, to forage alone, and that males, unable to defend access to a single female because of the size of her home range, had to cooperate to defend a number of females against other groups of males. Males were forced to travel in parties, as lone males were vulnerable to attack by other males, leading by escalation to mutually hostile male communities (Wrangham, 1987; Dunbar, 1988a).

Te Boekhorst & Hogeweg (1994) have claimed that this model is inadequate, as it fails to distinguish functions of male party and male community, assumes evolution from a solitary stage which for phylogenetic reasons seems unlikely, and provides no explanation for the formation of male associations; defence against aggression from larger groups begs the question of what was responsible for the formation of *these* groups. As a replacement, te Boekhorst and Hogeweg (*ibid*) propose that the evolution of chimpanzee society can be explained by 'self-structured' model, in which the social system emerges as a the result of simple mate-finding and feeding rules. However, as explained below, this model is itself inadequate.

In Chapter 5 an alternate model, dealing with the behaviour of male chimpanzees, was introduced. This model addresses the criticisms of Wrangham's model raised by te Boekhorst and Hogeweg, and furthermore accounts for details of the interactions between males. This model, of tactical association, separates the functions of community and male parties and provides an explanation for the evolution of male association. Furthermore the model does not require the postulation of a solitary stage prior to the evolution of a fission-fusion social system.

Males are seen as associating in order to form relationships with which they out compete other males, and male parties are the environment of within-group competition; it is in these parties that males contest and establish the alliances which later serve in competition for status, and, ultimately, females. Possible fitness benefits of high social status were discussed in Chapter 4, where it was suggested that while alpha status brings the greatest short-term benefits, at least in terms of access to females, it may be that over a life-time, holding high status may bring similar benefits.

While useful as a heuristic device, postulating a solitary stage is unnecessary for the model. Familiarity between males of the same social group would in fact make the formation of associations more likely than would be expected for solitary males. The model simply postulates that the ‘original’ grouping pattern became more fragmented with sub-groups and lone individuals becoming more common. This fragmentation can be seen as an extension of the tendency shown by many primates groups whilst foraging, perhaps made more extreme as the habitat become increasingly patchy as a result of a drying environment. Such drying, and the resulting fragmentation of forest habitats, occurred in Africa throughout most of the Miocene (Potts et al., 1992).

Parties, therefore, are concerned with formation of alliances. The composition of the party is more important than its size, and is seen as the result of association choices made by individuals. Most adult males are similarly social, but divide their social time differently. Two separate association strategies have been distinguished, with some males associating primarily with only a few individuals, and others associating more evenly with community males. Both of these strategies seemed useful in achieving the necessary interactions for an improvement in social status. During this study, individuals pursuing both social strategies improved their social status. The importance of allying with the right individuals was also apparent; the allies of an individual unsuccessfully challenging for high status seemed to suffer repercussions for their own social status.

The behaviour of male chimpanzees of the Sonso community appeared to support the community concept as described by Wrangham (1979, 1987). Males had similar boundaries to their home ranges, with smaller ranges tending to fall inside the boundaries of larger ranges. Parties of males made patrols, or incursions into areas beyond the identified community boundaries, during which they stopped often to listen, and did not feed until turning for home. Males were found to spend the majority of their time in relative small core areas, located away from the community range boundaries. In this, the males deviate from the expectations of Wrangham’s model, which assumed even ranging across the shared range. Other than a brief mention by Wrangham and Smuts (1980), such a core area phenomenon has not been reported before. I hypothesise that these core areas may function to enable prediction of the location of individual males, and are located away from the range edges to minimise the risks of accidentally encountering males from other communities. The results of the ranging analysis represent an interesting modification to the generally accepted model of chimpanzee communities.

The ‘self-structuring’ model presented by te Boekhorst and Hogeweg (1994), while an interesting exercise in computer modelling, mirrors only crude aspects of chimpanzee society, and does not reflect the behaviour of real chimpanzees. One of the assumptions of the model is that chimpanzees feed from a single food source until satiated, whereas in reality chimpanzees will often travel from one food source to another. More importantly, this model predicts that parties increase in size as more fruiting trees become available, a prediction which is not supported by observations in Budongo where the reverse is seen.

While in Kibale larger parties are associated with increasing food abundance, it seems that this may be the result of abundant food resources being highly clumped (Chapman & Wrangham, 1996). Such clumping is not incorporated in the te Boekhorst and Hogeweg model (1994).

The ‘self-structuring’ model also assumes that male chimpanzee move from one food source to another with parties forming simply as a byproduct of this movement. Such an assumption concerning the formation of parties seems erroneous. That males should be more sociable than females is an obvious outcome of the initial conditions of the model, but the resulting distribution of party sizes does not reflect that seen in real chimpanzees. Individual chimpanzees leave as well as join feeding parties, sometimes to feed elsewhere. The ‘self-structuring’ model only accounts for this in terms of males being satiated at different rates, which fails to explain the observed switching of food sources, and also fails entirely to explain the composition of parties. The ‘self-structuring’ model proposed by te Boekhorst and Hogeweg (1994) shows that an apparently fission-fusion social system can arise from simple ecological rules, free from the assumptions of a sociobiological model, but the result is inadequate as an explanation of the reality of chimpanzee society.

While this thesis has focused on cognitive demands of male social behaviour, female chimpanzees also show complex cognition. While they may respond in different ways to the fission-fusion society, it is well known that females have the capability to engage in typically male alliance formation (deWaal, 1982), and recent work suggests that in the wild females have dominance relationships which appear to have important reproductive consequences (Pusey et al., 1997). Females may use associations with their adult sons to improve status, and may make decisions concerning the identities of potential mates (Gagneux et al., 1996). Furthermore, and perhaps most critically, females may need to make complex decisions concerning associations when transferring between communities (Hiraiwa-Hasegawa, personal communication).

Understanding the extent of chimpanzee cognitive skills, and their use in the natural lives of chimpanzees is unlikely to illuminate the origins of the the deep analytical powers common to modern humans, but should clarify precisely what the differences are, and what the minds of the early hominids were like. If chimpanzees were recognised as members of the human genus, along with all hominid species, their similarities to humans might be less surprising, less contentious, and more informative.

The complexity of the chimpanzee social system, whether responsible for, or the product of, their cognitive skills, seems certainly to require such abilities; chimpanzees could not live the way they do without the cognitive abilities which, in captivity at least, they demonstrably possess.

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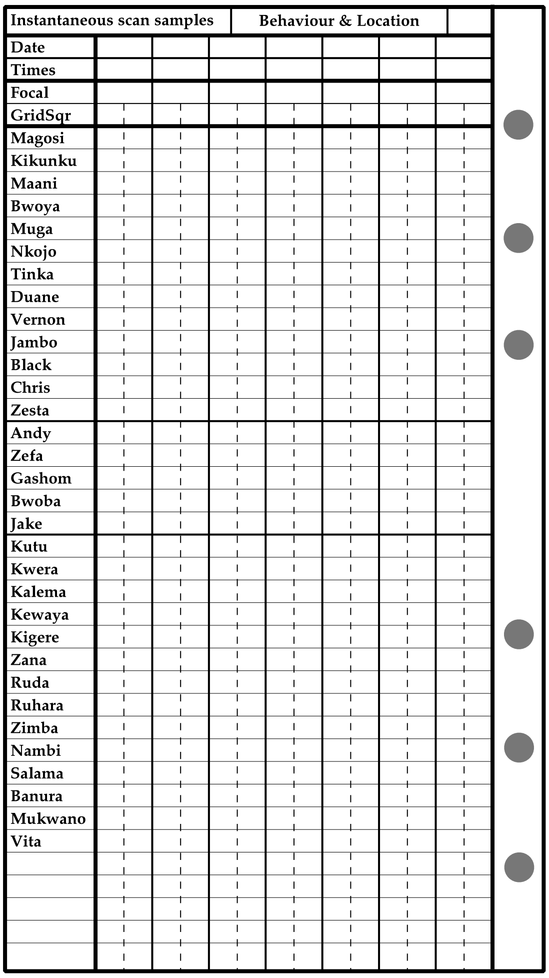
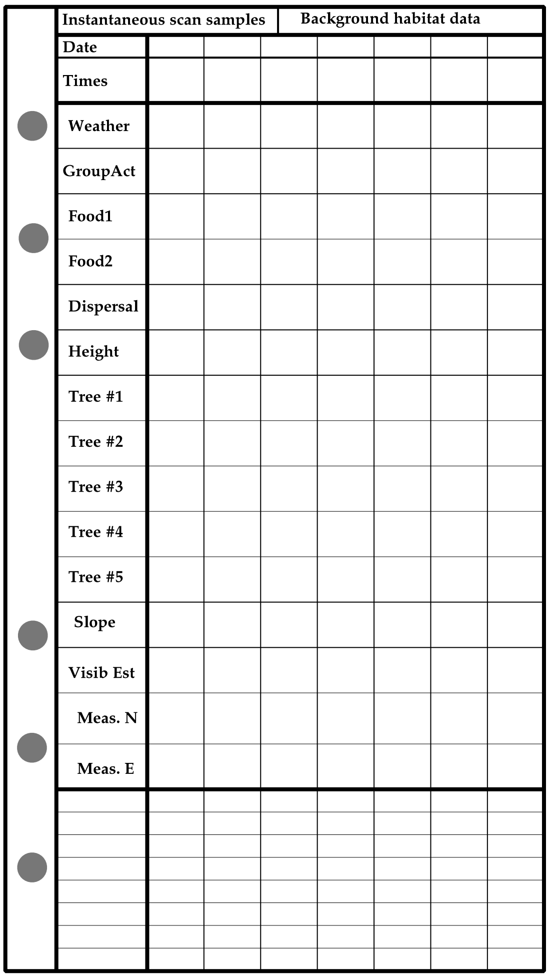
# Appendix 1

# EXAMPLES OF DATA SHEETS

## Instantaneous Scan Sampling



| Instantaneous scan samples | Behaviour & Location | | | | | | |
|---|---|---|---|---|---|---|---|
| Date | | | | | | | |
| Times | | | | | | | |
| Focal | | | | | | | |
| GridSqr | | | | | | | |
| Magosi | | | | | | | |
| Kikunku | | | | | | | |
| Maani | | | | | | | |
| Bwoya | | | | | | | |
| Muga | | | | | | | |
| Nkojo | | | | | | | |
| Tinka | | | | | | | |
| Duane | | | | | | | |
| Vernon | | | | | | | |
| Jambo | | | | | | | |
| Black | | | | | | | |
| Chris | | | | | | | |
| Zesta | | | | | | | |
| Andy | | | | | | | |
| Zefa | | | | | | | |
| Gashom | | | | | | | |
| Bwoba | | | | | | | |
| Jake | | | | | | | |
| Kutu | | | | | | | |
| Kwera | | | | | | | |
| Kalema | | | | | | | |
| Kewaya | | | | | | | |
| Kigere | | | | | | | |
| Zana | | | | | | | |
| Ruda | | | | | | | |
| Ruhara | | | | | | | |
| Zimba | | | | | | | |
| Nambi | | | | | | | |
| Salama | | | | | | | |
| Banura | | | | | | | |
| Mukwano | | | | | | | |
| Vita | | | | | | | |
| | | | | | | | |
| | | | | | | | |
| | | | | | | | |
| | | | | | | | |
| | | | | | | | |

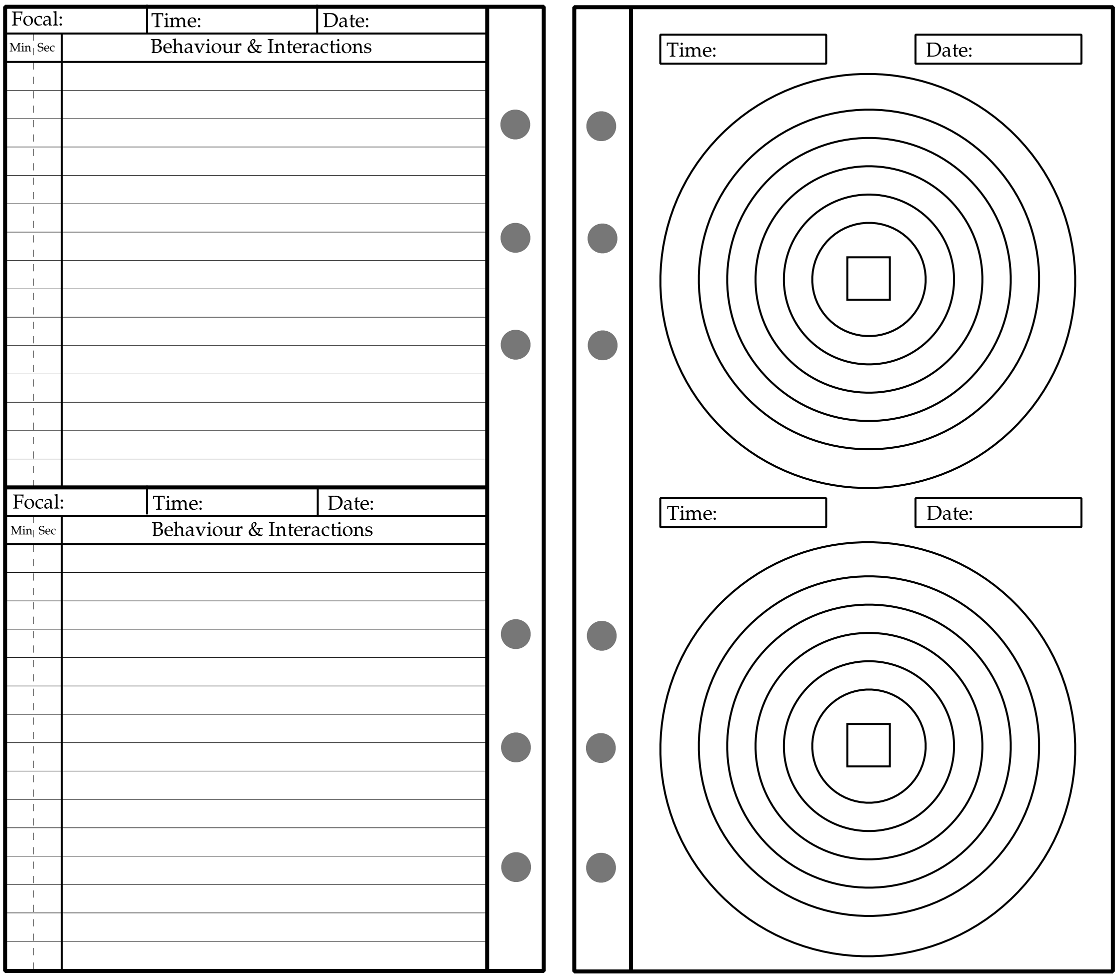


| Instantaneous scan samples | Background habitat data | | | | | | |
|---|---|---|---|---|---|---|---|
| Date | | | | | | | |
| Times | | | | | | | |
| Weather | | | | | | | |
| GroupAct | | | | | | | |
| Food1 | | | | | | | |
| Food2 | | | | | | | |
| Dispersal | | | | | | | |
| Height | | | | | | | |
| Tree #1 | | | | | | | |
| Tree #2 | | | | | | | |
| Tree #3 | | | | | | | |
| Tree #4 | | | | | | | |
| Tree #5 | | | | | | | |
| Slope | | | | | | | |
| Visib Est | | | | | | | |
| Meas. N | | | | | | | |
| Meas. E | | | | | | | |
| | | | | | | | |
| | | | | | | | |
| | | | | | | | |
| | | | | | | | |
| | | | | | | | |
| | | | | | | | |
| | | | | | | | |
| | | | | | | | |

**Notes**: For each individual, presence in a party, and behaviour (if visible) recorded. In addition the reproductive state of females (Perianal swelling = 1; No swelling = 0), and the presence of any dependent infants was recorded.

A1.2

# Focal Sampling



**Notes**: Behaviour of focal and nearest neighbour recorded in a short-hand form with time record to minutes and seconds on the left-hand sheet. Proximity relationships were recorded on the right-hand sheet. Focal individual was placed in the centre square, and other individuals placed according to their horizontal distance (circles represent 1,2,3,4,5 and 10 metres from the focal) with difference in vertical location indicated by + or - *x* metres. Distances recorded to nearest metre. Movements of individuals noted by the means of arrows, with the new location drawn to provide a continuous record of proximity. Multiple proximity diagrams were used during a single sample when necessary.

# Appendix 2

# IDENTIFIED FLORA OF THE BUDONGO FOREST RESERVE

**(Compiled by A. J. Plumptre)**

| *Botanical Name* | *Code* | *Botanical Name* | *Code* |
|---|---|---|---|
| *Acacia spp.* | Acs | *Caloncoba schweinfurthii* | Cls |
| *Acalypha spp.* | Acl | *Canarium schweinfurthii* | Cns |
| *Aidia micrantha* | Aim | *Canthium spp.* | Cth |
| *Alangium chinense* | Alc | *Canthium vulgare* | Cav |
| *Albizia spp.* | Alb | *Cassia spectabilis* | Cs |
| *Albizia coriaria* | Ac | *Celtis africana* | Caf |
| *Albizia ferruginea* | Af | *Celtis durandii* | Cdu |
| *Albizia glaberrima* | Agl | *Celtis mildbraedii* | Cmi |
| *Albizia gummifera* | Agu | *Celtis wightii* | Cwi |
| *Albizia zygia* | Az | *Celtis zenkeri* | Cze |
| *Alchornea laxiflora* | Al | *Chaetachme aristata* | Cha |
| *Allophyllus dummeri* | Ald | *Chlorophora* (*Milicia*) *excelsa* | Chl |
| *Alstonia boonei* | Ab | *Chrysophyllum albidum* | Cal |
| *Aningeria altissima* | Aal | *Chrysophyllum gorungosanum* | Cgo |
| *Annona* (*Lepsis*) *senegalensis* | Ans | *Chrysophyllum muerense* | Cmu |
| *Antiaris toxicaria* | Ant | *Chrysophyllum perpulchrum* | Cpr |
| *Antidesma laciniatum* | Anl | *Citropsis articulata* | Cit |
| *Antidesma venosum* | Anv | *Cleistanthus polystachyus* | Cpy |
| *Aphania senegalensis* | Aps | *Cleistopholis patens* | Cp/Clp |
| *Apodytes dimidiata* | Apd | *Clausena anisata* | Cla |
| *Argomuellera macrophylla* | Am | *Cola gigantea* | Cog |
| *Balanites wilsoniana* | Bw | *Combretum spp.* | Cms |
| *Balsamocitrus dawei* | Bd | *Combretum binderanum* | Cob |
| *Baphia wollastonii* | Bpw | *Combretum collinum* | Cbc |
| *Belonophora hypoglauca* | Beh | *Combretum ghasalense* | Cgh |
| *Belonophora glomerata* | Beg | *Cordia africana* | Coa |
| *Bequaertiodendron oblanceolatum* | Beo | *Cordia millenii* | Com |
| *Bersama abyssinica* | Bsa | *Craibia brownii* | Crb |
| *Blighia unijugata* | Blu | *Cratera adansonii* | Cta |
| *Blighia welwitschii* | Blw | *Crossonephelis africanus* | Cra |
| *Bombax spp.* | Bob | *Croton macrostachys* | Cmc |
| *Bosqueia phoberos* | Bp | *Croton megalocarpus* | Cmg |
| *Bridelia brideliifolia* | Brb | *Croton sylvaticus* | Csy |
| *Bridelia micrantha* | Brm | *Cynometra alexandrii* | Cya |
| *Broussonetia papyrifera* | Bpy | *Dasylepis eggelingii* | Dae |

| | |
|---|---|
| *Desplatsia chrysochlamys* | Dc |
| *Desplatsia dewevrei* | Dd |
| *Dichrostachys cinerea* | Dcc |
| *Dictyandra arborescens* | Dar |
| *Diospyros abyssinica* | Dia |
| *Diospyros mespiliformis* | Dim |
| *Discoclaoxylon sp.* | Dcx |
| *Dombeya burgessiae* | Dob |
| *Dombeya goetzenii* | Dog |
| *Dombeya mukole* | Dom |
| *Dovyalis macrocalyx* | Dvm |
| *Drypetes sp.* | Dsp |
| *Drypetes gerrardi* | Dgr |
| *Drypetes ugandensis* | Du |
| *Ehretia cymosa* | Ec |
| *Ekebergia capensis* | Ekc |
| *Ekebergia senegalensis* | Eks |
| *Entandrophragama angolense* | Ena |
| *Entandrophragama cylindricum* | Enc |
| *Entandrophragama utile* | Enu |
| *Erythrina abyssinica* | Ea |
| *Erythrina excelsa* | Ee |
| *Erythrophleum suaveolens* | Es |
| *Euadenia eminens* | Eu |
| *Euphorbia teke* | Et |
| *Fagara angolensis* | Fan |
| *Fagara leprieurii* | Fle |
| *Fagara macrophylla* | Fma |
| *Fagara mildbraedii* | Fmi |
| *Fagaropsis angolensis* | Faa |
| *Ficus spp.* | Fic |
| *Ficus asperifolia* (*urceolaris*) | Fa |
| *Ficus barteri* | Fb |
| *Ficus exasperata* | Fe |
| *Ficus lingua* | Fl |
| *Ficus mucuso* | Fm |
| *Ficus natalensis* | Fn |
| *Ficus ottoniaefolia* | Fo |
| *Ficus polita* | Fpo |
| *Ficus pseudomangifera* | Fps |
| *Ficus sansibarica* (*brachylepis*) | Fsa |
| *Ficus saussureana* (*dawei*/*lutea*) | Fss |
| *Ficus stipulifera* | Fst |
| *Ficus sur* (*capensis*/*vogelana*) | Fsu |
| *Ficus thonningii* | Fth |
| *Ficus trichopoda* (*congensis*) | Ftr |
| *Ficus vallis-choudae* | Fvl |
| *Ficus variifolia* | Fvr |
| *Funtumia africana* | Fua |
| *Funtumia elastica* | Fue |
| *Glyphaea brevis* | Gr |
| *Greenwayodendron suaveolens* | Gs/Gys |
| *Guarea cedrata* | Gc |
| *Harungana madagascariensis* | Hm |
| *Holoptelea grandis* | Hg |
| *Irvingia gabonensis* | Ig |
| *Khaya anthotheca* | Ka |
| *Khaya grandifoliola* | Kg |
| *Khaya senegalensis* | Ks |
| *Kigelia africana* | Kia |
| *Klainedoxa gabunensis* | Klg |
| *Lannea barteri* | Lb |
| *Lannea welwitschii* | Lw |
| *Lasiodiscus mildbreadii* | Lm |
| *Lacaniodiscus cupanioides* | Lc |
| *Lacaniodiscus fraxinifolius* | Lf |
| *Leptaulus daphnoides* | Lpd |
| *Leptonychia mildbreadii* | Lpm |
| *Lindackeria scweinfurthii* | Lis |
| *Linociera johnsonii* | Lj |
| *Linociera latipetala* | Ll |
| *Lovoa swynnertonii* | Ls |
| *Lovoa trichilioides* | Lt |
| *Lychnodiscus cerospermus* | Lyc |
| *Macaranga barteri* | Mbr |
| *Macaranga lancifolia* | Ml |
| *Macaranga schweinfurtii* | Ms |
| *Maerua duchesnei* | Md |
| *Maesopsis eminii* | Me |
| *Majidea fosteri* | Mf |
| *Mammea africana* | Ma |
| *Mango mangifera* | Mmf |
| *Manilkara butugi* | Mb |
| *Manilkara dawei* | Mad |
| *Manilkara obovata* | Mo |
| *Markhamia platycalyx* | Mp |
| *Maytenus arguta* | Mya |
| *Mildbraediodendron excelsum* | Mie |
| *Milletia sp.* | Mil |
| *Mimulopsis sp.* | Mps |
| *Mimusops bagshawei* | Mbg |
| *Mitragyna stipulosa* | Mst |
| *Monodora angolensis* | Moa |
| *Monodora myristica* | Mom |

| | |
|---|---|
| *Morus lactea* | Mol |
| *Musanga cecropioides* | Mc |
| *Myrianthus holstii* | Myh |
| *Neoboutonia macrocalyx* | Nm |
| *Newtonia buchananii* | Nb |
| *Ochna membranaceae* | Om |
| *Ochna schweinfurthii* | Osh |
| *Olea africana* | Ola |
| *Olea hochstetteri* | Olh |
| *Olea welwitschii* | Olw |
| *Oncoba spinosa* | Ons |
| *Ouratea spp.* | Ous |
| *Oxyanthus speciosus* | Oxs |
| *Pachystela brevipes* | Pcb |
| *Pancovia turbinata* | Pat |
| *Parinari excelsa* | Pe |
| *Parkia filicoidea* | Pf |
| *Paropsia guineensis* | Pg |
| *Phyllanthus* (*Margaritaria*) *discoideus* | Phd |
| *Phyllanthus inflatus* | Phi |
| *Picralima nitida* (“quinine”) | Pn |
| *Piptadeniastrum africanum* | Pa |
| *Pittosporum viridiflorum* | Pv |
| *Poemna angolensis* | Pa |
| *Prunus africana* | Pra |
| *Pseudospondias microcarpa* | Psm |
| *Psidium guajava* | Psg |
| *Pterygota mildbreadii* | Ptm |
| *Pycnanthus angolensis* | Pya |
| *Pyrecantha staudtii* | Pys |
| *Randia micrantha* | Rnm |
| *Raphia farinifera* | Rf |
| *Rauvolfia vomitoria* | Rv |
| *Ricinodendron heudelotii* | Rh |
| *Rinorea ardisiaeflora* | Ri |
| *Rinorea ilicifolia* | Rii |
| *Ritchiea albersii* | Ra |
| *Rothmania urcelliformis* | Rtu |
| *Sapium ellipticum* | Se |
| *Schrebera arborea* | Sa |
| *Scolopia sp.* | Scs |
| *Solanum wightii* | Sol |
| *Spathodea campanulata* | Sc |
| *Staudtia kamerunensis* | Sk |
| *Sterculia dawei* | Std |
| *Stereospermum kunthianum* | Stk |
| *Strombosia scheffleri* | Ss |
| *Strychnos mitis* | Sm |
| *Suregada procera* | Spr |
| *Symphonia globulifera* | Sg |
| *Syzygium guinense* | Szg |
| *Tabernaemontana holstii* | Th |
| *Tapura fischeri* | Taf |
| *Teclea nobilis* | Tn |
| *Terminalia brownii* | Tb |
| *Terminalia glaucescens* | Tg |
| *Tetrapleura tetraptera* | Tt |
| *Tetrorchidium didymostemon* | Td |
| *Treculia africana* | Tra |
| *Trema orientalis* | To |
| *Trichilia dregeana* | Trd |
| *Trichilia prieuriana* | Trp |
| *Trichilia rubescens* | Trr |
| *Trichocladus ellipticus* | Tce |
| *Turrea vogelioides/robusta* | Tv |
| *Uvaria welwitschii* | Uw |
| *Uvariopsis congensis* | Uc |
| *Uvariodendron magnificum* | Um |
| *Vangueria apiculata* | Va |
| *Vitex ferruginaea/adansonii* | Vf |
| *Vitex doniana* | Vd |
| *Warburgia ugandensis* | Wu |
| *Zanha golungensis* | Zg |
| **Climbers** | |
| *Alaphia sp.* | Alp |
| *Basella alba* | Ba |
| *Cyphostemma sp.* | Cyp |
| *Grewia calymatosepala* | Grc |
| *Mikania cordata* | Mic |
| *Piper guineense* | Ppg |
| *Uncaria africana* | Una |
| *Urera camaroonensis* | Urc |
| *Uvaria angolensis* | Uva |
| **Herbs** | |
| *Coffea spp.* | Cos |
| *Coffea canephora* | Cca |
| *Coffea robusta* | Cor |
| *Penisetum purpureum* | Ppr |
| **Others** | |
| Epiphyte | Epi |
| Mushrooms | Msh |
| Moss | Mss |
| Unknown species | Unk |

# Appendix 3

# TESTS OF OBSERVER ACCURACY

## Paced Distance, Estimates of Distance, and Visibility Quantification

### Paced Distances

Distances were paced primarily by my field assistant Geresomu Muhumuza. This table presents the results of 40 tests of his accuracy at pacing 25 metres (20 tests) and 50 metres (20 tests). Distance were measured using a 50 metre tape.

| | Distances (metres) | | | |
|---|---|---|---|---|
| Test # | Paced | Measured | Paced | Measured |
| 1 | 25 | 27 | 50 | 49 |
| 2 | 25 | 25 | 50 | 50½ |
| 3 | 25 | 25 | 50 | 51½ |
| 4 | 25 | 25½ | 50 | 48 |
| 5 | 25 | 26 | 50 | 49 |
| 6 | 25 | 25½ | 50 | 49 |
| 7 | 25 | 25 | 50 | 49 |
| 8 | 25 | 25 | 50 | 50½ |
| 9 | 25 | 25 | 50 | 49 |
| 10 | 25 | 25 | 50 | 49 |
| 11 | 25 | 24½ | 50 | 53 |
| 12 | 25 | 25 | 50 | 53 |
| 13 | 25 | 26½ | 50 | 54 |
| 14 | 25 | 27½ | 50 | 53 |
| 15 | 25 | 25½ | 50 | 52½ |
| 16 | 25 | 27½ | 50 | 51 |
| 17 | 25 | 25½ | 50 | 51 |
| 18 | 25 | 25½ | 50 | 51 |
| 19 | 25 | 27 | 50 | 52 |
| 20 | 25 | 26 | 50 | 53 |

## Estimated Distances

During data collection, distances were estimated by both myself (Observer 1: NNF) and my field assistant (Observer 2: GM). This table presents the results of 20 trials, estimating the distance from observer to a randomly chosen object. A range finder was used to measure distances. This had a maximum range of 30 metres, and was accurate to ± 1 metre. The rangefinder seemed to be less sensitive to differences in distance over 25 metres.

| | Measured Distance (m) | Estimated Distance (m) | |
|---|---|---|---|
| Trial # | (range finder) | Observ. 1 | Observ. 2 |
| 1 | 6 | 6 | 6 |
| 2 | 9½ | 9 | 9 |
| 3 | 12 | 10 | 11 |
| 4 | 20 | 16 | 20 |
| 5 | 9 | 8 | 8 |
| 6 | 22 | 21 | 22 |
| 7 | 6½ | 7 | 8 |
| 8 | 11½ | 11 | 10 |
| 9 | 21 | 24 | 22 |
| 10 | 11 | 10 | 12 |
| 11 | 23 | 22 | 23 |
| 12 | 14 | 12 | 14 |
| 13 | 9½ | 9½ | 10 |
| 14 | 5 | 5½ | 6 |
| 15 | 12 | 12 | 12 |
| 16 | 16 | 16 | 18 |
| 17 | 15 | 17 | 15 |
| 18 | 25½ | 27 | 24 |
| 19 | 4 | 4 | 4 |
| 20 | 18 | 16 | 17 |

## Visibility Quantification

Visibility was estimated as the maximum distance at a which a moving chimpanzee could be seen, standardised to height of 1 metre. The degree of visibility was quantified in fifty trials with the use of an A3 white card; the fraction of the card visible at the estimated maximum visibility, and at this distance plus five metres, was recorded to the nearest quarter. Observer 1 (NNF) conducted all visibility quantification.

| Trial # | Estimated Distance (m) | Fraction visible @ Estimate | Fraction visible @ Estimate+5 m |
|---|---|---|---|
| 1 | 15 | ¾ | ½ |
| 2 | 10 | ½ | 0 |
| 3 | 15 | ½ | 0 |
| 4 | 15 | ¾ | ½ |
| 5 | 15 | ¾ | 0 |
| 6 | 8 | ½ | 0 |
| 7 | 5 | 1 | 0 |
| 8 | 12 | ¾ | ¼ |
| 9 | 10 | ½ | 0 |
| 10 | 6 | 1 | ¼ |
| 11 | 20 | ¾ | ¾ |
| 12 | 18 | 1 | ¼ |
| 13 | 25 | ¾ | ½ |
| 14 | 20 | ¾ | 0 |
| 15 | 5 | ½ | 0 |
| 16 | 7 | 1 | ¼ |
| 17 | 15 | ¾ | 0 |
| 18 | 17 | 1 | ½ |
| 19 | 22 | ¾ | ¼ |
| 20 | 18 | ¾ | ¼ |
| 21 | 18 | ¾ | 0 |
| 22 | 10 | ¾ | ½ |
| 23 | 25 | ¾ | ¼ |
| 24 | 12 | ½ | 0 |
| 25 | 17 | ¼ | 0 |
| 26 | 27 | 1 | 1 |
| 27 | 11 | ¾ | ¼ |
| 28 | 20 | 1 | 0 |
| 29 | 13 | ¾ | 0 |
| 30 | 7 | ½ | 0 |

| Trial # | Estimated Distance | Fraction visible @ Estimate | Estimate+5 m |
|---|---|---|---|
| 31 | 15 | ½ | ¼ |
| 32 | 13 | ¾ | ¼ |
| 33 | 10 | 1 | ½ |
| 34 | 15 | ½ | ¼ |
| 35 | 7 | 1 | ½ |
| 36 | 19 | ½ | 0 |
| 37 | 12 | ½ | ¼ |
| 38 | 8 | ¾ | ¼ |
| 39 | 10 | ½ | 0 |
| 40 | 18 | ½ | 0 |
| 41 | 25 | ½ | ½ |
| 42 | 15 | 1 | 0 |
| 43 | 20 | ¾ | 0 |
| 44 | 17 | ½ | 0 |
| 45 | 15 | ½ | 0 |
| 46 | 12 | ¾ | 0 |
| 47 | 15 | ¼ | 0 |
| 48 | 17 | ½ | 0 |
| 49 | 15 | 1 | 0 |
| 50 | 16 | ¾ | ¼ |

# Appendix 4

# DIET OF SONSO CHIMPANZEES

## Main Food Species

Species accounting for 0.5% or more of feeding time. Diet assessed by percentage of time spent feeding on each species. The percentage of feeding time spent consuming the fruit of each species is also presented, together with the percentage of 'fruit-eating' time for each species. Data from all 15 minute scan samples, and includes observations of male-only, mixed sex, and female only parties.

| Species | All items | Fruit only | |
|---|---|---|---|
| | % time feeding | % time feeding | % time eating fruit |
| *Ficus sur* (*capensis*) | 23.0 | 23.0 | 35.6 |
| *Broussonetia papyrifera* | 22.7 | 4.0 | 6.2 |
| *Ficus mucuso* | 9.8 | 9.8 | 15.1 |
| *Maesopsis eminii* | 9.4 | 9.2 | 14.3 |
| *Celtis durandii* | 8.4 | 7.2 | 11.3 |
| *Celtis mildbraedii* | 4.6 | 0.1 | 0.2 |
| *Khaya anthotheca* | 2.9 | 0.0 | 0.0 |
| *Croton macrostachys* | 2.8 | 1.0 | 1.6 |
| *Ficus exasperata* | 2.2 | 1.5 | 2.3 |
| *Cordia millenii* | 1.7 | 1.4 | 2.1 |
| *Desplatsia dewevrei* | 1.3 | 1.3 | 2.0 |
| *Alstonia boonei* | 1.0 | 0.0 | 0.0 |
| *Ficus sansibarica* (*brachylepis*) | 0.9 | 0.9 | 0.1 |
| *Cleistopholis patens* | 0.8 | 0.1 | 0.1 |
| *Raphia farinifera* | 0.6 | 0.0 | 0.0 |
| *Ficus natalensis* | 0.5 | 0.5 | 0.7 |
| *Ficus varifolia* | 0.5 | 0.0 | 0.0 |
| | | | |
| Terrestrial Herbaceous Vegetation | 3.2 | | |
| Climbers | 1.5 | | |

# Time Spent Feeding

Percentage of time spent feeding, measured by the number of parties (see Chapter 5), in which each individual was present and feeding. The five food species on which each individual spent the most time feeding are also indicated, in decreasing order. See Appendix 2 for species codes. Individuals are arranged in order of decreasing social status (Chapter 4).

| | #Parties | | %Time | |
|---|---|---|---|---|
| Individual | Present | Feeding | Feeding | Primary Food Species |
| DN | 2093 | 809 | 38.65 | Bpy, Fsu, Me, Cdu, Fm |
| VN | 740 | 1758 | 42.09 | Bpy, Fsu, Fm, Cdu, Me |
| BK | 1118 | 478 | 42.75 | Bpy, Fsu, Fm, Cmc, Cmi |
| MG | 1532 | 595 | 38.84 | Bpy, Fsu, Cmi, Cdu, Cmc |
| MA | 1730 | 708 | 40.92 | Bpy, Fsu, Me, Cdu, Fm |
| CH | 1104 | 449 | 40.67 | Bpy, Fm, Fsu, Me, Com |
| JM | 730 | 273 | 37.95 | Bpy, Fsu, Fm, Ka, Com |
| BY | 1377 | 466 | 33.92 | Bpy, Fsu, Cdu, Ka, Cmi |
| KK | 1429 | 582 | 40.73 | Fsu, Bpy, Fm, Cmi, Cdu |
| NJ | 997 | 432 | 43.33 | Bpy, Fsu, Me, Fm, Cmi |
| MU | 1219 | 588 | 48.24 | Bpy, Fsu, Me, Fm, Cdu |
| TK | 974 | 487 | 50.00 | Bpy, Fm, Fsu, Me, Cdu |

## Plant Food Items Consumed

Data from this study and *ad libitum* observations of Budongo Forest Project field assistants. A ✓ indicates that chimpanzees were observed feeding on the item, a **?** that the species was recorded as a food source, without the precise food item being noted.

| | Food Items | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | leaves | | fruit | | | | | rotten | exudate/ | |
| Species | young | mature | unripe | ripe | seeds | flowers | bark | wood | sap | pith |
| *Albizia ferrungunea* | | | ✓ | | | | | | | |
| *Alstonia boonei* | **?** | | | | | | | | | |
| *Antiaris toxicaria* | | | ✓ | ✓( | | | | | | |
| *Brousonettian papyrifera* | ✓ | ✓ | ✓ | | | ✓ | | | | |
| *Carica papaya* | | | ✓ | | | | | | | |
| *Caloncoba schweinfurthii* | | | | | ✓ | ✓ | | | | |
| *Celtis durandii* | | | ✓ | ✓ | | | ✓ | | | |
| *Cetis mildraedii* | ✓ | ✓ | ✓ | ✓ | | | | | | |
| *Celtis wightii* | ✓ | | | | | | | | | |
| *Celtis zenkeri* | ✓ | | | ✓ | | | | | | |
| *Chrysophyllum albidium* | | | | ✓ | | | | | | |
| *Cleistanthus polystachyus* | | | ✓ | ✓ | | | | ✓ | | |
| *Cola gigantea* | | | | | ✓ | ✓ | | | | |
| *Cordia millenii* | | | | ✓ | | ✓ | | | | |
| *Croton macrostachys* | | | | ✓ | ✓ | | | | | |
| *Croton megalocarpus* | | | | | ✓ | | | | | |
| *Croton sylvaticus* | | | | ✓ | | | | | | |
| *Cynometra alexandrii* | ✓ | ✓ | | | ✓ | ✓ | ✓ | | | |
| *Depslatsia dewevrei* | ✓ | | ✓ | ✓ | | | | | | |
| *Entandrophragama sp.* | ✓ | | | | | | | | | |
| *Erythrophleum suaveolens* | | | | | ✓ | | | | | |
| *Ficus barteri* | | | ✓ | | | | | | | |
| *Ficus exasperata* | ✓ | ✓ | ✓ | ✓ | | | | | ✓ | |
| *Ficus mucuso* | | | ✓ | ✓ | | ✓ | | | | |
| *Ficus natalensis* | | | ✓ | ✓ | | | | | | |
| *Ficus polita* | | | | ✓ | | | | | | |
| *Ficus sansibarica* | | | ✓ | ✓ | | | | | | |
| *Ficus sur* | | | ✓ | ✓ | | | | | | |
| *Ficus thoningii* | | | ✓ | ✓ | | | | | | |
| *Ficus tricopoda* | | | ✓ | ✓ | | | | | | |
| *Ficus vallis-choudae* | ✓ | | | | | | | | | |
| *Ficus variifolia* | ✓ | | | | | | | | | |
| *Irvingi gabonensis* | | | | ✓ | | | | | | |
| *Kaya anthotheca* | | | | | | | ✓ | | ✓ | |
| *Klainedoda gasbunensis* | | | | ✓ | | | | | | |
| *Lannea welwitchii* | | | | ✓ | | | ✓ | | | |

| | Food Items | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | leaves | | fruit | | | | | rotten | exudate/ | |
| Species | young | mature | unripe | ripe | seeds | flowers | bark | wood | sap | pith |
| *Lasiodiscus mildraedii* | ✓ | | | | | | | | | |
| *Macaranga schweinfurthii* | ✓ | | ✓ | ✓ | | | | | | |
| *Maesopsis eminii* | ✓ | | ✓ | ✓ | | ✓ | | | | |
| *Mildraediodendron excelsum* | | ✓ | ✓ | | | | | | | |
| *Milicia excelsa* | ✓ | | ✓ | ✓ | | | | | | |
| *Monodora angolensis* | | | | ✓ | | | | | | |
| *Monodora myristica* | | | | | | ✓ | | | | |
| *Moros lactea* | ✓ | | ✓ | ✓ | | ✓ | | | | |
| *Myrianthus holstii* | | | | ✓ | | | | | | |
| *Penistum purpureum* | | | ✓ | | | | | | | ✓ |
| *Platycerium angolense* | ✓ | ✓ | | | | | | | | |
| *Pseudospondias microlarpa* | | | ✓ | | | | | | | |
| *Raphia farinifera* | | | | | | | ✓ | | | ✓ |
| *Ricinodendron heudelotii* | | | | ✓ | | | | | | |
| *Strychnos mitis* | | | | ✓ | | | | | | |
| *Teclea noblis* | | | | ✓ | | | | | | |
| *Trichilia sp.* | ✓ | ✓ | | | | | | | | |
| *Trichilia rubescens* | ✓ | | | | | | | | | |
| *Urera cameroonensis* | | | | ✓ | | ✓ | | | ✓ | |
| Unidentified climber spp. | | | ✓ | ✓ | | ✓ | | | | |
| Unidentified herbaceous spp. | ✓ | | | ✓ | | ✓ | | | | ✓ |

## Additional Food Items

Meat of blue monkeys, red-tailed monkeys, black & white colobus and infant chimpanzees.

Honeycomb, termite clay, and *Cubitermes* termites.

# Appendix 5

# OBSERVED FREQUENCIES OF INTERACTIONS

## STATUS INTERACTIONS

### *Agonistic*

Number of interactions in which individuals in rows were agonistic to individuals in columns. ‘Others’ refers to all members of the study community other than those indicated in the table. These individuals were primarily adult females and juvenile males.

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH | ZT | AY | ZF | Others |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | x | 2 | | | 2 | | | 2 | | 1 | | | | | 1 | 20 |
| KK | | x | | | 1 | | | | | 2 | | | 1 | | | 7 |
| MA | 1 | 2 | x | 1 | 2 | 1 | | | 1 | 1 | | | | | | 4 |
| BY | | | | x | | | 2 | 1 | | | 2 | | | | | 3 |
| MU | | | | 2 | x | | | | | | | | | 1 | | 4 |
| NJ | | 1 | | | | x | | | | | | | | | | 4 |
| TK | | | | | | | x | | | | | | | | | 9 |
| DN | 5 | 8 | 3 | 4 | 8 | | | x | 2 | 1 | 3 | 1 | 3 | 2 | | 34 |
| VN | 5 | 6 | 6 | 6 | | 1 | | | x | 4 | 1 | 1 | | 2 | | 15 |
| JM | | | | | 1 | | | | | x | | | | 1 | 1 | 5 |
| BK | 3 | 3 | 3 | 3 | 1 | 2 | | | | | x | 5 | | 1 | | 19 |
| CH | | 1 | | 1 | 1 | 1 | 1 | 1 | | 2 | | x | 1 | | | 16 |
| ZT | | | | | | | | | | | | | x | | | 2 |
| AY | | | | | | | | | | | | | | x | | 5 |
| ZF | | | | | | | | | | | | | | | x | 3 |
| Others | | | | | | | 2 | | | | | | 1 | | 3 | |

### *Pant-Grunts*

Number of interactions in which individuals in rows pant-grunted to individuals in columns. ‘Others’ refers primarily to adult females and juvenile males.

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH | ZT | AY | ZF | Others |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | x | | | | | | | 4 | 2 | | | | | | | |
| KK | 6 | x | | 1 | | | | 2 | 6 | | | | | | | |
| MA | | | x | | | | | 5 | 3 | | 2 | | | | | |
| BY | | | 2 | x | | | | 7 | 6 | | 1 | | | | | |
| MU | 1 | 1 | 3 | | x | 1 | | 22 | 10 | | 1 | 1 | | | | |

**Pant-grunts** (*cont.*)

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH | ZT | AY | ZF | Others |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| NJ | 1 | | | | | x | | 6 | 6 | | | | | | | |
| TK | 1 | 1 | 2 | 1 | | | x | | 1 | 1 | 1 | | | | | |
| DN | | | | | | | | x | | | | | | | | |
| VN | | | | | | | | | x | | | | | | | |
| JM | 1 | | | | | | | 2 | 2 | x | 1 | | | | | |
| BK | | | | | | | | 3 | | | x | | | | | |
| CH | 1 | | 1 | | | | | 2 | 2 | | 1 | x | | | | |
| ZT | 1 | | 1 | | | | | 5 | 2 | | | 1 | x | | | |
| AY | 4 | | 1 | | 1 | | | 10 | 7 | 1 | 1 | | | x | | 1 |
| ZF | 1 | | 3 | | | | | 4 | 6 | 1 | | | | | x | |
| Others | 6 | 3 | 4 | 2 | 1 | 2 | 1 | 49 | 9 | 2 | 8 | 11 | | 1 | | |

# AFFILIATIVE INTERACTIONS

## *Affiliative (combined)*

Number of interactions in which individuals in rows showed affiliative behaviour (joining or grooming) towards individuals in columns. Only adult and adolescent males are shown.

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH | ZT | AY | ZF |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | x | 3 | 10 | 22 | 1 | 1 | | 17 | 4 | 4 | 5 | 5 | | | |
| KK | 7 | x | 17 | 11 | 5 | 1 | 1 | 5 | 17 | 9 | 1 | 3 | 1 | 3 | |
| MA | 21 | 12 | x | 18 | 4 | 15 | | 29 | 30 | 8 | 14 | 2 | | 2 | |
| BY | 26 | 5 | 18 | x | 2 | 4 | | 15 | 27 | 8 | 13 | 16 | 2 | | |
| MU | 10 | 9 | 4 | 4 | x | 3 | | 6 | 8 | | | | | | |
| NJ | 5 | 1 | 21 | 5 | | x | | 1 | 5 | 5 | 3 | 3 | | | |
| TK | | 1 | 2 | 1 | | | x | | | 4 | 2 | 1 | | | |
| DN | 12 | 1 | 21 | 13 | 1 | | | x | 29 | 4 | 5 | 2 | | | 1 |
| VN | 3 | 4 | 14 | 16 | 1 | 2 | | 30 | x | 5 | 4 | 3 | | | |
| JM | 9 | 6 | 8 | 6 | | 4 | 2 | 6 | 8 | x | 6 | 2 | | | |
| BK | 9 | 2 | 15 | 10 | | 3 | 3 | 10 | 4 | 7 | x | 6 | | 1 | 1 |
| CH | 5 | 1 | 3 | 11 | | 4 | | 4 | 2 | 2 | 7 | x | | 1 | |
| ZT | | 1 | 1 | 1 | | | | | | | | | x | | |
| AY | 5 | 4 | 6 | 2 | 2 | 1 | | 1 | | | 5 | 1 | | x | |
| ZF | | | 1 | 1 | 2 | | 1 | 1 | 4 | | 1 | | | | x |

## *Grooming*

Number of interactions in which individuals in rows showed grooming behaviour towards individuals in columns. One interaction was recorded for each grooming bout in which the individual groomed. Grooming bouts were defined by breaks in grooming of more than one minute. Only adult and adolescent males are shown.

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH | ZT | AY | ZF |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | x | 2 | 10 | 18 | 1 | 1 | | 15 | 3 | 4 | 5 | 5 | | | |
| KK | 5 | x | 16 | 9 | 5 | 1 | 1 | 3 | 15 | 9 | 1 | 3 | 1 | 3 | |
| MA | 21 | 10 | x | 17 | 4 | 14 | | 25 | 28 | 8 | 14 | 2 | | 2 | |
| BY | 23 | 4 | 17 | x | 2 | 4 | | 15 | 26 | 7 | 13 | 14 | 2 | | |
| MU | 8 | 8 | 4 | 4 | x | 1 | | 5 | 8 | | | | | | |
| NJ | 4 | 1 | 18 | 3 | | x | | 1 | 3 | 5 | 3 | 3 | | | |
| TK | | 1 | 2 | 1 | | | x | | | 4 | 2 | 1 | | | |
| DN | 12 | 1 | 17 | 12 | | | | x | 26 | 4 | 5 | 2 | | | 1 |
| VN | 3 | 4 | 13 | 16 | 1 | 2 | | 27 | x | 5 | 4 | 3 | | | |
| JM | 7 | 6 | 8 | 5 | | 4 | 1 | 5 | 6 | x | 5 | | | 1 | 1 |
| BK | 9 | 1 | 15 | 10 | | 3 | 2 | 9 | 4 | 6 | x | 5 | | 1 | 1 |
| CH | 5 | 1 | 2 | 11 | | 3 | | 3 | 2 | 1 | 5 | x | | 1 | |
| ZT | | 1 | 1 | 1 | | | | | | | | | x | | |
| AY | 5 | 4 | 6 | 2 | 2 | 1 | | 1 | | | 4 | 1 | | x | |
| ZF | | | 1 | 1 | 2 | | 1 | 1 | 4 | | 1 | | | | x |

## *Frequency of Copulations*

Number of copulations, with males in rows and females in columns. UID refers to an unidentified female. Row and column totals are given. Females not present in the table were not seen to copulate with adult males during systematic data collection.

| | ZA | RD | RH | ZM | BN | MM | JN | MK | KY | SR | UID | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | | | | 11 | 9 | 3 | | 1 | | | | 24 |
| KK | | | | 6 | | 1 | | 2 | 2 | | | 11 |
| MA | | | | 8 | 2 | 1 | | 2 | 1 | | | 14 |
| BY | | | | 7 | 6 | 1 | | 2 | 1 | 3 | | 20 |
| MU | | 1 | 1 | | | 2 | | 4 | 2 | 2 | | 12 |
| NJ | 1 | | | | 1 | 2 | | 3 | | | | 7 |
| TK | | 1 | | 1 | | | | 2 | 3 | | | 7 |
| DN | | 4 | | 9 | 6 | 4 | 1 | 5 | 7 | 2 | 2 | 40 |
| VN | | | | 3 | 6 | | | 1 | | | | 10 |
| JM | | | | 2 | 1 | 2 | | 1 | 1 | 1 | | 4 |
| BK | | | | 9 | 1 | 2 | | 1 | 1 | 1 | | 15 |
| CH | | | | 4 | 2 | 4 | | 2 | 1 | | | 13 |
| ZT | | | | | | 2 | | 4 | 3 | | | 9 |
| AY | | | | | | | | | | | | |
| ZF | | | | | | | | | | | | |
| Totals | 1 | 6 | 1 | 60 | 34 | 24 | 1 | 30 | 21 | 9 | 2 | |

# ASSOCIATION INTERACTIONS

## *Frequency of Association*

Frequencies of pairwise associations, calculated from a data set in which consecutive records show a change in party composition.

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH | ZT | AY | ZF |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | | | | | | | | | | | | | | | |
| KK | 385 | | | | | | | | | | | | | | |
| MA | 448 | 465 | | | | | | | | | | | | | |
| BY | 427 | 407 | 477 | | | | | | | | | | | | |
| MU | 251 | 224 | 356 | 225 | | | | | | | | | | | |
| NJ | 217 | 238 | 312 | 206 | 215 | | | | | | | | | | |
| TK | 200 | 165 | 229 | 169 | 180 | 141 | | | | | | | | | |
| DN | 551 | 524 | 671 | 540 | 368 | 345 | 255 | | | | | | | | |
| VN | 415 | 485 | 616 | 452 | 351 | 330 | 168 | 733 | | | | | | | |
| JM | 213 | 234 | 223 | 203 | 118 | 117 | 94 | 277 | 263 | | | | | | |
| BK | 303 | 263 | 340 | 289 | 173 | 167 | 150 | 394 | 297 | 136 | | | | | |
| CH | 232 | 256 | 291 | 279 | 194 | 140 | 105 | 335 | 298 | 157 | 216 | | | | |
| ZT | 162 | 180 | 204 | 137 | 135 | 95 | 122 | 216 | 169 | 88 | 159 | 130 | | | |
| AY | 188 | 181 | 283 | 173 | 259 | 154 | 109 | 249 | 267 | 97 | 178 | 162 | 117 | | |
| ZF | 144 | 130 | 192 | 131 | 139 | 101 | 82 | 209 | 181 | 73 | 96 | 125 | 85 | 108 | |

## *Proximity*

### *Nearest Neighbours*

Frequencies at which each pair of males were nearest neighbours. Individual in row is the nearest neighbour of the individual in column. Data are from focal samples.

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | x | 2 | 6 | 11 | 3 | 6 | | 7 | 4 | 4 | 1 | 5 |
| KK | 4 | x | 9 | 8 | 1 | 3 | 2 | 9 | 9 | 4 | 6 | 4 |
| MA | 5 | 8 | x | 10 | 4 | 3 | 2 | 18 | 14 | 1 | 5 | 2 |
| BY | 10 | 4 | 9 | x | 3 | 3 | 3 | 11 | 7 | 2 | 4 | 7 |
| MU | 5 | 7 | 3 | 3 | x | 5 | 3 | 4 | 3 | 1 | 2 | 3 |
| NJ | 1 | 4 | 5 | 4 | 4 | x | 2 | 3 | 8 | 2 | 3 | 4 |
| TK | | 1 | 6 | 5 | 3 | 2 | x | 1 | 1 | 4 | 3 | 4 |
| DN | 5 | 6 | 9 | 7 | 4 | 5 | 4 | x | 21 | 2 | 8 | 5 |
| VN | 5 | 11 | 12 | 4 | 1 | 3 | | 18 | x | 4 | 4 | 6 |
| JM | 1 | 4 | 6 | 4 | 2 | 1 | 1 | 5 | 5 | x | | 3 |
| BK | 5 | 3 | 9 | 4 | 3 | 2 | 2 | 4 | 4 | 3 | x | 8 |
| CH | 7 | 3 | 4 | 5 | 2 | 5 | 1 | 3 | 9 | 1 | 5 | x |

## *Close Proximity*

Frequencies at which each pair of males were in close proximity (nearest or second nearest neighbours). Individual in row is the neighbour of the individual in column. Data are from focal samples.

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | x | 3 | 9 | 17 | 5 | 7 | 2 | 16 | 5 | 5 | 1 | 7 |
| KK | 9 | x | 9 | 17 | 6 | 3 | 4 | 13 | 15 | 5 | 9 | 6 |
| MA | 6 | 10 | x | 15 | 6 | 7 | 4 | 24 | 17 | 4 | 7 | 7 |
| BY | 12 | 8 | 15 | x | 3 | 3 | 4 | 20 | 13 | 3 | 6 | 12 |
| MU | 8 | 8 | 5 | 4 | x | 9 | 5 | 6 | 4 | 1 | 3 | 5 |
| NJ | 1 | 5 | 5 | 4 | 5 | x | 4 | 11 | 14 | 2 | 4 | 8 |
| TK | 5 | 1 | 6 | 5 | 4 | 4 | x | 3 | 2 | 4 | 4 | 6 |
| DN | 12 | 7 | 18 | 10 | 6 | 7 | 6 | x | 26 | 3 | 12 | 7 |
| VN | 5 | 14 | 20 | 10 | 6 | 3 | 0 | 28 | x | 8 | 7 | 10 |
| JM | 3 | 9 | 8 | 7 | 3 | 2 | 2 | 9 | 9 | x | 2 | 3 |
| BK | 7 | 5 | 11 | 6 | 3 | 3 | 3 | 10 | 9 | 4 | x | 7 |
| CH | 8 | 4 | 7 | 2 | 7 | 5 | 4 | 4 | 12 | 1 | 7 | x |

## *Nearest Neighbour Distances*

Median distances between nearest neighbours. Individual in row is the neighbour of the individual in column. Data are from focal samples.

| | MG | KK | MA | BY | MU | NJ | TK | DN | VN | JM | BK | CH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MG | x | 2.75 | 0.5 | 1 | 5 | 1.5 | | 4 | 2.5 | 1.25 | 0.5 | 1.5 |
| KK | 2 | x | 1 | 2.25 | 4 | 5 | 7 | 5 | 2 | 1.5 | 4.75 | 6 |
| MA | 1.5 | 3 | x | 2 | 4.75 | 2 | 10 | 1.5 | 2 | 9 | 0.5 | 4.5 |
| BY | 3.5 | 3.5 | 2.25 | x | 1 | 3 | 5 | 2 | 0.5 | 0.75 | 3.5 | 2 |
| MU | 5 | 2 | 2 | 4 | x | 3 | 6 | 5.75 | 5 | 1 | 2.75 | 4.5 |
| NJ | 1 | 1 | 0.5 | 2 | 3.25 | x | 5.5 | 1.5 | 2.75 | 2.25 | 0.5 | 5.25 |
| TK | | 10 | 4.5 | 5 | 5 | 7.25 | x | 5 | 4.5 | 3.55 | 5 | 4 |
| DN | 2 | 3.5 | 2.5 | 2 | 2.25 | 3.5 | 5 | x | 2 | 6.75 | 3 | 5.5 |
| VN | 1.75 | 3 | 2.25 | 2 | 5.5 | 2 | | 2 | x | 3.5 | 1.5 | 4 |
| JM | 3 | 1.75 | 1 | 2.5 | 2.5 | 3 | 10 | 0.5 | 3 | x | | 3 |
| BK | 1 | 3 | 2 | 2.25 | 4 | 4.25 | 1.25 | 2.5 | 3.25 | 0.5 | x | 3 |
| CH | 2 | 3 | 2 | 1.5 | 5.5 | 4.5 | 4.5 | 1 | 5 | 3 | 2.5 | x |

## GROOMING PARTNER SELECTION

Table of data relating to all observations of a selection of grooming partners. Individual ‘A’ is the selecting individual, individual B the selected grooming partner. ‘Behav.’ is a description of the initial phase of the grooming interaction, with either A grooming B, or B grooming A. ‘LatGrm’ is the ‘latency to groom’, the delay between the initial approach of A and the initiating of grooming. ‘Resp.’ is a description of the second phase of the grooming interaction, either the response of individual B, or where B does not respond, the termination of grooming by A. ‘LatResp.’ is the duration of initial grooming, before a ‘response’ occurs. Data for ‘Resp.’ & ‘LatResp.’ were only collected for some samples. C1-C6 are the identities of all possible grooming partners in each instance of selection, with D1-D6 the respective distances (in metres) from the selecting individual.

| A | B | Behav. | LatGrm | Resp. | LatResp. | C1 | D1 | C2 | D2 | C3 | D3 | C4 | D4 | C5 | D5 | C6 | D6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| KK | BY | AgrmB | 00:05 | Bterm | 02:58 | ch | 0.5 | by | 2.5 | vn | 4 | | | | | | |
| KK | BY | AgrmB | 00:51 | ABgroom | 03:07 | by | 2 | mu | 4 | zt | 4 | | | | | | |
| BY | JM | AgrmB | 01:53 | | | kk | 0.5 | jm | 2 | zt | 4 | | | | | | |
| DN | MU | AgrmB | 00:04 | | | mu | 3 | jm | 3 | kk | 4.5 | by | 5 | ma | 6 | zt | 6 |
| BY | NJ | AgrmB | 00:44 | Aterm | 06:51 | nj | 2 | vn | 3 | ay | 4 | | | | | | |
| MU | VN | AgrmB | 00:03 | Aterm | 05:17 | dn | 3 | vn | 4 | mg | 4 | | | | | | |
| KK | MU | AgrmB | 00:08 | | 09:27 | mu | 3 | by | 5 | vn | 7.5 | | | | | | |
| AY | BK | AgrmB | 00:10 | | | bk | 2 | bb | 2 | | | | | | | | |
| KK | MA | AgrmB | 02:57 | | | ma | 1 | zt | 1 | | | | | | | | |
| KK | CH | AgrmB | 00:06 | ABgroom | 02:15 | dn | 3 | ch | 3 | bk | 3 | vn | 3 | | | | |
| BY | ZT | AgrmB | 00:23 | ABgroom | 02:15 | ma | 2 | mg | 2.5 | zt | 5 | | | | | | |
| MA | MG | BgrmA | 00:09 | ABgroom | 00:21 | mg | 1 | by | 2.5 | zt | 3 | | | | | | |
| DN | VN | AgrmB | | BgrmA | 02:54 | vn | 0.5 | jk | 1 | | | | | | | | |
| AY | MA | AgrmB | 00:11 | Aterm | 01:32 | ma | 2 | mg | 2.5 | | | | | | | | |
| MA | BY | AgrmB | 00:06 | BgrmA | 01:15 | ch | 3 | by | 5 | | | | | | | | |
| DN | MG | AgrmB | 00:11 | Aterm | 00:06 | vn | 1 | mg | 2 | by | 2 | | | | | | |
| VN | MG | AgrmB | 00:02 | | | mg | 3 | dn | 3 | by | 3 | | | | | | |
| KK | BY | AgrmB | 00:08 | Aterm | 02:44 | by | 10 | ay | 12 | | | | | | | | |
| AY | BK | AgrmB | 00:06 | Aterm | 00:44 | bk | 2 | kk | 3 | | | | | | | | |
| BK | TK | BgrmA | 00:05 | BgrmA | 00:00 | tk | 3 | dn | 10 | | | | | | | | |
| BY | CH | AgrmB | | BgrmA | 03:22 | ch | 0.5 | mg | 1 | bk | 4 | dn | 7 | | | | |
| DN | MA | AgrmB | | Aterm | 00:22 | ma | 0.5 | by | 0.5 | mg | 2 | | | | | | |
| KK | MG | AgrmB | 00:15 | Aterm | 00:26 | by | 0.5 | ma | 1 | dn | 1 | mg | 3 | | | | |
| MG | DN | AgrmB | | Aterm | 00:11 | dn | 0.5 | kk | 0.5 | by | 0.5 | jm | 0.5 | | | | |
| MG | DN | | | ABgroom | 32:50 | | | | | | | | | | | | |
| MU | MG | AgrmB | | Aterm | 02:48 | mg | 0.5 | tk | 1 | | | | | | | | |
| DN | VN | AgrmB | 00:08 | Aterm | 01:11 | ma | 3 | vn | 4 | kk | 9 | | | | | | |
| KK | DN | AgrmB | | BgrmA | 02:17 | dn | 0.5 | ay | 0.5 | | | | | | | | |
| DN | MA | AgrmB | 00:08 | | | ma | 3 | by | 3 | tk | 5 | mg | 7 | | | | |
| JM | MA | AgrmB | 01:51 | BgrmA | 05:22 | ma | 2 | vn | 2 | dn | 5 | bk | 6 | by | 6 | mu | 7 |
| BK | BY | AgrmB | 00:04 | BgrmA | 02:32 | dn | 1 | mu | 2 | jm | 4 | ma | 4 | by | 5 | vn | 5 |
| DN | MA | AgrmB | | Aterm | 01:47 | vn | 0.5 | ma | 1 | | | | | | | | |
| CH | MG | AgrmB | | | | mg | 0.5 | vn | 0.5 | gs | 0.5 | | | | | | |
| BY | CH | BgrmA | 02:06 | | | ch | 10 | mg | 10 | vn | 10 | gs | 10 | | | | |
| DN | BY | AgrmB | | ABgroom | 04:03 | by | 0.5 | ma | 0.5 | | | | | | | | |
| VN | DN | BgrmA | 01:45 | | | nj | 4 | by | 6 | dn | 8 | ma | 14 | | | | |
| MA | JM | AgrmB | 00:37 | ABgroom | 00:00 | jm | 3 | ch | 4.5 | dn | 5 | vn | 6 | | | | |

| A | B | Behav. | LatGrm | Resp. | LatResp. | C1 | D1 | C2 | D2 | C3 | D3 | C4 | D4 | C5 | D5 | C6 | D6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ZF | VN | AgrmB | | | | vn | 0.5 | kk | 5 | dn | 7 | | | | | | |
| VN | BY | AgrmB | | | | by | 0.5 | ch | 1 | nj | 2 | mu | 2 | | | | |
| VN | BY | AgrmB | 07:01 | BgrmA | 01:49 | by | 0.5 | ch | 1 | mu | 2 | nj | 3 | | | | |
| MA | NJ | BgrmA | 01:55 | ABgroom | 00:15 | nj | 7 | dn | 8 | | | | | | | | |
| DN | MG | BgrmA | 00:02 | Bterm | 08:55 | mg | 5 | ma | 6.5 | nj | 6.5 | | | | | | |
| MA | DN | AgrmB | 01:42 | ABgroom | | dn | 5 | mu | 10 | zf | 10 | | | | | | |
| BY | MG | AgrmB | 00:02 | Aterm | 04:20 | mg | 1 | ch | 1 | | | | | | | | |
| BY | CH | AgrmB | | Aterm | 01:49 | mg | 0.5 | ch | 0.5 | | | | | | | | |
| BY | MG | AgrmB | | | | ch | 0.5 | mg | 0.5 | | | | | | | | |
| BY | VN | AgrmB | 00:02 | Bterm | 00:56 | mg | 1 | ch | 1 | vn | 5 | dn | 8 | | | | |
| VN | BY | AgrmB | 00:04 | BgrmA | 00:50 | dn | 2 | by | 3 | | | | | | | | |
| MA | DN | AgrmB | 00:04 | ABgroom | 02:46 | dn | 2 | kk | 3.5 | nj | 3.5 | mu | 4 | | | | |
| NJ | MA | AgrmB | 00:59 | ABgroom | 07:09 | ma | 2 | ay | 10 | | | | | | | | |
| BY | MG | AgrmB | 00:40 | ABgroom | 00:00 | vn | 3 | mg | 7 | | | | | | | | |
| DN | VN | AgrmB | 00:02 | | | by | 3 | vn | 4 | bk | 4 | ma | 4.5 | mu | 5 | | |
| BY | JM | AgrmB | 00:06 | ABgroom | 03:02 | jm | 2 | vn | 8 | | | | | | | | |
| BY | MG | AgrmB | | Aterm | 05:22 | mg | 3 | vn | 3 | ch | 5 | | | | | | |
| BY | CH | AgrmB | 04:19 | | | mg | 0.5 | vn | 0.5 | ch | 2 | | | | | | |
| KK | BY | AgrmB | 00:37 | ABgroom | 00:53 | by | 6 | ch | 6 | | | | | | | | |
| KK | MA | AgrmB | | | | ma | 1 | mg | 1 | | | | | | | | |
| DN | MG | AgrmB | 00:03 | ABgroom | 00:00 | mg | 2 | kk | 5 | | | | | | | | |
| BK | VN | AgrmB | | | | vn | 0.5 | jm | 0.5 | | | | | | | | |
| JM | VN | AgrmB | | Aterm | 01:58 | vn | 0.5 | bk | 0.5 | | | | | | | | |
| MG | BK | AgrmB | 00:28 | Aterm | 04:47 | bk | 5 | ma | 5 | dn | 10 | | | | | | |
| MG | MA | AgrmB | 00:11 | Aterm | 01:03 | ma | 1 | bk | 0.5 | dn | 5 | | | | | | |
| BK | VN | AgrmB | | Aterm | 00:29 | vn | 1 | jm | 1 | | | | | | | | |
| NJ | VN | AgrmB | 00:10 | ABgroom | 00:00 | vn | 3 | ma | 3.5 | | | | | | | | |
| ZF | BK | AgrmB | | ABgroom | 06:50 | bk | 0.5 | ma | 0.5 | | | | | | | | |
| ZF | MA | AgrmB | | | | bk | 0.5 | ma | 0.5 | | | | | | | | |
| VN | MA | AgrmB | | Aterm | 02:05 | ma | 0.5 | dn | 0.5 | | | | | | | | |
| DN | VN | AgrmB | | ABgroom | | vn | 0.5 | ma | 0.5 | | | | | | | | |
| KK | MA | AgrmB | 00:05 | BgrmA | 01:41 | jm | 2 | ma | 2.5 | | | | | | | | |
| KK | JM | AgrmB | 00:07 | BgrmA | 00:48 | ma | 0.5 | jm | 2 | | | | | | | | |
| KK | VN | AgrmB | 00:01 | Aterm | 03:43 | vn | 0.5 | dn | 0.5 | ma | 0.5 | | | | | | |
| MA | BY | BgrmA | 01:18 | ABgroom | 02:05 | dn | 1 | by | 3.5 | vn | 4 | mg | 4.5 | | | | |
| BY | MG | AgrmB | 00:11 | ABgroom | 01:40 | mu | 2 | dn | 3 | vn | 4 | mg | 4 | | | | |
| VN | JM | AgrmB | 00:02 | ABgroom | 00:00 | kk | 0.5 | jm | 4 | | | | | | | | |
| MA | BK | AgrmB | 00:04 | ABgroom | 07:39 | by | 2 | bk | 3 | vn | 10 | | | | | | |
| MU | MG | AgrmB | 04:30 | Aterm | 05:23 | mg | 10 | ch | 10 | | | | | | | | |
| MG | CH | AgrmB | 00:46 | ABgroom | 02:19 | vn | 10 | ch | 14 | by | 14 | | | | | | |
| CH | DN | AgrmB | 00:14 | Bterm | 03:19 | dn | 10 | tk | 10 | jm | 10 | | | | | | |
| MA | VN | AgrmB | 00:02 | ABgroom | 03:17 | nj | 1 | vn | 1 | | | | | | | | |
| BY | BK | AgrmB | | ABgroom | 00:00 | bk | 2 | dn | 2.5 | | | | | | | | |
| KK | DN | AgrmB | 00:02 | Aterm | 02:28 | vn | 3.5 | dn | 4 | | | | | | | | |
| VN | BY | AgrmB | 00:04 | BgrmA | 03:50 | dn | 0.5 | kk | 0.5 | by | 4 | | | | | | |