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AFFILIATION, AGGRESSION AND
RECONCILIATION IN MALE CHIMPANZEES OF
THE BUDONGO FOREST, UGANDA

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Chapter 1

Introduction

Animals should behave in such a way as to maximise their inclusive fitness (Dawkins, 1982). As is the case with other animal species, the function of some types of competitive and cooperative behaviour in primates can have direct consequences for reproductive success (Cheney *et al.*, 1987; Pusey & Packer, 1997). Though group living has many benefits including for example, reduced predation risks, better predator defence, communal rearing, and better access to resources (e.g. Krebs & Davies, 1987; Dunbar, 1988), it is also a competitive environment where the ability of individuals to secure resources is constrained by the behaviour of other group members.

The content, patterning and quality of repeated interactions with each group member can be described as a relationship (Hinde, 1979, 1983). Selection should act on individuals to maximise their reproductive potential by behaving in such a way as to manipulate relationships to their advantage (Kummer, 1978; Byrne & Whiten, 1988; Whiten & Byrne, 1997).

The distribution of affiliative, aggressive and post-conflict behaviours is the subject of this thesis. In this chapter I first review the nature of chimpanzee societies and the relationships within them. I then outline some of the aspects of chimpanzee behaviour which appear to be particularly profitable in terms of increasing reproductive success for males in particular. In this chapter I present widely

accepted interpretations of these behaviours. This subject matter is often expanded upon more critically in the relevant chapters that follow.

1.1 Chimpanzee societies

1.1.1 Social structure

Chimpanzee communities are composed of between 20 to 100+ individuals of all age-sex classes (Nishida & Hiraiwa-Hasegawa, 1987). Sex ratios are skewed in favour of females (Hiraiwa-Hasegawa *et al.*, 1984) although this does not lead to the formation of all-male groups and lone males are rare.

All chimpanzee populations have been reported to live in fission-fusion societies (Nishida, 1968; Kummer, 1971; Goodall, 1986) where members of a community regularly form temporary associations or parties that last from several minutes to a few days. The composition of these parties tends to be of mixed sex containing between 1 and 77 individuals (Hiraiwa-Hasegawa *et al.*, 1984) although parties of six or less are most common (Goodall, 1968; Reynolds & Reynolds, 1965; Nishida, 1968; Tutin *et al.*, 1983; Sakura, 1994; Clark & Wrangham, 1994; Chapman *et al.*, 1994; Boesch, 1996). A *community* (after Goodall, 1973) is defined as a closed network of male and female chimpanzees which share a common range area, show mutual tolerance and often engage in affiliative interactions; the same definition applies to a *unit-group* (Nishida, 1968). Members of different communities generally have hostile relationships.

Goodall (1986) has classified party types as follows:

All male party – 2 or more adult and/or adolescent males.

Family unit – a mother and her dependants, with or without older offspring.

Nursery unit – 2 or more family units, sometimes accompanied by nonrelated nulliparous females.

Mixed party – one or more adult or adolescent males with one or more adult or adolescent females, with or without dependants.

Sexual party – mixed party in which one or more of the females is in oestrus.

Consortship – exclusive relationship of one adult male with one adult female (oestrus or anoestrus) when they travel on their own, with or without her dependants or older offspring.

Gathering – group comprises of at least half of the members of the community, including at least half of the mature males.

Lone individual – completely alone.

The nursery party is the only long term-party and consists of a mother and her dependent offspring. Party composition is fluid and it is this fluidity which has led some researchers to suggest that chimpanzee societies are more complex than that of any other nonhuman primate (Goodall, 1986; Newton-Fisher, 1997).

1.1.2 Socioecology

Food abundance and distribution are variables that can, among others, be limiting factors on grouping patterns (Wrangham, 1980, 1986; Dunbar, 1988). In a fission-fusion social system, foraging parties can distribute themselves between a number of food patches within a community home-range, which individually would not be large enough to contain adequate resources for the entire community to forage efficiently together. Few, large food patches can facilitate large party sizes and more cohesive foraging patterns. Many small food patches can lead to smaller

party sizes due to increased feeding competition. Thus party size is subject to seasonal variation and average party sizes between populations will covary with food abundance.

Other factors may also influence party size and composition. Although the fission-fusion system is thought to allow greater flexibility in exploiting resource patches of different sizes, this explanation was proposed with the assumption of a lack of predation (Dunbar, 1988; Kummer, 1971; Symmington, 1990). This is, however, not the case for a number of populations of chimpanzees which are preyed upon by leopards or lions (Taï: Boesch, 1991; Mahale: Tsukahara, 1993). Bossou and Assirik chimpanzees seem to react to higher predation pressure by forming larger parties (Tutin *et al.*, 1983; Sakura, 1994). Hunting rate (Boesch, 1996) and sexual opportunities in terms of the number of females in oestrus have also been shown to affect social grouping patterns (Boesch, 1996; Goodall, 1986; Stanford *et al.*, 1994). Demographic factors will, of course, also affect party size. For example, many dependent infants may result in large nursery parties.

1.1.3 Social relationships

Chimpanzee societies are characterised by male philopatry. Adult females rarely associate with other community members except with their dependent female offspring, whilst foraging at large food patches or in nursery parties (Nishida, 1979; Halperin, 1979; Wrangham & Smuts, 1980. But see Sugiyama, 1988). Female coalitions are uncommon although they have been observed in captivity (de Waal, 1982; Baker & Smuts, 1994). Dominance relationships among females are relatively difficult to discern although high rank appears to be acquired with age. The general view is that females spend little or no time attempting to reach high status either in

the wild (Bygott, 1974) or in captivity, where interaction rates are vastly elevated (de Waal, 1982, 1984, 1993: but see Baker & Smuts, 1994).

The mother-offspring relationship lasts for several years beyond weaning and whereas females usually emigrate to other communities during late adolescence (11-14 yrs: Goodall, 1986), males continue to travel with their mothers even into adulthood. At late adolescence (13-15 yrs: Goodall, 1986) they begin to spend most of their time either with other males, with females in oestrus, or alone on the periphery of the community (Pusey, 1977; Halperin, 1979; Hayaki, 1985, 1988). When adult, and fully integrated into the male hierarchy, males may still continue to associate, and engage in prolonged grooming bouts with their mothers (Pusey, 1983).

Chimpanzee male-male social relationships are unusual among primates in that they are tolerant and co-operative (Nishida & Hiraiwa-Hasegawa, 1987). Males spend more time associating in parties than females and have frequent interactions in a variety of contexts. Wrangham (1979, 1987) has suggested that such relationships have been able to evolve in chimpanzees because overlapping female ranges enable males to co-operatively defend large home ranges containing a number of cycling females. The benefits associated with kin relationships, or perhaps mutualism, may outweigh the costs of competition for mates. Whereas females occupy small core territories, males occupy larger ranges that are patrolled in order to detect male intruders from neighbouring communities (Bygott, 1974; Chapman & Wrangham, 1993). Extracommunity males might constitute a threat in that they may try to solicit copulations with oestrus females who often spend time at the edge of the community range. There have also been a number of reports of

intercommunity infanticide (Goodall, 1977; Kawanaka, 1981) and lethal aggression (Goodall *et al.*, 1979; Nishida *et al.*, 1985).

Grooming is far more common among males than females. Grooming bouts occur more frequently between males than any other sex combination and are of longer duration. Males also appear to have more female grooming partners than females do (Nishida, 1979; Wrangham, 1986; Nishida & Hiraiwa-Hasegawa, 1987; Muroyama & Sugiyama, 1994. But see Sugiyama, 1988; de Waal, 1986). Social bonds, which are in part reinforced by grooming but also by other affiliative and cooperative social interactions, are significant in two contexts with regard to males. The first is alliance formation which enhances success rates in intragroup competition to achieve high status (Wrangham, 1986). High status is worth investing time and energy in as it facilitates access to resources such as oestrus females (Hasegawa & Hiraiwa-Hasegawa, 1983; Nishida, 1983; Sugiyama & Koman, 1979; Tutin, 1979). The second context in which strong male bonds are important is when intercommunity relations are hostile and cooperation between all adult males helps in defending community resources (Dunbar, 1988). In populations where this is the case, grooming between males is more intense and social bonds are stronger (Hutchins & Barash, 1976; McKenna, 1978).

Meat sharing appears to be another means whereby chimpanzees can affect relationships (Stanford *et al.*, 1994). Meat is a highly prized form of food, probably because of its high nutritional value. Males who hunt successfully sometimes distribute their catch among the gathered individuals either directly or indirectly. Bystanders are sometimes able to steal scraps of meat or win carcasses through aggression. Occasionally, the possessor of the meat hands portions to other individuals in response to begging. Recipients of such 'gifts' tend to be females,

especially those in oestrus (Goodall, 1986), but sometimes they are males with which the possessor has a close relationship (Goodall, 1986).

Relative status in chimpanzees is indicated by the direction of pant-grunt vocalisations (Goodall, 1986) which are always unidirectional within any dyad in the short term until such times as rank reversals occur. Subordinates always pant-grunt toward dominants and this signal is a very good indicator of relative agonistic competitive ability. Adult males always dominate adolescent males in agonistic interactions. Among adult males, dominance relations are not always clear cut except in the case of the alpha male who is dominant over all individuals in a community (Hayaki *et al.*, 1989). Females are usually subordinate to adult and adolescent males although captive studies have shown that females can outrank males in agonistic (de Waal, 1982) and competitive (Noë *et al.*, 1980) interactions. Linear hierarchies are more likely to be discernible in small communities (Nishida, 1979; Sugiyama & Koman, 1979) than in large ones (Appleby, 1983; Nishida & Hosaka, 1996; Newton-Fisher, 1997) where relationships are likely to be more complex (Dunbar, 1992). In some communities, researchers have only managed to categorise males as high, mid and low ranking due to the number of rank reversals observed in large numbers of dyads (e.g. Bygott, 1979). It is usually clear, however, which individual holds alpha status. Nonetheless, age is the best predictor of rank and most males which achieve alpha status do so at around the age of 20-25 years. In addition to age, size and physical condition are also factors involved in rank acquisition. The alpha male typically shows the highest levels of aggression towards others and frequently performs bluff displays in which he 'asserts' himself and his ability to dominate others (Reynolds & Luscombe, 1969; Riss & Goodall, 1977). Alpha status confers several advantages including the ability to supplant others from

feeding sites and reproductive benefits (Wilson, 1975; Nishida, 1979) although a number of field studies have not been able to confirm the latter (Goodall, 1973; Bygott, 1979; McGinnis, 1979).

1.2 Status acquisition through social interactions

In almost all writings on the nature of male chimpanzee social behaviour, emphasis is laid on the tactical nature of their interactions. Male chimpanzees are described as being motivated to achieve high status in almost all cases. It is argued that high rank confers benefits on individuals such as reproductive advantages over lower ranking competitors and so is an adaptive trait (reviewed by Silk, 1987). It is clear that this is the case for chimpanzees holding alpha status (Bygott, 1979; Takahata, 1990a; Nishida, 1979, 1983; Tutin, 1979) but there is generally no such correlation for other, non-alpha males. Mating opportunities for these males are generally described as opportunistic. It has been suggested by Newton-Fisher (1997, 1999a) that as chimpanzee communities are fragmented, there may be an advantage to being the highest-ranking male in any particular party. If a female in oestrus is located then such a male might be able to initiate a consortship without harassment from dominants.

Rank may be a factor in access to desired resources. A high-ranking male may be able to steal meat from a subordinate or supplant him at other types of desirable food sources.

In addition to the competitive advantage that high rank may confer, it has been suggested that fitness benefits accrue to different status levels through a physiological mechanism mediated by stress hormones. Research on monkeys has shown that levels of stress hormones are elevated in lower ranking animals (Keverne

et al., 1982; Sapolsky, 1993, 1996). Behavioural ‘style’, described in terms of personality differences, appears to mediate the effects of chronic stress (Virgin & Sapolsky, 1997) and has been reported as being important for tenure of alpha males (Takahata, 1990b; Nishida & Hosaka, 1996; Goodall, 1986).

1.2.1 Coalitions

Status, then, is worth striving for and the various means by which male chimpanzees acquire high status has been an important area of research for many years. One of the most important ways in which males can increase their relative status is through the formation of coalitions. A coalition is defined as two or more individuals joining forces against one or more conspecific rivals (Harcourt & de Waal, 1992). In terms of behaviour, coalitions involve an ongoing aggressive encounter that a third party joins, taking the side of one opponent by aggressing against the other. Coalition formation has been widely documented in mammals and birds (Harcourt, 1992) and so is not peculiar to chimpanzees or even primates. It is claimed that what is unique about coalition formation in male chimpanzees is the frequency and apparent complexity and flexibility with which this strategy is employed (Nishida & Hosaka, 1996; Newton-Fisher, 1997, see Chapters 5 & 7). When a coalition between a particular dyad persists over an extended period of time, then this relationship can be called an alliance. Coalitions, however, very often do not persist. Adult male chimpanzees show extreme opportunism, siding with one individual and then another in rapid succession (de Waal, 1982; Nishida, 1983; Goodall, 1986; Uehara *et al.*, 1994a).

Descriptions of coalitions and alliances between particular known individuals in communities which have been the subjects of long term field or

captive studies are now quite widespread in the chimpanzee literature (de Waal, 1982; Goodall, 1986). The most commonly documented, and of apparently greatest interest, are *long-term* coalitions also known as alliances. A good example is that of Figan and his brother Faben at the Gombe Stream Reserve, Tanzania. “First apparent in 1967 (after Figan became dominant to his elder brother) Figan and Faben’s alliance persisted until Faben’s disappearance and presumed death in 1975. Faben almost always supported Figan’s aggressive initiatives during this period. Even if he did not, on only one occasion was he observed to join forces against his brother, and never after 1973.” (Goodall, 1986, p. 418). Though this example involves brothers, stable alliances between more distant kin also occur. In primate species, which exhibit female philopatry, kin-based alliances are also common and persistent. Coalitions between nonkin are always rarer and tend to occur when the risk of retaliation is low. However, where the risk of retaliation is high (e.g. when the target is dominant to the supporter), it is in the interests of only closely related animals to support one another (for reviews, see Gouzoules & Gouzoules, 1987; Walters, 1987; Harcourt, 1988; Bernstein, 1991; Ehardt & Bernstein, 1992; Silk, 1992).

Besides kinship, there are other factors involved in analysing the relative costs of intervention. As mentioned above, there are risks associated with supporting a victim of aggression if the aggressor is dominant to the supporter. If the aggressor is subordinate, there may be little cost and perhaps some gain in that the relationship with the victim is strengthened, and dominance relations with the target of the coalition are cemented (Noë, 1992). Although some studies have demonstrated that the receipt of support increases the likelihood of winning an aggressive encounter (Harcourt, 1992; Silk, 1992) it is more difficult to show that the intervener is acting

in an altruistic manner in that it is not gaining something from the interaction. Recent studies of coalitions have concluded that they could better be described as mutually cooperative because both partners might gain benefits (e.g. Bercovitch, 1988; Noë, 1990; Watts, 1998).

1.2.2 Reciprocity

In situations where the intervening animal does not profit from any immediate gain, it is possible that reciprocity may be involved with respect to the costs and benefits of coalition formation. De Waal & Luttrell (1988), studying rhesus macaques, stumptail macaques and chimpanzees, found that solicitations for support during agonistic encounters were more likely to be responded to if the solicitor had previously aided the target. They also found that individuals were more likely to solicit those who had recently solicited them. Only chimpanzees, however, were demonstrated to more often join coalitions against those who had attacked them in the past than other members of the group. They termed this phenomenon ‘revenge’. One of the assumptions involved in any claims for reciprocation is that some form of mental record keeping is involved. Hemelrijk & Ek (1991), in challenging this assumption in a study on captive chimpanzees, showed that aid was most often given only to those individuals who were close in rank, and that high ranked chimpanzees gave more support in absolute terms. Interestingly, this pattern was observed during periods of instability when the alpha male position was unclear. The latter finding was again interpreted as an opportunity for chimpanzees with high status to assert their dominance over others and the former, to increase their competitive ability in an opportunistic fashion. Thus, they concluded that observed instances of reciprocation did not require mental record keeping or

explanations in terms of reciprocal altruism. Acts of agonistic support could equally be performed for selfish ends (see also, Hemelrijk, 1996; Hemelrijk *et al.*, 1991). Though this study was carried out on the same group of chimpanzees as the de Waal & Luttrell (1988) study, no evidence for any kind of revenge system was found.

Other studies have looked for evidence of reciprocation where the currencies to be exchanged differ, e.g. A might groom B in exchange for B's support in future agonistic interactions. These types of exchange, where currencies differ in kind, are called 'interchange'. Evidence of interchange of grooming and support has not been found in monkeys (vervet monkeys: Hemelrijk, 1990 a,b; Fairbanks, 1980; rhesus macaques: de Waal & Luttrell, 1988; stumptail macaques: Silk, 1982) except in the case of female baboons (Hemelrijk, 1990 a,b) and in a limited sense in longtail macaques (Hemelrijk, 1994). Hemelrijk & Ek (1991) found a similar correlation in female chimpanzees but not males. It is not clear, however, that either support or grooming are altruistic acts. Hemelrijk *et al.* (1992) found that male chimpanzees groomed oestrus females more than anoestrus ones, especially those with whom they mated more often. Again this result could not be interpreted as selfless behaviour on the part of the males. There was, however, no relationship between mating and agonistic aid. Overall, there is no strong evidence for reciprocation or interchange in either monkeys or chimpanzees. What evidence there is does not yet preclude the possibility that primates keep mental notes of which individuals have helped them in the past, but neither does it confirm it.

1.2.3 Problem solving

Another area of research which bears on the question of chimpanzee cooperation has sought to investigate their ability to solve problems which require

the participation of two or more individuals. The best known example of this type of behaviour in wild chimpanzees is cooperative hunting of other animals. The chimpanzees of the Taï forest have been reported to hunt monkeys (mostly red colobus monkeys, *Colobus badius*) in a way that no other known populations do (Boesch & Boesch, 1989). At Taï, like Gombe, monkeys are regularly caught opportunistically by single males (Busse, 1978; Goodall, 1986; Stanford *et al.*, 1994; Teleki, 1973). However, at Gombe, when two or more males hunt together, any cooperation is opportunistic and there are no reports of what might appear to be planned collaborations. All of the males chase monkeys in the same way at the same time and there is no differentiation in roles.

Though this kind of hunt is observed at Taï, approximately 50% of cases involve a joint effort on the part of the hunters. Hunting parties consist of 2-6 males which move quietly through the forest in relative silence in a similar manner to a boundary patrol. The group will stop occasionally and look up into the trees until a group of monkeys are found at which point individuals give a “hunting bark”. The males set a kind of ambush in which different individuals assume different roles (Boesch, 1994b). When the prey is captured, they give a “capture call” that alerts the other members of the party and the meat is then shared out.

This kind of ambush hunting is not unique to chimpanzees (Boesch & Boesch, 1989) and may not require that the individuals involved understand the roles of the others or have any knowledge of their goals. Each might be pursuing an individual strategy, which is guided by past experiences of what the other members of the party do. However, the fact of the capture call suggests that there may be some acknowledgement of the collaboration.

To distinguish between these alternative explanations we again turn to experimental studies. The first of these was the classic study of Crawford (1937, 1941) in which two juvenile chimpanzees were presented with a box containing food with ropes attached, which was out of reach and too heavy to be pulled by one chimpanzee. At first, when two chimpanzees were given access to the ropes, each tried to pull the box with no coordination between them. When they were taught to respond to the verbal cue “pull”, they pulled together. This cooperation persisted when the cue was no longer given. In the second experiment, food was delivered when a combination of 4 coloured keys were pressed in order. Pairs of chimpanzees were then tested in a situation where one cage contained a panel with two of the coloured keys, and another cage contained a panel with the other two coloured keys. One pair of dyads learned to coordinate their behaviour successfully with the use of solicitations. The other pair of chimpanzees never learned to coordinate their behaviour although these were less socially experienced. Chalmeau (1994) conducted a similar study in which two chimpanzees had to simultaneously pull two handles on a food dispensing apparatus in order to get the food. One individual, the dominant male learned to wait by the apparatus until another individual pulled a handle. He was even seen to lead females to one of the handles. Analysis of gazing patterns suggested that some understanding of the role of others was involved in that they had to be in an appropriate location before food could be obtained (Chalmeau & Gallo, 1996).

In another type of study, Povinelli *et al.* (1992a) trained chimpanzees to pull one of 4 pairs of handles associated with 4 pairs of baited cups divided by a partition. On the other side of the partition, a human had to pull the corresponding handle in order for both human and chimpanzees to obtain the food. In the first

experiment, the chimpanzees could see which pair of handles would release the food and had to indicate to the human by pointing or similarly gesturing to the correct handle. In the second experiment, the chimpanzee had to respond to indications by the human as to which handle to pull. One of the subjects of the experiment learned to switch from the role of informer to operator quite quickly but this individual had a history of extensive contact with humans and so may have learned how to comprehend a human pointing gesture (Tomasello & Call, 1997). Two other chimpanzees were given the same task but had to play the role of operator first and then switch to informant. These were also successful, although whether they learned to give an explicit sign as to the location of the food or whether they simply gave the location away by looking was not reported.

Both of these studies have been replicated with monkeys but evidence of their understanding of roles was not found (rhesus macaques: Povinelli *et al.*, 1992b; capuchin monkeys: Chalmeau *et al.*, 1997).

As yet, some of the cognitively richer explanations of the apparently complex behaviour that chimpanzees exhibit have not gained sufficient ground for them to be incorporated into our theories. However, it is too early to discount them and many would choose not to on the grounds that descriptions of the histories of wild chimpanzees suggest that their social lives are complex enough for such abilities to have evolved (e.g. Humphrey, 1976; Byrne & Whiten, 1988; Whiten and Byrne, 1997), and perhaps that they are necessary in order to successfully meet the challenges that this complexity presents (Newton-Fisher, 1997).

1.2.4 Reconciliation and consolation

The first study of post-conflict behaviour was carried out on captive chimpanzees by de Waal & van Roosmalen (1979) after they had noticed that former opponents often had affiliative contacts with one another soon after the conflict had ended. They called this phenomenon ‘reconciliation’. Initially, it was imagined that reconciliation might be peculiar to chimpanzees, or possibly apes, as it appeared to be a complex behaviour requiring a minimum cognitive capacity which could support self-awareness, empathy and attribution (Gallup, 1982). Since then studies have found that such selective attraction and affiliation between former opponents is a common phenomenon among primates and has also been found in some nonprimate species (extensively reviewed by Aureli & de Waal, 2000). Conflicts can often result in former opponents avoiding one another and indicators of anxiety, such as self-directed behaviours, occur at a higher rate (Maestripieri, 1992). Reconciliation has been shown to result in rates of dyadic affiliation and self-directed behaviours returning to baseline levels (Aureli & van Schaik, 1991b; Castles & Whiten, 1998b; Das *et al.*, 1998). So far, the hypothesis that best accounts for the distribution of reconciliation within groups is the ‘valuable relationships’ hypothesis (Cords & Thurneer, 1993; Cords & Aureli, 1996) which states that reconciliation should be more common among dyads containing individuals that are valuable to each other in some way. In the original captive chimpanzee study, reconciliation was found to most common among male-male dyads, which formed coalitions and had strong affiliative relationships, and least common among female-female dyads whose relationships were relatively weak (de Waal & van Roosmalen, 1979).

A second phenomenon which de Waal & van Roosmalen (1979) observed and recorded was ‘consolation’. Consolation is defined as affiliative contact initiated by an uninvolved individual and directed towards a victim of aggression (de Waal & van Roosmalen, 1979; de Waal & Aureli, 1996). It has been suggested that consolation, like reconciliation, may alleviate the victim’s distress (de Waal & Aureli, 1996) and may function as a substitute reconciliation (Watts, 1995b) although the relationship repair aspect of reconciliation is absent.

Consolation has been looked for in a number of species of primate (bonobos; de Waal, 1987; long-tailed macaques; Aureli *et al.*, 1989; Aureli & van Schaik, 1991a; Aureli, 1992; de Waal & Aureli, 1996; vervet monkeys; Cheney & Seyfarth, 1989; patas monkeys; York & Rowell, 1988; rhesus macaques; de Waal & Yoshihara, 1983; stumptail macaques; de Waal & Ren, 1988; Japanese macaques; Aureli *et al.*, 1992; ring-tailed lemurs and redfronted lemurs; Kappeler, 1993) but so far, it has only been found in chimpanzees.

A slightly different form of this behaviour has been observed in capuchin monkeys (Verbeek & de Waal, 1997) and spectacled leaf monkeys (Arnold & Barton, 2001b) in which victims actively approach bystanders in order to affiliate with them at a rate significantly higher than during control periods.

Despite similarities between the affiliation with bystanders exhibited by monkeys and true consolation performed by chimpanzees, de Waal & Aureli (1996) perceive this qualitative difference (i.e. direction of approach) as another indicator of the postulated cognitive difference between apes and monkeys, as reflected in the former’s abilities to use tools (e.g. Goodall, 1986; McGrew, 1992a; Nishida & Hiraiwa-Hasegawa, 1987), symbols (Gardner *et al.*, 1989; Parker & Gibson, 1990), mirror self-recognition (Gallup, 1982) etc. They suggest that consolation in

chimpanzees is facilitated by their ability to respond “empathically” to the distress they perceive in others (see also Preston & de Waal, *in press*). They further claim that their study measures “not so much empathy, however, but the active response to assist another, known as sympathy” (de Waal & Aureli, 1996, p. 83) which monkeys are not capable of.

1.2.5 Tactics and strategies

As mentioned above, there are many examples that indicate that primates and perhaps male chimpanzees in particular manipulate their relationships strategically and to do this they must integrate a complex set of information (Cords, 1997). Opportunistic coalition formation is one good example of such strategic behaviour but there are also many examples of strategies used in the long term, especially in the case of male chimpanzees where the pursuit and maintenance of high rank appear, for many, to pervade all areas of their social lives.

From an early age, male chimpanzees begin to prepare the ground in such a way that their competitive potential might be fully realised in the future. Adolescent males, although at the periphery of the community, begin to test their relationships with one another and with adult males to whom they are particularly attracted. They are especially motivated to associate with the alpha male (Kawanaka, 1989). Late adolescent males remain peripheral to the adult male network but make their presence known by frequent pant-grunting and other greeting behaviours. They unilaterally follow and groom adult males. Takahata (1990a) reports that prime males demand grooming from young males and that mutual grooming was infrequent. Late adolescent and young adult males begin to perform charging displays when females, particularly those in oestrus, but not adult males are in the

vicinity and begin their bid to dominate all adult females (Kawanaka, 1989). When young adult males become integrated into the 'adult male cluster', they increase their frequency of charging displays and may even dominate a few of the lower ranked adults. They are not, however permitted to associate intimately with them until they become better established.

It seems that males with a brother, particularly an elder brother, are at a distinct advantage in their efforts to achieve high rank (McGrew, 1992 cited in Byrne, 1995, p. 197). When both are young, they will have many opportunities to associate as they travel with their mother. During this period the elder brother is usually protective of his younger sibling. Even when the elder brother begins to spend more time away from his family, the relationship remains friendly and brothers will often feed, patrol and nest together. The younger will often rise quickly in rank under his brother's protection and eventually challenge his brother. At this point, there will be greater tension between the pair than at any other time. It is usually the younger brother who eventually dominates and after this, normal, friendly relations are resumed. The elder will continue to support his brother thus strengthening his position (Goodall, 1986).

The importance of such a relationship is clear in the case of Figan, a male of the extensively researched community at Gombe (see Goodall, 1968, 1986). Figan had an elder brother, Faben, who dominated Figan when they were young but with whom he enjoyed a relaxed and playful relationship. During Figans's late adolescence, Faben contracted polio and lost the use of one arm. Almost instantly, Figan began to challenge his brother until he had intimidated him enough to dominate him. Though Figan's aggression towards Faben ceased at this point, there followed a period of tension between the two for the next 2 years when they were

rarely seen together. In the following year the brothers began to associate again. They travelled and groomed together often and displayed in unison at other males. A few years later, Faben was Figan's staunchest ally and it was this relationship which allowed Figan to attain the position of alpha male. When, later, Faben disappeared, Figan lost this position temporarily and had to struggle to regain it.

There were other factors that apparently led to Figan's success. When young, Figan's mother was one of the highest ranked females in the community. His mother's support is likely to have affected his relationship with his peers and led to early domination of other females. According to Goodall (1986), Figan would probably have ascended to the position as alpha even without his alliance with Faben. Personality traits appear to affect an individual's potential for high rank. Figan is described as an opportunist, taking advantage of the ill health or any form of temporary weakness in his rivals.

Physical factors such as size can play a role although small males (such as Figan) can offset such disadvantages by using less direct forms of manipulation. Without a reasonable degree of social skill, even the largest males cannot always attain alpha status or hold this position for very long.

One of the most consistently shared characteristics of those males that are successful is persistence (Goodall, 1986). In his initial challenges on Faben, Figan would display repeatedly, up to 9 times in 15 minutes. Goblin was another male who used these tactics. He holds the record for persistence at Gombe (Goodall, 1986). In his early attempts to challenge the adult females, he was seen to display 12 times in 15 minutes. Although the females chased and attacked him, he repeated his displays the next time he encountered them.

As mentioned above, young males are attracted to the alpha male. If they are successful in building a friendly relationship with this individual, then they might in the future benefit from his protection. This is a tactic that Goblin used. His rapid rise in status over the females was unaided and showed that he had the qualities necessary to be successful. He also associated with Figan (alpha) and formed a close relationship with him. When Goblin was confident enough to start displaying toward the adult males, Figan would support him if any of the males retaliated (except in the case of Humphrey who was one of Figan's important allies). Very quickly he came to dominate all the other males, even when he was outnumbered. Eventually he took advantage of a period when Figan was lame to challenge him. Though all the other males formed a coalition against him, he finally dominated Figan and took over the alpha position in the community.

Though most males become alpha at some time in their prime (20-30 years old) some do not. This may be, as in case of Faben, because they will benefit from the indirect fitness gains that are accrued via a brother with which cooperative relationships are common, and/or because of some physical handicap. In some cases, though, they simply appear to lack motivation. Historical factors such as low frequencies of interaction when young may result in naivety when dealing with their rivals. Some particular event may reduce confidence such that a male may not take advantage of opportunities to intimidate his competitors.

Personality traits such as boldness and inventiveness have characterised chimpanzees which have been unusually successful at Gombe (Goodall, 1986). Displays are known to function as intimidation tactics and can be performed towards any member of the group, although they are most frequent in large groups and in the presence of other males (Riss & Buss, 1977). They usually consist of a behaviour

pattern in which the chimpanzee stands quadrupedally or bipedally with their hair erect, swaying from side to side. Hoots of increasing pitch begin, leading up to a scream, after which the animal charges at other individuals, towards objects which can be beaten (drumming display) or at branches which can be swayed so that they make a noise. There is quite a lot of individual variation in these displays where males incorporate idiosyncratic elements. Some beat their chests, others perform the charge at high speed. Bygott (1974) reported that one male would stamp on the ground very slowly and throw sticks and stones into the air. A famous example is that of Mike who would use kerosene cans, which he found lying around the camp, which he banged together (Goodall, 1968). This is a good example of the use of novel behaviour being used effectively to increase status.

An alternative way of increasing the effectiveness of the display is to add an element of surprise. Some males begin their displays out of sight and then emerge dramatically to great effect (Bygott, 1974) or at times when other males are off-guard. Figan occasionally performed his displays at dawn or dusk when the other males were asleep in their night nests (Goodall, 1986).

Although it is easy to see why displays might be an effective means of dominating individuals due to their aggressive appearance, there is evidence that they may function simply as a way of attracting attention to the displaying individual. Displays often result in immediate association initiated by onlooking males and those individuals which display at high rates are often not overtly aggressive in other ways (Chance, 1967; Reynolds & Luscombe, 1969).

Miller (1997) outlines some theoretical reasons why surprise tactics are adaptive. If an alpha male follows Miller's 'old man' strategy then the threshold at which the male will punish challenges or insults to his dominance will be set and

invariant. Subordinates will quickly learn what this threshold is and can behave in such a way as to further their interests at will, provided this threshold is not reached. Alternatively, the alpha male could adopt Miller's 'mad dog' strategy where the anger threshold is probabilistic. In this case punishment occurs at random when the threshold which is chosen from a normal curve is exceeded. This strategy results in enormous uncertainty in the subordinates as to whether even the slightest offence will, on this occasion, result in heavy punishment. This strategy is less costly for the alpha male and the uncertainty alone will do much of the work of intimidating subordinates. Perhaps some of the existing data on display and punishment behaviour in alpha male chimpanzees could be reanalysed and interpreted within this new framework.

As noted previously, males associate most with other males (Kawanaka, 1990; Hayaki *et al.*, 1989). It is a reasonable assumption that the spatial organisation of a set of individuals reflects the underlying nature of the relationships between those individuals (Kawanaka, 1993; White & Chapman, 1994; Furuichi & Ihobe, 1994). Males must choose which individuals to associate with and therefore which parties to join in order to further their goals. Newton-Fisher (1997) has suggested that these kinds of decisions are tactical in themselves. Proximity may be used tactically in that it might promote the strengthening of bonds, especially if those in close proximity are more likely to groom. Close proximity might also serve to deter others from approaching a particular individual. Newton-Fisher's (1997) data show that middle and high ranking males spend a great deal of time grooming when in close proximity, irrespective of whether or not they have strong association relationships with one another, and whether or not they are in close proximity more often than would be expected on the basis of their associations.

Middle and high status males must on the one hand form coalitions with one another to prevent younger males unseating them from their social positions, and on the other hand, form coalitions in order to compete with one another for status. This suggests that their relationships with one another must be ambivalent, unless they are allies. This ambivalence might be reflected in their grooming behaviour. Males often groom each other's faces and pant while doing so indicating a desire for intimacy despite the observable signs of physiological stress (Nishida & Hosaka, 1996).

In general though, there is a correlation between association strengths and time spent grooming. Those males involved in a dyadic alliance groom their alliance partner more than any other individual. Harcourt (1988, 1989) argues that primates' use of tactics to compete for access to the most effective alliance partners sets them apart from any other social animal. Other than achieving this through reciprocating specific supportive acts, their main method of cultivating cooperative relationships is through grooming (Seyfarth, 1976; Hemelrijk, 1990b, 1994; Hemelrijk & Ek, 1991; O'Brien, 1993).

An alpha male associates most often with other males (Kawanaka, 1989, 1990; Hayaki *et al.*, 1989) but restricts his association partners to only a few of those available (less than half at Mahale: Kawanaka, 1990). However infrequently other males associate with the alpha male, grooming relations are usually reciprocal and symmetrical (Kawanaka, 1990). Alpha males often associate with experienced, old males who have achieved alpha status and are declining in rank, and young males. Associations with closely ranked males are less likely as they will be the individuals who are in position to challenge for status. Associations with old males are mutually beneficial as they often retain the respect of challenging males and can enjoy the

protection of the alpha male (Uehara *et al.*, 1994). Old males tend to support the alpha male passively (Nishida & Hosaka, 1996). Alpha males often share meat with these males but refrain from sharing with other high-ranking males (Nishida *et al.*, 1992). Young males can safely challenge males who outrank them in the presence of the alpha male and by doing so deter his competitors from challenging him. An interesting case is that of a low ranking male at Mahale whose highest recorded position in the male hierarchy was 5th. He associated intimately with two successive alpha males but never challenged them and was outranked at times by some juvenile males. His relationship with the alpha males was similar in some respects to that of old males and he had symmetrical grooming relationships with them. There was evidence that the alpha males actively sought such relationships (Kawanaka, 1990). The alpha male often takes the initiative to groom those with whom he associates and grooms more often than he is groomed (Takahata, 1990a).

Other prime males often mutually groom one another. At Mahale, such males seldom pant-grunted at one another and inhibited overt displays of dominance (Hayaki *et al.*, 1989). The initiative to approach and follow another was taken irrespective of rank. These patterns were interpreted as an attempt by these males to keep their dominance relationships ambiguous (Takahata, 1990). They form coalitions against the alpha male in order to better their positions. Alpha males have been reported to try to break up these coalitions by charging at parties of grooming males (Nishida & Hosaka, 1996; de Waal, 1982). Similar tactics are used by males rising in rank to weaken alliances between dominant males (Goodall, 1986).

However, chimpanzee applications of power are not always used in competitive circumstances. Sometimes high rank is used to quell disputes through the use of 'pacifying interventions' (Boehm, 1992, 1994, 1997). Typically adult

aggression is quashed by an individual who outranks both protagonists. Most often it is the alpha or beta male who takes on this ‘control role’ and only when the hierarchy is stable. The most frequent tactic is to direct a charging display at both parties simultaneously. Interventions are impartial and are directed at nonkin more often than kin. Boehm (1992) also describes two other tactics, which he observed at Gombe. In one, Goblin directed a series of attacks at two females and herded them into separate trees. He immediately stopped his attacks once the females were separated. In another instance, Satan, having charged at two adolescents and failing to break up the fight, manually separated the two. A similar intervention tactic used by captive chimpanzees at Arnhem Zoo was reported by de Waal (1982). Boehm (1992, 1997) argues that chimpanzees have a genetic predisposition to intervene in disputes due to the marked similarities in the patterns of such behaviours in very different situations (i.e. Gombe Stream reserve, Tanzania and Arnhem Zoo, Netherlands). He suggests that these seemingly altruistic acts might be an extension of the protective tendency of adults towards young. However, this phenomenon remains far from clearly understood.

1.3 Aims of the present study

Initially, the aim of this study was to gain a better understanding of some of the more potentially complex aspects of chimpanzee behaviour such as the proximate mechanisms involved in coalition formation and, in particular, to ascertain the extent to which post-conflict behaviour of wild chimpanzees mirrored that reported in captivity. The first of these objectives, however, was not possible due to the scarcity of such events. The second objective was achieved to some

extent although consolation, the behaviour of greatest interest, was also extremely rare. A theme that was intended to pervade this thesis was the degree to which behaviours were coordinated and solicited, and the extent to which observable signals might be used in achieving desired outcomes. Instead, data concerning the form and distribution of affiliative, aggressive and post-conflict behaviours provide the basis of the content of each of the four data chapters that follow.

The aim of this thesis is to provide a description of social behaviour of the Sonso community of chimpanzees living in the Budongo Forest, Uganda. I shall also investigate the degree to which male chimpanzee behaviour in this population conforms to the standard view that chimpanzees, and that male chimpanzees in particular, are highly rank oriented and that their social behaviour reflects this predisposition in the pattern of affiliative and aggressive interactions.

The first of these, Chapter 3, describes the basic social structure of the Sonso community and tests the following hypotheses:

- 1) Males are attracted to reproductively active females showing full anogenital swellings and constituting potential mating opportunities, and also other males in order to take advantage of potentially beneficial social opportunities.

Predictions – (i) The proportion of males in parties should therefore increase according to the number of cycling females present. (ii) Males should tend to associate in parties containing a high proportion of other males. (iii) Male-male attraction should be reflected by higher association indices among males than between males and females.

- 2) High rank brings reproductive benefits to males.

Predictions – (i) High-ranking males should copulate more often than low-ranking males. (ii) High-ranking males should have more sexual partners than low-ranking males.

- 3) When co-occurring in parties, males seek to engage in positive social interactions more often than females do, and engage in such interactions more often with one another than with females.

Predictions – (i) Males should spend more time in proximity and grooming than females do. (ii) Males should engage in such activities with other males more often than with females. (iii) If spending time in close proximity provides enhanced access to grooming partners, then a time spent in proximity and time spent grooming should be correlated.

- 4) Males compete for access to high-ranking males in order to increase or maintain potentially beneficial relationships with them.

Predictions – (i) High-ranking males should spend more time in proximity with other males, as other males should compete for access to them while they, themselves, compete to have access to other high-ranking males. (ii) Males that are close in rank should spend more time in proximity than males that are more distantly ranked as access to one another should be less constrained by their competitors and their social interests should be more likely to be convergent.

Chapter 4 concentrates on grooming relationships in order to further investigate sex differences in social investment and the role of rank in structuring patterns of grooming among males. The following hypotheses are tested:

- 5) Grooming is a more important social activity among males than any other sex combination

Predictions – (i) Males should have a larger number of grooming relationships with available males than with available females. (ii) Males should devote more time to grooming one another than any other sex combination.

- 6) Given the ‘egalitarian’ nature of chimpanzee societies where power differentials are less pronounced than in more despotic species, grooming should be reciprocal.

Prediction – (i) Grooming reciprocity at the group level should be found in all age/sex combinations, irrespective of dyadic association frequencies and rank related grooming partner preferences.

- 7) Males should preferentially groom individuals from whom they could potentially receive the greatest benefits.

Predictions – (i) High-ranking males should receive more grooming than low-ranking males. (ii) High-ranking males should receive more grooming than they give. (iii) Males should groom sexually receptive females more than unreceptive ones. Given that males should be more differentiated in terms of their value than females, (iv) males should groom females more equitably than males.

- 8) Males compete for access to high-ranking grooming partners.

Predictions – (i) Males are constrained in their choice of grooming partners and so grooming between closely ranked males should be more common than between distantly ranked males. (ii) The observed distribution of grooming among males should fit models of grooming distribution that take competition into account.

Chapter 5 investigates patterns of aggression, coalition formation and the performance of aggressive displays. Under the assumption that it is in the interest of males to maintain their good relationships (those which include high levels of

affiliative behaviours), and also that males dominate others via aggression, the following hypotheses are tested:

- 9) Males are less likely to have conflicts with individuals with whom they affiliate relatively often.

Predictions – (i) There should be a negative relationship between dyadic conflict frequency and the amount of time spent in proximity and grooming. (ii) Males will direct fewer attacks at, and receive fewer attacks from those males that they groom most often.

- 10) High-ranking males use more force in their attempts to dominate others than low-ranking males.

Prediction – (i) High-ranking males initiate more conflicts than low-ranking males.

- 11) Competition should be most intense between closely ranked males.

Prediction – (i) Conflict frequency should increase with decreasing rank distance.

- 12) Grooming investment increases the likelihood of support during aggressive encounters.

Prediction – (i) There is a positive correlation between dyadic grooming investment and the receipt of support.

- 13) Rank determines the degree to which males perform aggressive displays and also the context of these displays, in terms of the number and rank of the other males present.

Predictions – (i) High-ranking males display more often than low-ranking males. (ii) High-ranking males should perform displays in the presence of larger number of males than low-ranking males. (iii) Low-ranking males should be inhibited from performing displays in the presence of higher-ranking males.

- 14) The performance of joint displays demonstrates close social bonds.

Predictions – (i) Male-male dyads that groom relatively often, display together relatively often. (ii) Males should display jointly in the presence of both larger numbers of males and males of higher rank than individual displays.

15) The performance of joint displays reflects the convergent interests of the males involved.

Prediction – (i) Closely ranked males should display more often than distantly ranked males.

16) The individual displays of high-ranking males are more likely to escalate into joint displays than the individual displays of low-ranking males.

Prediction – (i) High-ranking males should have a larger number of display partners than low-ranking males. (ii) High-ranking males should perform more joint displays than low-ranking males.

Chapter 6 investigates post-conflict behaviour within the Sonso community. Hypotheses and specific predictions relating to the patterns of reconciliation and other forms of post-conflict behaviour are set out in the introductory section of Chapter 6. In Chapter 7 I briefly discuss the findings of the previous chapters and take issue with the widespread view that male chimpanzees are the best example of a ‘political’ nonhuman primate.

Chapter 2

Study Site, Population and General Methods

2.1 Study site

The Budongo Forest Reserve lies between $1^{\circ} 35'$ - $1^{\circ} 55'$ N and $31^{\circ} 18'$ - $31^{\circ} 42'$ E in the Masindi district of western Uganda. With a total area of 793 km^2 the reserve is Uganda's largest remaining block of tropical rainforest, 428 km^2 of which is continuous forest cover (the remainder being savannah woodland or grassland). The area has a mean annual rainfall of c. 1600mm with two wet seasons, March to May and September to November, and a dry season falling between December and February.

The forest is classified as moist, medium altitude (average altitude: 1100m), semi-deciduous tropical forest (Eggling, 1947). Gaps created by the felling of trees during periods of logging and by a small population of forest elephants in the 1960's, together with natural variations in local environmental conditions has resulted in a mosaic of forest types. The four basic forest types are:

1. Swamp forest - the least common forest type. Dominated by *Raphia farinifera*, *Mitragyna stipulosa* and *Pseudospondias microcarpa*.
2. Colonising forest - found in large blocks around the edge of the forest. Dominated by *Maesopsis eminii*, *Cordia millenii* and *Diospyros abyssinica*.
3. Mixed forest - the most common forest type. Dominated by *Celtis mildbraedii*, *C. zenkeri*, *Khaya anthotheca*, *Chrysophyllum albidum* and *Funtumia elastica*.

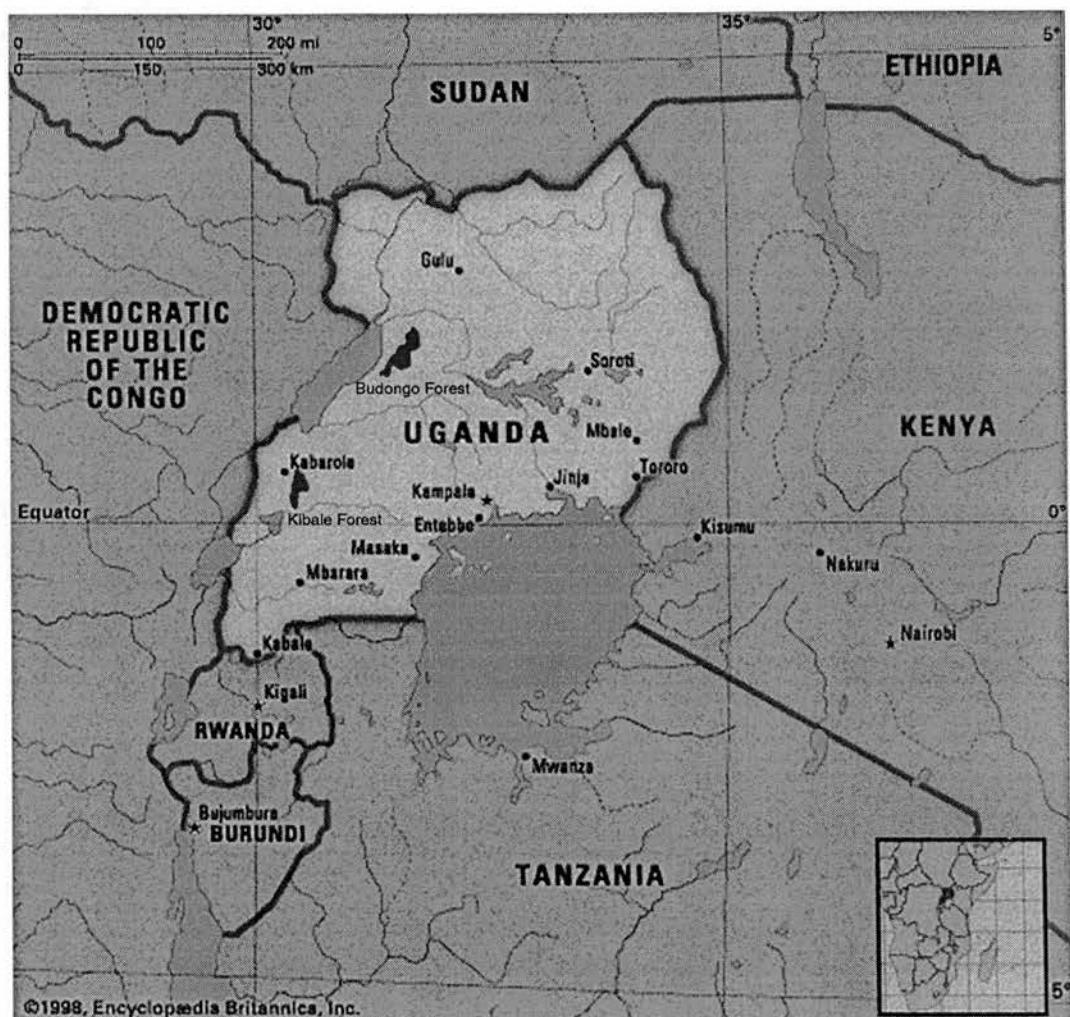


Figure 2.1 Map of Uganda showing the location of the Budongo Forest situated to the East of Lake Albert.

4. Ironwood forest - possibly the climax forest type and containing the fewest species. *Cynometra alexandrii* dominates forming 75% of the canopy with *Lasiodiscus mildbraedii* as the dominant understorey tree.

The forest is divided into 47 compartments. The Budongo Forest Project research station is situated close to the centre of compartment N3 and provided a base from which to carry out this study. It was originally founded, in 1991, to facilitate a study on the effects of logging on chimpanzee ecology and has

subsequently extended its scope to include studies of chimpanzee ecology and behaviour, the effects of logging on forest ecology and the importance of frugivorous primates on forest regeneration. Compartments N3, and the adjoining N15, contain a trail system which was cut to allow researchers to move efficiently through the forest and to identify their position relative to the camp. The trail systems consist of pathways cut in parallel, running north-south and east-west, which are approximately 100m apart. This system divides the compartments into blocks of 1 square hectare each of which are labelled. Altogether, the trail system covers approximately 31km² of the study community's range, the full extent of which is not yet known.

Notable fauna within the study area, aside from chimpanzees, include four species of diurnal primates; olive baboons (*Papio anubis*), black and white colobus (*Colobus guereza*), red-tailed monkeys (*Cercopithecus ascanius*) and blue monkeys (*C. mitis*). Other large mammals include bushbuck (*Tragelaphus scriptus*), red duiker (*Cephalophus natalensis*), blue duiker (*C. monticola*) and bushpig (*Potamochoerus porcus*). Potential predators such as lions (*Panthera leo*) and leopards (*P. pardus*) were absent from this part of the forest.

A very detailed description of the study site, including its history, climate, flora and fauna is given in Newton-Fisher (1997).

2.2 Study community

The Sonso community consisted of 50-51 named and individually recognisable individuals, members of the subspecies of Eastern chimpanzees (*Pan troglodytes schweinfurthii*). Habituation to human observers began in 1990 and is ongoing. Provisioning has never been employed to facilitate habituation of this

Table 2.1 Age/sex classification of the Sonso community of chimpanzees.

Age Class	October 1998		October 1999	
	Male	Female	Male	Female
Adult	11	11	9	12
Adolescent	4	5	3	4
Juvenile	5	6	4	6
Infant	4	5	4	8

community. The adult males were better habituated than the females and would tolerate researchers in moderately close proximity even when on the ground. Females were generally more wary and some would only descend from the trees and remain in view when males were present. While they were in trees, females and males were habituated to a comparable degree. Table 2.1 gives a breakdown of the study community by age and sex.

During the course of the study one adult male disappeared (VN: June, 1999) and two males died of unknown causes, one juvenile (KD: July, 1999) and one old adult male (MG: May, 1999). A further male, a young adult, died of lethal wounds inflicted during an intracommunity attack (ZT: November, 1998; Fawcett & Muhumeza, 2000). Table 2.2 gives details of the identities of the study community, including their names and two letter identity codes. At least one unnamed female with a dependant juvenile offspring was observed to associate with mixed sex parties but only when she was in estrous. Her status, with regard to community membership, is currently unknown and neither she, nor her offspring,

Table 2.2 Identities and age/sex classes of the Sonso community at the beginning of the study.

Age Class	Males	ID	Females	ID
Adult	Duane	DN	Banura	BN
	Vernon [†]	VN	Harriet	HT
	Black	BK	Kalema	KL
	Magosi [†]	MG	Kigere	KG
	Maani	MA	Kutu	KU
	Jambo	JM	Kwera	KW
	Bwoya	BY	Nambi	NB
	Muga	MU	Ruda	RD
	Nkojo	NJ	Ruhara	RH
	Tinka	TK	Zana	ZN
Adolescent (late)	Zesta [†]	ZT	Zimba	ZM
	Zefa*	ZF	Kewaya*	KY
	Andy (NB)	AY	Janie	JN
			Mukwano	MK
			Clea	CL
Adolescent (early)	Nick (RH)	NK		
	Bwoba (ZA)	BB		
Juvenile	Gashom	GS	Gonza (ZM)	GZ
	Kato (KU)	KT	Grinta (RH)	GT
	Kadogo [†] (KG)	KD	Muhara (MM)	MH
	Bob (RD)	BO	Vita	VT
	Musa (NB)	MS	Shida (BN)	SH
Infant			Emma	EM
	Kwezi (KW)	KZ	Bahati (KL)	BH
	Hawa (HT)	HW	Nora (NB)	NR
	Zig (ZM)	ZG	Rachael (RD)	RC
	Zalu (ZA)	ZL	Betty (BN)	BT
			Rose (RH)	RS
			Keti [‡] (KG)	KE
			Katya [‡] (KY)	KA
			Kana [‡] (KU)	KN
	? [‡] (JN)			

*Denotes individuals which moved into an older age class; [‡]denotes individuals that were born;
[†]denotes individuals who died or disappeared during the course of the study. ID codes in parentheses indicate the identity of the mother where known.

has not been included in Table 2.2.

Unfortunately, kin relationships within the community are unknown except where females have given birth or have been observed with dependant offspring since 1990. A study is currently underway which should provide information about kin relations in the near future (Reynolds, pers. com.).

2.3 Data collection

After an initial pilot study of one month in June 1998, the main study was carried out between 28th September 1998 and 15th October 1999. The field site was located within the community range of the Sonso chimpanzees and from here searches were begun at approximately 7.30 am, six days a week. Searches would begin at the last known location of a group, or groups, of chimpanzees and from thereafter, would consist of walking the trail system in that area, and then further afield if no chimpanzees were encountered. The most common method of pinpointing a subgroup was by overhearing calls, usually long-distance pant-hoots, and then following these calls to their source. If chimpanzees were still not found, then random walks in different parts of their range were begun together with listening carefully while stationary at intervals. If no chimpanzees were located within approximately four hours, a new search would begin in the afternoon when the chimpanzees became active again following the likely resting and socialising period around midday. Mixed sex, multi-male parties were preferentially searched for in order to maximise chances of observing conflicts. I was allocated a field assistant, James Kakura, who was employed by Budongo Forest Project. His primary role was to aid in the identification of individuals, especially in the early stages of the study, and to navigate the forest. He had been trained in data collection

techniques by previous researchers and so was able to help collect and record scan samples while I simultaneously collected focal animal data. Together, we were able to monitor whole subgroups provided they were not too large or dispersed over a wide area. Both myself and my field assistant used binoculars (10 x 40) for observing and identifying chimpanzees in tall trees or at a distance on the ground.

2.3.1 Sampling methodology

Given that I was interested in relatively complex and rare behaviours such as post-conflict and coalitionary behaviour, I chose to focus primarily on males as among chimpanzees, it is the males who have been shown to be more likely to engage in such behaviours as aggression, displays, interventions, coalitionary behaviour and so on. What follows is a description of the sampling regime and methods that I used.

Focal animal sampling

I took continuous focal animal samples (Altmann, 1974) of 30 minutes of all independent male individuals. These consisted of all the adult and adolescent males in the community and also a single orphaned, and therefore independent, juvenile. Focal samples were collected in a randomised order and an attempt was made to sample each focal animal equally within each month. A fifteen minute interval followed each sample in order to reduce dependence within the data set. A new focal was selected from the same party if one was available, preferably one which was next on the randomised list. Rarely seen individuals, however, were primary targets. This method of selecting focals reduced the amount of time spent looking for focals. The short duration of focal samples permitted a number of individuals to

be sampled each day and minimised the amount of time wasted if the focal animal was lost from view.

The objective of each 30 minute sample was to accurately record a continuous account of the social behaviour of the focal animal although other activities, e.g., foraging, were also recorded but in less detail. A hand held computer was employed for this purpose (Hewlett-Packard 200LX) running The Observer v.3 event recording software package (Noldus Information Technology B.V.). The Observer allows data to be recorded in the same format as more traditional paper checksheets but eliminates the need for laborious transformation of raw data into frequency counts and durations of behaviour into proportions of activity budgets, for example. The software includes minimal analysis tools that automatically convert raw data into a number of types of simple statistical reports if required. At the end of each day, focal animal samples were downloaded to a laptop computer, edited if necessary, and backed up. This type of data provided information on the frequency and duration of behavioural events which were unlikely to be recorded by other methods such as changes in proximity and rare behaviours such as genital inspection, together with identities of the initiator of social behaviours e.g., grooming. A list of behaviours recorded by this method, and further details, are given in an ethogram (see sections 2.3.2 & 2.3.3). One drawback of this method of data collection was that, occasionally, the speed with which sequences of behaviour were performed was beyond that which I could input the two or three letter codes for those behaviours. In such cases I used a dictaphone, which was always to hand, to record spoken accounts of the observed behaviours in real time. These records were timed, and then edited into the focal animal sample at the end of the day.

Table 2.3 The total number of 30 minute focal animal samples collected per focal subject, and the number of hours spent in the field and with the chimpanzees, per month.

	Month												
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Total
F-hrs	123	99	56	72	106	130	68	110	105	114	89	162	1233
C-hrs	100	69	20	21	36	50	32	40	22	57	19	67	534
Focal													
DN	8	6	1	2	4	4	5	3	0	5	2	6	46
VN	10	4	0	1	3	6	4	3	1	-	-	-	32
BK	10	4	3	1	2	5	3	3	5	6	2	5	49
MG	11	3	2	1	2	4	3	3	-	-	-	-	29
MA	10	6	0	1	2	5	4	2	3	5	2	9	49
BY	7	8	1	1	2	4	4	3	1	7	0	1	39
JM	3	6	0	0	3	6	3	5	4	7	1	7	45
NJ	9	5	0	2	2	4	3	2	0	6	0	6	39
MU	4	9	1	4	2	2	2	4	1	7	5	7	48
TK	6	5	1	5	5	5	1	2	3	5	5	4	44
ZT	11	1	-	-	-	-	-	-	-	-	-	-	12
AY	10	6	2	2	3	3	3	4	0	5	3	8	49
ZF	5	5	1	2	3	4	1	5	2	0	0	8	36
NK	4	6	0	3	3	7	2	2	3	5	2	4	41
BB	11	2	2	2	1	4	3	5	1	2	3	8	44
GS	9	5	0	3	2	3	3	4	0	6	3	6	44
Total	128	81	14	27	39	66	44	50	24	66	28	79	646

F-hrs = no. of hrs spent in the field, C-hrs = no. of hrs spent in contact with chimpanzees. A dash (-) indicates that a subject is no longer available for sampling due to death or disappearance.

Focal behaviour sampling

Focal behaviour sampling (Altmann, 1974) was employed to record all instances of aggression and coalitions where observational conditions allowed detailed recording of the behaviours in question. This methodology enabled the collection of complete bouts of behaviour without being constrained by a fixed time

period focused on a single individual. All observed occurrences of the specified behaviour pattern, involving at least one of the subject animals, for which initiation was observed, were recorded. This rule ensured that comparable data were recorded for all subjects. This data was recorded as a spoken account using a dictaphone. If opportunities to collect this kind of data occurred during focal animal sampling, the latter was abandoned. Information of the following type was recorded:-

Aggression:

Date/time at which aggressive episode begins.

Intensity: 1. low intensity threat, 2. high intensity threat, 3. display, 4. chase, 5. chase with body contact, 6. fierce biting. See section 2.3.3.

Identities of participants

Responsibility for initiation.

Direction - unidirectional/bidirectional.

Context - behaviour of aggressor/target, prior to aggression (if possible).

Outcome - identity of winner/loser or undecided.

Coalitions - identity of supporter, identity of recipient of support, outcome.

Scan sampling

Scan sampling (Altmann, 1974) provided information about party composition, location, activity and also interindividual distances. Samples were taken every 15 minutes by my field assistant and were integrated with focal animal sampling in the following way. Once a party had been located and the individuals comprising the party had been identified, I chose a focal subject according to the

protocol described above. At this point, my field assistant and I synchronised our watches and set the timer to beep at 15 minute intervals. This meant that a scan sample began at the same time as focal samples, with one scan falling at the mid-point and another at the end of a focal sample. There then followed a 15 minute interval during which time a new focal animal was selected. This sample interval was chosen as it has been used in previous studies of chimpanzees (e.g. Chapman *et al.*, 1994; Wrangham *et al.*, 1996; Newton-Fisher, 1997) and provided a reasonable compromise between using a time-frame suitable for limiting the amount of dependence between samples while increasing opportunities for sampling relatively short lived activities or behavioural states and brief periods of party membership. It also made the synchronisation of the overall sampling regime somewhat automatic, thereby reducing the amount of communication necessary between myself and my potentially distant and invisible field assistant.

Each scan sample was recorded on a special purpose checksheet (see Appendix A) and included the following:

- 1) The identity of all individuals that were considered to be members of the party under observation. Party membership was defined as those individuals who were present within a discrete subgroup, usually located within a radius of approximately 40m or less.
- 2) The date and time.
- 3) The grid location or, if the party was outside the grid system, the location relative to the nearest known point on the grid system.
- 4) The tree species in which the majority of the party was located (recorded as 'ground' if the party was on the ground).

- 5) The activity of all visible party members. Activities were categorised according to the following definitions:

Resting: individual is stationary, either sitting or lying and may or may not be vigilant.

Travelling on the ground: individual walks on the forest floor.

Moving in the tree: individual is walking, climbing or brachiating along the branches or trunk of a tree.

Foraging: feeding including moving short distances and handling food items.

Self-grooming: individual uses fingers and lips to push apart its fur to locate and remove ectoparasites and other foreign bodies from own fur and skin.

Grooming: individual grooms (as above) another individual. The identity of grooming partner was noted, as was the direction of grooming.

Other social: any other social activity including playing and aggression. The identity of the social partner was noted.

- 6) The relative distance in metres of all party members from the individual which was the subject of the focal observation being collected simultaneously.

All individuals of both sexes were included as subjects of scan samples with the exception of infants who were assumed to be present if their mothers were recorded as being present. Additionally, a five point scale indicated the cycling stage of each female as estimated by the degree of swelling of the anogenital region: 0 (no swelling); 1 (some swelling visible); 2 (small but pronounced swelling); 3 (pronounced but not fully tumescent swelling); 4 (fully tumescent swelling).

Table 2.4 The number of scan samples per month collected over the study period.

Month													
Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Total	
277	259	58	80	110	168	140	151	93	204	96	205	1841	

Ad libitum sampling

Unsystematic sampling of behaviour was necessary when that behaviour was infrequent but informative. All instances of dominant or submissive behaviour were recorded using this method (see Ethogram, section 2.3.3) when the individual performing the behaviour was not the subject of a focal observation, in order to construct a dominance hierarchy. Additionally, any examples of rare behaviours such as hunting, tool use, gestures, particularly those considered to be soliciting gestures, copulations etc., were recorded in a notebook or as a spoken account using a dictaphone. In all such cases, as many of the relevant contextual details as possible were also recorded, including responsibility for initiation.

All observations relating to post-conflict behaviour were recorded *ad libitum* in that they were not sampled according to any protocol. Any example of aggression that could be observed accurately, and then followed by a post-conflict observation, was recorded immediately. Details of recording methods associated with post-conflict behaviour are given in Chapter 6. If a conflict was observed during the course of a focal animal sample, the focal animal sample was abandoned in favour of the post-conflict observation. Interrupted focal animal samples were begun from scratch 15 minutes after the termination of the post-conflict observation. Thus, focal animal samples rarely contain instances of aggression but this measure was necessary given that one of the major aims of the study was to

examine the nature of these chimpanzees' post-conflict behaviour, and opportunities for collecting data on this behaviour were rare.

2.3.2 Recording behaviour

Behavioural codes were programmed into the Configuration Designer of the Observer software package. The sampling method (one-animal focal sampling), independent variables (two letter subject ID code, weather conditions, group activity and forest grid location), and duration for each focal (30 minutes elapsed time) were set and determined the entire configuration. Observer uses 'classes' to group behaviours, each class is a set of mutually exclusive behaviours, or 'behavioural elements', which can be either states or events. This means that within one class of behaviour, only one behavioural state can be active at one time although any number of behavioural events can be recorded at any time. It is possible to associate a maximum of two 'modifiers' to each behavioural element which can be used to give further details of the behaviour in question, e.g. state: grooming; modifier 1: individual ID code; modifier 2: mutually. A notepad function also enabled the recording of time stamped additional details where appropriate and necessary which were automatically appended to the focal sample. The Observer program was configured in the following way:

Independent variables

Independent variables were recorded at the beginning of each focal sample and could be edited at the end of the 30 minute period if conditions changed and the initial inputs were regarded as nonrepresentative of the focal sample as a whole.

1. Group activity: resting, travelling, foraging.

2. Weather: sunny, fine, overcast, cloudy, storm.
3. Grid location: the grid within the trail system occupied by the party.
4. Focal: identity of the focal individual.

Behavioural elements: states

The event recorder of the Observer program has been configured so that behavioural categories shown in Table 2.5 can be entered as "states". A behaviour has been classified as a "state" if the duration of the behaviour is considered to be relevant to the study, or if the duration of the behaviour is likely to be such that it may influence the calculation of the durations of other behaviours and so should not be classified as an "event".

Behavioural elements: events

The behavioural categories shown in Table 2.6 were recorded as events. Such behaviours were generally of short duration and only the frequency of occurrence were considered relevant to the study.

Definitions of each of the behavioural states, events and modifiers are given in section 2.3.3.

2.3.3 Ethogram

Behaviours Coded as States

Rest - modifier: rest class

Inactive. No energy expenditure above that needed to maintain posture and to maintain basic metabolic processes.

Travel

Terrestrial locomotion, generally quadrupedal.

Move

General arboreal locomotion.

Forage - modifier: height

Feeding while stationary or when locomoting.

Build - modifier: height

The construction of a night or day nest.

Autogroom

Manipulation of own fur or skin with the hands or mouth.

Allogroom - modifier: ID

Manipulation of the fur, skin or eyes of another individual, using the hands or mouth.

Aggression - modifier: ID/intensity

Threats, chasing, hitting, biting, charging, slapping. Alone or in combination. With or without physical contact. (See intensity).

Play - modifier: ID

Social interaction characterised by apparent low tension and an absence of stereotyped sequences that include: wrestling, sham biting, jumping on, jumping over, chasing, fleeing and related activities. Typically accompanied by a play face (open mouth and relatively relaxed facial features).

Embrace - modifier: ID

Two individuals embrace, oriented towards each other's ventral surface.

Table 2.5 Behavioural states and their corresponding codes and modifiers.

Element name	Code	Modifier 1	Modifier 2
Rest	re	rest class	-
Travel	tr	-	-
Move arboreally	mv	-	-
Forage	fo	height	-
Build nest	bl	height	-
Autogroom	sg	ID	-
Allogroom	gm	ID	-
Receive grooming	GM	ID	-
Aggress	ag	ID	intensity
Receive aggression	AG	ID	intensity
Play	pl	ID	-
Copulate	cp	ID	-
Genital inspect	gi	ID	-
Genitals inspected by other	GI	ID	-
Anal inspect	ai	ID	-
Anus inspected by other	AI	ID	-

Modifier: rest class

Modifier name	Code
Lying	l
Sitting	s
Vigilant	v
Not vigilant	n

Modifier: intensity

Modifier name	Code
Intensity 1	1
Intensity 2	2
Intensity 3	3
Intensity 4	4
Intensity 5	5

Modifier: Height

Modifier name	Code
Arboreal	a
Terrestrial	t

Modifier: ID

Modifier name	Code
Individual name	see table 2.2

Table 2.6 Behavioural events and their codes and modifiers.

Element name	Code	Modifier 1	Modifier 2
Approach	ap	ID ¹	proximity
Approached by	AP	ID	proximity
Leave	lv	ID	-
Left by	LV	ID	-
Vocal communication	vc	voc. comm.	ID
Ignore	ig	ID	-
Ignored by	IG	ID	-
Genito-genital contact	gg	ID	-
Self scratch	ss	-	-
Yawn	yn	-	-
Displace	dp	ID	-
Displaced by	DP	ID	-
Present	pr	ID	-
Presented to by	PR	ID	-
Avoid	av	ID	-
Avoided by	AV	ID	-

¹See Table 2.5

Modifier: voc. comm.

Modifier	Code
Pant-hoot	pho
Pant-bark	pba
Pant-scream	psc
Whimper	whi
Hoo	hoo
Squeak	sqk
Scream	scr
Bark	bar
Waa-bark	wab
Cough threat	cth
Laugh	laf
Pant	pnt
Copulation pant	cpt
Lipsmack	lsm
Tooth clack	tcl
Pant-grunt	pgr
Food-aa	faa
Huu	huu

Modifier: proximity

Modifier	Code
Proximity	p
Body contact	b

Half-embrace - modifier: ID

Individual puts one arm around the shoulders or torso of another.

Genital inspect - modifier: ID

Subject looks intently at, or touches another's' genitalia.

Anal inspect - modifier: ID

Subject looks intently at, or touches another's' anus.

*Modifiers***Rest class**

Lying - resting in a prone position, trunk in contact with substrate.

Sitting - trunk upright. Additional support may be provided by leaning against a solid structure or by clutching a branch with a hand or foot.

Vigilant - showing signs of alertness, scanning the environment or watching another individual.

Not vigilant - showing no signs of alertness.

Height

Arboreal - subject is located off the ground at any height.

Terrestrial - subject is located on the ground.

Intensity of Aggression

Intensity 1 - mild threat: head tip, arm raise, hitting toward, flapping, sitting hunch, quadrupedal hunch (see Goodall, 1986, pp. 314-315).

Intensity 2 - aggressive threat: swaying branches, throwing objects, flailing or hitting toward with stick or branch, bipedal swagger, running upright

toward, charging.

Intensity 3 - Any of the above including a chase of > 4m.

Intensity 4 - Any of the above including body contact such as pushing, slapping, hitting or grappling.

Intensity 5 - Any of the above combined with fierce biting.

Display - charging at a fast or slow run and showing piloerection.

Behaviours coded as Events

Approach - modifier: ID/proximity

Movement to within 2 metres of another individual.

Leave - modifier: ID

Movement to beyond 2 metres of another individual.

Ignore - modifier: ID

Subject pays no attention to another individual who is directing behaviour towards the subject.

Genito-genital contact - modifier: ID

Genito-genital rubbing or brief contact.

Present - modifier: ID

Subject orientates hindquarters toward another individual.

Copulate - modifier: ID/intromission

Male mounts female with erect penis and thrusts intermittently.

Displace - modifier: ID

Subject moves towards another individual, other individual moves away and subject rests at the former location of the other.

Avoid - modifier: ID

Movement from the path of an approaching individual before that individual moves to within 2 metres of the approacher.

Vocal communication - modifier: ID/vocal communication.

Subject emits a sound produced in the throat.

Yawn

Yawn may indicate tension.

Self scratch

Raking the fingernails through the fur repeatedly.

*Modifiers***Proximity**

Proximity - located within 3 metres of another individual.

Body contact - sitting or standing with contact with at least 25% of another individual's body surface.

Intromission

Intromission - thrusting with intromission

No intromission - thrusting without intromission.

Vocal communication (taken from Goodall, 1986)

Pant-grunt - directed by a subordinate towards an individual of higher rank.

Pant-bark - louder than a pant-grunt; associated with apprehension.

Pant-scream - louder still and associated with fear.

Whimper - soft but may grade into screams. Associated with distress.

Hoo - usually uttered by infants but occasionally by adults when begging for food.

Squeak - short, shrill calls given in series of 2-5 per second; response to threats from dominant individuals. May grade into screams.

Scream - high-pitched, loud and given in series; heard in the context of aggression or social excitement. 4 types of scream have been identified: SOS scream, victim scream, tantrum scream, copulation scream.

Bark - loud, sharp sounds, usually given by females during periods of excitement.

Waa-bark - similar to "bark" but given in agonistic contexts, usually threats or counter aggression.

Cough-threat - mild threat directed down the hierarchy.

Laugh - wheezing laughter associated with play.

Pant - usually without voice; occurs during grooming or greeting.

Copulation-pant - with or without voice; associated with copulation.

Lip-smack - without voice using lips and tongue; associated with grooming.

Tooth-clack - banging the teeth together; associated with grooming.

Grunt - exchanged when two or more familiar individuals travel or forage together.

2.4 Statistical data analysis

Details of the various statistical tests used in this study are provided in the relevant chapters. Parametric tests were used when data met the necessary assumptions of normality after transforming the data where necessary. Where these assumptions were not met, nonparametric tests were used. All statistical tests were

two-tailed with $\alpha = 0.05$. Corrections for ties were applied throughout. Analyses were conducted using Microsoft Excel 97 or SPSS for Windows v. 6.0 unless otherwise stated.

Chapter 3

Social Structure

3.1 Introduction

Some of the most basic parameters which operate on chimpanzee community structure, as in other primate societies, include 1) environmental and demographic factors, e.g. the nature of the food supply, the number of community members, the male/female sex ratio; 2) the availability of cycling females; 3) social factors, such as the existence of dominance hierarchies and their form at any given time, or the gregariousness of community members (Goodall, 1986). Predator pressure is also likely to have contributed to the evolution of the chimpanzee social system (Wrangham, 1986; Dunbar, 1988; Boesch & Boesch-Achermann, 2000) but was not likely to be a proximate factor in the social organisation of the Sonso chimpanzees as potential predators, such as leopards (*Panthera pardus*) or lions (*P. leo*), are known to occur only in the north-eastern areas of the Budongo Forest, far from the Sonso community range (Newton-Fisher, 1997). Other environmental factors such as food supply have just begun to be investigated at Budongo. Newton-Fisher *et al.* (2000) have demonstrated that party sizes of the Sonso chimpanzees are dependant on the size of food patches, as has been shown in other communities (Wrangham, 1977). Sonso party sizes are not, however, affected by habitat-wide measures of food abundance or overall levels of food dispersion. Feeding competition is therefore not as important a factor in the social organisation of this community as it is at other sites, due to the overall abundance of food (Newton-Fisher *et al.*, 2000).

The ecological factors affecting social organisation are not the subjects of investigation here. Instead, I will focus on a number of social factors which are common to all chimpanzee populations and which should provide a general framework within which to understand the particular community under study, and male chimpanzee behaviour in particular.

3.1.1 Dominance hierarchies

As with many other animal species, primates often form dominance hierarchies that are usually measured in terms of the direction of aggressive and submissive behaviours or the direction of approach-retreat behaviours (Walters & Seyfarth, 1987). Within any dyadic relationship, the dominant animal tends to be the aggressor in agonistic confrontations, and the winner in competition for resources. The subordinate animal tends to respond fearfully or avoid the dominant when threatened or attacked, and will generally lose access to a contested resource when challenged by the dominant. Dominance relations, therefore, are essentially dyadic (Hinde, 1976, 1978), but when all such dyadic relationships within a group are considered, the consequences of summing these relationships is often the emergence of a hierarchy within which each animal can be ranked according to the number of individuals it dominates. In a perfectly transitive hierarchy in a group of four animals for example, A dominates B, B dominates C, and C dominates D consistently; A also dominates C and D, while B also dominates D, etc. Such a hierarchy is also described as linear if the relative differences in *intrinsic* power (that which is derived from an individual's own physical and temperamental endowment: Datta, 1983) are the same between adjacently ranked animals. Linearity requires transitivity but the reverse is not true. Ranking animals ordinally

can result in the loss of information about relative intrinsic power where hierarchies are not strongly linear, whereas the use of cardinal ranks retains information about the magnitude of these differences (Boyd & Silk, 1983).

The picture so far outlined can be complicated where *extrinsic* power also operates on the probability of a favourable outcome in contests (Datta, 1983). In species which form coalitions, extra-dyadic influences can raise the probability of winning contests because two animals can potentially intimidate a single animal, despite the latter's higher rank. In many species of macaque, for example, coalitions tend to reinforce the dominance hierarchy insofar as both the aggressor, and the supporter, will attack a third animal that is subordinate to both (e.g., Gouzoules & Gouzoules, 1986; Walters, 1987; Harcourt, 1988; Ehardt & Bernstein, 1992; Silk, 1992; Widdig *et al.*, 2000). The potential effects of extrinsic power are, perhaps, more important in species that are considered to be relatively egalitarian, of which chimpanzees are a prime example (de Waal, 1989). Rowell (1966) suggested that the behaviour of subordinates toward dominants is as important in maintaining dyadic dominance relationships as the (more intuitive) reverse. Whereas this possibility was inferred from avoidance behaviour in baboons, it is evidenced in the initiation of dominant-subordinate interactions among chimpanzees. Status-signalling behaviours such as pant-grunting, which are directed by subordinates toward dominants and are often not elicited by any other observable behaviours on the part of the dominants, are an everyday feature of chimpanzee social life (e.g. van Hooff, 1967; Goodall, 1986; Hayaki, 1990). These kinds of interactions imply that individuals 'know' their status in relation to others, at least at the level of the dyad. However, where coalitions are formed against a higher-ranking animal, this 'knowledge' does not always determine the course of competitive events and

subordinate animals can flout existing social conventions when benefiting from increased extrinsic power conferred upon them by their supporters. Coalition formation in such species constitutes a strategy which can result in increased status, or in gaining the benefits that follow from undermining social constraints, which would otherwise only be achieved by exploiting heritable, intrinsic qualities. Thus, the importance of dominance in primate social systems is further demonstrated by the evolution of counter-strategies that buffer the negative consequences of low rank on reproductive success (Dunbar, 1988).

It remains unclear, however, just how rank impacts on reproductive success in chimpanzees. There is some evidence that females mate preferentially with high-ranking males, especially during the latter phase of oestrus when the likelihood of conception is highest (Nishida, 1983; Hasegawa & Hiraiwa-Hasgawa, 1990; Matsumoto-Oda, 1999). High-ranking males can also restrict access to oestrus females by aggressively deterring other males from attempting to copulate with them (Nishida, 1979, 1983; Tutin, 1979; Hasegawa & Hiraiwa-Hasgawa, 1983, 1990; Takasaki, 1985; Watts, 1998). However, females show preferences for particular males and the development of strong affiliative relationships between specific males and females appears to influence mating patterns, irrespective of male rank (Tutin, 1979; Goodall, 1986; Takehata *et al.*, 1996; Nishida, 1997). Males can also induce females to enter into consortships, thereby securing exclusive mating opportunities (Tutin, 1979; Goodall, 1986; Boesch & Boesch-Achermann, 2000) although again, female choice operates in determining whether or not consortships can be successfully initiated. Finally, sperm competition is thought to be an important component of male reproductive success in species in which females mate promiscuously and exert post-copulatory choice (e.g. Dixon, 1991)

thereby, potentially, nullifying any advantages that high-ranking males may have in gaining priority of access to cycling females.

3.1.2 Party size and composition

The fission-fusion patterns of association characteristic of chimpanzee societies is thought to have arisen in response to the dispersed nature of their food sources which vary in size at different locations, and from season to season, in habitats free of predator pressure (Dunbar, 1988). Other primate species have converged on the same solution to similar foraging conditions, e.g. Guinea baboons, hamadryas baboons, pigtail macaques and spider monkeys (Klein & Klein, 1977; Izawa *et al.*, 1979; Sigg *et al.*, 1982; Kawai *et al.*, 1983; Caldecott, 1986). Group size in frugivorous primates is constrained not only by the size of food patches, but also by the cost of additional travel imposed by extra travel companions (Janson & Goldsmith, 1995). Travel is energetically more costly for females with dependant offspring than for males where the degree of dimorphism is small, as it is in chimpanzees (Hunt, 1989; Wrangham, 2000). Males, therefore, can be expected to travel together more often and consequently are able to interact more socially than females. Female chimpanzees without offspring also tend to be more social, free of the burden of infant care (Goodall, 1986). Thus, male bonding in chimpanzees can be explained without reference to other factors, such as the potentially differential benefits to males and females (Wrangham *et al.*, 1996; Wrangham, 2000).

Chimpanzee parties contain only a small subsection of any community with an average of five individuals per party across study sites (Bossou, Budongo, Gombe, Kibale, Mahale, Taï: Boesch & Boesch-Achermann, 2000, p. 93). Mean party size varies between sites; larger communities typically containing more

individuals, on average, than smaller communities, resulting in a mean party size of between 9% and 21% of the entire community (mean = 16% across all sites). Smaller communities, which typically form smaller parties, tend to be less fluid in their patterns of fission and fusion since smaller parties tend to be more stable than large parties (Boesch & Boesch-Achermann, 2000). Mixed-sex parties are the most common types across all communities, although their frequency depends upon the prevailing ratio of males to females. The males of Budongo and Gombe, however, have been shown to associate with females in mixed-sex parties less often than other communities when the community sex ratio is taken into account (Boesch & Boesch-Achermann, 2000).

Whereas feeding competition is thought to determine female grouping patterns, male grouping patterns are dependent upon those of the females. It has been suggested that males join parties containing females in order to locate those which might be in oestrus and with whom they might gain mating opportunities (Wrangham, 1980). Male foraging requirements are still met, as most encounters with females will occur at feeding sites. The flexibility of the fusion-fission system, while accommodating differential foraging strategies, also allows ample scope for individuals to follow differential social strategies over and above those that might lead directly to increased reproductive success via mating opportunities.

3.1.3 Association

It has been suggested that fitness might be more closely related to feeding success in female chimpanzees than in males (Wrangham, 1986). Consequently, a high priority for a female chimpanzee should be access to feeding sites of sufficient size and quality to satisfy the nutritional requirements of both her and her

dependant offspring. A number of studies have shown that females spend more time alone than males (e.g. Wrangham & Smuts, 1980; Baker & Smuts, 1994) and solitary foraging might be more efficient than when foraging in parties where feeding competition is necessarily more intense. Social strategies that require association with key individuals are, for the most part, less important for females except under certain circumstances. Immigrant females, for example, have been shown to benefit from strong relationships with males that serve to protect them against aggression from resident females (Pusey *et al.*, 1997) and are more likely to be in a position to pursue social strategies, unhindered by dependant offspring. Males, on the other hand, are relatively unconstrained in their movements within the community range and are able to associate with other individuals according to the value of these social relationships (Wrangham & Smuts, 1980). Almost all studies of wild chimpanzee association patterns have found that male-male associations are stronger, on average, than male-female associations, which are, in turn, stronger than female-female associations (e.g. Gombe: Goodall, 1986; Kibale: Ghiglieri, 1984; Wrangham *et al.*, 1992; Mahale: Nishida, 1968, 1979; Nishida & Hosaka; Taï: Boesch & Boesch-Achermann, 2000; Budongo: Fawcett, 2001). Males also appear to have a particular interest in forming relationships with other males and some of the possible reasons for this have been investigated extensively. These will be discussed below, and in subsequent chapters.

3.1.4 Why are male chimpanzees more gregarious than females?

That males are the philopatric sex in wild chimpanzees means that they should be much more closely related to one another than they are to females, or than females are to one another (Morin *et al.*, 1994). Kinship is often used to

explain patterns of affiliation and cooperation in a wide variety of animals according to the theories of inclusive fitness and kin selection (Hamilton, 1963; Maynard Smith, 1964) and wild male chimpanzees are, on average, more strongly affiliative and cooperative with one another than they are with females, or than females are among themselves (Nishida, 1968, 1979; Goodall, 1968, 1986; Simpson, 1973; Bygott, 1979; Wrangham, 1986; Nishida & Hiraiwa-Hasegawa, 1987; Watts, 2000a; but see Pepper *et al.*, 1999). Male relatedness has traditionally been thought to be a major factor underpinning the pattern of bond formation within communities and this assumption is an entirely sensible one. Cooperative behaviour such as coalition formation is far more prevalent in males than in females, at least in chimpanzees' natural habitat (Riss & Goodall, 1977; Nishida, 1983; Walters & Seyfarth, 1987; van Hoof & van Schaik, 1994). Males also hunt cooperatively (Boesch & Boesch, 1989; Nishida *et al.*, 1992; Stanford, 1998; Mitani & Watts, 1999) and participate in territorial boundary patrols (Goodall *et al.*, 1979). It has also been suggested that chimpanzees may have the ability to recognise kin relationships at the phenotypic level, although only those between mothers and sons (Parr & de Waal, 1999). Recent studies, however, have failed to find a correlation between affiliative bond strength, or coalition formation, and maternal relatedness in chimpanzees or bonobos (*Pan paniscus*: Goldberg & Wrangham, 1997; Hashimoto *et al.*, 1996; Hohmann *et al.*, 1999; Mitani *et al.*, 2000), and in Taï at least, males were found to be no more closely related to one another than females were (Gagneux, *et al.*, 1999). That closely related males at Kibale were not found to be more cooperative than distantly related ones, in terms of meat sharing or coalition formation (including coalitionary mate guarding: Watts, 1998; Mitani *et al.*, 2000), is of particular significance given the important fitness consequences of

such behaviours (Goodall *et al.*, 1979; Nishida, 1983; Nishida *et al.*, 1992; Nishida & Hosaka, 1996).

Why, then, should males cooperate and affiliate as they do? To date, no explanation has been forwarded which explicitly deals with this question, presumably because the findings outlined above have only recently been published. However, Watts (1998), who predicted the lack of correlation between maternal relatedness and coalitionary mate guarding among the Ngogo males in the light of the Goldberg & Wrangham (1997) study, suggested an alternative explanation to kin selection. He proposed that coalitionary mate guarding, which has not been documented elsewhere, could, in fact, be a form of mutualism. Such coalitions were stable for between one and four days and involved two or three males cooperating with one another to aggressively prevent other males from copulating with an oestrus female. These males shared opportunities for mating with one another and each achieved more matings than they would have if they had attempted to mate guard alone, or if they had mated opportunistically (Watts, 1998). Dyads, or triads of males that regularly took part in such coalitions were also allies in other contexts and showed reciprocity in agonistic support (Watts, unpublished data cited in Watts, 1998). This phenomenon was explained as a strategy that was particularly suited to overcoming male-male competition for mates in an unusually large community containing many males. Watts (1998) pointed out that power asymmetries inherent in male-male relationships means that high-ranking chimpanzees could defect from such a coalition by failing to incur the costs of aggressively deterring other males, or by preventing the lower-ranking coalition partner from mating. Lower-ranking males, however, cannot defect by preventing a higher-ranking male from mating. Watts (1998) considers it unlikely that males face

a Prisoner's Dilemma under these conditions, as neither partner has the opportunity to defect unilaterally, and R (the reward for mutual cooperation) would probably not be less than T (the temptation to defect); rather, the conditions for mutualism were more likely to be met ($R > T$; Dugatkin, 1997a). Costs would have been incurred by mate guarding males if refusal to form mate guarding coalitions resulted in the breakdown of this system and mating became opportunistic. Copulation interference between coalition partners might have encouraged defection and also resulted in males resorting to opportunistic mating strategies instead (Watts, 1998).

Mutualism has also been cited as the most likely explanation for male cooperation in intercommunity aggression (Wilson *et al.*, 2001). Wilson *et al.* (2001) found that low-ranking males counter-called on hearing extracommunity pant-hoots, and approached the source of the sound, as often as high-ranking males. In other primate species, high-ranking males participate more actively than low-ranking males in intergroup contests (Schaller, 1963; Waser, 1976; Cheney & Seyfarth, 1977; Yamagiwa, 1985; Oi, 1990) and it has been suggested that this is because higher-ranking males have more to gain from defending group resources, of which they can secure the lion's share (Nunn, 2000). But male chimpanzees cannot defend their territory alone and must rely on mutual cooperation. Each male, irrespective of his rank, can expect to gain similar benefits from territorial defence despite differences in mating success (Wilson *et al.*, 2001).

Cooperative hunting in chimpanzees could also be explained by mutualism. Collaborative hunts have been reported at Taï (Boesch & Boesch, 1989; Boesch, 1994a,b; Boesch & Boesch-Achermann, 2000) and at Gombe (Busse, 1978; Teleki, 1973). Hunting success in the Taï chimpanzees increases with hunting group size

(Boesch & Boesch-Achermann, 2000) whereas at Gombe, high hunting efficiency is much higher for lone hunters than it is at Taï, and lone hunting is more common. Cooperative hunts at Taï result in meat being distributed to individuals that were not involved in the hunt although hunters each receive significantly more meat than bystanders do, and hunters receive meat proportional to the amount of effort they exert, or skill they employ (Boesch & Boesch-Achermann, 2000). That “these meat-sharing rules strongly restrict the possibility of cheating” (Boesch & Boesch-Achermann, 2000, p. 180) suggest that $R > T$ in this situation and again the conditions for mutualism are met, although Boesch & Boesch-Achermann (2000) do not explicitly state as much.

Taking all of these examples together, there exists a distinct possibility that mutualism might account for a range of persistent, cooperative relationships among males, provided that the results of studies of the influence of relatedness on the distribution of such relationships, are replicated in other populations. Affiliation patterns appear to be geared toward servicing these relationships in which females play almost no part. Males groom other males more than they groom females and grooming occurs in almost all male-male dyads (Goodall, 1968; Takahata, 1990; Nishida & Hosaka, 1996; Newton-Fisher, 1997; Boesch & Boesch-Achermann, 2000). Successful territory defence benefits from the participation of as many effective males as are available and is a constant requirement where communities are adjacent to one another. Assuming that a grooming network that includes all or most males promotes greater cohesiveness among this portion of any community, males should invest some of their grooming effort in all effective males, as all are allies in the face of extracommunity males (Wrangham, 1979; Nishida *et al.*, 1985; Goodall 1986; Manson & Wrangham, 1991). Strong associations among males,

which may result from greater compatibility in terms of travel velocity, and time budgets which allow more time for socialising than is the case for females, give ample opportunity to affiliate and strengthen male bonds. The ability of males to have differential affiliative relationships in terms of the time and effort spent servicing those relationships, and a closer convergence of interests among subsections of males, promotes the formation of smaller units which can potentially outcompete individual males or other units and result in greater reproductive success.

Against this background, the modest aim of this first data-chapter is to describe the social structure of the Sonso community of chimpanzees in order to estimate the extent to which it resembles, or diverges from, descriptions of other communities in terms of a number of basic parameters. From this starting point, the nature of the social relationships within the community can be assessed in the light of current theories concerning the distribution and quality of wild chimpanzee social relationships, with particular reference to males.

3.2 Methods

3.2.1 Data collection

Data were collected according to the procedures set out in Chapter 2. Data concerning agonistic behaviours and copulations were collected *ad libitum* due to their infrequent occurrence. All other data were collected using scan sampling methods. Definitions for terms used in this chapter are set out in Chapter 2.

3.2.2 Data analysis

I used de Vries' (1995) revised version of Appleby's (1983) test to ascertain whether or not the dominance hierarchy was linear. I assigned ranks to the males by following a method used by Fournier & Festa-Bianchet (1995) which has been used in previous studies at Budongo (Newton-Fisher, 1997; Fawcett, 2001), thereby producing directly comparable results. For agonistic dominance rank, a ratio of (wins + 1)/(losses + 1) yielded an 'agonism index'. For rank based on 'conferred respect' (after Newton-Fisher, 1997), a ratio of (pant-grunts received +1) / (pant-grunts given +1) yielded a 'respect index'. These values were transformed (natural logarithms of square roots) and summed to give cardinal ranks for each individual. Ordinal ranks were derived from the cardinal ranks. Rank distance was defined as the number of individuals ranking between a dyad, plus one.

A second method of determining agonistic rank based on the proportion of individuals dominated was also used. Dominance value (DV) is the square root, arcsine transformation of this proportion: $DV = \text{arcsine}(\sqrt{x})$ (Fournier & Festa-Bianchet, 1995).

Indices of association were calculated for each dyad using a 'twice weight' method (Cairns & Schwager, 1987), which is the least biased index where there is a sampling bias in favour of finding individuals together, as in the case of wild chimpanzees.

$$I_{AB} = S_{AB}/(S_A + S_B - S_{AB})$$

Where S_{AB} is the number of scans in which individuals A and B are both present, S_A is the total number of scans in which individual A is present, and S_B is the total number of scans in which individual B is present. These values were converted into

measures of dyadic association strength; a relative measure of association that indicates deviation from the mean level of association in all dyads including adult, adolescent and juvenile subjects.

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

Where I_{AB} is the dyadic association index, I is the mean association index across all subjects, and s is the standard deviation of the sample.

Cluster analysis of the association strength matrix, calculated over the entire 13 month period, was carried out to achieve a graphic representation of the association relationships between individuals. This employed the ‘unweighted pair group’ method using arithmetic averages’ (UPGMA) or ‘average linkage’ method also used by Newton-Fisher (1997) for comparative purposes.

For analyses of party size, I included in the data set only those records which represented a change in party composition, i.e. where one or more individuals either joined or left a party between consecutive 15 minute scan samples, or when a new party was encountered. This method of measuring party size is similar to that used in other studies of wild chimpanzees (White & Burgman, 1990; Boesch, 1991; Chapman *et al.*, 1994). The addition of a minimum time interval between successive counts to this method should further decrease the dependence between successive records (Newton-Fisher, 1997).

For comparisons of time budgets, individuals were classified as engaged in one of seven behavioural categories: ‘self-grooming’ (grooming own body), ‘grooming’ (allogrooming another individual), ‘groomed’ (other individual allogrooms self), ‘mutual grooming’ (allogrooms, and is allogroomed by the same individual at the same time), ‘forage’ (feeding and moving to alternative feeding

locations in close proximity to the original), ‘rest’ (sitting, standing, or lying still while not engaged in any other activity) and ‘other’ (any other activity not falling into one of the above categories).

Frequencies and durations of interactions were estimated from scan samples and corrected for observation time using the ‘dyad-correction’ method. The sum of each dyadic interaction was divided by the number of samples for each dyad. These corrected figures were multiplied by an integer which represented the number of scan samples collected which concerned the most common dyad (DN-MA = 556). The resulting scores, thus became effectively the predicted values for frequencies of interaction if each dyad was sampled as many times as the most frequent dyad. Data concerning frequencies of agonistic interactions, copulations, grooming durations and the amount of time spent in proximity were corrected in this way.

3.3 Results

3.3.1 Dominance

A total of 189 aggressive interactions were observed between 135 specific dyads (16.5% of all possible dyads, Table 3.1). Of these, 102 aggressive interactions occurred between males, and these involved 57 specific male-male dyads (47.5% of all possible dyads). The small number of female-female conflicts together with a low incidence of submissive behaviours performed by females precluded the construction of a dominance hierarchy for the whole community and so analyses of agonistic data are restricted to male-male interactions. Submissive

behaviours were observed 220 times in 60 male-male dyads (50% of all possible dyads). The frequency of male-male submissive behaviours is given in Table 3.2.

A hierarchy was constructed by combining the dyad-corrected rates of aggressive and submissive behaviours (Table 3.3 and Table 4.3) after checking that the dominance hierarchy was linear. De Vries' (1995) revised version of Appleby's (1983) procedure which compares the number of circular triads, given random dominance relationships, revealed a significantly non-random dominance hierarchy among the males ($\chi^2 = 73.7$, $df = 23$, $p < 0.001$) although this hierarchy was not particularly linear ($h' = 0.74$, $p < 0.04$). On this basis, a male hierarchy was constructed.

Ordinal rankings resulting from the derived indices relating to agonistic interactions and conferred respect were highly significantly correlated (Spearman rank-order correlation coefficient: $r_s = 0.897$, $N = 16$, $p < 0.001$. Figure 3.1). I therefore combined these indices to give an overall status score, which was then used to assign an overall ordinal rank to each male.

Ordinal rankings based on overall status scores for each individual, together with agonistic and respect indices, individual dominance values and the number of dominants and subordinates as indicated by the number of individuals towards whom pant-grunts are directed are given in Table 3.5.

The use of ordinal ranks, while providing a useful and simple way of describing relative status, results in the loss of information regarding the magnitude of relative differences in rank. Cardinal ranks, however, preserve such information and permit the use of parametric statistical tests (Boyd & Silk, 1983) after the data (in this case, the dyad-corrected frequencies of interactions) has been normalised by an appropriate transformation. Following Newton-Fisher (1997) I performed a

Table 3.1 Matrix of aggressive interactions. Individuals in rows are aggressive toward those in columns and numbers indicate the number of displacements and one-way threats, displays, chases and aggression involving body contact. Female = independent females. Other = dependent individuals.

	DN	BK	JM	BY	MG	MA	VN	ZF	ZT	MU	NJ	TK	AY	BB	NK	GS	female	other	Total
DN		4	1		1	2		2		3	1	1	1	2			10	1	29
BK	1			2	1	4	3			1	2	1	2	5	2	3	3	1	31
JM								1					1		1		2	1	6
BY		1				1		1		1	1	1		1	1	2	4		14
MG										1				1	1	1	1		5
MA		1		2				1			1		2	2	1		3	2	15
VN		1				1				1				1			1	2	7
ZF													2	2	1	7	2	14	
ZT																		0	
MU				1							1	1		1	1		2	2	9
NJ														2	1	1		4	
TK														2		6	1	9	
AY								1							1	4	3	9	
BB	1														0	1	1		
NK														1	4	2	7		
GS																		0	
female		1					2			6		2		1	14	6	32		
Total	1	8	1	5	2	8	3	8	0	7	6	10	6	17	13	11	62	24	189

Table 3.2 Matrix of submissive behaviours. Individuals in rows are submissive to those in columns and numbers indicate the number of pant-grunts, pant-screams, crouches and head-bobs.

	DN	VN	BK	JM	MA	BY	ZT	NJ	MG	MU	AY	ZF	TK	BB	GS	NK	Total
DN																	0
VN	2		1														3
BK	5	1				1						1					8
JM	3		1														4
MA	10						2										12
BY	6		2		1						1						10
ZT	1																1
NJ	7	1															8
MG	6		4														10
MU	29		2		2												33
AY	27	4	2		1		1				1						36
ZF	11	1	3	1	2												18
TK	8		2	1	2												13
BB	10	3	4		1	2		1		1	2	1					25
GS	10		2	1				1				1	1	1			18
NK	9	1	4	2							4	1					21
Total	144	11	4	5	10	4	1	2	4	6	3	1	1	1	0	0	220

Table 3.3 Matrix of dyad corrected frequencies of aggressive interactions.

	DN	BK	JM	BY	MG	MA	VN	ZF	ZT	MU	NJ	TK	AY	BB	NK	GS	Total	
DN		5.57	1.49		2.27	2.00		3.89		4.74	1.24	2.52	1.28	5.32			30.32	
BK	1.39				3.23	2.22	4.39	5.70		1.78	3.20	2.41	2.44	9.96	3.97	4.91	45.60	
JM								2.09					1.77		2.55		6.41	
BY		1.62					1.39		2.38		2.17	1.69	2.55		2.94	2.44	4.26	21.44
MG											2.25				1.82	3.80	1.32	9.19
MA		2.19			2.79				1.32			1.19		2.04	3.68	1.87		15.08
VN		1.90					1.50				2.20				2.89			8.49
ZF														4.92	5.40	2.11		12.43
ZT																	0.00	
MU				2.17							2.27	3.09		2.34	2.87			12.74
NJ															4.69	1.57		6.26
TK															5.88			5.88
AY								1.41								1.37		2.78
BB																	0.00	
NK																2.60		2.60
GS																	0.00	
Total	1.39	11.28	1.49	8.19	4.49	9.28	5.70	11.09	0.00	13.14	9.59	10.57	7.53	33.87	33.47	18.14	179.22	

Table 3.4 Matrix of dyad corrected frequencies of submissive interactions.

	DN	VN	BK	JM	MA	BY	ZT	NJ	MG	MU	AY	ZF	TK	BB	GS	NK	Total
DN																	0.00
VN	2.38		1.9														4.28
BK	6.97	1.9				1.1					2.22						12.19
JM	4.47		1.81														6.28
MA	10				2.79												12.79
BY	7.33		3.23		1.39					2.07							14.02
ZT	2.7																2.70
NJ	8.64	1.65															10.29
MG	13.6		8.87														22.47
MU	45.8		3.55		2.84												52.20
AY	35.5	6.09	2.48		1.04		1.17			1.68							47.97
ZF	21.4	2.89	5.45	2.09	2.64												34.45
TK	20.1		4.81	3.45	4.2												32.59
BB	26.6	8.66	7.97		1.84	5.88		2.32	1.82	4.67	1.66						61.42
GS	19.6		3.27	2.54				1.57			1.37	2.11	1.88	1.53			33.85
NK	19.7	2.71	7.94	5.1						11.5	2.04						48.95
Total	244.8	23.90	51.28	13.18	15.05	8.67	1.17	3.89	7.79	16.13	5.07	2.11	1.88	1.53	0.00	0.00	396.45

Table 3.5 Overall ordinal and cardinal ranks based on combined status scores, together with dominance values and the number of dominants and subordinates as indicated by pant-grunts given and received, for each of the 16 focal males of the Sonso community.

ID	Status score	Rank		Index		DV	Number of	
		Ordinal	Cardinal	Agonism	Respect		superiors	subordinates
DN	252.2	1	2.78	6.20	246.00	1.57	0	15
BK	7.75	2	1.02	3.79	3.96	1.02	4	11
VN	6.14	3	0.91	1.42	4.72	0.68	2	6
JM	4.92	4	0.80	2.97	1.95	0.55	2	4
BY	3.08	5	0.56	2.44	0.64	0.37	4	2
MA	2.74	6	0.50	1.57	1.17	0.76	2	7
MG	2.23	7	0.40	1.86	0.37	0.55	2	4
ZT	1.59	8	0.23	1.00	0.59	0.26	1	1
MU	1.29	9	0.13	0.97	0.32	0.37	3	2
ZF	1.20	10	0.09	1.11	0.09	0.25	5	1
NJ	1.12	11	0.06	0.69	0.43	0.37	2	2
TK	0.68	12	-0.19	0.59	0.09	0.26	4	1
AY	0.56	13	-0.29	0.44	0.12	0.47	6	3
BB	0.17	14	-1.06	0.10	0.04	0.26	9	0
NK	0.12	15	-1.06	0.10	0.02	0.00	6	1
GS	0.05	16	-1.50	0.02	0.03	0.00	8	0

Figure 3.1 The relationship between ordinal rankings of agonistic dominance and conferred respect (pant-grunts). Low numbers indicate high ranks. Letters indicate individual IDs.

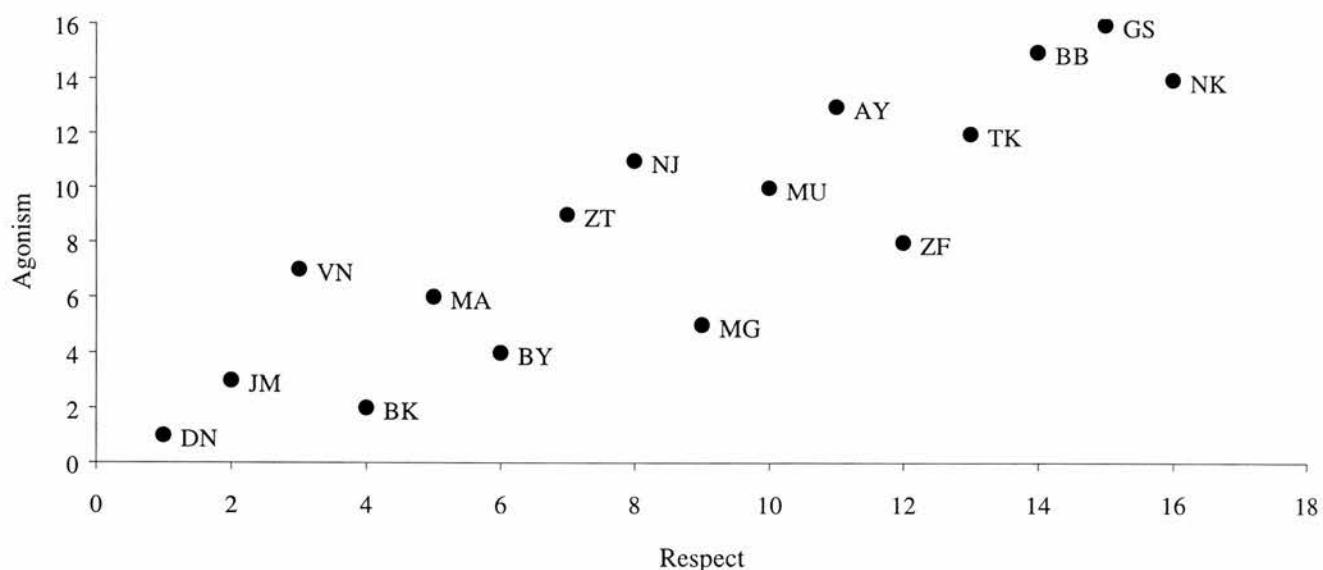
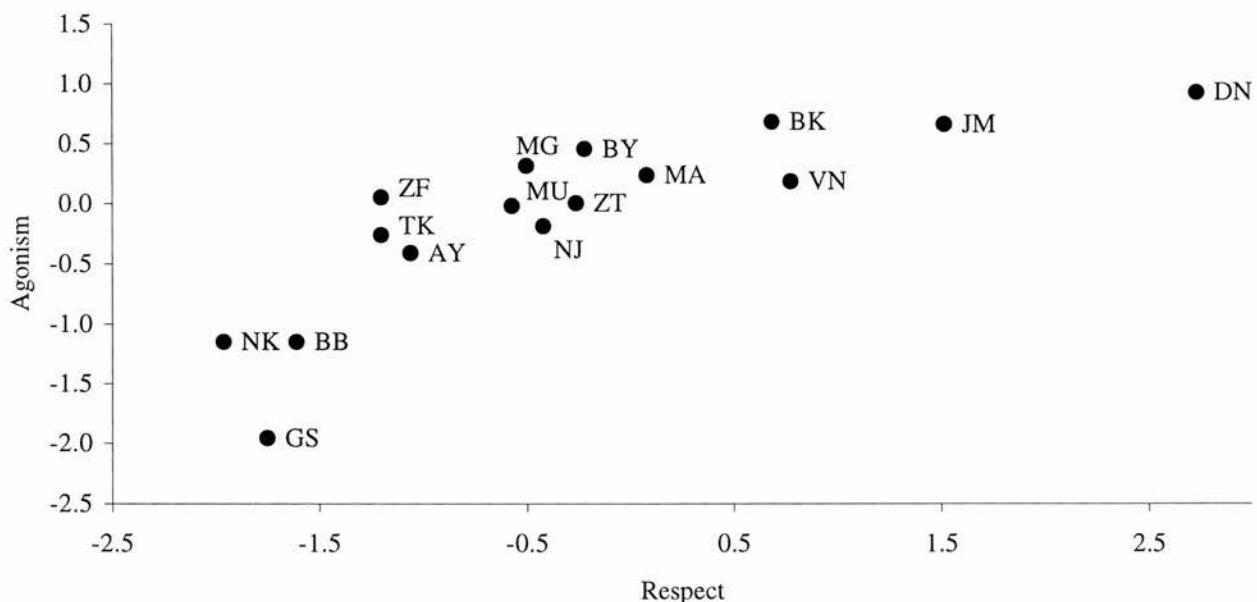


Figure 3.2 The relationship between cardinal rankings of agonistic dominance and received respect (pant-grunts). Low numbers indicate low ranks.



double transformation (natural logarithms of square roots) to give cardinal ranks, then repeated the correlation of agonistic dominance and conferred respect. The correlation remained highly significant (Pearsons: $r = 0.833$, $N = 16$, $p < 0.001$. Figure 3.2). This treatment of the data showed that the alpha position, occupied by DN, was unambiguous while the rank differences among the remaining males was fairly evenly spaced with the exception of a larger rank difference between this group and the youngest adolescent males, NK and BB, together with the independent juvenile GS. I then plotted the cumulative difference in cardinal rank between each male and the male ranked immediately above in order to determine the extent to which relative rankings were clustered (Bygott, 1979: Figure 3.3) and this pattern was confirmed. The greatest differences in cardinal ranks were between the alpha and beta males (difference = $1.76 > 3$ S.D.s from mean difference in cardinal ranks between adjacently ranked males). The second greatest difference in

Figure 3.3 Cumulative differences in cardinal status scores.

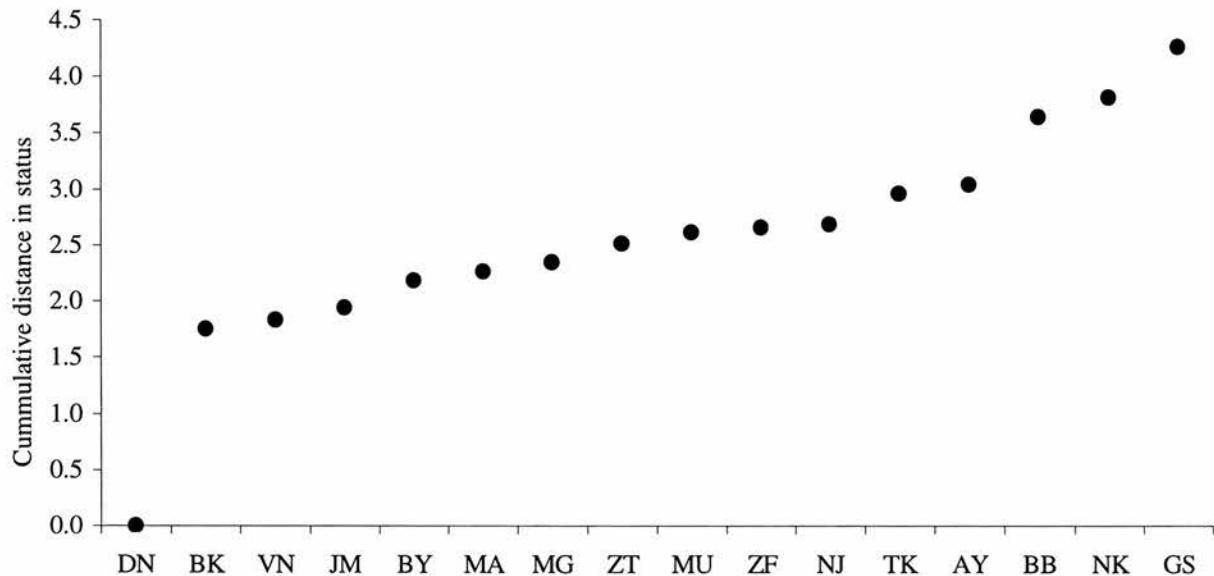


Figure 3.4 The relationship between cardinal rank and dominance value. High numbers indicate high ranks.

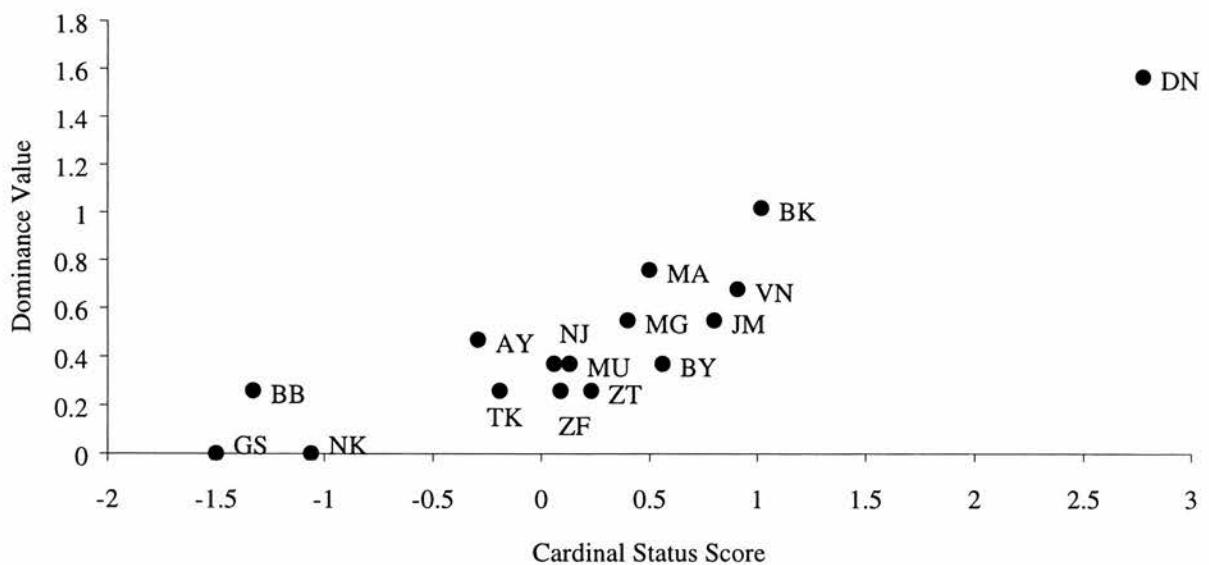


Figure 3.5 The relationship between dyad corrected frequencies of aggressive acts performed and submissive behaviours received.

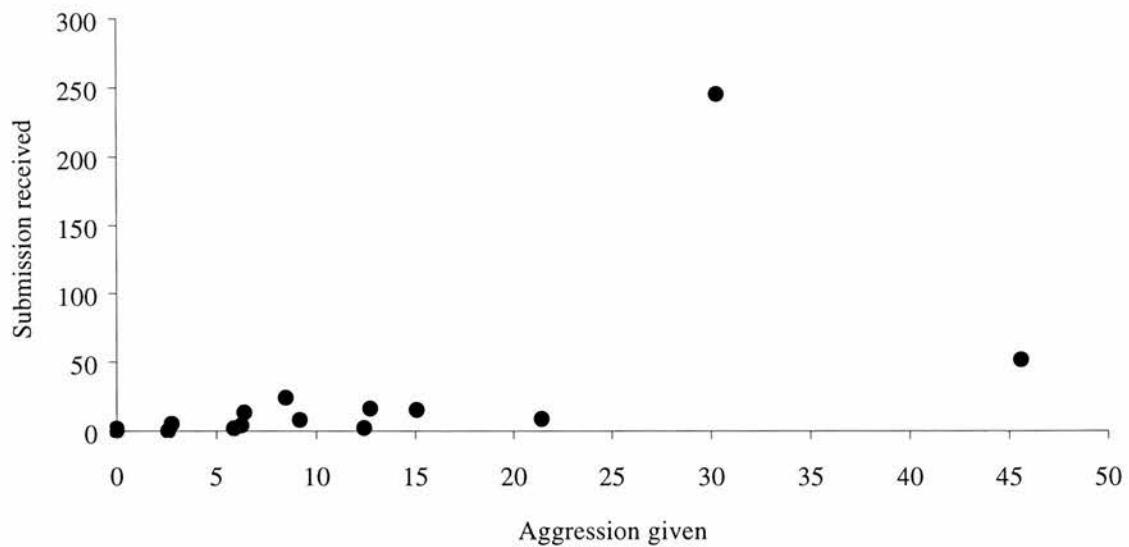


Table 3.6 The relationship between ordinal and cardinal ranks, and status level.

	Ordinal rank	Cardinal rank	Status level	Status description
DN	1	2.78	6	alpha status
BK	2	1.02	5	beta status
VN	3	0.91	4	Mid status (high)
JM	4	0.80	4	Mid status (high)
BY	5	0.56	4	Mid status (high)
MA	6	0.50	4	Mid status (high)
MG	7	0.40	3	Mid status (mid)
ZT	8	0.23	3	Mid status (mid)
MU	9	0.13	3	Mid status (mid)
ZF	10	0.09	3	Mid status (mid)
NJ	11	0.06	3	Mid status (mid)
TK	12	-0.19	3	Mid status (low)
AY	13	-0.29	3	Mid status (low)
BB	14	-0.89	2	Low status
NK	15	-1.06	2	Low status
GS	16	-1.50	1	Very low status

cardinal ranks was between the lowest ranking older adolescent male, AY, and the highest ranking younger adolescent male, BB (difference = $0.6 > 1$ S.D. from mean) although this second grouping was not so clear. Dominance value and cardinal rank were also highly correlated ($r = 0.893$, $N = 16$, $p < 0.001$) and a plot of this relationship (Figure 3.4) revealed another high status group containing VN, MA, JM, MG; it also showed that BK's position as beta male was also clear over the study period as a whole. Lastly, males which were often aggressive also received submissive signals relatively often ($r_s = 0.85$, $N = 16$, $p < 0.01$. Figure 3.5).

Again following Newton-Fisher (1997), I scaled the cardinal ranks from Table 3.5 by rounding cardinal ranks to 1 significant figure and allotting a status level to each individual such that individuals within the same numerical level have the same cardinal rank (Table 3.6). The lowest ranked individual was allotted a status level of '1' and the highest, '6'. Status levels are described as 'alpha', 'beta', 'mid', 'low' and 'very low', with the category 'Mid' further subdivided to reflect the possible distinction between VN, JM, BY and MA and the other males within the 'mid' category. I do not claim that these are natural categories insofar as they are recognisable by the chimpanzees themselves, but rather that they might be more useful than linear, ordinal rankings for describing patterns of behaviour involving different types of male chimpanzee, with respect to dominance (*sensu* Bygott, 1974).

3.3.1.1 Changes over time

During the course of the study no major upheavals in the male dominance hierarchy were apparent. The analyses of dominance status presented above reflect a reasonably good reflection of relative male status. However, certain analyses

Figure 3.6 Plots of cumulative cardinal status scores for each quarter of the study period.

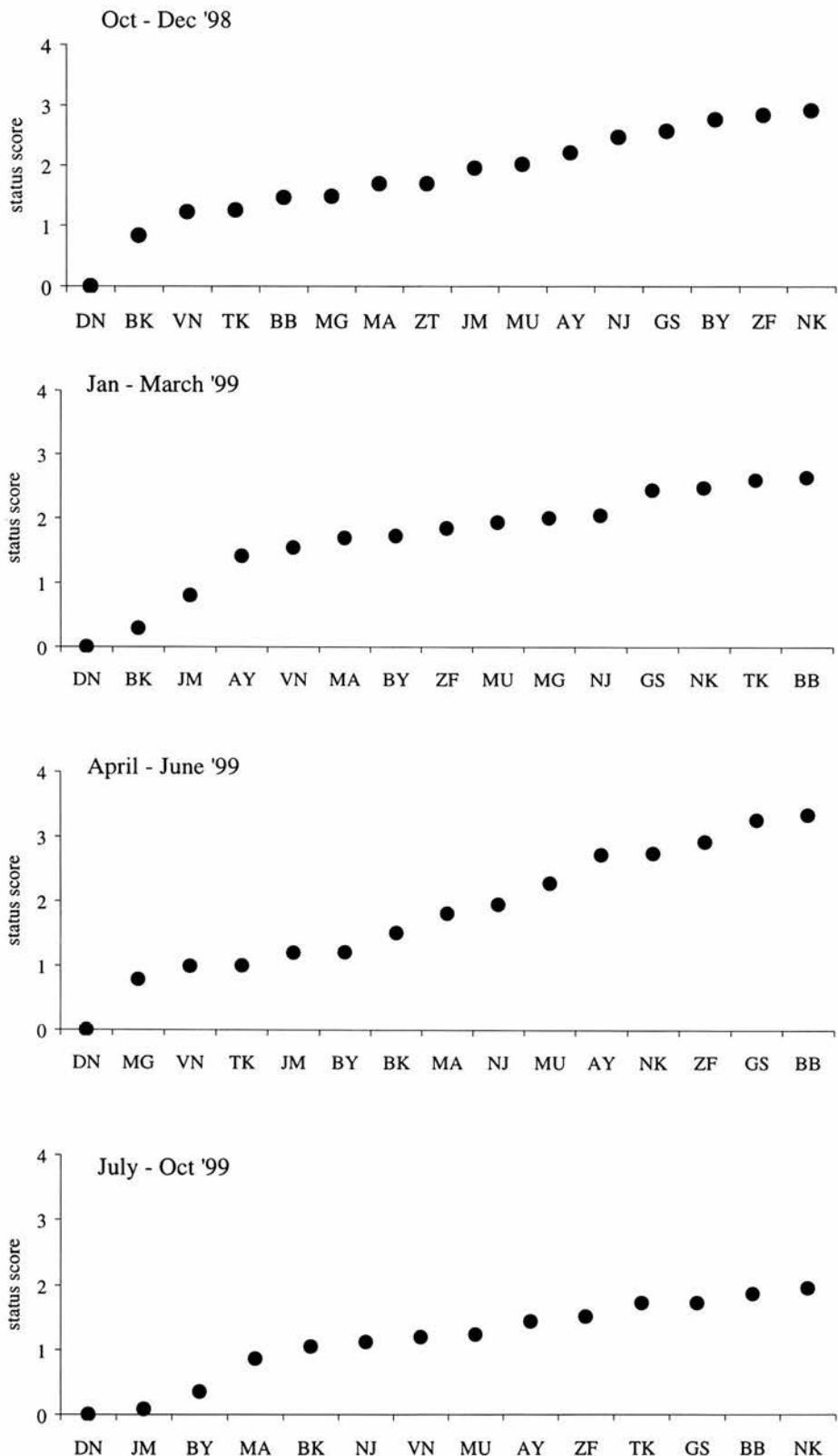


Figure 3.7 The number and frequency of agonistic behaviours during the four quarters of the study period.

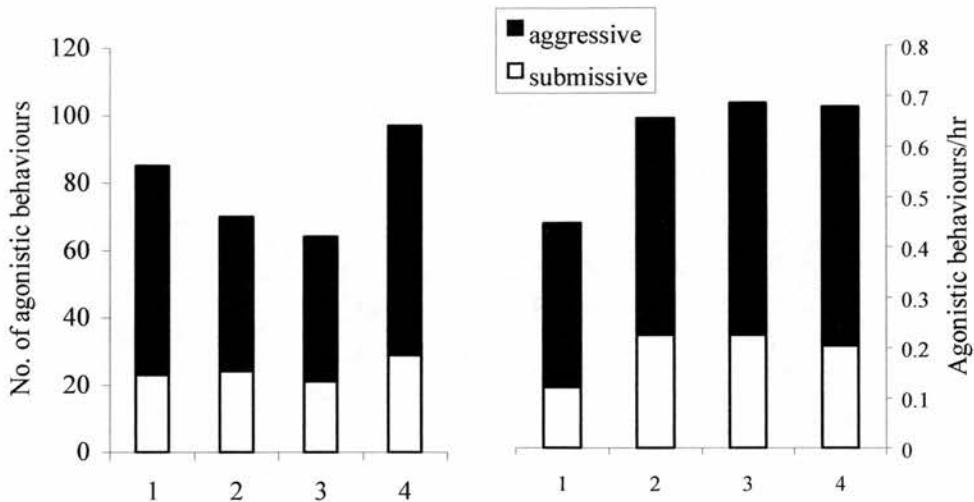
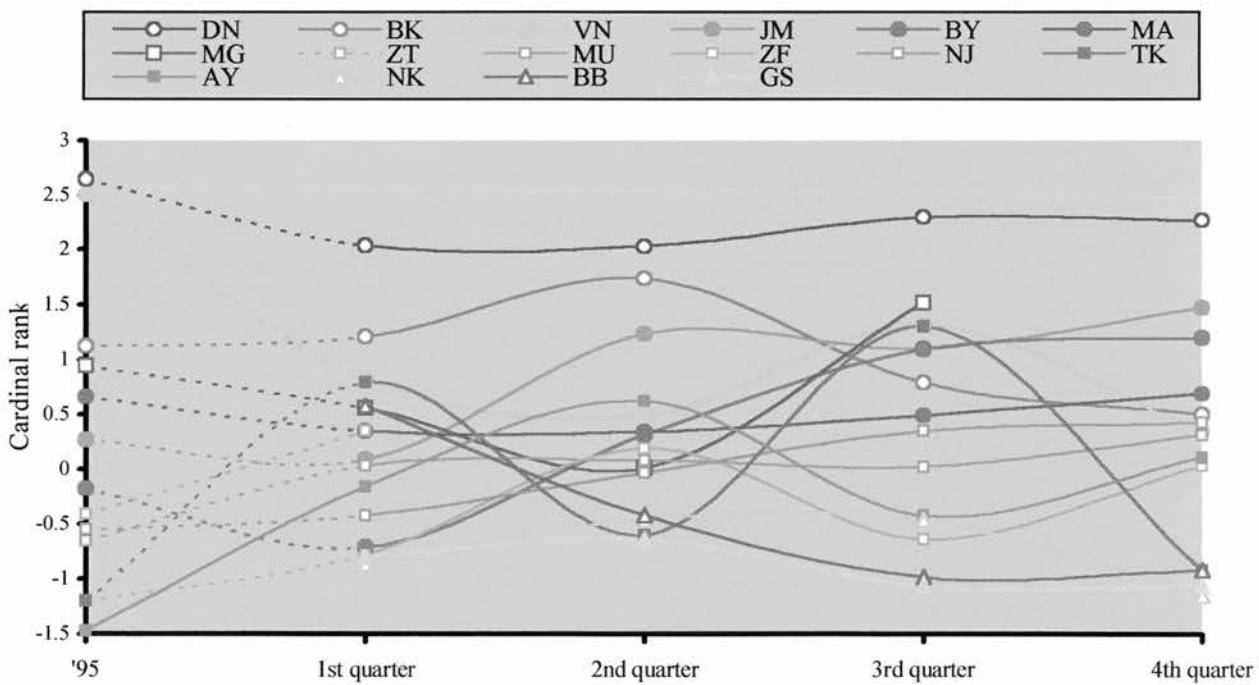


Figure 3.8 Smoothed plot of individual cardinal ranks over time. Overall status levels are indicated by the following symbols: open circles = alpha and beta; closed circles = mid (high); open squares = mid (mid); closed squares = mid (low); open triangles = low status; closed triangle = very low status. Data points joined by dashed lines indicate overall cardinal status during 1995 and are taken from Newton-Fisher (1997).



relating to rank presented throughout the thesis require a more accurate representation of the prevailing dominance relations. For this reason, together with a more general interest in the dynamics of male social relationships throughout the study, I have presented data concerning relative status changes over time.

Data on dominance interactions were analysed separately in four blocks of approximately three months duration. Figure 3.6 shows the relative distance between cardinal ranks over the four quarters of the study period. During each quarter the relative distances between cardinal ranks were fairly even: the largest differences lying between the three highest ranking males and the remaining males during the second quarter, and the alpha male and the remaining males during the first and third quarters. During the fourth quarter, the males were relatively undifferentiated. The number of dominance interactions observed varied between quarters due to variation in time spent in contact with the chimpanzees, and were particularly low during the second and third quarters, although their frequency was comparable across all quarters (Figure 3.7). The low frequency of dominance interactions resulted in a rather non- intuitive rank order in some cases and, to this extent, quarterly data should be interpreted with caution. Figure 3.8 represents changes in cardinal rank of the 16 focal males during the period October 1998-October 1999 and includes their overall cardinal rank during the period of 1994-1995 (given in Newton-Fisher, 1997). In 1995 DN rose dramatically in status and became the alpha male due, in part to an alliance with VN (Newton-Fisher, 1997). DN had retained his position and was still the alpha male by a large margin throughout this study (see Figure 3.3). This margin was reduced in the second quarter of the study. Evidence that this can be interpreted as a concerted effort by BK to increase his status as beta male is as follows. First, BK's aggressive

encounters were primarily directed toward DN's ally VN, who fell in status during that period. Secondly, BK was observed, on a number of occasions, to join parties that contained VN but not DN, and then immediately attack VN. Under these circumstances, VN was the loser of such conflicts. If, however, BK attempted to harass VN when DN was present, DN always supported VN and chased BK away. During the second half of the study period BK fell dramatically in status after this failed attempt to challenge DN by these apparent indirect means. VN also fell in status during the last quarter and finally disappeared toward the end of the study: he never returned (Vernon Reynolds, pers. comm.).

Also of interest was the rapid increase in status of MG, who had occupied the alpha position prior to DN's takeover. He remained as a mid status male until the third quarter when he appeared to rise dramatically in rank due, primarily, to an increase in the number of submissive behaviours which were directed towards him by others. During this third quarter he seemed much weaker than he had done previously and eventually died, possibly due to old age.

JM, who had been rather elusive during the first quarter of the study, rose gradually in rank and finally occupied the beta role once he had become better established within the group. BY also rose in status throughout the same period to occupy the gamma position.

TKs position appeared to fluctuate dramatically, but this is entirely due to an increase in the frequency of agonistic interactions directed at adolescent males during the third quarter, together with low rates of aggression received. His high rank at this time is unlikely to be representative of the true position within the male hierarchy which was generally low. Similarly, BB's position is perhaps artificially high for similar reasons in the first quarter. The relative ranks of the remaining

Figure 3.9 A comparison of mean party size by month of the Sonso chimpanzees for two periods of study. '98 – '99 data refers to this study; '94 – '95 refers to data taken from Newton-Fisher (1997).

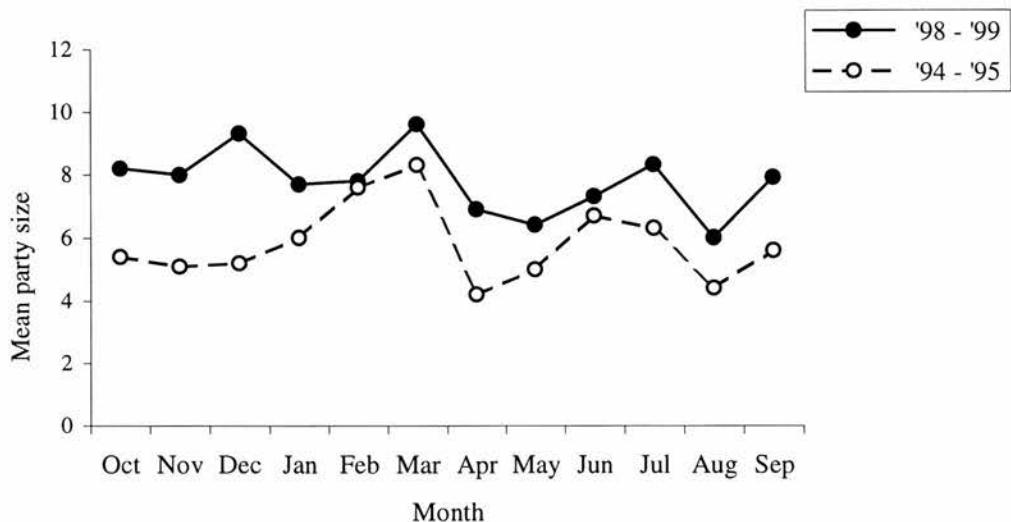


Table 3.7 Party structure by age/sex class.

Class	Mean	Median	Mode	Range
Adult male	3.2	3	1	0-11
Adult female	1.2	1	0	0-9
Adolescent male	1.3	1	1	0-4
Adolescent female	0.8	1	0	0-4
Juvenile male	0.8	1	0	0-4
Juvenile female	0.5	0	0	0-3

Figure 3.10 Party size (closed circles) and the proportion of males in parties (open circles).

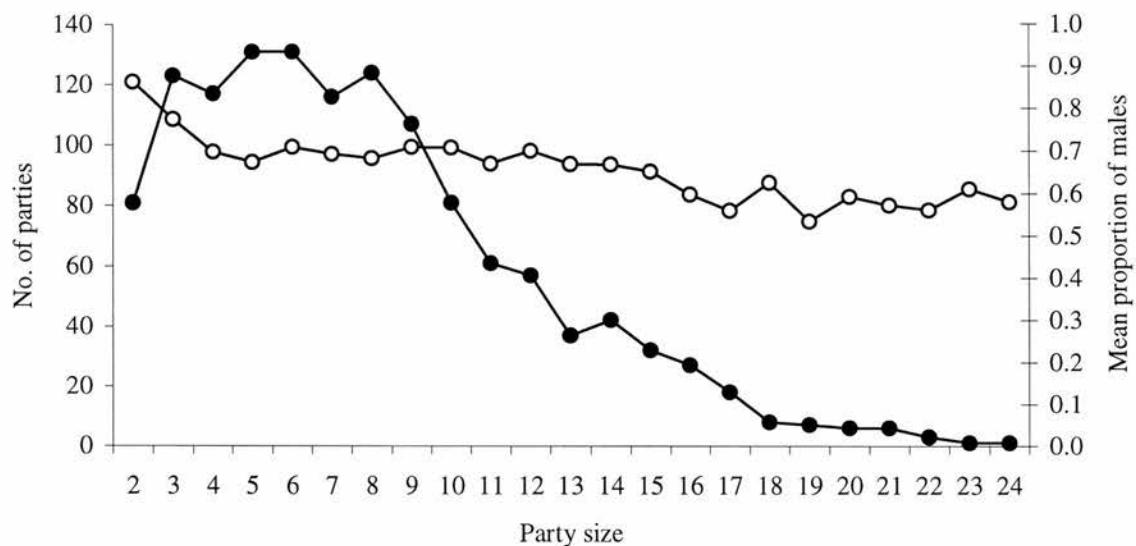
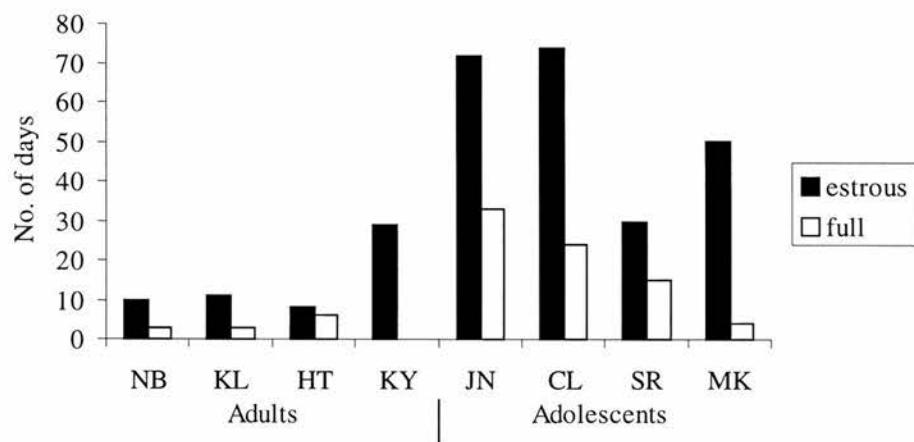


Figure 3.11 The number of days on which females were observed to show oestrus swellings and the number days that these swellings were maximally tumescent.



males were fairly stable throughout.

3.3.2 Party size and composition

The mean party size (excluding infants) for all party types was 7.8 ± 4.2 ($N = 1317$, median = 7, mode = 6, range = 1 – 24). This number was at the upper end of the range of party sizes reported for other study sites (see Chapman *et al.*, 1994, p. 53; Boesch & Boesch-Achermann, 2000, p. 93) and higher than that previously reported at Budongo (3.9, $N = 215$, Reynolds & Reynolds, 1965; 4.4, $N = 514$, Sugiyama, 1968; Sonso community, 5.7, $N = 5171$, Newton-Fisher, 1997). Figure 3.9 shows the monthly variation in mean party sizes during this study and during Newton-Fisher's (1997) study for comparison. Despite larger mean party sizes for every month in this study, the pattern of variation is very similar for both study periods. The modal party size during this study of 6 was much larger than the modal party size of 2 during Newton-Fisher's study. However, when Newton-Fisher considered only parties that included at least one adult or adolescent male, mean and modal party sizes increased to 5.9 and 4 respectively. These figures provide a better comparison, as this study did not include data on party membership when parties did not include focal males. It should be expected that communities containing a large number of individuals should also form relatively large parties (Boesch & Boesch-Achermann, 2000). The relative mean party size, given as,

$$\text{(mean party size / community size)} \times 100,$$

for the Sonso chimpanzees was 15.6 which falls in the middle of the range given for other study sites (Bossou, Gombe, Kibale, Mahale, Tai: Boesch & Boesch-

Achermann, 2000, p. 93). This figure is similar to relative mean party sizes calculable from data previously collected at Budongo (12: Reynolds, in press; 15: Newton-Fisher, 1997).

Table 3.7 gives the mean, median and modal number of adult, adolescent and juvenile males and females occurring in parties. Sonso parties were dominated by males like those of the Kanyawara community, Kibale, Uganda, (Chapman *et al.*, 1994) in which sex ratios were similar (Budongo: 0.71-0.56; Kanyawara: 0.66) although this proportion may have been inflated by this study's bias in favour of finding parties containing males. Parties of between 3 and 9 individuals were most frequently encountered and smaller parties were more common than large parties (Wilcoxon-Mann-Whitney test: $z = 3.86$, $p < 0.001$. Figure 3.10). The proportion of males in parties remained fairly constant across party sizes (Kolmogorov-Smirnov one-sample test: $D = 0.045$, $N = 23$, NS).

Only 29.6% of parties contained one or more oestrus females. Of the 16 resident adult and adolescent females, 8 were observed to come into oestrus. One of these, KY, was never observed to reach full oestrus and was pregnant. She ceased cycling after the birth of her infant. Figure 3.11 shows the number of days on which each cycling female displayed oestrus swellings and the number of days during which those swelling were maximally tumescent. The four adult females that were cycling did so only irregularly. All adult females had infants and three were just beginning to resume cycling after the period of infant dependency. MK was a young adolescent that only rarely displayed maximal tumescence. JN and CL were older adolescents and were regularly observed in mixed-sex parties. SR, who was also an older adolescent, was less gregarious. Figure 3.12 shows the number of parties that contained between 0 and 3 females in oestrus.

Figure 3.12 The percentage of parties containing males and cycling females.

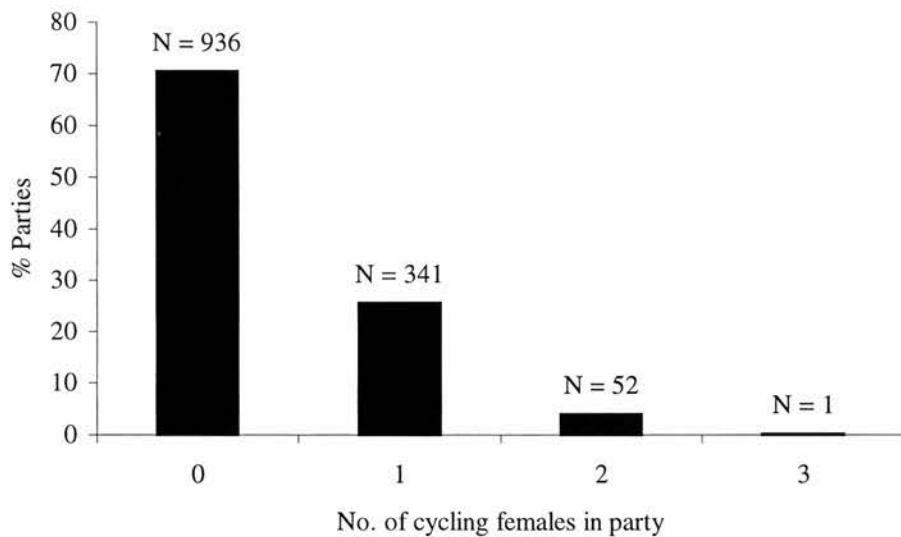


Figure 3.13 The effect of the number of cycling females present in parties on (a) median party size, and (b) number of males present (including interquartile ranges).

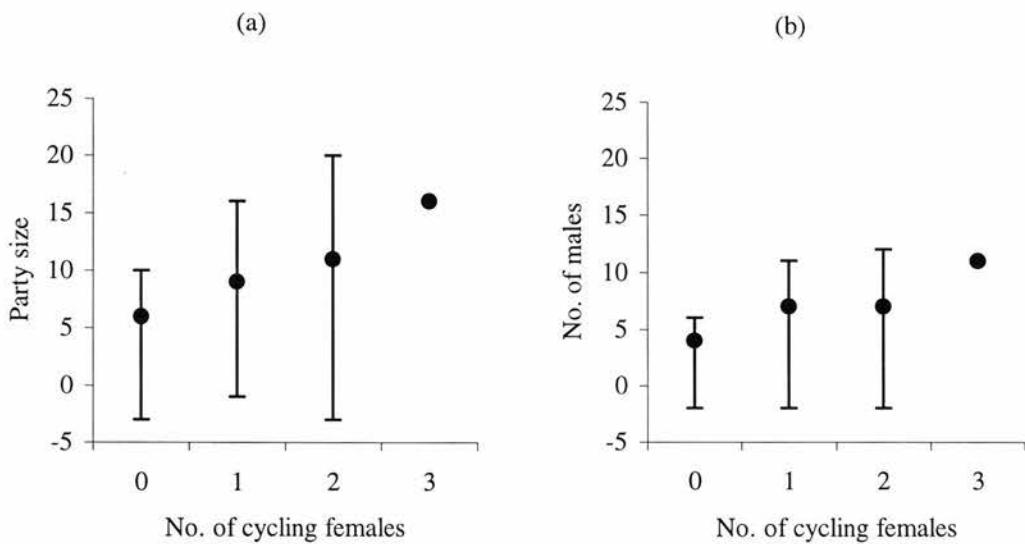


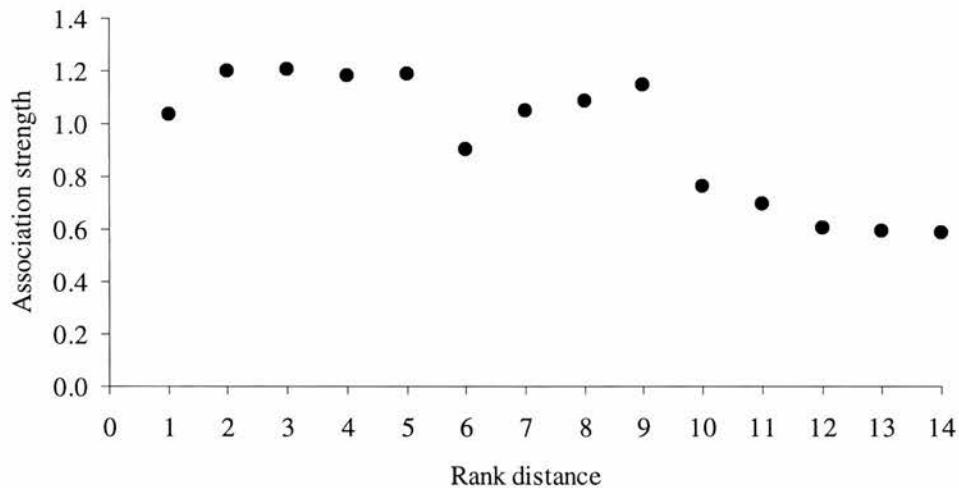
Table 3.8 Mean dyadic association strength among male and female dyads*.

Class	N	Mean	Median	S.D.	Max	Min
M-M	105	0.24	0.23	0.07	0.48	0.13
M-F	255	0.11	0.10	0.07	0.29	0.00
F-F	136	0.09	0.08	0.07	0.43	0.00

M = male; F = female; * only independent individuals are included.

Cycling females were absent in 70.4% of all parties; one cycling female was present in 25.6% of all parties; two cycling females were present in 3.9% of all parties; three cycling females were present in 0.1% of all parties. The size of parties differed according to the number of cycling females (Kruskal-Wallis one-way ANOVA: $H = 302.2$, $df = 3$, $p < 0.001$. Figure. 3.13a). Dunn's *post hoc* multiple comparisons test (Siegal & Castellan, 1988, p. 213) showed that parties containing two cycling females were significantly larger than parties containing one cycling female, which were in turn, significantly larger than parties containing no cycling females. A similar analysis revealed that the presence of cycling females influenced the number of males in parties (Kruskal-Wallis one-way ANOVA: $H = 467.7$, $df = 3$, $p < 0.001$. Figure. 3.13b). In this case the Dunn's post hoc multiple comparisons test revealed that the number of males in parties was significantly greater when there were one or two cycling females in a party compared with parties containing no cycling females. There was no difference in the number of males present when parties contained one female compared to parties containing two or three cycling females. In short, the number of males in parties was greater when cycling females were present, irrespective of the number of cycling females that were present.

Figure 3.14 The effect of rank distance on dyadic association strength.



3.3.3 Association patterns

Using the dyadic association index (DAI) as a relative measure of the degree to which pairs of individuals associated with one another in parties, association was strongest among male-male dyads and weakest among female-female dyads (Table, 3.8). All males had higher mean DAI's with other males than they did with females (Wilcoxon signed ranks test: $T^+ = 120$, $N = 120$, $p < 0.0001$). Mean DAI's were not significantly different for females' association with other females compared with females' association with males ($z = 0.44$, $N = 17$, NS). High-ranking males did not have stronger dyadic associations, on average, than lower-ranked males. Male rank was not correlated with either male-male, or male-female, mean DAI's (Spearman rank-order correlation: male-male, $r_s = 0.50$, $N = 15$, NS; male-female, $r_s = 0.22$, $N = 17$, NS). Rank distance did have an effect on dyadic association strengths among

Figure 3.15 Dendrogram showing the results of a cluster analysis of dyadic association indices (males are shown in bold type; adolescents and juveniles are shown in lower case; only independent individuals are included).

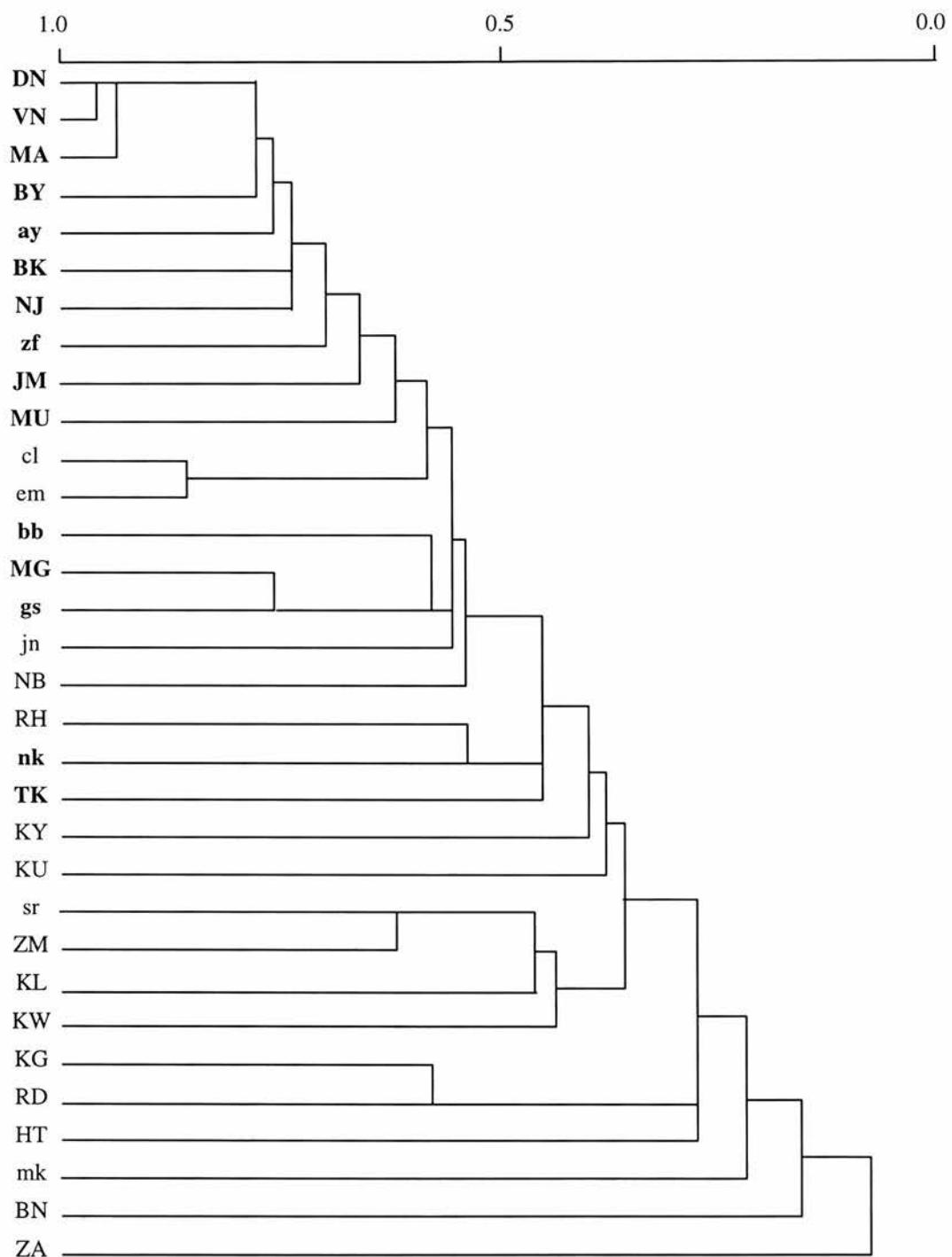
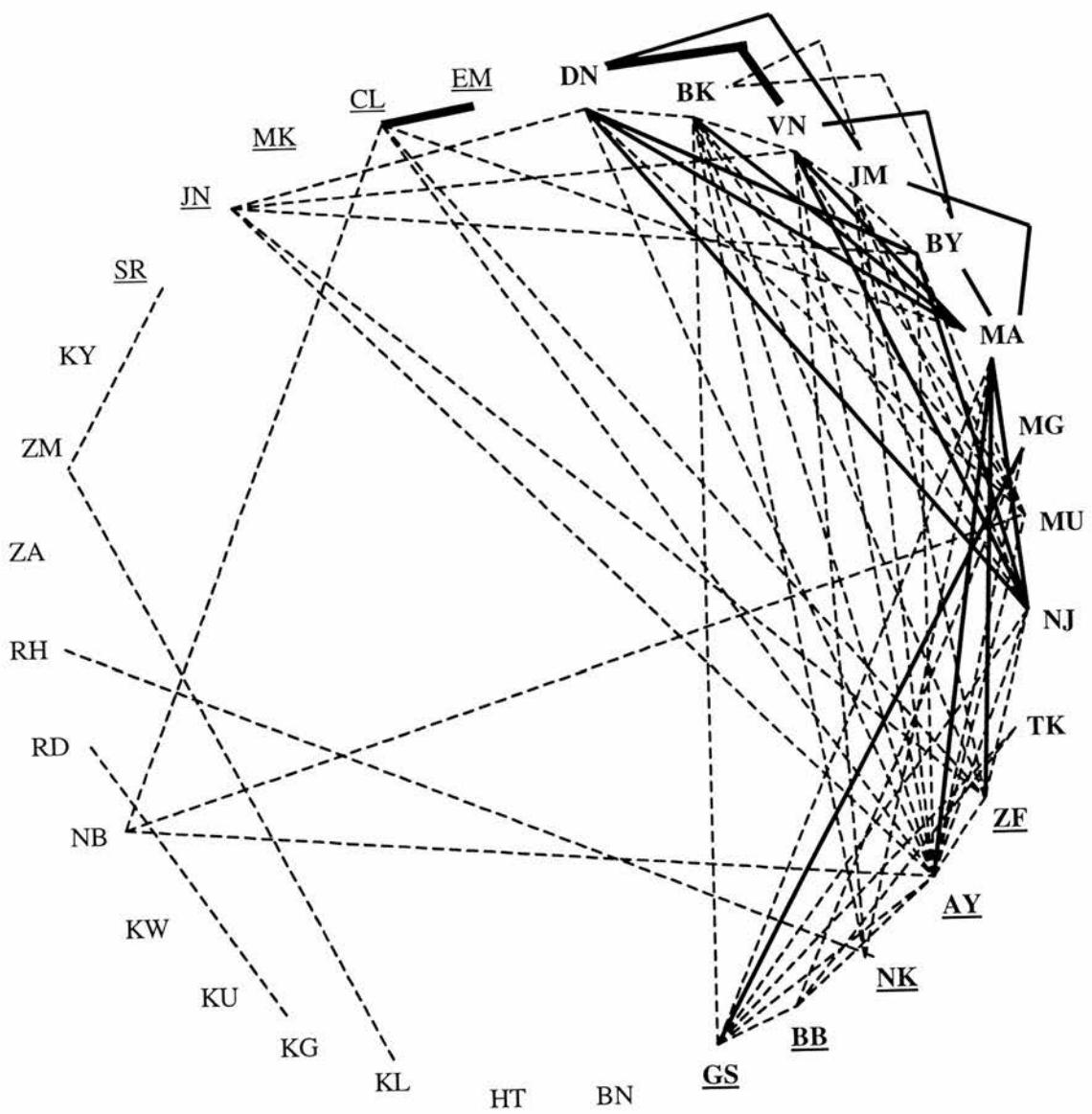


Figure 3.16 Sociogram of association among independent males and females. Males are denoted by bold type in bold, adolescents are underlined: — indicates > 3sd above mean DAI; — : indicates > 2sd above mean DAI; ----- indicates > 1sd above mean DAI.



the males. Closely ranked males associated more often than more distantly ranked males although this result was only marginally significant when only adult males were considered (all males: $r_s = 0.81$, N = 14, p = 0.001; adult males: $r_s = 0.57$, N = 10, p < 0.1. Figure 3.14). Rank distance did not affect association strengths among adult males or between adult males and subadult focal males (adult-adult: $r_s = 0.42$, N = 10, NS; adult-subadult: $r_s = 0.34$, N = 14, NS).

Figure 3.15 shows the results of a cluster analysis of dyadic association indices for all independent individuals including one juvenile male, GS, and one time with the orphaned juvenile, GS, and young adolescent BB. The tightest cluster included the alpha male, DN, his ally, VN (Newton-Fisher, 1997) and MA. Another close association included adolescent female, CL, and the orphaned juvenile female, EM. Otherwise, the adult and older adolescent males associated with one another relatively often, whereas among the females, comparably close associations were rare and most showed no strong patterns of association. Three females, MK, BN and ZN, spent very little time with any other community members. Figure 3.16 depicts the same association data in the form of a sociogram in order to show dyadic association strengths in more detail. Of note are the relatively strong associations between adolescent female, JN, three high-ranking males and the two oldest adolescent males. CL also had strong associations with these adolescent males and also with MA who was the focus of many associations with both high and low-ranking males. Only two females were known to have independent male offspring and these relationships are reflected in relatively strong DAI's between RH and NK, and between NB and her adult and adolescent sons, MU and AY.

Table 3.9 Mean number of scans in which adult and adolescent males and females spent time in proximity with one another. Observed/expected frequencies are also given in parentheses (M = male; F = female; Ad = adult; Adol = adolescent).

Class	Mean	Median	S.D.	Max	Min
Ad M - Ad M	19.1 (1716/611)	17.2	12.2	62.7	1.8
Ad M - Adol M	11.1 (889/543)	9.3	8.3	32.1	0.0
Adol M - Adol M	4.3 (52/81)	4.4	3.0	8.5	0.0
Ad M - Ad F	5.4 (920/1628)	0.0	10.3	72.5	0.0
Ad M - Adol F	8.8 (350/543)	6.5	9.4	39.7	0.0
Adol M - Ad F	5.8 (277/651)	0.0	10.0	44.5	0.0
Adol M - Adol F	4.4 (71/217)	2.3	5.1	14.3	0.0

3.3.4 Affiliation

Table 3.9 shows the dyad-corrected amount of time male and female, adults and adolescents spent in proximity (within 3m) of one another. The amount of time combinations of members of each age/sex class spent in proximity was significantly different (Kruskal-Wallis one-way ANOVA: $H = 33.0$, $df = 6$, $p < 0.001$). Dunn's *post hoc* multiple comparisons test (Siegal & Castellan, 1988, p. 213) revealed that adult males spent more time in proximity with other adult males than they did with adult females; adult males spent more time in proximity than adolescent males spent in proximity with one another, with adult or with adolescent females.

Differences in the amount of time other age/sex combinations spent in

Figure 3.17 The influence of rank on the amount of time males spent in proximity with (a) other males, and (b) females (dyad-corrected).

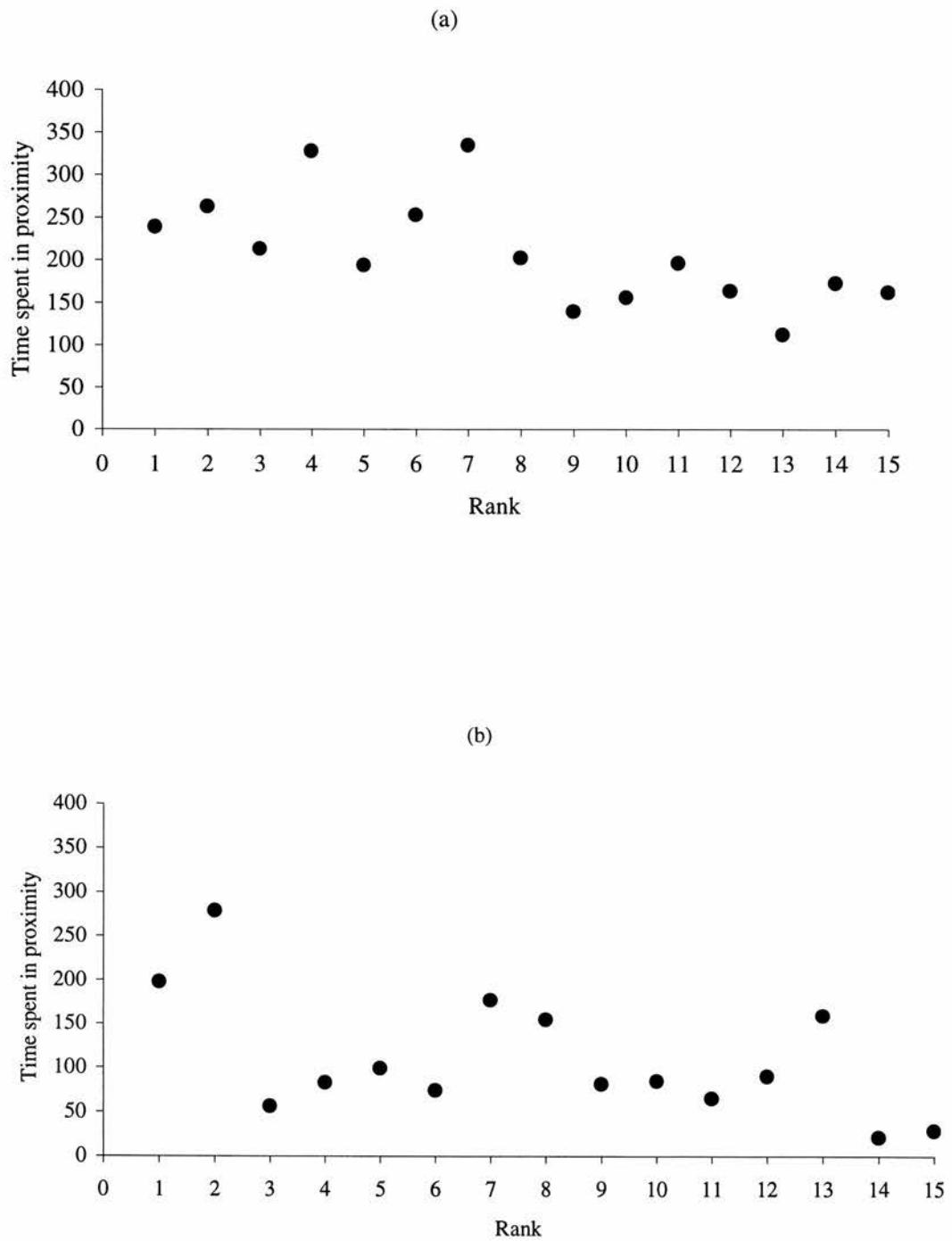
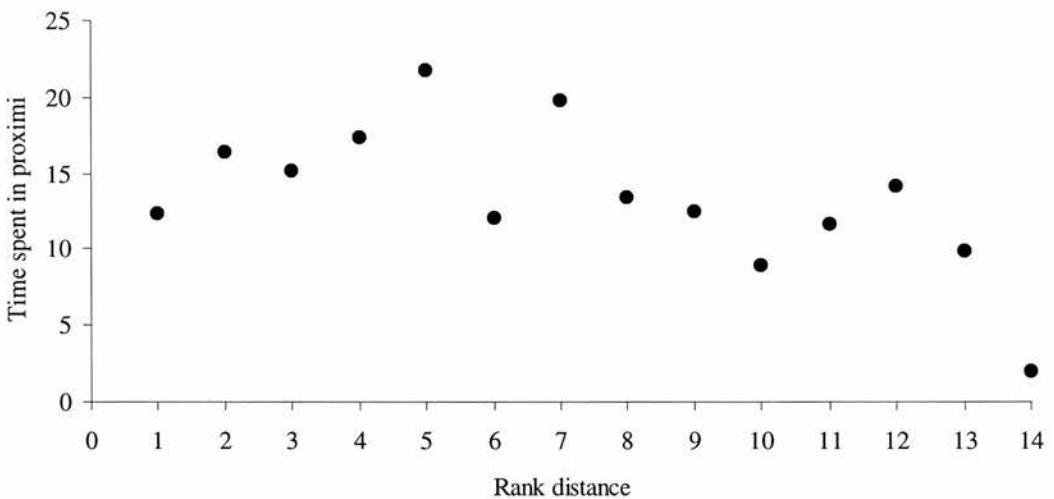


Figure 3.18 The relationship between rank distance and time spent in proximity.



proximity were not significant. Observed and expected amounts of times spent in proximity were significantly different in all cases (Chi-square goodness-of-fit tests: $df = 1$, $p < 0.001$, Yates' correction applied).

The amount of time males spent within 3m of other males was influenced by their rank. Using dyad corrected data, high-ranking males spent more time close to other males than low-ranking males did ($r_s = 0.71$ $N = 15$, $p < 0.005$. Figure 3.17a) although this relationship did not hold when only adult males were considered ($r_s = 0.44$, $N = 10$, NS). Adult males, spent more time in proximity with all males, and other adult males, than adolescent males or the juvenile focal male did (all males: $W_x = 16.5$, $p < 0.0007$; adult males: $W_x = 21$, $p < 0.01$). Male rank did not affect the amount of time spent in proximity with females ($r_s = 0.48$, $N = 10$, NS. Figure 3.17b) and adult males did not spend more time in proximity with females than adolescent males or the juvenile male ($W_x = 30$, NS). Males that were close in rank spent more time in proximity to each other than distantly ranked males ($r_s = 0.61$, $N = 14$, $p < 0.05$. Figure 3.18). This correlation was not significant, however, when

Figure 3.19 The amount of time males spent in proximity with (a) males and (b) females.

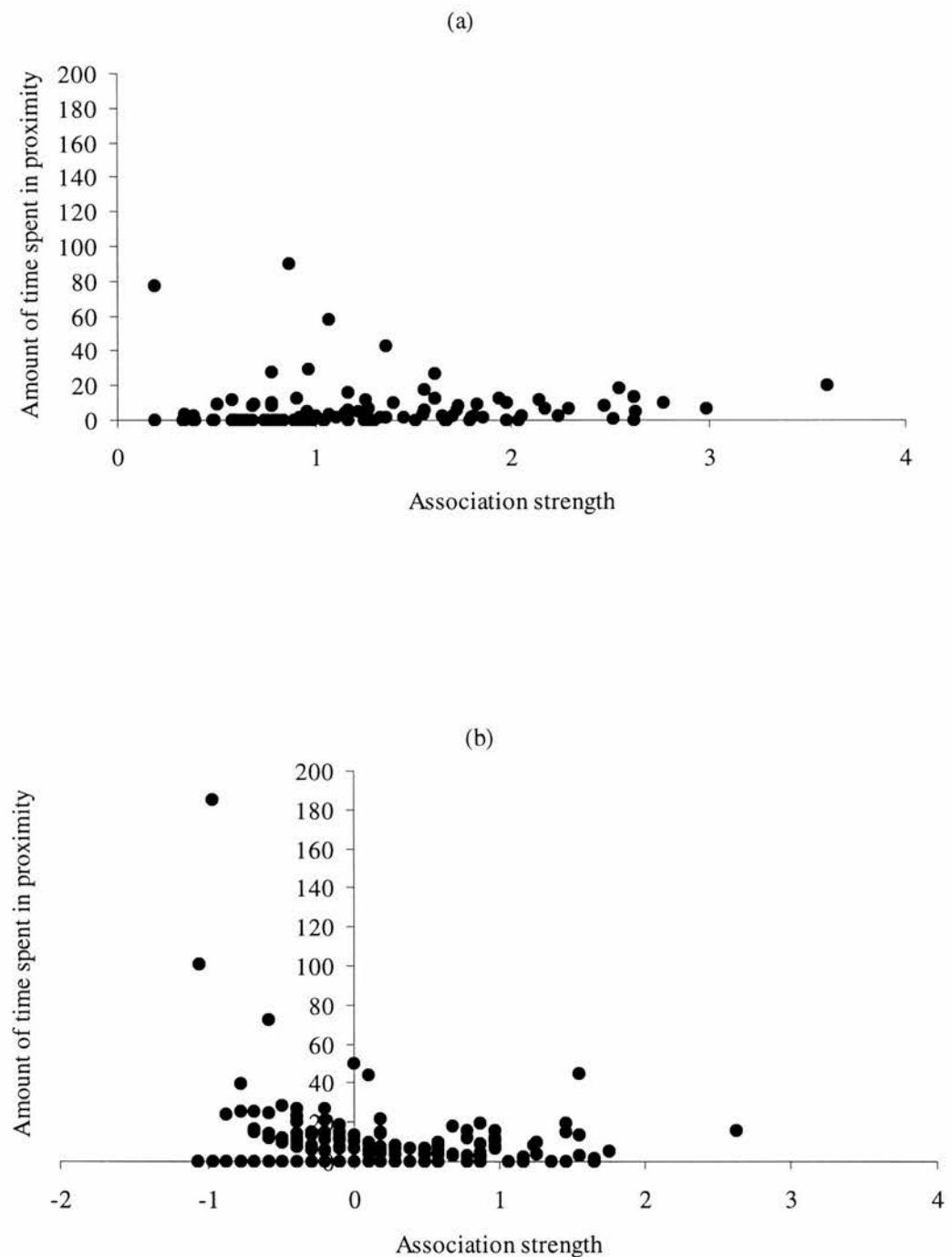
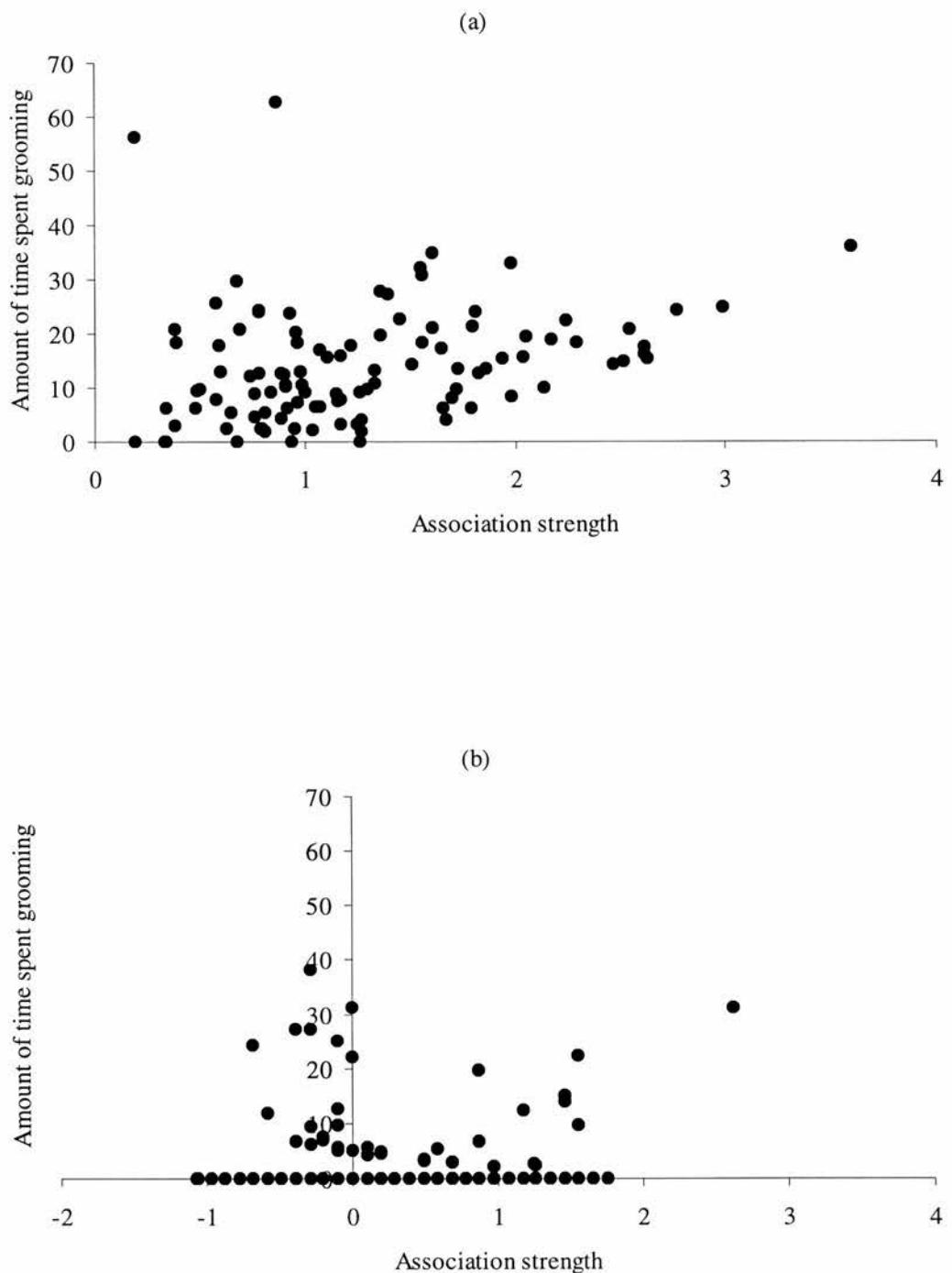


Figure 3.20 The amount of time males spent grooming with (a) males and (b) females.



only adult males were considered ($r_s = 0.42$, $N = 10$, NS).

Dyads with strong associations spend more time in proximity than those with weak associations (Pearson's: $r = 0.199$, $v = 377$, $p < 0.05$). This positive correlation was weak, but significant, for all male-male dyads (Spearman's: $z = 3.47$, $N = 105$, $p < 0.006$. Figure 3.19a) and marginally significant for adult male-adult male dyads ($z = 1.92$, $N = 45$, $p < 0.06$). The same was true for all male-female dyads ($z = 4.69$, $N = 256$, $p < 0.0006$. Figure 3.19b) and for adult male-adult female dyads ($z = 3.18$, $N = 126$, $p < 0.001$).

A stronger positive correlation was found between association and grooming. Dyads with strong associations spent more time grooming than those with weak associations (Pearson's: $r = 0.261$, $v = 377$, $p < 0.001$). This correlation was significant for all male-male dyads (Spearman's: $z = 3.47$, $N = 105$, $p < 0.006$. Figure 3.20a), marginally significant for adult male-adult male dyads ($z = 1.92$, $N = 45$, $p < 0.06$), and significant for all male-female dyads ($z = 3.83$, $N = 256$, $p < 0.00014$. Figure 3.20b) and for adult male-adult female dyads ($z = 3.05$, $N = 126$, $p < 0.002$). Dyads that were often in proximity were also more likely to groom one another than those which were rarely in proximity (Pearson's: $r = 0.391$, $v = 377$, $p < 0.002$). This correlation held for male-male dyads (Spearman's: $z = 6.12$, $N = 105$, $p < 0.0001$), male-female dyads ($z = 16.80$, $N = 256$, $p < 0.0001$) and adult male-male dyads ($z = 4.18$, $N = 45$, $p < 0.0001$). Grooming is examined in more detail in Chapter 4.

3.3.5 Time budgets

Table 3.10 shows the proportion of time individuals of each age.sex class devoted to each category of activity. Adolescent males spent more time self-

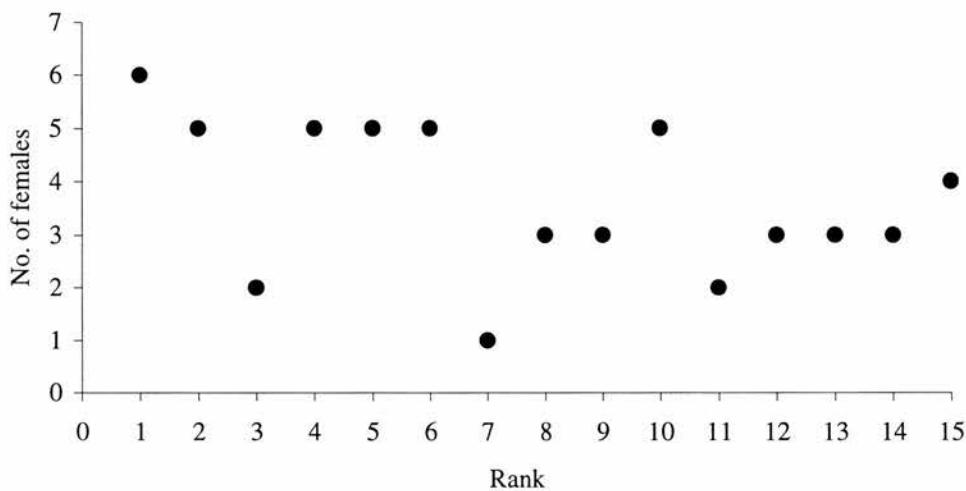
Table 3.10 Time budgets of individuals of different age/sex classes. Numbers indicate the mean percentage of time spent occupied in each activity. Ad = adult, Adol = adolescent, M = male, F = female.

Class	Self-groom	Grooms	Groomed	Mutual groom	Forage	Rest	Other
Ad M	10.3	5.0	6.0	4.6	39.4	22.7	12.0
Ad F	8.2	4.8	3.1	3.8	50.4	17.3	13.2
Adol M	10.8	3.8	1.3	1.8	44.0	24.0	14.5
Adol F	10.1	3.7	1.3	3.9	45.6	22.5	14.1
Juv M	6.4	1.2	3.8	0.6	42.0	23.6	22.4
Juv F	3.1	0.8	3.5	0.4	45.0	23.1	24.1

grooming than juvenile females (adolescent males v juvenile females, $W_x = 13$, $p < 0.03$). Adult males and females self-groomed significantly more than juvenile females (adult males v juvenile females, $W_x = 27$, $p = 0.04$; adult females v juvenile females, $z = 1.96$, $p = 0.05$). Adult males and females groomed significantly more than juvenile females (adult males v juvenile females, $W_x = 27$, $p < 0.04$; adult females v juvenile females, $z = 2.04$, $p < 0.05$). All of the remaining differences in the proportion of time each age/sex class spent on each activity (including total grooming) were not significant.

3.3.6 Copulations

Eight resident females were observed in the oestrus condition over the course of the study although only the four adolescent females were cycling regularly. Another unidentified adult female and her juvenile offspring, presumed to be part of a neighbouring community, was observed to join parties containing males on a number of occasions when she was maximally tumescent. Copulations were observed between males and all of these females at some time.

Figure 3.21 Male rank and the number of females with which each male copulated.**Table 3.11** The number of copulations observed between each female, and males of different age categories. Percentages are given in brackets.

	Adolescent females				Adult females			
	JN	SR	CL	MK	KY	KL	NB	HT
Ad M	26 (65.0)	17 (81.0)	7 (31.8)	4 (57.1)	1 (100)	10 (100)	4 (100)	9 (75.0)
Adol M	12 (30.0)	3 (14.3)	9 (40.9)	0	0	0	0	2 (16.7)
Juv M	2 (5.0)	1 (0.5)	6 (27.3)	3 (42.8)	0	0	0	1 (0.1)
Total	40	21	22	7	1	10	4	12

Ad = adult; Adol = adolescent; Juv = Juvenile.

One hundred and twenty four incidents of copulation were observed involving males of all ages. Adolescent females were involved in 76.6% of copulations. Four copulations involved ZT who is not included in the following analyses as the data concerning him is unlikely to be representative given his death after only one month of observation. Adult males were observed to copulate, on

average, 8.1 times (range = 1-16) with 3.9 females each (range = 1-6) during 533.5 observation hours. Adolescent males copulated 6.5 times (range = 3-9) on average with 3 females each. Juvenile males copulated 2.2 (range = 0-6) times with 1.4 females (range = 0-4) on average. The number of observed copulations between each female with adult, adolescent and juvenile males is given in Table 3.11.

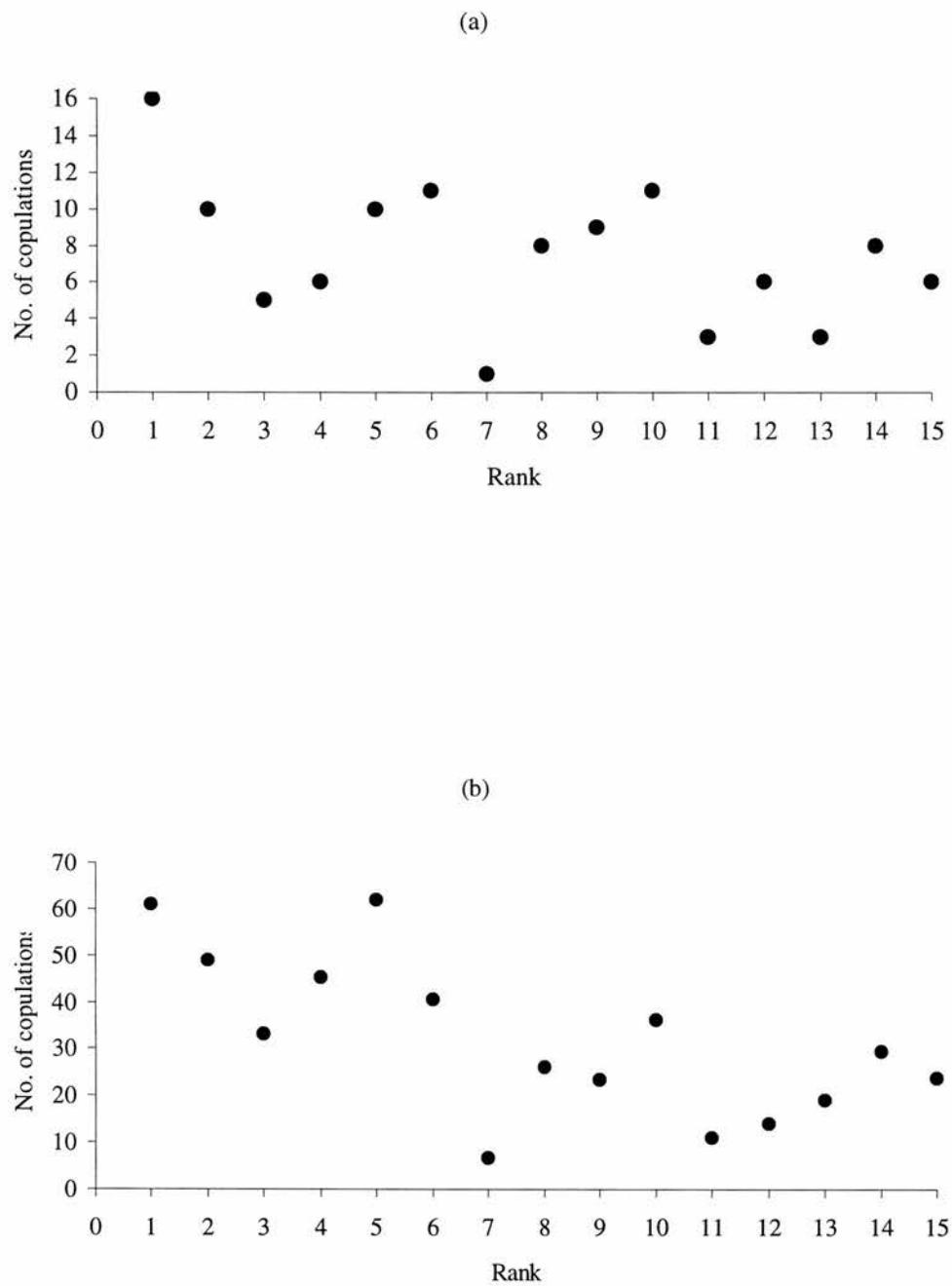
Male rank did not significantly influence the number of females with which males copulated ($r_s = 0.40$, $N = 15$, NS. Figure 3.21). Neither did rank affect the number of observed copulations achieved (all females: $r_s = 0.38$, $N = 15$, NS; adult females: $r_s = 0.45$, $N = 15$, NS) although the alpha male, DN, did have more copulations than any other male (Figure 3.22a). This correlation was significant when using dyad-corrected copulation frequencies ($r_s = 0.66$, $N = 15$, $p < 0.01$. Figure 3.22b). However, a number of males copulated once with females that rarely associated with them, resulting in extremely elevated dyad-corrected copulation frequencies in such cases. This last analysis should therefore be interpreted with caution.

3.4 Discussion

3.4.1 The dominance hierarchy

Few agonistic interactions, either aggressive, or submissive, were observed in this community throughout the course of the study, and most of these involved males. Construction of a female dominance hierarchy was therefore not attempted. Female chimpanzees rarely engage in dominance interactions among themselves (de Waal, 1982; Goodall, 1986), perhaps because the female hierarchy might be based upon

Figure 3.22 Male rank and (a) the frequency of observed copulations, (b) dyad-corrected copulations.



'respect' rather than overt shows of competitive superiority and, instead, determined by age and personality, as suggested by de Waal (1982). Aggressive interactions were shown not to be good predictors of female-female dominance relations at Gombe and Arnhem (Bygott, 1979; de Waal, 1982). When they can be established, female dominance relations are more stable over time than those among males, although they can display status striving tactics like those characteristic of male chimpanzees (Baker & Smuts, 1994). It has been hypothesised that these tactics might be important at rare but crucial stages in female life histories such as the period during which they establish core areas within which they spend most of their time foraging for themselves and their dependant offspring (Baker & Smuts, 1994). Immigrant females at Budongo have recently been shown to participate in a larger number of female-female agonistic interactions than established females (Fawcett, 2001). The amount of 'resource holding power' (RHP: Parker, 1974) that each female has may influence the quality of the core area that she is capable of acquiring and maintaining, and afford her priority of access to food where core areas overlap (Baker & Smuts, 1994). Analysis of 35 years of data from Gombe has revealed that female dominance has direct consequences in terms of reproductive success. High-ranking females produced offspring more frequently, had significantly higher infant survival rates, and daughters that matured more rapidly, than low-ranking females over the course of their respective lifetimes (Pusey *et al.*, 1997).

A hierarchy was discernible among the Sonso males although it was neither fully linear nor fully transitive. Males were cardinally ranked according to the direction in which both dyadic aggressive, and submissive interactions, were observed to occur. De Waal was the first to distinguish between 'real' and 'formal'

dominance (de Waal, 1982, 1986; de Waal & Luttrell, 1985) in order to account for the finding that some species possess ritualised agonistic displays which are consistently shown by just one member of a dyad but not the other, despite variations in the outcome of competitive interactions which appear to be resource, or context, specific (e.g. Kummer, 1971; Bygott, 1979; Strum, 1982). Chimpanzees possess such a display, the ‘pant-grunt’, which is a vocalisation performed by the subordinate member of the dyad, and directed toward the dominant member (Goodall, 1968, 1986; equivalent to the ‘rapid oh-oh’: van Hooff, 1973). However, it has been suggested that pant-grunts are not submissive behaviours, as they are rarely observed in aggressive contexts, but instead they are a means to indicate subordinate status, and are given spontaneously (Goodall, 1986; Newton-Fisher, 1997). Ordinal rankings derived from aggressive and submissive interactions (pant-grunting included) were significantly correlated and so ‘real’ (agonistic) dominance relations mirrored ‘formal’ dominance relations in most cases.

Despite significant correlations between all of the measures of dominance used, these measures produced slightly different rank orders. Five status levels based on cardinal ranks were distinguished following Bygott (1979) and Newton-Fisher (1997). This broad method of ranking males was not useful in the present study, because relative differences in cardinal rank values were not large between adjacently ranked males, and these values did not naturally fall into distinct categories, as shown by a plot of cumulative differences in cardinal values. Previously, during a period of instability in the male hierarchy, the Sonso males fell more neatly into five status categories. At that time, these distinctions were more useful as differences in the values of cardinal ranks between status levels were large (Newton-Fisher, 1997). Changes in the dominance hierarchy over time were

apparent in the present study although many of these could be explained by the relative activity, or even presence, of certain males during each quarter of the study period. Sample sizes for each quarter were small and consequently, small changes in the frequency of agonistic behaviours for each male exerted a disproportionate effect on their relative positions within the hierarchy. Three cases illustrate this well: (i) the change in status of TK, from a high point of 4th ranked to a low of 14th, occurred because his behaviour toward subadult males resulted in an artificially inflated status; (ii) MG's position as beta male before his death was due to the high frequency of submissive behaviours shown to him by the young males that he associated with at the time; and (iii) JM was rarely observed to associate with other community members during the first quarter of the study and his low status at that time is likely to have been another artefact of small sample sizes given that he was a prime male and never ranked lower than 5th during subsequent quarters. Otherwise, the male hierarchy appeared to be stable. The only change in status which is likely to be real (not a product of small sample sizes) was that of BK, who fell from his position as beta male and became progressively lower-ranking during the latter part of the study, evidenced by his failure to dominate males that he had dominated previously.

DN was clearly the alpha male according to all measures of dominance. The degree to which he dominated the males in the Sonso community was particularly marked with respect to the number of submissive and subordinate signals he received from all of the other males. BK, ranked second overall, was high-ranking according to all measures of dominance. He maintained this position throughout the first half of the study period by frequently showing aggressive behaviour toward the other males. However, VN, the previous beta male (Newton-Fisher, 1997)

outranked him in terms of the degree of subordination others demonstrated toward each of them (respect index) and it is possible that the rank reversal between these two males was not yet acknowledged or accepted by the other males in the community. BK's superior status was acknowledged, however, by more males than any other individual within the male hierarchy with the exception of DN. BK pant-grunted to four males during the course of the study although these incidents occurred during the last half of the study when BK dropped in rank. That BK pant-grunted to these males accounts for the finding that he ranked below VN according to measures based on conferred respect. VN, like the ex-alpha male, 7th ranked MG and also the 4th ranked JM, pant-grunted to only two males, DN and BK. Many males, particularly adult males, were not observed to pant-grunt to all those males that were superior to them and this is often the case among chimpanzees (e.g. Goodall, 1986; Boesch & Boesch-Achermann, 2000, p. 111; Nishida & Hosaka, 1996; Newton-Fisher, 1997). This suggests that certain dominance relations between males might have been ambiguous. Nishida & Hosaka (1996) found that dominance relationships among four middle-ranking males of M group, Mahale, were non-transitive and unstable. They explained this as a facet of the behaviour of younger males, which attempt to dominate high-ranking males that are past their prime, before tackling adjacently ranked, but capable, competitors. Nishida & Hosaka, like Newton-Fisher (1997), consider the withholding of acknowledgement of superior status to be a tactic that chimpanzees use in order to further their own interests with respect to the acquisition of status. Newton-Fisher (1997) goes on to attempt to substantiate this claim by appealing to the findings of a relatively new area of research that indicates that there are psychological repercussions for winners and losers of conflicts that are positively reinforcing. There is a growing body of

evidence across many taxa that prior social experience affects the outcomes of subsequent aggressive interactions (e.g. Frey & Miller, 1972; Bakker & Sevenster, 1983; Bakker *et al.*, 1989; Chase *et al.*, 1994; Bekoff & Dugatkin, 2000) via transient changes in CNS activity and hormone levels (Raleigh *et al.*, 1984). Winners of competitions are more likely to win subsequent conflicts than they would otherwise, all things being equal, and prior losers are more likely to lose again, even when more than twenty four hours elapse between fights. However, these findings are based on the outcomes of aggressive, competitive interactions. It is not clear how the receipt, or production, of status signals alone could achieve the same degree of reinforcement without correspondingly large changes in hormonal activity. Given the apparent stability of the male hierarchy during this study, it is questionable whether or not withholding such signals lends itself to interpretation as tactical behaviour in all cases. Males that were more aggressive also received more submissive signals. Pant-grunting might serve simply to pacify such males. Similarly, males that were high-ranking but relatively unaggressive, such as JM and BY, were pant-grunted to less often.

The consequences of dominance relations are further addressed in the chapters that follow.

3.4.2 Party size and composition

The mean party size, excluding infants, was 7.8 individuals. It is likely that this is not a true reflection of mean party sizes at Budongo as only parties containing males were sampled and males tend to be more gregarious than females. However, mean party sizes reported previously at Budongo which also contained at least one adult or adolescent male were smaller and contained 5.9 individuals

(Newton-Fisher, 1997), whereas overall mean party sizes recorded in recent years were between 5.7 (Newton-Fisher, 1999a) and 5.1 (Reynolds, unpublished). The relative mean party size, which takes into account the size of the community under study, fell within the middle of the range of relative party sizes at other study sites (Boesch & Boesch-Achermann, 2000, p. 93) although this figure was higher than that calculated for the larger communities within the sample presented which were of comparable size (*ibid*). It is possible that the absolutely large party sizes, relative to other sites, found at Budongo were supported by a superabundance of food which, it has been suggested, is less of a limiting factor than for other chimpanzee populations (Newton-Fisher, *et al.*, 2000). Food abundance was not measured in this study and so whether or not high food availability promoted large parties could not be assessed.

Parties of seven individuals or less were more common than larger parties and this pattern has been reported previously at Budongo (Newton-Fisher, 1997). Parties were dominated by males who constituted a similar proportion of party members, irrespective of the size of parties. Given that the sex ratio within the Sonso community was between 1.1 and 1.3 in favour of females, this result indicates that males were more attracted to, and spent more time in, mixed sex parties than females did. Mixed-sex parties are always the most common party type reported (Budongo, Bossou, Gombe, Kibale, Mahale, Taï: Boesch & Boesch-Achermann, 2000, p. 96) and males spend more time in mixed sex parties than single sex parties (Newton-Fisher, 1999a; Boesch & Boesch-Achermann, 2000).

Aside from food availability, one of the major factors thought to influence party size, and particularly the number of males in parties, is the presence of oestrus females. (Goodall, 1986; Newton-Fisher, 1999a; Boesch & Boesch-Achermann,

2000; Reynolds, unpublished data). Just under thirty percent of parties contained one or more oestrus females in the present study, which is a lower number than that reported previously at Budongo (50.2%: Newton-Fisher, 1999a). This was very probably due to the fact that only four adolescent females were cycling regularly, while four adult females cycled very irregularly, and the remaining adult females had not resumed cycling after the birth of their infants. Party sizes increased significantly when one oestrus female was present, and increased again when two females were present. The presence of a further cycling female did not affect party sizes. Parties containing three cycling females were very rare ($N = 1$) and so the lack of effect on party size of a third cycling female cannot be representative although this result is the same as that reported by Newton-Fisher (1999a). The number of males in parties also increased significantly when one oestrus female was present but did not increase further with the addition of more oestrus females. This last result is a little surprising but could be explained by the fact that only three females mated regularly and might have been considered popular, and the probability that more than one of these females were cycling at the same time was low. At Mahale, females do not show synchronisation of their oestrus cycles or the timing of ovulation (Takahata *et al.*, 1996). One of these females at Budongo, the adolescent, CL, showed a distinct lack of receptivity and often avoided sexual contact with adult males even though she regularly joined parties containing males when she was in oestrus. As many as 27% of observed copulations with CL ($N = 22$) involved juvenile males. Her lack of willingness to mate with adult males may have made her relatively unattractive. Another adolescent female, MK, was never observed to come into full estrous and copulated infrequently, so was also unlikely to have attracted males to parties in which she was present. It is possible that

cycling females were more likely to occur in large parties simply because a larger proportion of the community were necessarily present in such parties, and one or more females present were in oestrus, as opposed to individuals being attracted to oestrus females and forming large parties around them as proposed by Goodall (1986). There may be some benefit to mothers of dependent juvenile sons in exposing their offspring to oestrus females in order that they may gain experience of sexual behaviour. Male rank did not affect the number of copulations achieved, or the number of sexual partners that they had, except in the case of the alpha male who copulated more times than any other male. Adolescent females, in particular, were prepared to copulate with low-ranking males including juveniles and, on one occasion, even an infant male. Certain females with dependent male offspring, however, were relatively asocial and did not seek out these opportunities.

3.4.3 Association

As in most other populations, association was strongest among male-male dyads and weakest among female-female dyads (Nishida, 1979; Ghiglieri, 1984; Goodall, 1986; Wrangham *et al.*, 1992; Boesch & Boesch-Achermann, 2000). All focal males associated with other males more often than with females. Although females associated more often with males than with other females, this difference was small and insignificant.

Male rank did not appear to influence mean association strengths with other males or with females. Males that were relatively closely ranked were more likely to associate with one another than males that were more distantly ranked. This difference, however, was a marginal one when only adult males were considered which suggests that subadult males associated with other subadult males, which

were also close in rank, more often than with the more distantly ranked adult males. The effect of rank distance on association among adult males alone was not significant. Neither did rank distance affect association between adult males and subadult males. These results indicate that males did not systematically choose their association partners according to their absolute, or relative, status. Newton-Fisher (1999a) argues that male chimpanzees associate strategically in order to further their own 'social interests' and presents data to support this view concerning party membership and the flexibility of association patterns. It would be surprising if strategies concerning the social interests of male chimpanzees did not coincide, to some extent, with strategies concerning the acquisition of reproductive benefits. Strong group level male-male relationships are considered to promote successful defence of resident community females, and differentiated relationships between community males are thought to promote individual interests in gaining access to reproductive females, either directly (Watts, 1998) or indirectly, via coalitions. Unfortunately, Newton-Fisher (1999a) does not provide information concerning the rank of closely associating males, or on coalition formation despite his suggestion that males prefer to associate in small parties in order to develop relationships or to increase their access to cycling females within those parties. The data presented here indicate that although some males may choose to associate with profitable males, in term of rank, such preferences were not evident on a wide scale. Priority of access constraints are unlikely to operate on party membership and any male could seek to associate with high-ranking males in order to attempt to develop better relationships with them. But the mean association strengths for high-ranking males did not reflect such strategies. If it were unlikely that distantly-ranked males might form mutually beneficial relationships, then a better option would be to

attempt to develop relationships with closely-ranked, but slightly higher-status, males. The lack of a relationship between association strength and rank distance, while far from conclusive, also fails to reflect choices, or constraints, on party membership.

Perhaps male chimpanzees make choices about whom to associate with based on other criteria such as individual characteristics. It would be very difficult to ascertain what characteristics might be considered attractive in a male chimpanzee aside from intrinsic power. A male that was more predisposed than average to intervene on behalf of high, or low, ranking males might be attractive to males which fall into one of these two categories, for example. Few coalitions were observed during this study and so this possibility could not be explored. The majority of interventions in which adult males were involved were, however, loser-support coalitions and so low-ranking males might do well to associate with high-ranking males who might protect them in the face of aggressors (see Chapter 5). Males of the Mahale M group were also more likely to support losers, defined as those which had recently lost contests to the same aggressor, although they were also more likely to support aggressors in the conflicts presented, and the determination of which individual was more likely to be the loser had the conflict remained dyadic was reported to be difficult and, in the end subjective (Nishida & Hosaka, 1996). Inspection of data concerning association and intervention patterns (Nishida & Hosaka, 1996, p. 123 and p.124) does not support the existence of such a relationship overall, although there is a relationship between association and interventions among the highest-ranking males. The Sonso males rarely intervened in fights and no patterns emerged, except that DN intervened on behalf of his ally,

VN, on both of two occasions when VN was attacked in the presence of DN. DN and VN were also each other's closest associates.

It was unclear what motivated other close associations. Previously, Newton-Fisher (1999a) categorised the Sonso males as either intense, or gregarious, association strategists according to the strengths of their associations with other males. Two clusters of intense strategists spent more time, and in smaller parties, with the males within their association cluster. Gregarious strategists tended to associate in larger parties with larger numbers of males. In the present study, only one cluster of similarly intense association strategists was identified. This group, containing DN, VN and MA appears to have re-formed since Newton-Fisher's (1997, 1999a) study after an intervening period during which MA associated closely with BK (Fawcett, 2001). Interestingly, MA was a close associate of DN and VN, whose alliance led to the overthrow of the previous alpha male, MG in 1995. BK's subsequent close association with MA coincided with a phase leading up to BK's repeated challenges to VN's status in the first part of this study. MA then began associating regularly with DN and VN again and, together with two other high-ranking males, supported a third high-ranking male when he was attacked intensely by BK. After this incident, BK began to fall sharply in rank and was observed to pant-grunt to MA.

For some reason, MA appears to be an influential male within the Sonso community. Many individuals associated with MA closely. Of all the individuals within the community, it was DN and MA who were primarily responsible for the shape of the dendrogram (Figure 3.15) depicting the association patterns presented above. MA and DN were the closest associates of 54% and 29%, respectively, of the adult and adolescent males. DN was likely to have been attractive due to his

alpha status. MA, however, was a relaxed and highly social male who was amongst the most intense grooming partners of both high-ranking and adolescent males. Perhaps this sociability was his most desirable characteristic.

MG and GS also associated relatively intensely. GS was an orphaned juvenile male who associated with MG a great deal. MG and GS were never observed to groom one another but the ex-alpha male tolerated GS' presence and may have served as protection for GS. A young adolescent, BB, also associated with these two regularly. BB's mother is thought to be ZA, who was the least social community member. Two other adolescent males, AY and NK, were of comparable age with BB, associated with their mothers regularly, whereas BB appears to have relinquished the company of his mother in order to have closer contact with the other community males. BB, GS and MG were often found alone together and these small parties may have provided a safe environment for the two young males, providing a social base from which they could begin to integrate themselves into the male network. Also within the larger main association cluster were the two adolescent females, CL and JN. These were the two most recently immigrated females and they regularly associated with the males in mixed sex parties. SR immigrated into the community during the same year that JN did, although she spent much less time in association with the males, as did MK who had joined the community three years earlier. An orphaned juvenile female, EM, associated with CL regularly but was also seen to travel with single high-ranking males from time to time. Other than JN, CL and EM, the female that associated with males most often was the adult, and highest ranked female (Fawcett, 2001) NB, whose ties with her adult and adolescent sons, MU and AY, seem to have remained close.

The association patterns within the community supported Wrangham's (2000) hypothesis that the potential for gregariousness in any individual might depend upon their ability to travel in parties, which in turn is dependent upon individual travel velocities. According to this hypothesis, mothers, whose travel velocity is likely to be reduced by the need to carry, or attend to, their offspring should be the least social community members. Males and females without dependants can travel at the same speed and can therefore move together from one feeding site to the next. As predicted, JN, CL and EM associated with males more frequently than any other females although SR and MK associated with males irregularly. Also, in support of this hypothesis, TK, a crippled adult male, was relatively asocial and was often encountered travelling alone.

3.4.4 Affiliation

Adult males spent more time in proximity with one another than any other age/sex combination did. Adolescent males spent less time in proximity with one another than any other age/sex combination and spent more time than expected within proximity of adult-males. This result is consistent with previous findings at Kibale (White & Chapman, 1994). All other age/sex combinations, which included adult and adolescent males and females, spent less time in proximity than expected. Adult males spent more time within 3 metres of other adult males than adolescent males, or the juvenile male did. This result was consistent with the findings of Kawanaka (1993) who also reported that the proximity relations of males of different age classes were not differentiated when interindividual distances of 10 metres were considered at Mahale. Kawanaka (1993) suggested that these differences reflected the relationship between adolescent males and adult males, in

which adolescent males were attracted to adult males but were rarely allowed, or were not confident enough, to position themselves in such a way as to increase their chances of having physical contact with them such as grooming.

Neither rank, nor rank distance, had a strong effect on the likelihood that males would spent time within 3 metres of one another, although there was some relationship when males of all ages were included in the analyses. This relationship disappeared when only adult males were considered. There was a stronger relationship between close proximity and dyadic association. Males and females that associated regularly also spent more time within 3 metres of one another than those that were more rarely found in association did. Familiarity, therefore, was a better predictor than rank of the likelihood that individuals would tolerate one another at close range. If familiarity promotes tolerance, then it should also affect the likelihood of relationship formation. This appeared to be the case as individuals that had close associations also were more likely to groom one another, and dyads which spent more time in proximity also spent more time grooming. Grooming behaviour is investigated further in the following chapter.

3.4.5 Summary

It was possible to rank the males of the Sonso community according to the direction in which aggressive and submissive interactions were performed, although the emergent dominance hierarchy was neither fully linear nor fully transitive. Throughout the study period, rank relations appeared largely stable.

Mixed sex parties of seven individuals or less were the most common party type. Hypothesis 1 (given in section 1.3) which stated that males were attracted to reproductively active females and other males was supported. The number of males

in parties increased when there was at least one cycling female present although the presence of additional cycling females did not result in even larger aggregations of males. It is possible that these results merely indicate that larger parties are more likely to include oestrous females while the proportion of males in parties remain fairly constant across party size. Male dominated mixed sex parties were more common than female dominated parties. Male-male attraction was reflected in higher mean DAIs among males than among male-female dyads.

Hypothesis 2, that high rank brings reproductive advantages to males, was largely unsupported. There was no positive correlation between rank and the number of female sexual partners or the number of copulations achieved although the alpha male did achieve more copulations than any other male. Instead, females appeared to display idiosyncratic sexual preferences based on other factors. However, the data presented here may not be properly representative of the sexual behaviour within this community as the females that were the most sexually active were all nulliparous and may not have elicited as many sexual advances as receptive, parous females. Male competition may, therefore, have been relatively weak. Nonetheless, it is unclear why high-ranking males should not compete for access to even relatively low quality females in the absence of higher quality ones.

Hypothesis 3, that males seek to engage in positive social interactions with one another more often than with females, was supported. There were positive correlations between mean dyadic association indices (DAIs) and the amount of time spent in proximity (within 3m) and grooming for male-male and male-female dyads. Adult males spent more time in proximity with other males, and less time in proximity with females, than expected. The amount of time dyads spent in proximity and the amount of time spent grooming within those dyads was positively

correlated for both male-male and male-female dyads. Thus, given the stronger associations between males and the relationship between association and affiliation, males were more affiliative than females and positioned themselves such that opportunities for male-male grooming were more frequent than for male-female grooming.

Hypothesis 4, that males compete for access to high-ranking males in order to improve, or maintain, potentially beneficial relationships with them, was not supported. Neither rank nor rank distance influenced the amount of time spent in proximity with other males. This suggests that high-ranking males did not form a nucleus within parties around which other males aggregated. Furthermore, these results do not indicate that males sought affiliative contact with high-ranking males more often than with low-ranking males.

Overall, males did emerge as the more social sex. They associated with one another more often spent more time at close quarters than females. The influence of rank on general social organisation, however, appeared to be weak according to all measures. Neither did high rank bring any advantages in terms of sexual opportunities, except for the alpha male. In the next chapter, I will concentrate on grooming relationships, the most widespread and directly affiliative behaviour in which chimpanzees engage, in order to examine sex differences and the effect of rank on the distribution of what is considered to be a valuable currency, exchangeable for fitness enhancing services.

Chapter 4

Grooming Relationships

4.1 Introduction

4.1.1 Grooming in primates

Grooming is an activity that involves the removal of parasites, foreign bodies, debris, dead skin etc., from accessible body parts: its function is primarily hygienic (Hutchins & Barash, 1976; Barton, 1985; Tanaka & Takefushi, 1993). Grooming is therefore an essential daily activity for the maintenance of good health and is found among many animal species from damselflies (*Ischnura verticalis*: Baker & Smith, 1997) and crayfish (*Cherax quadricarinatus*: Batang & Suzuki, 2000) to wallabies (*Macropus parma*: Ord *et al.*, 1999) and primates. Grooming is often self-directed autogrooming but where body parts are inaccessible, conspecifics or even members of other species will sometimes invest time in allogrooming. However, interspecific grooming is almost always unidirectional and often provides direct benefits for the groomer, usually in the form of food, e.g., cleaner wrasse (*Labroides dimidiatus*: e.g., Grutter, 1995). In primates, by-products of this utilitarian activity include positive physiological changes e.g., stress relief (Terry, 1970; Boccia, 1987; Schino *et al.*, 1988) and the release of endorphins (Keverne *et al.*, 1989).

Allogrooming (hereafter "grooming") is the most common form of affiliative behaviour exhibited by primates (Goosen, 1981). Time spent grooming does not correlate with body size but does correlate with social group size (Dunbar, 1991). This strongly suggests that grooming has an important social function. In gelada baboons, grooming is the last behaviour exhibited in a four stage sequence of relationship

development between unfamiliar individuals (Kummer, 1975). This may well apply to many other Old World primate species in particular. Grooming is considered to be a key feature of primate society, as it is extremely important in facilitating interindividual familiarity and bonding (Carpenter, 1942; Dunbar, 1988). Frequent grooming partners tend to spend a large proportion of their time together and are relaxed in each other's presence. It is a behaviour that initiates and maintains friendly relationships (Harcourt, 1992; Cords, 1997). Grooming is also the most common affiliative behaviour observed during reconciliation between former opponents in many studies of post-conflict behaviour (e.g. rhesus macaques, *Macaca mulatta*: de Waal & Yoshihara, 1983; Japanese macaques, *M. fuscata*: Aureli *et al.*, 1993; moor macaques, *M. maurus*: Matsumura, 1996; pigtail macaques, *M. nemestrina*: Castles *et al.*, 1996; black-and-white colobus monkeys, *Colobus guereza*: Björnsdottir *et al.*, 2000; spectacled leaf monkeys, *Trachypithecus obscurus*: Arnold & Barton, 2001a; Chapter 6). Direct physical contact in such situations serves to reassure or appease former opponents by demonstrating friendly intentions and disinclination toward further antagonistic interactions (de Waal, 1986, 1989).

4.1.2 The benefits of allogrooming

On the face of it, grooming could be considered an altruistic act (e.g., Kurland, 1977). Kin should therefore groom more than nonkin so that the costs of grooming can be offset against the indirect benefits gained through kin selection (Silk, 1987). This has been shown to be the case in numerous studies of despotic species for which kinship is an important variable in all aspects of social organisation. But there are other more or less direct benefits to be gained in addition to better health in one's relatives, increased familiarity and the ability to restore a relationship after a conflict.

First, grooming can be reciprocated, immediately in the form of turn taking or within a bout of mutual grooming, or further into the future. Thus, an investment can be recouped on a tit-for-tat basis. Second, grooming can be 'exchanged' (or interchanged) for tolerance around resources (e.g. Stammbach, 1988) or temporary tolerance *per se* i.e., the groomer is less likely to be aggressed against or displaced while in proximity to the gromee. Tolerance can be gained in the short term and can be increased via an ongoing long term grooming relationship. Third, grooming can be interchanged for a commodity. The commodity which has traditionally been the focus of greatest interest is agonistic support (see e.g. Seyfarth, 1977; Seyfarth and Cheney, 1984; Dunbar, 1988; de Waal & Luttrell, 1988; Harcourt, 1992; Hemelrijk, 1990a, 1996; Barrett *et al.*, 1999; Watts, 2000b). Other currencies that might be traded for grooming include sex (e.g. Hemelrijk *et al.*, 1992, 1999), food (Hemelrijk, 1996; de Waal, 1997) or allomothering (Muroyama, 1994).

Food sharing among adults has been documented in a number of primate species both in captivity (e.g. brown capuchin monkeys, *Cebus apella*: de Waal *et al.*, 1993; de Waal, 2000; long-tailed macaques, *M. fascicularis*: Schaub, 1996; bonobos, *Pan paniscus*: Vervaecke *et al.*, 2000; chimpanzees: de Waal, 1997; Hemelrijk, 1996; Hemelrijk *et al.*, 1999), and in the wild (e.g. white-faced capuchin monkeys, *Cebus capucinus*: Rose, 1997; Perry & Rose, 1994; bonobos: Hohmann & Fruth, 1993; lar gibbons, *Hylobates lar*: Nettelbeck, 1998; chimpanzees: Boesch & Boesch, 1989; Kuroda *et al.*, 1996; Newton-Fisher, 1999b; Bethell *et al.*, 2000). There have been two studies that have investigated the relationship between food sharing and grooming, both in captive chimpanzees. De Waal (1997) found that food sharing with a particular individual was more likely when grooming had been received from that individual within the previous 2 hrs although the effect was small. Grooming within the same

dyad dropped after the opportunities for food sharing had passed. By contrast, Hemelrijk (1996) reports that young chimpanzees cooperated in a food acquisition task but that there was no correlation between willingness to cooperate and grooming behaviour.

Hemelrijk *et al.* (1992) investigated the possibility that females were more likely to receive more social benefits from males when they were in oestrus than at other times, and whether males would confer more benefits on those females with whom they mated more often. Males were found to preferentially groom oestrus females and those with whom they mated frequently. However, the authors point out that this pattern was not reflected in analyses of food sharing by males, and oestrus females actually received less support during aggressive encounters with males than they would when they were not in oestrus (although this may have been due to increased aggression intensity during male-female conflicts at such times). These intense grooming relationships were not maintained when the females in question were not sexually receptive. In a follow-up study, Hemelrijk *et al.* (1999) combined this data with a DNA-typing study on the same colony and found that males did not sire more offspring with females that they groomed (or supported, or shared food with) more frequently and so direct fitness benefits were not accrued via increased affiliation.

Whether grooming is a currency which is valuable enough to be exchanged for other services, especially in captivity where grooming time is not so limited by other time consuming activities such as foraging, has been called into question (Hemelrijk *et al.*, 1992; Hemelrijk, 1996). Neither is it clear that grooming can be considered an altruistic act in the sexual arena. Hemelrijk *et al.* (1992) suggested that grooming may have a direct function in this context as it may serve to counteract the aggressive

tendencies of males and the tendencies of females to flee during solicitations for copulation. Thus, grooming may have direct and immediate benefits for males. Even in other contexts, grooming need not be considered in terms of time lost to the groomer any more than to the groomee (Dunbar, 1988). Grooming positively influences the opiate system in the groomer as well as the groomee (Keverne *et al.*, 1989) and might reinforce grooming with certain partners leading to the observed reciprocity in grooming (Hemelrijk, 1996) which has been reported in chimpanzee studies (e.g. Hemelrijk & Ek, 1991; Newton-Fisher, 1997; Boesch & Boesch-Achermann, 2000; Watts, 2000a; and also vervet monkeys: Hemelrijk, 1990a).

4.1.3 Theories concerning the distribution of grooming in primates

4.1.3.1 Priority of access models

The currency that has received most attention in studies concerning the possibility of interchange for grooming is coalitionary support. For many years primatologists have explained the distribution of grooming effort of their subjects within the framework proposed by Seyfarth (1977). Seyfarth assumed that 1) there must be benefits to be accrued from grooming otherwise animals would not be predisposed to invest heavily in this activity, and that a likely benefit is the receipt of support in agonistic encounters, 2) all animals are equally skilled at parasite removal but successful support is directly related to the relative rank of the supporter to the aggressor, 3) individuals are selected to maximise the total amount of benefit received from all others over a finite period. In addition, the distribution of grooming effort will depend upon the assumptions that attractiveness as a grooming partner is directly related to rank, females will be selected to maximise time spent with high-ranking

individuals and competition for grooming partners will force some individuals to compromise. Seyfarth suggested that asymmetrical dominance relationships force the lower-ranking partner to invest more grooming than the higher-ranking partner, as the higher-ranking partner is the more attractive of the two as a supporter. Thus, adjacently ranked individuals are predicted to groom with the highest degree of reciprocity. Thus, grooming will be directed up the hierarchy and individuals will spend most time grooming those to which they are adjacently ranked.

The predictions generated by this model have been poorly supported by studies of both wild and captive groups of despotic female-bonded species (vervet monkeys, *Cercopithecus aethiops*: Seyfarth, 1980; Fairbanks, 1980; bonnet macaques, *M. radiata*: Silk, 1982) and female-bonded New World monkeys (wedge-capped capuchin monkeys, *C. olivaceus*: O'Brien, 1993; brown capuchin monkeys: Di Bibetti, 1997; Linn *et al.*, 1995; Parr *et al.*, 1997). Hemelrijk (1994) did provide some support for Seyfarth's model in her study of long-tailed macaques in which she induced grooming within a triad of monkeys by dropping a sticky mixture on to back of the intended groomee, and then provoked a conflict. In this case, aggressor support followed more often when a recent grooming bout between the aggressor and the third party had preceded the conflict. Victim support was not observed. However, Hemelrijk points out that this artificial test environment did not provide conclusive positive evidence as the possibility that grooming caused a general increase in the tendency to support could not be ruled out.

In a recent study of captive bonobos (Vervaecke *et al.*, 2000) support for Seyfarth's model was claimed, although this amounted to a positive correlation between grooming given and support received, grooming being directed up the hierarchy, and high-ranking females being groomed most frequently. Increased

grooming between individuals adjacent in rank was not confirmed, and neither was competition for high-ranking partners (see also Franz, 1999). Interestingly, subjects also gave more support to those that they groomed more. The authors suggest that this could, in fact, account for the correlation between grooming given and support received.

Seyfarth's (1977) original model was modified by Sambrook *et al.* (1995) to increase the impact of competition for grooming partners on the distribution of grooming in a large versus a small group of female olive baboons (*Papio cynocephalus anubis*). Sambrook *et al.* incorporated three further constraints into models of grooming: 1) Engagement model - in which the desired grooming partner may already be engaged in grooming with a higher-ranking grooming partner; 2) Interference model - in which the groomer has learnt that access to some partners is likely to be constrained by interference from higher-ranking competitors and so attempts to get access to those partners are inhibited; 3) Rank difference model - in which variation in partner attractiveness is taken into account. The fit of Sambrook *et al.*'s data to the models was very poor for the small group of baboons and only slightly better for the large group. However, Sambrook *et al.* (1995) were unable to distinguish between the models in terms of their predictive power. They found that in a multiple regression analysis, rank, but not rank distance, explained a significant amount of the variance in grooming for the small group, but not the large group. Conversely, rank distance, but not rank, explained a significant amount of variance for the large group, but not the small group. This implicated group size as an important factor to be incorporated into any model as group size is likely to play a role in the distribution of grooming relationships and social structure generally.

Watts (2000b) used the attraction-to-high-rank and rank-distance models formulated by Seyfarth (1977) together with those outlined above (Sambrook *et al.*, 1995) to test hypotheses concerning the effect of rank on the distribution of grooming in wild chimpanzee males, under the assumption that rank relates to attractiveness, and that alliances among males are dependant upon grooming relationships. Watts used data concerning two groups, one with a large number of males ($N = 22-24$: Ngogo community, Kibale, Uganda) and another with a small number of males ($N = 9$: M group, Mahale, Tanzania). He found that in the larger group, males were attracted to high-ranking grooming partners and grooming was predominately directed up the hierarchy. Both rank and rank distance were important variables in determining the distribution of grooming. The attraction-to-high-rank and rank-distance models were well supported for this group. Neither rank, nor rank distance, was successful in explaining the distribution of grooming in the smaller Mahale group. In comparing his results with the baboon study of Sambrook *et al.* (1995), Watts (2000b) suggested that the difference in rank effects between the small baboon and chimpanzee groups may be due to a greater degree of mutualism in the formation and maintenance of agonistic alliances in chimpanzees as opposed to the more kin-biased, less opportunistic strategies of female cercopithecines. In male chimpanzees, high-ranking males are more susceptible to successful challenges from below and so lower-ranking males have more to gain from alliances than do female cercopithecines. In a small group of male chimpanzees, such strategies might be more apparent and sufficient to mask rank-related effects. In a large group these details are more likely to be obscured.

4.1.3.2 Grooming as a currency in biological markets

More recently, ideas that concentrate on the characterisation of grooming as a currency which can be exchanged for the same or different currencies in a biological market (Noë & Hammerstein, 1995) have received attention (Henzi & Barrett, 1999; Barrett *et al.*, 1999; see also Stopka & Macdonald, 1999, for mice). According to this view, the primary function of grooming in primates is to reduce aggression and increase tolerance in dominants toward subordinates, thereby decreasing power differentials, or at least their potential limiting effects on subordinates. Within any dyad, one member trades tolerance while the other trades grooming, or both might trade grooming. Among egalitarian species, grooming traders predominate and trade with each other. Here, grooming is likely to be reciprocal. Among despotic species where power differentials are much greater, and dominance gradients much steeper, traders of tolerance will be more common and grooming is likely to constitute a currency for interchange. Grooming reciprocity is still to be expected in despotic species if time constraints and reduced access to high-ranking grooming partners (competition) influence grooming distribution, resulting in grooming occurring most frequently between closely ranked individuals. Interchange between grooming and tolerance should be less common in wild primates than captive ones as avoidance is a more viable option for them (Henzi & Barrett, 1999). This model predicts that: 1) reciprocal grooming should be immediate so that there will be no net underpayment by either party; 2) the amount of variance in grooming reciprocation explained should co-vary with the steepness of the power gradient for any particular group. In groups with more asymmetric power relationships, the possibility for interchange will be reflected in the dominant investing the minimum amount of grooming necessary to initiate a bout of received grooming that is equal to the value of the interchangeable

commodity (e.g. reduced food related aggression). Time-matching in grooming investment in such cases will be low; 3) time matching should become weaker as rank distance between individuals increases.

These predictions were tested in a study of two populations of chacma baboons (*P. cynocephalus ursinus*) in which different ecological conditions promoted large differences in levels of food related aggression and dominance gradients (Barrett *et al.*, 1999). Significant time matching was found in both groups, although for the group with the weakest power differentials, this was more pronounced. Rank distance influenced the degree of time matching in the more despotic population, as predicted by the model.

4.1.4 Grooming in chimpanzees

As with other primates, grooming is considered to play a major role in chimpanzee social strategies. Males are the philopatric sex and therefore have the strongest relationships. Males are more gregarious than females (Nishida, 1968; Halperin, 1979; Wrangham & Smuts, 1980; Goodall, 1986; Wrangham *et al.*, 1992; Pepper *et al.*, 1999) and generally spend more time grooming, mostly with other males (Nishida, 1968, 1979; Goodall, 1968, 1986; Simpson, 1973; Bygott, 1979; Wrangham, 1986; Nishida & Hiraiwa-Hasegawa, 1987; Watts, 2000a; *c.f.* Muroyama & Sugiyama, 1994). Females spend more time alone (or with their offspring) than males except when they are in oestrus, when they can become very social (Kortlandt, 1962; Reynolds & Reynolds, 1962; Riss & Buss, 1977; Sugiyama & Koman, 1979; Goodall, 1986; Furuichi & Ihobe, 1994).

Males groom with other males in order to establish and maintain alliances that help to influence their dominance ranks within their community (de Waal, 1982;

Goodall, 1986; Nishida & Hosaka, 1996). Female grooming relationships have received much less attention. Kin relationships among females have been shown to positively affect grooming frequency and duration at Gombe and Bossou (Goodall, 1986; Sugiyama, 1988). Generally, female-female grooming relationships are relatively uncommon, being less frequent than expected when compared with grooming frequencies generated according to sex ratios (Goodall, 1986; Wrangham *et al.*, 1994; Takahata, 1990a,b; Boesch & Boesch-Achermann, 2000). An exception to this tendency was reported by Sugiyama (1988) in his study of grooming relationship at Bossou, where female-female grooming was reported to occur at chance levels, probably due to the size of the study group which included a mean of only 2.5 adult males and 7 females. A similar trend was found in de Waal's (1986) study of captive chimpanzees at Arnhem Zoo, where a similar number of adult males (3) and females (8) may have resulted in female-female grooming being relatively common. Association and proximity have been shown to influence grooming rates in wild chimpanzees (Sugiyama, 1988; Boesch & Boesch-Achermann, 2000). This is not at all surprising since individuals that often associate with one another have more opportunities to groom than those who do not. Most studies have shown that females tend to spend relatively little time in parties (Nishida, 1979; Ghiglieri, 1984; Goodall, 1986; Wrangham *et al.*, 1992; Boesch & Boesch-Achermann, 2000) and so groom less.

It is thought that there is little need for wild females to form alliances via grooming relationships or other means, as they do not appear to compete amongst themselves once they have established adequate core areas (Pusey, 1980; Goodall, 1986; Nishida, 1989; Baker & Smuts, 1994). Competitive interactions are rare compared to males (de Waal, 1982; Goodall, 1986; Fawcett, 2001; *c.f.* Wrangham *et*

al., 1992) and are not always a good predictor of rank (Bygott, 1979; de Waal, 1982) although rank does appear to be an important component of female reproductive success (Pusey, *et al.*, 1997). Nonetheless, females have been reported to form coalitions in captivity that have been described as 'familiarity-dependant' by de Waal (1978, 1984) with support being given to the more familiar of the two individuals involved in a conflict. Here, female support strategies primarily serve to maintain the status quo. In another study of captive chimpanzees (Baker & Smuts, 1994) opportunistic coalitions were observed, thereby weakening the link between support choices and social bonds in females. Data concerning reciprocation and interchange of grooming for other services is lacking for wild female chimpanzees. However, the low grooming rates that are reported suggest that the social function of grooming among females is far less important than it is for males and may be restricted to the maintenance of kin orientated social relations.

Male-female grooming is more variable between communities. Again, this is likely to be due to differences in demography and association patterns. Boesch & Boesch-Achermann (2000) consider these factors to be important in the distribution of grooming in wild chimpanzees more generally. They note that male-female grooming is not centred around the highest-ranking (male) individuals at Taï but that males show marked preferences in their choice of female grooming partners, independent of associations. The males that were the most active groomers of females were not high-ranking males but those which hunted regularly. It seems likely that these males followed a strategy for reproductive success that involved the giving of services in return for access to females rather than the more commonly cited rank orientated route. Although males and females do sometimes have 'special' affiliative relationships, male-female interactions are most frequent when they involve females,

which are in oestrus. Oestrus females associate frequently in mixed sex parties. In Takahata's (1990a) study of male-female relationships at Mahale, both males and oestrus females were active in maintaining close proximity to one another. The alpha male was the most active in this respect. He approached oestrus females often and had symmetrical grooming relationships with them. Young males also had fairly symmetrical grooming relationships with females but other prime males groomed oestrus females more frequently than they were groomed by them. Oestrus females were primarily responsible for maintaining proximity with non-alpha males.

Among chimpanzees, male-male grooming patterns should perhaps most closely resemble those of female Old World primates. Males are philopatric and form discernible and reasonably linear dominance hierarchies (Hayaki, 1989, 1990; Takahata, 1990b; Newton-Fisher, 1997) although when the number of males in a community is large, dominance relationships can be ambiguous (Bygott, 1979; Nishida & Hosaka, 1996; Watts, 2000b). Consequently, males vary in their quality as potential allies and competition for alliance partnerships should influence grooming relationships (Watts, 2000a). Evidence that males sometimes interfere with male-male grooming bouts gives support to this hypothesis (de Waal, 1982, 1984). Group size might affect grooming distributions, since finite time-budgets should impose constraints on the number of possible grooming partners. As group size increases, so does the number of potential grooming partners, allies and competitors. Males might then continue to groom with all possible partners, although the amount of time available to devote to each partner will decrease with increased group size; alternatively, they might prioritise grooming of a subset of all possible partners so maintaining those relationships, then groom others only if time allows (Dunbar, 1984, 1991). It is likely that increased competition for grooming partners would force males

to groom at elevated rates as the market value of grooming partners increases (Dunbar, 1984, 1991). Increased competition might also result in less reciprocal grooming relationships (Hemelrijk & Luteijn, 1998) and a shift toward differentiated trader classes within dyads of the type described in section 4.1.3.2. In this case, the lower-ranking member of the dyad will be a grooming trader and the higher-ranking will be a support trader.

Competition for allies among male chimpanzees has received much attention (de Waal, 1978, 1982; Nishida, 1983; Nishida & Hosaka, 1996) but only very recently has the possibility of an exchange of grooming for support been investigated. Watts (2000a) compared grooming distributions of males within a large community (Ngogo, Kibale) with those of a much smaller community (M group, Mahale). He found that the number of male grooming partners was comparable between groups despite the Ngogo community having between 24 and 25 males while M group had only 9. Grooming was equally diverse between groups, i.e. given the number of available males, the proportion of grooming given to, or received from, each grooming partner was similar. However, the Ngogo males groomed less equitably, i.e. they concentrated their grooming effort on a smaller subset of their grooming partners. Males of both communities devoted 10% of their grooming to 3 partners. Grooming reciprocity was demonstrated in both groups. As at other sites (Gombe: Goodall, 1968, 1986; Simpson, 1973; Mahale: Nishida, 1979; Nishida & Hosaka, 1996; Kanyawara, Kibale: Wrangham *et al.*, 1992) males groomed other males more than females. In fact, Ngogo males groomed almost exclusively with other males, possibly due to intense competition for allies combined with time-budget constraints (Watts, 2000a) but possibly due to the fact that females were less habituated than males. Grooming with adolescent males was also uncommon. Again this could be due to the

same constraints operating on male choice of grooming partners. Interchange of grooming for tolerance may have operated during one period in which adolescent males groomed the alpha male often and were tolerated by him. Otherwise, most grooming between adults and adolescents involved low-ranking adult males. Grooming predominately was directed up the hierarchy. High-ranking males had many male grooming partners and received more grooming than low-ranking males (Watts, 2000b). Grooming was also more common among males that were close in rank. Rank and rank distance, however, were not good predictors of grooming distribution for the M group males. Males formed alliances (Watts, 1998) and often groomed with their alliance partners (Watts, in prep.).

Watts (2000b) also tested a number of priority of access models including Seyfarth's (1977) and those of Sambrook *et al.* (1995) described in section 4.1.2.1. Data concerning the Ngogo males strongly supported the attraction-to-high-rank, rank-distance and rank-difference models, but support for the interference and engagement models was weak or non-existent when grooming reciprocity and association frequency was taken into account. The M group data did not support any of the models.

The first aim of this chapter is to describe grooming behaviour in the Sonso community of chimpanzees, comparing my findings with those from other wild chimpanzee communities. This will help build a much needed descriptive base, essential if comparative studies are to identify general patterns of chimpanzee social behaviour and, more generally, grooming behaviour in primates. At present, one very common conclusion drawn from studies of wild chimpanzees is that different populations at different times are highly variable. As yet, we do not know the extent of this variability for grooming. A secondary aim of the chapter is to examine the extent

to which models of rank-related grooming distributions predict grooming relationships among these males during a relative stable period.

4.2 Methods

For information regarding the study site, subjects and sampling regime, see Chapter 2.

4.2.1 Data collection

Data on grooming interactions presented here were primarily collected using scan sampling methods at 15 minute intervals. The identities of any individuals that were observed self-grooming or allogrooming were recorded together with those of their grooming partners. Focal samples of 30 minute duration were collected on focal subjects in order to ascertain grooming durations and frequency of grooming bouts both for self-grooming and allogrooming. Grooming bouts in which both partners allogroomed simultaneously were recorded as bouts or instances of 'mutual grooming'.

4.2.2 Data Analysis

The amount of time spent grooming by each individual or within each dyad was based on 1841 scan samples. I calculated the percentage of each individual's grooming time, given and received, by a particular individual or class of individuals from the total number of scans during which he groomed, or was groomed. Data drawn from focal samples should have provided a better estimate of the amount of time involved in grooming interactions but this data set was much smaller than that based on scan samples and consequently provides information on fewer dyadic grooming partner relationships. However, there was good agreement between the data

set based on scan samples and that based on focal samples. The distribution of grooming given and received according to scan sample data correlated significantly with the number of grooming bouts in which grooming was given and received (grooming given: $K_r = 580$, $\tau_{Kr} = 0.633$, $p < 0.0002$; grooming received: $K_r = 467$, $\tau_{Kr} = 0.543$, $p < 0.0002$) and with grooming duration, given and received (grooming given: $K_r = 482$, $\tau_{Kr} = 0.551$, $p < 0.0002$; grooming received: $K_r = 438$, $\tau_{Kr} = 0.522$, $p < 0.0002$) according to focal samples. Therefore scan sampling data were considered to provide the most accurate representation of grooming distributions within the community as a whole and allowed a realistic representation of grooming interactions involving females, in particular, in mixed sex parties at least.

Dyad-corrected scores of time spent grooming were used throughout in order to take account of the variation in the amount of time dyads had access to one another as grooming partners, i.e. the amount of time spent in the same party. Details of the rationale for using this method and its implementation are given in Chapter 3.

I measured the diversity of individuals which males groomed, or were groomed by, using the Shannon-Weaver information index (Dunbar, 1984):

$$H = p_i \times \ln p_i,$$

in which p_i is the percent of a male's grooming given to or received from the i th male. H for each grooming partner was summed to give H' for either grooming given or received. Equitability takes into account variation in the distribution of grooming among grooming partners (Pielou, 1969):

$$E = H' / H_{max},$$

Where $H_{max} = \ln (1 / \text{number of individuals in the group})$. This index produces values between 0 (indicating complete equitability) and 1 (indicating that grooming is given to, or received from only one individual). In this case, the group consists of 15

individuals for analyses of male-male grooming, and 31 individuals for analyses of male-female grooming.

Grooming reciprocity occurred if individuals gave more grooming to those from whom they received more grooming (Hemelrijk, 1990a). I used Hemelrijk's MATRIXTESTER matrix permutation program to measure correlations between grooming given and received. MATRIXTESTER is an updated version of MATSQUAR and MATRECT (Hemelrijk, 1990a) combined into one program and contains an improved permutation procedure compared to MATSQUAR and MATRECT (C. Hemelrijk, pers. comm.). Matrix permutation methods avoid problems caused by the non-independence of dyads involving the same individual and unknown sampling distributions for data on dyadic interactions. They also avoid biases arising from individual variation in the tendency to direct certain kinds of acts to others (Hemelrijk, 1990a). Reciprocity can be *relative*, i.e., individuals groom others on an ordinal scale that corresponds to the rank order of grooming received from others, or *absolute*, i.e., individuals groom others at the same frequency or duration as they receive grooming from those others. Absolute reciprocity is expected to occur when individuals are similar in their capacities and inclinations to groom others but does not imply a directly proportional relationship between the performance and receipt of directed behaviour.

MATRIXTESTER calculates a number of association indices between an actor-receiver matrix and a receiver-actor matrix and then randomly permutes rows and columns to generate sampling distributions with which to establish the significance of test statistics derived from the original data matrix. I carried out these tests based on 5000 permutations in every case. The tests carried out by MATRIXTESTER are the K_r test, Mantel's Z test and the R test. The K_r test measures

relative reciprocity or interchange and gives a multivariate version of Kendall's S statistic corrected for individual variation and sample size, τ_{kr} (Hemelrijk, 1990a). Mantels' Z coefficient and R coefficient measure absolute reciprocity by assessing the symmetry in the matrices being tested. The R coefficient is a nonparametric version of the Z test and is used alongside the Z test to make up for any deficiencies of the Z test.

MATRIXTESTER also calculates Partial τ_{kr} for the association between two variables, with a second independent variable held constant (Hemelrijk, 1990b). This test was used (in combination with Kr test) when testing models of the distribution of grooming according to partner ranks in order to preclude the possibility that a fit between the actual distributions of grooming given or received and the distributions predicted by the models was not, in fact, due to reciprocity.

4.2.3 Hypotheses concerning grooming distribution according to partner rank

I tested a number of models which predict the distribution of grooming among partners according to rank (and therefore presumed attractiveness). These were:

1. *The attraction-to-high-rank model* (Seyfarth, 1976, 1977; Hemelrijk, 1990a; Sambrook *et al.*, 1995; Watts, 2000b): There is a positive association between amount of grooming given and partner rank. Grooming is given preferentially to higher-ranking partners over lower-ranking partners. An alternative version of this model generates a hypothesis matrix containing expected values of grooming given or received. The attractiveness of the grooming partner increases with rank and individuals groom others in proportion to their attractiveness. The top-ranked individual is unconstrained in his grooming preferences and grooms according to the attractiveness of all other individuals. The individual

ranked second is only constrained by the top-ranked individual; the third is constrained by the preferences of the two higher-ranking individuals etc. The attractiveness of each individual is calculated as:

$$\text{Attr} = (n + 1) - \text{rank}$$

where n is the number of individuals in the group. The expected percentage of grooming devoted by male #2 to male #1 in a group of four males is:

$$[\text{Attr } \#1 / (\text{Attr } \#1 + \text{Attr } \#3 + \text{Attr } \#4)] \times 100$$

2. *The engagement model:* a modification of the attraction-to-high-rank model based on an assumption that high-ranking males have priority of access to one another resulting in lower than expected amounts of grooming being directed towards them by middle and low-ranking individuals simply because the desired partner may already be engaged in a grooming bout (Seyfarth, 1977; Sambrook *et al.*, 1995; Watts, 2000b). It is assumed that each individual has a quota of 100 units of grooming time for grooming given, and 100 units for grooming received, and this will be filled up by higher-ranking individuals thus denying the lowest ranked individuals any opportunity to groom them. According to this model, the lowest-ranking individual may fail to fill his grooming quotas.
3. *The interference model:* this model was formalised by Sambrook *et al.* (1995) and assumes that an individual may not always groom another higher-ranking individual according to the idealised distribution predicted by the attraction-to high-rank model, as competition from other higher-

ranking individuals may interfere with his access to that individual. For the highest ranked individual, expected percentages are identical to those in the engagement model. For the individual ranked second, expected percentages are reduced for all individuals except the alpha, due to competition with the alpha for access to other partners, etc. The cell values are then scaled so that each animal gives and receives a grooming quota of 100 units. By allowing for competition for grooming partners, this model might be considered more realistic than the relatively idealised models above. Individuals groom higher-ranking individuals in inverse proportion to their ranks, but groom lower-ranking individuals in direct proportion to their ranks (Watts, 2000b). This model assumes that prior experience will inform decisions about partner choice and cause lower-ranking individuals to have more modest ambitions than higher-ranking animals in their choice of grooming partners.

4. *The rank-distance model:* as rank difference increases, grooming decreases due to attraction to high-ranking partners and competition for those partners (Seyfarth, 1977). The entries in the hypothesis matrix are the rank distance between pairs of individuals, plus one (Hemelrijk, 1990a; de Waal, 1991; Watts, 2000b).
5. *The rank-difference model:* Sambrook *et al.* (1995) modified the rank-distance model such that variation in rank-related partner attractiveness is taken into account. The entries in the engagement model hypothesis matrix are divided by the absolute value of the rank distance between partners when the groomee is ranked higher than the groomer. These values are then scaled so that each individual gives and receives 100 units of

grooming and then converted to represent percentages of expected grooming for each dyad. Thus the higher ranked of two equidistant partners may receive less grooming than the lower ranked partner due to competition from other high-ranking individuals.

4.3 Results

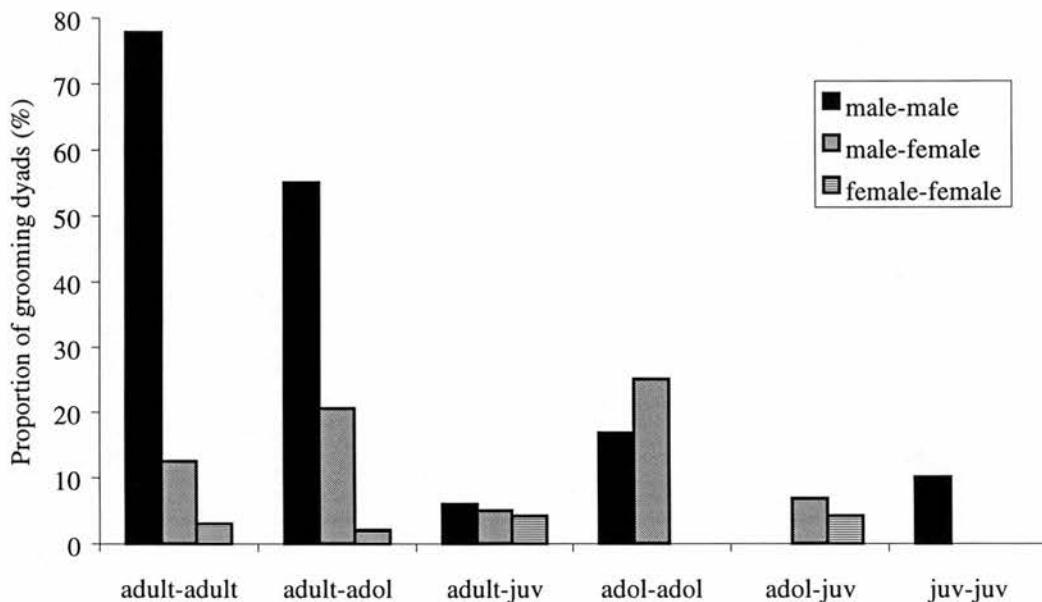
4.3.1 Self-grooming

All of the male focal subjects regularly engaged in self-grooming and this activity occupied between 3 and 19 % of their time budgets (mean = 9.4%). Adult and adolescent males self-groomed for, on average, 10.3% and 10.8% of their time respectively. Juvenile males devoted a smaller proportion of their time (6.4%) to self-grooming (Wilcoxon-Mann-Whitney test: adult-adolescent, $W_x = 36$, $N = 16$, NS; adult-juvenile, $z = 1.96$, $N = 16$, $p < 0.05$; adolescent-juvenile, $W_x = 26$, $N = 16$, $p < 0.1$). Rank did not affect time spent self-grooming when corrected for observation-time (Spearman rank-order correlation coefficient: $r_s = -0.1$, NS).

4.3.2 The effect of age and sex on the distribution of grooming

Grooming was observed in 14.0% of all possible dyads. Here, a grooming relationship is defined as one in which at least one member of the dyad groomed the other on at least one occasion. Grooming occurred in over a third of all male-male dyads (36.3%) compared to 11.0% of all male-female dyads. Grooming among female-female dyads was rare (3.0%). Most adult males had grooming relationships (77.8% of adult male-male dyads), and just over half of all adult male-adolescent male dyads groomed (55%). Grooming also occurred in 25.0% of adolescent male-

Figure 4.1 The proportion of dyads in each age-sex class that had grooming relationships (adol = adolescent, juv = juvenile).



adolescent female dyads. Of the remaining age-sex combinations, the most notable were the number of grooming dyads among adult male-adolescent female dyads (20.5%), and adolescent male-adolescent male dyads (16.7%). The remaining age-sex classes contained few grooming dyads (Figure 4.1). Thus, grooming was not distributed evenly among all age-sex classes. Adult males had on average 12.5 grooming partners of either sex (range = 7-17) of which 7 were adult males (range = 2-9). Adolescent males had 9 grooming partners (range = 6-13). Juvenile males had 3.4 grooming partners on average (range = 4-7). Adult females had only 2.7 grooming partners of either sex of which 1.3 were adult males (range = 0-4) and 0.17 were adult females (range = 0-1). Adolescent females had 5.5 grooming partners (range = 4-7) and 3.5 of these were adult males (range = 0-5). Juvenile females had 1.3 grooming

Table 4.1 Observed and expected frequencies of grooming, given and received by individuals of all age/sex classes.

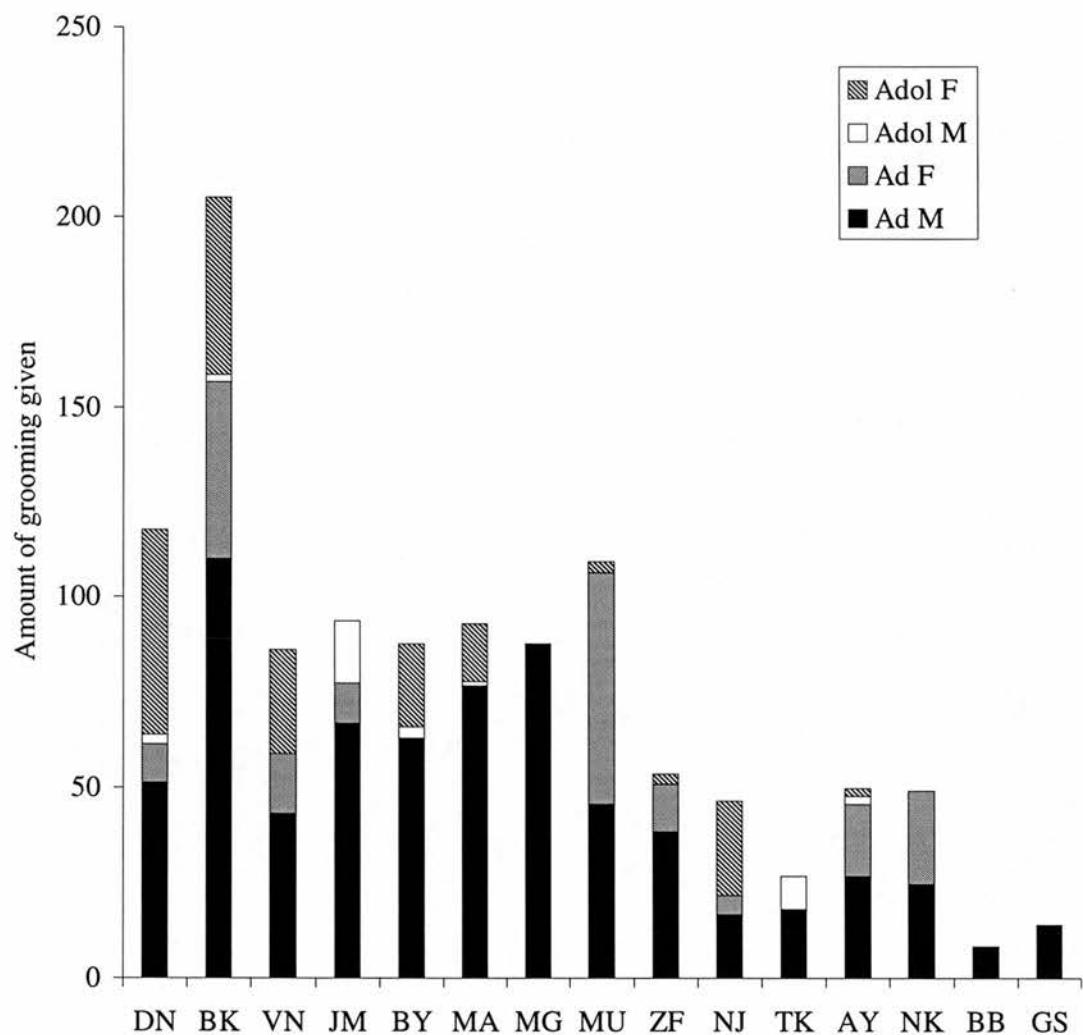
Given	Received					
	Ad M	Adol M	Juv M	Ad F	Adol F	Juv F
Ad M	579 (113) ***	33 (101) ***	1 (126) ***	148 (301) ***	192 (101) ***	6 (150) ***
Adol M	99 (101) ***	2 (14) ***	0 (49) ***	35 (122) ***	5 (41) ***	5 (60) ***
Juv M	12 (126) ***	0 (49) ***	10 (25) **	22 (150) ***	0 (49) ***	7 (76) ***
Adult F	100 (301) ***	60 (122) ***	435 (150) ***	13 (165) ***	5 (122) ***	48 (181) ***
Adol F	126 (101) *	37 (41) ***	0 (49) ***	5 (122) ***	0 (14) ***	23 (60) ***
Juv F	0 (150) ***	16 (60) ***	0 (76) ***	17 (181) ***	14 (60) ***	0 (37) ***

Ad = Adult; Adol = Adolescent; Juv = Juvenile; M = Male; F = Female. Expected frequencies are given in parentheses. Probabilities associated with the results of Chi-square goodness-of-fit tests (Yates' correction applied) are given as: * = $p < 0.02$; ** = $p < 0.01$; *** = $p < 0.001$.

partners (range = 0-4).

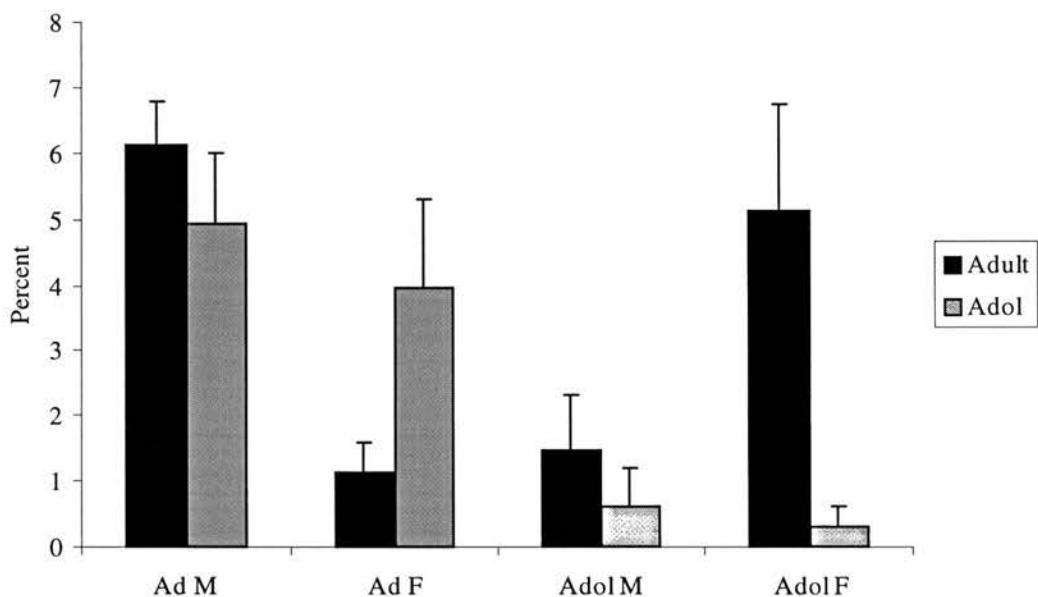
Grooming given and received was not evenly distributed among all age/sex classes and differed from expected frequencies ($\chi^2 = 470607$, df = 25, $p < 0.001$) where expected frequencies of grooming were calculated by multiplying the total amount of grooming by the proportion of dyads of each age/sex class. Table 4.1 gives the amount of grooming given and received by all age/sex classes and indicates which age/sex combinations contribute to differences between observed and expected frequencies.

Figure 4.2 Amount of grooming (dyad-corrected) given by each male to individuals of different age/sex classes. Males are arranged in rank order. Ad M = adult male, Ad F = adult female, Adol M = adolescent male, Adol F = adolescent female.



Overall, individual adult males invested the majority of their grooming effort in other adult males (61.6%). Adolescent females accounted for 18.6% of adult males' grooming and adult females, for 15.6%. The least amount of grooming was invested in adolescent males (4.3%). Figure 4.2 shows the amount of grooming invested by all males, including adolescent and juvenile males, in other adult and adolescent males and adult and adolescent females. These proportions are meaningful, but they do not properly reflect grooming effort as a measure of the potential value of each class of individual. While there were approximately equal numbers of adult males and adult females in the community (10 and 12), there were only 4 adolescent males and 4 adolescent females. A better reflection of investment takes these proportions into account by dividing individual investment by the number of members of each age and sex class. After this correction, individual adult males still invested the majority of their grooming time in other adult males (mean = 6.1% per male), and significantly less in adult females (mean = 1.1% per female. Wilcoxon signed ranks test: $T^+ = 54$, $N = 10$, $p = 0.002$) and adolescent males (mean = 1.4% per male. $T^+ = 54$, $N = 10$, $p = 0.002$). But, they invested a mean of 5.1% of their grooming effort in each *adolescent* female; not significantly less than in other adult males ($T^+ = 34.5$, $N = 10$, NS). Adolescent males also groomed adult males most, but groomed adolescent females least. They also differed from adult males in that they groomed individual adult females twice as much as adult males did (adult males: mean = 6.9%; adult females: mean = 2.3%; adolescent males: mean = 0.6%; adolescent females: mean = 0.3%. Figure 4.3), although sample sizes were too small to show significant differences between age/sex classes. The orphaned juvenile, GS, only groomed three adult males ranked 9th, 11th and 12th in the dominance hierarchy. It should be noted that GS was the only juvenile male observed to have grooming relationships with adult males. No

Figure 4.3 Mean percentage of grooming time per individual that adult and adolescent males devoted to different age and sex classes (corrected for the number of individuals with each age and sex class). Ad = adult, Adol = adolescent, M = male, F = female.



juvenile male had grooming relationships with adolescent males.

We now consider the types of individuals from which males received grooming. Overall, individual adult males received most grooming from other adult males (57.4%). They received 17.8% of grooming from adolescent females and 15.3% from adult females. Males received the least amount of grooming from adolescent males (8.1%). All proportions are very similar to those reported for grooming investment by males. Figure 4.4 shows the amount of grooming received by males from adult and adolescent, males and females. Again, the mean proportion of grooming received by members of each age/sex class was calculated by applying the correction described above. Individual adult males received most grooming from other adult males (mean = 6.4% per male), and significantly less from adult females (mean

Figure 4.4 Amount of grooming (dyad-corrected) received by each male from individuals of different age/sex classes. Males are arranged in rank order. Ad M = adult male, Ad F = adult female, Adol M = adolescent male, Adol F = adolescent female.

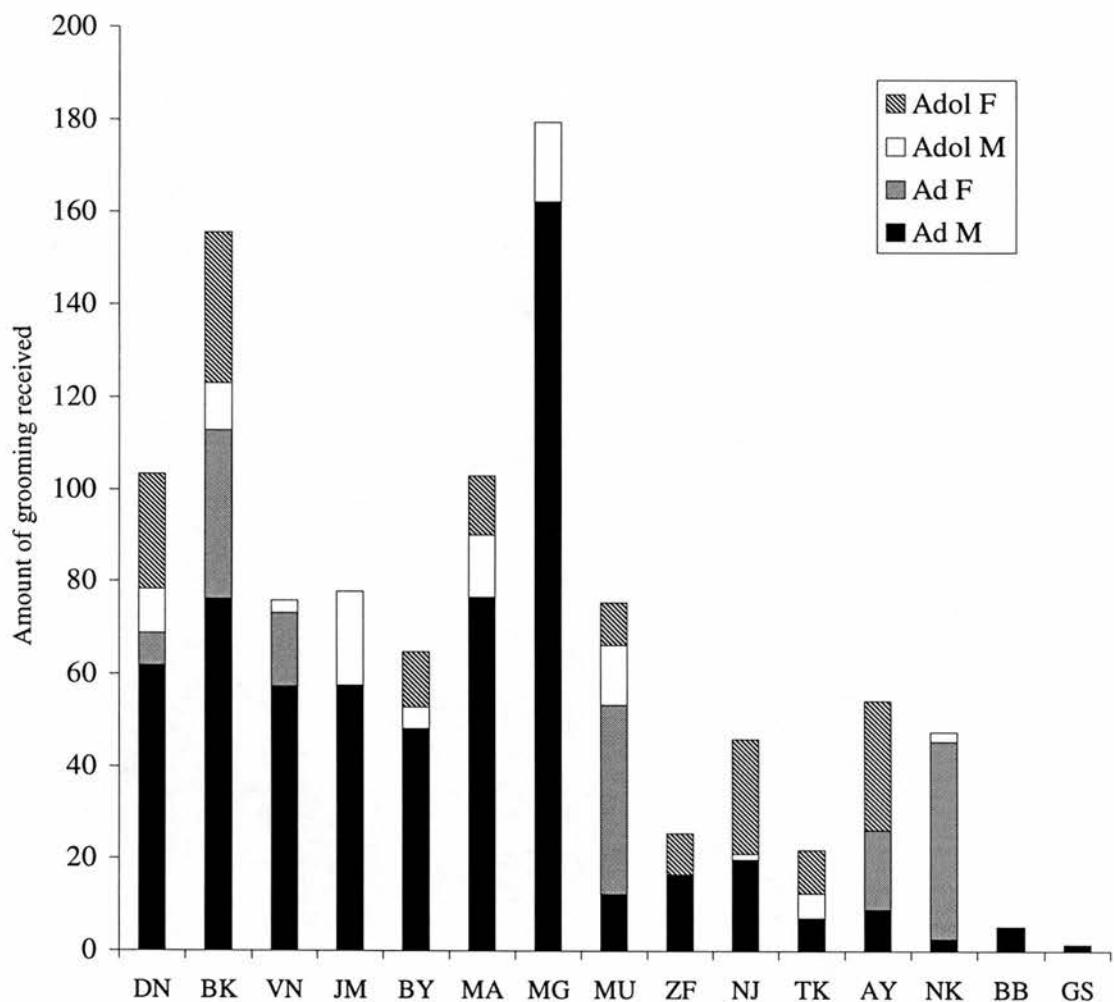
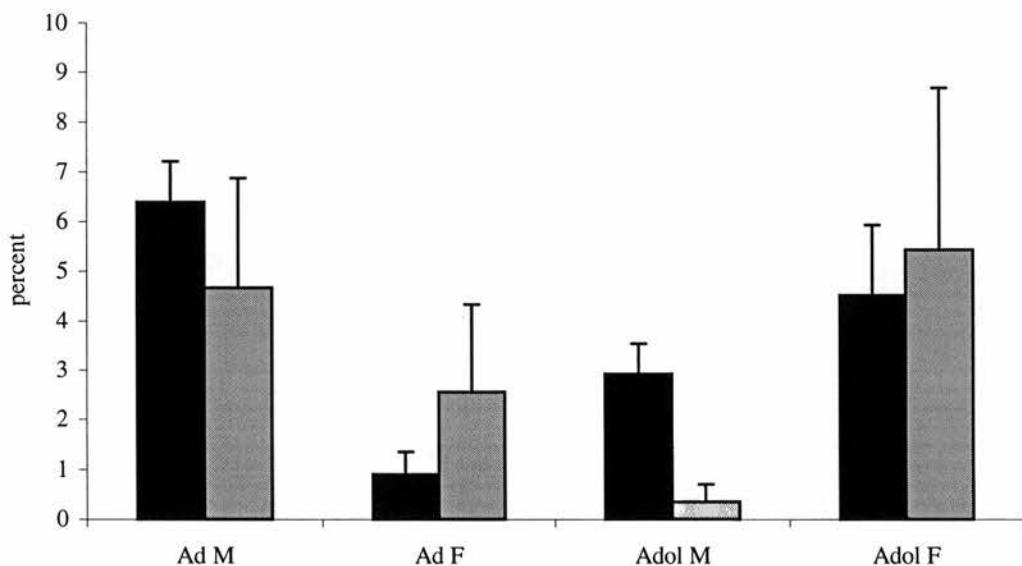


Figure 4.5 Mean percentage of grooming received by adult (black bars) and adolescent males (grey bars) from members of each age/sex class (corrected for the number of individuals with each age and sex class). Ad = adult, Adol = adolescent, M = male, F = female.



= 0.9% per female. Wilcoxon signed ranks test: $T^+ = 54$, $N = 10$, $p = 0.002$) and adolescent males (mean = 2.9% per male. $T^+ = 52$, $N = 10$, $p = 0.005$). Males received 4.5% of their grooming from each adolescent female; not significantly less than from other adult males ($T^+ = 27$, $N = 10$, NS). Adolescent males differed from adult males in so far as each adolescent female contributed more to their grooming, on average, than they contributed to adult males (grooming received from adolescent females: mean = 5.4%; adult males: mean = 4.7%; adult females: mean = 2.6%; adolescent males: mean = 0.4%; adolescent females: Figure 4.5). The juvenile GS only received grooming from one adult male, MA, who was ranked 6th in the male hierarchy.

4.3.3 The effect of sex on diversity and equitability in grooming distribution

Despite similar numbers of male and female subjects (male = 15; female = 16), males gave and received grooming from a greater diversity of male partners than female partners (grooming given: male-male v male-female, $H' = 1.55$ v 0.85 , $T^+ = 76$, $N = 12$, $p = 0.0007$; grooming received: male-male v male-female, $H' = 1.47$ v 0.54 , $T^+ = 75$, $N = 12$ $p = 0.0012$, Figure 4.6). The mean diversity of male-male grooming given was slightly higher than for grooming received although this difference was not significant (grooming given v received, $H' = 1.55$ v 1.47 , $T^+ = 65.5$, $N = 15$, NS). Males gave grooming to a wider range of females than that from which they received grooming (grooming given v received, $H' = 0.85$ v 0.54 , $T^+ = 49$, $N = 10$, $p = 0.014$).

The distribution of grooming among partners was more equitable for male-male dyads than for male-female dyads (grooming given: male-male v male-female, $E = 0.57$ v 0.31 , $T^+ = 76$, $N = 12$, $p = 0.0007$; grooming received: male-male v male-female, $E = 0.67$ v 0.19 , $T^+ = 76$, $N = 12$ $p = 0.0007$, Figure 4.7). The mean equitability for male-male grooming given was slightly lower than for grooming received but the difference was not significant ($T^+ = 54$, $N = 15$, NS). The mean equitability of grooming given to females was significantly lower than for grooming received from females ($T^+ = 49$, $N = 10$, $p = 0.014$).

A previous study compared the diversity and equitability of grooming distributions among 22-24 adult males from the Ngogo community in Kibale during two study periods in 1995/1996 and 1997, and 9 adult males from M group in Mahale (Watts, 2000a). These three data sets gave mean diversity values of approximately 1.8, 1.5 and 1.7 for grooming given and 1.8, 1.5 and 1.65 for grooming received, respectively. For comparative purposes, I calculated diversity among the adult males of Sonso. Mean diversity among the adult males for grooming given was 1.49, and

Figure 4.6 The mean diversity (H') of grooming partners, both for grooming given and received, for male-male and male-female dyads.

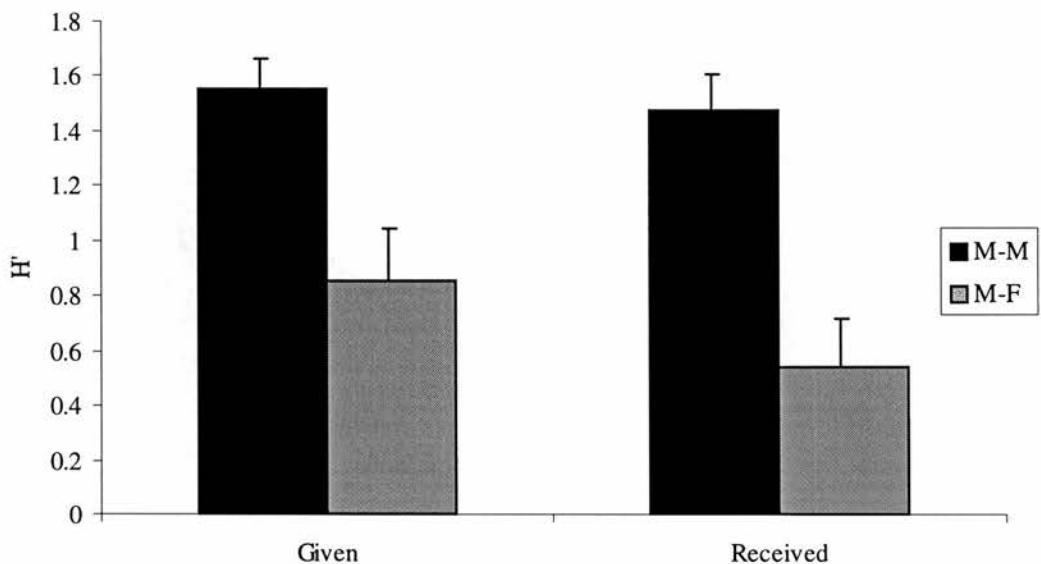
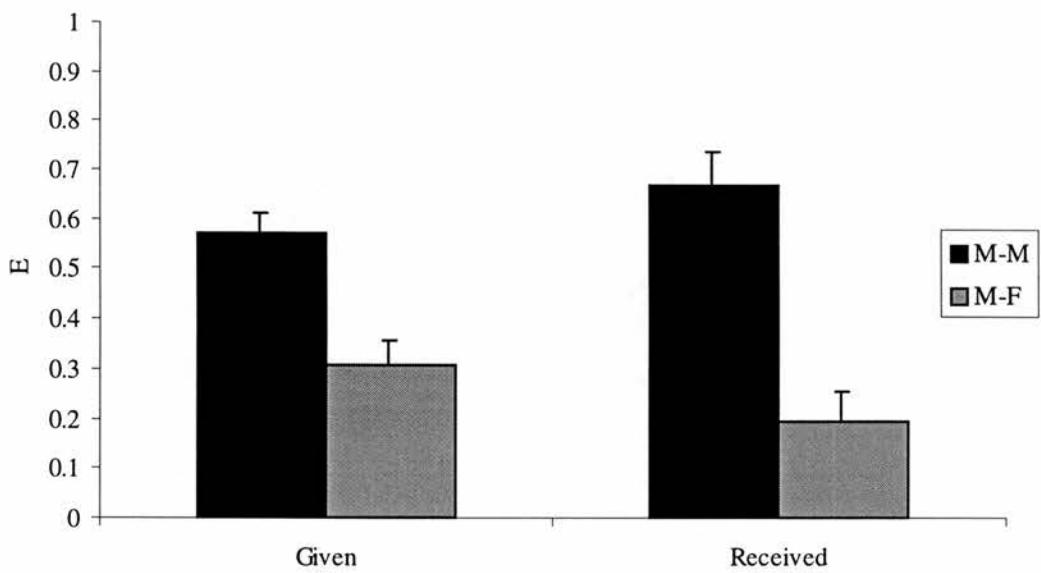


Figure 4.7 The mean equitability (E) of grooming partners, both for grooming given and received, for male-male and male-female dyads.

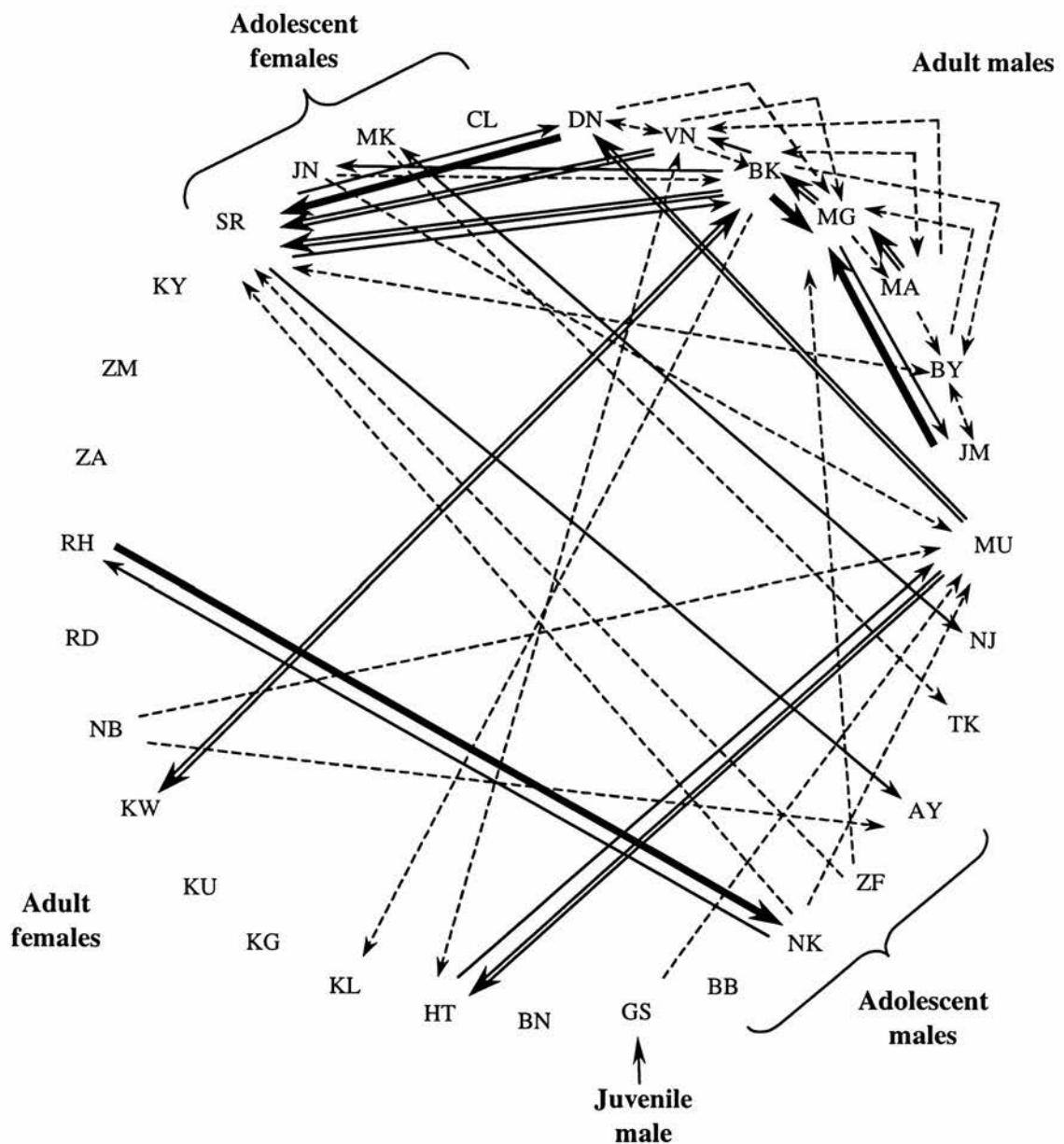


1.56 for grooming received. Mean equitability for Ngogo 1995/1996 and 1997, and Mahale was approximately 0.59, 0.49 and 0.78 for grooming given and 0.45, 0.49 and 0.62 for grooming received, respectively. For the Sonso males, mean equitability for grooming given was 0.65, and 0.38 for grooming received. On average, Ngogo males gave $\geq 10\%$ of their grooming to 3.6 (1995/1996) and 3.2 (1997) partners and received $\geq 10\%$ of their grooming from 3.7 and 3.2 partners respectively. Mahale males gave $\geq 10\%$ of their grooming to 3.9 partners and received $\geq 10\%$ of their grooming from 3.2 partners (Watts, 2000b). The equivalent values for the Sonso males were 1 ± 0 partners for grooming given and 1 ± 0 partners for grooming received. Sonso males showed much clearer preferences for certain individuals despite similar diversity and equitability values to both the Ngogo and the Mahale males. In fact, 3 individuals accounted for a mean of $64.3 \pm 16.3\%$ of grooming given and $58.2 \pm 11.0\%$ of grooming received. For 2 males, *one* of their top 3 grooming partners were females and for 4 males, *two* of their top 3 grooming partners were females, for grooming given. For grooming received, 5 males had *one* female among their top 3 grooming partners, and 2 males had *two* females as two of their top 3 partners.

4.3.4 Distribution of grooming among individuals

Figure 4.8 shows the distribution of grooming among individuals. The strongest grooming relationships were those among the 7 highest-ranking males, and between these males and adolescent females. SR in particular was the focus of male grooming attention although she did not reciprocate the same level of grooming to those males that groomed her. BK, the 2nd ranked male, and MU, the 8th ranked male, received more than the average amount of grooming from 3 females each. BK also groomed 4 females at a high rate and therefore had the largest number of relatively

Figure 4.8 Sociogram of grooming given and received by all independent males and females: → indicates > 3sd above mean amount of grooming; → : indicates > 2sd above mean; → : indicates > 1sd above mean; → indicates above mean. Double-ended arrows indicate grooming is reciprocated at the same level.



intense grooming relationships with females. The previous alpha male, MG, was the centre of much grooming attention from other males although he did not reciprocate in most cases. Where he did reciprocate, he always received more grooming than he gave.

4.3.5 Reciprocity

All age/sex classes showed relative grooming reciprocity; that is individuals directed relatively more grooming towards those from which they received grooming more frequently, but did not necessarily return as much grooming as they received.

This high degree of grooming reciprocity was not at all surprising given that many grooming bouts were bi-directional, i.e. both partners groomed the other at the same time. Adult and adolescent males engaged in mutual grooming for 28.6% (s.d. = $\pm 9.4\%$), and 24.0% (s.d. = $\pm 5.3\%$), of their total grooming time, respectively. However, when mutual grooming scores were removed from the data set, grooming remained reciprocal between all age/sex combinations except adult male-adult female dyads, where asymmetries occurred but with no pattern in terms of which sex contributed more grooming.

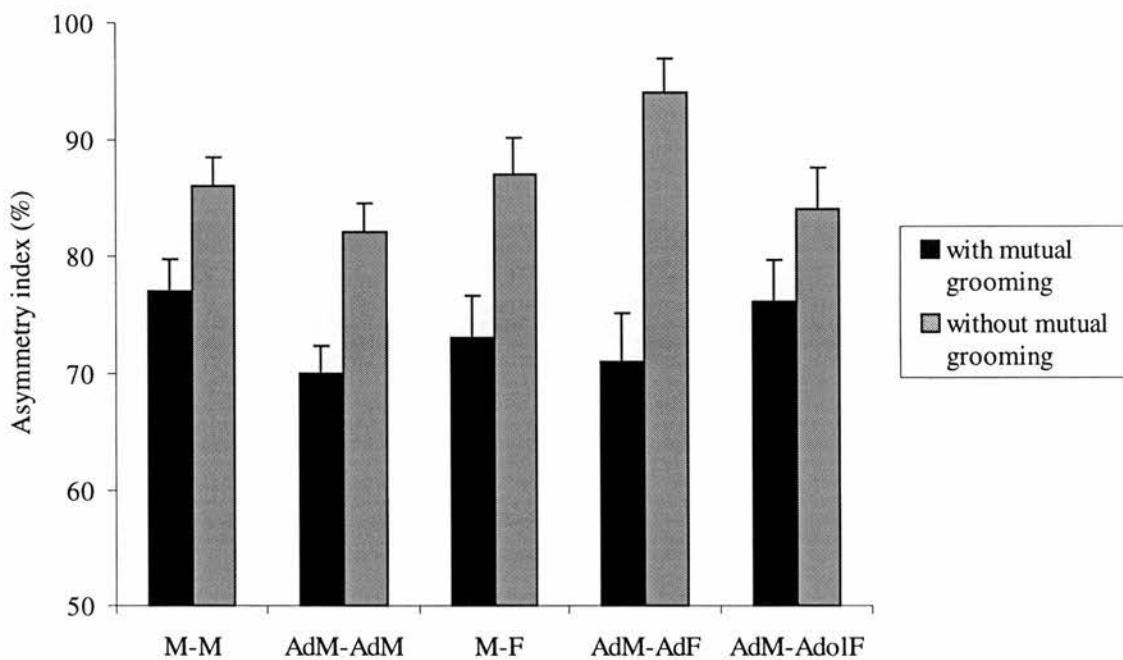
Reciprocity could be a by-product of association if individuals most often groom those with which they frequently associate. Both grooming given and received were significantly correlated with association frequency among male-male dyads (grooming given: $K_r = 223$, $\tau_{Kr} = 0.203$, $p < 0.0218$; grooming received: $K_r = 206$, $\tau_{Kr} = 0.196$, $p < 0.009$). Among male-female dyads the correlation between grooming given and association was significant but for grooming received, the correlation was not quite significant (grooming given: $K_r = 159$, $\tau_{Kr} = 0.202$, $p < 0.0378$; grooming received: $K_r = 117$, $\tau_{Kr} = 0.179$, $p < 0.0546$).

Table 4.2 Results of K_r correlation tests for grooming reciprocity among different age/sex classes. Tests are for correlations between grooming given and received. Results of Partial τ_{Kr} tests control for the influence of rank and association on grooming reciprocity. ‘Less mutual grooming’ indicates tests using data sets from which mutual grooming interactions have been removed. M = male; F = female; Ad = adult; Adol = adolescent.

Age/sex class	N	K_r	τ_{Kr}	p	Partial τ_{Kr}	p
No control						
M-M	15	505	0.557	0.0002	0.500	0.0002
Ad M-Ad M	10	230	0.561	0.0002	0.527	0.0002
Control for rank						
M-M					0.539	0.0002
Ad M-Ad M					0.557	0.0002
Control for association						
M-F	31	317	0.803	0.0002	0.796	0.0002
Ad M-Ad F	21	83	0.835	0.0004	0.803	0.0004
Ad M-Adol F	14	10	0.646	0.0190	0.656	0.0200
Less mutual grooming						
M-M	15	219	0.309	0.0004	0.284	0.0004
Ad M-Ad M	10	91	0.334	0.0006	0.311	0.0006
M-F	31	164	0.532	0.0002	0.513	0.0006
Ad M-Ad F	21	13	0.270	0.1226	0.119	0.2492
Ad M-Adol F	14	12	0.899	0.0098	0.897	0.0040

However, grooming reciprocity remained significant when association was controlled for using Partial correlation tests (τ_{Kr}) in all age/sex combinations. Neither was reciprocity among males influenced by male rank. However, the lack of reciprocity among adult male-adult female dyads when mutual grooming was removed from the data set was confirmed when association was controlled for. An asymmetry index (de Waal & Luttrell, 1988) was calculated for each dyad in order to determine the level of grooming reciprocity at the level of individual relationships.

Figure 4.9 Dyadic asymmetry indices for grooming among different age/sex combinations (mean and SE). M = male, F = female, Ad = adult, Adol = adolescent.



This index is defined as the amount of grooming given by the most frequent groomer in the dyad as a proportion of the total grooming given by both partners. For male-male grooming the mean asymmetry index for all grooming dyads = $77 \pm 21\%$; for adult male-male grooming = $70 \pm 18\%$; for male-female grooming = $73 \pm 22\%$; for adult male-adult female grooming = $71 \pm 25\%$; for adult male-adolescent female = $76 \pm 22\%$. A matrix correlation test comparing dyadic asymmetry indices with rank distance showed that grooming relationships were not more symmetrical among male-male dyads of similar rank ($K_r = 26$, $\tau_{K_r} = 0.059$, $p = 0.2667$).

When mutual grooming, which is inherently symmetrical, was removed from the data set, the asymmetry indices for all age/sex classes increased (see Figure 4.9).

For male-male grooming the mean asymmetry index for all grooming dyads = $86 \pm 19\%$; for adult male-male grooming = $82 \pm 19\%$; for male-female grooming = $87 \pm 17\%$; for adult male-adult female grooming = $94 \pm 15\%$; for adult male-adolescent female = $84 \pm 19\%$. This increase in asymmetry was significant for all of the dyadic age/sex combinations listed above except among all males (all male-male, $z = 0.68$, $N = 31$, NS; adult male-adult male, $z = 2.18$, $N = 23$, $p = 0.015$; all male-female, $z = 4.16$, $N = 18$, $p < 0.001$; adult male-adult female, $T^+ = 27$, $N = 7$, $p = 0.016$; adult male-adolescent female, $T^+ = 20$, $N = 6$, $p = 0.031$).

4.3.6 Effect of rank

Grooming tended to be directed up the hierarchy. Lower-ranking males tended to groom higher-ranking partners in 55% (34/62) of dyads in which grooming occurred. The reverse occurred in only 27% of dyads (17/62). The remaining dyads groomed each other equally often.

The ranks of all the independent focal males (adults, adolescents and the juvenile, GS) were strongly correlated with number of observed grooming partners ($r_s = -0.707$, $N = 16$, $p < 0.005$). Figure 4.10). This result was primarily due to the strong influence of rank on the number of male grooming partners ($r_s = 0.734$, $N = 16$, $p < 0.002$). Rank had only a weak effect on the number of female grooming partners ($r_s = 0.481$, $N = 16$, $p < 0.1$).

This result was mirrored by analyses of the effect of rank on grooming diversity (H'). High-ranking males gave grooming to more male partners than low-ranking males ($r_s = 0.544$, $N = 15$, $p < 0.05$). The effect of rank was much stronger when related to the diversity of male partners from which males received grooming ($r_s = 0.761$, $N = 15$, $p < 0.002$). Rank had no effect on the diversity of female grooming

Figure 4.10 The relationship between male rank and number of grooming partners, (a) all partners, (b) male grooming partners, (c) female grooming partners.

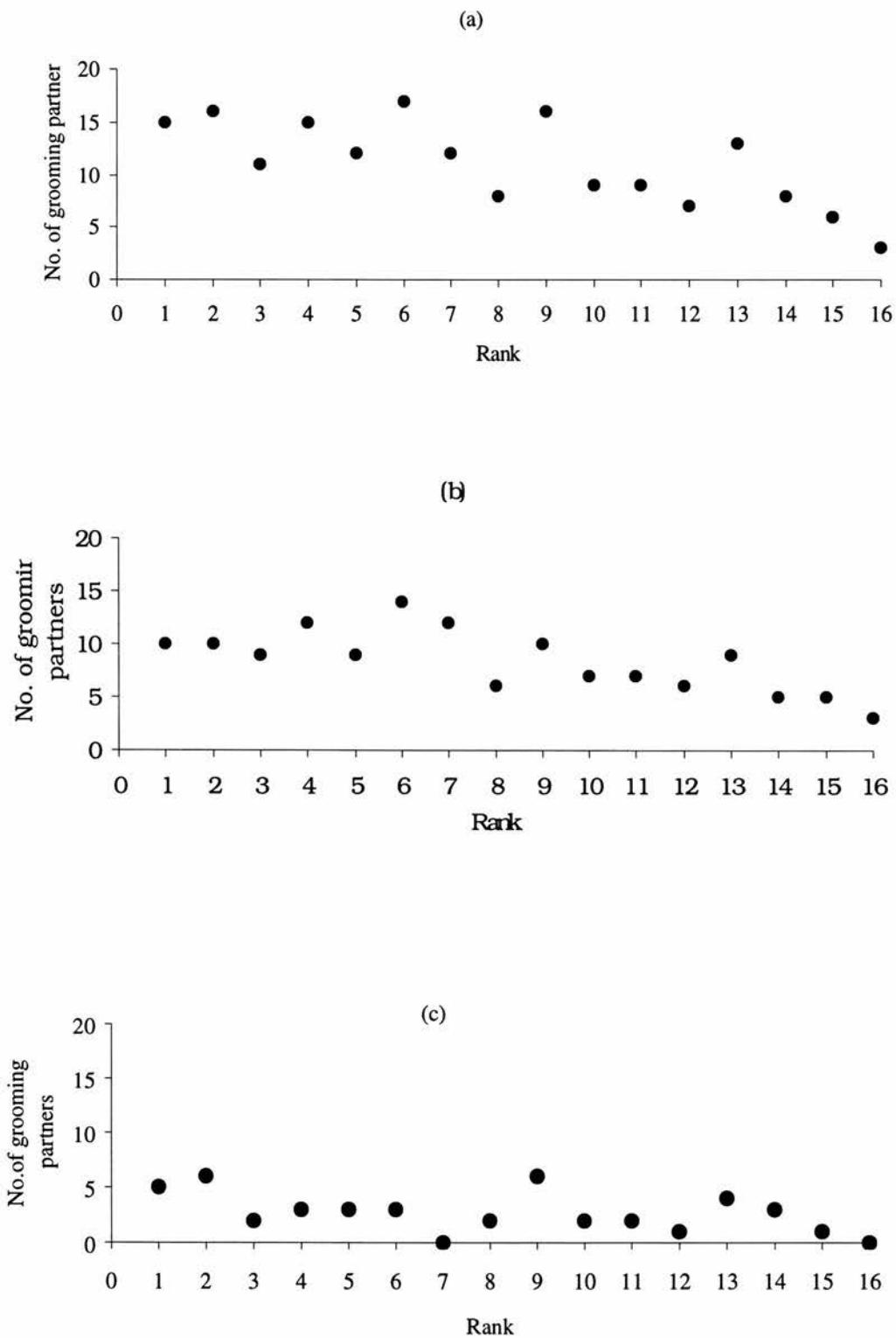
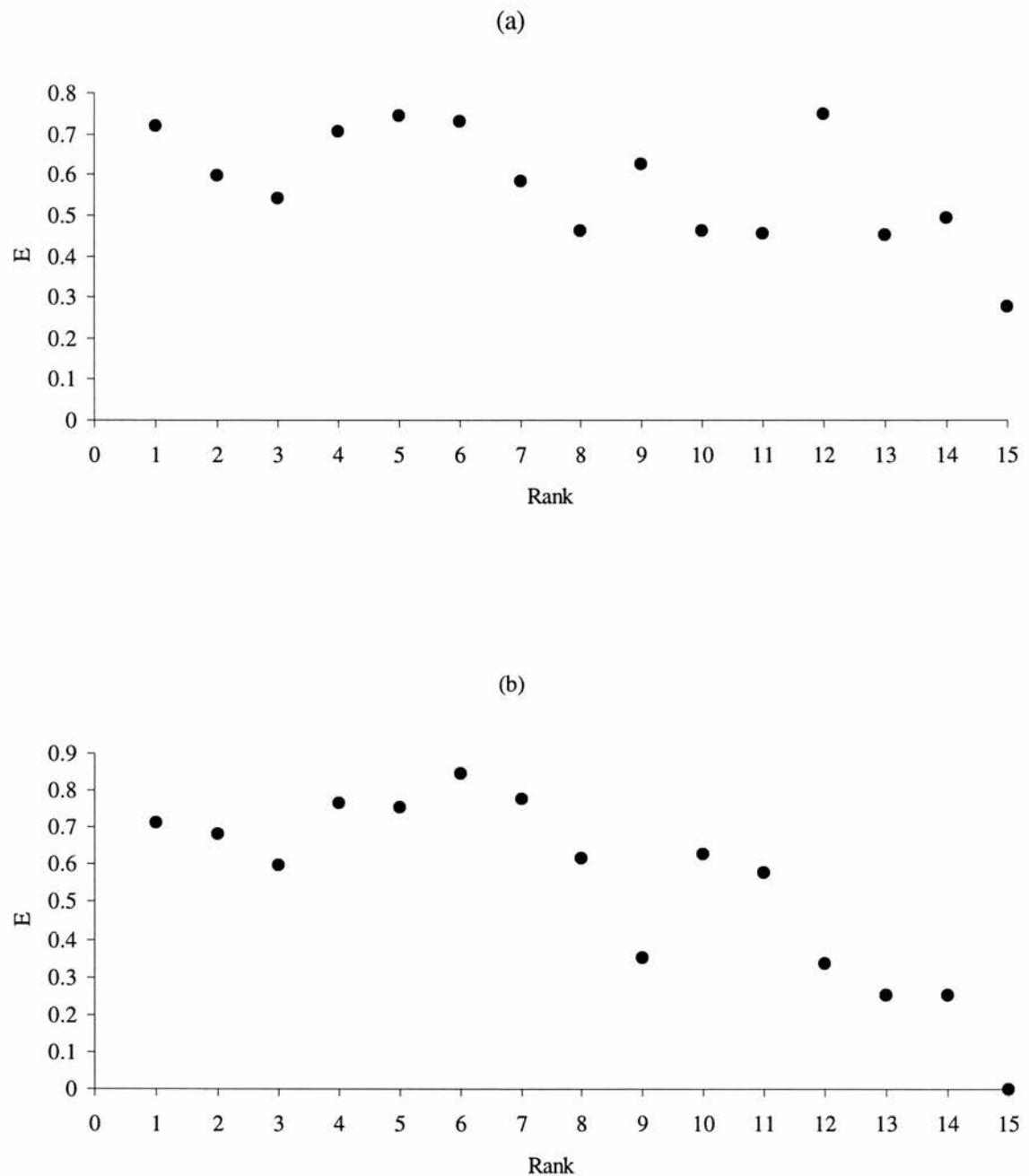


Figure 4.11 The effect of rank on Equitability for grooming (a) given, and (b) received for male-male dyads.



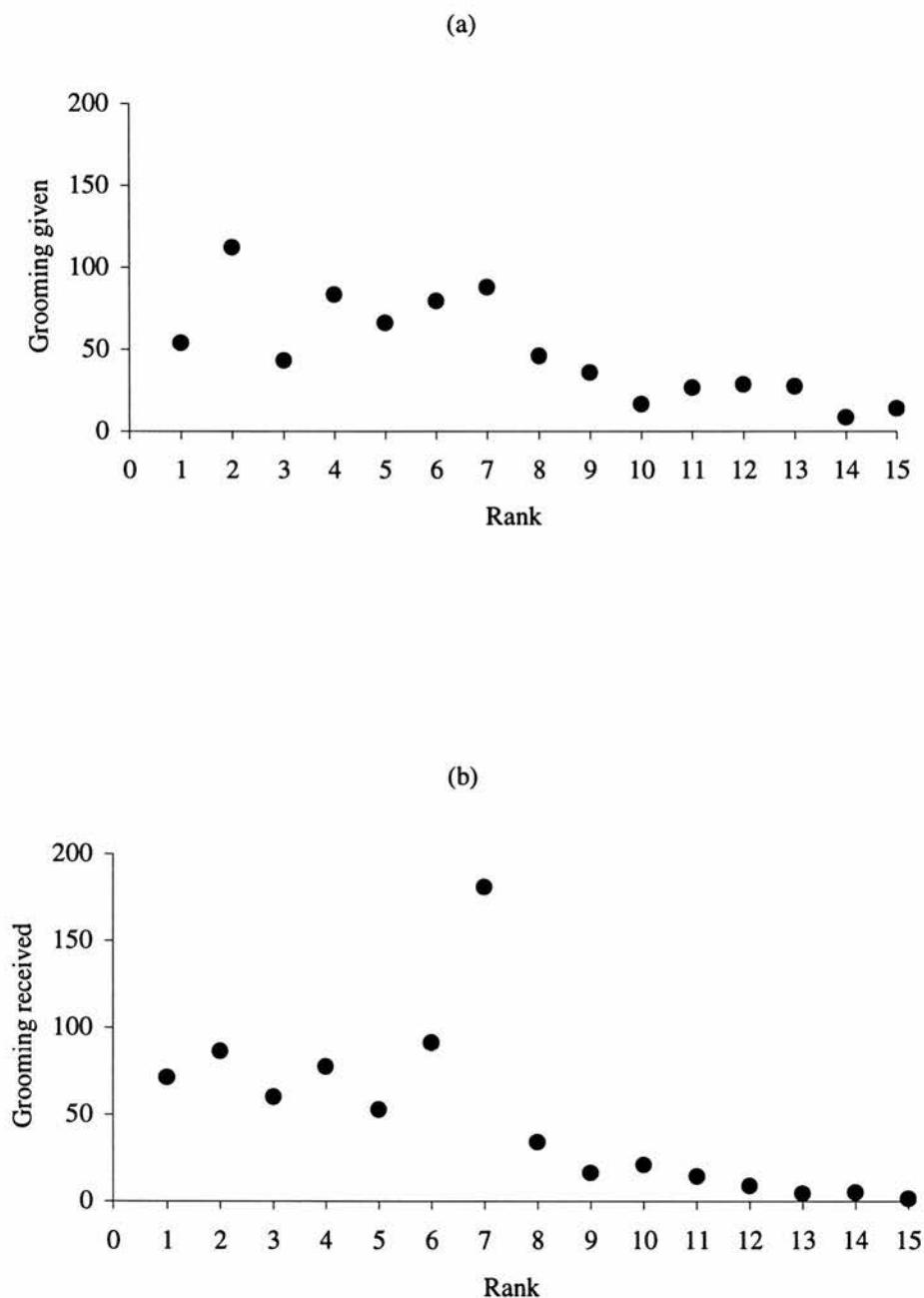
partners (grooming given: $r_s = 0.364$, N = 12, NS; grooming received: $r_s = 0.239$, N = 12, NS).

Rank had a very similar effect on equitability (E). High-ranking males distributed grooming given more equally among their male grooming partners than low-ranking males ($r_s = 0.539$, N = 15, $p < 0.05$). High-ranking males also received grooming more equitably from male grooming partners than low-ranking males ($r_s = 0.761$, N = 15, $p < 0.002$. Figure 4.11). Rank had no effect on the evenness of the distribution of grooming given or received in the case of female grooming partners (grooming given: $r_s = 0.371$, N = 12, NS; grooming received: $r_s = 0.239$, N = 12, NS).

However, when adult male dyads were considered alone, rank had no effect on either the diversity or equitability of grooming distributions (diversity: grooming given, $r_s = 0.548$, N = 10, NS; grooming received, $r_s = 0.221$, N = 10, NS. Equitability: grooming given, $r_s = 0.552$, N = 10; grooming received, $r_s = 0.248$, N = 10, NS).

The alpha male, DN, did not score highest on the number of grooming partners for males although he was among the males in the upper quartiles of the ranges for each sex combination. MA, ranked 6, had the largest male grooming network and the largest grooming network overall. BK, ranked 2, and MU, ranked 9, had more female grooming partners than any of the other males. Using dyad-corrected grooming scores, the amount of grooming given and received within male-male dyads was strongly influenced by rank when young males were included. High-ranking males gave, and received more grooming than low-ranking males (grooming given: $r_s = 0.811$, N = 15, $p < 0.001$; grooming received: $r_s = 0.864$, N = 15, $p < 0.001$. Figure 4.12) and this was confirmed by matrix correlation tests (grooming given: $K_r = -431$, $\tau_{Kr} = -0.383$, $p = 0.0008$; grooming received: $K_r = -330$, $\tau_{Kr} = -0.307$, $p = 0.0008$). For adult males only,

Figure 4.12 The effect of rank on the amount of grooming (a) given, and (b) received, within male-male dyads.



neither grooming given nor grooming received were correlated with male rank (grooming given: $r_s = 0.467$, N = 10, NS; grooming received: $r_s = 0.527$, N = 10, NS). The outlier shown in Figure 4.12b is MG (ranked 7), the previous alpha male, who was the recipient of the highest proportion of grooming given to any one individual by four out of the six highest-ranking males. High-ranking males also groomed females more than low-ranking males although the effect was much weaker than for male-male grooming (grooming given: $r_s = 0.614$, N = 15, $p < 0.02$). However, rank did not affect the amount of grooming received from females (grooming received: $r_s = 0.307$, N = 15, NS. Figure 4.13). When only adult males were considered, the effect of rank was reduced to a trend for grooming given (grooming given: $r_s = 0.564$, N = 10, $p = 0.1$; grooming received: $r_s = 0.0321$, N = 10, NS).

Most males (66.7%) gave more grooming than they received from other males. On average, in 64.1% of each male's male-male grooming dyads more grooming was given than received. The percentage of male-male grooming dyads in which each male received more grooming than he gave increased with male rank ($r_s = 0.575$, N = 15, $p < 0.05$. Figure 4.14). When adult males were considered alone, 50% gave more grooming than they received and in only 49.2% of each male's grooming dyads, more grooming was received than given. In this case the effect of rank was reversed. The percentage of adult male-male grooming dyads in which each male received more grooming than he gave decreased slightly with male rank although this relationship was not significant ($r_s = -0.358$, N = 15, NS. See Figure 4.14. Data points for adult males fall to the left of the dashed line).

Among the males, grooming was most likely between individuals of similar rank and became less likely as dyadic rank distance increased. The mean amount of grooming per dyad was significantly correlated with rank distance for both grooming

Figure 4.13 The effect of rank on the amount of grooming (a) given, and (b) received, within male-female dyads.

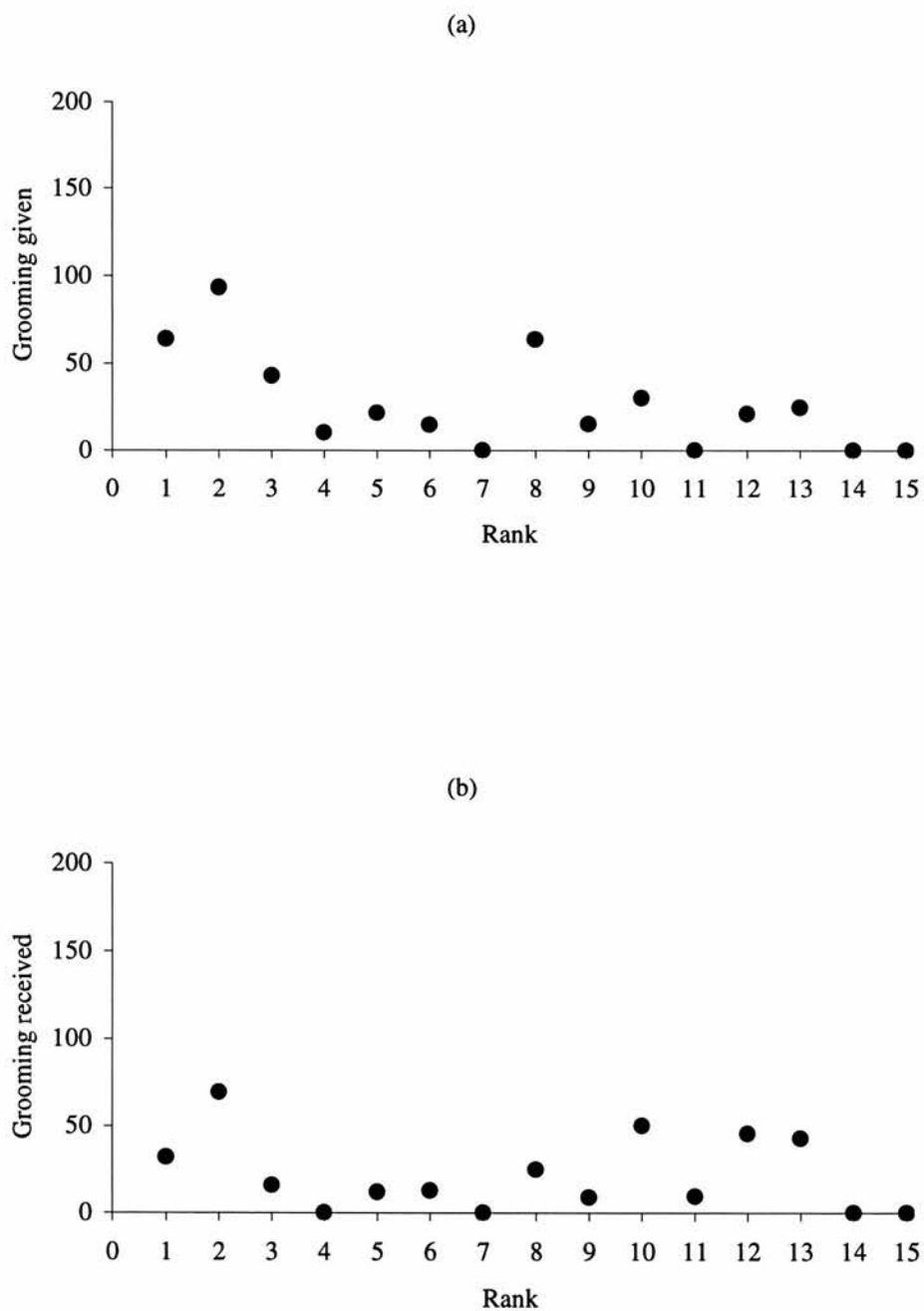
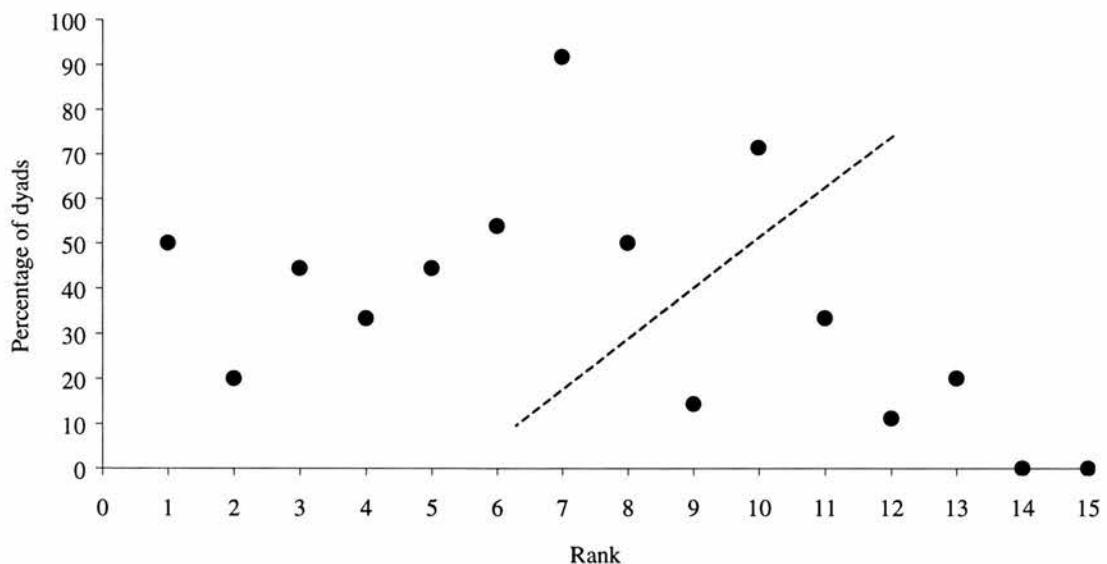


Figure 4.14 The percentage of each male's grooming dyads in which more grooming is received than given. Adult males fall to the left of the dashed line.



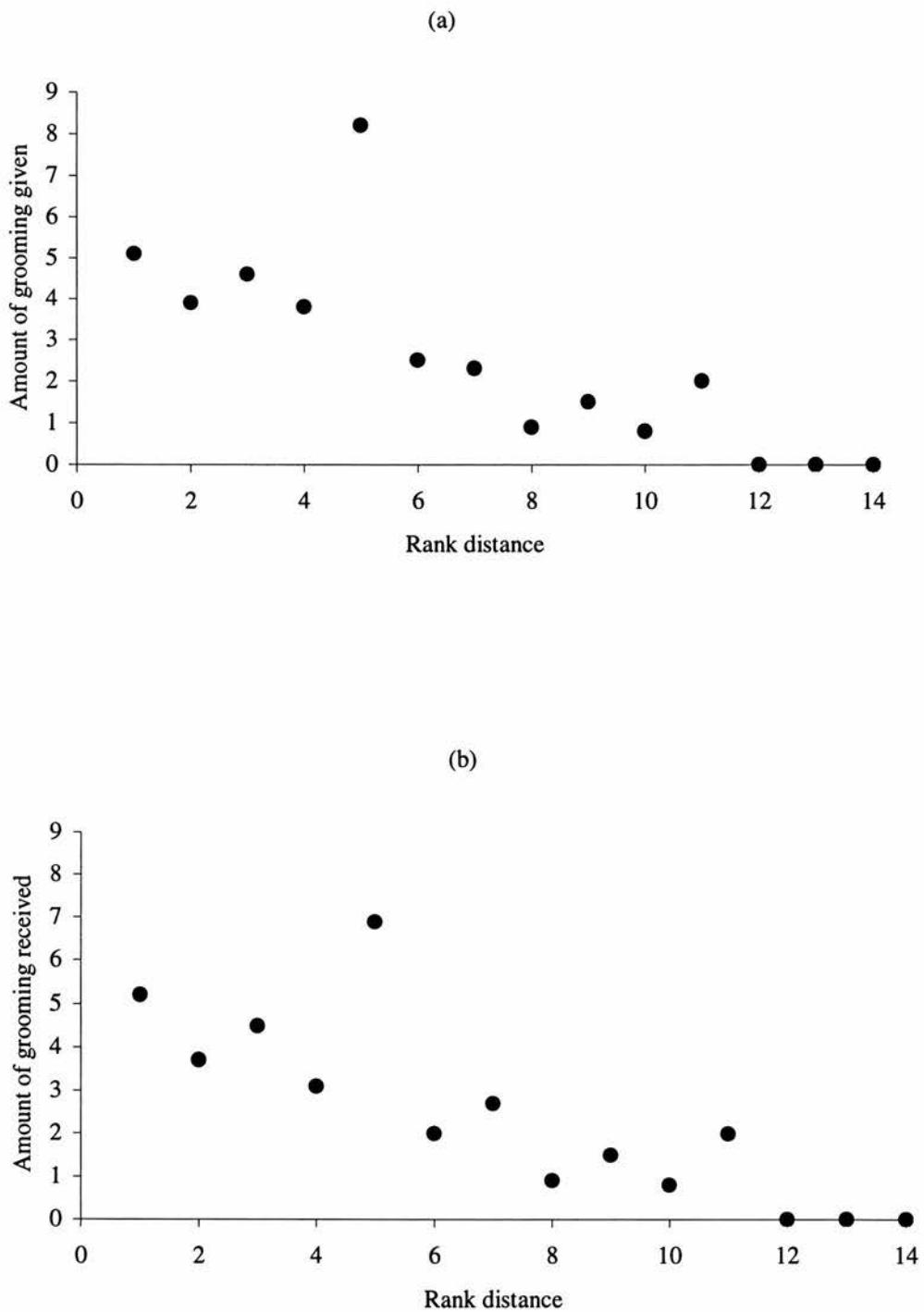
given (all males: $r_s = -0.921$, $N = 14$, $p < 0.001$; adult males = -0.783 , $N = 9$, $p = 0.02$)

and received ($r_s = -0.916$, $N = 14$, $p < 0.001$; adult males = -0.783 , $N = 9$, $p = 0.02$).

Figure 4.15).

Grooming reciprocity among males may be a by-product of rank (as grooming tended to be directed up the hierarchy), or rank distance (if grooming tends to be performed by dyads that are close in rank). However, partial correlations of grooming given with grooming received remained significant when rank and rank distance were controlled for (rank controlled: partial $\tau_{Kr} = 0.5$, $p = 0.0002$; rank distance controlled: partial $\tau_{Kr} = 0.547$, $p = 0.0002$).

Figure 4.15 The effect of rank distance on the mean amount of grooming (a) given and (b) received between males.



4.3.7 Tests of the models of the relationship between rank and grooming distribution

Each of the models was tested using data from 10 adult males and one adolescent male, ZF. ZF was ranked 9th and so was included in the analyses as he must be considered a potentially more attractive grooming partner than those adult males ranked below him despite his youth. In addition, although ZF was considered an adolescent during the study period, within the last 2 months he began to approach the body size of a fully grown adult and to become more integrated into the adult male social network.

‘Ngogo P1’ refers to the first study period at Ngogo during 1995/1996; ‘Ngogo P2’ refers to the second study period during 1997. ‘M Group’ refers to one study group of chimpanzees at Mahale. Data were collected on grooming distribution among M Group males in 1992 and originally presented in Nishida & Hosaka (1996). Results of tests of these models carried out on two separate data sets concerning adult males from these two study periods at Ngogo, and one from Mahale, were taken from Watts, (2000b) and are included for comparative purposes. K_r tests are relative and based on rank-order correlations between observed grooming distributions and those predicted by each of the models. Significant Partial τ_{K_r} values indicate that significant K_r correlations are not the result of reciprocity.

The Attraction-to-High-Rank Model

K_r tests were based on rank-order correlations between grooming given and partner dominance rank (Table 4.3). The Sonso males appeared to show weak support for this model. However, Partial τ_{K_r} values must be considered that give the association between grooming given and groomee rank when grooming received is held constant. When grooming received was controlled in this way, the significant

Table 4.3 Results of matrix permutation tests of the attraction-to-high-rank model. The results given in bold are for the Sonso males and results for males at Ngogo and Mahale are given for comparison (Watts, 2000b).

Group	N	K_r	τ_{Kr}	p	Partial τ_{Kr}	p
M Group	9	-25	-0.10	0.26		
Sonso	11	-109	-0.24	0.0722	-0.09	0.3001
Ngogo P1	22	-810	-0.24	0.0005	-0.23	0.0075
Ngogo P2	24	-1,287	-0.31	0.0002	-0.17	0.0005

correlation between grooming given and partner rank disappeared, which indicates that the trend in favour of there being a correlation between grooming given and partner rank was, in fact, a by-product of grooming reciprocity among these males. The data from Ngogo do support the attraction-to-high-rank model but the data from Mahale do not. Only one male, the previous alpha male, MG, received more grooming than he gave. The percentage of grooming dyads in which each male received more grooming than he gave did not correlate positively with rank ($r_s = 0.182$, N = 11, NS).

The Engagement Model

K_r tests examine the relative association between observed values of grooming given or received and those predicted by the model. Again, the Sonso data appear to support this model for both grooming given, and received. But again, Partial τ_{Kr} values which control for grooming received in the former case, and grooming given in the latter, indicate that the significant fit is a by-product of grooming reciprocity (Table 4.4). The data from Ngogo also achieve a good fit with the model but this fit is due to reciprocity; Mahale data do not fit the model.

Table 4.4 Results of matrix permutation tests of the engagement model. The results given in bold are for the Sonso males and results for males at Ngogo and Mahale are given for comparison.

Group	N	K_r	τ_{Kr}	p	Partial τ_{Kr}	p
Grooming given						
M Group	9	25	0.11	0.26		
Sonso	11	72	0.176	0.059	0.10	0.1834
Ngogo P1	22	1,147	0.33	0.0005	0.04	0.3074
Ngogo P2	24	985	0.25	0.005	0.03	0.3098
Grooming received						
M Group	9	28	0.12	0.22		
Sonso	11	97	0.23	0.021	0.11	0.1704
Ngogo P1	22	733	0.23	0.0005	0.04	0.2629
Ngogo P2	24	930	0.30	0.0005	0.03	0.3183

Table 4.5 Results of matrix permutation tests of the rank-distance model. The results given in bold are for the Sonso males and results for males at Ngogo and Mahale are given for comparison.

Group	N	K_r	τ_{Kr}	p	Partial τ_{Kr}	p
Grooming given						
M Group	9	-24	-0.10	0.23		
Sonso	11	-94	-0.21	0.021	-0.16	0.0662
Ngogo P1	22	-607	-0.18	0.0005	-0.16	0.0005
Ngogo P2	24	-722	-0.18	0.0010	-0.18	0.0005
Grooming received						
M Group	9	-29	-0.12	0.19		
Sonso	11	-64	-0.15	0.07	-0.04	0.3701
Ngogo P1	22	-781	-0.23	0.0005	-0.09	0.0470
Ngogo P2	24	-793	-0.20	0.0005	-0.10	0.0250

Table 4.6 Results of matrix permutation tests of the interference model. The results given in bold are for the Sonso males and results for males at Ngogo and Mahale are given for comparison.

Group	N	K_r	τ_{K_r}	p	Partial τ_{K_r}	p
Grooming given						
M Group	9	29	0.10	0.2189		
Sonso	11	81	0.20	0.048	0.12	0.1592
Ngogo P1	22	749	0.22	0.0005	0.09	0.0490
Ngogo P2	24	953	0.23	0.005	0.10	0.0215
Grooming received						
M Group	9	44	0.18	0.108		
Sonso	11	118	0.28	0.0066	0.14	0.1122
Ngogo P1	22	701	0.22	0.0005	0.13	0.0095
Ngogo P2	24	971	0.25	0.0005	0.09	0.3183

The Rank-Distance Model

K_r tests examine the relative association between observed values of grooming given or received and those predicted by the model. The Sonso data fit this model moderately for grooming given, as significance is marginal when grooming received is controlled for (Table 4.5). For grooming received, significance does not remain when grooming given is controlled and so this significant result was due to grooming reciprocity. Ngogo males groomed, and were groomed by partners close in rank more often than partners distant in rank in both periods although the results for grooming received for Ngogo P1 were, again, due to grooming reciprocity. Rank distance was not related to either grooming given or received in the Mahale males.

The Interference Model

K_r tests examine the relative association between observed values of grooming given or received and those predicted by the model. The results of K_r tests were

Table 4.7 Results of matrix permutation tests of the rank-difference model. The results given in bold are for the Sonso males and results for males at Ngogo and Mahale are given for comparison.

Group	N	K_r	τ_{K_r}	p	Partial τ_{K_r}	p
Grooming given						
M Group	9	22	0.09	0.2559		
Sonso	11	64	0.16	0.0314	0.13	0.0732
Ngogo P1	22	1,033	0.29	0.0005	0.15	0.0165
Ngogo P2	24	1,070	0.26	0.0005	0.12	0.0195
Grooming received						
M Group	9	29	0.12	0.1864		
Sonso	11	39	0.10	0.1424		
Ngogo P1	22	836	0.19	0.0005	0.17	0.0195
Ngogo P2	24	749	0.12	0.0005	0.10	0.0245

significant for both grooming given and received for the Sonso males but Partial τ_{K_r} values were not significant in either case (Table 4.6). Again therefore, grooming reciprocity accounts for the significant fit of the data to the model. Ngogo P1 data support the model for grooming received but only marginally support it for grooming given when grooming received is held constant. Data from Ngogo P2 support the model for grooming given but not for grooming received when grooming given is held constant. M group data do not support the model.

The Rank-Difference Model

K_r tests examine the relative association between observed values of grooming given or received and those predicted by the model. This model was moderately supported by the Sonso males. K_r values were significant for grooming given but not grooming received and marginal significance remained for grooming given when grooming received was held constant (Table 4.7). Data from Ngogo also support this

Table 4.8 The influence of association.

Group	τ_{Kr}	<i>p</i>	Partial τ_{Kr}	<i>p</i>
Attractiveness	-0.281	0.0998	-0.228	0.0780
Engagement	0.175	0.0758	-0.165	0.0702
Interference	0.137	0.1646		
Rank-distance	0.066	0.3465		
Rank-difference	-0.035	0.3195		

model although Mahale data do not.

The influence of association

It is possible that the tendency to associate in multimale parties, and therefore the potential for gaining access to grooming certain partners, may be limited by rank. Significant correlations between rank-related expected grooming frequencies and observed grooming frequencies may be misleading if agonistic interactions lead to party membership based on rank or rank distance or males simply groom others that are frequently in proximity (Hemelrijk, 1996). Grooming given and received were correlated with association frequencies (see section 4.3.5).

In order to ensure that significant correlations between observed grooming distributions and those expected according to each of the models were not a by-product of association frequencies, I compared the frequencies with which males associated in parties with rank, rank distance or expected values for grooming given, given under the engagement, interference and rank-difference models. Partial τ_{Kr} values are correlations between the observed and expected values for grooming given, with association held constant.

Only the attraction-to-high-rank and engagement models were marginally significantly correlated with association frequencies and this level of significance remained when association was controlled for (Table 4.8).

4.4 Discussion

4.4.1 Grooming among different age and sex classes

Grooming patterns among the Sonso chimpanzees were similar to those reported for other communities. Grooming was observed in just over one third of all male-male dyads and in three-quarters of all adult male-male dyads. As in other communities (Gombe: Goodall, 1986; Kanyawara, Kibale: Mahale: Takahata, 1990a,b; Taï: Boesch & Boesch-Achermann, 2000; Ngogo, Kibale: Watts, 2000a) adult males spent more time grooming other adult males than any other age/sex class combination and much more than expected based on age/sex class ratios (see Table 4.1). Ten percent of all male-female dyads groomed although this proportion was higher between both adult and adolescent males and adolescent females. Adult males and adolescent females gave and received significantly more grooming to one another than expected although among adolescent males and females, females gave as much grooming as expected while adolescent males gave less. Only 3% of all female-female dyads groomed. They devoted significantly less time to grooming one another than expected in every age combination. It is possible that the amount of female-female grooming was underestimated due to the sampling bias in favour of parties containing males. The occurrence of all-female parties (including juveniles and infants of either

sex) may have promoted female-female grooming. However, this seems unlikely given the amount of grooming adult females gave to juveniles.

Each adult male invested most heavily in grooming adult males and adolescent females and received similar amounts of grooming from them. Adolescent males gave adult males more grooming than they received and received more grooming from adolescent females than they gave. Adult male-female dyads gave and received only a small proportion of grooming to one another.

Males had a wider diversity of grooming partners than females. Each male had, on average, 12.5 grooming partners of both sexes compared to 2.7 for females. Adult males had 7 adult male grooming partners while adult females had 1.3, and only 0.17 adult female grooming partners. Males groomed more females than they received grooming from and showed strong preferences for certain female grooming partners. They groomed, and were groomed, more equitably with males than with females. Females on the other hand groomed males more equitably.

Male-female grooming was probably influenced by the fact that the majority of adult females had young infants and were not coming into full oestrus, thereby reducing their attractiveness to males. Adolescent females on the other hand were cycling regularly and were, perhaps, disproportionately attractive during this study period. One of these females, CL, actively avoided close contact with adult males and became distressed if they persisted in their attempts to solicit her. All adolescent females were active in contacting adolescent males although these males seemed more reticent. Though competition for access to these females was not as strong as expected, probably due to the fact that they were young, nulliparous females, it seems likely that adolescent males were intimidated in the presence of adult males and avoided conspicuous attempts to solicit females by grooming with them. This was

despite the fact that adult male interventions in this context were rare. In fact only one conflict between an adult male and an adolescent was observed.

4.4.2 Comparison with adult male grooming in other communities

The mean proportion of grooming that adult males gave to, and received from, each other was slightly higher than that reported for Gombe (Goodall, 1986) and Mahale (Nishida, 1979) but lower than that for Ngogo (Watts, 2000a). They had fewer adult male grooming partners than the much larger group of Ngogo males (Watts, 2000b) but the same number as the Mahale males of Nishida & Hosaka's (1996) study which were comparable in number. The diversity of grooming partners was similar in both of these studies but lower for the Sonso males.

Equitability of grooming given was intermediate between the Ngogo and Mahale studies, but lower for grooming received. Following Dunbar (1984, 1991), Watts (2000a) argued that the number of males within a grooming clique should stay reasonably constant irrespective of the number of available grooming partners as time budget constraints do not permit adequate maintenance of a large number of close relationships. The Ngogo males groomed with more partners than the Mahale or Sonso males but concentrated most of their grooming on a subset of them. Mahale males distributed their grooming fairly evenly among partners. The equitability of grooming given for the Sonso males appeared to be scaled according to their group size but received grooming came primarily from a much smaller subset of their grooming partners. Whereas the Ngogo and Mahale males gave and received >10% of their grooming to between 3 and 4 individuals, Sonso males devoted the same proportion of their grooming to only one partner and received much of their grooming from one partner. Each of these partners were rarely the same individual and so this

finding was not the product of symmetrical grooming relationships. In fact, the top three grooming partners accounted for 64% of grooming given and 58% of grooming received, some of which were females. Important grooming relationships with females were very rare in the Ngogo study.

4.4.3 Individual differences

Adult males invested a high proportion of their time budgets to grooming (see Chapter 3) and so it is unlikely that such intense grooming relationships were due to time constraints forcing them to concentrate on a few key individuals. Such intense grooming relationships were in part due to the behaviour of certain individuals. The ex-alpha male, MG, attracted a great deal of grooming from a number of high-ranking males, which he reciprocated. Lower-ranking males including adolescents also groomed him although he did not groom adolescent males at all, and low-rankers, only rarely. On average, he received nearly 18% of all adult males' total grooming and was groomed more than he groomed (see Simpson, 1973; Nishida & Hosaka, 1996; Watts, 2000a, for similar observations). It seemed that his alpha status, lost in 1995, gave him special status despite his greatly reduced rank during the study. He did not appear to be a particularly influential member of the community, except for his attractiveness as a grooming partner, and died during the course of the study. MA, ranked 6th also had a strong though less reciprocal grooming relationship with MG, but the development of an increasingly close relationship with adolescent male ZF, who was beginning to rise within the ranks of the adult males, appeared to strengthen his position. Toward the end of the study, MA successfully challenged BK on two occasions. MU had an almost 'sycophantic' relationship with the resident alpha male (see Chapter 3) and devoted more than 20% of his grooming to him despite also

having a close relationship with his own mother. The low-ranking NJ was especially attracted to adolescent female MK and on one occasion appeared to be attempting to solicit a consortship. The beta male, BK, spent more time grooming than any other individual. He groomed females often, especially during a period in which he made a concerted effort to intimidate VN, the gamma male (previously beta) and ally to the alpha male, DN (Newton-Fisher, 1997). He groomed VN and MG often but did not receive support from them or any other adult male in this apparent attempt to increase his rank further. Some reasonably strong male-female grooming relationships were between mothers and their male offspring, e.g., top-ranked female NB (Fawcett, 2001) and her sons, MU and AY, and RH and her son NK. The maternal relationships of the adult males are unknown at present. Adolescent females, JN and especially SR, had strong grooming relationships with adult males.

4.4.4 Reciprocity

Grooming reciprocity has been demonstrated among captive male and female chimpanzees at the Arnhem Zoo (Hemelrijk & Ek, 1991) during periods in which the hierarchy was both stable and unstable. More recently, Watts (2000a) demonstrated grooming reciprocity in 2 communities of wild adult male chimpanzees (Ngogo & Mahale) for the first time. It was also inferred by Boesch & Boesch-Achermann (2000) for the adult males at Taï, as mutual grooming, where grooming is performed by two grooming partners synchronously, was observed in 73% of all grooming interactions. That grooming reciprocity was observed in the Sonso community further suggests that it is likely to be prevalent in the wild. Reciprocity at a group level was found even when all instances of mutual grooming were removed from the data set. Grooming reciprocity was not found to be a by-product of association frequencies (in

the case of males and adolescent females) or male rank. Nonetheless, the occurrence of group-level-reciprocity does not mean that grooming given and received was symmetrical for all dyads. In fact, 11 out of 62 male-male dyads groomed absolutely equally and in 22 dyads, one member did not reciprocate grooming at all. On average, one member of each dyad contributed around 75% of the total dyadic grooming. But, if individual A groomed B most often, then A was groomed most often by B, though not necessarily equally often.

If mutual grooming is conventional as it was at Taï (Boesch & Boesch-Achermann, 2000), then the ability to keep records of payments and deficits does not need to be implicated. Mutual grooming was less common in this community but grooming reciprocity was still significant at the group level. Whereas grooming between males and adolescent females remained reciprocal when mutual grooming was removed from the data set, grooming between adult males and adult females was not found to be reciprocal when only uni-directional grooming was analysed. This result is a little surprising given that reciprocity seems prevalent in all other age sex categories.

Recently, the study of reciprocity has used relatively simple models that assume that the tendency to reciprocate is fixed and that some kind of record keeping is involved (Hemelrijk, 1990a). However, Hemelrijk (1996; Hemelrijk & Ek, 1991) found the results of her research hard to interpret as evidence for reciprocal altruism or of record keeping, as reciprocity and interchange, in particular, were not consistently demonstrated in the way that the theory would predict, and in many cases, could be explained as a side-effect of other processes. She suggested that a simpler mechanism than record keeping could be involved (Hemelrijk, 1996). Instead, it might be that subjects experience an ‘urge’ to reciprocate shortly after having received an act, and

that this tendency wanes exponentially over time if the opportunity to reciprocate does not present itself. The intensity of this tendency is also dependent on the identity of the partner and on the specific act received. The prevalence of mutual grooming in any community might be dependent on the strength of this tendency to reciprocate immediately and subject to variation, both between communities, and over time. That grooming was not found to be reciprocal between adult females and adult males may give some support to Hemelrijk's proposal. The lack of reciprocity within these categories of individual may be due to the fact that the tendency for males to associate frequently with one another, and for males and adolescent females also to associate frequently, results in opportunities to reciprocate acts before the act is forgotten. Adult females on the other hand associate far less regularly with adult males and so this tendency may be weakened or even lost if a number of days have passed since the receipt of the act.

That other services were interchanged for grooming is also a possibility. However, coalitions were rarely observed during this study and few of them involved support on behalf of females (see Chapter 5). There was one example of meat sharing but again, females were not the main beneficiaries. In any case, adult males groomed females more than the converse and so females could not be said to be 'owed' anything.

It could be said that reciprocal altruism in chimpanzees is inherent insofar that mutual grooming tends to equalise the net gains for each party, but assumptions about the level of cognitive complexity involved in the proximate mechanisms whereby this is achieved may need to be re-evaluated. Most investigations of reciprocity have been carried out on captive subjects. According to Hemelrijk's logic, this is an environment in which reciprocity is most likely to be statistically demonstrated. Further studies on

wild primates, especially those living in fission-fusion societies, are needed before explanations that incorporate more minimal cognitive mechanisms that may result in reciprocity of beneficial acts, can be ruled out.

4.4.5 The effect of rank

Male rank influenced male-male grooming relationships to some extent, but not male-female grooming relationships on the whole. Grooming tended to be directed up the male hierarchy and grooming was most likely between closely ranked males. High-ranking males had more grooming partners than low-ranking males. High-ranking males gave grooming to a wider diversity of partners than low ranking males did and this effect was even more marked for grooming received. High-ranking males also distributed their grooming more evenly among their male grooming partners and received grooming more equitably from them than did low-ranking males. However, when only *adult* male relationships were considered, rank had no effect on grooming partner diversity or the equitability of grooming. Male rank had only a weak effect on the number of female grooming partners and no effect on partner diversity and equitability.

The male with the largest male grooming network was MA, ranked 6th overall. He rose in rank toward the end of the study at which point he ranked 4th (see Chapter 3). Male grooming and bond formation with a wide variety of other males may have been a strategy, which helped to promote his rise in status. BK was the most active groomer of males and females. He also appeared to be more active than any other male in his ‘status striving’ attempts. During the first half of the study, he was ranked 2nd and made a number of attempts to intimidate the 3rd-ranked male, VN, who was also the alpha male, DN’s, ally. BK also groomed VN a great deal. BK appeared to be

using a mixed strategy of intimidation and bond formation that could have resulted in breaking the alliance between VN and DN, allowing BK to form a new alliance with VN. Meanwhile, BK attempted to improve his relationships with other members of the community, including the females. However, after VN's disappearance, BK fell sharply in rank. He had failed to form any alliances within the community and without them, he did not attempt to challenge DN. In fact, he was soon outranked by the gregarious MA.

It is thus plausible that grooming could be a tool used in rank acquisition strategies by males (de Waal, 1982, 1984, 1989; Harcourt, 1992; Boehm, 1994, 1999). High-ranking males gave and received more grooming than low-ranking ones and also received more grooming than they gave. However, for adult males, rank did not affect the ratio of grooming given to grooming received. One male stood out as a particularly popular grooming partner. The ex-alpha male, MG, had a large number of male grooming partners and invested less grooming in them than he received from them. Although he was ranked 7th overall in this study, his former rank may have substantially influenced his grooming relationships despite his loss of status.

High-ranking males also groomed females more than lower-ranking males although male rank did not effect grooming received by females. Rank, therefore, influenced access to females but was not particularly attractive to females. However, this may have been due in part to a high frequency of male-female grooming which involved mothers and also the adolescent females who were as likely to interact with lower-ranking and younger males as the more powerful males.

The influence of rank on grooming has been shown in many primate species. Positive relationships between grooming given and groomee rank have been demonstrated in female baboons (Seyfarth, 1976; Sambrook *et al*, 1995), female

rhesus macaques (de Waal, 1991; Kapsalis & Berman, 1996), vervet monkeys (Seyfarth, 1980; Hemelrijk, 1990b), white-faced capuchins (Perry, 1996) and bonobos (Franz, 1999; Vervaecke *et al.*, 2000). Rank distance effects have also been shown in rhesus macaques (de Waal & Luttrell, 1986; de Waal, 1991; Kapsalis & Berman, 1996) brown capuchins (Parr *et al.*, 1997), female vervet monkeys (Seyfarth, 1980) and females in some baboon groups (Seyfarth, 1977; Sambrook *et al.*, 1995). However, rank and rank distance are not always important structural variables (e.g. bonnet macaques: Silk, 1982; chacma baboons; Silk *et al.*, 1999).

The effect of rank on chimpanzee grooming has not been shown to be consistent across a number of studies. Neither rank nor rank distance had any effect in the Mahale M group males (Watts, 2000b) although it did in the Ngogo males (Watts, 2000b). Other studies of wild chimpanzees have failed to show a consistent relationship between dominance rank and the distribution of grooming. Whereas Simpson (1973) argued that Gombe males preferentially groomed high-ranking males, Bygott (1979) identified age as the most important factor. Takahata (1990b) found that the alpha male in the Mahale M group gave more grooming than he received. Hemelrijk & Ek (1991) found that rank did not influence grooming among males in a captive group although it did affect grooming positively among females. The findings so far indicate that the strength of the influence of rank on grooming might be dependent on the size of the groups under study. The number of males in the Arnhem and Mahale groups were between three and seven, and nine respectively. There were between 22 and 24 males in the Ngogo group. In small groups, other factors might mask the effect of rank whereas in large groups, the effect is statistically visible (Watts, 2000b). The Sonso group containing 10 adult males is also a relatively small

group. Both rank and rank distance did not effect grooming distributions among adult males.

4.4.6 Models of grooming distribution

Given the lack of positive correlations between grooming and rank among the Sonso adult males, it is not surprising that attempts to fit the data to the models were largely unsuccessful. The Sonso data gave some support to the rank-distance and rank-difference models when grooming given was considered, but not grooming received. Neither of these models tries to incorporate the effect of direct or indirect competition quantitatively (Watts, 2000b). Males groomed other males that were close in rank, independently of grooming reciprocity. This result supports the ‘similarity hypothesis’ which predicts that bonds are established between individuals who most resemble one another (de Waal & Luttrell, 1986). Rank distance may be a good indicator of similarity and similarity might translate into convergent interests in coalition formation and rank acquisition (Watts, 2000b). This correlation disappeared, however, when association frequencies were controlled for. In addition, grooming was not found to be more symmetrical between dyads of similar rank. Neither the attraction-to-high-rank, engagement nor the interference models were supported when reciprocity was taken into account. However, the structure of engagement model lends itself to being undermined when reciprocity is controlled for (Watts, 2000b). Individuals that are relatively unconstrained should groom and be groomed relatively often, while those whose access to a particular partner is heavily constrained, may not be attractive as a groomee to that partner (Sambrook *et al.*, 1995).

Access to grooming partners for chimpanzees must be limited not only by competition for access to partners but also must depend very much on association

patterns due to their fission-fusion social system. The distributions of grooming expected under the engagement and attraction-to-high-rank models were alone in being marginally correlated with association frequency but correlations between observed and expected values for grooming given remained marginally significant when association was controlled for. Thus, all significant correlations were by-products of either grooming reciprocity or association frequencies. However, given that the engagement model was weakened by reciprocity in grooming (which could be said to be built into the model) but not association frequencies, this was arguably the most successful model. But, chimpanzees are often not so constrained by their preferred grooming partner being already engaged with another because, unlike cercopithecine females, triadic or even polyadic grooming is not uncommon.

Sambrook *et al.* (1995) argued that the degree to which rank influences grooming distribution is dependent on group size. Sambrook *et al.* (1995) showed that the grooming distributions within the large group of baboons gave a better, though non-significant, fit to the engagement, interference and rank-difference models than the grooming distributions within the small group. Rank influenced grooming distributions in the small group, where low-ranking individuals could gain access to high-ranking grooming partners. In the large group, where competition for high-ranking grooming partners might be expected to be greater, rank distance had a significant effect on grooming distributions.

The data on the Ngogo and Mahale males support this argument (Watts, 2000b). Both rank and rank distance were both significantly correlated with grooming distributions in the large Ngogo group, but not in the small Mahale group. In the Sonso group, which was slightly larger than the Mahale group and half the size of the Ngogo group, rank-difference was a better predictor of grooming distributions than

was rank. It is possible that rank effects in the smaller groups were invisible due to individual peculiarities of the group members (Sambrook *et al.*, 1995). The lack of agonism and the small number of incidents of coalitionary support within the Sonso group were notable. Evidence of status striving was only apparent in BK and he tended to avoid contact with the alpha, DN, and showed, like some other high and mid-ranked males, a strong preference toward the mid-ranked ex-alpha male, MG, as a grooming partner. MU, ranked 8th, gave DN more than double the amount of grooming given by any other male. Competition for access to attractive grooming partners was not much in evidence. Such peculiarities were evident in both the Mahale and Ngogo groups but did not obscure rank effects in the larger group (Watts, 2000b). However, it should be noted that the Ngogo group was unusually large and although the Mahale and Sonso groups have been denoted ‘small’ they are far more representative of the average number of adult males found in a typical chimpanzee community (e.g. Boesch & Boesch-Achermann, 2000, p. 115).

How competition for access to attractive partners operates among chimpanzees remains unclear. Neither this study, nor Watt’s (2000b) have been able to discriminate between the available models. The importance of coalitions and alliances for male chimpanzees is undisputed, but Watts (2000b) suggested that the instability of male dominance hierarchies and opportunistic support strategies (de Waal, 1982; Nishida, 1983; Hemelrijk & Ek, 1991; Nishida & Hosaka, 1996), compared to female cercopithecines, favours more mutualistic, less kin biased and more unpredictable rank acquisition strategies. Grooming relationships with young ascendant males may pay off in the long run if they can develop into agonistic alliances, for example. Although chimpanzees might associate strategically with those with whom they wish to maintain or improve their relationships (Newton-Fisher, 1999a), their fission-fusion

system may prevent them from accessing their preferred partners at all times and excluding others from gaining access to them.

4.4.6 Summary

Males had more extensive grooming networks than females. One third of all possible male-male dyads groomed compared with only 11% of all possible male-female dyads and 3% of all possible female-female dyads. Of all possible adult male-male dyads, 78% had grooming relationships.

Hypothesis 5 (see section 1.3), that grooming is a more important social activity among males than any other sex combination, was partially supported. Adult males devoted more time to grooming other adult males than any other class of individual. They also groomed adolescent females relatively often but groomed adolescent males least of all. The pattern of received grooming for adult males from different age/sex classes was identical. When the proportion of grooming given and received was calculated at the individual level, males devoted a similar amount of grooming per individual to both adult males and adolescent females. Adult males also received similar amounts of grooming per individual from adult males and adolescent females. Adolescent males, however, received more grooming per adolescent female than they did from adult males and devoted most grooming to adult males and least to adolescent females. Adult males, therefore, each invested as much in the sexually active adolescent females as they did in other adult males. Adolescent males, on the other hand, focused the majority of their grooming on adult males but were largely groomed by adolescent females.

Hypothesis 6, that given the egalitarian nature of chimpanzee societies, where power differentials are less pronounced than in more despotic species, grooming

should be reciprocal, was supported. Grooming reciprocity was found at the group level in all age/sex classes, except among adult male-adult female dyads, even when association was controlled for, and when mutual grooming, which is inherently reciprocal and symmetrical, was removed from the data set. This finding raises the possibility that reciprocity might depend on record keeping over short time scales and may not operate where dyads associate only very rarely. Grooming reciprocity was, however, not a feature of many dyads. The mean asymmetry index for all age/sex combinations indicated that one member of the dyad contributed between 70-80% of total grooming.

Hypothesis 7, that males preferentially groom individuals from whom they could potentially receive the most benefits, was partially supported. Grooming was generally directed up the hierarchy. High-ranking males had a greater diversity of male grooming partners, but not female grooming partners, than low-ranking males. High-ranking males did receive more grooming than low ranking males although this relationship did not hold when only adult males were considered. Again, high-ranking males received more grooming than they gave but when only adult males were considered, this correlation became a negative one. As mentioned previously, adult males groomed sexually receptive adolescent females more than the irregularly or noncycling adult females. Adolescent males, however, groomed adult males most often and adolescent females least often. Adolescent males, therefore, were more interested in affiliative relationships with adult males who could, potentially, serve as future allies. That adolescent males groomed adolescent females rarely seems peculiar, although they were often groomed by them. However, adolescent females devoted a large amount of grooming to adolescent males and so these dyadic relationships could be considered secure. In this case, adolescent males appeared to

paying little for the services they received considering that adolescent females often initiated copulations with them. Results of the analyses concerning the equitability of grooming showed that males distributed grooming more evenly among themselves than they did with females which indicates that male-female grooming relationships were more differentiated than male-male grooming relationships. Thus, certain females were frequent affiliates while others were rarely, if ever, affiliates while male-male relationships were much less differentiated. This result contradicts the predictions set out in section 1.3 and is likely to be heavily influenced by the fact that very few females could provide short-term benefits to males in terms of mating opportunities during this study. Males, on the other hand, are always of some value to one another during cooperative territory defence at least. In more typical circumstances where a larger proportion of females might be expected to be sexually receptive over the course of a year, females should be less differentiated in terms of their value as many will be valuable at some time, but many will also be of little interest to males in intervening periods. Males, however, groomed moderately equitably in comparison with previous studies but received a disproportionate amount of grooming from a small number of males. Thus, grooming among males was far from randomly distributed but the observed distribution did not appear to be heavily influenced by rank.

Hypothesis 8, that males compete for access to high-ranking grooming partners, was not well supported. Low-ranking males distributed grooming less evenly than high-ranking males, which suggests that low-ranking males were more constrained in their choice of grooming partners. If such constraints were in operation more generally, then closely ranked males should groom more than distantly ranked males. However, this was not the case. Attempts to fit observed grooming

distributions among adult males to models that specifically take competition for high-ranking grooming partners into account, were unsuccessful. It has been suggested that only in large groups is the influence of rank statistically visible, and other factors might mask what is a real effect in smaller groups. However, as the number of adult males in the Mahale and Sonso groups are more typical for wild chimpanzees and dominance relations may be more ambiguous in larger groups, it seems reasonable to suggest that, in fact, rank might not be an important structural variable in the majority of wild populations but is, instead, one of a number of interacting characteristics and contingencies which can affect grooming partner choice. The apparently atypical status of adolescent females during this study and also the popularity of the ex-alpha male, are cases in point. The stability of the male hierarchy, possibly due to a lack of competition between males, may have contributed to the weakness of rank effects although there is little evidence that this is an unusual situation for wild chimpanzees.

Chapter 5

Conflicts, Coalitions and Displays

5.1 Introduction

5.1.1 Conflict

Aggressive behaviour is the most obvious manifestation of competition within primate groups. As with many non-primate animals, aggression often takes the form of displays. Displays are conspicuous signals exchanged between two or more animals that rarely lead to physical contact but usually result in the displayer gaining access to a resource (Walters & Seyfarth, 1987). Aggressive displays vary from species to species and include eyelid-flashing in baboons (*Papio cynocephalus*: Hall & DeVore, 1965), chest-beating in gorillas (*Gorilla gorilla*: Schaller, 1963) and pheromone-smeared-tail-waving in adult male ring-tailed lemurs when competing for females (*Lemur catta*: Jolly, 1972). Displays often grade into threats that are forms of aggression that can be directed more easily at specific individuals when combined with visually attending to those individuals. The threats of many primate species include staring, head jerking, branch-shaking and ground-slapping and may be combined with chasing, which then constitutes a more intense form of aggression. Finally, aggression may escalate into physical attacks such as hitting, grappling and biting, although prior signalling that such an attack will occur is sometimes omitted (Walters & Seyfarth, 1987).

Aggression is, in fact, only sometimes linked directly to competition for access to resources. Often, one individual will supplant another from feeding or resting sites and no overt show of aggression is necessary, especially when the

individual who is supplanted is subordinate to its competitor and is willing to defer to them, thus forestalling the risk of physical harm or raised stress levels. This last type of interaction is common, and physical attacks are rare in this context (Walters & Seyfarth, 1987). Competition between males for access to reproductive females, however, is far more likely to manifest itself in terms of contact aggression and can sometimes result in serious injury or wounding (e.g. Fawcett & Muhumuza, 2000). In multimale societies males will also direct aggressive acts towards females when they are most likely to conceive, deterring them from mating with other males, or from bonding with outgroup males at other times (e.g. hamadryas baboons, *Papio hamadryas*: Kummer, 1968).

However, much of the competition within groups is not directly related to competition for access to particular resources, but indirectly through the establishment and maintenance of dominance relationships which will, to some extent, then determine the level of access to limited or desirable resources. Many studies have found that the majority of aggression occurs for reasons which are not apparent, at least not to the observer (e.g. vervet monkeys, *Cercopithecus aethiops*: Seyfarth, 1980; rhesus macaques, *Macaca mulatta*: Lindburg, 1971; Japanese macaques, *M. fuscata*: Koyama, 1997 chacma baboons, *P. cynocephalus*: Seyfarth, 1976; chimpanzees, *Pan troglodytes*: Bygott, 1979). Dominants will sometimes threaten or, more rarely, attack subordinates without provocation, thereby eliciting demonstrations of their subordinate status (e.g. chimpanzees, de Waal & Hoekstra, 1980; bonnet macaques, *M. radiata*: Silk *et al.*, 1981; Japanese macaques: Kurland, 1977; olive baboons, *P. cynocephalus anubis*: Wasser & Barash, 1983). Severe aggression, however, is more common when the status of a dominant is challenged,

or in retaliation for attacking one's kin (chimpanzees: Goodall, 1971; gorillas: Harcourt, 1979; bonnet macaques: Silk, 1982).

Though aggression between individuals within a group can be viewed as a destructive force, this may not always be the case. There is often a cost associated with receiving aggression from others, in terms of reduced accessibility of resources, subordination, increased stress, energetic costs and loss of time which could be better spent on other occupations etc. But if such aggression is of low intensity and the costs are not high, there can be a net gain on the part of the victim, who might acquire information about its aggressor and modify expectations about future interactions with her (Lyons, 1993). Aggression can function to establish and maintain beneficial social relationships over the long term (Bernstein & Gordon, 1974; Kummer, 1975; Nishida, 1979; de Waal, 1989, 1996) and, as a consequence, crystallise the social structure of the group. Once social rules and norms are established and (re-established) within a group, aggression may become less frequent and intense (Bernstein *et al.*, 1974).

5.1.2 Coalitions

A coalition is defined as cooperation in an aggressive or competitive context; it is a social tool used to defeat others. For students of animal behaviour, a coalition refers to the joining of forces by two or more parties during a conflict of interest with other parties (de Waal & Harcourt, 1992). Long-term dyadic relationships which involve one partner supporting the other unilaterally, or both partners supporting each other mutually are called *alliances* (Chapais, 1992; de Waal, 1992). Coalition formation has excited a great deal of interest among primatologists as it is a potentially complex social interaction which lends itself to

cost-benefit analysis. Benefits accrue to the recipient of support in the form of increased long-term competitive abilities, access to resources and protection. Costs may be borne by the supporter in terms of risk of injury or damage to his existing relationship with his opponent (Cords, 1997). It is unlikely, however, that the costs of forming a coalition are equal to the benefits gained by the recipient of support in many cases. Supporting the aggressor, who is likely to be dominant to the victim of aggression in cercopithecine primates, may have immediate benefits and very limited costs, assuming that enhancing a relationship with a higher-ranking individuals is more valuable than with a lower-ranking one. Even victim-support under these circumstances might not be costly where the supporter outranks the original aggressor and benefits might be gained if the status of the aggressor (and competitor) is undermined (Noë, 1992; Chapais, 1992). In such cases, mutualistic cooperation might be a better description of this relationship than altruism, as both the supporter and the recipient of support gain from the interaction (Bercovitch, 1988; Noë, 1990).

Triadic interactions are inherently more complex than dyadic ones as there are more relationships to consider among three individuals, than two. Two animals must take one relationship into account, A's relationship with B. The interaction of three animals involves the interaction of three relationships, one for each of the pairings in the triangle (Whiten & Byrne, 1988). An analysis of triadic relationships, therefore, is computationally more complex than the analysis of dyadic relationships. Triadic interactions are therefore considered to be cognitively more demanding than dyadic ones. The decision to support another requires an assessment of who, when and under what circumstances support should be given, and what the payoff would be (Harcourt, 1988). Evidence that such considerations

might operate comes from studies of coalition formation among cercopithecine primates. Most studies agree that kin are supported more often than non-kin, support is given most often when the target is a subordinate, high-risk support strategies are usually associated with kin-biased coalitions, and younger animals are supported more often when they are most at risk (Gouzoules & Gouzoules, 1986; Walters, 1987; Harcourt, 1988; Ehardt & Bernstein, 1992; Silk, 1992; Widdig *et al.*, 2000). Reciprocation of support has also been demonstrated in certain primate species such as chimpanzees, bonnet macaques (*Macaca radiata*), rhesus macaques (*M. mulatta*), stumptail macaques (*M. arctoides*), and vervet monkeys (*Cercopithecus aethiops*: Hunte & Horrocks, 1987; de Waal & Luttrell, 1988; Hemelrijk, 1990a; Hemelrijk & Ek, 1991; Silk, 1992). Reciprocity of contra-interventions have been reported for male bonnet macaques (Silk, 1992) and chimpanzees (de Waal & Luttrell, 1988, but see also Hemelrijk & Ek, 1991). Thus, the complexity of coalition formation among primates deserves attention as a candidate for use in delineating primate and nonprimate cognition.

Coalitions have been reported in a wide range of other mammals including lions (*Pantera pardus*: Bertram, 1975; Bygott *et al.*, 1979; Packer & Pusey, 1982) for which coalitions function to increase the probability of obtaining, maintaining and defending prides of females. Male cheetahs form coalitions that allow them to gain territories and access to females (*Acinonyx jubatus*: Caro & Collins, 1987). Dwarf mongooses (*Helogale parvula*: Rood, 1978; Rasa, 1983) and slender mongooses (*Herpestes sanguineus*: Waser *et al.*, 1994) may form coalitions for similar reasons. Male stallions form long term coalitions (or alliances) in order to defend harems of breeding females (*Equus caballus*: Feh, 1999). Captive spotted hyenas (*Crocuta crocuta*: Zabel *et al.*, 1992) and wolves (*Canis lupus*: Zimen,

1976; Fentress *et al.*, 1986; Jenks, 1988) appear to form coalitions that share some of the characteristics of primate coalitions. They form opportunistic coalitions that tend to support the existing dominance hierarchy although subordinates do join coalitions against dominant individuals (Zabel *et al.*, 1992). However, like cercopithecine primates, hyenas and wolves are less likely to aid another individual when they rank below the opponent, although such occurrences have been observed (Zabel *et al.*, 1992; Jenks, 1988). In hyenas, coalitionary behaviour has been explained as socially facilitated behaviour, or synchrony, whereby animals simply join in the activities that they observe others performing. This social 'contagion' can extend to other, even solitary activities such as scent-marking defecating and surveying the surroundings. This behavioural coordination is likely to be adaptive in animals that hunt cooperatively.

Coalition formation in primates, however, is generally considered to be more complex than in nonprimates. Although coalitions in both primates and nonprimates function to bring about the same ends, e.g. protection, especially of kin, facilitation of resource acquisition in others, improvement of status in kin and improved access to resources for the supporter, the way primates obtain some of the benefits of cooperation in contests may be unique. Only primates appear to reciprocate support, cultivate potentially beneficial relationships with dominant group members and compete for these potential allies (Harcourt, 1988, 1992). They have also been shown to have the ability to opportunistically switch coalition partners according to partner availability over short time spans, i.e., according to circumstances (Marsden, 1968; Chapais, 1985). However, though primate coalitions and alliances may differ substantially from those of nonprimates, it is not yet clear that they do (Harcourt, 1988). It is possible that the triadic conflicts of other

mammals such as wolves and hyenas will be found to be just as complex. Redirection of aggression, for example, has been documented in hyenas (Zabel *et al.*, 1992).

In the mean time, the apparent dichotomy between nonprimates and the comparatively large brained primates suggests that information-processing ability may be a constraint on the complexity of some of the more subtle aspects of coalition formation and also that a positive feedback loop, or ratchet effect, between selection for more complex alliance formation strategies, and the information-processing abilities required to instantiate them, may have emerged at some point in the evolution of the primate order.

5.1.3 Chimpanzee aggression and displays

Aggression and the establishment of dominance hierarchies is a central and constant feature of social life for many primate species. This statement is certainly true of male chimpanzees whose ‘political manoeuvrings’ in this context, via coalition formation in particular, have been the source of much attention (e.g. de Waal, 1982; Goodall, 1986; Nishida & Hosaka, 1996; Boehm, 1997). Details of wild chimpanzee conflicts, however, are sparse except where complex interactions are concerned. Blow-by-blow accounts of chimpanzee conflicts abound in the literature, but basic quantitative data are somewhat lacking and usually consist of matrices of individual agonistic interactions used for determining dominance hierarchies among males.

Two of the more complete accounts are given by Bygott (1979) and Goodall (1986) who describe the agonistic behaviour of the Gombe chimpanzees in some detail, although with few quantitative data. Nishida and Hosaka (1996) provide a

more quantitative account of agonism and coalition patterns in the adult male chimpanzees of Mahale. Otherwise, quantitative data tend to focus on very broad aspects of wild chimpanzee conflicts and can be summarised as follows.

At Gombe, 90% of all agonistic interactions involved at least one adult male (Bygott, 1979). During 1978, aggressive acts between adult males and adult females were most frequent (34%). Aggression between adult males and between adult females accounted for a further 23% and 11% of all conflicts in which adult males and females were aggressors, respectively (Goodall, 1986). However, Bygott (1979) reported that only 4% of all aggression was observed between females during his male-orientated study. Adult males were most often aggressive towards adult females (48%) and other adult males (34%). Adult females directed the majority of their aggression at other adult females (33%) and adolescent males (34%: Goodall, 1986). Severe contact aggression was involved in 15.4% of all conflicts. The mean attack rate for males was 0.016 attacks per hour (range = 0.037 – 0.005) and 0.009 attacks per hour for females (range = 0.021 – 0). Males were most often aggressive in the context of reunions (33%), meat sharing (15%) and sexual activity (14%). The context of a further 14% of aggressive acts was not apparent. Female aggression occurred most often in the contexts of feeding (35%) and protection of their offspring and familiar partners (35%: Goodall, 1986). Analysing the data presented in Goodall (1986, p. 342), Baker and Smuts (1994) report that when the reunion and social excitement categories used by Goodall were combined and included as those having no obvious context, 58% of all male conflicts occurred in no apparent context compared with 13% for females. Male attacks tended to occur in clusters. Thirty percent of male attacks followed within 5 minutes of a previous attack (Bygott, 1979). Wrangham (1974) found that the

frequency of attack per individual increased with group size. This was confirmed in Bygott's (1974, 1979) study where the median group size was 3 but the median group size in which attacks occurred was 9. Male displays are described in Goodall (1986) as the most dramatic form of threat observed in chimpanzees. Displays often include such elements as pilo-erection, running, stamping, ground-slapping, tree-drumming, branch swaying, exaggerated brachiation and branch dragging. Bygott (1979) noted that joint displays tended to be performed by males who were often in association and that there was a positive correlation between rank and display/attack ratios. High-ranking males displayed more often than low-ranking males and did not display more often than a dominant if one was present.

At Mahale, Nishida and Hosaka (1996) report that simple dyadic conflicts accounted for 50% of all conflicts between adult males. Male rank and conflict frequency was positively correlated. Side-directed behaviours which were directed at bystanders included mount, approach with screaming, embracing, hold-out-hand gestures and touching (given in order of frequency). Forty-three percent of 21 incidents of side-directed communication resulted in support being given to the soliciting individual. Hayaki *et al.* (1989) reported that adult males directed 47% more aggression at adolescent males than at other adult males, whereas adolescent males did not aggress against adult males at all. The aggressive interactions of the three adult males of Nishida's (1983) study were most often threats (42%) and chases (51%) and contact aggression accounted for only 7%. Takahata (1990b) found no correlation between male rank and the frequency of displays.

At Budongo, Newton-Fisher (1997) reports that male-male aggression accounted for 37% of all aggression observed in his male orientated study. Sugiyama (1969) found that that the majority of the aggression that he observed

occurred between adult or subadult males (94%). The remaining 6% involved males and females. Female-female aggression was never observed although it is very likely that the high frequency of conflicts involving males but not females was due to habituation effects.

These results demonstrate consistency between communities with respect to the frequent involvement of males in agonistic interactions, and the low frequencies of severe aggression. Inconsistencies arise when considering the proportion of aggression that is directed by males at other age/sex classes. Many aspects of aggressive behaviour in wild chimpanzees have been addressed in one study or another but a comparative base has hardly begun to be assembled. The prevalence of qualitative accounts in the literature is noteworthy; although these are undoubtedly interesting and intuition forming, it is quantitative data that will define the behaviour of chimpanzees in relation to other primates.

Captive studies provide some further insights into chimpanzee conflicts but even here, little comparative work has been attempted and only a few, quite specific questions have been posed. In a comparative study of wild female chimpanzees at Gombe, and captive female chimpanzees at Arnhem and Detroit zoos, Baker and Smuts (1994) showed that both male and female chimpanzees interacted aggressively for no apparent reason more often in captivity than in the wild. They concluded that in a captive setting where limited resources are experienced less than in the wild, both males and females devote more of their time and energy to competing for high, or at least improved, status. They suggest that females are not uncompetitive as has been suggested by de Waal (1978, 1993), but are capable of deploying strategies similar to males as evidenced by patterns of female coalition formation and reconciliation (Baker & Smuts, 1994). Female-female competition

and social bonds may be vital in wild chimpanzees for establishing and maintaining core areas of sufficient quality (Pusey, 1980; Goodall, 1986; Nishida, 1989).

De Waal's studies of the Arnhem zoo colony of chimpanzees mirror those of wild chimpanzees in that males were involved in most conflicts, but male-male conflicts were more frequent than male-female conflicts, the converse of what was found at Gombe (de Waal, 1994; de Waal & Hoekstra, 1980). Conflicts were most often preceded by agonistic exchanges or displays. The most common context of adult male aggression was a sexual one, although the context for many conflicts was unknown. Female aggression centred on third party interactions with infants and on object possession (de Waal & Hoekstra, 1980). Sixty percent of conflicts were dyadic, although 43% of these involved "side-directed" or other behaviours involving bystanders (de Waal & van Hooff, 1981). Side-directed behaviours included approaches, vocalisations, touches, hold-out-hand gestures, contact-sitting, bared-teeth displays, mounting and embracing (given in order of frequency). Side-directed behaviours resulted in the receipt of support during 25% of conflicts during which these behaviours were observed. Side-directed behaviours were also given to individuals that were already supporters in an ongoing conflict. Hemelrijk *et al.* (1991), however, found that side-directed behaviours rarely resulted in the receipt of support despite their often being directed at individuals from whom support had been most forthcoming previously.

Shefferly and Fritz (1992) report that the presence of oestrus females positively influenced the rate of male-male agonistic behaviours in three captive groups. Conversely, Bloomsmith *et al.* (1992) reported no such increase in two well-established chimpanzee groups of comparable size.

Casperd's (1997) captive study found that over half of all conflicts were between males and females. Female-female conflicts were more frequent than male-male conflicts. High and low-intensity conflicts were most often initiated by high-ranking aggressors. Mid-ranking aggressors were less aggressive on average. Kinship had no effect on the frequency of observed agonistic interactions. Conflicts were more common among dyads that invested little time in grooming one another. Aggressors were more likely to engage in conflicts of high intensity with individuals with whom they had strong grooming relationships. Casperd (1997) interpreted this last result as evidence that escalation was more likely when conflicts of interest occurred between individuals who invested most heavily in one another.

The only study of displays in captive chimpanzees was carried out by Reynolds and Luscombe (1969) who observed that 'full' displays were only performed by adult males, although adolescents and females performed attenuated versions. They concluded that displays might function to attract attention to the display, in terms of subsequent approaches and affiliation, and agreed with Chance's (1967) proposition that the basis of rank order in primates might be related to the concentration of attention on dominants rather than the outcomes of competitive interactions.

5.1.4 Chimpanzee coalitions

Coalition formation among wild male chimpanzees has been reported in many studies (e.g. Nishida, 1983; Goodall, 1986; Nishida & Hosaka, 1996; Watts, 1998; Boesch & Boesch-Achermann, 2000) and is considered to be the primary social tool used for the acquisition of status and resources, over and above those

based on individual qualities such as size, strength, aggressiveness and resourcefulness. Rich descriptions are given in the literature but very little quantitative data are presented (e.g. Riss & Goodall, 1972; Goodall, 1986; Nishida, 1983; Uehara *et al.*, 1994).

More recently however, empirical data of better quality have begun to be published on coalitions in wild chimpanzees. Nishida & Hosaka's (1996) study of the adult males of M group, Mahale, documented coalition formation together with a number of other aspects of male affiliation and cooperation. They observed that the two highest ranked males supported the third-ranked male more often than any other male and interpreted this as evidence for competition for this potentially powerful ally although neither succeeded in their attempts to recruit him. Coalitions were just as likely to favour aggressors as targets of aggression and age appeared to be the most important factor governing which of two opponents was supported, as the older male was supported in 79% of all dyadic combinations (Nishida & Hosaka, 1996). Support was given to the subordinate more often than the dominant combatant, although one of the coalition members was often dominant over his target, thus reinforcing the existing dominance hierarchy. The two top-ranking males never groomed one another but groomed the third-ranking male often. The alpha male, in particular, groomed the third-ranked male more than any other male, and groomed him more often than he was groomed by him, thus supporting the idea that grooming strengthens male bonds and fosters alliances. Meat sharing by the alpha male, however, was confined to two old males and females.

At Taï, the alpha male and the oldest male were involved in over half of all coalitions both as supporters and recipients of support (Boesch & Boesch-Achermann, 2000). The old male was also the only male that was supported

regularly by high-ranking females. The subordinate individual involved in conflicts was supported in the vast majority of cases and the supporter was dominant to the target in less than half of the observed coalitions. Half of all joint attacks involved two individuals attacking a higher-ranking one; a common occurrence in wild chimpanzees and the opposite of what is observed in cercopithecine monkeys (see Boesch & Boesch-Achermann, 2000, p.123). Females were often involved in coalitions against males and also performed joint attacks against males. This unusual phenomenon in wild chimpanzees was interpreted as the result of strong male-female bonds in a community that relies on cooperation during hunting episodes.

Watts (1998) has documented the occurrence of coalitionary mate guarding in the Ngogo community, Kibale, Uganda. In most cases males copulate opportunistically but sometimes a single male may induce a female to consort exclusively with him, thereby excluding the possibility that she may mate with other males. Mate guarding, however, involves the aggressive maintenance of exclusivity within multimale parties and is therefore dependant on the competitive abilities of the guarding male (Watts, 1998). Coalitionary mate guarding, while relinquishing exclusivity, may be preferable where solo mate guarding is rendered too difficult by the number of males competing for access to an oestrus female. Members of the coalition would each have a better chance of successfully fertilising the female than if they mated opportunistically (Watts, 1998). Coalitionary mate guarding was observed frequently in the unusually large Ngogo community (≥ 115 members including 26 adult males) and usually involved the alpha male and one other high-ranking male. The remaining high-ranking males, and even some mid-ranking males, also successfully guarded females when they were not in association

with males that outranked them. Coalitions of high-ranking males could successfully guard oestrus females in large parties where individual attempts were thwarted because the demands involved in performing separating interventions, chases and vigilance could not be met (Watts, 1998).

Mitani *et al.* (2000) carried out a study of the role of kinship and its effects on patterns of male affiliative and cooperative behaviours within the Ngogo community. Kinship has often been cited as a principal factor in explanations of male social behaviour. It has been assumed that relatedness underlies the relative strength of male bonds, compared to female bonds in chimpanzees (e.g. Goodall, 1986; de Waal, 1982). However, Mitani *et al.* (2000) found that matrilineally related adult males did not affiliate closely (in terms of grooming, proximity and association). These results were consistent with Goldberg & Wrangham's (1997) study of the Kanyawara community, also in the Kibale forest, where mtDNA haplotype sharing was positively correlated with high levels of association, but not with other measures of bond strength, namely, grooming and proximity. Not only was relatedness *not* correlated with affiliation in Mitani *et al.*'s (2000) study, but it was also not related to a number of cooperative behaviours. There was no relationship between kinship and participation in coalitions, boundary patrols and meat sharing. This was surprising, as cooperation should bring greater fitness benefits than mere affiliation, which is usually taken to be a tool for servicing potentially cooperative relationships (Goodall *et al.*, 1979; Nishida, 1983; Nishida *et al.*, 1992; Nishida & Hosaka, 1996; Watts, 1998; Mitani *et al.*, 2000).

Coalition formation has been the primary focus of a number of studies of captive chimpanzees. De Waal's observations of the Arnhem colony constitute the bulk of this research, concentrating on the political nature of chimpanzee coalition

formation (see de Waal, 1982). In a study of sex differences in coalition formation de Waal (1984), found that adult males were most likely to intervene in conflicts involving all combinations of adult males and adult females, whereas adult females were likely to intervene in conflicts between adult males or between adult females but not in conflicts between adult males and adult females. Adolescent females only intervened in conflicts that involved all age categories of females and juveniles. This result provided confirmation of de Waal's earlier suggestion (de Waal, 1978, 1982) that in this captive colony, females had a considerable influence on the adult male hierarchy, which included only four males. With so few males present, females can become influential in power struggles amongst these males in a way not observed in wild communities. Adult males were more flexible in their support choices than females and regularly switched allegiances over a five-year period. Females showed a much more consistent pattern in this respect although they showed greater variation in their patterns of male-support which paralleled the males' own support strategies (de Waal, 1984). Female support choices were often in favour of familiar individuals (i.e. those with which they spent relatively more time in proximity and in contact). The two oldest adult males did not follow this pattern, although for one, the alpha male, this may have resulted from his reduced ability to affiliate with two other individuals which he often supported (the second ranked male and the highest-ranked female), due to frequent separating interventions by the third-ranked male (de Waal, 1984). The remaining two males behaved more like females in this aspect of their coalitional behaviour. The three highest-ranking males showed a greater tendency to follow familiarity-dependant support strategies during periods when the dominance hierarchy was stable than when it was unstable. This result suggests that males give priority to strategies that

may result in increased status when the opportunity arises, at the expense of more generalised social bond-orientated support patterns which they display at other times. Winner-support was the most common intervention pattern shown by males and females, especially under crowded conditions. De Waal (1984) interpreted this finding as evidence that when tensions are high, coalitions will tend to favour the reinforcement of the existing dominance hierarchy. The two highest-ranking males, however, often supported the subordinate individual involved in a conflict. He also noted that males would sometimes prevent others from intervening on behalf of the subordinate party. This lead de Waal (1984, p. 248-249, 1992) to speculate that males exhibit a protective tendency ('the control role') which may function to demonstrate their abilities as "arbitrators in disputes" and will compete for this 'role' (see also Boehm, 1994). Through such demonstrations, males can influence subordinates' perception of them as responsible leaders. Females appeared to be divided into supportive subgroups, where cliques of females tended to support one another, based on familiarity. Males' associates, however, were not more likely than any other individual to receive support from others that had relationships that involved support, with a particular male.

A later study addressed the question of whether chimpanzees reciprocated support, in a comparative study including rhesus and stump-tail macaques (de Waal & Luttrell, 1988). The findings of de Waal & Luttrell (1988) were positive for all three species and no distinction was made between male and female coalition patterns. They also found that, unlike the macaques, chimpanzees reciprocated *opposition* as well. In other words, chimpanzees more often intervened against a particular individual if that individual often intervened against them. This result was not replicated in a later study by Hemelrijk & Ek (1991) which was carried out on

the same captive group of chimpanzees. Hemelrijk & Ek's (1991) data did, however, agree with de Waal's (1984) when assessing sex differences in coalition formation. They found that familiarity influenced patterns of male coalition formation during periods of stability of the dominance hierarchy but not when the hierarchy was unstable. Females followed familiarity-dependant support strategies at all times. Also in contradiction to de Waal & Luttrell's (1988) study was Hemelrijk & Ek's (1991) finding that males reciprocated support during periods of instability but not at other times, and females did not reciprocate support at all.

This chapter will investigate a number of aspects of chimpanzee conflicts with the aim of providing some basic information that can extend the comparisons across chimpanzee populations as reviewed above, as well as comparisons between primate species. As mentioned previously, this kind of information is relatively sparse except where coalitions are concerned. Data concerning displays is particularly lacking and this chapter will, to some extent, fill this gap.

5.2 Methods

5.2.1 Data collection

Data on conflicts, coalitions and displays were recorded *ad libitum* due to the comparative rarity of these behaviours. Any conflict in which either the aggressor or the victim of aggression could not be identified was not included in the data set. All adult, adolescent and juvenile males and females were included as focal subjects.

Conflicts were categorised as occurring at one of five intensities:

Intensity 1 - mild threat: head tip, arm raise, hitting toward, flapping, sitting hunch, quadrupedal hunch (see Goodall, 1986, pp. 314-315).

Intensity 2 - aggressive threat: swaying branches, throwing objects, flailing or hitting toward with stick or branch, bipedal swagger, running upright toward, charging.

Intensity 3 - Any of the above including a chase of > 4m.

Intensity 4 - Any of the above including body contact such as pushing, slapping, hitting or grappling.

Intensity 5 - Any of the above combined with fierce biting.

Conflicts of intensity category 5 were never observed. Displays were recorded as conflicts when the display was directed at another individual. Such directed displays were most often categorised as conflicts of intensity category 2 unless the display developed into a more direct attack including chasing and contact aggression in which case the relevant category was chosen according to the severity of the attack.

Scan samples were collected every 15 min during periods of contact with a party of chimpanzees. Scan samples recorded the identities of all party members and the nature of the activity that occupied each of them. Further details are given in Chapter 2.

5.2.2 Data analysis

For analyses concerning rank, the rank position ascribed to each individual is based on calculations concerning the three-month period during which the agonistic interaction occurred. This approach takes into account the variation in

rank order over time. All graphical representations of the effect of rank give results for each individual based on the approach described above but individuals are arranged in the overall rank order based on calculations for the entire study period.

Some analyses include dyad-corrected frequencies of certain behaviours. Details of the methods used to calculate dyad-corrections are given in Chapter 3.

Matrix-permutation tests (Hemelrijk, 1990a) were used to compare distributions of conflicts with distributions of affiliative behaviours at the group level. Further details of these tests are given in Chapter 4.

5.3 Results

5.3.1 Conflict characteristics

A total of 157 conflicts between 37 adult, adolescent and juvenile individuals were recorded during the study period. Of these, the vast majority (92.3%) were simple dyadic conflicts. Very few conflicts were more complex: triadic and polyadic conflicts each accounted for 3.9% of the remaining conflicts (table 5.1). Further information on patterns of coalition formation during dyadic and triadic conflicts are given in sections 5.3.6 and 5.3.7.

Table 5.2 shows the number of conflicts between individuals of different combinations of age and sex classes. A large proportion of conflicts (70.3%) involved dyads consisting of adults and adolescents. Almost a quarter (23.3%) of all conflicts occurred between adult males and a further 19% involved dyads consisting of adult and adolescent males. A significant proportion of conflicts involved adult-adult and adult -adolescent males. Another large proportion of

Table 5.1 Numbers of dyadic, triadic and polyadic conflicts involving individuals of different sex classes.

Conflict Type				
	dyadic	triadic	polyadic	Total
M-M	87 (54.8)	4 (2.6)	2 (1.3)	93 (58.7)
M-F	43 (27.7)	2 (1.3)	4 (2.6)	49 (31.6)
F-F	15 (9.7)	0	0	15 (9.7)
Total	145 (92.3)	6 (3.9)	6 (3.9)	157

Numbers in parentheses indicate percentage of total conflicts.

Table 5.2 Number of conflicts between individuals of each age and sex class.

Age class	Sex combinations			Totals
	M-M	M-F	F-F	
Adult-adult	44 (23.3)	21 (11.1)	5 (2.6)	70 (37.0)
Adult-adolescent	36 (19.0)	22 (11.6)	5 (2.6)	63 (33.3)
Adult-juvenile	16 (8.5)	5 (2.6)	7 (3.7)	28 (14.8)
Adolescent-adolescent	5 (2.6)	4 (2.1)	1 (0.5)	10 (5.3)
Adolescent-juvenile	7 (3.7)	9 (4.8)	1 (0.5)	17 (9.0)
Juvenile-juvenile	0	0	1 (0.5)	1 (0.5)

Numbers in parentheses indicate percentage of total conflicts (189) where triadic and polyadic conflicts were analysed as consisting of a number of separate dyadic conflicts.

Table 5.3 Number of conflicts involving aggression of different intensities.

Conflict type	Conflict intensity				Totals
	1	2	3	4	
Dyadic	19 (12.1)	71 (45.2)	55 (35.0)	12 (7.6)	157
Poly/triadic	4 (12.5)	11 (34.4)	13 (40.6)	4 (12.5)	32
Totals	23 (12.2)	82 (43.4)	68 (43.3)	16 (8.5)	189

conflicts involved male-female dyads (totalling 22.7%) made up of both adult-adult and adult-adolescent age combinations. All-male, adult-juvenile dyads contributed 8.5% conflicts to the data set and conflicts involving other age/sex combinations were rare.

5.3.2 Conflict Intensity

Very intense conflicts were not observed except in one case which resulted in the death of a young adult male (ZT) from fatal injuries (Fawcett & Muhumeza, 2000). Unfortunately, no observer arrived at the scene of the conflict in time to record any details or the identities of many of the individuals involved. Only BK was observed charging and stamping on the incapacitated ZT during the last phase of what was likely to have been a polyadic attack (Fawcett & Muhumeza, 2000). However, DN, the alpha male, was implicated as the main attacker due to the presence of fresh puncture wounds and cuts observed a few hours after the attack (pers. obs.). Additionally, chimpanzee flesh and fur was found to be present in his dung the following day (Fawcett & Muhumeza, 2000). BK and AY were also

Figure 5.1 Conflict intensity within and between sex classes.

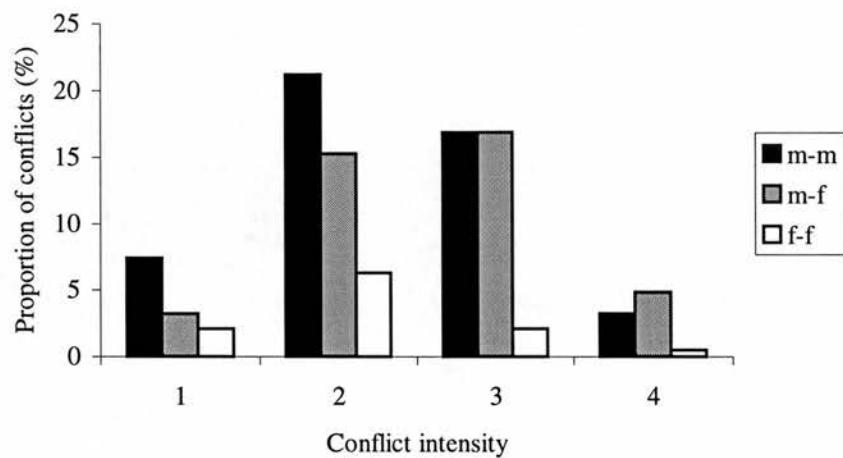
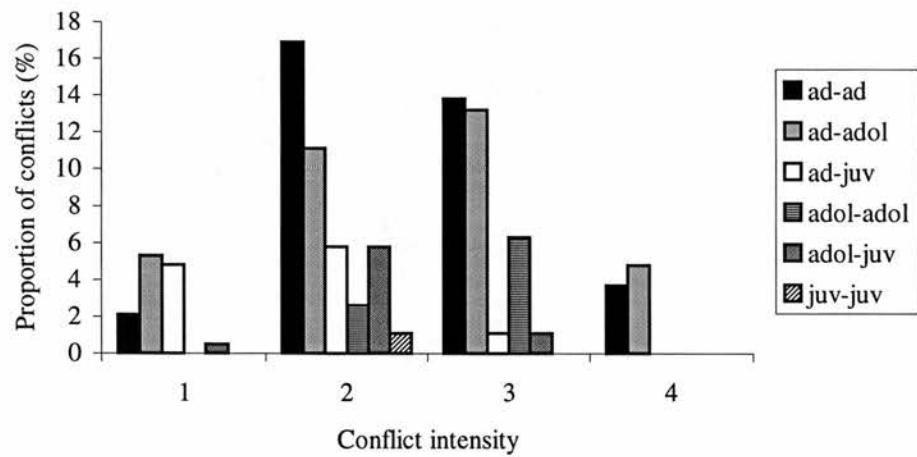


Figure 5.2 Conflict intensity within and between age classes.



observed to have received puncture wound injuries when they were encountered later on in the day of the attack and were likely to have been involved in the coalition against ZT.

No observed conflict involved biting or very severe aggression, although one individual, NJ, was seen with puncture wounds. It is unknown, however whether these injuries were the result of intracommunity aggression or an encounter with extracommunity males. The proportion of conflicts involving aggression of different intensities is given in table 5.3.

There was no difference in the proportion of conflicts of different intensities observed during dyadic and triadic/polyadic conflicts ($\chi^2 = 1.17$, $df = 3$, $p < 0.8$) and so triadic and dyadic conflicts are treated as separate dyadic conflicts and included in the data set for the following analyses.

Figure 5.1 shows the proportions of conflicts of each intensity within and between the sexes. There appears to be a slight bias toward low intensity conflicts for male-male and female-female conflicts and a skew in the opposite direction for male-female conflicts. However, these differences were not significant ($\chi^2 = 8.18$, $df = 6$, $p < 0.3$).

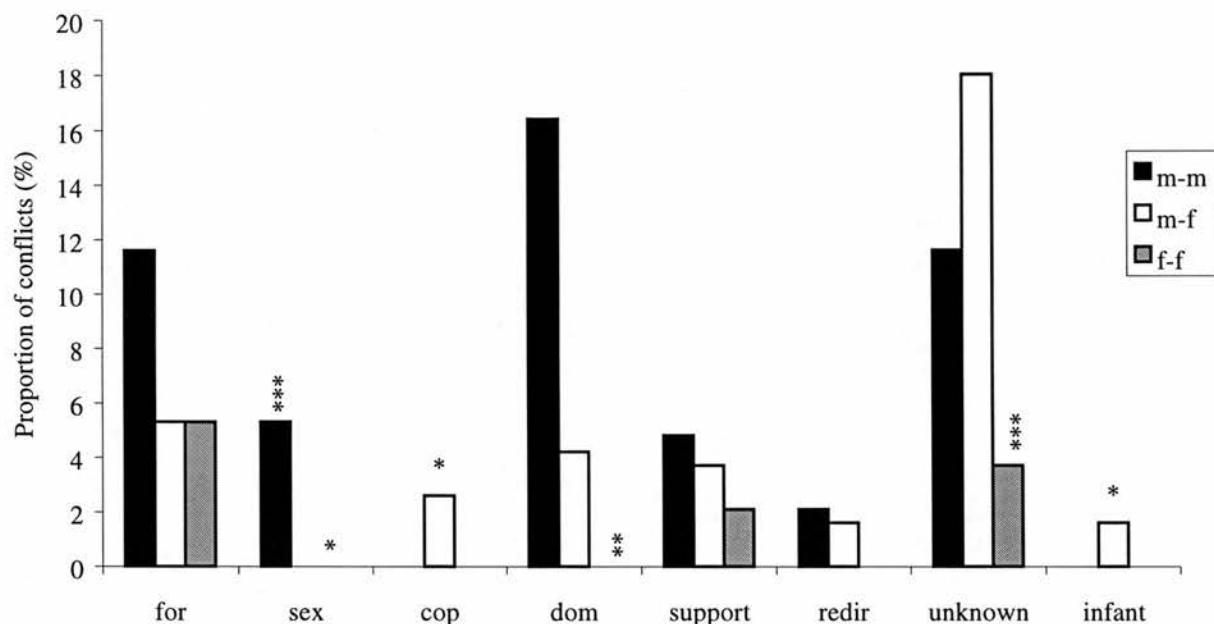
Figure 5.2 shows the proportions of conflicts of each level of intensity within and between age classes. Aggressive threats (intensity 2) made up 43.3% of all conflicts and were observed to occur within all age combinations. Aggression involving chases (intensity 3) made up 35.5% of conflicts and occurred with all age combinations except juvenile-juvenile conflicts. Mild threats (intensity 1) were rare (12.7%) and tended to occur between age classes where older individuals, usually adults, threatened younger ones. High intensity conflicts which involved aggressive body contact (intensity 4) were observed only within adult-adult and adult-

adolescent combinations. Sample sizes were too small to allow comparisons within and between all age classes, even when age-classes with the smallest frequencies were combined. It was possible to compare the effect of age-category combinations that included adult subjects on the intensity of conflicts, however. There was a significant difference in the distribution of conflicts of each intensity for adult-adult, adult-adolescent and adult-juvenile dyads ($\chi^2 = 23.85$, $df = 6$, $p < 0.001$). After partitioning the degrees of freedom, these differences were significant when adult-adult and adult-adolescent conflicts were combined and compared with adult-juvenile conflicts at intensities 1 and 2 ($\chi^2 = 6.73$, $df = 1$, $p < 0.01$), and when the same age categories were compared with conflict intensities 1 and 2 combined and contrasted with the frequency of conflicts at intensity 3 ($\chi^2 = 10.04$, $df = 1$, $p < 0.001$). In other words, adults had more conflicts with other adults and with adolescents than with juveniles, and when adults did have conflicts with juveniles, they were of lower intensities, consisting mainly of threats.

5.3.3 Context

Conflict context was categorised as one of the following: foraging (for), sex competition (sex), copulation attempt (cop), dominance interaction (dom), support of third party (support), redirection of aggression (redir), context unclear (unknown), or where possession of a dead infant was disputed (infant). There was a significant difference in the distribution of male-male, male-female and female-female conflicts in these contexts ($\chi^2 = 54.78$, $df = 14$, $p < 0.001$). Figure 5.3 shows the distribution of conflicts between different sex classes and the results of an analysis of these differences after partitioning the degrees of freedom. The majority of male-male conflicts were dominance interactions (31.6%) which were

Figure 5.3 Proportion of conflicts in each context within and between the sexes (probabilities are given as * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).



characterised by aggression which sometimes included display elements, e.g. piloerection, did not result in the acquisition of a resource and resulted in the performance of some form of submissive behaviour on the part of the aggressor. Foraging and unknown causes each making up a further 22.4% of conflicts. The context of almost half (48.6%) of all male-female conflicts was unknown. Most female-female conflicts were a result of feeding competition (47.6%) and a proportion of unknown conflicts were likely to have been similarly motivated although in some instances this was unclear. Males competed over access to females but females never competed over males. Neither did females show any inclination to aggress with the sole purpose of dominating one another.

5.3.4 Association and affiliation

It would be reasonable to suppose that conflict frequency for a particular dyad might depend, first, on the regularity with which pairs of individuals encounter one another, and second, on the strength of that dyad's relationship. Strong social bonds should increase the likelihood of tolerance around resources and buffer individuals against the physiological costs of competition for those resources. Relatively few conflicts within dyads with strong social bonds should also reduce the probability of weakening such relationships and therefore losing any benefits associated with them. Competitive interactions should be more frequent between individuals with weaker relationships, who have less to lose in terms of the time and effort involved in forming and maintaining friendly social relationships.

I investigated the effect of association strength on the frequency of dyadic conflicts (dyad-corrected). An analysis of the relationship between the relative strength of association between individual independent males and other independent individuals, both male and female, revealed a trend in favour of frequent associates having more conflicts than infrequent associates (Pearson's correlation: $r = 0.09$, $p < 0.1$, square root transformation). There was no relationship between conflict frequency and amount of time spent in proximity ($r = 0.09$, NS) and so it is unlikely that the distribution of conflicts was simply a function of relative distance. Surprisingly, there was also a trend in favour of a relationship between conflict frequency and time spent grooming ($r = 0.1$, $p < 0.1$). This suggests that, contrary to the above prediction, dyads with strong social bonds were more likely to have conflicts than dyads with weak social bonds. However, when data for male-male and male-female dyads was analysed separately, none of the correlations were significant although a new trend emerged in favour of a negative

relationship between association and conflict frequency for male-male dyads (male-male: association, $r = -0.15$, NS, $p < 0.1$, proximity, $r = 0.04$, NS, grooming, $r = 0.02$, NS; male-female: association, $r = 0.01$, NS, proximity, $r = -0.04$, NS, grooming = 0.1, NS).

A second set of analyses compared dyad-corrected conflict frequencies between dyads falling within the upper and lower quartiles of the range of each individual's dyad-corrected proximity and grooming counts. There was no difference in the number of conflicts between males and the 8 individuals with whom they spent the greatest time in proximity compared to the 8 individuals with whom they spent the least amount of time in proximity when their relationships with both males and females were included (Wilcoxon signed ranks test: frequent proximity v rare proximity = 1.4 v 2.8 conflicts; $T^+ = 57$, $N = 14$, NS). When male-male and male-female relationships were analysed separately, a trend emerged in favour of male-male dyads having more conflicts with other males with whom they spent little time in proximity compared to those with which they spent most of their time (frequent proximity v rare proximity = 1.6 v 2.4 conflicts; $T^+ = 88$, $N = 15$, $p < 0.06$). There was a higher frequency of conflicts among the male-female dyads which spent the least amount of time in proximity compared to those which spent the greatest amount of time in proximity but the difference was not significant (frequent proximity v rare proximity = 1 v 2.5 conflicts; $T^+ = 45$, $N = 12$, NS, Figure 5.4).

This analysis was repeated for grooming relationships except that a correction was needed where there were too many or too few individuals in some of the categories that were compared, preventing comparisons between upper and lower quartiles. Where there were sufficient individuals to compare quartiles, the

Figure 5.4 The number of conflicts per dyad between male-male and male-female dyads which spend time in close proximity either frequently or rarely (mean and S.E.).

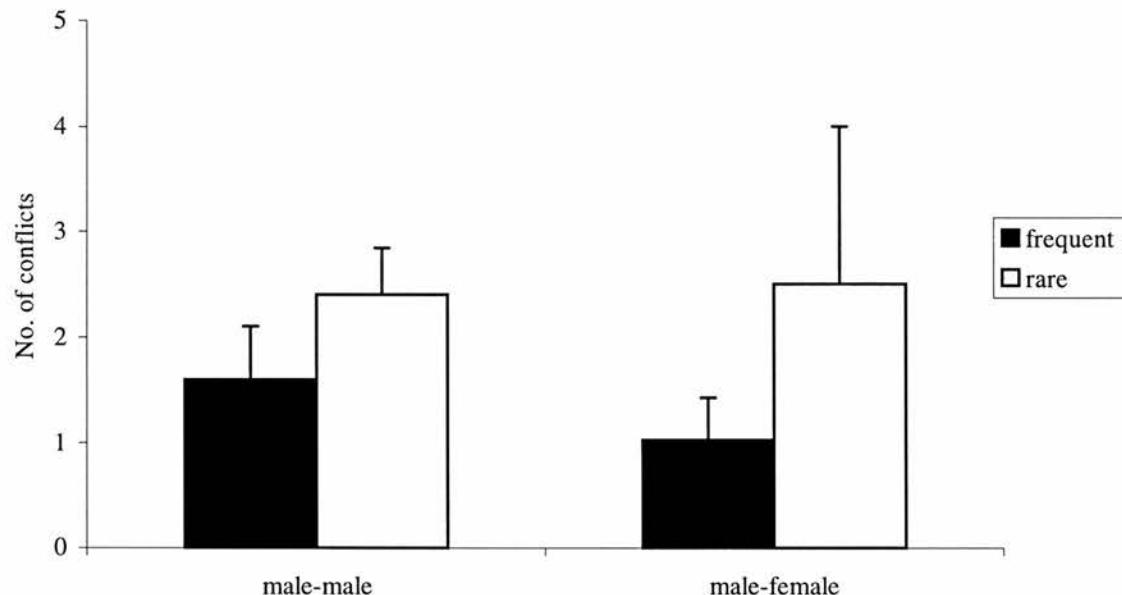
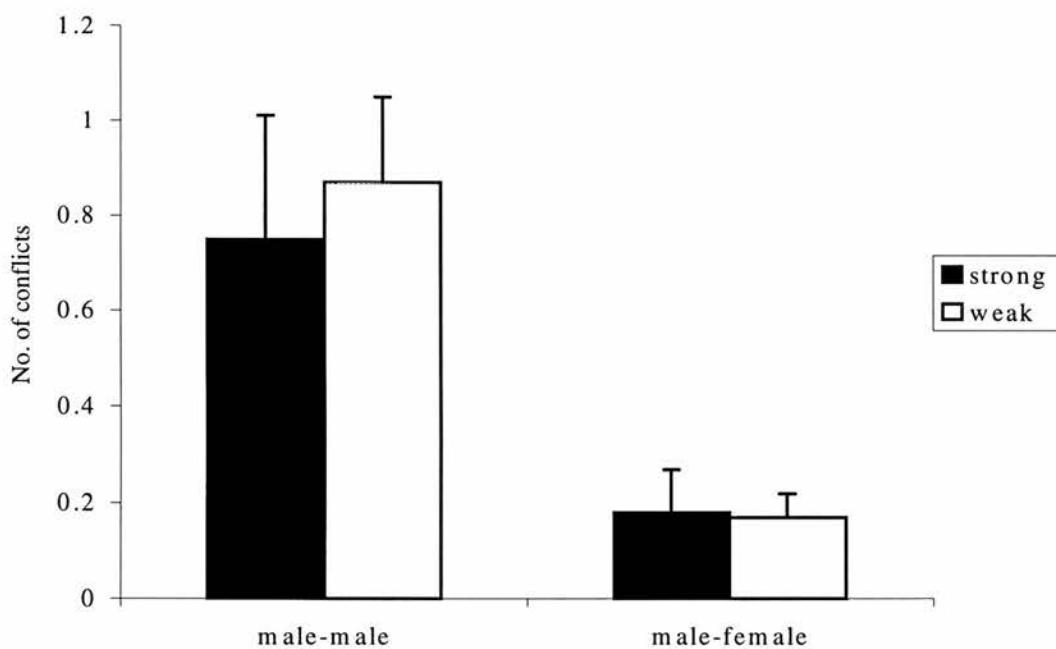


Figure 5.5 The number of conflicts per dyad between male-male and male-female dyads with strong or weak grooming relationships (mean and S.E.).



mean number of conflicts between dyads in each category were compared. Where there were too many non-grooming partners to compare quartiles, the mean number of conflicts between x_n non-grooming partners were compared with the mean number of conflicts between the x_g highest investment grooming partners, where $x_n = x_g$.

There was no difference in the frequency of male-male conflicts between males with strong or weak grooming relationships (strong v weak = 0.75 v 0.87 conflicts/dyad; $T^+ = 54$, $N = 13$, NS: mean number of individuals in each category = 4.6 ± 0.1 v 6.4 ± 2.6). Neither was there a difference in the frequency of male-female conflicts with strong and weak grooming relationships (strong v weak = 0.18 v 0.17 conflicts/dyad; $T^+ = 40$, $N = 13$, NS: mean number of individuals in each category = 4.6 ± 0.1 v 6.4 ± 2.6 . Figure 5.5). However, for males the relationship between individual investment in reinforcing relationships via grooming and the number of conflicts instigated, supported the hypothesis outlined at the beginning of this section according to the following analysis. Males directed significantly fewer attacks at individuals in whom they invested grooming time than they directed at males which they did not groom (high investment v no investment = 0.6 v 1.3 conflicts; $T^+ = 87$, $N = 13$, $p = 0.0009$: mean number of individuals in each category = 4.87 ± 1.1 v 7.7 ± 2.7 . Fig 5.6). For male-female dyads, few females groomed males and so comparisons were made according to whether females invested grooming time in males or not. In this case there was no difference in the mean number of attacks received from males which females groomed or never groomed (investment v no investment = 1.15 v 1.85 conflicts; $T^+ = 61$, $N = 13$, NS; mean number of individuals in each category = 2.8 ± 1.4 v 13.2 ± 1.4).

I then investigated whether males were less likely to direct aggression at

Figure 5.6 The number of dyad-corrected conflicts per dyad directed at individuals in which each subject invested most grooming time compared with individuals in which the subject invested no grooming time (male-male conflicts only).

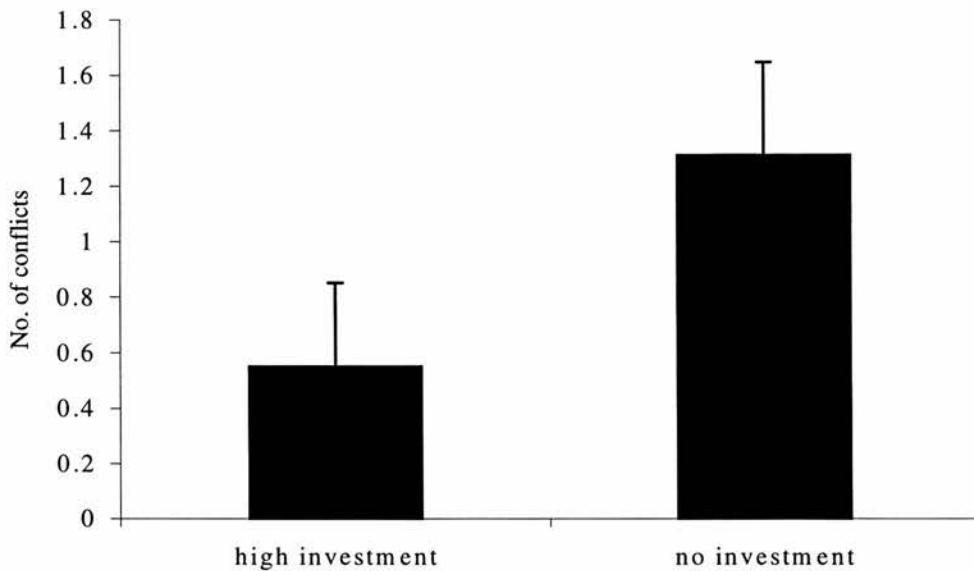
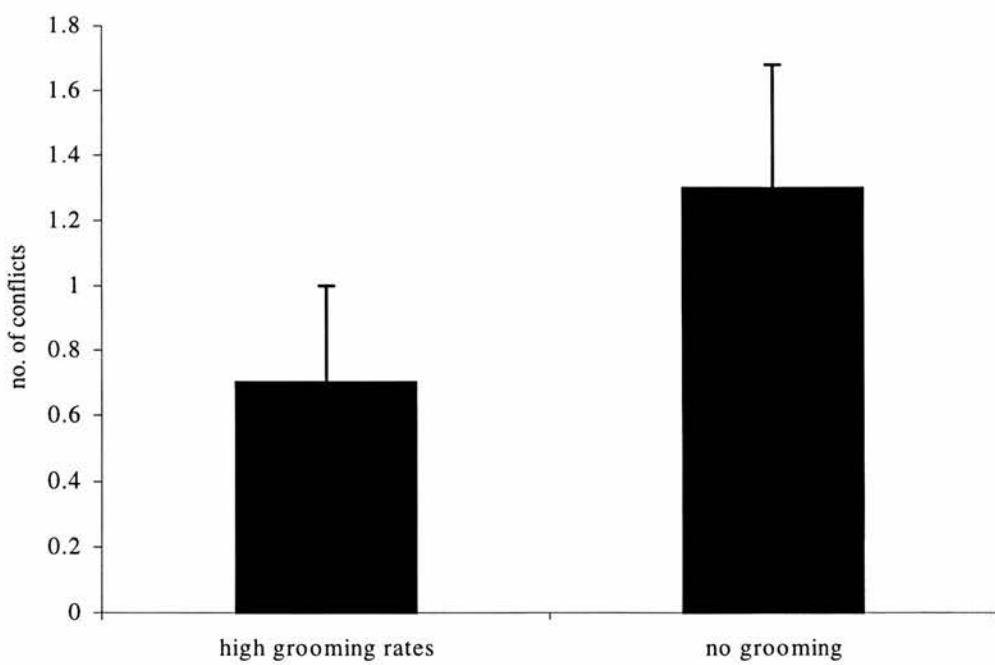


Figure 5.7 The number of dyad-corrected conflicts per dyad directed at individuals from which each subject received most grooming time compared with individuals in which the subject received no grooming (male-male conflicts only).



those individuals from which they *received* grooming at high rates compared to those from which they received no grooming using the same methods as in the above analyses. Again, for male-male dyads, males received significantly less aggression from other males in which they invested high proportions of grooming time compared to those in which they invested little or no time (high rates of grooming v no grooming = 0.7 v 1.3 conflicts; $T^+ = 85$, $N = 14$, $p = 0.02$; mean number of individuals in each category = 4.3 ± 1.9 v 7.8 ± 3.6). However, for females there was no significant difference (grooming investment v no grooming investment = 2.0 v 1.9 conflicts; $T^+ = 32$, $N = 12$, NS; mean number of individuals in each category = 1.9 ± 1.8 v 12.8 ± 4.2). Figure 5.7). I performed a matrix correlation test (Hemelrijk, 1990a) to investigate whether there might be a relationship between aggression given and grooming received but there was no such correlation for either all male-male dyads ($N = 15$, $K_r = -40$, $Tau_{kr} = -0.056$, NS), or all male-female dyads ($N = 31$, $K_r = 38$, $Tau_{kr} = 0.105$, NS), where the correlation was between male aggression toward females and grooming received by males from females.

5.3.5 Rank

Analyses of the effect of rank on aggressive interactions only concern male-male dyads as female-female aggressive interactions were rare. It is unlikely that it would have been possible to construct a linear hierarchy for females as an attempt to do so in a previous study concerning female ecology and social behaviour in this community, failed to do so (Fawcett, 2001).

High-ranking males were more likely to be aggressors against other males and females than low-ranking males; the frequency of attacks increased with

Figure 5.8 The relationship between conflict frequency and rank for (a) all conflicts involving males, (b) male-male conflicts, (c) male-female conflicts.

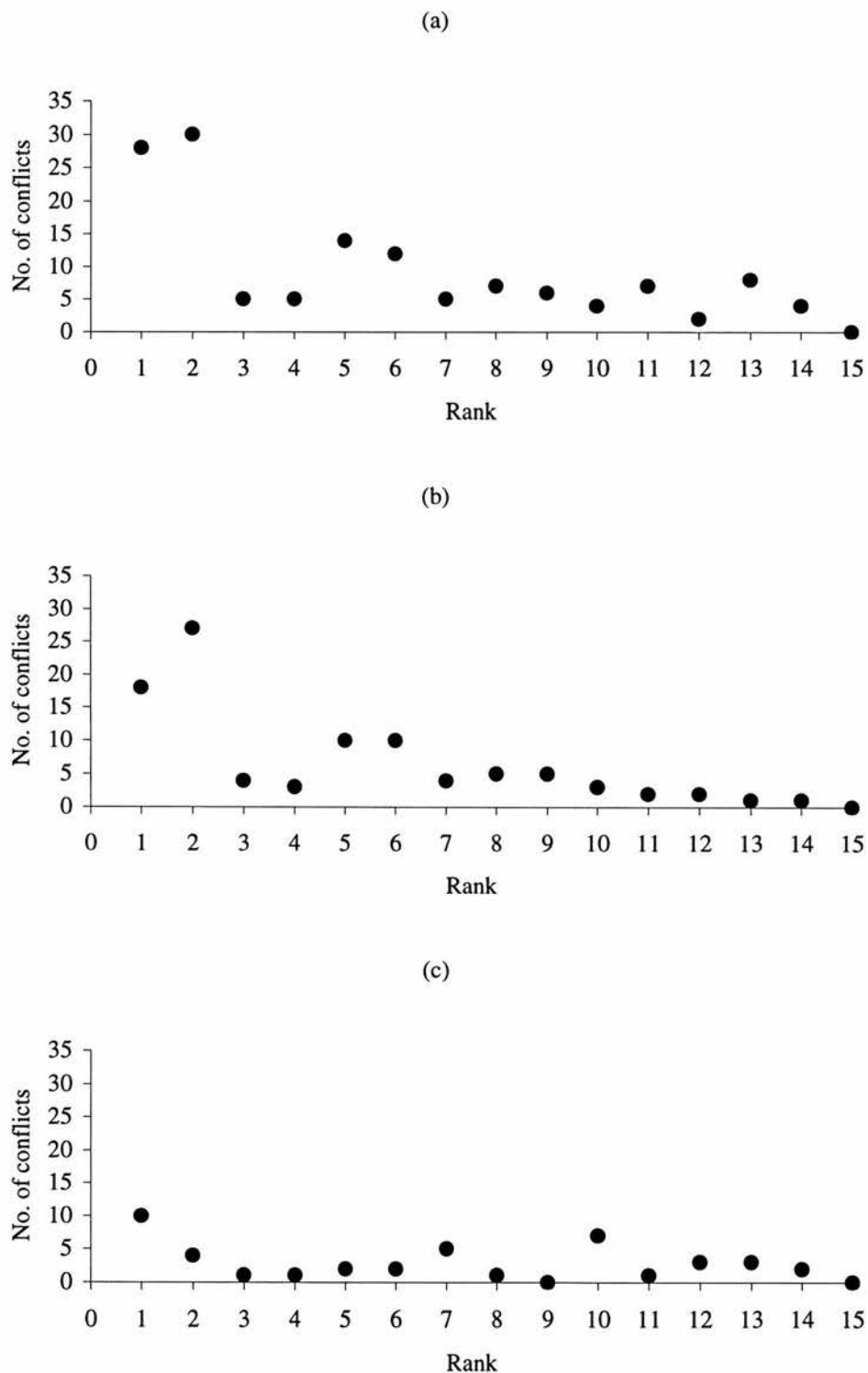
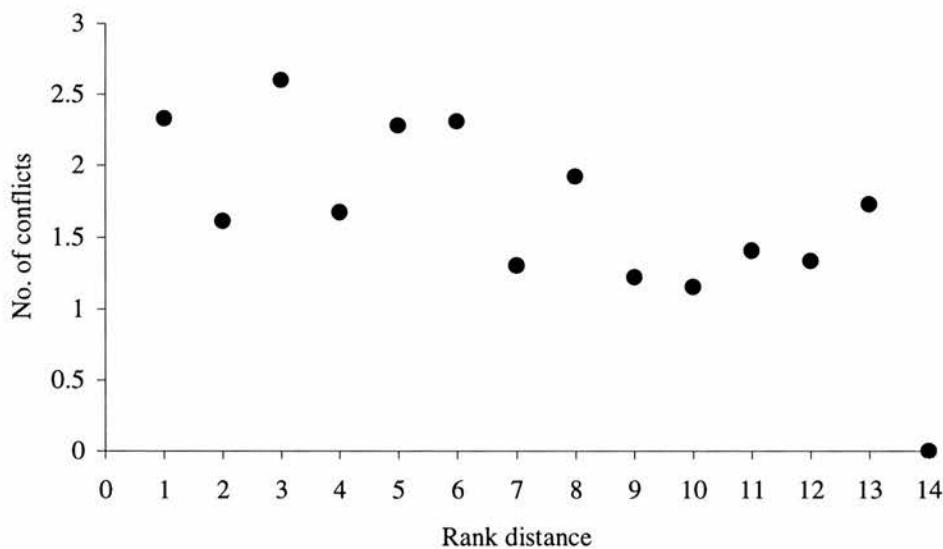


Figure 5.9 The effect of rank distance on the frequency of conflicts per dyad.



increasing male rank (Spearman rank-order correlation coefficient: $r_s = 0.63$, $N = 15$, $p < 0.05$). This correlation was much stronger when only male attacks on other males were considered ($r_s = 0.85$, $N = 15$, $p < 0.001$). Rank did not affect the likelihood of male attacks on females ($r_s = -0.28$, $N = 15$, NS. Figure 5.8). Among the males, the number of conflicts per dyad decreased with increasing rank distance ($r_s = -0.65$, $N = 14$, $p < 0.02$. Figure 5.9).

5.3.6 Triadic and polyadic conflicts

The overwhelming majority of male-male conflicts were dyadic (93.5% of 93) with triadic and polyadic conflicts accounting for only 6.5% of the total number of conflicts. Females were never observed to become involved in ongoing male-male conflicts and so these incidents of triadic or polyadic conflicts were cases in which support for one or other party was given by other males. A similar proportion of conflicts involving males and females were also dyadic (87.8% of 49). Mixed-

sex triadic and polyadic conflicts accounted for only 12.2% of all male-female conflicts; these were situations in which the original conflict involved male-female dyads, or female-female dyads where a male supported one of these females or her supporters.

5.3.7 Coalitions

Only 20 coalitions occurring during the course of 12 conflicts were observed during the study and these included coalitions between both sex classes. This was an unexpectedly small number, averaging 0.04 coalitions/observation hr, compared with e.g. 0.54/hr reported for M group males at Mahale (Nishida & Hosaka, 1996), and a similar figure of 5/day for captive chimpanzees at Arnhem Zoo (de Waal, 1984). Table 5.4 gives details of the individuals involved in conflicts where coalitions were observed.

Eighty percent of coalitions involved support for the victim of aggression, which was also the lower ranked individual in every case. Where aggressors were supported, 2 out of 4 such coalitions involved close kin. Kinship played a role in 2 further coalitions and could be considered as having a protective function. Other types of coalitions were classed as follows:

Control intervention: support is given to the lower ranking individual when the aggressor is a high ranking individual who might grow in status via aggressive interactions. Level of aggression used is of medium to high intensity.

Protective intervention: support is given to a low ranking individual, usually a juvenile or adolescent, against a much higher ranking individual. Level of aggression is usually of low intensity. (Similar to Boehm's (1994) 'partial pacifying intervention' category).

Table 5.4 Individuals involved in aggressive episodes during which support was given, and intervention type.

Aggressor ⇒ Victim	Support from	Pro	Contra	Kin?	Intervention type
BK ⇒ VN	DN	VN	BK		VA, LS, LA/CI
MG ⇒ MU	DN	MU	MG		VA, LS, CI
BK ⇒ BY	VN	BY	BK		VA, LS, CI
	MA	BY	BK		VA, LS, CI
	JM	BY	BK		VA, LS, CI
BK ⇒ VN	DN	VN	BK		VA, LS, LA/CI
MA ⇒ MS	DN	MS	MA		VA, LS, PI
	VN	MS	MA		VA, LS, PI
NB ⇒ GS	BY	GS	NB		VA, LS, PI
	ZF	GS	NB		VA, LS, PI
SR ⇒ KZ	KW*	KZ*	SR	Y	VA, LS, PI
AY ⇒ KW	NB*	AY*	KW	Y	AA, HS
TK ⇒ KY	ZM	KY	TK		VA, LS, CI/OP/PI
	GZ	KY	TK		VA, LS
ZM ⇒ CL	GZ*	ZM*	CL	Y	AA, HS
	RH	ZM	CL		AA, HS, CI/OP
	DN	CL	RH		VA, LS, PI
ZF ⇒ ZM	GZ*	ZM*	ZF	Y	VA, LS, PI
	TK	ZF	ZM		AA, HS, OP
DN ⇒ AY	BB	AY	DN		VA, LS, PI/OP

Pro = support for; contra = support against; VA = supports victim; AA = supports aggressor; LS = supports lower ranked individual; HS = supports higher ranked individual; Y = supports known kin (* marks the related individuals involved); CI = control intervention; PI = protective intervention; OP = opportunistic coalition; LA = long term alliance.

Ally support: support is given to a long-term ally. Aggression may be of any intensity.

Opportunistic coalition: support is given which could serve to increase status or reinforce higher status over the victim, and/or improve or maintain the relationship with the aggressor or victim of aggression. Aggression may be of any intensity.

Table 5.4 includes 8 examples of control interventions and 9 protective interventions. Four interventions were probably opportunistic in nature and 4 were mother-support for offspring or vice versa.

5.3.7.1 Sex differences

Male-male coalitions occurred in only two contexts. The first might be described as suppression, where attempts by a high ranking male to intimidate other adult males were quashed. On two occasions, BK (beta male) attacked VN (gamma male), in response to which, DN, alpha male, and VN's long-time ally, intervened. DN also prevented MG, the previous alpha male, from intimidating MU. On another occasion, BK attacked BY and this was countered with a coalition between three other high-ranking males. Otherwise, male-male coalitions were of a protective nature, intervening when juvenile males were being intimidated by older males. One other example of a protective coalition involved BB, a low ranking adolescent, aggressively threatening DN during an attack on another adolescent male, AY.

Cooking involving males and females began with aggression by a low-ranking male directed at a female, followed by female-female support on three occasions. On one of these occasions, support for the male aggressor was also given by another low-ranking male. On a further two occasions, an adult female aggressed

against a juvenile male. In one case, the mother of the juvenile supported the juvenile; in the other, two adult males gave support to an orphaned juvenile male. The other incident of this type involved female-female aggression where two females supported the aggressor, one of whom was her daughter, and the alpha male aggressed against one of these supporters, thus indirectly supporting the victim of aggression. There were no examples of triadic or polyadic aggression involving only females although the last incident described did begin as such.

5.3.8 Displays

Aggressive displays were observed on 124 occasions and males performed all of them. The majority (72.6%, 90/124) were performed by just one male. Only rarely (17 times) was it clear which individual or individuals were the target of the display, and in most cases it is likely that the display was not directed at a particular individual at all. On one occasion, a display was performed by BK who was associating with one other male, MG, shortly after pant-hoots were heard which probably came from a neighbouring community. This incident was not included in the following analyses, since although this display could have influenced BK's relationship with MG, the display was not directed at him, nor was it likely to be perceived as a dominance display in the context of this relationship.

5.3.8.1 Individual displays

Table 5.5 gives details of the number of individual aggressive displays performed by each male, the number of males in the party, the number of higher- and lower-ranking males present, the number of females, and the number of oestrus females present. Individual displays occurred in parties containing 4.4 ± 2.6 males

Table 5.5 The number of aggressive displays given by individual males and the mean number of males of higher and lower rank, females and oestrus females, present. Males are listed in rank order.

ID	Number of displays	Mean number of				
		Males present	Higher-ranking males present	Lower-ranking males present	Adult and adolescent females present	Oestrus females present
DN	13	5.8	0	4.8	2.4	1.1
BK	14	4.4	0.3	3.1	2.0	0.5
VN	3	3.3	0	2.3	1.3	0
JM	8	7.5	0.9	5.6	3.8	1.5
BY	2	7.5	3.0	3.5	4.0	2.5
MA	13	4.2	1.2	2.1	1.8	0.5
MG	1	5.0	1.0	3.0	2.0	0
MU	1	5.0	1.0	3.0	0	0
ZF	10	3.2	1.6	0.6	3.2	1.0
NJ	4	4.8	2.0	1.8	2.8	0.8
TK	7	2.3	0.4	0.9	2.4	0
AY	7	3.3	1.0	1.3	2.3	0.4
NK	1	2.0	1.0	0	1.0	1.0
BB	3	4.7	3.0	0.7	3.0	1.3
GS	1	4.0	3.0	0	0	0

and 2.4 ± 1.8 adult and adolescent females including 0.8 ± 1.1 oestrus females, on average.

The number of displays performed by each male was related to age but not to rank. There was a trend in favour of high-ranking males performing more displays than low-ranking males when all males were considered ($r_s = 0.51$, $N = 15$, $p < 0.1$; Fig. 5.10), but when data concerning only adult males (ranked 1-8, 10, 11)

Figure 5.10 The relationship between rank and the number of individual displays performed.

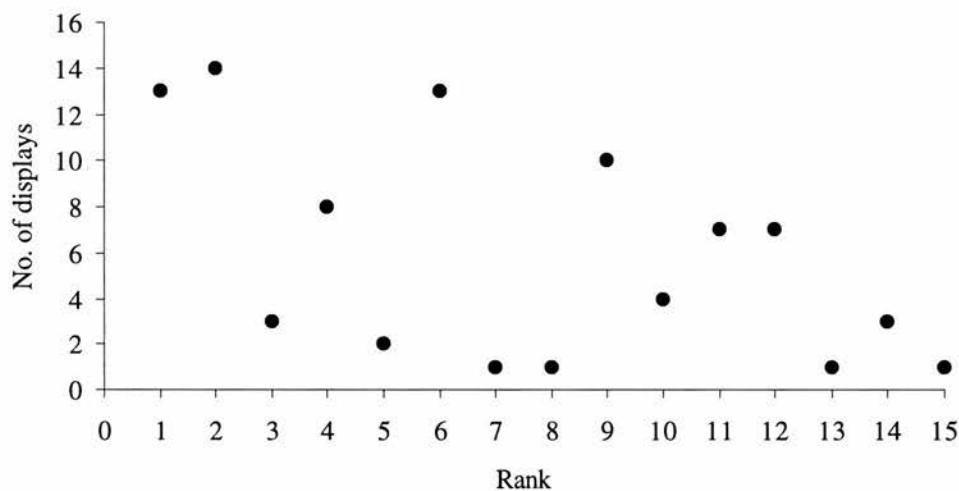


Figure 5.11 The relationship between rank and the mean number of males present in a party during the performance of individual displays (mean and SD).

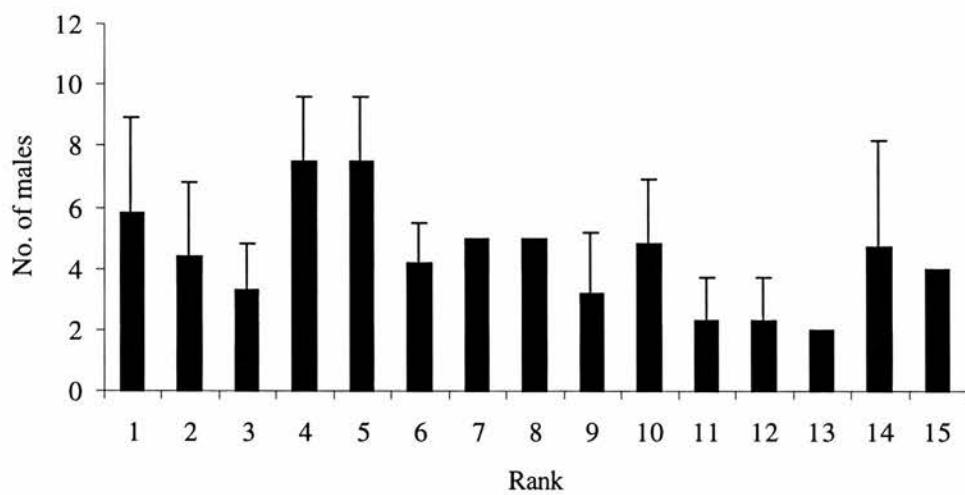
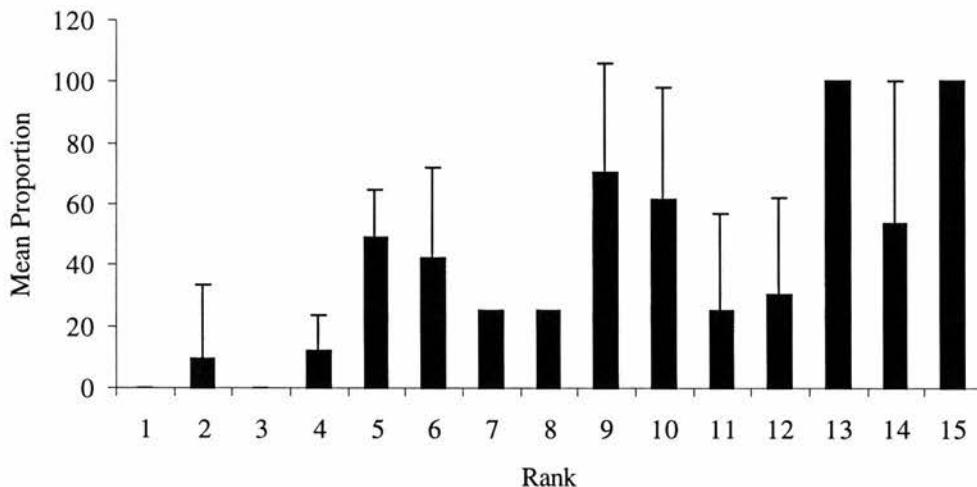


Figure 5.12 The relationship between rank and the mean proportion of males of higher-rank present during the performance of individual displays (mean and SD).



was analysed, this trend disappeared ($r_s = 0.49$, $N = 10$, NS). There was also a trend in favour of high-ranking males performing displays in the presence of a larger number of males than low-ranking males did ($r_s = 0.50$, $N = 15$, $p < 0.1$; Fig. 5.11). Again when only adult males were considered, this trend disappeared ($r_s = 0.30$, $N = 10$, NS). High-ranking males performed displays in the presence of fewer higher-ranking males than low-ranking males did (all males: $r_s = 0.79$, $N = 15$, $p < 0.001$; adult males: $r_s = 0.72$, $N = 10$, $p < 0.05$). Of course it follows from the rank relations of the males that the higher each male is ranked, the smaller the likelihood that males could be present that out-rank him. However, Figure 5.12 shows the proportion of males that are present and out-rank the display and perhaps indicates the ‘willingness’ of each male to perform displays in the presence of higher-ranking males. This proportion should be zero if males are strongly inhibited by the presence of higher-ranking males, which they are clearly not. The number of

adult and adolescent females in a party had no effect on the likelihood of display performance by males of high or low rank (number of females present: $r_s = 0.20$, N = 15, NS; number of oestrus females present: $r_s = 0.20$, N = 15, NS). The result of the same analysis remained nonsignificant when only adult males were considered (number of females present: $r_s = 0.01$, N = 10, NS; number of oestrus females present: $r_s = 0.40$, N = 10, NS).

5.3.8.2 Joint displays

On 34 occasions, displays were observed which involved two or more individuals. Of these, two displays were performed shortly after hearing pant-hoots which were likely to have been produced by a party from the neighbouring community, but, in this case, the displays were included in the following analyses as the dyadic and triadic nature of these displays may have had consequences for, or have been reflective of, the relationships of the individuals involved. Most displays were dyadic (88%, 30/34). Three displays were triadic and one involved four males. Joint displays occurred when in parties consisting of 5.8 ± 2.6 males and 1.4 ± 1.6 adult and adolescent females including 0.4 ± 0.8 oestrus females, on average. Table 5.6 gives details of the number of joint displays performed by each male, the number of males in the party, the number of higher- and lower-ranking males present, the number of females, and the number of oestrus females present. One adult, one adolescent and one juvenile male did not take part in any joint displays.

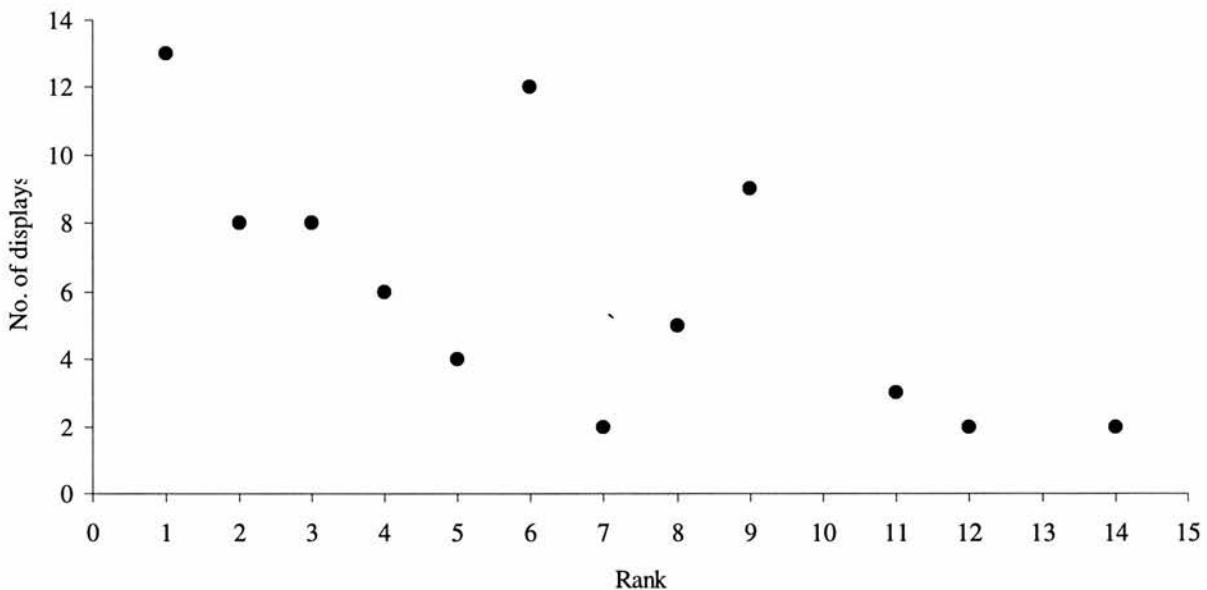
High-ranking males performed joint displays more often than low ranking males (all males: $r_s = 0.68$, N = 12, $p < 0.02$; adult males: $r_s = 0.73$, N = 9, $p < 0.02$. Figure 5.13). High-ranking males performed joint displays in the presence of a

Table 5.6 The number of joint displays performed by each male and the mean number of males of higher and lower rank, females and oestrus females, present. Males are listed in rank order.

ID	Number of displays	Mean number of				
		Males present	Higher-ranking males present	Lower-ranking males present	Adult and adolescent females present	Oestrus females present
DN	13	7.1	0	6.1	1.8	0.9
BK	8	7.3	0.8	3.9	2.0	0.1
VN	8	5.8	0.1	2.9	1.5	0.6
JM	6	7.5	1.3	5.2	3.2	0.7
BY	4	7.5	0.7	3.3	0.8	0.5
MA	12	4.8	1.4	2.3	1.0	0.3
MG	2	4.6	2.0	2.5	1.0	0
MU	5	6.2	3.8	2.0	0	0
ZF	9	4.7	1.8	2.3	0.8	0
NJ	0	-	-	-	-	-
TK	3	4.3	2.3	1.3	1.0	0.3
AY	2	3.0	0.5	1.5	2.0	0
NK	0	-	-	-	-	-
BB	2	5.0	3.5	0.5	2.0	0.5
GS	0	-	-	-	-	-

larger number of males than low-ranking males did (all males: $r_s = 0.70$, $N = 12$, $p < 0.02$; adult males: $r_s = 0.65$, $N = 9$, $p < 0.02$. Figure 5.14). Again, low-ranking males performed joint displays in the presence of a larger proportion of higher-ranking males than high-ranking males did (all males: $r_s = 0.76$, $N = 12$, $p < 0.01$; adult males: $r_s = 0.96$, $N = 9$, $p < 0.001$. Figure 5.15). High-ranking males did not perform displays in the presence of more females or more oestrus females than low-

Figure 5.13 The relationship between rank and the number of joint displays performed.



ranking males (number of females present: $r_s = 0.11$, $N = 12$, NS; number of oestrus females present: $r_s = 0.54$, $N = 9$, NS), although there was a trend in favour of high-ranking adult males doing so (number of females present: $r_s = 0.65$, $N = 9$, $p < 0.1$; number of oestrus females present: $r_s = 0.62$, $N = 9$, $p < 0.1$).

I investigated the possibility that males would be more likely to take part in joint displays than perform them individually. This was not the case as there was no difference in the number of displays performed individually (mean = 5.9) compared to those performed jointly (mean = 4.9; Wilcoxon-Mann-Whitney test: individual v joint displays $T^+ = 71.5$, $N = 14$, NS). Joint displays occurred in parties containing a slightly larger number of males than individual displays did (mean number of males, individual v joint = 4.6 v 5.5, $T^+ = 56$, $N = 11$, $p = 0.02$). All but one of the adult males were more likely to perform joint displays than individual displays in a

Figure 5.14 The relationship between rank and the mean number of males present in a party during the performance of joint displays (mean and SD).

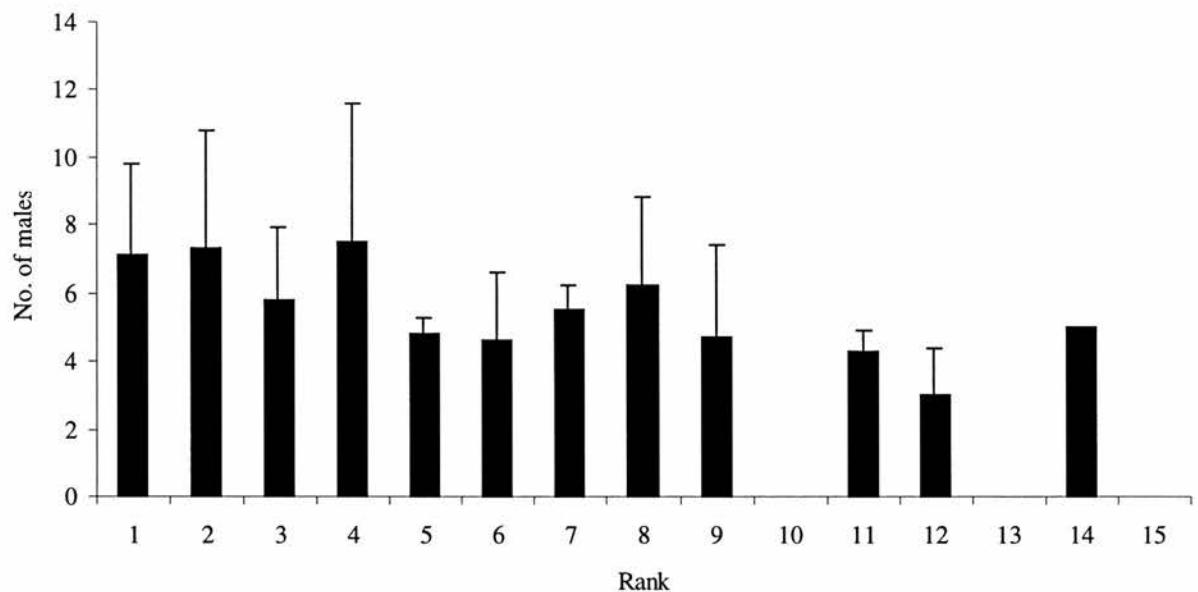
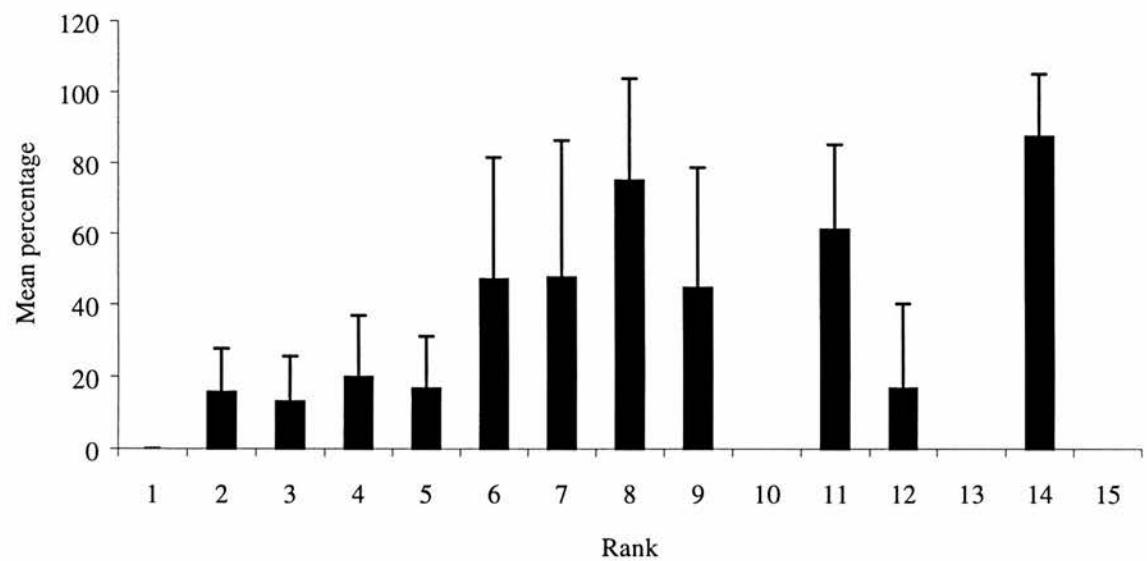


Figure 5.15 The relationship between rank and the mean proportion of males of higher-rank present during the performance of joint displays (mean and SD).



party that contained a higher proportion of higher-ranking males, including those which were also displaying (proportion of higher-ranking males present during individual v joint displays = 20.8% v 32.8%, $T^+ = 30$, $p = 0.055$). Those males which were displaying jointly were included as party members since the possibility of reprisals for taking part in joint displays existed and was observed on one occasion when an adolescent male displayed with high-ranking adult males. The inclusion of adolescent males in this analysis resulted in the disappearance of this trend (proportion of higher-ranking males present during individual v joint displays = 28.5% v 37.0%, $T^+ = 46$, NS). Joint displays were performed more often in parties containing fewer adult and adolescent females, and fewer oestrus females, than individual displays (adult and adolescent females: joint v individual displays = 1.4 v 2.4, $T^+ = 65$, $N = 11$, $p = 0.001$; oestrus females: joint v individual displays = 0.3 v 0.7, $T^+ = 43$, $N = 11$, $p = 0.02$).

Thus, it seems likely that joint displays were associated with large aggregations of males and were not influenced by female presence. Individual displays, however, might be slightly more tuned to the presence of oestrus females. For five males in particular (VN, JM, BY, ZF, BB ranked 3, 4, 5, 9 and 14 respectively), the coincidence of the performance of individual displays with the presence of oestrus females was marked (see tables 5.5 and 5.6). However, of these males, the adults VN and JM were observed to copulate with females on five and six occasions respectively compared to the average number of copulations for adults of 8.1. The adult BY copulated ten times. The adolescents ZF and BB copulated 9 and 8 times respectively compared to the average number of copulations for adolescents of 6.5. High-ranking males displayed with a larger number of partners than low-ranking males did ($r_s = 0.64$, $N = 12$, $p < 0.05$. Figure

Figure 5.16 The relationship between rank and the number of joint display partners.

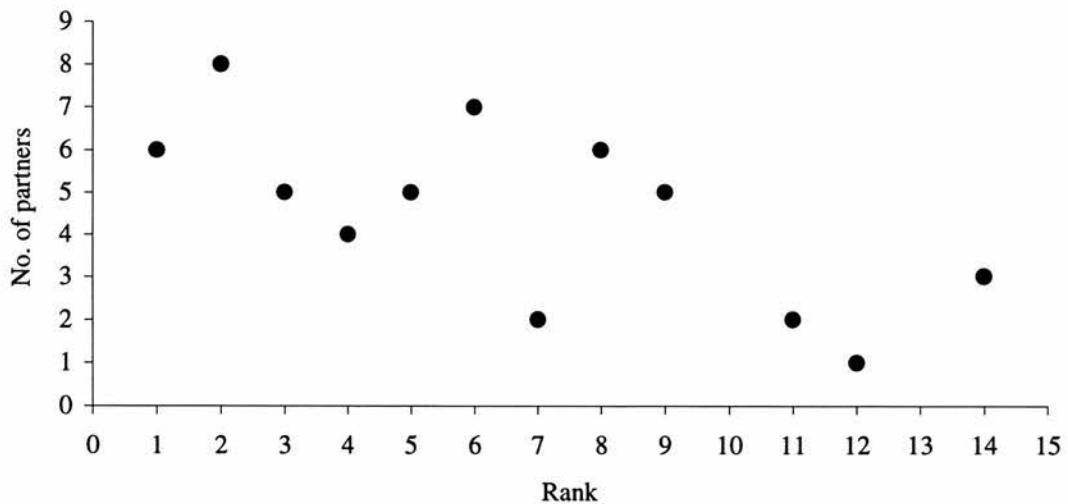


Figure 5.17 The relationship between rank and the mean rank of joint display partners (mean \pm SD).

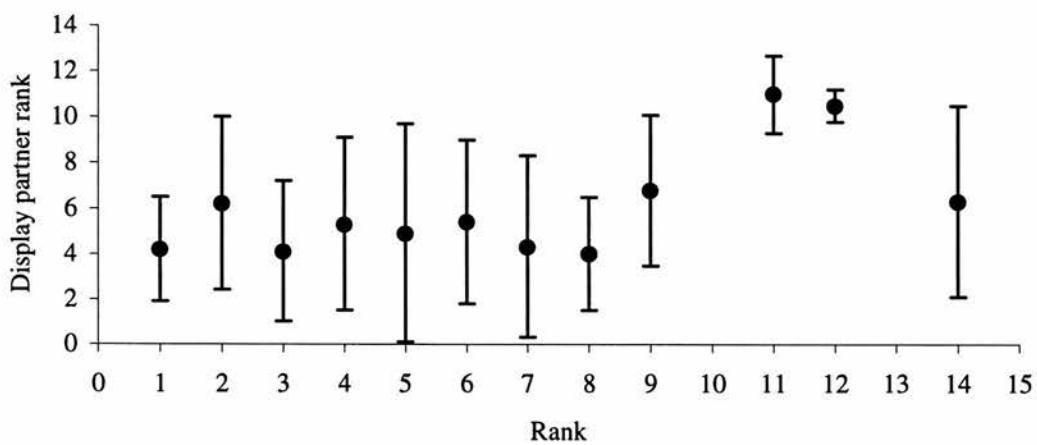
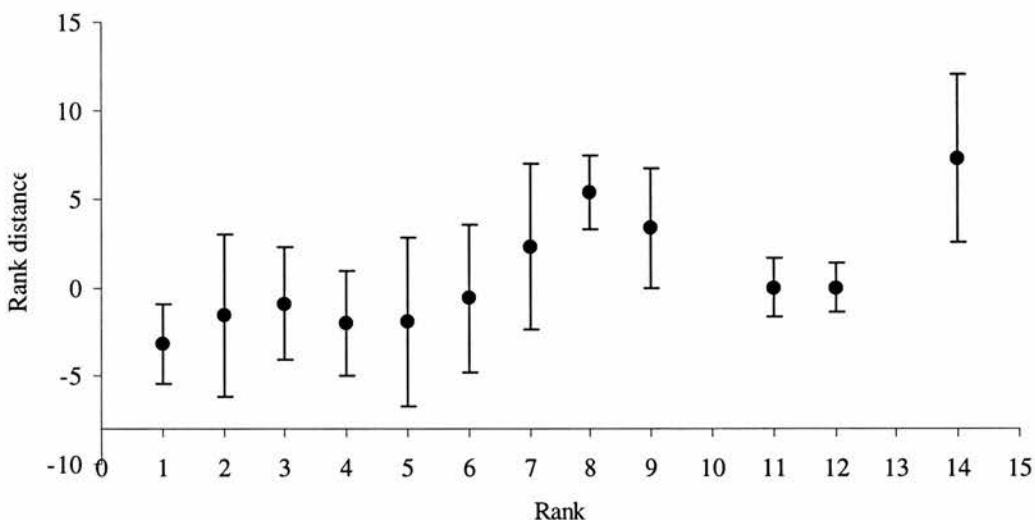


Figure 5.18 The relationship between rank and the mean rank distance of joint display partners (mean \pm SD).



5.16) although as this relationship did not hold when only adult males were considered ($r_s = 0.48$, $N = 9$, NS). Thus, rank did not affect the number of display partners, but adult males had more partners than adolescents.

The independent juvenile, GS, did not take part in joint displays. There was no relationship between the rank of a display and the rank of his display partners (all males: $r_s = 0.41$, $N = 12$, NS, Figure 5.17). The mean ranks of display partners were similar for all displaying males, especially the adults (adult males only: $r_s = 0.13$, $N = 9$, NS). High-ranking males displayed with others that were closer to them in rank than low-ranking males ($r_s = 0.60$, $N = 12$, $p < 0.05$) although this relationship disappeared when only adult males were considered ($r_s = 0.20$, $N = 9$, NS). Only four low-ranking males (ranked 7, 8, 9 and 14) displayed with males ranked higher than themselves, on average (see figure 5.18).

Males jointly displayed more often with other males in which they invested most heavily in grooming (i.e. those males who fell in the upper quartile of grooming investment scores for each male, hereafter "intense" grooming relationships) than with those with which they had "intermediate" or "weak" relationships (intermediate = middle quartiles, weak = lower quartile. Percentage of joint display partners with whom each male had intense v weak grooming relationships: 51.3% v 21.6%, $T^+ = 55.5$, $N = 11$, $p < 0.03$; intense v intermediate: 51.3% v 27.1%, $T^+ = 37$, $N = 9$, $p < 0.05$. See Figure 5.19). There was no difference between the proportion of display partners with whom each male had intermediate or weak grooming relationships (intermediate v weak = 27.1% v 21.6%, $T^+ = 31.5$, $N = 9$, NS). A similar pattern emerged when only adult males were considered. Display partners were more often those with which each male had an intense grooming relationship than a weak one (intense v weak = 52.7% v 11.2%, $T^+ = 36$, $N = 8$, $p = 0.004$); however, there was no difference between the proportion of display partners with which they had intense or intermediate grooming relationships (intense v intermediate = 52.7% v 36.1%, $T^+ = 20$, $N = 7$, NS). A further difference was that adult males also displayed more often with intermediate as opposed to weak grooming partners (intermediate v weak = 52.7% v 11.2%, $T^+ = 27$, $N = 7$, $p < 0.02$).

A similar analysis, this time focusing on proximity with close, intermediate and rare categories equating to proximity scores falling in the upper, mid and lower quartiles, gave a slightly different result (Figure 5.20). Males displayed more often with others which were often in close proximity and in the intermediate category, compared with those who were rarely in proximity (close v rare = 42% v 12.2%, $T^+ = 36$, $N = 8$, $p = 0.004$; intermediate v rare = 45.9% v 12.2%, 42% v 12.2%, $T^+ =$

Figure 5.19 The influence of grooming relationships on the number of joint displays performed (mean and SE).

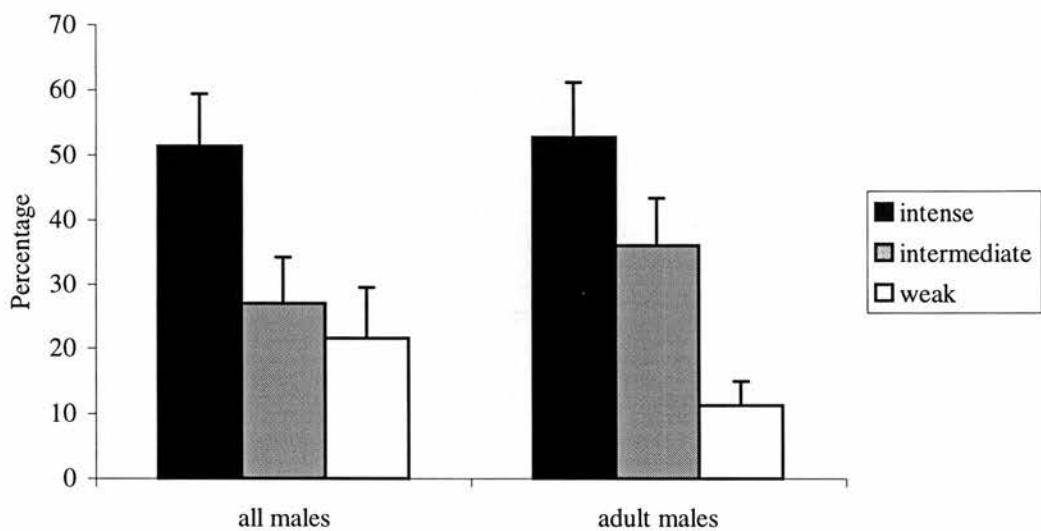


Figure 5.20 The influence of proximity frequency on the number of joint displays performed (mean and SE).

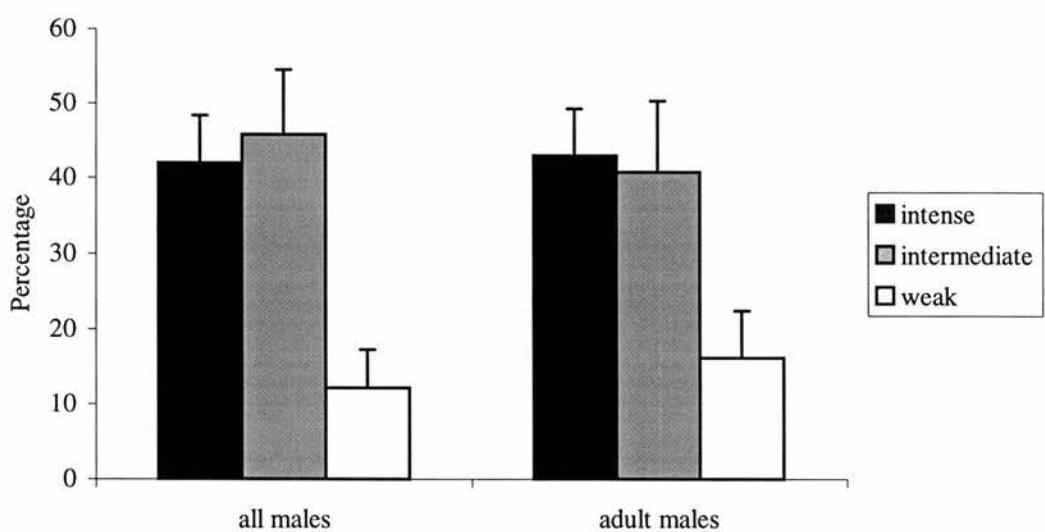
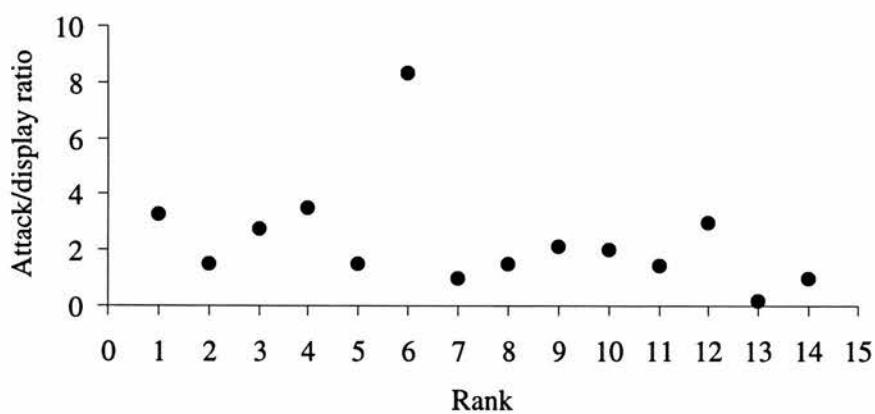


Table 5.7 The ratio between the number of displays v the number of attacks of intensity 3 or higher performed by each male (listed in rank order).

Display/attack ratio	
DN	3.3
BK	1.5
VN	2.8
JM	3.5
BY	1.5
MA	8.3
MG	1.0
MU	1.5
ZF	2.1
NJ	2
TK	1.4
AY	3
NK	0.2
BB	1.0
GS	0

Figure 5.21 The relationship between rank and display/attack ratios.



57, N = 11, p < 0.02). There was no difference in the number of displays performed with males in the close and intermediate categories (close v intermediate = 42% v 45.9%, $T^+ = 22.5$, N = 10, NS). The same analysis concerning adult males alone gave the same result (close v rare = 43.0% v 16.2%, $T^+ = 21$, N = 8, p < 0.02; intermediate v rare = 40.8% v 16.2, $T^+ = 28.5$, N = 8, p < 0.01; close v intermediate = 43% v 40.8%, $T^+ = 24.5$, N = 8, NS).

When both individual and joint displays were considered, the ratio of displays performed v attacks was not influenced by rank when all males were considered ($r_s = 0.41$, N = 15, NS) although there was a trend in favour of a positive correlation between rank and display/attack ratios when only adult males were considered ($r_s = 0.61$, N = 10, p < 0.1, see figure 5.21). Individual display/attack ratios are given in Table 5.7.

5.4 Discussion

Relatively few conflicts were observed among the Sonso chimpanzees, despite a sampling regime biased toward observing parties containing males. I was able to record details of only 157 conflicts during the thirteen-month period of the study. Agonistic confrontations have been recorded at much higher frequencies at other study sites (e.g. 319 at Gombe in 1978, Goodall, 1986; 212 between Mahale M Group males in 3 months during 1992, Nishida & Hosaka, 1996; 197 between males at Taï during 1993, Boesch-Boesch-Achermann, 2000) and also at Budongo during Newton-Fisher's (1997) 14 month study during which he recorded 357

conflicts. This low frequency (0.3 hr^{-1}) immediately suggests that this community was not experiencing high levels of competition during the study period.

5.4.1 Conflict characteristics

The vast majority of conflicts were simple dyadic conflicts; triadic and polyadic conflicts were rare (7.8% of all conflicts). Among males, only 3.9% of conflicts involved coalitions of one type or another. Conflicts involving coalitions among the remaining sex combinations accounted for a further 3.9% of the total number of conflicts. This contrasts with results obtained at Mahale where 50% of conflicts between males involved coalitions during a period in which the dominance hierarchy was stable although there were rivalries amongst the three highest-ranked males (Nishida & Hosaka, 1996). Dyadic conflicts constituted only 60% of all conflicts among the captive colony at Arnhem where again, there were rivalries among the three highest ranked males, and females were often involved in coalitions. If coalitions are more likely to occur when competition for status is intense, the male hierarchy within the Sonso community appeared to be very stable during my study period with virtually no collaboration between males in their attempts to acquire higher status. Patterns of coalition formation will be discussed later in this chapter.

Very intense conflicts involving biting or wounding were never observed with the exception of one very severe, and very likely polyadic, attack on a young adult male, ZT during the first month of the study which is described in Fawcett & Muhumuza, (2000). This was the first observed instance of a lethal *intracommunity* attack in the history of wild chimpanzee research although a similar incident may have occurred at Mahale (Nishida, 1996; Wrangham, 1999). Like the Mahale M

group (Hayaki *et al.*, 1989), the most common forms of aggression observed among the Sonso chimpanzees were aggressive threats and chases which accounted for 86.6% of all conflicts. More severe forms of aggression that involved physical contact were least represented in the data set and slightly more common during coalitions. The most common forms of aggression between males were aggressive threats, then chases (in order of frequency). Aggressive threats were also the most common conflict-type between females. Mild threats and chases were less, but equally, common. Male-female conflicts were slightly more intense with chases being the most common form of aggression.

Adult-adult aggression also tended to take the form of aggressive threats and chases. Patterns of aggression between adults and adolescents were similar although chases were slightly more common. Adults and adolescents threatened juveniles but were rarely more aggressive toward them.

5.4.2 The context of aggression

Male-male conflicts frequently appeared to be dominance interactions although the context of a high proportion of conflicts was unknown and could also have been related to demonstrations of status. Only ten percent of male-male conflicts were observed in the context of sexual activity. This was slightly less than at Gombe where fifteen percent of conflicts between males involved sex competition (Goodall, 1986). Competition between females for sexual partners was not observed and has not been reported at other sites. The huge majority of male-female aggression was also classified as having no obvious context although many of these conflicts were between adolescent males and adult females and could also have been dominance related. Dominance interactions between females were not

observed except in the context of foraging which was also the most common context of female-female aggression. This was also the case at Gombe (Goodall, 1986) although the females of this community were also often aggressive in the context of the protection of familiars which was not observed at Budongo.

5.4.3 The effect of relationship quality

The effects of dyadic characteristics on the frequency of chimpanzee aggression have been given little attention except where the sex, and relative rank, of combatants is concerned. This study, however, has attempted to provide information on other characteristics such as the degree of bondedness measured in terms of proximity and grooming investment. If chimpanzees cultivate utilitarian relationships with certain individuals via affiliation, then, for the most part, they should avoid conflicts with those individuals rather than risk disrupting their ‘good relationships’. Association is also a factor that should affect the frequency of aggression, since the coincidence of competing individuals within the same party will provide opportunities for conflict. Newton-Fisher (1997, 1999a) suggested that male chimpanzees associate tactically in order to maximise the benefits gained from certain important relationships. If chimpanzees do take social factors into account when making ‘decisions’ about which parties to join and which to leave, then they should also avoid parties containing individuals which are likely to harass them, or join parties containing individuals which would be advantageous to target as part of a status-improving strategy.

To examine these questions we can consider relationships between the frequency of aggression and the characteristics of those dyads that become involved in conflicts. In common with most other studies, males were more likely to

demonstrate the effects of intragroup competition through aggressive interactions, than females. The majority of conflicts were between adult males, and between adult and adolescent males (42.3%). Conflicts between adult and adolescent males and females accounted for a further 22.7% of all conflicts. At Gombe, 90% of all conflicts involved at least one adult male (Bygott, 1979). In this study a very similar pattern was observed as males were involved in 89% of all conflicts. Conflicts among females, therefore, were very infrequent in mixed sex parties. All-female parties were rarely sampled and so it is likely that this is an underestimation of conflict frequency among the females of this community. However, Fawcett (2001) observed only 38 female-female conflicts during a two year study which was intentionally biased in favour of all-female parties which is comparable to the findings of this study (20 conflicts in 13 months). Female-female competition was therefore much less evident than male-male competition although there is the possibility that female-female aggression is rarer in mixed sex parties than in all-female parties if there is the potential for males to intervene and escalate fights. This was observed on one occasion when during a conflict between females, the alpha male intervened on behalf of a coalition of female aggressors and attacked their target. However, if the costs of defending resources outweigh the costs of securing alternative ones then conflicts should be avoided (Maynard Smith, 1982). The most common context of conflicts among females was foraging, and since the vast majority of conflicts for which the context was unknown occurred arboreally and could have been related to feeding competition in some cases, alternative sources of food could easily be located in most cases. Conflicts involving juveniles were rare, although adolescents of both sex classes had more conflicts with juveniles than they did with other adolescents. Adult aggression directed at

juveniles was usually a consequence of the juvenile concerned interfering with activities such as feeding from a very clumped food source.

Those individuals which often associated together in parties were slightly more likely to become involved in conflicts than those that were relatively unfamiliar with one another although this result was only marginally significant. This is to be expected as regular associates have more opportunities to have aggressive interactions than those who spend less time together do. This correlation, however, already took the frequency of association into account, as dyad-corrected conflict frequencies were used in this analysis. There was no relationship between conflict frequency and the amount of time spent in close proximity and so it was not the case that individuals that were particularly accessible to one another, in terms of spatial proximity, were the ones that were most likely to become involved in aggression. There was also a trend in favour of frequent grooming partners being more likely to have conflicts than more weakly bonded dyads. However, when male-male and male-female conflicts were analysed separately, all of these trends disappeared and instead, a slight negative correlation between male-male association and conflict frequency emerged. According to this analysis, then, there was *some* indication that males that often co-occurred in parties had fewer conflicts than those that avoided one another, although this relationship was weak.

A second set of analyses were carried out which compared conflict frequencies among dyads whose grooming and proximity scores fell in the upper and lower quartiles for each individual. For male-male dyads, and male-female dyads, no difference was found in the frequency of conflicts between dyads with strong grooming relationships compared with weak ones, and between dyads which spent a great deal of time in proximity compared with those that spent very little

time in proximity. But males directed less aggression at, and received less aggression from, individuals that they groomed regularly compared with those that they never groomed at all. Whether females gave grooming to, or received grooming from, males had no effect on the likelihood that they would receive aggression from those males.

Thus on balance, familiarity and bond strength, as defined by grooming relationships, proximity and association, had an indeterminate affect on the distribution of conflicts. Male-male and male-female dyads with strong affiliative relationships were not significantly less likely to experience aggression than those with weak affiliative relationships. This was confirmed for male-female dyads as the frequency with which conflicts were initiated was not affected by the amount of grooming given to instigators of aggression, or by the amount of grooming instigators invested in others. Thus, good relationships, indexed by grooming investment, did not result in lowered probabilities of receiving aggression among male-female dyads. Males, however, were less likely to initiate conflicts with other males in which they invested most of their grooming compared with those in which they invested little or no grooming. They also have fewer conflicts with males that invested relatively high proportions of grooming in them. Thus, males seemed to behave in a way that preserved close relationships by preferentially directing aggression at other males in whom they invested least grooming.

High-ranking males were more often aggressors than low-ranking males, especially for male-male conflicts. Data concerning male-male conflicts at Mahale also show this pattern (Nishida & Hosaka, 1996) together with many studies of other primate species with discernible linear hierarchies. Male dyads which were close in rank were more likely to have aggressive interactions than those which

were ranked further apart although this could have been a by-product of the relationship between association frequencies and rank-distance (see Chapter 3). Alternatively, this result may have reflected a greater tension between closely ranked males which are the most likely candidates for rank reversals and between whom competition for increased status is likely to be most intense. Another possibility is that males can expect to compete successfully against lower-ranked males. Among dyads that are made up of individuals which are distantly ranked, the lower-ranked male will attempt to avoid provoking aggressive interactions which, according to their experience, they are likely to lose. Within dyads containing individuals that are closely ranked, the lower-ranked individual is not at such a competitive disadvantage and so may act in such a way as to maximise any benefits potentially available to it. This strategy may then result in overt competition between closely ranked individuals, for whom asymmetries in competitive abilities are small, and conflicts ensue (Mason, 1993). Male rank had no effect on the likelihood that males would attack females. All adult males dominated females and though the relative status of adolescent males and adult females may not have been clear, attacks by adolescent males were common and *vice versa*. Females were only ever observed to aggress against the lowest ranked adult male, TK, who was crippled.

5.4.4 Coalitions

Coalitions were a rare occurrence during the course of this study. Triadic and polyadic conflicts involving males and females were twice as common as those involving only males were. Coalitionary aggression occurred at a rate of 0.04 incidents/hr compared to 0.54/hr at Mahale (Nishida & Hosaka, 1996) and 5/day in

the captive colony at Arnhem (de Waal, 1984). Opportunities for reinforcing or disrupting the dominance hierarchy, therefore, were rarely taken (Packer, 1977; de Waal, 1977, 1978). Neither was there any evidence of long term coalitionary partnerships, or alliances, with the exception of an ongoing alliance between the alpha male, DN and the third-ranked male, VN (Newton-Fisher, 1997). DN intervened on behalf of VN on both of the two occasions when DN was present during attacks on VN by the second-ranked BK. Both of these episodes occurred during a period in which BK was observed to join parties containing VN, attack VN, and then leave. DN appeared to be preventing BK from intimidating his alliance partner. VN was never observed to join in an attack initiated by DN except where VN followed DN in threatening a juvenile when he interfered with feeding activities. VN's role in the alliance was, therefore, not clear. He appeared to be the recipient of aid but contributed little more to the relationship than DN in terms of other services such as grooming. DN and VN groomed one another equally often (bouts: from scan data) although grooming bouts in which VN groomed DN were longer than the reverse (duration: from more limited focal data). DN and VN were one another's closest associates over the course of the study until VN's disappearance. Their alliance, therefore, appeared to be based on 'friendship' although knowledge of their relationship history may help to shed more light on this issue. What is known is that DN's rise to the alpha position was probably a consequence of their alliance. After DN and VN's deposition of the ex-alpha male, MG, VN held the alpha position temporarily until he was overthrown by DN in 1995 (Newton-Fisher, 1997). VN was then the beta male for some time afterwards until BK's domination of him during the course of this study. The prevention of BK from intimidating other males may have been a preoccupation of other males in the

community, however, and so DN's intervention on behalf of VN may have simply been part of a general attempt to restrict BK's abilities to dominate other males. On another occasion, BK attacked the high-ranking BY. This resulted in a polyadic coalition of three high-ranking males (VN, MA, JM) against BK in the absence of DN. DN also supported a mid-ranking male, MU, when he was attacked by the ex-alpha male, MG. MU groomed DN far more than the reverse and so this may have been an example of a grooming-for-support trading relationship. Alternatively, DN may again have been behaving in such a way as to undermine the influence of a once powerful male. Unfortunately, detailed analyses of the interchange of support for grooming or any other currency could not be carried out due to the small number of observations of coalitions.

No other intervention patterns involving particular combinations of individuals were evident in this community. Eighty percent of coalitions were victim- or loser-support interventions. Half of only four aggressor-, or winner-support coalitions involved the support of close kin. Two further loser-support coalitions involved kin and probably had a protective function. Many of the observed coalitions could have had multiple functions (see e.g. Ehhardt & Bernstein, 1992) and were classified in a number of different ways. If these classifications were correct then protective interventions were the most common type of coalition observed and opportunistic coalitions that might have served to establish good relationships with the aggressor in an ongoing conflict were rare. I shall describe these in some detail as interpretation of these incidents can be related to existing theories regarding coalition formation. Two opportunistic coalitions involved the intervention of females on behalf of other females. On one occasion, an adult female (ZM) and her juvenile daughter (GZ) defended a young adult female against

a low ranking male (TK). Although this may have helped to cement the relationship between the females involved, it is just as, if not more, likely that this was in fact a control intervention that might have functioned to deter this male from harassing females. Observations of the agonistic interactions involving this male suggest that he did not dominate some of the more senior adult females within this community. On another occasion, the same adult female and then her daughter attacked an immigrant adolescent female (CL). Another adult female joined the coalition at which point the alpha male intervened on behalf of the adolescent female and the conflict ended. Pusey *et al.* (1997) have suggested that it is in the interest of immigrant females to form close relationships with males in order to buffer the effects of female-female competition. Although CL's relationship with DN was not particularly close, DN adopted the 'control role' (e.g. Bernstein & Sharpe, 1966; Boehm, 1981; de Waal, 1984, 1992; Bernstein & Ehardt, 1992) in such a way as to promote their mutual interests. For CL, this was to establish herself in the community and for DN, access to cycling females. Two further opportunistic coalitions involved males: one in which the low ranking TK joined an attack by ZF on the adult female, ZM. This may have been an attempt to improve his relationship with up-and-coming ZF. Alternatively TK may have been taking the opportunity to dominate ZM who had attacked him previously. Lastly, the young adolescent male BB intervened in an aggressive attack by DN on adolescent male AY by distracting DN, which enabled AY to escape. A truly cognitivistic interpretation of this incident would call this evidence of empathy (e.g. de Waal, 1996b) and it is difficult to imagine why BB should have taken such a risk as a reprisal from DN could potentially have been very costly. However, again BB may have acted in this way to improve his relationship with the higher-ranking AY.

Males were involved in coalitions of three basic types: 1) suppressive, 2) protective, and 3) opportunistic. Females were not observed to form coalitions that were unequivocally opportunistic although they did form coalitions of the first two types. The latter observation is consistent with findings of de Waal's (1984) and Hemelrijk & Ek's (1991) studies of captive chimpanzees in that females seemed to show familiarity-dependant support strategies. The Arnhem males, however, regularly switched allegiances over time in a way that appeared to be profitable in terms of improving their status. The Sonso males may also show this tendency but the duration of this study, the stability of the hierarchy and relative peacefulness of the male-male relationships prevented any conclusions being drawn on this matter. The predominance of loser-, or victim-support coalitions also suggests that tensions were not high within the Sonso community. The proportion of winner-support coalitions at Arnhem increased when the group was housed in the relatively cramped conditions of their winter quarters. At Mahale, loser-support strategies were the norm despite tensions among the three highest-ranking males (Nishida & Hosaka, 1996). At Taï, support patterns also favoured subordinates in most cases (Boesch & Boesch-Achermann, 2000). If protective or suppressive interventions are the most common coalition types found among different communities of wild chimpanzees, then this sets chimpanzees apart from other (at least cercopithecine) primates and makes their characterisation as a relatively egalitarian species (de Waal, 1989; Boehm, 1997, 1999) more robust. Unlike at Taï, the alpha male was not the most active intervener in conflicts, and joint attacks of higher-ranking individuals were not observed. Again, this may be reflective of the Sonso community's stability during the study. The lack of interventions by the alpha male, except where suppression of obvious rivals was concerned, was surprising,

however. My own impression of his style of leadership suggested that he did not adopt a dictator-style of strategy as he was tolerant in many situations where tolerance would not be expected according to the literature, but neither was he particularly benign. He might instead have had a 'Mad Dog' disposition which, according to Miller's (1997, p. 323) logic, would benefit an alpha male in that other community members would be unable to predict his tolerance threshold and therefore gauge his reaction to their misdemeanours at any given time. Thus, DN would tolerate male solicitations of maximally tumescent females often but on the occasion of ZT's death, the same behaviour led to an extremely severe, and eventually lethal, attack. During the following few days, even the slightest threat from DN toward the other males resulted in extremely fearful reactions and avoidance on their part. Observations similar to Watts' (1998) on the formation of mate-guarding coalitions were not observed although this was to be expected given Watt's reasoning that this phenomenon was a consequence of the intense competition for sexual partners in a very large community that included many males.

5.4.5 Displays

Only males were observed to perform aggressive displays in this community. Female displays have not been reported in wild chimpanzees although Reynolds & Luscombe (1969) observed attenuated versions in captivity. There was one report of an adolescent female performing a drumming display in the absence of any adult males that involved the drumming of her feet on a tree trunk (J. Karamaji, pers. comm.) although this display may have had a communicative function rather than an aggressive one. Most male displays were performed

individually and were rarely directed at specific individuals. Adult males displayed more often, and in the presence of a larger number of males, than adolescent males did, but no relationship was found between adult male rank and individual display frequency or the number of males present. Bygott (1979) reported a strong correlation between rank and display/attack ratios among males at Gombe. Within each age group, the highest-ranking males attacked relatively often while the lower-ranking males displayed more than they attacked. Low-ranking males, therefore, preferred to behave in an aggressive but not directly confrontational way. Most of the Sonso males, among whom the relationship between display/attack ratios and rank was weak, had rather low display/attack ratios in comparison to those reported by Bygott (1979). An exception was MA who displayed very often toward the end of the study period during which he rose in rank. Goodall (1968, 1986) describes how one male, Mike, attained alpha position through the novelty and vigour of his displays. Male displays, therefore, can play an important part in their perceived social status.

Joint displays, where two or more males displayed in tandem were most often dyadic. Only 12% of joint displays involved more than two males. Rank *did* influence the performance of joint displays, unlike individual displays. High-ranking males performed more joint displays in the presence of a larger number of males than low-ranking males did, even when only adult males were considered. Males were not more likely to begin joint displays or to take part in the displays of other males than they were to perform them alone. Adult males were more likely to take part in joint displays in the presence of larger numbers of males, and in the presence of a larger proportion of higher-ranking males, than they did when performing individual displays. The number and relative rank of males in a party

did not affect the tendency of adolescent males to perform individual or joint displays. Individual displays were more often performed in the presence of larger numbers of females than joint displays and this pattern also applied to the presence of oestrus females. Thus, large numbers of males promoted the performance of joint displays whereas large numbers of females promoted the performance of individual displays. It seems reasonable to suppose that joint displays were demonstrations of male bonds, or that males took the opportunity to display in front of other males that they would be otherwise be inhibited from displaying in front of individually, or both. Individual displays, however, may function to draw the attention (see Reynolds & Luscombe, 1969) of females generally and oestrus females in particular. Four males were particularly likely to perform individual displays in the presence of oestrus females. Two of these males were adults and both of them copulated with females at below average frequencies for adult males. The remaining two males were adolescents and they both copulated at above average frequencies for adolescent males, and at frequencies equivalent to the average for adult males. Only adolescent females were cycling regularly and they were more likely to approach adolescent males in order to copulate with them than adult males. If displays were attention-getting devices, then in the prevailing climate that lacked more confident cycling females, this strategy appeared to pay for adolescent males at least. It is possible that the adult males discussed above were also attempting to use this strategy, though unsuccessfully, given their under-performance in securing copulations compared to other adult males.

Adult males had a wider range of display partners than adolescent males. Rank did not affect the mean ranks of males' display partners although high-ranking males displayed with partners that were closer in rank than low-ranking

males did, suggesting that high-ranking males that displayed together might have had convergent interests in terms of demonstrations of dominance or aggressiveness, whereas low-ranking males may have been taking advantage of an ongoing display to promote their own standing. On one occasion, an adolescent male was aggressed against when he attempted to display with high-ranking males and so it was not the case that any male within a party could take advantage of the potential benefits that might be associated with joint displays.

In agreement with the hypothesis that males jointly displayed in order to demonstrate male bonds, males displayed more often with males in which they had intense grooming relationships and least often with those with whom they had weak grooming relationships. This relationship held, although less strongly, in the case of male dyads that spent more than the average amount of time in proximity.

Thus, it seems that male displays might indeed function primarily to attract attention as Reynolds & Luscombe (1969) suggested. In the case of individual displays, females might be the intended targets and certain males who displayed frequently in their presence achieved more copulations than expected. Joint displays, however, appeared to be directed at other males and could serve to draw attention to close, and potentially rewarding relationships. My impression was not that males necessarily intended to perform displays jointly as I was unable to perceive any signalling of intent, but rather, when one male displayed the other joined them on the spur of the moment. This impression resembles that of Goodall's (1986) interpretation of the dynamics of coalition formation which she explained as the result of contagion. Signals may have been exchanged which were too subtle to observe but it is equally likely that displays were joined spontaneously. Bygott (1979) reported that displays were most common when males encountered another

party. It seems plausible that males who had been travelling together for some time might behave synchronously on joining a party together. Males who travelled together in pairs were often close affiliates and behavioural synchronisation has been reported to function as marker of pair-bonds in a number of primate species (e.g. play behaviour in barbary macaques, *M. sylvanus*, Preuschoft, 1992; duetting in siamangs, *Hylobates syndactylus*, Geissmann & Orgeldinger, 2000) including chimpanzees (call convergence, Mitani & Gross-Louis, 1998) and humans (e.g. demonstrations of attraction, Capella, 1997). Unfortunately I did not collect detailed enough data on the context of displays to examine this possibility. However, these preliminary results suggest that the relationship between the performance of joint displays in relation to male bonds deserves further attention.

5.4.6 Summary

Conflicts within the Sonso community were rare by comparison with previous studies carried out at Budongo and elsewhere. Males were involved in 89% of conflicts and 42% of conflicts were between males. Simple dyadic conflicts were the most common form of aggression by far. Conflicts involving chases were most common among male-female dyads whereas less intense forms of aggression were most often used during single sex conflicts. A high proportion of conflicts between males appeared to be dominance interactions while conflicts among females were predominately food related. Male-male competition in the context of sex was less common than previously reported at Gombe (Goodall, 1986).

Hypothesis 9 (given in section 1.3), that males are less likely to have conflicts with individuals with whom they affiliate relatively often, gained some support. Although males had marginally fewer conflicts with other males with

whom they often associated, dyads who groomed often were not less likely to have conflicts than those that groomed rarely or not at all. However, males directed less aggression toward, and received less aggression from, those individuals that they groomed frequently compared with those that they groomed rarely. This was not the case for male-female dyads as females were just as likely to experience aggression from males irrespective of whether they received grooming from them or gave grooming to them. Thus, there was some evidence that grooming relationships promoted tolerance among males. If a male groomed another, he was also less likely to disrupt the relationship by initiating overt competition with him. Equally, if a male received grooming from another, he was less likely to direct aggression toward him.

Hypothesis 10, that high-ranking males use more force in their attempts to dominate others than low-ranking males, was supported in the case of male-male conflicts. High-ranking males directed aggression toward other males more often than low-ranking males did. There was no difference, however, in the frequency of aggression displayed by high and low-ranking males toward females. It is to be expected that intrasexual competition should be more intense than intersexual competition. Assuming that male-female competition revolves mainly around access to resources utilised by both sexes, e.g. food in the case of this community, then competition should be equally intense between males and females irrespective of rank. That high-ranking males were more aggressive toward other males than low-ranking males indicates that male-male competition for something was a feature of the Sonso community although the findings of the previous chapters have rarely indicated that this might be the case. It is possible that high status among male chimpanzees might constitute an end in itself, thus promoting their image as

political primates. It is equally possible, however, that males chimpanzees simply behave in such a way as to maximise their chances of getting their own way as often as they can. Dominating as many males as possible through intimidation would count as workable strategy for achieving this.

Hypothesis 11, that competition should be most intense among closely ranked males, was supported. There was a negative correlation between male rank distance and conflict frequency. Males whose relative positions in the dominance hierarchy were the least clear experienced more competition than those whose relative positions were clearly differentiated.

Hypothesis 12, that grooming investment increases the likelihood of receiving support during aggressive encounters, was not tested. Coalitions were so rare in this community that such a relationship between grooming and support could not be investigated. However, the majority of coalitions were in fact interventions on behalf of victims of aggression. Only a very small proportion of coalitions included individuals that associated frequently or had strongly affiliative relationships. The DN-VN alliance provides the only example of a positive relationship between grooming and support and so this phenomenon cannot be considered widespread in this community.

Hypothesis 13, that rank determines the degree to which males perform aggressive displays and also the context of these displays, in terms of the number and ranks of the other males present, was not supported. This was a little surprising given that high-ranking males were more aggressive than low-ranking males and that displays are also considered to function as intimidation strategies. This finding presents the possibility that displays serve purposes other than straightforward attempts at dominating others. The only finding in favour of this hypothesis was

that adult males displayed more often than adolescent males. There was also no relationship between rank and the number of males present during the performance of displays. Neither were low-ranking males inhibited from displaying by the presence of higher-ranking males which could be considered risky if displays are merely shows of aggression. The possibility that displays might serve some alternative function was further investigated.

Hypothesis 14, that the performance of joint displays demonstrates strong social bonds, was supported. Dyads that included males that groomed often were more likely to display together than dyads that groomed at intermediate levels or rarely. Males were also more likely to perform joint displays in the presence of larger numbers of males and males of higher rank, than when they performed individual displays. Thus, the presence of large numbers of relatively powerful males promoted the performance of synchronised displays which might serve to demonstrate the potential for future coalitions.

Hypothesis 15, that the performance of joint displays reflects the convergent interests of the males involved, was not supported. Males that were close in rank were no more likely to display jointly than males that were distantly ranked.

Hypothesis 16, that the individual displays of high-ranking males are more likely to escalate into joint displays than the individual displays of low-ranking males, was partially supported. High-ranking adult males did not have more display partners than low-ranking males although they did perform more joint displays than low-ranking males which suggests that males were more likely to take opportunities to demonstrate, or attempt to demonstrate, close bonds with other powerful males.

Again, although it was impossible to assess the influence of rank on the distribution of coalitions, rank had little effect on patterns of joint displays which

could be considered to be a measure of cooperative behaviour. Instead, the observed patterns of display behaviour were underpinned by the strength of grooming relationships.

Patterns of post-conflict behaviour have been shown to reflect the relative value of various dimensions of relationship quality for both wild and captive primates using both observational and experimental methods. Following conflicts, primates, and other mammals, reconcile with those individuals that are valuable in some way, whether as social partners, protectors or co-operators. In the next chapter I investigate patterns of reconciliation and other forms of post-conflict behaviour that should shed further light on which characteristics are most valued in a social partner, irrespective of what objective use they are and what kinds of relationships are worth repairing after a conflict.

Chapter 6

Post-Conflict Behaviour¹

6.1 Introduction

Since the first study of post-conflict behaviour in captive chimpanzees (de Waal & van Roosmalen, 1979) a considerable amount of research effort has been devoted to the study of how primates maintain group cohesion, and its benefits, in the face of intragroup conflict (for an extensive review, see Aureli & de Waal, 2000). Primates have been shown to 'reconcile' a significant proportion of conflicts within minutes of their termination. Reconciliation is defined as some form of affiliative interaction between former opponents occurring soon after an aggressive episode, and has been suggested to be a mechanism for restoring a dyadic relationship to a state similar to that which prevailed prior to the conflict (de Waal & van Roosmalen, 1979). Conflict often results in elevated stress levels, and reconciliation has been shown to reduce rates of behavioural indicators of stress back to baseline levels in both aggressors and victims in a number of baboon and macaque species (olive baboons, *Papio anubis*: Castles & Whiten, 1998a; chacma baboons, *P. cynocephalus ursinus*: Cheney & Seyfarth, 1997; long-tailed macaques, *Macaca fascicularis*: Aureli & van Schaik, 1991a; Aureli, 1997; Das *et al.*, 1988; Barbary macaques, *M. sylvanus*: Aureli, 1997; see Aureli & Smucny, 2000 for a review).

Reconciliation has been demonstrated in almost thirty species of primate (Aureli & de Waal, 2000) including members of all of the major primate groups. It has

¹ Published version, Arnold, K. & Whiten, A. (2001). Post-conflict behaviour in wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Behaviour*, 138, p. 649-690.

also been shown to occur in domestic goats (*Capra hircus*: Schino, 1998), captive bottlenose dolphins (*Tursiops truncatus*: Samuels & Flaherty, 2000) and wild spotted hyenas (*Crocuta crocuta*: Hofer & East, 2000).

Despite the fact that de Waal & van Roosmalen's (1979) chimpanzee study initiated the field, there has been no study of post-conflict behaviour in wild chimpanzees. Indeed, the vast majority of studies of post-conflict behaviour have been carried out on captive subjects and it has largely been assumed that theories constructed in the light of these data are equally applicable to their wild counterparts. Only one study has set out to test these assumptions by gathering data in the wild for a species already studied in captivity (long-tailed macaques, *M. fascicularis*: Aureli, 1992). This, and other studies concerning wild primates (vervet monkeys, *Cercopithecus aethiops*: Cheney & Seyfarth, 1989; mountain gorillas: Watts, 1995a,b; olive baboons: Castles & Whiten, 1998a,b) have generated findings consistent with principles derived from the captive studies.

The study of post-conflict behaviour in wild chimpanzees is thus overdue. The considerable literature on captive primate reconciliation that has accumulated since de Waal & van Roosmalen's (1979) study allows us to structure our analysis in accordance with a number of principles.

The first concerns how reconciliation varies according to the dominance style of the species under investigation. Species which can be described as 'despotic' are those whose societies are characterised by strict hierarchies, asymmetrical contests and a high degree of kin bias in the distribution of valuable relationships (de Waal, 1989a). For these species, valuable partners may be limited to quite a small subset, or clique, of the social group. The conciliatory tendency of any particular dyad of e.g. rhesus macaques (*M. mulatta*) may be high, but mean conciliatory tendencies for this

species are amongst the lowest reported. Stumptail macaques (*M. arctoides*: de Waal & Luttrell, 1989), Tonkean macaques (*Macaca tonkeana*: Thierry, 1984, 1985, 1986) and spectacled langurs (*Trachypithecus obscurus*: Arnold, 1997) show relaxed and 'tolerant' dominance styles (de Waal, 1989a) demonstrated in the frequent bi-directionality of aggression, low intensity of aggression and high frequency of grooming. The conciliatory tendency of all three species has been reported as high (stumptail macaques: de Waal & Ren, 1988; Tonkean macaques: Demaria & Thierry, 1992; spectacled langurs: Arnold & Barton, 1997, 2001a) and all have a rich repertoire of reassurance gestures and show behavioural specificity in conciliatory contexts.

The post-conflict behaviour of captive chimpanzees, which exhibit a relatively egalitarian society (Boehm, 1992), has been reported to have much in common with the post-conflict behaviour of these more tolerant species (de Waal, 1989a). In captive studies, chimpanzees show behavioural specificity during post-conflict reunions and reconcile at a high rate (de Waal & van Roosmalen, 1979; Casperd, 1997). It has been hypothesised that such specificity marks such reunions thus making reconciliation explicit (de Waal & Ren, 1988). It is important to establish whether these principles apply to wild chimpanzees. Findings from captive studies may not be representative of chimpanzee post-conflict behaviour, as it is known that chimpanzees are very able to adapt to captive conditions by displaying patterns of social behaviour which are rarely observed in the wild (de Waal, 1982, 1994).

Another set of principles concern the likelihood of reconciliation within a particular dyad of any given species. Although reconciliation is an option for former opponents, it is not always taken, nor is it always possible. Attempts to approach a former opponent may result in further aggression (e.g. Aureli & van Schaik, 1991a; Cords, 1992) and might therefore be costly. Alternatively, former opponents might not

be sufficiently motivated to expend time and energy on a conciliatory effort if the benefits of doing so are not particularly great. One of the most robust findings of studies of post-conflict behaviour is that the kinds of dyads that are most likely to reconcile are those which consist of individuals that are valuable to one another in some way (Cords & Thurneer, 1993; Cords & Aureli, 1996). For example, many macaque and baboon species show higher rates of reconciliation between kin than between non-kin, and these group members are most likely to be intense affiliates, protectors and coalition partners relative to nonkin group members (e.g., de Waal & Yoshihara, 1983; Aureli *et al.*, 1989, 1997; Castles & Whiten, 1998b). In mountain gorillas, males are important to females as protectors and social partners, but females rarely affiliate and interactions are often antagonistic (Watts, 1996). As this predicts, conflicts between males and females are reconciled but not those between females (Watts, 1995a).

According to what is known about the social behaviour of wild chimpanzees, we predict that reconciliation should be influenced by relationship quality in the following ways:

- 1) Reconciliation should be most frequent among males, reflecting the close and co-operative nature of their relationships. Males are known to have strong social bonds and form the most frequent grooming partnerships (Goodall, 1986). They also hunt and defend community ranges co-operatively and are important to one another as potential allies in individual struggles for high status (Riss & Goodall, 1977; de Waal & van Roosmalen, 1979).
- 2) Male-female dyads would be expected to reconcile conflicts less often than male-male dyads as social bonds tend to be weaker between the sexes.

- 3) Reconciliation, however, should be more common when the female is in oestrus in order that males can get access to them; moreover, males would be expected to be primarily responsible for the initiation of reconciliation and to be especially motivated to maintain good relationships with females at this time.
- 4) Females should reconcile least as they rarely cooperate with one another and spend relatively little time socialising.

Male chimpanzees have often been described as 'political' (de Waal, 1982; Byrne & Whiten, 1988). Accordingly we also predict that:

- 5) Conciliatory tendencies should correlate with levels of affiliation and association (Newton-Fisher, 1999a) reflecting individuals' motivation to selectively seek to maintain relationships with high ranking individuals.
- 6) Adults should reconcile conflicts with other adults more frequently than with adolescents and juveniles as the latter have less potential as allies, or in the case of male-female relationships, provide few benefits in terms of reproductive success. Younger individuals should be more motivated to attempt reconciliation with adults thereby enabling continued social contact.
- 7) Chimpanzees should also withhold opportunities for relationship repair from individuals with whom dominance relationships are ambiguous, as reconciliation often involves the acknowledgement of relative status through ritualised submissive signals before it can be achieved (de Waal, 1986, de Waal & Ren, 1988). We would therefore expect status signals to precede reconciliation in most cases and low conciliatory tendencies between individuals which are closely ranked.

In addition to post-conflict interactions between former opponents, conflicts sometimes have consequences for uninvolved third parties. Among the despotic

species of primate, redirection of aggression toward uninvolved third parties is common. It is possible that redirection by the victim serves to divert the attention of the former aggressor toward a new target (for a review see Scuccchi *et al.*, 1988), solicit the aggressors' support against a third party, thereby restoring the relationship (de Waal, 1977) or indirectly impose a fitness cost on the aggressor by attacking her kin (Cheney & Seyfarth, 1989; Aureli & van Schaik, 1991b; Aureli, 1992; Aureli *et al.*, 1992).

Victims in more tolerant species initiate affiliative interactions with third parties, which may serve as a substitute for reconciliation by reducing stress levels and reduce the likelihood of further attacks (Watts, 1995b, Verbeek & de Waal, 1997, Watts *et al.*, 2000; Arnold & Barton, 2001b).

Another form of post-conflict affiliation with third parties has only been observed in chimpanzees. 'Consolation' is defined as an affiliative contact, initiated by a third party and directed toward a victim of aggression (de Waal & van Roosmalen, 1979; de Waal & Aureli, 1996). In de Waal & van Roosmalen's (1979) study, reconciliation and consolation were distinguished by a high incidence of kissing in the former, and embracing, in the latter, thereby explicitly marking the affiliative contact as one which was directly linked to the previous conflict (de Waal & Ren, 1988). Consolation has been looked for in a number of studies of monkeys but has not been found at elevated rates in post-conflict periods (e.g., long-tailed macaques: Aureli & van Schaik, 1989a; Aureli, 1992; vervet monkeys: Cheney & Seyfarth, 1989; rhesus macaques: de Waal & Yoshihara, 1983; stump-tail macaques: de Waal & Ren, 1988; olive baboons: Castles & Whiten, 1998b). Neither has it been found in other great apes (bonobos, *P. paniscus*: de Waal, 1987; gorillas: Watts, 1995a; Watts *et al.*, 2000). De Waal & Aureli (1996) propose two alternative hypotheses that might account for

the occurrence of consolation in chimpanzees but not in macaques. First, the 'social cognition' hypothesis relies on the proposal that chimpanzees, but not macaques, empathise with the distress perceived in the victim. Second, the 'social constraints' hypothesis suggests that this type of post-conflict behaviour is more advantageous or less risky in chimpanzee society than in macaque society. Chimpanzee society is less strictly hierarchical and more tolerant than that of macaques and, unlike macaques, coalitions may be directed up the hierarchy indicating greater symmetry in power relationships and a less fearfulness in the face of dominants.

All of these principles of social dynamics, the influence of valuable relationships, redirection and affiliative third party contacts, thus make predictions for chimpanzees that beg investigation in the wild. In addition, captive studies have produced some contradictory results. At Arnhem Zoo in the Netherlands, males were the most conciliatory sex (de Waal & van Roosmalen, 1979) whilst at Chester Zoo, UK, males and females reconciled conflicts equally often and male-male dyads had the lowest conciliatory tendencies (Casperd, 1997). The more detailed results of the Chester study were surprising as males were important coalition partners, yet reconciled relatively infrequently. They were also important social partners in terms of time spent affiliating, so would be expected to reconcile relatively often according to the 'good relationships' hypothesis which states that reconciliation should be more common among individuals which have intensely affiliative relationships with low frequencies of aggression (Aureli *et al.*, 1989). It was not the case that males simply did not have particularly conciliatory dispositions as males reconciled often with females. In contrast with the findings of the Arnhem study, victims, losers and high-ranking individuals at Chester were more likely to initiate reconciliation than aggressors, winners and low ranking individuals.

The goal of this study was thus, most basically, to remedy a surprising gap in our knowledge of post-conflict behaviour by a study of wild chimpanzees. Additionally, captive studies to date have generated contradictory results that beg resolution by studies under natural conditions, and a number of proposed social principles that structure the specific analyses that follow.

6.2 Methods

6.2.1 Subjects

All of the members of the community, with the exception of infants (less than 4 years old) were considered as subjects and 37 of a possible 42 were sampled at least once as either aggressor or victim of aggression.

6.2.2 Data collection

Data were collected from September 1998 to October 1999. I collected continuous focal animal samples of 30 min duration (Altmann, 1974) with 15 min inter-observation intervals, and post-conflict and matched control observations (see below). Scan samples were collected every 15 mins by a second observer and these provided basic information of three types.

First, the identity of all individuals that were considered to be members of the party under observation was recorded. Party membership was defined as those individuals who were present within a discrete subgroup, usually located within a radius of approximately 40m or less. Second, the activity of all visible party members were categorised according to the following definitions and noted:-

Resting: individual is stationary, either sitting or lying and may or may not be vigilant.

Travelling on the ground: individual walks on the forest floor.

Moving in the tree: individual is walking, climbing or brachiating along the branches or trunk of a tree.

Foraging: feeding including moving short distances and handling food items.

Self-grooming: individual uses fingers and lips to push apart its fur to locate and remove ectoparasites and other foreign bodies from own fur and skin.

Grooming: individual grooms (as above) another individual. The identity of grooming partner was noted, as was the direction of grooming.

Other social: any other social activity including playing and aggression. The identity of the social partner was noted.

Third, the relative distance of all party members from the individual which was the subject of the focal observation being collected simultaneously. Data concerning agonistic dominance interactions were collected *ad libitum* for the construction of dominance hierarchies and are listed below.

Females were given an oestrus condition score ranging from 0 = no swelling to 4 = maximal swelling. Incidents of copulation and the identities of those involved were noted

Post-conflict behaviour was investigated in the following way. Observational procedures were based on those developed by de Waal & Yoshihara (1983) and Aureli *et al.* (1989). Whenever aggression was observed, a description of the interaction was noted including the following information:

1. The identities of the aggressor and victim.
2. The intensity of the aggression: low intensity aggression was defined as threats e.g., hitting toward, flailing, swaying branches, lunging, charging displays,

aggressive vocalisations; high intensity aggression was defined as chases of > 4m which may or may not be combined with threats and contact aggression including body contact including pushing, slapping, hitting, grappling, stamping on (for definitions see Goodall, 1986).

3. The date and time of the interaction.
4. The context in which the aggression occurred, e.g. feeding, resting, travelling, and any other factors considered to be potentially relevant, e.g. female in oestrus.
5. The approximate height relative to the forest floor.
6. The identities of other individuals involved in the aggressive episode and the nature of their involvement, e.g. if they were supporters of either party.

In most cases, levels of visibility either allowed all of the above information that required good observation conditions to be collected, or very little of it. In cases where the victim and aggressor could not be reliably identified or where the conflict resulted in both parties moving out of sight, post-conflict (PC) observations were not made. If at least one former opponent was still visible at the point when the conflict was terminated, a PC observation was begun immediately. If the conflict was resumed within 30s then the PC was restarted again as soon as the aggression ceased. A former opponent was selected as the focal individual with a bias toward victims of aggression. Victims were preferred because we were interested in interactions between victims and third parties. However, the bias did not affect the sampling distribution, as victims were more likely to move out of sight than were aggressors resulting in roughly equal sampling of each class of opponent. The relative distance (using 5m classes) of the former opponents was recorded at the beginning of the PC and subsequently at 5 min intervals. PC observations consisted of a continuous record of all agonistic interactions (high and low intensity aggression, displays, screaming,

fleeing, crouching, pant-grunting, pant-screaming) affiliative interactions (allogrooming, playing, sitting in contact, gentle touches, mounting, presenting, embracing, arm around, genital inspection, approach) and other signals (hold-out-hand, overhead branch-hold, shake-testicles) involving the focal subject, the identity of the interaction partner and the identity of the initiator of the interaction. 'Overhead branch-hold' is defined as grasping an overhead branch with one hand. It was used to solicit contact, particularly allogrooming. 'Shake-testicles' is defined as grasping the testicles with one hand and shaking them. This behaviour was recorded in an appeasement context and was observed being performed by the appeaser, both on himself, and on the individual being appeased. Scratching and self grooming were also recorded and were scored as one bout when the such self-directed behaviours were resumed <5s after a previous bout. Scratching was categorised as either gentle-scratching (soft raking of the fingers through the fur) or rough-scratching (vigorous, audible and repetitive raking of the fingers through the fur). If the focal animal moved out of sight for more than 1 min within the first 10 mins of the PC and a potential social partner was known to be close by (within 5m) and also out of sight, the PC was abandoned in order to minimise the risk of underestimating the occurrence of reconciliation and third party contacts. Focal subjects that moved out of sight but which were not near other individuals did not present a problem for determining the occurrence of post-conflict interactions. In addition to social behaviour, the occurrence and duration of non-social activities (as defined for scan sampling above) were also recorded.

To determine whether or not post-conflict affiliative contacts are influenced by the recent conflict, a matched control observation (MC) mirrors the corresponding PC in as many respects as possible except that it is not preceded by a conflict, thus

constituting a record of 'normal' behaviour with which to compare post-conflict behaviour. Traditionally, the MC focuses on the same individual as the PC and is collected on the day following the PC and at the same time of day therefore controlling for seasonal and diurnal patterns of activity. Additionally, the distance between former opponents may affect the likelihood of reconciliation and so MCs should ideally begin when former opponents are at the same relative distance as they were at the start of the PC (Call, 1999).

All of the above criteria may easily be met in captive studies but studies of wild subjects, and especially of wild chimpanzees, present more of a problem. The fission-fusion nature of chimpanzee societies means that former opponents may well not co-exist in the same party at any time on the day after the conflict which gave rise to the PC. Therefore, the criteria for the collection of MCs had to be relaxed. MCs were collected on the next day that the same dyad was seen together in the same party. Rather than matching the observation with respect to time of day, MCs were instead matched according to the general activity of the party, e.g., resting, travelling, feeding (a PC following a conflict in a large fruit tree is better matched by an MC taken while the dyad is feeding in another large tree than one taken at the same time of day but while the party is resting on the ground). MCs would begin when former opponents were within 10m of their relative distance at the start of the corresponding PC. If, after 15 mins, the former opponents did not reach a relative distance that satisfied this criterion, the MC was begun rather than risk the possibility that either individual might leave the party altogether. A more suitable MC was collected if the opportunity arose within 2 days of the original MC. The mean number of days between the collection of PCs and MCs was 6 (max = 23).

6.2.3 Data Analysis

The analyses of reconciliation were based on 120 PC-MC pairs (median = 3 per focal individual) which represented all age-sex combinations in the roles of aggressor and victim (table 1). Eighty two percent of these consisted of unique aggressor-victim dyads. The targeted duration of PCs was 30 mins and the mean duration was 28.3 mins (min = 22.7 mins). MCs were of the same duration as the corresponding PC, thus eliminating the possibility of underestimating the occurrence of post-conflict interactions. In only 9 cases were PCs abandoned because of the possibility of unobservable contacts with former opponents or third parties. In 26 PCs, focal subjects could not be followed continuously and so analyses of rates of self-directed behaviours and maintenance activities were confined to the remaining 94 PCs.

I tested for the occurrence of reconciliation, using two methods. First, the 'PC-MC' method (de Waal & Yoshihara, 1983) by which I assessed whether former-opponents contacted one another earlier in the PC than in the corresponding MC, or only in the PC. If this was the case then the PC-MC pair of observations was labelled an 'attracted pair'. If such contacts were made earlier in the MC than in the PC, or only in the MC, then this PC-MC pair was labelled 'dispersed'. If no contact was made in the PC and in the MC, then the PC-MC pair was labelled 'neutral'. Attracted pairs are considered to indicate the occurrence of reconciliation. The second method I employed was the 'time rule' (Aureli *et al.*, 1989; Aureli & van Schaik, 1991). Here, the minute block in which the first affiliative behaviours occurred was determined for PCs and MCs. The distribution of these contacts over time was examined and, if significantly different in PCs compared to MCs, this difference was considered to be due to the preceding conflict.

Table 6.1 The number of PC-MC pairs per age-sex class.

	Victim						Total
	AM	AF	AdM	AdF	JM	JF	
Main Aggressor							
AM	25	17	17	10	9	0	78
AF	3	3	2	2	1	3	14
AdM	0	7	5	4	4	1	21
AdF	0	0	0	1	1	1	3
JM	0	0	0	0	0	1	1
JF	1	0	1	0	0	1	3
Total	29	27	25	17	15	7	120

A = adult, Ad = adolescent, J = juvenile; M = male, F = female

These two methods were also used to demonstrate the occurrence of conflict influenced affiliative contacts with third parties and redirection of aggression by substituting the relevant type of contact in the analyses.

For comparison of the frequency of reconciliation across different classes of individuals I calculated the mean Conciliatory Tendency (CT: Veenema *et al.*, 1994) for each class. Individual CT = $(a - d)/t$, where a is the number of attracted pairs, d is the number of dispersed pairs and t is the total number of PC-MC pairs for that individual. This index fully controls for baseline levels of affiliation.

Nonparametric statistical tests are used throughout. Where sample sizes prohibited comparisons at the individual level, I used Chi-squared and Fisher Exact tests on pooled data. For these analyses I compared the proportion of conflicts which were reconciled (attracted pairs) with the proportion which were not (neutral and dispersed pairs). Where possible, Wilcoxon signed ranks and Wilcoxon-Mann-Whitney tests (Siegal & Castellan, 1988) were used to confirm differences in mean

Conciliatory Tendencies at the individual level using subjects with at least 3 qualifying PC-MC pairs unless otherwise stated. Analyses were two-tailed and the level of significance was set at 5%.

6.3 Results

6.3.1 Sampling distribution

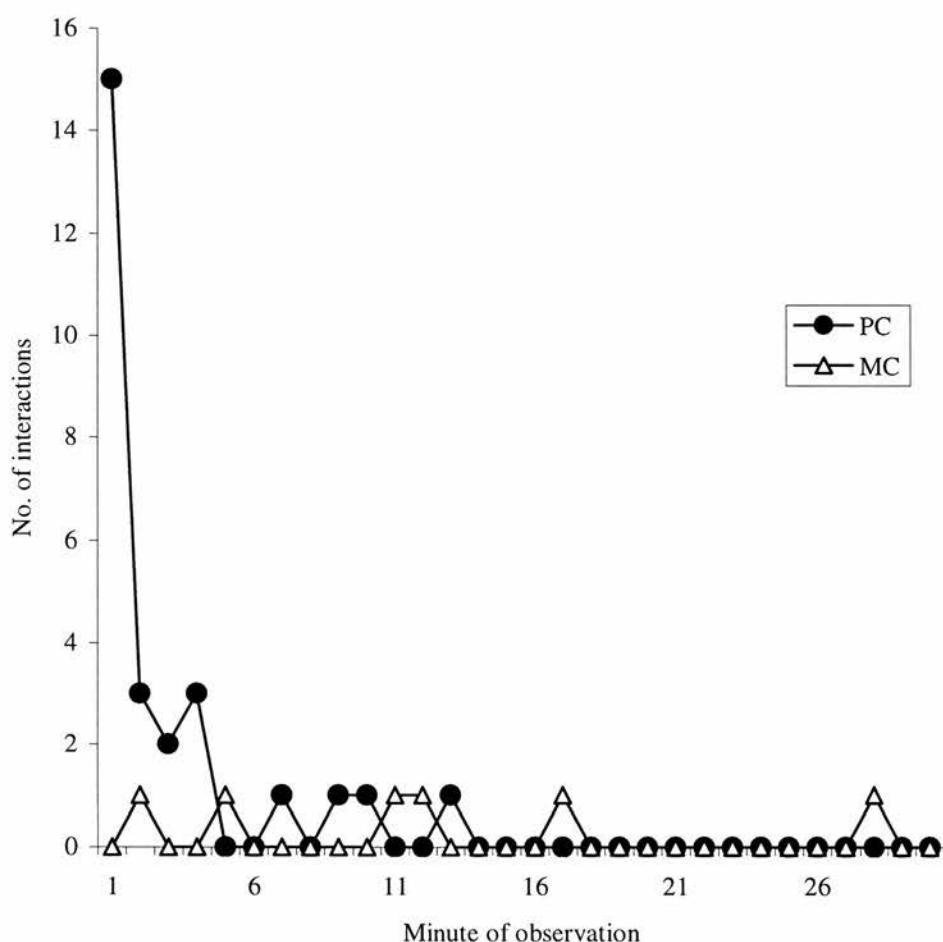
The necessity of *ad libitum* sampling combined with the lack of observed conflicts among many dyads resulted in some pseudoreplication in the sampling of PC-MC pairs in this study due to a small number of dyads (18%) being sampled on more than one occasion. Only 11.5% (94/820) of all possible dyads were sampled, and males were slightly better represented than females (male-male and male-female dyads: 13.9%, 82/589; female-female and female-male dyads: 7.7%, 50/649).

6.3.2 The demonstration of reconciliation

A greater proportion of post-conflict affiliative acts between former opponents occurring earlier in PC than in the corresponding MC confirmed that reconciliation was characteristic of post-conflict behaviour according to the PC-MC method (pooled data: earlier pairs = 22.5%, later pairs = 3.3%, $\chi^2 = 15.61$, $df = 1$, $p > 0.001$) and this was confirmed at the individual level (mean proportion of earlier pairs = 26.4%, later pairs = 2.3%, Wilcoxon signed ranks test: $N = 17$, $z = 3.5$, $p < 0.001$).

According to the time-rule, former opponents made friendly contacts earlier in PCs than in MCs. There was a significant difference in the cumulative distributions of the timing of these contacts in post-conflict and control periods (Kolmogorov-

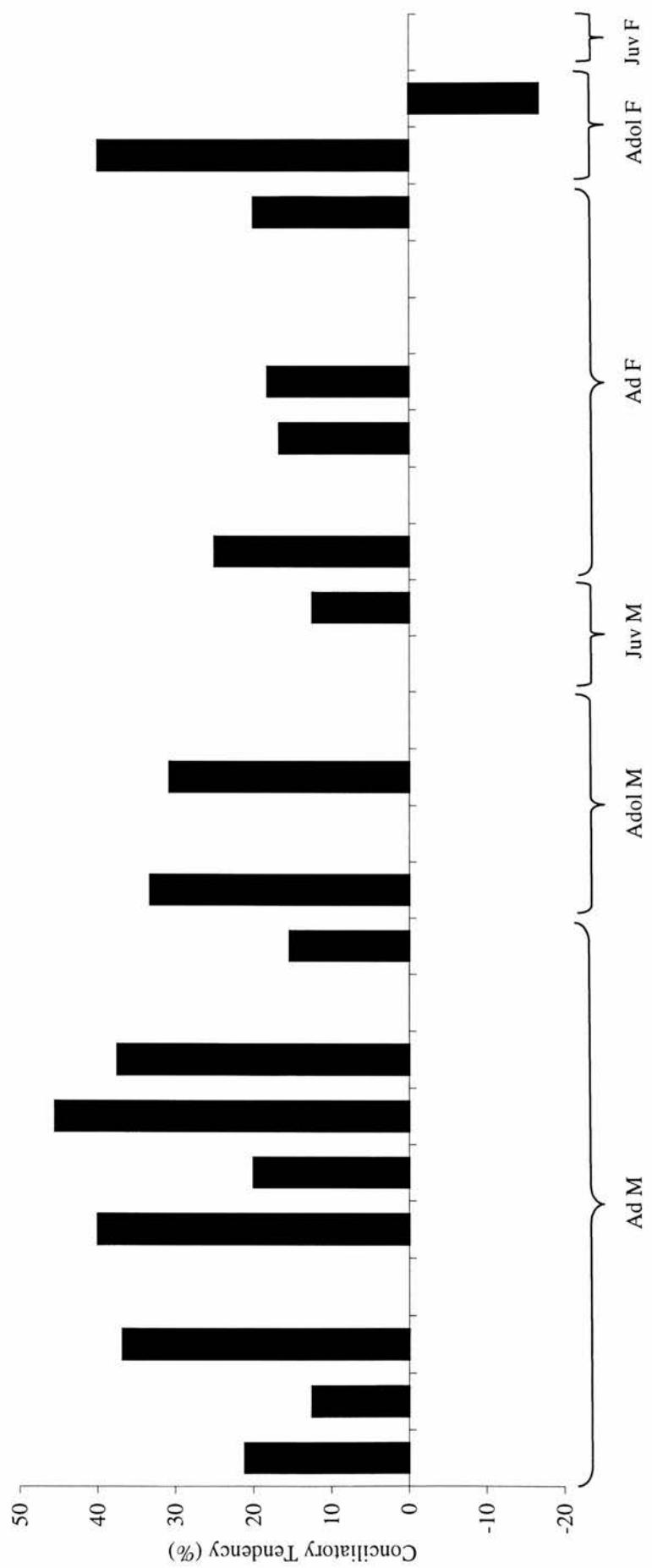
Figure 6.1 Distribution of first affiliative interactions between former opponents during 30 min post-conflict (PC) and matched control (MC) observations.



Smirnov test: $D = 0.68$, $p < 0.025$). The time window within which the greatest difference in distributions occurred was four minutes and this can be taken to be the critical period within which reconciliation is most likely to occur (Figure 6.1). The mean latency to reconcile was 2.3 mins (S. E. = 38s).

The conciliatory tendency of the group was 19.2% (attracted pairs = 27; dispersed pairs = 4; total pairs = 120) when calculated using pooled data and 12.3% ($N = 26$, $SD = 15.8\%$) when taking the mean of individual conciliatory tendencies for individuals with ≥ 3 PC-MC pairs (figure 6.2).

Figure 6.2 Conciliatory tendencies associated with individuals with at least 3 PC-MC pairs. Ad = adult; Adol = adolescent; Juv = juvenile; M = male; F = female.



6.3.3 Selective attraction

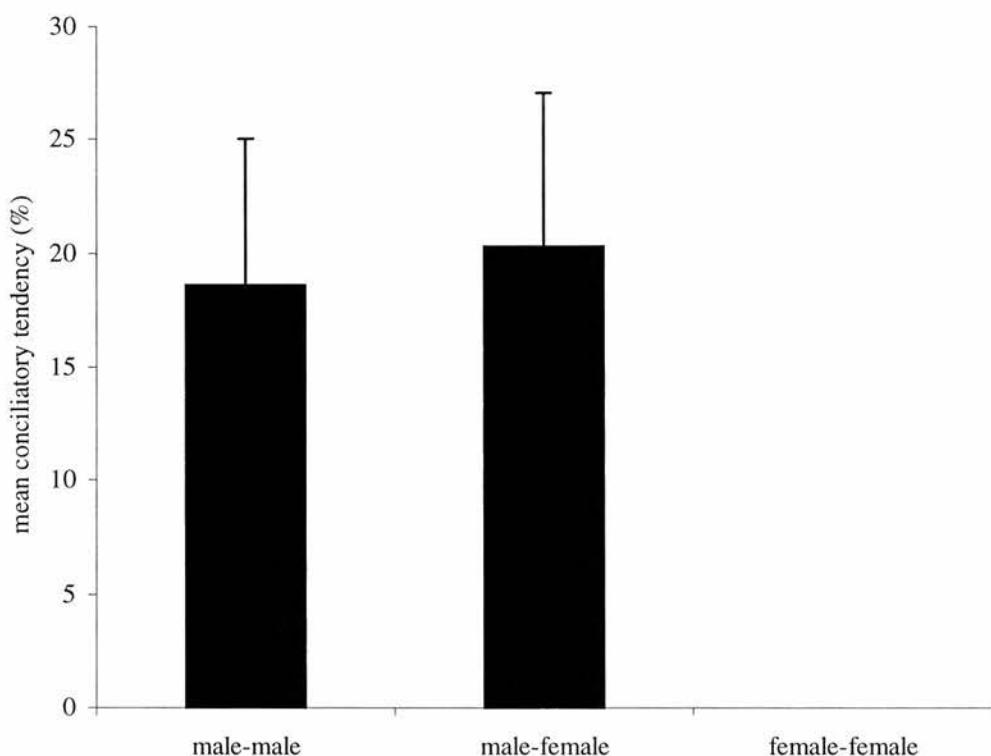
It is possible that the early contacts made by former opponents might simply be a by-product of a widespread increase in activity and affiliation among party members following a disturbing conflict. To rule out this possibility I considered the proportion of PC contacts which were made with a former opponent as opposed to other party members and compared this with the equivalent proportion in MCs. 65.4% of affiliative contacts in PCs were between former opponents while only 11.3% of such contacts involved former opponents in MC observations (Wilcoxon signed ranks test: $N = 12$, $T^+ = 78$, $p < 0.0002$).

6.3.4 Distance

It was not always possible to match PC and MC observations with respect to the distance between opponents at the beginning of the observations. Therefore it was possible that the occurrence of post-conflict affiliation was due to a greater likelihood of contact when former opponents were in closer proximity at the beginning of PCs than the beginning of MCs.

I selected those PC-MC pairs in which the distance between the former opponents was within 5 m of the recorded distance at the beginning of each type of observation. There were 61 such PC-MC pairs and within these there was a higher proportion of reconciled than unreconciled pairs (24.6% v 8.1%; Wilcoxon signed-ranks test: $N = 7$, $T^+ = 25$, $p < 0.04$). This confirms that the probability of the occurrence of reconciliation was not simply due to differences in proximity between former opponents in each context.

Figure 6.3 Conciliatory tendencies associated with conflicts among different sex combinations (mean \pm SE).



6.3.5 Sex differences

Males were not shown to be significantly more conciliatory than females (male mean CT = 19.1%, female mean CT = 12.0%; Wilcoxon-Mann-Whitney test: $z = 1.01$, NS). There was no difference in the mean conciliatory tendencies associated with male-male as opposed to male-female conflicts (male-male v male-female = 32.8% v 27.1%; Wilcoxon signed-ranks test: $N = 5$, $T^+ = 9$, NS) and this result was not affected when the 3 PC-MC criterion was relaxed to include more individuals in the analysis or when only adults or adults and adolescents were considered. However, of 12 female-female conflicts, none were reconciled. Only one female had enough conflicts with other females so that the > 3 PC-MC pair criterion was satisfied. Pooled data were therefore analysed and the difference in the proportion female-female conflicts as

opposed to female-male conflicts that were reconciled was significant (female-female v female-male = 0 v 0.25; Fisher exact test: $p < 0.001$). Similarly, female-female conflicts were reconciled less often than male-male conflicts (female-female v male-male = 0 v 0.25; Fisher exact test: $p < 0.05$, Figure 6.3). Females initiated reconciliation more often than males whereas the responsibility for initiating affiliative contact in non-agonistic contexts was roughly equal ($PC = 83.3\%$, $MC = 53.8\%$) although the difference was not significant ($\chi^2 = 1.32$, $df = 1$, NS).

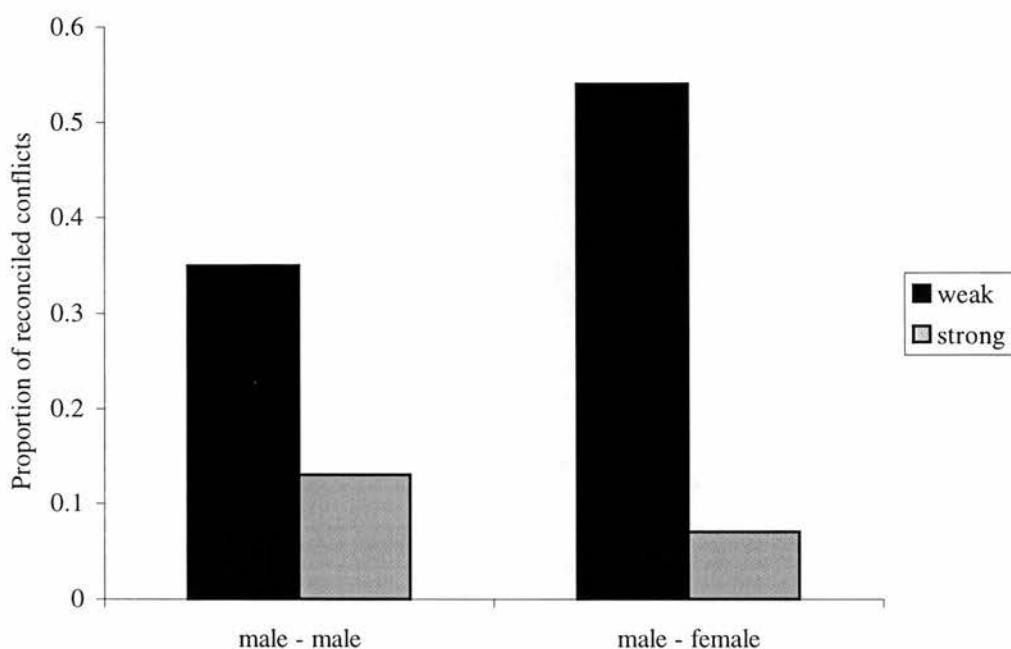
6.3.6 Compatibility

All dyads were given an affiliation score which was calculated by summing the amount of time spent grooming, in body contact or within proximity of one another. The dyadic affiliation scores for each individual were ranked and those which fell within the top quartile were labelled 'strongly compatible' while those which fell within the bottom quartile were labelled 'weakly compatible' ($N = 4$).

Analysis of pooled data revealed that among males, strongly compatible dyads were more likely to reconcile conflicts than weakly compatible dyads (proportion of conflicts reconciled between strongly v weakly compatible dyads = 0.35 v 0.13; Fisher Exact test: $p < 0.05$). Analysing this difference at the individual level with no criterion for the minimum number of opponent pairs confirmed this result (mean CT for strongly v weakly compatible dyads = 36.0% v 9.5%; Wilcoxon signed-ranks test: $N = 6$, $T^+ = 19$, $p < 0.05$. Figure 6.4).

Male-female conflicts were also more likely to be reconciled when opponents were strongly compatible as opposed to weakly compatible although this could not be tested at the individual level as there were too few individuals who had conflicts with both classes of opponent (proportion of conflicts reconciled between

Figure 6.4 The proportion of reconciled conflicts among strongly and weakly compatible dyads (pooled data).



strongly v weakly compatible dyads = 0.54 v 0.07; Fisher Exact test: $p < 0.05$.

A similar analysis concentrating on grooming relationships alone did not follow this pattern for male-male conflicts (proportion of conflicts reconciled between intense v weak grooming partners = 0.35 v 0.15; $\chi^2 = 1.09$, $df = 1$, NS). However, intense male-female grooming relationships were reconciled significantly more often than weak ones (proportion of conflicts reconciled between intense v weak grooming partners = 0.70 v 0.07; Fisher Exact test: $p = 0.0002$).

6.3.7 Oestrus females and copulation rates

Whether females were in oestrus or not had no effect on the probability of male-female reconciliation (male-oestrus female v male-anoestrus female = 0.23 v

0.30; Fisher Exact test: $p = 0.81$). Females were primarily responsible for the initiation of reconciliation in both cases (proportion of female initiated reconciliation when in oestrus = 100%, $N = 10$; when anoestrus = 77.7%, $N = 9$).

Rates of reconciliation appeared to be higher between males and females with whom they had copulated at some time though not necessarily around the date of the conflict (proportion of conflicts reconciled between copulating v non-copulating dyads = 0.60 v 0.17; Fisher Exact test: $p < 0.0001$) although this relationship did not hold when tested at the individual level (mean CT copulating v non-copulating dyads = 35.0% v 22.5%; Wilcoxon signed-ranks test: $N = 5$ $T^+ = 8.5$, NS). There was also no correlation between arcsine transformed dyadic conciliatory tendencies and the number of copulations (Pearson's correlation: $r = 0.04$, $N = 39$, NS).

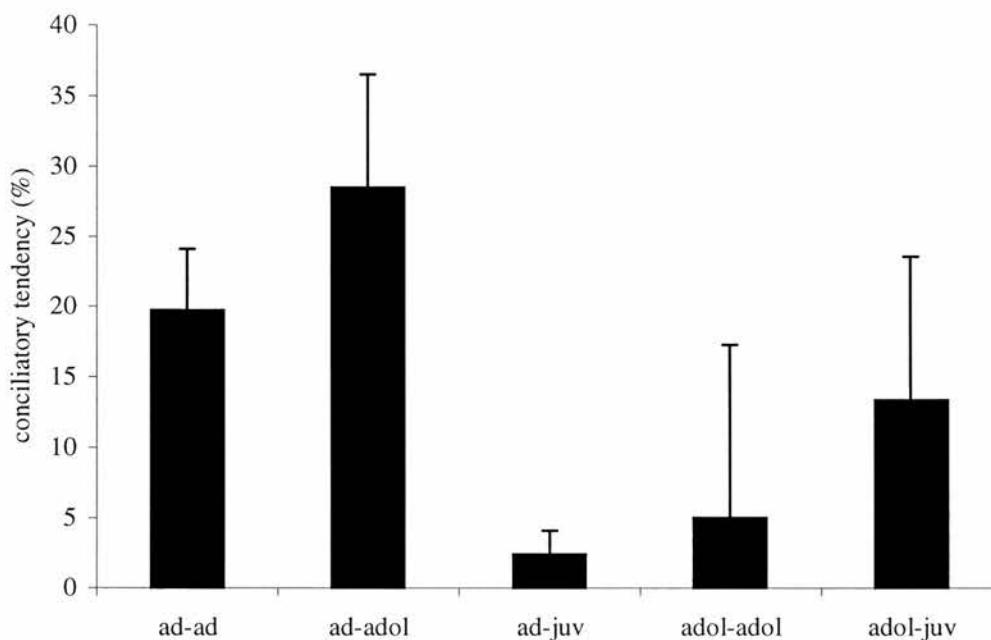
6.3.8 Association

There was no correlation between association strength (see section 3.2.2) and conciliatory tendency where individual conciliatory tendencies were calculated with no criteria for the minimum number of PC-MC pairs (Spearman rank-order correlation coefficient: $z = 0.71$, $N = 83$, NS). The mean conciliatory tendency for dyads which fell in the upper quartile, mid quartiles, and lower quartile of the range of association strength scores were 26.5% ($N = 21$), 16.7% ($N = 41$) and 16.7% ($N = 21$) respectively. There was no difference in the proportion of reconciled conflicts in the upper and lower quartiles (upper = 0.31, lower = 0.27; $\chi^2 = 0.005$, $df = 1$, NS).

6.3.9 Age

Conflicts between adults were more often reconciled than those between adolescents but this apparent difference in conciliatory tendencies was not significant

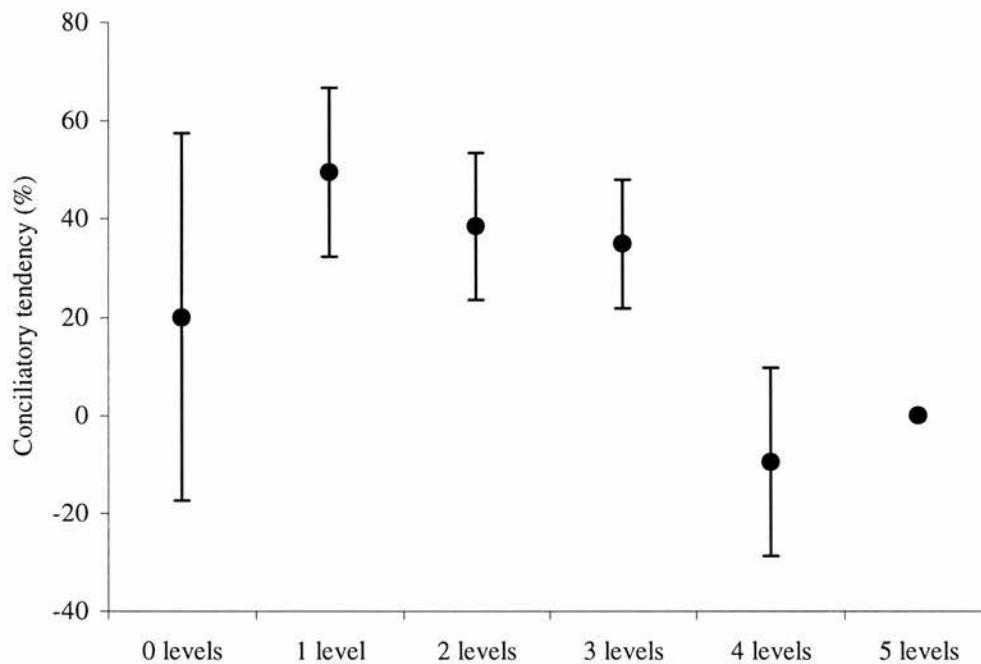
Figure 6.5 Conciliatory tendencies associated with conflicts between individuals of different age classes (ad = adult,adol = adolescent, juv = juvenile; mean \pm SE).



when analysed at the individual level (adult-adult = 23.7%, N = 15, adolescent-adolescent = 5.0%, N = 5; Wilcoxon-Mann-Whitney test: $z = 1.57$, $p = 0.12$). There were not enough conflicts between juveniles to permit analysis. Insufficient PC-MC pairs for most individuals in conflicts between age classes precluded analysis at the individual level.

Pooled data revealed no difference in the proportion of reconciled conflicts between age classes (adult-adult v adult-adolescent, proportion reconciled = 0.28 v 0.36; $\chi^2 = 0.21$, $df = 1$, $p < 0.5$. Adult-adult v adult-juvenile, proportion reconciled = 0.28 v 0.07; Fisher exact test: $p = 0.1$. Adolescent-adolescent v adolescent-juvenile, proportion reconciled = 0.1 v 0.14; Fisher exact test: $p = 0.96$. Juvenile-adult v juvenile-adolescent, proportion reconciled = 0.07 v 0.14; Fisher exact test: $p = 0.90$). However, if young adolescents were placed in the juvenile class, then adults

Figure 6.6 The effect of rank distance on conciliatory tendency (mean \pm SE).



reconciled significantly more often with the remaining adolescents than with juveniles (adult-adolescent v adult-juvenile, proportion reconciled = 0.5 v 0.11; $\chi^2 = 6.07$, $df = 1$, $p < 0.02$). Figure 6.5 shows mean conciliatory tendencies associated with conflicts within and between the various age classes.

6.3.10 Rank distance

Rank distance among males had no effect on the likelihood of reconciliation (Spearman rank-order correlation coefficient: $r_s = -0.166$, $N = 13$, NS). Males were also categorised as high, mid-high, mid-low, low and very low status as this might be a more meaningful way to classify individuals given that differences in cardinal rank values were small between certain individuals. This analysis confirmed that there was

no correlation between rank distance and conciliatory tendency (Spearman rank-order correlation coefficient: $r_s = -0.60$, $N = 6$, NS, Figure 6.6).

6.3.11 Reciprocated aggression

10% of the 120 PC-MC pairs were bi-directional. In every case where aggression was met with counter-aggression the outcome of the conflict was unambiguous in that a clear winner and loser could be identified. Of the bi-directional conflicts, 16.7% (2/12) were reconciled. Of the unidirectional conflicts, where the victim did not return the aggression, 22.2% (24/108) were reconciled. This small decrease in the likelihood of reconciliation when aggression was returned was not significant (Wilcoxon signed ranks test: $N = 11$, $T^+ = 40$, NS).

6.3.12 Initiative

I examined which former opponent was most likely to initiate reconciliation. In every case, reconciled conflicts resulted in a clear winner and so there was no ambiguity regarding the outcome. Victims of aggression were initiators of affiliative contact in 88.9% of PCs ($N = 27$) as opposed to 50.0% of MCs ($N = 6$; Fisher exact test: $p < 0.1$) but this only indicated that there was a trend in favour of victims initiating reconciliation. However, five males occupied the role of aggressor and victim in conflicts that were reconciled. In every case, they initiated reconciliation when they were victims but never as aggressors.

Given that such low rates of former opponent contact in MCs might not accurately reflect initiative to contact in non-conflict contexts, I also compared initiative to contact in PCs with data concerning contact initiative among former opponents which was, instead, drawn from focal data. In this case, victims initiated

64.5% ($N = 93$) of contacts compared to 88.9% in PCs and the increase in victim initiated contacts in PCs was significant ($\chi^2 = 4.82$, $df = 1$, $p < 0.05$).

6.3.13 Aggression intensity

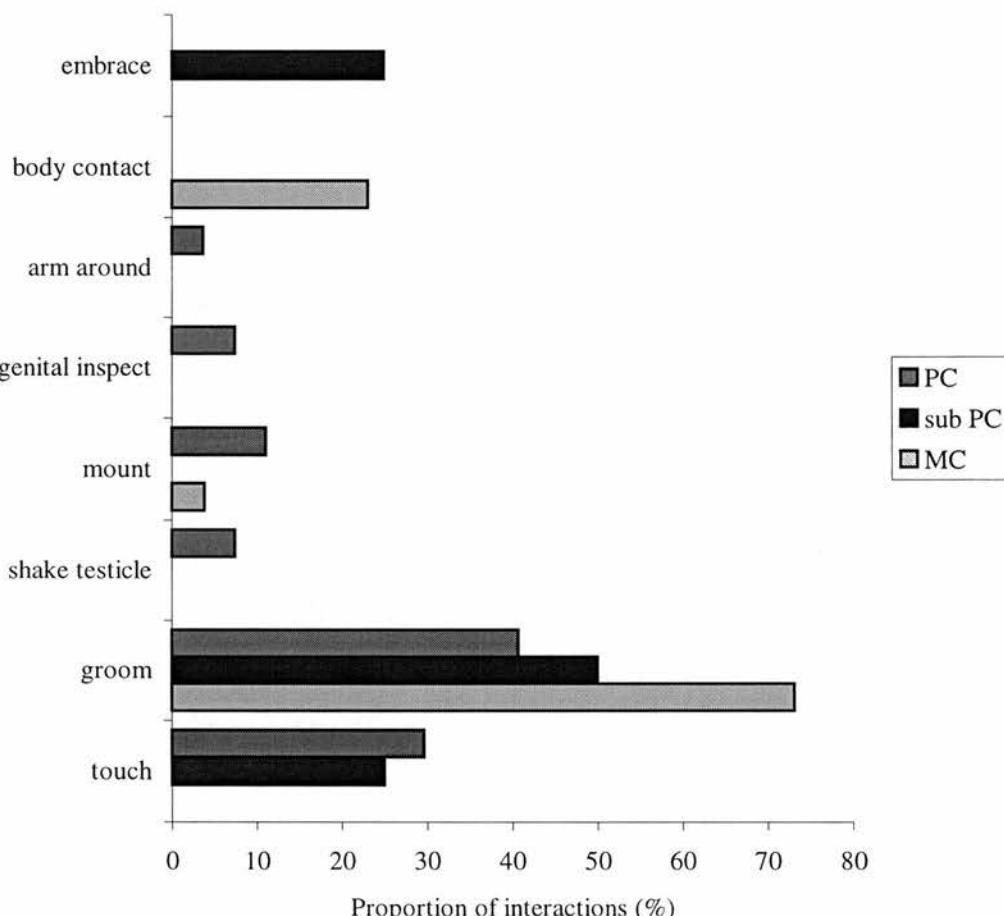
Conflicts were categorised as either low or high intensity aggression. Low intensity conflicts, defined as threats and lunges, made up 54.1% of all recorded conflicts. The remaining 45.9% of conflicts were of high intensity and this category comprised chases of over 3m, contact aggression and bi-directional conflicts.

Using only data concerning dyadic conflicts ($N = 70$) after which each former opponents settled at a particular location for at least 20 seconds, the mean recorded distance between opponents after low intensity conflicts was 5.8 m as opposed to 11.4 m after high intensity conflicts (Wilcoxon signed ranks test: $N = 22$, $z = 3.89$, $p < 0.001$). On only two occasions did a conflict result in the victim of aggression leaving a party completely and each time this followed a high intensity conflict. These results demonstrate that high intensity conflicts were more dispersive than those of low intensity. The mean conciliatory tendency associated with low intensity conflicts was 36.1% as opposed to only 16.7% associated with high intensity conflicts (Wilcoxon signed ranks test: $N = 12$, $T^+ = 59.5$, $p < 0.06$). Although the difference in conciliatory tendencies was not quite significant, there was a trend indicating that low intensity aggression was more often reconciled than high intensity aggression.

6.3.14 Specific affiliative acts

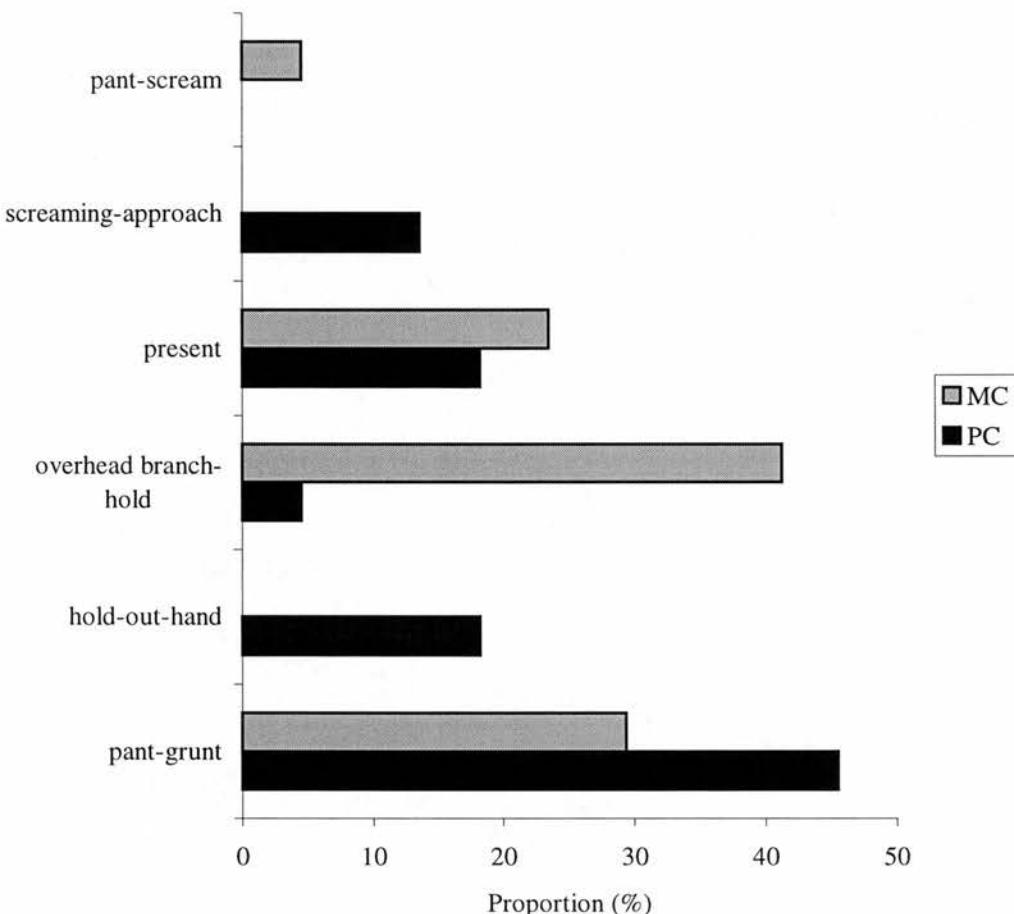
I was interested in whether or not certain behaviours were more frequently associated with reconciliation than other affiliative contexts. Figure 6.7 shows that a wider variety of affiliative behaviours were involved as a first contact behaviour

Figure 6.7 The occurrence of eight classes of affiliative behaviour occurring in three contexts: the first contact behaviour in PCs (PC), subsequent affiliative behaviour in PCs (sub PC) and first affiliative behaviour in MCs (MC).



during post-conflict reunions (PC) than at other times. Due to the low frequency of affiliative contacts between former opponents in MC observations I supplemented these data with observations from 20 focal samples which had been collected soon after an MC observation and involved affiliative contacts concerning the relevant dyad for comparative purposes. These made up the data set of first contacts during non-conflict contexts (MC). If a post-conflict affiliative behaviour was quickly followed by another and might then be considered relevant to reconciliation, I called this the subsequent affiliative behaviour (sub PC) and included information about the

Figure 6.8 The occurrence of vocal and gestural signals prior to affiliative contact in PCs and MCs given as the proportion of all signals observed in PCs ($N = 22$) and MCs ($N = 17$).



distribution of these behaviours in Figure 6. In total, the distributions of 27 PC contacts, 4 sub PC contacts and 26 MC contacts were analysed. I found no difference in the distribution of these behaviours in the three contexts (Friedman Two-way ANOVA: $N = 8$, $k = 3$, $F_r = 2.07$, NS).

In some cases, a signal was given before post-conflict affiliation was attempted (Figure 6.8). These signals were not considered to mark reconciliation proper as these attempts to initiate reconciliation would sometimes be rejected. As would be expected, pant-grunt-approach was always performed by the victim of aggression, as was the

screaming-approach and present. Hold-out-hand was performed by both victims and aggressors. One example of overhead-branch-hold was performed by the aggressor and was immediately followed by an approach resulting in reconciliation, on the part of the victim. Such pre-reconciliatory signals lead to reconciliation in 18.3% of all PCs. In only 2 PCs (1.7%) were such signals observed but not responded to by the former opponent and both of these were examples of hold-out-hand.

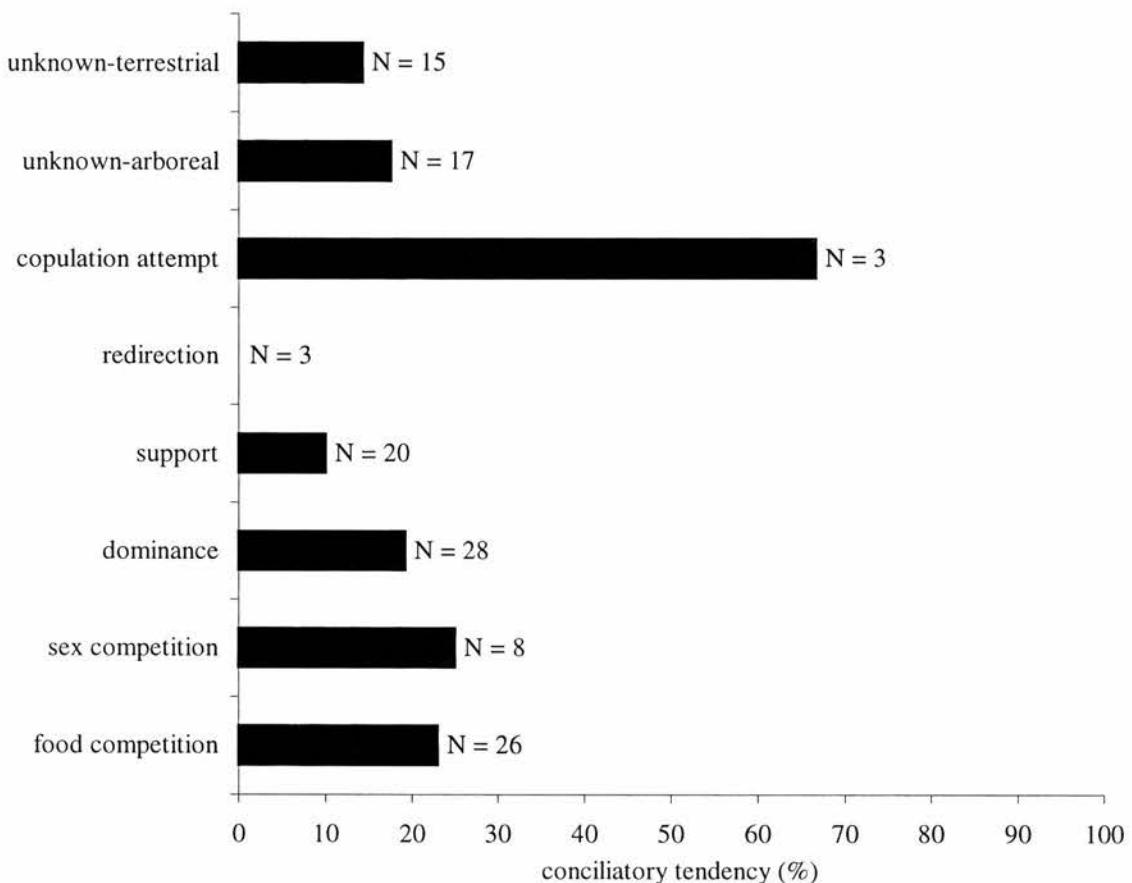
6.3.15 Context

The context in which conflicts occurred was shown not to have any discernible effect on the likelihood of reconciliation. Figure 6.9 shows group level conciliatory tendencies associated with aggression and the contexts in which it occurred, together with the number of times conflicts of each type occurred. Analysing these differences at the individual level revealed no difference between contexts (Kruskal-Wallis one-way ANOVA: $\chi^2 = 8.40$, $df = 6$, NS). Categorising conflicts as either food related or social revealed a nonsignificant trend in favour of food related conflicts (food = 27.3%, social = 11.5%; Wilcoxon signed-ranks test: $N = 5$, $T^+ = 13.5$, $p < 0.1$) but when the 3 PC-MC pair criterion was relaxed in order that more individuals were represented, this trend disappeared (food = 31.2%, social = 24.5%; $N = 14$, $T^+ = 62.5$, NS).

6.3.16 Ecological consequences

In order to investigate the effect of conflicts on activity budgets, I analysed PCs during which reconciliation did not occur and also excluded those PCs which involved relocation of the entire party to a new site. I compared the proportion of time spent foraging, resting and locomoting during PCs with MCs and found that conflicts had little effect on activity budgets when separately analysing the behaviour of

Figure 6.9 Group level conciliatory tendencies following conflicts categorised as one of eight conflict contexts.



aggressors and victims (Figure 6.10) and males and females (Figure 6.11). Only the amount of time males spent resting differed between contexts and was elevated from 29.1% to 39.2 (%) (Wilcoxon signed ranks test: $N = 13$, $T^+ = 70$, $p < 0.05$).

6.3.17 Post-conflict stress

I investigated the occurrence of gentle-scratching, rough-scratching and self-grooming as possible indicators of stress in PCs and MCs. Surprisingly, 40.6% ($N = 32$) of focal subjects were not observed to engage in any of these behaviours during PCs as opposed to 28.1% in MCs. Mean rates (bouts min^{-1}) of all three of these self-

Figure 6.10 Activity budgets of (a) victims and (b) aggressors during PC and MC observations.

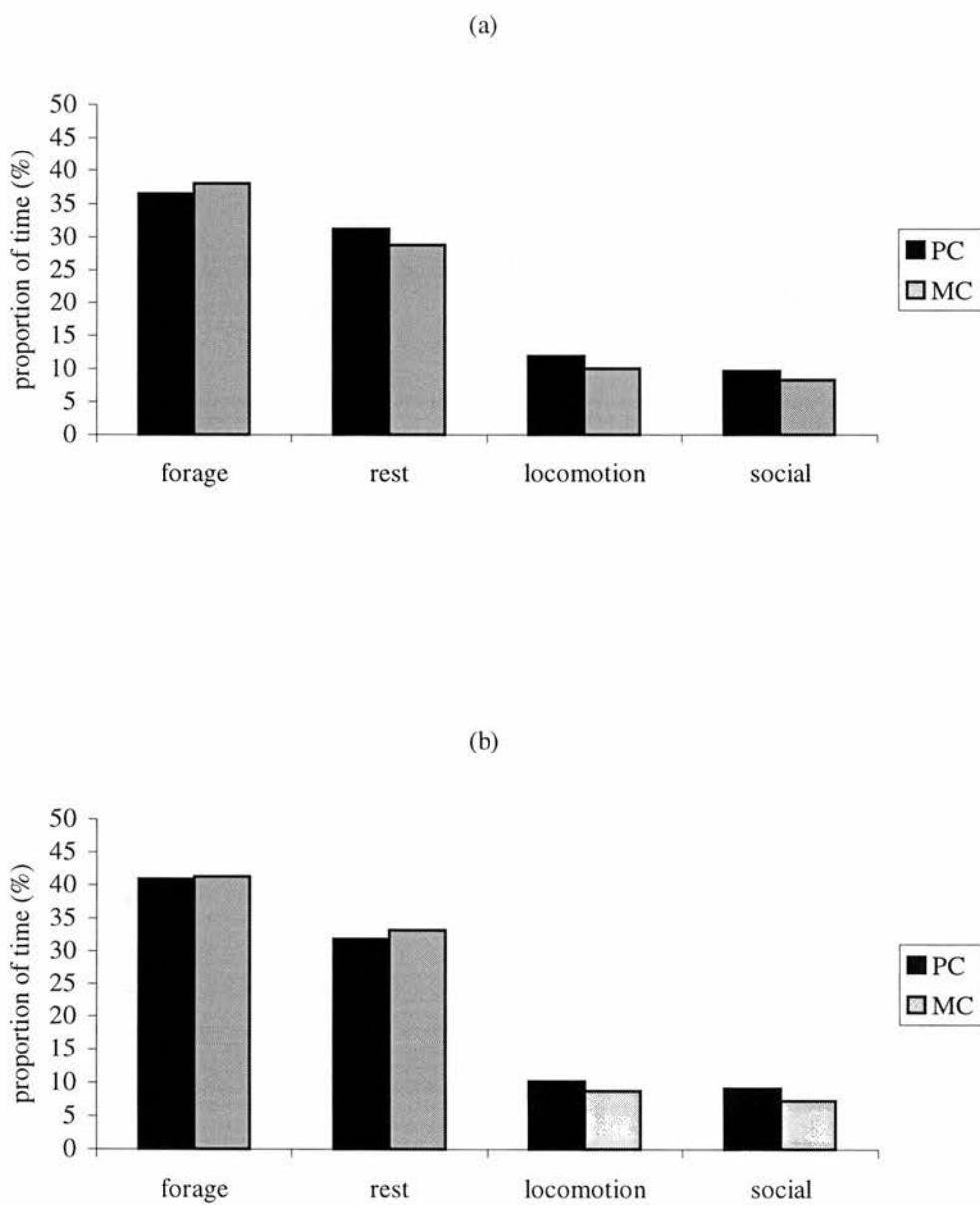


Figure 6.11 Activity budgets of (a) males and (b) females during PC and MC observations.

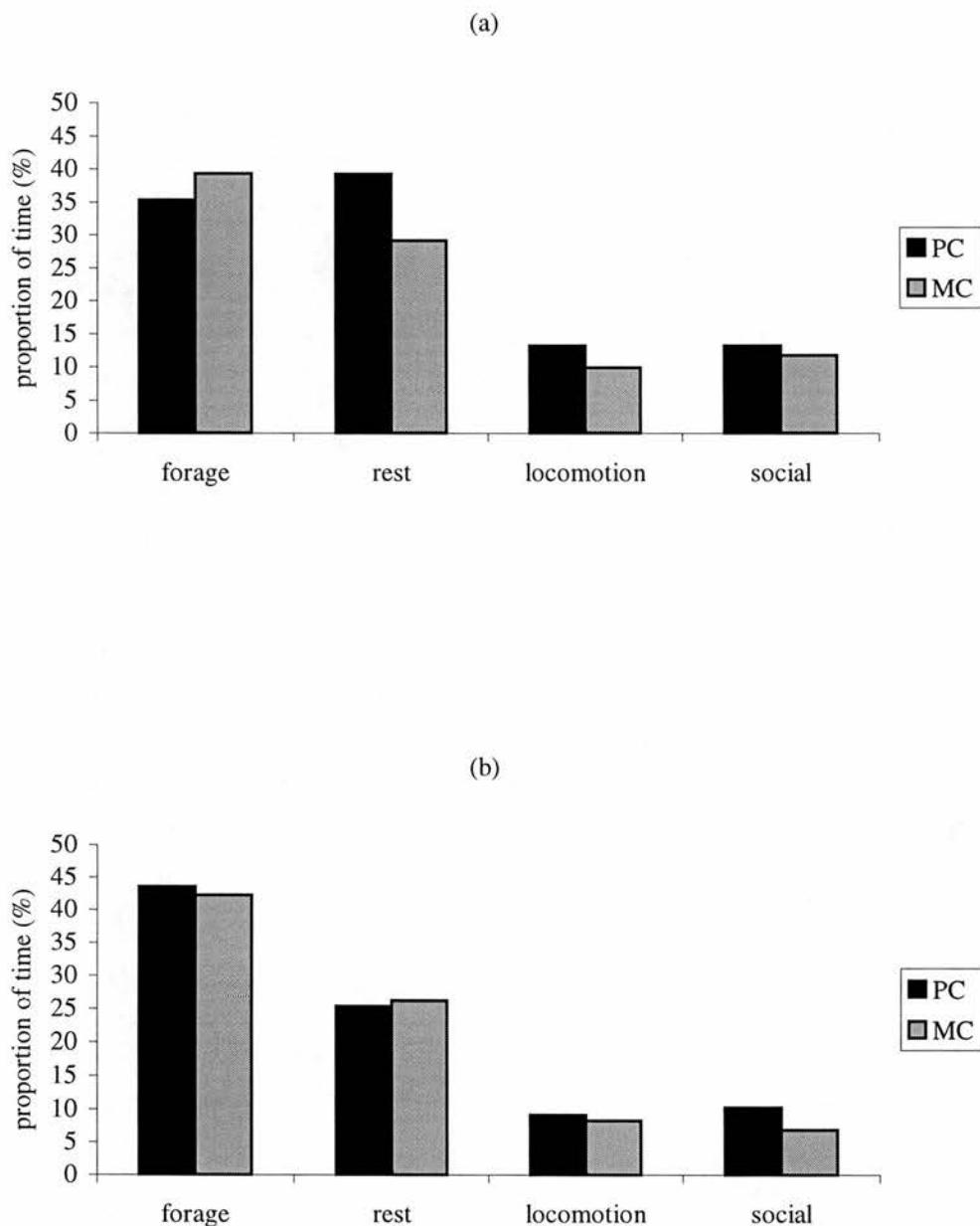
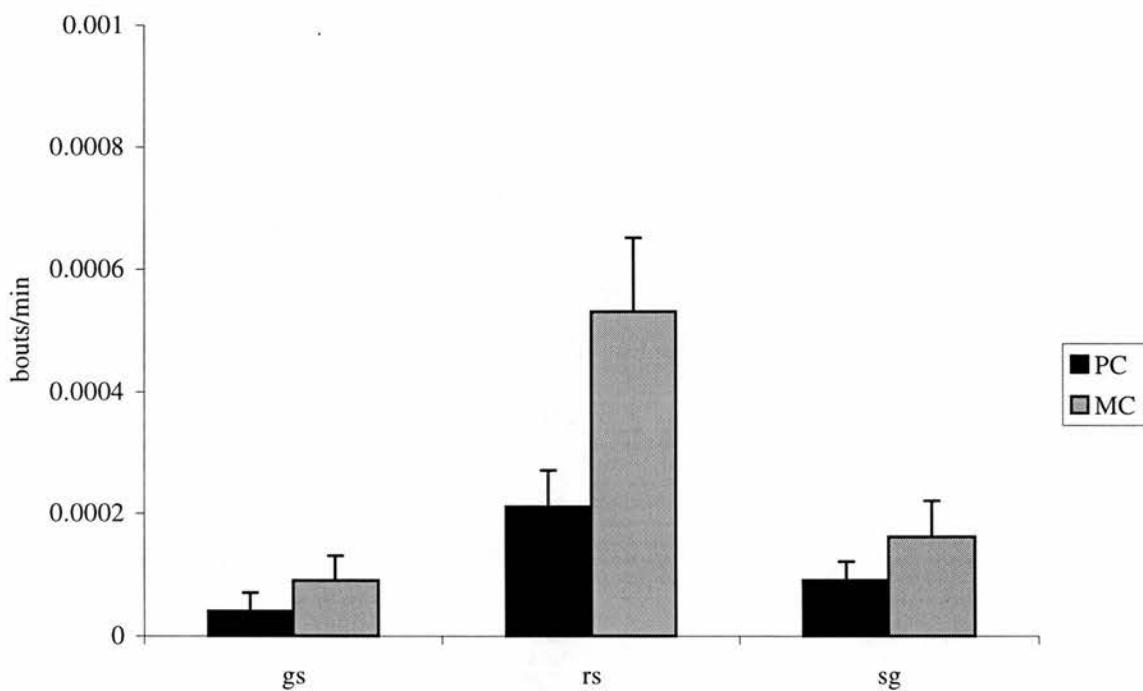


Figure 6.12 Rates of three self-directed behaviours in PCs and MCs (gs = gentle-scratch, rs = rough-scratch, sg = self-groom; mean and SE).



directed behaviours (SDBs) were lower during PCs than MCs although for gentle-scratching, this was not quite significant (PC v MC = 0.00004 v 0.0009; Wilcoxon signed-ranks test, $N = 11$, $T^+ = 52$, $p = 0.051$), whereas rates of rough-scratching were significantly lower during PCs (PC v MC = 0.00021 v 0.00051; $N = 21$, $z = 2.36$, $p < 0.02$) and rates of self-grooming were similar in PCs and MCs at the individual level (PV v MC = 0.00009 v 0.00016; $N = 15$, $T^+ = 76$, NS, Figure 6.12).

It might be expected that high intensity conflicts would result in higher rates of SDBs than low intensity conflicts if SDB rates are indicative of stress levels in chimpanzees. But, this was not the case. Combined rates of rough and gentle-

scratching were not significantly different during PCs following high compared to low intensity conflicts (high v low = 0.00022 v 0.00017; N = 14, T⁺ = 55, NS).

Despite the low rates of SDBs during post-conflict periods, mean rates of rough-scratching and gentle-scratching, were higher in unreconciled PCs than those which were reconciled (gentle-scratching: unreconciled v reconciled = 0.00008 v 0.00001; N = 5, T⁺ = 15, p < 0.05; rough-scratching: 0.00025 v 0.00013; N = 14, T⁺ = 80, p < 0.05, Figure 6.13). Rates of self-grooming were not elevated during PCs although there was a slight tendency in favour of self-grooming bouts taking up a higher proportion of PC time after unreconciled conflicts than after those which were reconciled (rate: unreconciled v reconciled = 0.00009 v 0.00011; N = 11, T⁺ = 45, NS; duration: 1.83% v 1.46%; N = 10, T⁺ = 42, p = 0.08).

For those conflicts which were reconciled, however, the combined rates of gentle and rough scratching did not decrease significantly once reconciliation had occurred (mean rate before reconciliation v after reconciliation = 0.00067 v 0.00043; N = 6, T⁺ = 13, NS, Figure 6.14).

6.3.18 Post-conflict aggression involving third parties

Aggression in PC and MC observations was very rare. On only one occasion did a victim of aggression direct aggression at a third party soon after a conflict and victims were never involved in conflicts in control situations. Aggressors directed aggression at third parties in 4.2% of PCs, and 1.7% of MCs. The difference in the distributions of this type of aggression was most marked within the first six minutes after the conflict but was not significant (Kolmogorov-Smirnov test: D = 0.8, NS).

Figure 6.13 Rates of self-directed behaviours during PCs following reconciled and unreconciled conflicts (gs = gentle-scratch, rs = rough-scratch, sg = self-groom; mean \pm SE).

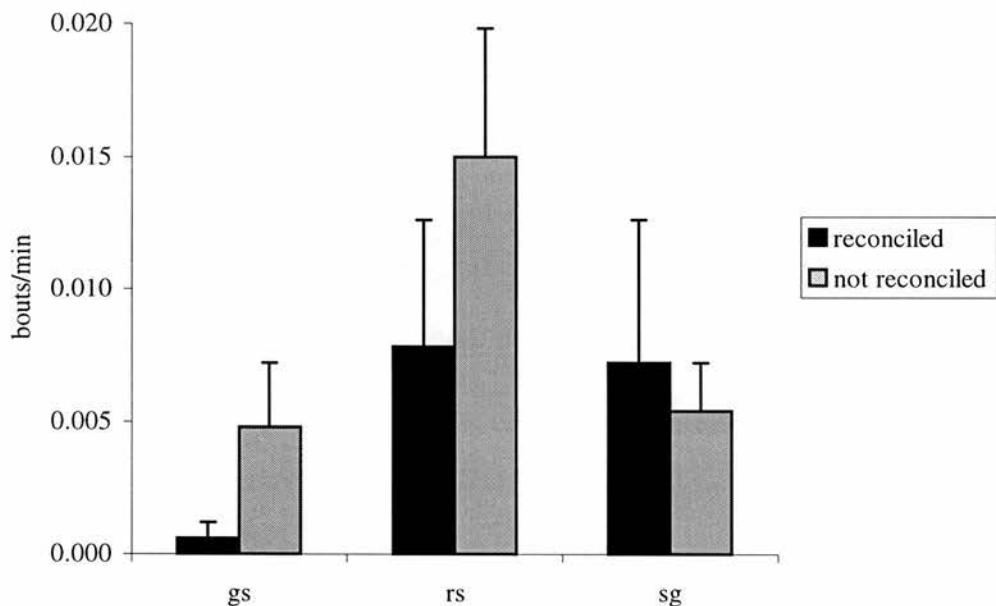
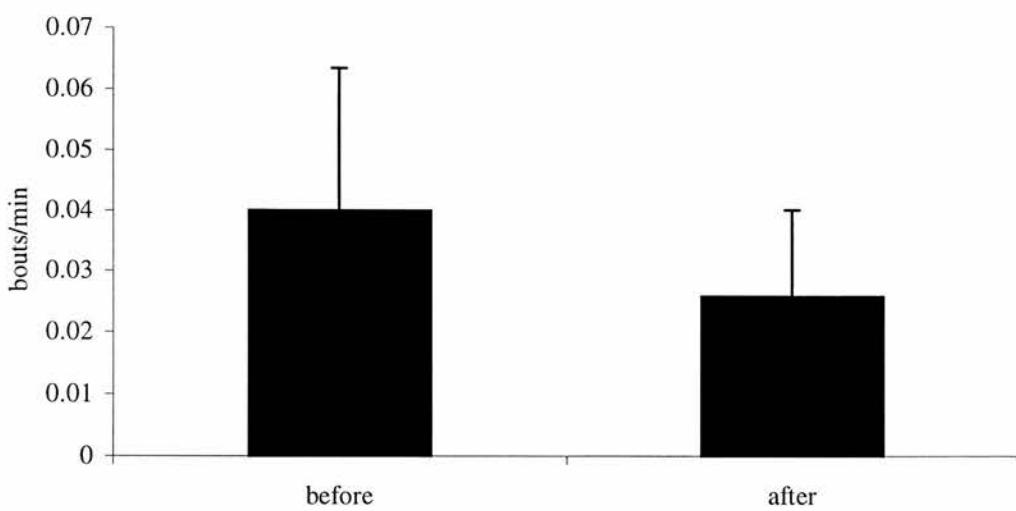


Figure 6.14 Scratch rates before and after reconciliation (mean \pm SE).



6.3.19 Post-conflict affiliation involving third parties

Victim initiated affiliative contacts with third parties were observed at least once in a similar proportion of PCs and MCs (9.2% v 7.5%) although in PCs, the majority occurred soon after the end of the conflict. The time-rule method revealed that the distributions of these contacts over time were significantly different in PCs compared to MCs and this difference was greatest within the first three minutes following the conflict (Kolmogorov-Smirnov test: $D = 81.0$, $p = 0.01$, Figure 6.15). The PC-MC method indicated a trend at the individual level, in favour of these contacts occurring earlier in PCs than in MCs (Wilcoxon signed ranks test: $N = 11$, $T^+ = 49$, $p < 0.09$). The mean latency to contact was 2.8 mins (S. E. = 1.6 mins).

Only 5.8% of PCs contained at least one aggressor initiated affiliative contact as opposed to 21.7% in MCs but the distributions of these contacts were not significantly different (Kolmogorov-Smirnov test: $D = 36.6$, NS, Figure 6.16).

Consolation, where third parties approached and affiliated with victims of aggression, occurred in a very small proportion of PCs (3.3%). Similar contacts were observed in 6.6% of MCs. Despite the extremely small sample sizes, the distribution of this type of contact in PCs and MCs was significantly different as all of these contacts in PCs occurred within the first two minutes (Kolmogorov-Smirnov test: $D = 28$, $p = 0.05$, Figure 16). This effect could not be confirmed at the individual level.

Further analyses of the characteristics of the third parties, that were contacted by victims, showed that the post-conflict context did not affect the choice of affiliation partners. The proportion of affiliation partners in PCs and MCs which were highly compatible v weakly compatible (45.5% v 37.5%. Fisher exact test: $p = 0.99$) and intense v weak grooming partners (45.5% v 62.5%. Fisher exact test: $p = 1$) was no different. For male-male contacts, victims contacted higher ranking males in both

Figure 6.15 The distribution of victim initiated first affiliative interactions with uninvolved third parties in PCs and MCs.

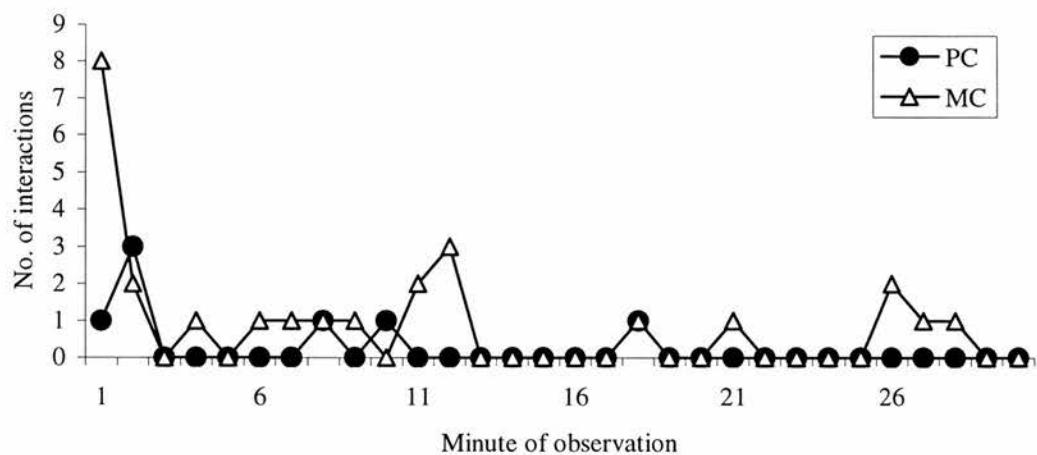


Figure 6.16 The distribution of aggressor initiated first affiliative interactions with uninvolved third parties in PCs and MCs.

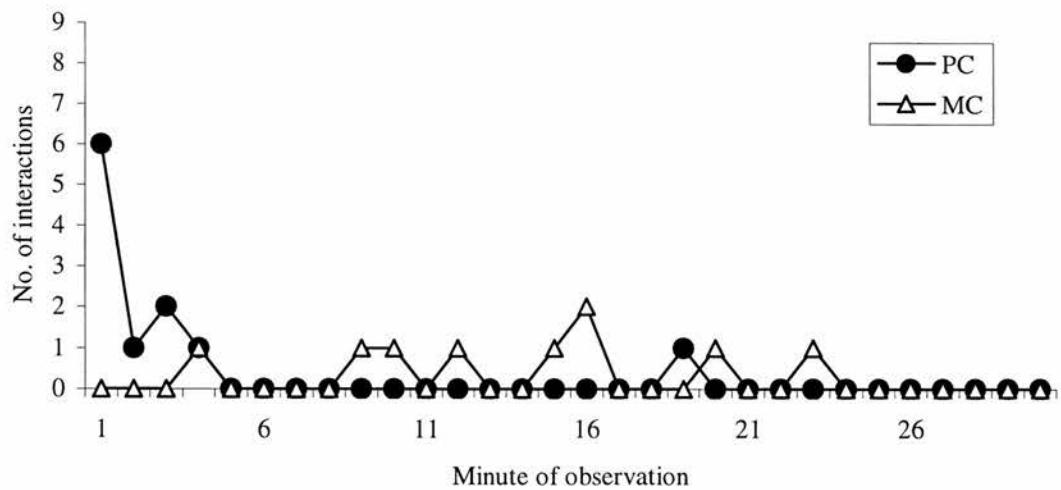


Figure 6.17 The distribution of third party initiated affiliative interactions with victims.

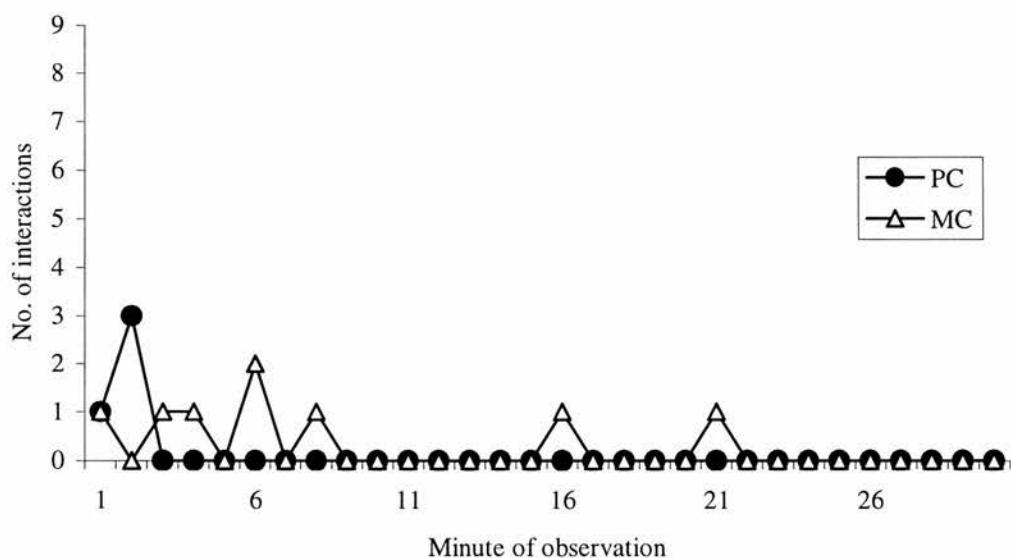
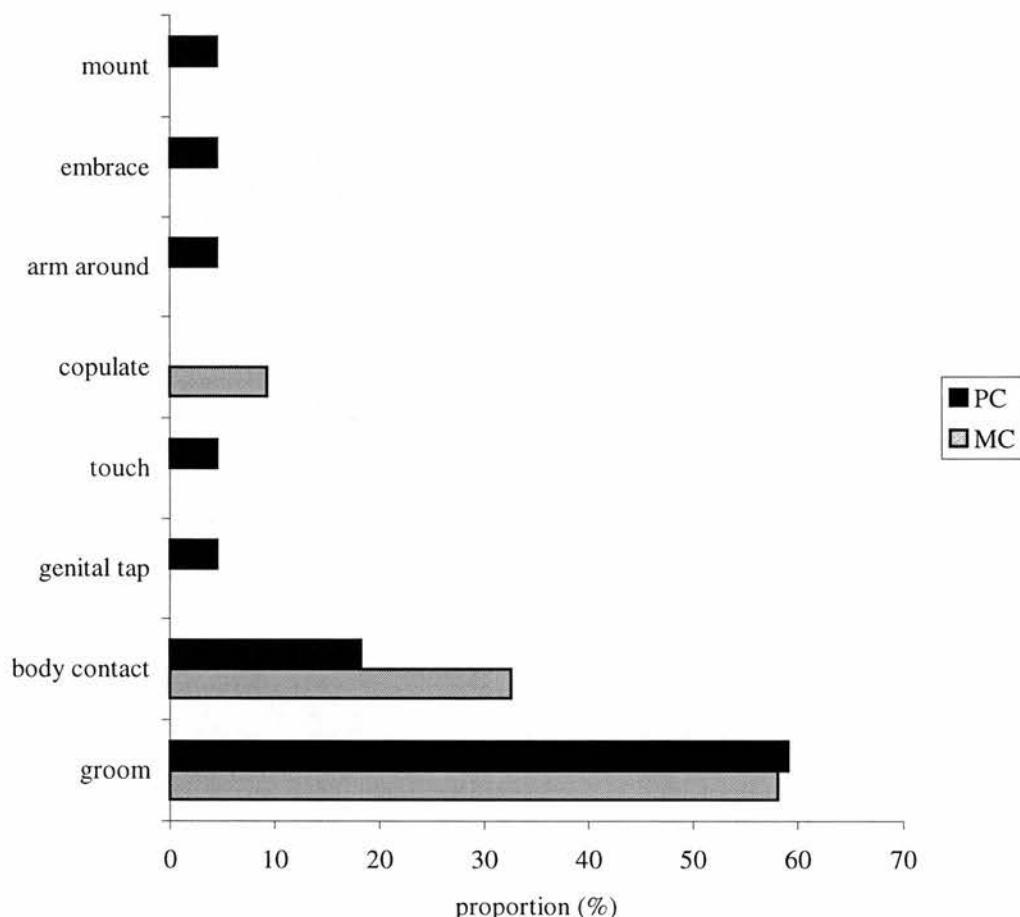


Table 6.2 The frequency of affiliative behaviours patterns in PCs and MCs between former opponents and third parties.

	Victim initiated contact		Aggressor initiated contact		Consolation		Totals
	PC	MC	PC	MC	PC	MC	
	PC	MC	PC	MC	PC	MC	
groom	6	5	5	15	2	5	38
body contact	3	3	1	8	-	3	18
copulate	-	1	-	3	-	-	4
arm around	-	-	1	-	-	-	1
embrace	-	-	-	-	1	-	1
touch	1	-	-	-	-	-	1
genital tap	1	-	-	-	-	-	1
mount	-	-	-	-	1	-	1
Totals	11	9	7	26	4	8	65

Figure 6.18 The occurrence of eight classes of affiliative behaviour occurring as the first affiliative contact behaviour in PCs (PC) and in MCs (MC) between individuals previously involved in a conflict and third parties.



PCs and MCs and the difference in rank was very similar in both cases (PC: median = 5.5; MC: median = 5). Analysing the distribution of contacts over time revealed that highly compatible dyads and intense grooming partners were contacted earlier in PCs than in MCs. This was not true of dyads whose relationships were moderate (scores falling within the middle quartiles) or weak (highly compatible dyads: $D = 15$, $p = 0.05$; moderately and weakly compatible dyads: $D = 20.1$, NS; intense grooming partners: $D = 25$, $p = 0.01$; moderate and weak grooming partners: $D = 14.95$, NS). Therefore, victims of aggression contacted individuals with whom they had close

affiliative relationships soon after the end of a contact but not individuals with whom they had weaker relationships.

6.3.20 Specific acts involved in affiliation with third parties

Eight classes of affiliative behaviour were observed as first post-conflict contacts between former opponents and uninvolved third parties in PCs and MCs. Sample sizes were too small to analyse differences in the distribution of these behaviours according to the whether it was the victim or the aggressor that initiated the contact or consolation. The distribution of the behaviour patterns observed in PCs were not significantly different from those in MCs ($\chi^2 = 2.97$, $df = 2$, $p < 0.1$) using the categories, groom, body contact, and other, where 'other' includes mount, embrace, arm around, copulate, touch and genital tap (see Figure 6.18).

6.4 Discussion

6.4.1 The conciliatory tendency of chimpanzees

This study demonstrated reconciliation in a wild population of chimpanzees. Former opponents were selectively attracted to one another and the occurrence of these friendly post-conflict contacts was not due to closer proximity at the beginning of PC observations than at the beginning of MC observations. However, the mean conciliatory tendency was only 12.3% compared with 35-41% in captivity (de Waal & van Roosmalen, 1979; Casperd, 1997; Preuschoft *et al.*, in press).

The high proportion of reconciled conflicts reported in captivity has placed chimpanzees among the most conciliatory species. Generally, studies of reconciliation

in primates have shown a relationship between the 'dominance style' of that species and the proportion of conflicts which are reconciled (de Waal, 1992; Chaffin *et al.*, 1995; Castles *et al.*, 1996; Thierry, 2000). The chimpanzee social system has much in common with that of the more 'tolerant' monkey species in that levels of aggression are low, and dominant-subordinate relationships are relaxed and tolerant around resources. Chimpanzee society is also described as relatively 'egalitarian' because coalitions among subordinates can reduce the effectiveness of dominants' efforts to overpower or out-compete them (de Waal, 1996a). Tolerant species tend to have higher mean conciliatory tendencies than despotic species (see Aureli & de Waal, 2000, p. 383). How, then, are we to interpret the lower mean conciliatory tendency we found in the wild?

One possibility derives from the finding that the degree of confinement of a group of primates affects the rate at which certain types of behaviour are manifest, although only very rarely are unique behaviour patterns exhibited either in captivity or in the wild (e.g. Rowell, 1967; Judge & de Waal, 1997). Rates of aggression are often elevated in captive conditions and this is true of chimpanzees (Nieuwenhuijsen & de Waal, 1982); submissive and affiliative behaviours are also shown more frequently. However, studies of macaques have shown that more or less crowded conditions do not affect rates of reconciliation (Aureli, 1992; Judge & de Waal, 1993; Aureli *et al.*, 1995; Call *et al.*, 1996; Judge & de Waal, 1997). It seems that the motivation to reconcile remains dependent on the relative value of relationships and perhaps the context of the conflict (Cords & Thurneer, 1993; Castles *et al.*, 1996; Judge, 2000) rather than simply being part of a set of coping mechanisms deployed when conditions become more extreme, as was suggested by de Waal (1989b). A puzzle thus remains about why rates of reconciliation were so low in this study. In Aureli's (1992) study of

wild long-tailed macaques, no difference was found in the rate of reconciliation from that observed in captivity. A number of possibilities present themselves. Perhaps monkeys are not flexible in the number and types of relationship that they consider valuable under varying circumstances, whereas chimpanzees are. Alternatively, the dominance style of the Sonso chimpanzees during this study might have been much stricter and more rule-bound than that of the captive chimpanzees studied so far. Another possibility is that the Sonso chimpanzees did not often perceive their relationships to be disturbed after a conflict, or at least not enough to warrant attempts to reconcile when other occupations, such as foraging, might be more profitable; wild chimpanzees live within constraints which are different to, and more severe than, their captive counterparts.

6.4.2 The influence of relationship quality

I next consider the extent to which relationship quality, as predicted by current models of chimpanzee social behaviour, is reflected in the patterns of reconciliation observed in this study. It is well known that male chimpanzees have a greater need than females to cooperate with one another, preventing extracommunity males from having access to oestrus females (Bygott, 1974; Dunbar, 1988; Chapman & Wrangham, 1993). They increase their status and ultimately their reproductive success through agonistic alliances (e.g., Goodall, 1986; Wrangham, 1986; de Waal, 1992). Males tend to be far more sociable than females and spend a great deal of their time actively developing and maintaining relationships with other males. Occasionally, males and females have close affiliative relationships, especially mothers and male offspring (Pusey, 1983). But male-female relationships are often short term and might take the form of exclusive consortships or a general interest in maintaining friendly

contact with females in oestrus. Females have very little direct contact with each other in the wild, tending to aggregate around resources or in 'nursery' parties (Nishida, 1979; Halperin, 1979; Wrangham & Smuts, 1980).

Contrary to predictions (1 and 2), males were not more conciliatory than females in general, and that the rate of reconciliation between males was comparable with that between males and females. Throughout the study period, only the adolescent females displayed normal oestrus cycles as almost all of the adult females had dependant offspring. The tendency to reconcile in this condition was primarily due to the behaviour of the adolescent females toward the alpha male, with whom they had intense grooming relationships, compared with other males (see Chapter 3). Thus proper tests of the effect of reproductive status on reconciliation was not possible. It might be expected that it would be in the interest of males to reconcile conflicts with females more often when females were in oestrus, thereby preserving good relationships with females and enhancing access to them even in the short term (c.f. Hemelrijk *et al.*, 1992), but this was not the case. Whether females were in oestrus or not, did not affect the likelihood of reconciliation. Nor did males reconcile conflicts more often with females with whom they had copulated. Moreover, it was almost always the females who were responsible for initiating reconciliation, whereas in non-conflict situations, affiliative interactions were initiated equally often by males and females. A number of studies by Hemelrijk and colleagues have shown that a female's value as a sexual partner may not be reflected in reciprocal or exchange relationships with males (e.g., Hemelrijk & Eck, 1991) and neither do relatively good relationships result in relatively high reproductive success (Hemelrijk *et al.*, 1999). Females might be more motivated to initiate reconciliation with males as good relationships with

males may buffer the effects of female-female competition, especially for immigrant females (Pusey *et al.*, 1997) and reduce male harassment.

The third prediction was confirmed in that female-female conflicts were reconciled least. However, it is unlikely that Sonso females never reconcile. This study was biased toward observing post-conflict behaviour involving males and so behaviour in-all female parties was not well represented in the data set. On one occasion, a clear attempt to reconcile was made by a female after a fight with a high ranking female but the attempt was rejected.

In relation to our fourth prediction, highly compatible males - those who spent more time affiliating and in close proximity - did reconcile conflicts significantly more often than weakly compatible males. This was also the case for male-female conflicts.

These results thus provide some support for the valuable relationship hypothesis. The compatibility or 'friendliness' of another individual can be considered a valuable quality, as the probability of beneficial and relaxed social interactions with such individuals is increased (Cords & Aureli, 2000; Kummer, 1978). Evidence for the positive influence of compatibility on the tendency to reconcile has previously been documented in a number of species, including captive chimpanzees (de Waal & Yoshihara, 1983; de Waal & Ren, 1988; Aureli *et al.*, 1989; Cords & Aureli, 1993; Watts, 1995a; Castles *et al.*, 1996; Casperd, 1997; Schino *et al.*, 1998; Call *et al.*, 1999; Arnold & Barton, 2001a; Preuschoft *et al.*, in press). However, the finding that oestrus females were not more likely to achieve reconciliation with males, and that males appeared to be less motivated to reconcile than females was a surprising result. It is possible that the sample sizes in this study were too small to reveal what is a

highly predictable relationship between reconciliation and sexual receptivity, but Casperd's (1997) captive study produced a similar result.

With regard to prediction 6, levels of association, which could be described as 'familiarity', might be a relevant measure of relationship quality in the fission-fusion society of chimpanzees. It has been suggested that male chimpanzees might associate tactically with one another and that regular association partners might be of some value to one another (Newton-Fisher, 1999a). However, there was no relationship between association strength and conciliatory tendency for male-male or male-female dyads.

Contrary to the sixth prediction, the relative age of former opponents was not shown to influence the probability of reconciliation occurring despite the fact that adults are likely to be more useful to one another as coalition partners and most adults devote more time to socialising with one another than with adolescent or juvenile members of the community. Consequently, adolescents and juveniles tend to socialise with each other or with their mothers, although as adolescent males approach maturity they tend to seek out the company of adult males and place themselves within the male hierarchy. In this study, no significant results pertaining to age were obtained using pooled data, although adults tended to reconcile more often with other adults than with juveniles. When young adolescents were placed in the juvenile category, adults also reconciled more often with the remaining adolescents than with juveniles. Adolescent males which are close to maturity are almost fully integrated into the adult male social network and their value as social and coalition partners is much greater than their younger counterparts, who have little contact with adults and are rarely involved in triadic agonistic encounters. All of the adolescent females in the community were close to maturity and were regularly coming into oestrus.

Rank distance did not predict the probability of reconciliation (prediction 7) although rank did influence which party initiated reconciliation when it occurred. Victims of aggression, which were always ranked lower than the aggressor took the responsibility for initiating reconciliation in the vast majority of cases suggesting that victims were more motivated to restore the relationship than aggressors. Casperd's (1997) study found the same pattern although in de Waal & van Roosmalen's (1979) study victims and aggressors were equally likely to initiate friendly post-conflict contacts. That victims of aggression are able to approach a dominant aggressor soon after a conflict is in keeping with the characterisation of chimpanzees as a more tolerant primate species. Another indication of this is that bi-directional conflicts were as likely to be reconciled as uni-directional conflicts although it should be noted that bi-directional conflicts were rare. Bi-directional conflicts always resulted in a clear winner and any show of lack of intimidation or uncertainty about dominance relationships did not reduce the chance of reconciliation in the form of withholding opportunities for relationship repair or status signalling. In fact, none of the bi-directional conflicts that were reconciled involved an acknowledgement of status on the part of the victim.

However, 54% of all successful attempts at reconciliation were preceded by some form of submissive signal; most commonly the 'pant-grunt' which is always given by the subordinate and is considered to be a reliable indicator of relative status. A further 19% of successful reconciliations were preceded by a gesture of invitation or solicitation of friendly contact. This frequency is about double that found during Casperd's (1997) study. 'Hold-out-hand' was observed on four occasions and 'arm-up', a gesture often associated with grooming, was observed to precede reconciliation once. These gestures were produced exclusively by the dominant party. There was no

significant difference in the distribution of first contact behaviours in PCs and MCs and so this community of chimpanzee's style of reconciliation can be considered to be 'implicit' as the behaviours involved occur frequently in other contexts (de Waal & Ren, 1988). The 'explicit' reconciliation of tolerant species involves friendly interactions with the former opponent which are characteristic of the post-conflict context in that they are rarely observed in other contexts and may serve to signal the occurrence of reconciliation. Such contacts include embracing, clasping and hold-bottom gestures (e.g. *M. tonkeana*: Thierry, 1984; *Rhinopithecus roxellanae roxellanae*: Ren *et al.*, 1991; *Colobus guereza*, Björnsdottir, *et al.*, 2000; *T. obscurus*: Arnold & Barton, 2001a; *M. arctoides*: de Waal & Ren, 1988). Chimpanzees are also considered to have an explicit style of reconciliation which is characterised by mouth-to-mouth kissing (de Waal & van Roosmalen, 1979). Kissing was also observed during 14% of conciliatory contacts in Casperd's (1997) study although the frequency of this behaviour in MCs was not reported, so it is unclear whether or not kissing was characteristic of reconciliation in this group. Kissing was never observed in any context during this study and this, together with the rarity if bi-directional conflicts, call into question the assumption that chimpanzees are an archetypal tolerant species with regard to their post-conflict behaviour.

Only one of the dimensions of relationship quality we investigated influenced the likelihood of reconciliation: compatibility. This suggests that a history of friendly contacts constitutes a relationship that is sufficiently valuable for one or other opponent, usually the lower ranking victim of aggression, to seek to restore the relationship. As mentioned previously, the value of coalition partners would be expected to be reflected in patterns of reconciliation. Few coalitions were observed, however, and most instances of third party involvement in conflicts were, in fact,

control interventions (Boehm, 1994) on behalf of the victim which ended conflicts rather than conferred a competitive advantage on either opponent. Conflicts between interveners and recipients of support were very rare and so an analysis of the relationship between agonistic support and reconciliation could not be carried out. However, of five dyads that had relationships involving both aggression and support on at least one occasion, only one dyad reconciled a (single) conflict. In this case the reconciled conflict and the coalition were temporally distant and so unlikely to be related. Intriguingly, no such relationship has been found in captive chimpanzee studies (Casperd, 1997; Preuschoft *et al.*, in press), which challenges the notion that chimpanzees, themselves, perceive any stability in the supporter-recipient relationship, as well as our intuition that the inherent value of coalition partnerships should be recognised by them. Support for this scepticism lies in the sparse evidence for reciprocation of support, or interchange involving other currencies in chimpanzees (Hemelrijk & Eck, 1991; Hemelrijk *et al.*, 1991; Hemelrijk, 1996). Alternatively, the valuable relationship hypothesis may simply not hold as predictably for chimpanzees as it does among other primate species. As yet, only the two studies cited above have shed any light on this issue.

Kinship has widely been reported to be an important factor influencing reconciliation in kin-based monkey societies (e.g. Aureli *et al.*, 1989; Cheney & Seyfarth, 1989) and might also be an important determinant of post-conflict behaviour of chimpanzees, particularly males. Chimpanzee society is philopatric and thus the relatedness of males is assumed to be high unlike adult females who are usually immigrants from neighbouring communities. Again, analysis of the effects of kinship could not be analysed as too few kin relationships are known in this community and conflicts among kin were rare. It is likely, however, that if kinship is important

enough among chimpanzees to influence reconciliation, then it will also be reflected in patterns of association and affiliation as well. No relationship between kinship and reconciliation was found in captive chimpanzees (Casperd, 1997) but such a relationship needs further investigation and this will be possible when an ongoing study of the genetic relationships of the Sonso community is completed (Reynolds, pers comm.).

Previous studies have shown that the context of a conflict can affect the probability of reconciliation. Conflicts concerning access to food are less likely to be reconciled than purely social conflicts (Aureli, 1992; Matsumura, 1996; Koyama, 1997; Verbeek & de Waal, 1997; Castles & Whiten, 1998a). It has been suggested that food related conflicts might not disturb social relationships as dominance interactions should be 'expected' at such times, or that reconciliation might be delayed until feeding was over (Aureli, 1992) although Koyama failed to find such an effect in her study of free ranging, semi-provisioned Japanese macaques (1997). Chimpanzees, however, have been predicted to reconcile conflicts over clumped food resources (Verbeek & de Waal, 1997), as they have been shown to employ a wide range of reassurance behaviours in these situations, both in captivity (de Waal, 1989) and in the wild (Goodall, 1986). Our results confirm this prediction, showing a trend favouring reconciliation in this context. There were no differences in rates of reconciliation in other contexts.

Activity budgets were generally not affected by aggression although males were more likely to rest after a conflict than at other times. Resting gives the opportunity for vigilance and it is possible that the males spent some time assessing the current situation before continuing with other activities. Further aggression

following conflicts, however, was very rare, as were opportunistic attacks by third parties.

6.4.3 Reconciliation and anxiety

Self-directed behaviours such as scratching and self-grooming are commonly observed in non-human primates and rates of such behaviours have been shown to be a reliable indicator of anxiety (Schino *et al.*, 1996). Rates of self-directed behaviours have been shown to increase following conflicts and then return to, or fall below, baseline levels after reconciliation (Aureli & van Schaik, 1991b; Castles & Whiten, 1998b; Das *et al.*, 1998). Baker & Aureli (1997) have shown that rates of rough scratching, in particular, increase when captive chimpanzees perceive an increased probability of agonism. Rough scratching was also found to increase in frequency under conditions of high population density (Aureli & de Waal, 1997). We investigated the occurrence of rough scratching, gentle scratching and self-grooming under post-conflict conditions but found that the rate of rough scratching was actually significantly lower during unreconciled PCs than MCs whereas rates of gentle scratching and self grooming were roughly equal. Nonetheless, rates of rough and gentle scratching were lower during PCs that were reconciled compared with those which were not, and although bouts of self-grooming were not more frequent, they were of longer duration.

Low intensity conflicts resulted in smaller inter-opponent distances than high intensity conflicts at the beginning of PCs and were reconciled more frequently. This suggests that victims of low intensity aggression were less concerned with increasing their distance from former aggressors and should be less stressed. But I found no difference in scratch rates after conflicts of different intensities. I therefore conclude

that rates of self-directed behaviours were not a good measure of stress in this wild population, although there was some indication that reconciliation affected post-conflict rates of these behaviours. The lower frequencies found in PCs might not reflect a lack of anxiety, but rather that these behaviours are frequently displayed in other contexts for different reasons. For example, scratch rates were high during grooming sessions, even when individuals were not actually involved in allogrooming themselves.

6.4.4 Post-conflict contacts with third parties and implications for cognition

Redirection of aggression on the part of the victim was very rare in this study, and has not been documented previously in chimpanzees unlike many macaque species (e.g., Aureli & van Schaik, 1991a; Aureli, 1992; Aureli *et al.*, 1992). This is despite the prediction that the cost of this form of aggression should be relatively low in a non-nepotistic, non kin-based society where reprisals from relatives of the target of redirection should be infrequent (Watts *et al.*, 2000), whereas the benefits might include stress reduction (Levine *et al.*, 1989; Aureli & van Schaik, 1991b), direction of attention toward a third party, or might actually facilitate reconciliation (Aureli & van Schaik, 1991a). Redirection towards an opponent's kin might also impose indirect fitness costs which would constitute an effective counter strategy (Aureli *et al.*, 1992). The lack of redirection in chimpanzees is a little surprising, as it is a strategy which holds many possibilities for the tactical imposition of fitness costs on rivals via triadic conflict management; an arena in which chimpanzees should excel over monkeys. However, the ability to counter-attack might make redirection unnecessary (Thierry, 1985) but counter-attacks were rarely observed.

Conflict management in all of its forms has great potential for the manifestation of sophisticated cognitive abilities via the manipulation of relationships (Cords, 1997; Castles, 2000). To date, no evidence exists that demonstrates a greater complexity in nonhuman primate conflict management, than in nonprimate conflict management, primarily due to a severe lack of data for nonprimates (Schino, 2000). Even within the primate order there are few data uncontroversially suggestive of different strategies which require differential cognitive loads in terms of social knowledge (Castles, 2000). One possibility was suggested by de Waal & Aureli (1996) and concerns the affiliative behaviour of former opponents and uninvolved third parties after conflicts. Affiliation between aggressors and third parties at higher rates after conflicts compared with non-conflict contexts has been documented in a number of macaque species (de Waal & Yoshihara, 1983; Judge, 1991; Das *et al.*, 1997; for a review see Das, 2000). Such contacts are thought to reconfirm alliances between the affiliating individuals; they might not count as a conflict management strategy as such, even though social tension might be dissipated by this means. Similarly high rates of affiliation between victims and third parties has been demonstrated in a small number of species, but not macaques (*P. papio*: Petit & Thierry, 1994; *G. g. beringei*: Watts, 1995b; *P. troglodytes*: de Waal & Aureli, 1996; *Cebus apella*: Verbeek & de Waal, 1997; *T. obscurus*: Arnold & Barton, 2001b; *P. hamadryas*: Zaragoza & Colmenares, unpublished). This 'solicited consolation' has been proposed to alleviate stress, provide protection from further attacks in the same way that reconciliation does, and might also help to induce reciprocal behaviour in the future (Watts, 1995b; Arnold & Barton, 2001b; for a review see Watts *et al.*, 2000). However, in all of these cases it is the victim of aggression that initiates these contacts.

'Consolation' proper is defined as an affiliative interaction between a victim of aggression and a third party, which is initiated by the third party. Only chimpanzees have been demonstrated to console one another and it has been suggested that this difference between chimpanzees and other primate species might be explained by a difference in social styles or a difference in cognitive abilities (de Waal & Aureli, 1996). The 'Social Constraints Hypothesis' (de Waal & Aureli, 1996) predicts that third parties will initiate affiliation when the benefits of doing so will be high and the risks of receiving aggression themselves are low. Therefore species with despotic dominance styles, such as some macaque species are precluded from consoling victims. The 'Social Cognition Hypothesis' (de Waal & Aureli, 1996) predicts that only species that are capable of empathising with others, and expressing the desire to alleviate the distress of victims, will show consolatory behaviour. The data so far support the social cognition hypothesis, as species with tolerant dominance styles have not been demonstrated to show consolation and no monkey species is thought to be capable of attributing knowledge states to others (e.g., Povinelli *et al.*, 1991). Whether chimpanzees have the ability to attribute emotions or other states of mind is controversial (Povinelli & Eddy, 1996; Whiten, 1997) although recent evidence indicates that they may (Hare *et al.*, 2000; Hare *et al.*, 2001). Observational field studies cannot resolve this issue.

However, only one study has successfully demonstrated the occurrence of consolation in chimpanzees (de Waal & Aureli, 1996). The original study of de Waal & van Roosmalen (1979), where the term 'consolation' was first coined, did not consider responsibility for initiation and so cannot be counted as good evidence for consolation in chimpanzees. Unfortunately, our results are difficult to interpret. Aggressors did not contact third parties at higher rates in PCs compared with MCs.

Aggressors were most often adult males who had higher affiliation rates than any other age-sex class. Victims of aggression did contact third parties at higher rates during PCs than in MCs and this positive result was due, in particular, to the distribution of contacts with individuals with whom victims were highly compatible. Post-conflict affiliation in this community of chimpanzees is therefore dependent on good relationships with others whether they are former opponents or bystanders. The latency to contact third parties was 2.8 minutes, only slightly longer than the latency to contact former opponents, at 2.3 minutes, and so might serve as substitute reconciliation as suggested above.

Consolation was also demonstrated statistically although this result was the product of only four consolatory episodes and a very low interaction rate between these four victims of aggression and third parties in MCs. I am therefore reluctant to conclude that consolation was part of this community's post-conflict repertoire due to the rarity of the behaviour. Chimpanzees are said to reconcile explicitly and kiss one another more often during reconciliation than at other times. Similarly, their style of consolation is explicit in that embracing marks the occasion (de Waal & van Roosmalen, 1979). I found no evidence for explicit third party contacts and embracing, in particular, was never observed. This provides further evidence that third party contacts in this wild population might be different from those observed in captivity.

Our data are thus limited and firm conclusions cannot be drawn. Nor can I judge the competing (though not mutually exclusive) hypotheses for the occurrence of consolation in captive chimpanzees. But our data do suggest that consolation might not be a ubiquitous phenomenon among chimpanzees. Further study is needed to identify the conditions under which consolation occurs.

6.4.5 Summary

This community did not appear to possess as rich a repertoire of communicatory gestures as that described in other populations (e.g., Goodall, 1986; de Waal, 1982) and this may have resulted in the rather sparse evidence for complex social interactions presented here. It should be noted, however, that social tension in the Sonso community was rather low throughout the study. Only sixty conflicts between adult and adolescent males were observed in total compared to 132 in a previous study of similar length during which the previous alpha male was ousted and replaced by the current one. The social dynamics of the males as a whole, in terms of status, were rather more fluid (Newton-Fisher, 1997) than during this study. The low availability of adult females in oestrus was also a factor that was likely to have reduced male competition. It is therefore possible that the stability of the group reduced the potential value of individuals, particularly males, to one another during a period when coalitionary partnerships and 'political' manoeuvrings generally, were not as important as they might be at other times.

Additionally, our limited data set might not accurately reflect patterns of post-conflict in these chimpanzees. However, they are similar in many respects to those reported in Casperd's (1997) captive study based on a larger data set. I therefore conclude that chimpanzee post-conflict behaviour is potentially more variable than that of monkeys and dependent on the prevailing ecological and demographic situation. Predictions derived from the relationship quality hypothesis were partially supported although a number of measures of relationship quality did not influence the tendency to reconcile. The post-conflict behaviour of these chimpanzees is consistent with their characterisation as relatively a tolerant, or egalitarian, species as severe aggression was infrequent, bi-directional conflicts were reconciled as often as

unidirectional conflicts and victims of aggression were most often responsible for initiating post-conflict affiliative contacts. However, the lack of behavioural specificity and low rates of reconciliation make this characterisation less secure in these wild chimpanzees. The nature of contacts with third parties was also similar to tolerant monkey species; it does not set them apart from monkeys in the ways previously reported for captive chimpanzees.

Lastly, rank effects were limited to the indication of which of the former opponents were more likely to initiate reconciliation. The dimension of relationship quality that most strongly influenced patterns of post-conflict behaviour in wild chimpanzees was compatibility, indexed by the amount of time dyads spent grooming and in proximity. It is possible that compatibility might have been underestimated as a pervasive influence in previous studies concerning other species of primate. For example, among wild mountain gorillas, male-female reconciliation is far more common than female-female reconciliation and this has been explained in terms of the value that males carry as female protectors and interveners in disputes (Watts, 1995a). However, male and female mountain gorillas have far stronger affiliative relationships than than females do with each other (Watts, 1996). Similarly, the high rates of reconciliation between kin compared with non-kin in a number of species of macaques and baboons (e.g., de Waal & Yoshihara, 1983; Aureli *et al.*, 1989, 1997; Castles & Whiten, 1998b) might well reflect the distribution of intense affiliative relationships which correspond very closely with the distribution of co-operative relationships. In such species it is very difficult to tease apart the most salient features of relationships in the context of reconciliation. However, the lack of obvious co-operative relationships within the Sonso community of chimpanzees has afforded the opportunity to do so and compatibility, in terms of affiliation at least, appears to be an

important factor in its' own right in determining which relationships are worth actively maintaining or improving, and which are not.

Chapter 7

Concluding Discussion

Each of the previous chapters include extensive, and often cumulative, discussions of the results of this study and of some more general issues. This chapter represents an opportunity to briefly reflect on the significance of the results in relation to some of the received images of chimpanzee social life.

7.1 Male bonds, not rank, influenced male relationships

One of the most striking aspects of the Sonso chimpanzees during 1998 and 1999 was the degree to which bond strength, as opposed to rank, was important in structuring male social behaviour. Grooming relationships were intense by the standards of two previously studied communities (Mahale and Ngogo: Watts, 2000a). Males directed less aggression at other males if they were frequent grooming partners than if they had weak grooming relationships or none at all. The strength of male-male and male-female bonds was the most important factor determining patterns of reconciliation.

Rank was a factor in the degree to which males affiliated with one another. High-ranking males gave and received more grooming, and distributed their grooming among a wider circle of partners than low-ranking males did, but this effect was lost when only adult males were considered. This result was similar to that found at Mahale, although rank was an important variable influencing grooming distribution in the large Ngogo community at Kibale (Watts, 2000a). Although it would make sense that females should seek to form bonds with high-

ranking males as such males are more likely to be able to provide benefits such as protection or possibly high quality genes, females did not appear to prefer high-ranking males as grooming partners. High-ranking males did groom females more than low-ranking males but these attentions did not result in higher copulatory rates or a larger number of sexual partners among adult males. Rank-based priority of access models of grooming distribution were not predictive of real grooming distributions at Sonso or Mahale (Watts, 2000b). Relative rank also had no effect on the likelihood of the occurrence of reconciliation.

During my study I was surprised, given that my initial intention was to gain a better understanding of post-conflict behaviour, by the lack of dominance interactions and conflicts within the Sonso community. I saw little evidence of the effects of rank in my day to day observations. I was even a little perturbed when I watched mid-ranking males frantically branch-shaking at the most popular adolescent female displaying a fully tumescent sexual swelling while the alpha male sat one metre away gently soliciting her himself. Why did DN not exercise his 'right' to monopolise her when there was no other cycling female available? He surely had nothing to lose, and his grip on the other males in terms of their displays of submission toward him seemed an iron one. Why strive for status if not to reap the rewards?

Another striking aspect of this study was the lack of evidence for social manipulation. I saw no grooming interventions, relatively few dominance interactions, and coalitions were rare. The coalitions I did see did not appear to be particularly strategic because loser-support coalitions, outside of the DN-VN alliance, often favoured individuals who were at a serious competitive disadvantage and, in these cases, the intensity of aggression involved was often the minimum

required to end an attack. Winner-support coalitions were extremely rare. On asking colleagues why I might have seen so little of the behaviour that is generally considered to characterise male chimpanzees in the literature, a common response is that dominance relations in this community at that time must have been stable. I do not consider this a satisfactory answer. It is not clear why the male hierarchy should ever be stable. If males have the ability to use tactics and strategies of manipulation to increase their status, why do they not employ them often? Why should the hierarchy be allowed to stabilise over periods of a year or more? In any case, it is not quite true to say that the hierarchy was entirely stable over the entire study period. There did appear to be an attempt on the part of BK to subordinate VN, the outcome of which was not evident due to VN's disappearance toward the end of the study. MA also came to dominate BK shortly afterward. How or why this should have occurred is impossible to say as no event/s were observed to precede this rank reversal which could have shed light on this matter. If rank reversals were possible it is surprising that males should settle for their existing status, assuming there are benefits associated with high status.

It has been suggested (Newton-Fisher *et al.*, 2000) that feeding competition is not as important for chimpanzees at Budongo as it is at other sites due to the abundance of food, and of fruiting trees in particular. The Budongo Forest was logged extensively during the 1960's, creating gaps within which colonising species eventually gave way to secondary forest and allowed various important fruit species to thrive in many locations. Areas containing climax forest made up only a small proportion of the Sonso chimpanzees community range. Any resultant decrease in feeding competition might render high rank less advantageous in terms of the ability to obtain the largest share of a desired resource and exclude others from it.

Nonetheless, fruit of the *Ficus sp.*, a very popular and attractive food source, tends to be very clumped and high rank should still afford priority of access to discrete food patches. The lack of cycling adult females may also have reduced male-male competition for mates although it seems unlikely that males might entirely opt out of competition for mates despite adolescent females' possible status as unproven breeders and less attractive than mothers. The alpha male still gained the largest number of observed copulations and so *was* interested in these females, as were the remaining males of all ages. These factors may have contributed to stable dominance relations among the males. However, I now take issue with the conception of male chimpanzees as 'dominance driven' entities (de Waal, 1982, p. 188) striving to realise their potential through the use of cunning manipulations and well executed plans.

7.2 Power struggles

Male chimpanzees are considered to be far more active than females in asserting their dominance over others and the 'tactics' that they appear to employ in doing so was influential in building the conception of nonhuman primates as 'Machiavellian' in their use of social strategies for the acquisition of power (de Waal, 1982; Byrne & Whiten, 1988; Whiten & Byrne, 1997). Most of the published accounts of male 'status striving' refer to periods of instability within the male hierarchy when major upheavals result in one or more males ascending or declining in rank fairly rapidly, or rank reversals are documented over more extended periods of time, concentrating on important events during this process that are described at the level of individual interactions (e.g. de Waal, 1982; Nishida, 1983; Goodall, 1986). These kinds of descriptions tend to promote the impression that power

struggles are a constant feature of the social life of male chimpanzees. However, de Waal's (1982) documentation of the rise of Luit to the alpha position states that the reorganisation of the male hierarchy took one year to complete, although the most important events took place between the spring and autumn of 1976. The initial hierarchy included Yeroen, occupying the alpha position, Luit, the beta, and Nikkie, the gamma male. After the reorganisation, the rank order was Luit, Yeroen, and then Nikkie. Rank reversals occurred again after a period of stability during which Nikkie became alpha, Luit dropped to the beta position, and Yeroen dropped again to occupy the gamma position. This, again, took one year to accomplish. This whole process took place over the course of two years, involved only three males, and occurred in a captive setting.

Goodall (1986) also provides rich descriptions of the ascendance of Gombe males together with data which charts their rise in rank, periods of tenure, and then their decline (Fig. 15.2, p. 414). Out of eight males for which data are presented, four never reached alpha status, two of these did attain high rank, while the remaining two males died at 17 and 26 years of age. Four males attained the alpha position after 8.5 ± 5 years of adult life, on average, when they were between the ages of 20-26 years (Goodall, 1986). This in itself is suggestive that age alone could contribute significantly to male success in gaining high rank, as three of these males attained alpha status when they were in their prime, and fell in rank between the ages of 28-32 when they were ousted by younger males (Goodall, 1986). The fourth male, Goblin, became alpha male when he was only 15 years old and represents the best example of a meteoric rise in status at Gombe. What was Goblin's remarkable strategy that allowed him to dominate all of the community males so quickly, and at such a tender age? Goblin's closest associate, from his becoming an independent

juvenile through to adulthood, was Figan who became alpha male when Goblin was 10 years old. According to Goodall (1986), the most important feature of Goblin's character was his *persistence* in attacking and eventually dominating first the adult females, and then with Figan's support, the other adult males. Eventually, he overthrew Figan and became alpha male. Goblin's success, then, was due in part to an unusual character trait, combined with a 'strategy' which he used consistently throughout his independent life until he had achieved his 'goal'. Whether or not Machiavelli would have been impressed with these tactics is debatable.

Mike was unusual in that he displayed at a very high rate and incorporated the use of noisy kerosene cans in these displays. He was described as persistent and determined (Goodall, 1986, p. 426). Humphrey overthrew Mike during a single fight and "no special strategy was involved" according to Goodall (1986, p. 424). Mike held his position for only a short time. Figan then became alpha male and retained this position for eight years. Figan was also notable for his persistence and determination together with the effectiveness of his displays. Goodall also writes that Figan's brother and ally, Faben, was crucial in his attainment of alpha status (1986, p. 427). Figan withstood sixteen coalitions involving three or four males in one year without the support of his then absent ally. Goodall goes on to suggest that Figan's ability to do this was a result of the characteristics outlined above, together with the failure of the other males to capitalise on their immediately strengthened positions in relation to him. Rather than actually jointly attacking him, they ended their attack once they had caught up with him, and excitedly groomed one another (Goodall, 1986).

I describe such examples at such length in order to demonstrate that these two major sources of descriptive information (de Waal, 1982; Goodall, 1986) which

have helped to shape many researchers' impressions of male chimpanzee power struggles as complex and requiring greater social intelligence and forethought than that exhibited by other species including monkeys, are not altogether compelling. The course of events which result in rank reversals taking place are often quite protracted, especially in the wild, and although this certainly does not preclude the possibility that plans are constructed and executed profitably, neither does it preclude the possibility that many of the 'strategies' that we perceive are not premeditated over long time spans, but are simply the product of the adherence to a 'rule', e.g. where opportunities arise, temporary weaknesses in your competitors should be exploited. Rank reversals can sometimes occur after just one fight while others result from a series of intimidation attempts. Winner and loser effects (e.g. Chase *et al.*, 1994; Dugatkin, 1997b) which probably operate widely in primates (Raleigh, 1984), via changes in blood serotonin levels, could then help to fix any resultant changes in the perception of the competitors' status in relation to one another. These changes could then be further stabilised by bystander effects which have been found to reinforce rank orders in theoretical models (Dugatkin, 2001) and have been demonstrated in birds and fish (e.g. Chase, 1985; Johnsson & Akerman, 1998; Oliveira *et al.*, 1998). After a series of such events leading to a positive outcome for a particular individual, it is easy to see an elaborate plan where there may, in fact, be none.

It is not clear what exactly is meant by the term 'status striving'. This term certainly implies goal-directed behaviour and that chimpanzees and other animals are capable of this is not in question (see Tomasello & Call, 1997 for a review). Whether chimpanzee behaviour could be directed in such a way as to accomplish previously considered long-term goals (achievable over a span of up to eight years)

which incorporate calculated moves that bring the subject closer to its goal little-by-little is unknown. De Waal is explicit in his view that chimpanzees are capable of such long term planning (1982, p. 191-192). De Waal even considers chimpanzees to have a concept of truth which guides their plans; a view which he also makes explicit when he states that "For Yeroen to have continued his policy he ...must have been certain that he was right" (de Waal, 1982, p. 191). Such beliefs undoubtedly intervene in de Waal's interpretation of chimpanzee behaviour and have encouraged others to tackle some important problems in the study of primate cognition, on his terms. Alternative possibilities, such as Mason's (1993) 'minimax' model in which individuals simply strive to have their own way wherever they can, has received little or no attention, although problems arise when competing hypotheses predict similar outcomes and naturalistic observations alone cannot distinguish between them.

7.3 Jumping the gun?

More recently, researchers have turned to computer modelling of the behaviour of artificial entities which follow simple rules in virtual worlds in order to examine the efficacy of more parsimonious scenarios concerning social organisation than those currently available, and from which emerge a number of recognisable features of apparently complex societies. For example, Hemelrijk (1999) created artificial entities living in a homogenous world which aggregated, and on meeting one another, performed dominance interactions in which the effects of winning and losing were self-reinforcing. She found that by making these entities intensely aggressive (fierce entities), behaviour resembling despotic primate societies emerged. When the entities were programmed to be less aggressive (mild

entities), a more egalitarian society emerged. The society of fierce entities that emerged came complete with larger rank distances, lower cohesiveness, lower interaction frequencies, less symmetrical attack patterns and more rank-related behaviours than emerged in the society of mild entities. These results mirrored differences in the societies of despotic versus egalitarian, or tolerant, macaque species about which many of the details are known compared with other primate species (de Waal & Luttrell, 1989; Thierry, 1990). As Hemelrijk points out, this simple model generated an astonishing number of emergent effects that could not have been predicted by inference from what we know about the evolution of social systems alone.

At present it seems that the slowly accumulating evidence that primates, and chimpanzees in particular, are capable of certain relatively high level cognitive functions, together with the fact that not only can humans seem to recognise aspects of their own mentalities in the behaviour of chimpanzees but also it makes perfect sense that we should have much in common with them given our shared evolutionary histories, seduces us into explaining their behaviour according to what would make most sense if we were in their place. If some researchers are correct in deducing from the results of carefully controlled experiments that chimpanzees are able to understand some of the relations between objects, animate or otherwise, but not *why* those relations obtain or that the understanding of these relations are part of the subjective experience of conspecifics (e.g. Tomasello, 2000), then it seems unlikely that their behaviour could be guided by such things as long-term plans, empathy or predictions about possible counterstrategies (de Waal, 1982; de Waal & Aureli, 1996; Preston & de Waal, in press).

As yet we simply do not have a sufficiently sophisticated descriptive base from which to robustly characterise the cognitive capacities of chimpanzees or to assess the complexity of chimpanzee societies within which these capacities have evolved and are utilised. Moreover, attempts at more minimal explanations, as opposed to richer ones, are often unpopular and are seen as 'killjoy'. But we may be surprised (or dismayed) by what apparent complexity can be generated out of quite simple rules and regularities, as Hemelrijk's (1999) virtual entities have shown. We should make careful note in the future of what such approaches can tell us about what we might need to explain, and what we might not need to explain, in terms of the complexity of social living and the cognitive capacities which underpin it, or are necessary to deal with it.

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Appendix A: Scan Sampling Check Sheet

Checksheet: Party size and composition/ distance from focal and activity.