-Chapter 1-

General Introduction

Human-induced change on ecosystems over the past 11 500 years associated with the spread, growth and development of human populations are having detrimental consequences for our ecosystems. Habitats are being destroyed, with the result of an unknown number of species having been harvested or hunted to extinction. The colonization of new regions and the introduction of alien species have all too often led to the exclusion of indigenous taxa and due to the way that the loss of one species can cascade through an ecosystem, many other species have also been lost. As human populations increase so the planet's resource base decreases, and never before has one species been responsible for not only the extinction of other species but for its own extinction.

Our closest relatives the other primates are also caught within this trap of disaster. Their populations are under constant pressure from encroaching human populations into their already diminishing habitat. Extant primate species currently lie between 200 to 230 species, which are expected to decline drastically if conservation plans to conserve habitat is not taken (Cowlishaw and Dunbar 2000). Several primate species are already on the brink of extinction (Mittermeier et al. 2006). For example, the snub-nosed monkeys (*Rhinopithecus spp)* of Vietnam and China, consisting of four species with very restricted distributions, are highly threatened by both hunting and habitat loss (Kirkpatrick 1995). Even primate species that have adapted to coexisting with humans are unsafe.

Uncontrolled live trapping catalysed by deforestation and 'problem animal control' is resulting in the drastic decline of among others, rhesus monkeys (*Macaca mulatta),* savanna baboons (*Papio ursinus*) and vervet monkeys (*Cercopithecus aethiops)*.

By aiming to provide sound knowledge and guidance to implement effective conservation strategies to sustain natural biodiversity, we may be able to preserve biological systems that support living systems. The conservation of primates justifies this concept in terms of the ecological value that they have to natural ecosystems. It has been suggested that primates are important pollinators (Carthew and Goldingay 1997) although this is largely based on speculation than hard evidence. A great more is however, known about the significance of primates as seed dispersers. A wide range of primates including gorillas *Gorilla gorilla* (Tutin et al. 1991; Voysey et al. 1999 a,b), chimpanzees *Pan troglodytes* (Wrangham et al. 1994), orangutans *Pongo pygmaeus* (Payne 1995) and baboons (Slater and du Toit 2002) have been identified as being significant contributors to seed dispersal. Some plants may rely solely on an individual primate species for dispersal of its seeds (Tutin et al. 1991). There is evidence to suggest that by removing primates from forests, forests may be unable to regenerate due to the importance of primates as seed dispersal agents (Chapman and Onderdonk 1998) and if the forests disappear, climate regulators and water catchments systems may also disappear. There is also intellectual value to the conservation of non-human primates due to their similarities both physically and cognitively to ourselves. Socioecologists can use differences between sites and populations to understand either ecological (Wrangham et al. 1996) or cultural (McGrew et al. 1997) factors which influence social systems and behaviour. Palaeontologists and palaeoecologists often utilise non-human primates as models to contribute to our understanding of extinct hominoids (Moore 1996). The more that we understand about comparative primate biology, the more we will be able to understand about ourselves.

One of the main objectives of primate socio-biology is to generate a greater understanding of the variations observed in social behaviour and how they tie in with biological function. One of the most frequently observed social behaviours in primates is allogrooming, (one individual grooms another). Despite other activities such as feeding, sleeping, mating, playing and autogrooming (self grooming) individuals are often seen grooming other individuals, therefore indicating willingness to invest time and effort in relationships with other group members (Walters and Seyfarth 1987; Dunbar 1991, 1992; Hemelrijk and Lutjein 1998), which may be essential for the development of cooperative relationships (Van Hoof and Van Schaik 1994) and used to establish and reinforce social relationships between group members (Walters and Seyfarth 1987).

Grooming helps to remove ectoparasites and other debris from an individual's coat (Poirier 1970; Tanaka and Takefushi 1993), whilst, also stimulating the productions of endorphins (Keverne et al. 1989). Seyfarth (1980) suggested that allogrooming occurs more frequently than is necessary for hygienic purposes alone and therefore, probably has social significance. Support for this suggestion of social reinforcement through grooming interactions between group members comes from demonstrations of grooming reciprocity (chimpanzees: Hemelrijk and Ek 1991; Watts 2000; vervet monkeys: Hemelrijk 1990), preference of allies to groom each other (tufted capuchins *Cebus apella:* Di Bitetti 1997), gaining of social acceptance by group members (Poirier 1970), tolerance at feeding sites (Barton and Whiten 1993), support during conflicts (Seyfarth 1976; Hemelrijk 1990), mating opportunities (Weingrill 2000), access to new born infants (Seyfarth 1976; Altmann 1980; Henzi and Barrett 2002) and sharing of food (De Waal 1989, 1997).

Constraints on an individual's grooming time due to other demands of daily activities, results in individuals having to choose whether to give small amounts of grooming to all potential partners or groom with fewer more important partners for the amount of time needed to maintain relationships (Dunbar 1991). Important partners are those that could offer some form of benefit in exchange for being groomed and these benefits should influence choice of grooming partners. Benefits could be influenced by the age and sex of individuals, with adults being able to offer more benefits than younger age classes.

Chimpanzees have a fission–fusion social structure (Sugiyama 1968) where group members do not move around as a single unit such as in baboons and vervet monkeys, but rather have a social grouping system which involves temporary units coming together and separating as the need arises. This reduces opportunities for individuals to groom others and therefore, based on time and association constraints alone grooming is expected to be unevenly distributed among group members.

Previous studies on chimpanzees indicate that males are philopatric and are usually more gregarious than females (Nishida 1968; Wrangham and Smuts 1980; Goodall 1986; Pepper et al. 1999). Males also spend more time grooming other males than other sexes (Goodall 1968; Nishida 1968; Simpson 1973; Wrangham 1986; Nishida and Hiraiwa-Hasegawa 1987; Watts 2000). Males are thought to utilise grooming to establish and reinforce alliances with each other, which in turn influences their dominance status as well as the their ability to gain access to females for mating opportunities (De Waal 1982; Goodall 1986; Nishida and Hosaka 1996).

Most studies have indicated that adult females spend little time in social groups (Nishida 1979; Ghiglieri 1985; Goodall 1986) and therefore have fewer opportunities for grooming other individuals. Female-female grooming relationships have generally been reported to be uncommon (De Waal 1986; Goodall 1986; Wrangham et al. 1994) but this could be due to females being less easy to habituate and studies having concentrated mainly on male social relationships.

Female chimpanzees display sexual receptiveness through the swelling of their anogenital region during oestrus periods (Wallis 1992). It has been found that grooming activity between males and oestrous females increases in captive groups (Hemelrijk et al. 1992), and although Goodall (1986) observed similar behaviour in free-living chimpanzees, it has not been empirically investigated. Adults are regarded as the reproductive individuals within a group, but subadult females also display anogenital swellings, even though they are usually infertile for approximately their first 19 menstrual cycles (Tutin 1980; Boesch and Boesch-Achermann 2000). The effect of these swellings on grooming relationships between different age-sex classes together with the possibility that males increase their grooming of females in oestrous as a means to increase their chances of copulations with females, it would be expected that there would be a correlation between the amount of grooming that males give to females and the number of copulations that they receive. It would also be expected that any correlations that do exist would be stronger between adults than subadults.

Over the years many publications have arisen from studies of primates in both free-living and captive environments. What have also surfaced with these publications are the debates as to which sampling methods for the purpose of behavioural studies produces the most reliable results. Scan and focal animal sampling methods have been the most widely recommended methods, whilst *ad libitum* methods have been criticised as being biased towards behaviour types that are most likely to attract the observer (Altmann 1974). A further complication is that when comparing results from different populations it is not always clear whether the results are true reflections of behaviour or due to outcomes of using different sampling methods. By comparing the results of different sampling methods from the same study group over the same time period would help to justify whether different sampling methods do in fact produce similar results.

Given the background above, the objective of the present study is to investigate the grooming behaviour of a group of free-living chimpanzee population in the Budongo Forest, Uganda and by doing so increase the knowledge base that exists for the social dynamics of a potentially endangered species (Oates 2006).

1.1 Relevance of study

With the rate at which species are being exterminated it is imperative that we obtain as much information about these threatened species as possible so that efforts can be made based on our understanding to conserve habitats and with them, populations that are true representations of what they should be.

This study is part of a larger, long term study of the Budongo Forest in Uganda. The project was initially undertaken to study the dynamics of the forest and its wildlife. It was to explore the effects of the logging that had been conducted for over 60 years and its impact on the forest and especially the chimpanzees. By studying one of the few remaining free-living populations of chimpanzees (referred to as the Sonso group in this study) we will be able to add to the existing information on the social dynamics of chimpanzees with special reference to grooming and how various factors influences its distributions. By doing this the findings can then be used as comparative knowledge when investigating social behaviour of other chimpanzee populations. With chimpanzees sharing 99% genetic similarities to ourselves and having shared a common ancestor with modern day humans between 4 and 6 million years ago, by understanding the socio-biology of chimpanzees we may be able to gain a clearer understanding of our own evolutionary behaviour.

1.2 Key Questions and dissertation outline

The following key questions (and their associated parts of this dissertation) will be addressed in the present study

Key Question I: Is there variation in grooming behaviour across chimpanzee age-sex classes?

The first part of this study (Chapter 2) is directed towards obtaining a clearer understanding of how different age-sex classes of the Sonso chimpanzees distribute their grooming to other group members in terms of: total grooming time, allocation of unidirectional and mutual grooming bouts, numbers of grooming partners and reciprocation of unidirectional grooming?

Key Question II: How do sexual swellings influence grooming behaviour between males and females of different age classes within the Sonso group of chimpanzees?

Chapter 3 investigates whether sexual swellings displayed by females during oestrous periods influences grooming behaviour of males and females. It further investigates if age class may be a contributing factor to any differences observed.

Key Question III: How does the grooming of sexually receptive females by males influence copulations between males and females of different age classes?

The idea that grooming may be a strategy used by chimpanzees in exchange for access to copulations is investigated in chapter 4. Looking at whether there is a correlation between grooming and copulations across different age classes is also investigated

Key Question IV: Do scan-focal and *ad libitum* sampling methods generate different results when used to collect grooming behaviour?

Chapter 5 compares different sampling methods used to record behavioural data. Scan-focal and *ad libitum* sampling methods were used to collect grooming data for independent studies over the same period. The question that is addressed in this chapter is whether the results of these different sampling methods are comparable or are there significant differences found?

The final chapter (chapter 6) provides a synthesis and general discussion of the major findings of the study.

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-Chapter 2-

Grooming distributions across age-sex classes

Abstract

Grooming in primates is a social interaction used to establish and reinforce social relationships between group members. Chimpanzees have a fission–fusion social organisation where group members do not move around as a single unit, but rather have a social grouping system which involves temporary units coming together and separating as the need arises. This reduces opportunities for individuals to groom others and therefore, based on time and association constraints alone grooming is expected to be unevenly distributed among group members. Five and a half years of grooming data were examined from a group of free-living chimpanzees (*Pan troglodytes*) in the Budongo Forest, Uganda, to investigate how grooming is distributed across different age-sex classes. Mutual grooming bouts accounted for 28.6% whilst unidirectional bouts accounted for 71.4% of grooming interactions within the group. Wilcoxon signed rank tests found that with the exception of grooming interactions between adult and infant males and between subadult females and juvenile males, most grooming interactions that took place were unidirectional. Kruskal Wallace ANOVA revealed that all age-sex classes with the exception of infant females distributed their grooming significantly unevenly across the group. Adult males, subadult males and adult females had grooming interactions mostly with adult males, whilst juveniles and infants groomed mainly with their mothers. The number of grooming partners varied between age-sex classes, ranging from one partner for infants to a mean of 21.82 for adult males. Except for grooming interactions between adult males and juvenile females and between subadult males, individuals were found to more likely groom those individuals from whom they received grooming. Overall, grooming patterns found among the Sonso Chimpanzees are comparable to those observed in other free-living populations, and variations could be attributed to variables including resource base, population numbers and differences in age-sex class composition.

Keywords: Chimpanzees, Pan troglodytes, grooming, Budongo Forest

Running Title: Grooming distributions of free-living chimpanzees of the Budongo Forest, Uganda

2.1 Introduction

In many species allogrooming (where one individual grooms another) is a social interaction used to establish and reinforce social relationships between group members (Walters and Seyfarth 1987). Allocating time to allogrooming instead of other activities such as feeding and autogrooming (self grooming) indicates an individual’s willingness to invest in reinforcing relationships with others (Walters and Seyfarth 1987; Dunbar 1992; Hemelrijk and Lutjein 1998), which may be essential for the development of cooperative relationships (Van Hoof and Van Schaik 1994). Grooming helps to maintain hair free of ectoparasites and other debris (Poirier 1970; Tanaka and Takefushi 1993) whilst also stimulating the production of endorphins (Keverne et al. 1989) and has been found to lower heart rate in horses (Feh and De Mazieres 1993). Seyfarth (1980) suggested that more grooming is performed than is necessary for hygienic purposes alone and, therefore, probably has social significance, which is supported by demonstrations of: grooming reciprocity in chimpanzees (Hemelrijk and Ek 1991; Watts 2000), vervet monkeys (Hemelrijk 1990) and Impala *Aepyceros melampus* (Hart and Hart 1992); preference of allies to groom each other in tufted capuchins *(*Di Bitetti 1997); gaining of social acceptance by group members (Poirier 1970); tolerance at feeding sites (Barton and Whiten 1993); support during conflicts (Seyfarth 1976; Hemelrijk 1990); mating opportunities (Weingrill 2000); sharing of food between allogroomers (De Waal 1989, 1997) and indirect benefits such as access to new born infants (Seyfarth 1976; Altmann 1980; Henzi and Barrett 2002).

Constraints on an individual's grooming time due to the necessity of other activities results in individuals having to choose whether to give small amounts of grooming to all potential partners or groom with fewer but more important partners for the amount of time needed to maintain relationships (Dunbar 1991). The choice of partners would be influenced by the benefits that individuals could offer in exchange for being groomed. These benefits may be influenced by the age and sex of individuals, with adult age classes being able to offer more benefits than younger age classes and males being able to offer different benefits than females, for example adult males may offer females protection from harassment by younger males, whereas adult females will be able to offer males reproductive opportunities that subadult females cannot. Rhesus monkeys groom their close genetic relatives more than unrelated members of a group (Sade 1965), therefore suggesting that if there are direct benefits to grooming like removal of external parasites, then individuals should have more grooming interactions with relatives, but if social relationships and alliance formation are more important grooming drivers, grooming interactions should be dominated by intergenetic interactions. This should not under represent the strength of grooming with kin, as there is evidence to suggest that male chimpanzees in particular do not show a strong preference for association and coalition formation with kin (Mitani et al. 2002). This may be due to the slow reproductive rate and high infant mortality of chimpanzees, which results in there seldom being maternal siblings growing up together (Mitani et al. 2002). Therefore, it may be that if kin was present there would be a preference for grooming between them, but in the absence of close kin, males may then choose alternative grooming partners.

Chimpanzees have a fission–fusion social structure (Sugiyama 1968) where group members do not move around as a single unit such as in baboons and vervet monkeys, but rather have a social grouping system which involves temporary units coming together and separating as the need arises. This reduces opportunities for individuals to groom others and therefore, based on time and association constraints alone grooming is expected to be unevenly distributed among group members. Studies on chimpanzee grooming have concentrated largely on that of adult males (Goodall 1968; Nishida 1968; Simpson 1973; Wrangham 1986; Nishida and Hiraiwa-Hasegawa 1987; Watts 2000; Arnold and Whiten 2003) and to a lesser extent on adult females (Hemelrijk and Lutejin 1998; Fawcett 2000; Stumpf and Boesch 2005). Previous studies indicate that males are philopatric and are usually more gregarious than females (Nishida 1968; Wrangham and Smuts 1980; Goodall 1986; Wrangham et al. 1992; Pepper et al. 1999). Males also spend more time grooming other males than other sexes (Goodall 1968; Nishida 1968; Simpson 1973; Wrangham 1986; Nishida and Hiraiwa-Hasegawa 1987; Watts 2000). Males are thought to utilise grooming to establish and reinforce alliances with each other, which in turn influence their dominance status as well as the their ability to gain access to females for mating opportunities (De Waal 1982; Goodall 1986; Nishida and Hosaka 1996). Most studies have indicated that adult females spend little time in social groups (Nishida 1979; Ghiglieri 1985; Goodall 1986; Wrangham et al. 1992) and therefore have fewer opportunities for grooming other individuals. Female-female grooming relationships have generally been reported to be uncommon (De Waal 1986; Goodall 1986; Wrangham et al. 1994) but this could be due to females being less easy to habituate and therefore under represented during data collections. Juveniles and infants have been largely neglected in studies of grooming, probably due to a combination of factors: low numbers of infants and juveniles during proposed study periods, shyness of adult females with young infants, inaccessibility to nests for observations of youngsters, lack of frequent grooming interactions by juveniles and infants when visible.

Behavioural studies are increasingly indicating that chimpanzee social behaviour is variable between populations due to differences in population demographics and the ecology of areas. The aim of this chapter is to describe how grooming is distributed across and within age-sex classes found in a group of free-living chimpanzees within the Budongo Forest, Uganda. The advantage of this study is that it uses data that were collected over a continuous five and a half year period using *ad libitum* sampling methods. Therefore, by not focusing on specific age-sex classes I hope to obtain a broader description of grooming that has previously not been possible for free-living chimpanzees.

This study aims to specifically investigate variation in grooming behaviour across chimpanzee age-sex classes in terms of: (1) Total grooming time generated by the group; (2) allocation of unidirectional and mutual grooming bout frequency; (3) grooming time directed from each age-sex class to all others; (4) numbers of grooming partners per individual; and (5) reciprocity of unidirectional grooming.

2.2 Study area and methods

2.2.1 Study area

The Budongo Forest Reserve is made up of 793 km² of moist, semi-deciduous forest and grassland, and is situated at a mean altitude of 1100m on the edge of the western Rift Valley in western Uganda (Eggeling 1947; Plumptre 1996). The average rainfall of the region is approximately 1400 mm per year with a dry season between December and February. Daily mean temperatures range between 14ºC and 28ºC (Eggeling 1947).

The Sonso region (1º44' N, 31º33 E'), in which this study was carried out, lies well within the forest and is named after the river flowing through the area. Although most of the forest was selectively logged in the past, the logging industry halted operations within the study area between 1947 and 1952 (Plumptre 1996). This, together with the forest dynamics, has resulted in the Sonso region of the forest being made up of various forest types including mixed forest, colonizing forest, swamp forest and ironwood *Cynometra* *alexandrii* forest (Eggeling 1947; Reynolds 1992). The study site was established in 1990 and is maintained by the Budongo Forest Project (Reynolds 1992; Plumptre et al. 1997). A system of trails covering an area of approximately 31km² aids travel through the study area, allowing researchers relatively easy access to the forest.

2.2.2 Study group

Between 1990 and 1994 with the effort of Nick Newton-Fisher and field assistants Geresomu Muhumuza and Zephyr T. Kiwede the chimpanzees were followed and eventually allowed observers to follow them at close quarters throughout the day. Individual chimpanzees of the Sonso group have subsequently been habituated, sexed and identified, and have all been given a two-letter identification code (Appendix A). The chimpanzees spend most of their time within an area of about 7km² with each individual having its own 'core' area (Newton-Fisher 2000).

During the study, the Sonso chimpanzee group consisted of between 26 and 54 individuals (Table 2.1). Eleven of the chimpanzees have injured limbs as a result of being caught in snares, set by the local people to catch duiker (*Cephalophus spp)* and forest pigs (*Potamochoerus porcus)* (Waller and Reynolds 2001). Four other groups of chimpanzees are known to occur within the forest, two (Busingiro and Kaniyo-Pabidi groups) of which are currently being habituated for tourism purposes. The other two groups (The Nature Reserve and Waisoke groups) have not yet been habituated or studied but both share boundaries with the study group. The following abbreviations will be used throughout the remainder of the chapter to refer to different age-sex classes: AM – adult males, AF - adult females, SM – subadult males, SF – subadult females, JM – juvenile males, JF – juvenile females, IM – infant males and IF – infant females.

Table 2.1 The number of individuals within each age-sex class from which grooming interactions were recorded during the five and a half year study period.

Age-sex class	1995/96	1996/97	1997/98	1998/99	1999/2000	2000/2001
Adult males (AM)	12	13	11	12	10	10
Adult females (AF)	10	12	10	15	13	11
Subadult males (SM)	1	2	4	4	3	1
Subadult females (SF)	5	5	5	3	3	2
Juvenile males (JM)	4	4	3	4	4	1
Juvenile females (JF)	0	4	6	7	5	0
Infant males (IM)	4	5	5	4	1	0
Infant females (IF)	5	3	2	5	1	1
Total	**41**	**48**	**46**	**54**	**40**	**26**

2.2.3 Data collection

Data were collected continuously between September 1995 and April 2001 as part of a long-term study on the behaviour and ecology of the Sonso chimpanzees. Eleven field assistants (a mean of four at any given time) employed by the Budongo Forest Project conducted sampling, daily (weather permitting) between 07:30 and 13:00 and then again between 14:00 and 16:30 on an *ad libitum* basis (Altmann 1974) whilst following the chimpanzees. Each sample recorded the identities of individuals present, interactions between individuals (grooming, playing, aggression, copulations etc) initiators and terminators of interactions, duration of interactions (recorded to nearest minute) and female anogenital swellings.

2.2.4 Analysis

Individuals were placed into age-sex categories as determined by the Budongo Forest Project. Individuals were classified as infants if they were under two years of age and either continuously clinged to their mother or moved very short distances away, whereas juveniles were those individuals between three and six years of age, characterized by being one quarter of adult size and carried on their mothers back. Subadults were between seven and ten years of age, between half and three quarters of adult size and showed increasing independency from their mothers. Adults were older than ten years and fully covered with black hair, and face usually dark. For further information on the criteria used for age determination of the chimpanzees, see Reynolds and Reynolds (1965).

A total of 4819 grooming interactions making up 1301.4 hours of grooming bouts were extracted from the data set, sorted into dyads (grooming interaction involving two individuals) and grouped into different age-sex class combinations. From this the percentage of grooming time (minutes) that each age-sex class combination contributed to the total grooming time of the study group was calculated as well as the percentage of mutual and unidirectional bouts that occurred between different dyads. For each individual the percentage of their grooming time (mutual, unidirectional given and received) allocated to different age-sex classes was also calculated together with the number of grooming partners between age-sex classes. Since many of the individuals were adults at the commencement of the data collection and no genetic studies had been conducted on this group at the time of the study, the kinship relationships of these individuals is largely unknown and therefore for the purpose of this study, only grooming bouts involving known mother-offspring and sibling dyads were classed as kin. All other dyads were thus regarded as non-kin.

Grooming duration varied across individuals (some individuals groomed more than others) and, due to the fission-fusion social system of chimpanzees, not all individuals were sampled equally. This should however, not affect how grooming is distributed amongst different age-sex classes as there should be no systematic sampling bias. Samples including juveniles and infants were quite small, and therefore grooming patterns of these age classes may have been an under representation of their grooming behaviour. Due to the time span over which the data were collected, some individuals occurred in more than one age class. These individuals therefore represented more than one age-sex class and may appear to have increased the group size. The study was, however, investigating grooming distributions of age-sex classes and not individuals and therefore might not have affected results reflecting grooming distributions of the group. Wilcoxon signed rank tests were used to establish whether the percentages of mutual and unidirectional bouts were significantly different within age-sex class combinations.

Kruskal Wallace ANOVA was used to establish whether different age-sex classes distributed their grooming time unevenly across the group. The post hoc test ‘comparison of means’ was run to indicate where any significant differences were. Unidirectional bouts were used to determine whether grooming was reciprocated at the group level. Mutual bouts were excluded because the difference in grooming given and received by individuals engaged in mutual grooming bouts will equal zero and therefore reflect absolute reciprocity. Due to any given dyad being recorded more than once, samples become statistically dependant. Sampling distributions for grooming interactions are not specifiable *a priori* (Schnell et al. 1985) and therefore matrix permutation methods that avoid these problems by using observed values to generate a sampling distribution against which to assess the significance of a sample correlation statistic were used (Hemelrijk 1990). Grooming reciprocity (grooming exchanged for grooming) is said to occur if individuals give more grooming to those from which they receive more grooming (Hemelrijk 1990). I used Hemelrijk’s (1990) MATRIXTESTER matrix permutation program as it takes into account individual variation in the tendency to direct a particular behaviour, e.g. grooming to others and calculates several association indices between an actor-receiver grooming matrix and its inverse to analyse the degree of reciprocity. The program randomly permutes columns and rows to generate a sampling distribution for the test statistics derived from the original data matrix. The Kr test statistic (a multivariate version of Kendall's S statistic corrected for individual variation and sample size) to measure relative reciprocity (Hemelrijk 1990) and a Tau$_{kr}$ value, which corrects the Kr value for sample size and ties is also generated. MATRIXTESTER further calculates a multivariate Mantel's Z coefficient and a multivariate R statistic to 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 in conjunction with the Z test to make up for any deficiencies of the Z test. All tests using this programme were carried out using 2000 permutations (Daniel 1978).

2.3 Results

2.3.1 General grooming distributions between age-sex classes

The 1301.4 hours of grooming interactions analysed shows that with the exception of grooming between AM (30.7%) and between AM and AF (11.70%), the percentage of overall grooming time that was contributed by each age-sex class was quite low (between 1.4 and 7.1%) (Figure 2.1).

2.3.2 Mutual versus unidirectional grooming bouts

Mutual grooming bouts accounted for 28.6% whilst unidirectional bouts accounted for 71.4% of grooming interactions within the group. With the exception of grooming interactions between AM - IM and between SF - JM, most grooming interactions that took place between age-sex classes were unidirectional, and in most cases made up a significantly higher percentage of grooming bouts (Table 2.2).

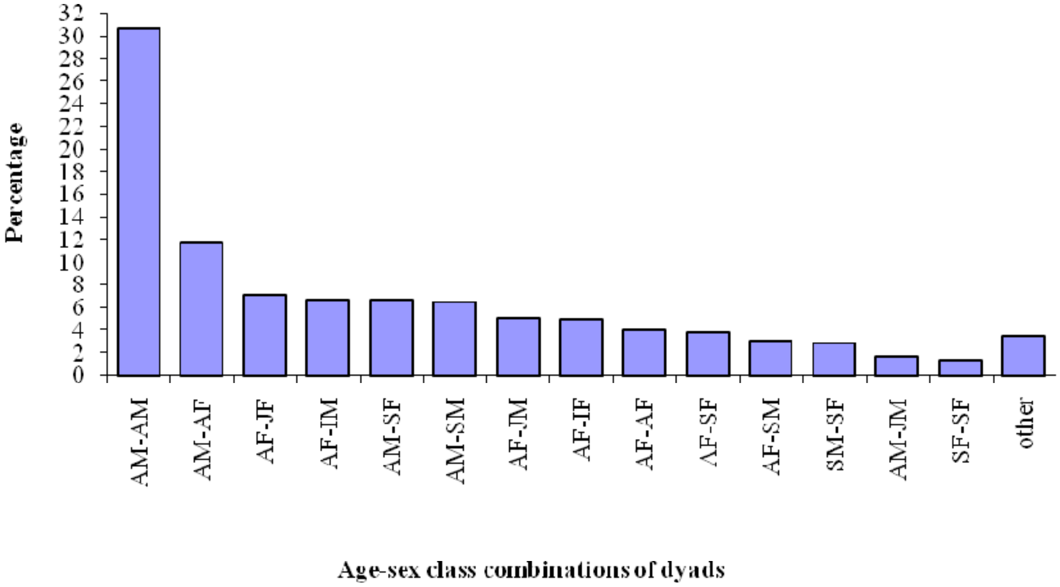

Figure 2.1 The percentage of the study group's total grooming time (1301.4 hours) that different age-sex class combinations contributed. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, other = sum of percentages of grooming between age-sex classes that were < 1%. N=17 AM, 17 AF, 6 SM, 7 SF, 11 JM, 7 JF, 7 IM and 9 IF.

Table 2.2 Comparison between the percentages of mutual and unidirectional grooming bouts between age-sex class combinations using Wilcoxon signed rank test. Mean values (± SE) are given. (N=4819 bouts). A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female

Age-sex class combination	No. of grooming dyads	Mutual (%)	Unidirectional (%)	T+	p-value
AF - IM	6	9.33 (± 4.29)	90.17 (± 4.35)	0	0.031
AF - JF	22	14.46 (± 3.69)	85.32 (± 3.73)	0	0.0001
SM - SM	5	11.60 (± 7.22)	88.20 (± 7.36)	0	0.063
AM - JM	21	13.48 (± 5.67)	86.48 (± 5.68)	11.5	0.0003
AM - SM	52	20.54 (± 3.94)	79.21 (± 3.95)	14.9	0.0001
AF - AF	26	20.86 (± 3.83)	78.73 (± 3.90)	9	0.0001
AF - IF	8	14.63 (± 12.38)	85.25 (± 12.33)	5	0.078
AF - AM	96	24.52 (± 3.11)	75.21 (± 3.11)	484	0.0001
AF - SF	21	23.62 (± 4.39)	75.86 (± 4.46)	6.5	0.0001
AF - SM	26	22.69 (± 6.04)	77.04 (± 6.07)	46	0.008
AM - AM	98	26.62 (± 2.82)	72.94 (± 2.83)	633	0.0001
AM - SF	49	26.45 (± 3.06)	73.04 (± 3.08)	64.5	0.0001
AM - JF	10	20.00 (± 13.33)	80.00 (± 13.33)	11	0.106
JF - JF	6	29.67 (± 4.94)	69.67 (± 4.83)	0	0.062
SF - JF	7	21.43 (± 14.00)	78.29 (± 14.02)	5	0.156
SF - SM	28	31.68 (± 5.48)	67.96 (± 5.50)	61	0.003
SM - JF	8	33.75 (± 13.88)	66.25 (± 13.88)	5	0.312
AF – JM	13	38.62 (± 10.61)	60.92 (± 10.58)	30	0.305
SF - SF	10	38.40 (± 11.06)	61.20 (± 11.09)	17	0.322
SM – IM	4	31.25 (± 23.66)	68.75 (± 23.66)	3	0.625
SF – JM	10	59.10 (± 11.81)	40.80 (± 11.82)	18	0.578
AM – IM	5	63.20 (± 22.68)	36.60 (± 22.57)	10.5	0.813

2.3.3 Grooming distributions of different age-sex classes

All age-sex classes except for IF (p = 0.06), distributed their grooming significantly unevenly across the group (p = 0.0001). Due to sample sizes being small in relation to the number of variables, post hoc tests were not always sensitive enough at the 95% confidence level to indicate where the significant differences were (Daniel 1978) and therefore to standardise methods, no post hoc results were used. It can in most cases, however, be clearly seen from the graphs where the significant differences occur.

a) Adult Males (Figure 2.2)

Adult males (N=17) had grooming interactions mostly with other AM [67.78% (mutual – 21.56 ± 3.11%, give – 27.33 ± 3.31%, receive – 18.89 ± 2.50%)]. A higher percentage of grooming was given to AM (27.33 ±3.31 %) and AF (6.98 ± 2.40%) in the form of unidirectional bouts, but more grooming was received from them during mutual bouts. AM received more grooming from SM (3.86% ± 1.03) than from AF (2.01± 0.59%), SF (1.09 ± 0.29%) or JM (1.00 ± 0.56%). AM allocated less than 3.5% of their total grooming time to juveniles and infants, with less than 1% of grooming received from JF and IM and no grooming from IF. AM engaged in similar amounts of mutual grooming with SM (2.43 ± 0.83%) and SF (3.33 ± 1.08%), and gave similar amounts of unidirectional grooming to them both (1.98 ± 0.63% and 1.09 ± 0.29% respectively).

b) Adult females (Figure 2.3)

Adult females (N=17) allocated most of their grooming time to AM [32.64% (mutual – 10.12 ± 2.78%, give – 8.11 ± 2.64 %, receive – 14.41 ± 4.59 %)]. Adult females received more grooming from AM (14.41 ± 4.59%) and SM (5.18 ± 4.54%) than what they gave them (8.11 ± 2.64% and 1.07 ± 0.5% respectively). Adult females prefer being involved in grooming interactions with unrelated (14.67%) rather than related AF (1.33%), but there was only one grooming dyad recorded that involved known kinship between AF and therefore the difference may be due to small sample size rather than a real preference. With the exception of grooming received by SM, grooming with subadults is similarly distributed. Not surprisingly, AF appear to allocate more grooming time to their own juveniles and infants rather than unrelated individuals.

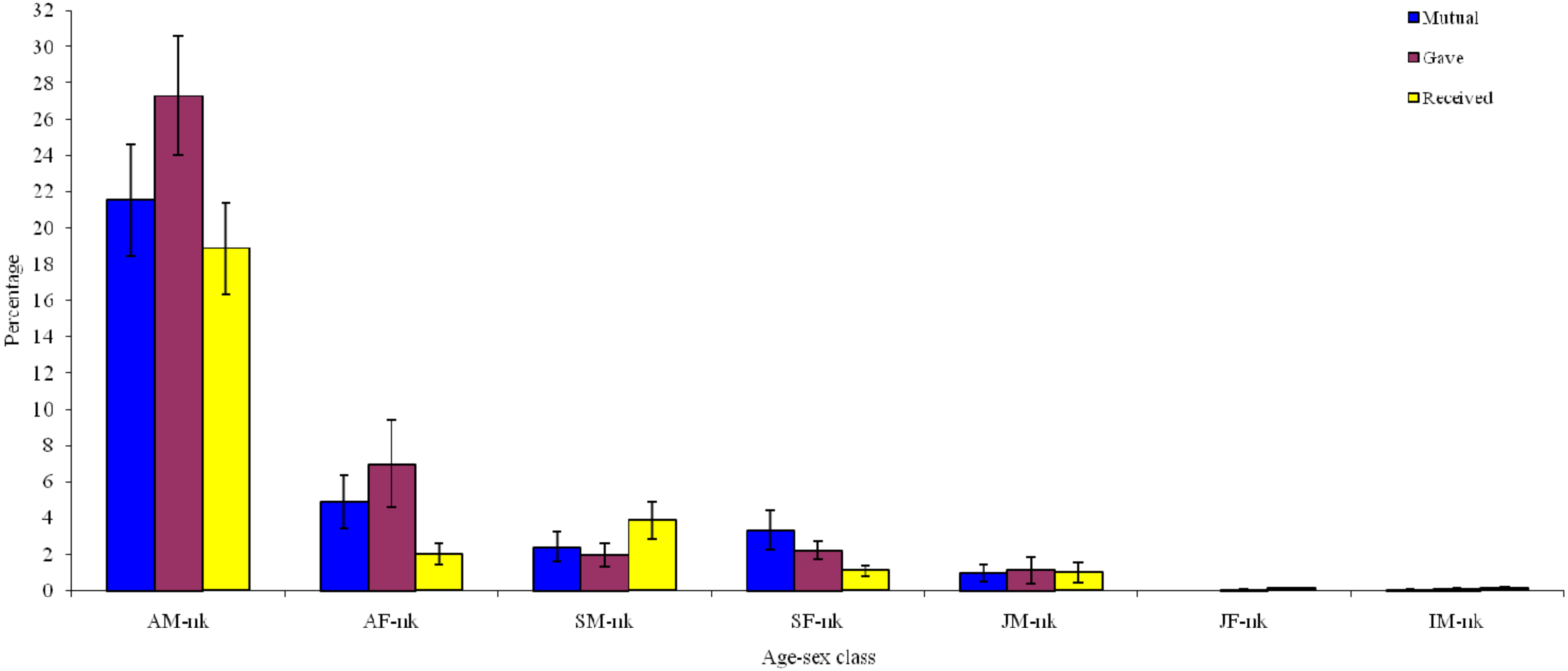

Figure 2.2 The percentage of adult male's total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, nk-nonkin. Column height gives mean across all adult males (N=17); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by adult males to different age-sex classes (unidirectional bouts) and received = grooming received by adult males from other age-sex classes (unidirectional bouts).

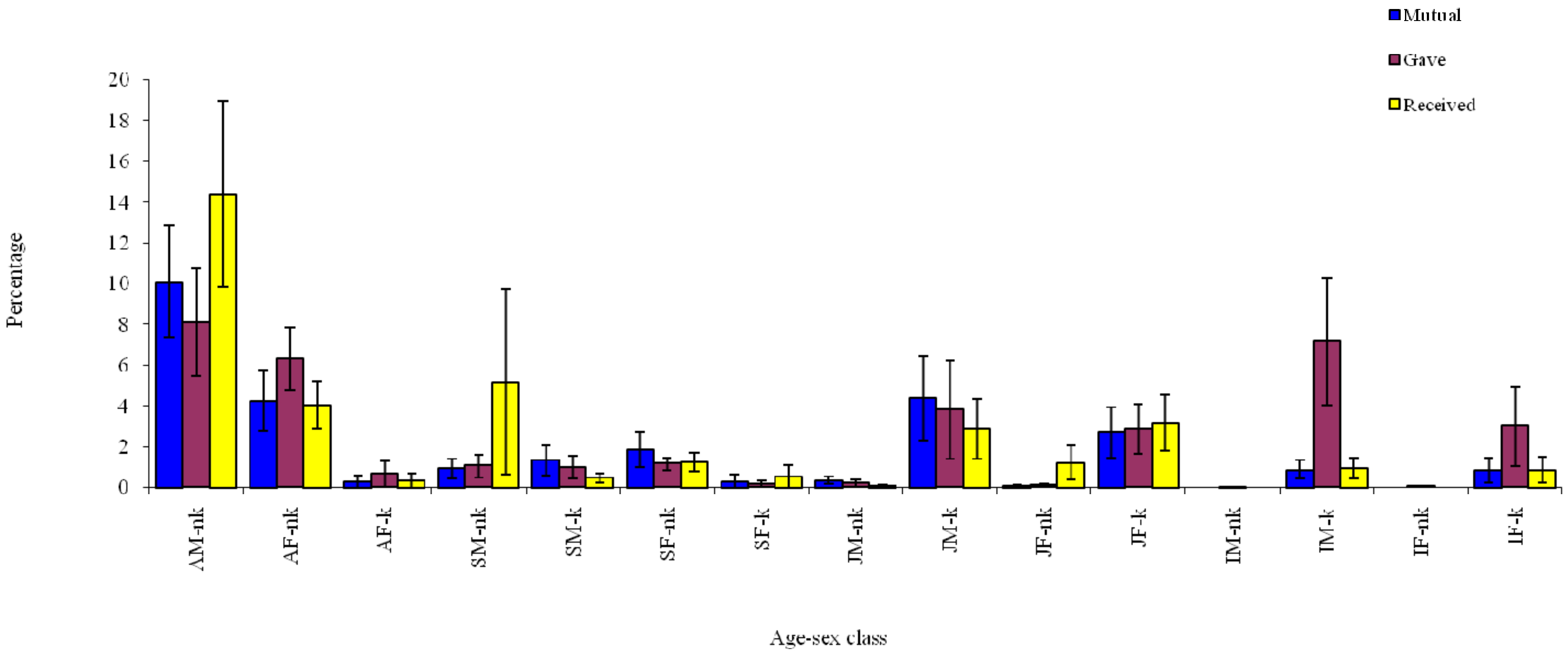

Figure 2.3 The percentage of adult female's total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all adult females (N=17); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by adult females to different age-sex classes (unidirectional bouts) and received = grooming received by adult females from other age-sex classes (unidirectional bouts).

c) Subadult males (Figure 2.4)

Subadult males (N=6) allocated most of their grooming time to AM [46.06% (mutual – 11.02 ± 3.39%, give – 26 ± 4.58 %, receive – 9.05 ± 3.90%)]. Grooming interactions with related (mothers) and unrelated AF were similar, but with slightly more grooming being received from mothers (3.70 ± 1.71) than from other AF (2.15 ± 1.46%). Subadult males seem to have more grooming interactions with SF than other SM (24.51% and 2.5 % respectively). Except for unrelated JM which received 3.05 ± 2.18% of SM grooming time, very few or no grooming interactions were recorded with juveniles and infants.

d) Subadult females (Figure 2.5)

Although the graph shows that SF (N=7) gave most grooming to AM (19.02 ± 13.55%), one individual allocated 100% of her grooming to AM therefore increasing the mean. When this female was removed from the data set the mean changed to 5.53 ± 1.49%, which would then indicate that SF received (11.32 ± 3.04%) more grooming from AM than they gave them. Taking this into account, SF would then give most grooming to unrelated SM (8.33 ± 5.75%). There seems to be a tendency for SF to engage in grooming interactions with unrelated AF rather than their mothers. Very little or no grooming took place with juvenile and infants.

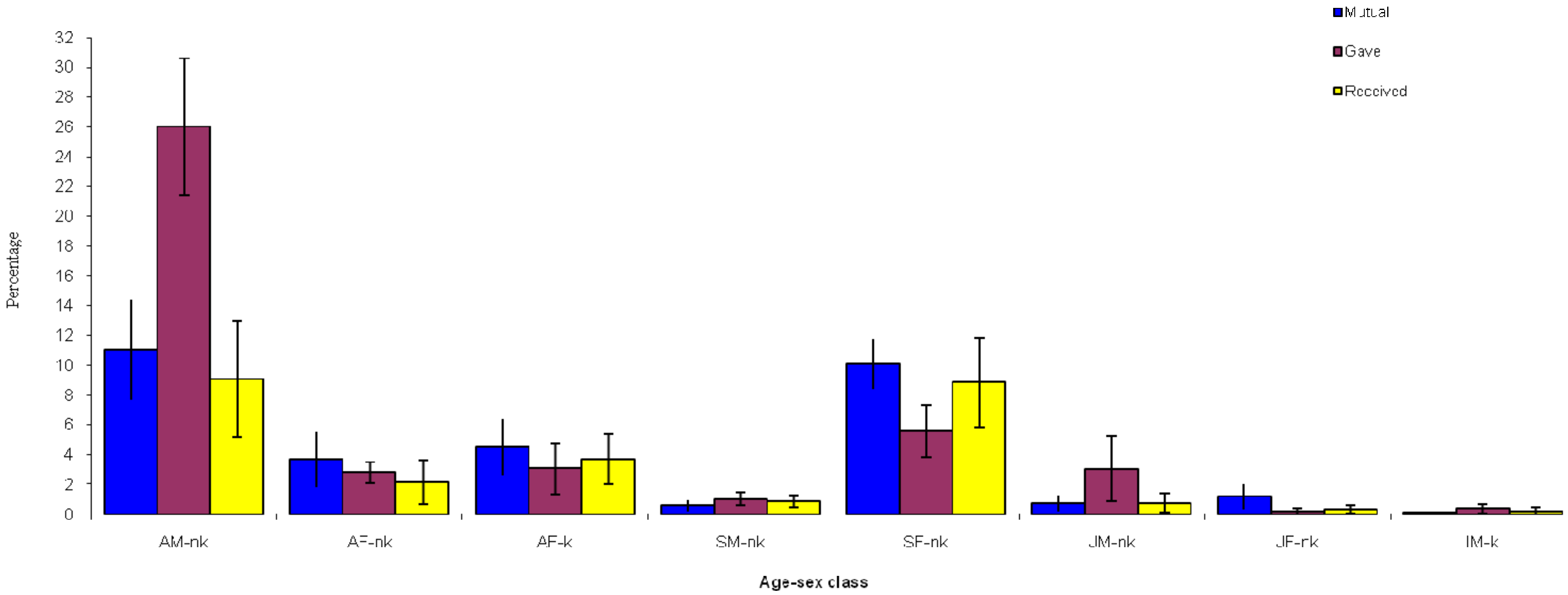

Figure 2.4 The percentage of subadult male's total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all subadult males (N=6); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by subadult males to different age-sex classes (unidirectional bouts) and received = grooming received by subadult males from other age-sex classes (unidirectional bouts).

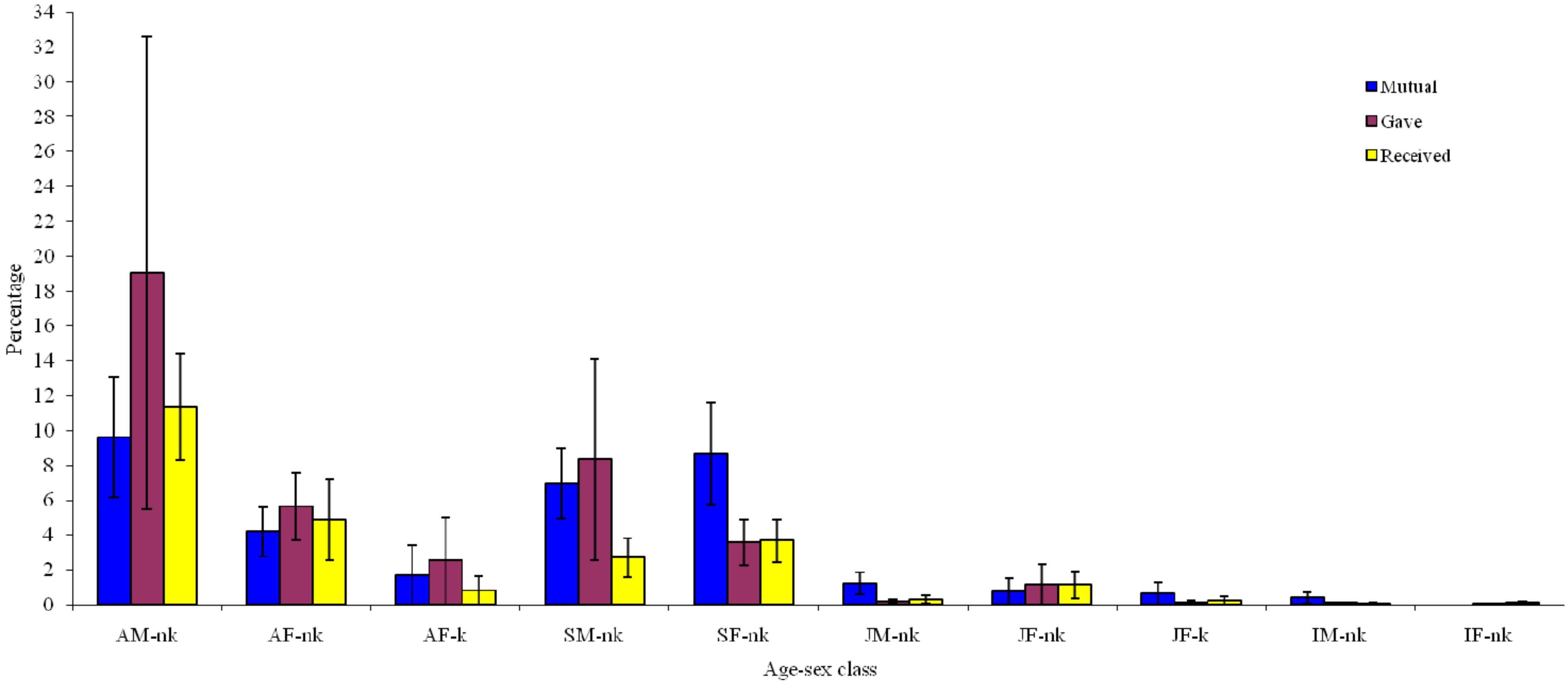

Figure 2.5 The percentage of subadult female's total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all subadult females (N=7); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by subadult females to different age-sex classes (unidirectional bouts) and received = grooming received by subadult females from other age-sex classes (unidirectional bouts).

e) Juvenile males (Figure 2.6)

Juvenile males (N = 11) received most of their grooming from their mothers (15.30 ± 5.385 %) whilst grooming received from other age-sex classes was low (< than 4%). Within unidirectional grooming bouts, JM groom AM (17.84 ± 5.65%) more than their mothers (14.20 ± 4.18%), but if mutual grooming bouts are taken into account, mothers receive more grooming. No grooming was recorded with related juveniles or infants simply because there were none available to groom with.

f) Juvenile females (Figure 2.7)

Most grooming involving JF (N = 7) was with their mothers (total - 58.42 %, mutual - 16.37 ± 6.58%, gave - 23.66 ± 9.19% and received - 18.39 ± 5.8). There were few grooming interactions recorded with other age sex classes. The low percentage of grooming between siblings was once again due to the absence of siblings.

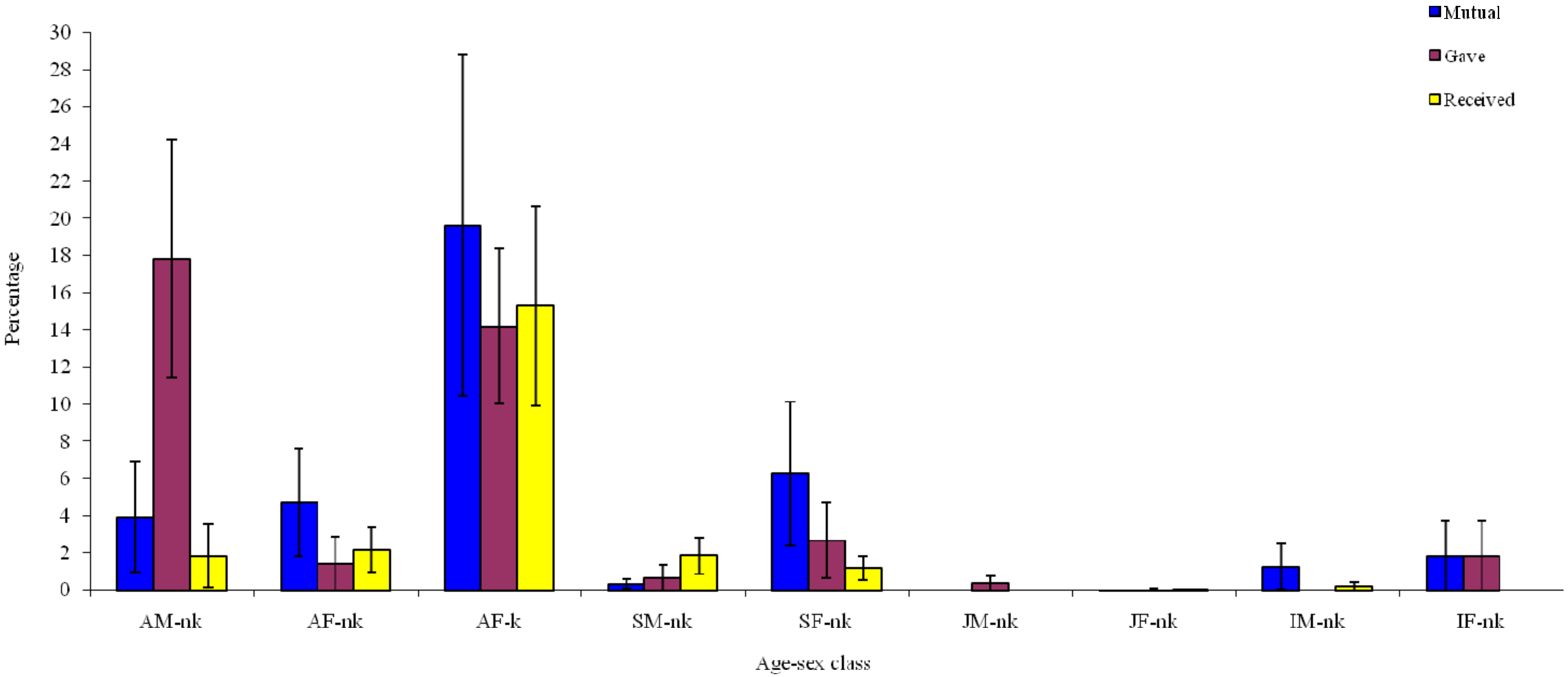

Figure 2.6 The percentage of juvenile male's total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all juvenile males (N=11); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by juvenile males to different age-sex classes (unidirectional bouts) and received = grooming received by juvenile males from other age-sex classes (unidirectional bouts).

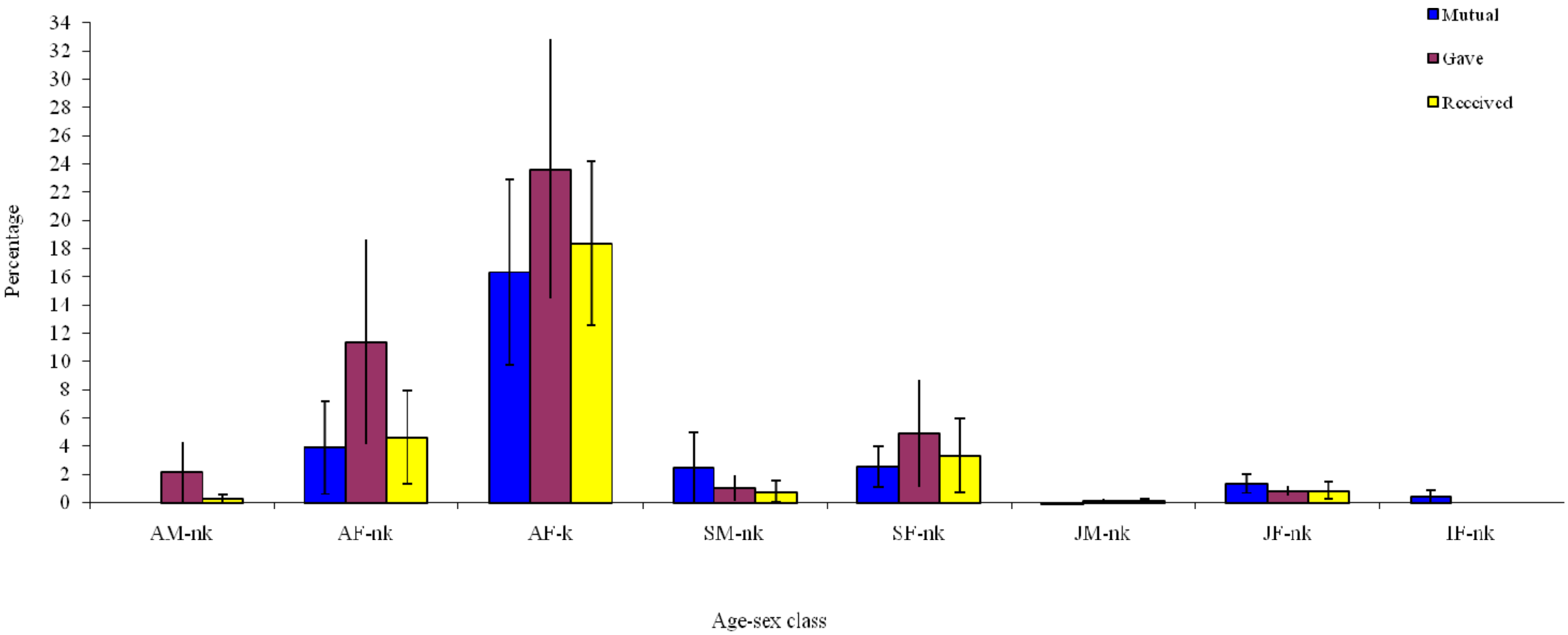

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Figure 2.7 The percentage of juvenile female's total grooming time distributed to different age-sex classes A-adult, S-subadult, J-juvenile, I-infant, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all juveniles females (N=7); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by juveniles females to different age-sex classes (unidirectional bouts) and received = grooming received by juveniles females from other age-sex classes (unidirectional bouts).

g) Infant males (Figure 2.8) and Infant females (Figure 2.9)

Infant males gave little grooming to most classes, with the majority being directed to or from their mothers (Total -70.26%, Mutual – 7.06 ± 3.19%, give – 8.39 ± 3.05% receive – 54.81 ± 12.21%. Infant males gave slightly more grooming to AM than what they received from them, but received slightly more grooming from unrelated AF and SF. Few or no grooming interactions with subadult, juveniles or infants were recorded.

Grooming interactions involving IF (N=9) were mostly with their mothers and very occasionally other age-sex classes.

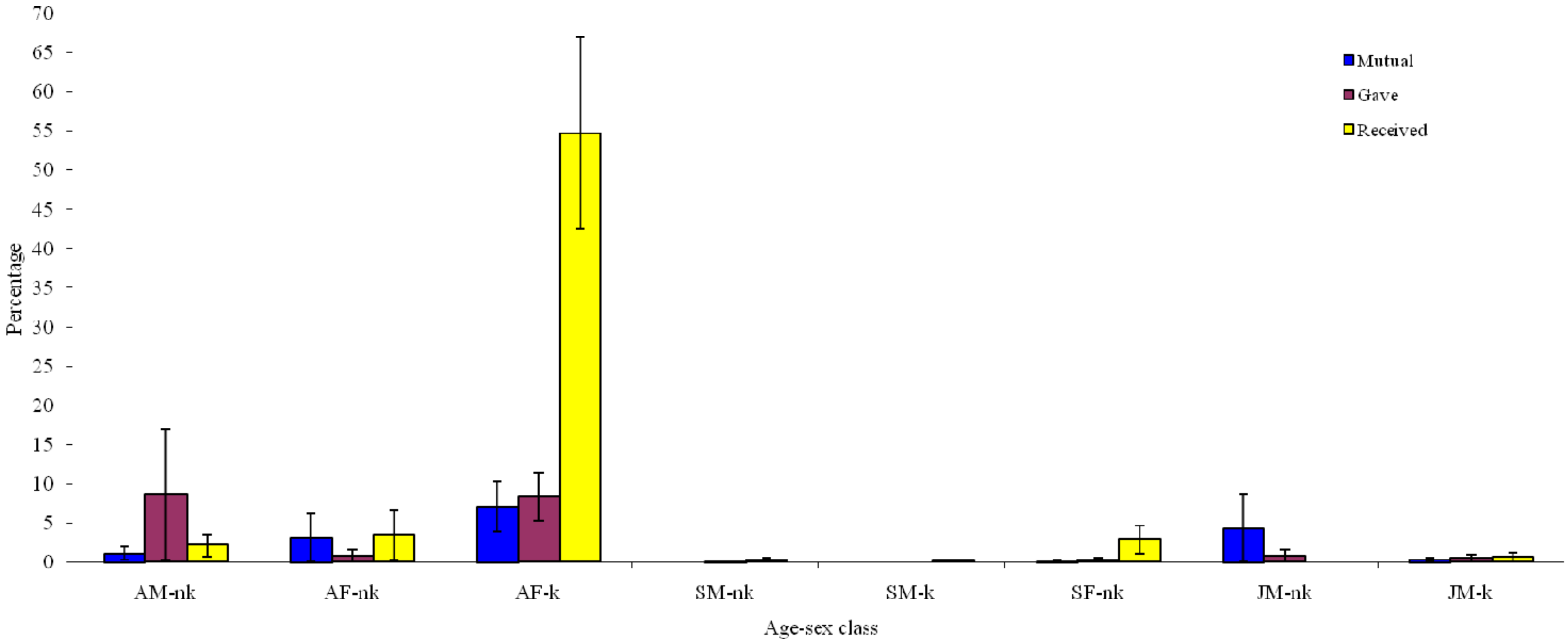

Figure 2.8 The percentage of infant male's total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all infant males (N=7); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by infant males to different age-sex classes (unidirectional bouts) and received = grooming received by infant males from other age-sex classes (unidirectional bouts).

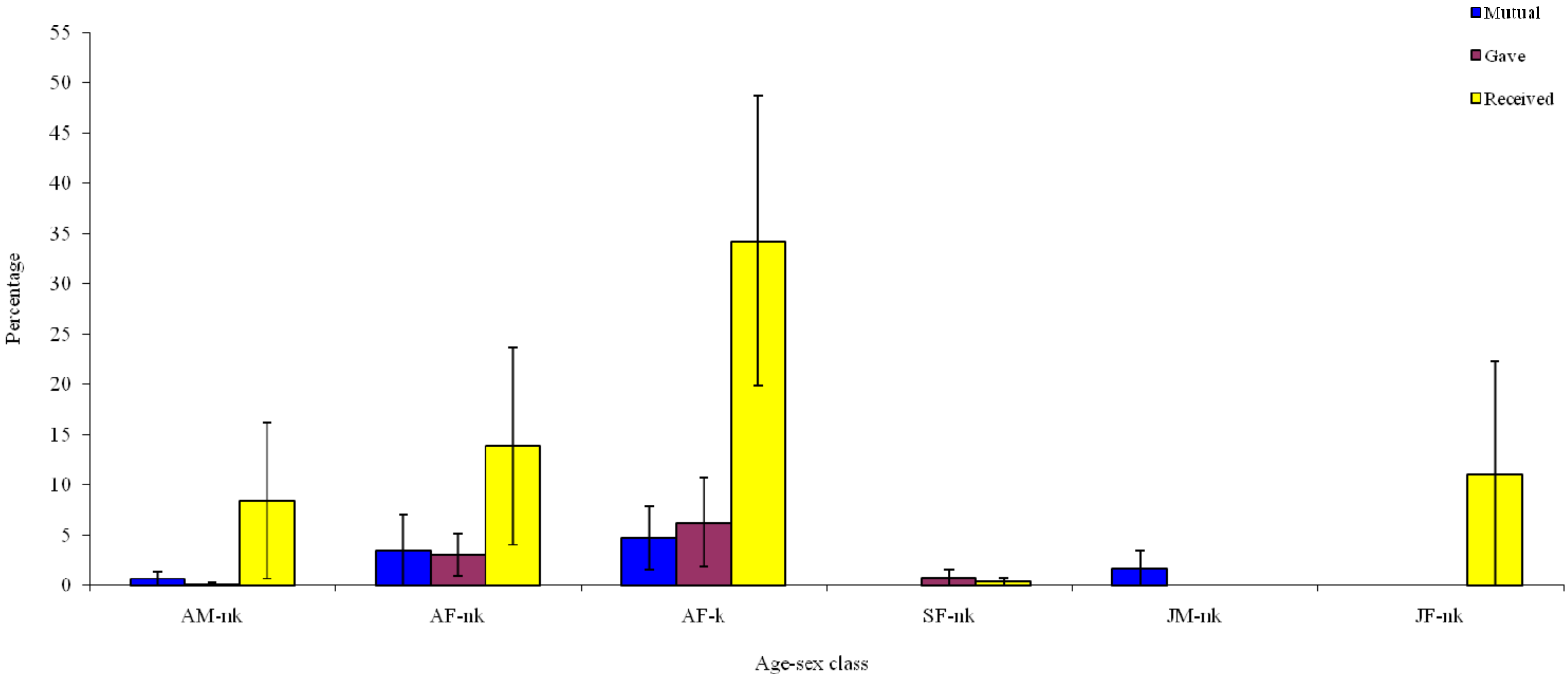

Figure 2.9 The percentage of infant female's total grooming time distributed to different age-sex classes. A-adult, S-subadult, J-juvenile, M-male, F-female, k-kin, nk-nonkin. Column height gives mean across all infant females (N=9); bars give std error. Mutual = mutual grooming bouts, Gave = grooming given by infant females to different age-sex classes (unidirectional bouts) and received = grooming received by infant females from other age-sex classes (unidirectional bouts).

2.3.4 Number of grooming partners

Adult males had a mean of 21.82 grooming partners (range: 2-39) of which 8.24 were other AM (range: 0-19). Adult females had a mean of 13.65 partners (range: 2-22). Eleven AF (64.7%) had mostly AM as partners, four (23.53%) had mostly other AF as partners but one AF, ZN had mostly SF as partners but allocated more of her grooming time to other AF (20%) than to SF (9.2%). Subadult males had a mean of 18.83 grooming partners of which most were AM, except for one individual (ZT) who had an equal number of AM and SF partners, but allocated a higher percentage of his total grooming time to AM (40%) than to SF (15%). Subadult females (N=7) had a mean of 18.29 partners of which five had mostly AM partners, and one had mostly AF. One individual, MH had equal number of AM, AF and SM partners, but allocated 13.90%, 32.00% and 53.49% of her grooming time to them respectively.

Juvenile females (N= 7) had a mean of 5.43 partners, most of which were AF. One individual (EM) had mostly AM grooming partners, but was thought to be an orphan and therefore would try and establish relationships with males to gain acceptance into the group. One JF had equal numbers of AF, SM and JF partners. She allocated her grooming time to them as follows: AF - 53.68% (35% of this to her mother), 18% - SM, 11.06% - JF. Juvenile males had a mean of 5.36 partners. Three of the 11 JM had mostly AM as partners and three had mostly AF. Of the three that had mostly AM partners one allocated most of his grooming time to AM, one of them allocated 59.68% to AF (45.70% to his mother) and the third allocated most of his grooming time to SF (43.33%). The three that had mostly AF partners allocated most of their grooming time to their mothers. One individual (KD) had one AF, one SF and one JF grooming partner, but distributed his grooming time as follows: 97.43% (mother), 1.56% to SF and 1.01% to a JF. Both male and female infants had between one and three grooming partners. With the exception of two infants (GS and BT) all infants had their mother as one of their partners.

2.3.5 Grooming reciprocity between age-sex classes

Most age-sex class combinations showed relative grooming reciprocity ($p < 0.05$), (Table 2.3) so individuals are more likely to groom those individuals from which they received grooming. Grooming between AM – SF, SF – JM, SM and juveniles, SF and infants, SM – IM and JF – JF were also positively correlated but not significantly reciprocated. AM – JF and SM - SM combinations had negative correlation (Taukr) values, which indicates unidirectionality between the age-sex classes, so individuals within these combinations do not necessarily groom those individuals from which they receive more grooming.

Table 2.3 Results of Kr, R and Z tests[1] for grooming reciprocity between different age-sex classes. All results are based on 2000 permutations. N=17 adult males (AM), 17 adult females (AF), 6 subadult males (SM), 7 subadult females (SF), 11 juvenile males (JM), 7 juvenile females (JF), 7 infant males (IM) and 9 infant females (IF).

Age-sex class	**Taukr**	**p**	**R**	**Z**
AF - AF	0.662	0.0005	5588704.75	24569
AF - AM	0.509	0.0005	6572409.5	50717
AM - AM	0.520	0.0005	6167352.5	547865
AF - SM	0.772	0.0005	462792.75	8798
AF - SF	0.477	0.0015	957022.5	40542
AM - SM	0.583	0.0005	1018428.5	33862
AM - SF	0.522	0.0710	1013977	18865
AM - JM	0.680	0.0005	2171701	11820
AF - JF	0.662	0.0005	1692705	23440
AF - JM	0.739	0.0005	2203379.5	162554
AM - JF	-0.111	1.0000	1242530	0
AF - IF	1	0.0070	918384.5	203483
AF - IM	1	0.0005	655787	47354
SF - SF	0.649	0.0075	108104.75	7991
SM - SM	-0.097	0.7116	21246	346
SF - JF	0.874	0.0005	254428.5	1276
SF - JM	0.674	0.1459	323459.5	30
SM - JF	0.725	0.0810	118504	117
SM - JM	1	0.098	155128	1501
SF - IM	1	0.1209	97200	35
SF - IF	1	0.1004	137781	98
SM - IM	1	0.0990	65488.5	775
SM - SF	0.562	0.007	72936.5	6372
JF - JF	0.714	0.1239	350301	160
JM - JF	1	0.0075	592317.5	139

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[1] The Kr test statistic (a multivariate version of Kendall's S statistic corrected for individual variation) measures relative interchange, and the Taukr value, corrects the Kr value for sample size and ties. Mantel's Z coefficient multivariate and the R statistic measures absolute interchange by assessing the symmetry in the matrices being tested. The R coefficient is a nonparametric version of the Z test and is used in conjunction with the Z test to make up for any deficiencies of the Z test.

2.4 Discussion

As recorded at other sites (Gombe: Goodall 1968, Mahale: Nishida 1979; Nishida and Hosaka 1996; Kanyawara in Kibale: Wrangham et al. 1992; Tai: Boesch and Boesch-Achermann 2000; Ngogo: Watts 2000), male chimpanzees of the Budongo Forest distribute most of their grooming to other males, although distributions of grooming interactions between different age-sex classes will vary among individuals and with time (Goodall 1986). This predominance of grooming among males reinforces the argument that male bonds are central to chimpanzee sociality (Wrangham 1979; Van Hooff and Van Schaik 1994). The mean percentage of inter-male grooming was lower than that for Ngogo (Watts 2000), possibly due to the higher number of adult males at Ngogo (n = 24) compared to this study (n = 17). Subadult males will invest time grooming AM because they need to establish relationships with stable males for acceptance and coalitionary support (Bygott 1979), and by investing time grooming AM, SM are indicating a willingness to invest time and effort in the AM. Adult males only allocated 4.41% of their grooming time to SM males supporting the suggestion that like SM at Gombe (Pusey 1990, Goodall 1986) and Mahale (Takahata 1990), SM at Budongo only establish themselves within adult grooming networks once they themselves have reached maturity.

Males develop grooming relationships with all other age-sex classes albeit for different reasons. Reproductive females are an essential resource to males in order to pass on their genes, and if males are to gain access to females they may be able to use grooming as a strategy to establishing familiarity with them as females are more likely to allow copulation’s from males with whom they are ‘friends’ with than those they have not formed a strong relationship (Seyfarth 1978a, 1978b; Smuts 1983, 1985; Weingrill 2000).

Furthermore, by grooming preferred males regularly, this may help reduce harassment from less preferred males when the female is in oestrous (Smuts and Smuts 1993) and thus ensure successful matings are with preferred males. Grooming interactions between AM and SF could be insight by the males into future reproductive potential or possibly these are low ranking or very young AM (Tutin 1979a).

Grooming interactions involving subadults, juveniles and infants are discussed below in relation to other populations of chimpanzees (Goodall 1968, Pusey 1978), but no direct comparisons could be made since no other published studies have investigated the amount of grooming that these individuals contribute to the population's total grooming time. I suggest that the small number of grooming interactions between AM, juveniles and infants is due to one of the following reasons: Firstly, juveniles and infants have no incentives to offer an AM in exchange for being groomed and therefore AM would rather invest time in grooming older individuals that could possibly offer some benefit. Secondly, AF with young infants or juveniles may be reluctant to allow other individuals in close contact with their offspring (Van Lawick-Goodall 1975; Nicolson 1987). Grooming that does take place could be a strategy used by AM to gain acceptance by AF as has been suggested for baboons (Smuts 1985). Adult males that invest time and effort in an AF infant or juvenile offspring may have a better chance of being accepted by that female. Males copulating with females are often pushed away by infants (Goodall 1968, Van Lawick-Goodall 1975; Tutin 1979b) so males familiar to infants through grooming and play interactions are more likely to be tolerated.

Grooming allocated by juveniles to AM may have been a result of a particular male being in close proximity to (but not necessarily grooming) the mother of the juvenile in question. Two JM allocated 92.86% (MS) and 24.14% (AY) of their grooming time to one AM (BK). These two individuals happened to be the sons of the alpha female NB and therefore this AM may have been trying to maintain relationships with their high-ranking mother. Four other JM allocated more than 35% (range: 35.48 – 89.79%) of their grooming time to AM. The dominance status of their mothers is unknown, but they are not expected to have high status for a number of reasons. ZF allocated 73.17% of his grooming time to AM but his mother (BN) was known to be an old, disabled chimp. The mothers of the other three juveniles were known not to be very sociable. It therefore does not seem likely that AM – juvenile interactions are only as a result of AM associating with high-ranking females.

An alternative explanation is that if JM do give reasonable amounts of their grooming time to AM, it may be that their mothers are of low social status and therefore gain acceptance by AM by investing time in establishing relationships with older males from a young age thereby ensuring acceptance once they themselves become adults. This may be essential, especially if an individual chimpanzee's social status is influenced by that of its mother, as has been indicated in baboons (Cheney 1977) and vervets (Horrocks and Hunte 1983). This idea, however, needs to be investigated further. Alternatively, grooming interactions between juveniles and AM could be over-represented by this data set because juveniles and infants spend time together with their mothers in sleeping nests which are inaccessible to observers, and therefore many grooming interactions between mothers and young offspring may not have been sampled. What does stand out though, is that grooming between AM and juveniles does occur, supporting observations of Gombe chimpanzees (Pusey 1990). Adult females spend a large amount of their time alone with their offspring, explaining why they allocate more of their grooming time to juveniles and infants than to other females. With AF only producing infants every 3-5 years (Reynolds and Reynolds 1965) there are seldom AF that have subadult, juvenile and infant offspring around at the same time. The interactions of infants and juveniles are mainly in the context of play (Van Lawick-Goodall 1975) and are dependent on their mothers interacting with each other, explaining the low number of grooming bouts recorded for these age classes.

The finding that AM–IF and SF–JF dyads had more mutual than unidirectional grooming interactions between them whereas all other age-sex class combinations had a higher percentage of unidirectional bouts between them is in contrast to Pusey (1990) and Boesch and Boesch-Achermann (2000) who found that most grooming interactions are likely to be mutual. An earlier study of the Budongo chimpanzees in 2001 found that of 709 grooming bouts 403 (57%) were unidirectional (Reynolds 2005). These differences may be resource based and if chimpanzees represent 'biological markets' where individuals can exchange 'commodities' (Noë and Hammerstein 1995) depending on the strength of resource competition, mutual grooming may dominate when there are shallow 'dominance gradients' (Henzi and Barrett 1999) whilst unidirectional bouts may dominate when grooming can be used to exchange for other resources. This suggestion is however, beyond the scope of this study and has therefore not been investigated further.

Based on an infant's complete dependence on its mother (Reynolds and Reynolds 1965, Pusey 1983), AF grooming their own offspring more than other AF offspring is supported by this study. As individuals reach adolescence they become more independent and spend increasingly more time without their mother, which facilitates interactions with other age-sex classes (Nishida 1979; Pusey 1983, 1990), explaining why subadults have both more grooming interactions and grooming partners than juveniles or infants. Subadult females eventually carve out their individual core areas either in their natal group or in a new one whilst SM integrate themselves into their natal group (Pusey 1983). In agreement with Pusey's (1990) study, SM allocated most of their grooming time to AM, SF and AF, all being age-sex classes that SM could benefit from developing social relationships with. Subadult males receive more grooming from their mothers than from other AF, but give equal amounts to their mothers as unrelated AF, which is explained by their increased independence as they make the transition from constant association with their mother to social integration into their natal groups as AM. Similar observations have been made of SM in red colobus monkey groups which groom AF at high rates (Struhsaker and Leland 1979). By investing grooming time in unrelated AF, SM may be able to enhance their acceptance by the rest of the group.

It is possible that SF would prefer to groom AM, but would have to compete with AF for access to AM and if AF are present, they are probably supplanted by them and therefore select SM as alternative grooming partners. Although SF invest time in establishing relationships with AM and other age-sex classes they still spend a proportion of their time with their mothers, especially when anoestrus (Pusey 1983, 1990). Similar to Pusey (1990), both JF and JM gave and received most of their grooming to and from mothers, but JF gave a higher proportion of their grooming to mothers than did JM.

Adults and subadults had more grooming partners than juveniles or infants and given both the fission – fusion social structure of chimpanzees and the significance of social grooming for social reinforcement this is not surprising. Adult males are more gregarious than other age-sex classes and therefore need to service relationships with as many partners as possible, and so they would be expected to have more grooming partners. Adult males from this study had more partners (21.82 ± 2.48) than those recorded at Ngogo (1995/96: 11.6 ± 4.3; 1997: 8.6 ± 4.1) and Mahale (7.3 ± 0.9) (Watts 2000) despite Ngogo's population consisting of about 114 individuals (Watts 2000). Arnold and Whitten's 2003 study on the Budongo chimpanzees showed that AM had a mean of 13 partners. This discrepancy may suggest that results could be influenced by the duration over which data is collected as the above studies were conducted over a period of less than 12 months.

Although the results indicate most infant grooming is with their mothers, there are some irregularities with regards to the grooming distribution patterns of infants and therefore this should not necessarily be interpreted as a general grooming pattern of infants. For example infants are completely dependent on their mothers and therefore, their mother should be at least one of their grooming partners. There were however, no samples recorded for grooming of two IF and their mothers. Infant grooming may therefore be under-represented in the sampling due to difficulty in observing mother-infant interactions whilst in nests.

The chimpanzees in this study show relative reciprocity in grooming at the group level as has been found in other studies (Hemelrijk and Ek 1991; Watts 2000; Arnold and Whitten 2003). In other words, individuals are more likely to give grooming to those from which they receive grooming. However, grooming was not necessarily reciprocated equally within dyads. Arnold and Whitten (2003) observed that one member of each grooming dyad contributed about 75% of the grooming and that grooming asymmetry was found to be more pronounced within more distantly ranked dyadic members in male grooming dyads in this study population. Although some of the grooming between age-sex classes was found to be statistically not significant, this does not necessarily mean that the results are not biologically important. The relationship is still positive which indicates that there is a trend towards reciprocation and may have been a function of sample size. The negative correlations observed between AM - JF and SM - SF indicate that grooming was not reciprocated. The interactions between AM and JF were due mainly to one juvenile female (EM) who was thought to be an orphan and therefore probably groomed various AM in an attempt to be accepted by them which would allow her integration into the group. AM would receive no short-term benefits from returning her grooming as she is sexually unreceptive and does not have a mother to which the males would try and gain access to through grooming her.

In conclusion, overall grooming patterns found among the Budongo chimpanzees are comparable to those observed in other free-living populations. Variations in grooming patterns could be attributed to a number of variables including resource base, population numbers and differences in age-sex class composition. In order to tease out the influence of these various factors further investigation is required.

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-Chapter 3[*]-

Grooming distributions between anoestrous and oestrous females

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Abstract

It has been suggested that allogrooming among primates is a strategy for enhancing reproductive success, either by allowing males to enhance their proximity to oestrous females, or by influencing female choice through the development of affiliative relationships with males. Female chimpanzees have obvious swollen anogenital regions at or close to ovulation, which males could recognise as signalling receptivity and therefore, by adapting their grooming investment accordingly, males could increase their copulatory success. Swollen females may also increase grooming interactions with males so as to keep preferred males close by during a period characterised by considerable harassment from other males, and thereby obtain protection and increase the likelihood of copulation with preferred partners. Five and a half years of grooming data from a group of free-living chimpanzees (*Pan troglodytes*) in the Budongo Forest, Uganda, were examined to investigate how sexual swellings influence grooming behaviour between males and females of different age classes. Based on the availability of oestrous females, Bonferroni confidence intervals revealed that anoestrous adult and subadult females gave and received significantly less grooming to and from adult males than expected, but that oestrous adult and subadult females gave and received significantly more grooming to and

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from adult males than expected. Adult (anoestrous and oestrous) females gave and received significantly less grooming to and from subadult males, whereas subadult females gave and received significantly more grooming to and from subadult males than expected. Wilcoxon rank sum tests revealed that oestrous adult females devoted more time to giving and receiving grooming to and from adult males than did anoestrous adult females. Oestrous subadult females gave both adult males and subadult males more grooming than did anoestrous subadult females. Grooming interactions between adult males and oestrous adult females were initiated significantly more often by males, but those between anoestrous subadult females and adult males were initiated significantly more frequently by females. Grooming interactions between adult males and oestrous adult females were more likely to be terminated by males. Both age and oestrous swellings influence grooming interactions between chimpanzees, and grooming may be a strategy used by males to increase their access to copulation opportunities, whereas females may use grooming to increase protection from harassment during swollen periods and the likelihood of copulation with preferred partners.

Keywords: Chimpanzees, Pan troglodytes, grooming, oestrous, Budongo Forest

Running Title: The influence of oestrous swellings on the grooming behaviour of chimpanzees of the Budongo Forest, Uganda

3.1 Introduction

One of the main objectives of primate socio-biology is to generate a greater understanding of the variations observed in social behaviour and how they tie in with biological function. One of the most frequently observed social behaviours in primates is allogrooming, (one individual grooms another) indicating willingness to invest time and effort in relationships with other group members (Walters and Seyfarth 1987; Dunbar 1992; Hemelrijk and Lutjein 1998), which may be essential for the development of cooperative relationships (Van Hoof and Van Schaik 1994) and used to establish and reinforce social relationships between group members (Walters and Seyfarth 1987). Grooming helps to remove ectoparasites and other debris from an individuals coat (Poirier 1970; Tanaka and Takefushi 1993) whilst also stimulating the productions of endorphins (Keverne et al. 1989). Seyfarth (1980) suggested that allogrooming occurs more frequently than is necessary for hygienic purposes alone and therefore, probably has social significance. Support for this suggestion of social reinforcement through grooming interactions between group members comes from demonstrations of grooming reciprocity (chimpanzees: Hemelrijk and Ek 1991; Watts 2000; vervet monkeys: Hemelrijk 1990), preference of allies to groom each other (tufted capuchins*:* Di Bitetti 1997), gaining of social acceptance by group members (Poirier 1970), tolerance at feeding sites (Barton and Whiten 1993), support during conflicts (Seyfarth 1976; Hemelrijk 1990), access to new born infants (Seyfarth 1976; Altmann 1980; Henzi and Barrett 2002) and sharing of food (De Waal 1989, 1997).

An additional suggestion is that grooming may be used by individuals to increase reproductive success (Weingrill 2000). By using grooming to strengthen social bonds, chances of copulations may also be increased (Michael et al. 1978; Tutin 1979). It may consequently be in a male’s best interest to invest time and effort in grooming potentially reproductive females rather than non-reproductive ones, whereas females may benefit more by developing grooming relationships with strong healthy adult males rather than generally smaller, weaker subadult males. (Anderson and Bierlet 1994)

Males may be able to recognize that females are sexually receptive, through visual cues such as anatomical changes during the periovulatory period (Hamilton 1984; Anderson and Bielert 1994). As females progress through their reproductive cycles, changes in oestrogen and progesterone levels cause swelling of the female’s anogenital region (e.g., chimpanzees and baboons). Males would benefit if they were able to use these visual cues to assess a female’s sexual receptivity and invest his grooming investment accordingly.

Between 26 and 35 species of primates are known to have sexual swellings (Clutton-Brock and Harvey 1976; Hrdy and Whitten 1987; Anderson and Bielert 1994) but none of these are prosimians or new world monkeys (Dixson 1983). Within the Old world species that do have sexual swellings, they occur mainly in species that have a multimale social organization (Clutton-Brock and Harvey 1976) such as red colobus monkeys *Colobus bodius*, macaques, baboons, mangabeys *Cercocebus spp* and chimpanzees.

Suggestions as to why sexual swellings have only evolved in some species include: Being used as a ‘passport’ by young females to safely join new groups (Nishida 1979; Pusey 1979; Moore 1984; Wallis and Goodall 1993; Boesch and Boesch-Achermann 2000); strategies used by females to compete with each other for access to mating opportunities with preferred males (Pagel 1994) although experimental data do not support this idea (Radwan 1995; Wiley and Poston 1996); initiating competition between males and females to help determine male quality (Clutton-Brock and Harvey 1976); the many-male hypothesis (Hrdy 1981; Hrdy and Whitten 1987), suggesting that females mate with a number of males, resulting in positive interactions between males and offspring thereby suggesting an illusion of paternity and decreasing the chances of infanticide (Goodall et al. 1979; Hrdy 1979; Taub 1980; Harcourt 1981; Hrdy 1981; Zinner and Deschner 2000) and serve as accurate ovulation indicators (Hamilton 1984) due to positive associations between females with swollen swellings and sexual behaviour having been observed in many species displaying this phenomenon (Rowell 1972; Wallis 1982; Dixson 1983).

If grooming is one of the strategies that males use to increase their chances of copulation, grooming with females would be expected to increase during female oestrous periods as has been found in captive chimpanzees (Wallis 1992). Observations suggest that this may also occur in free-living chimpanzees, but this has not been empirically investigated (Goodall 1986). Swollen females may also increase grooming interactions with specific males to keep preferred males close by during a period sometimes characterised by considerable harassment from other males. Females thus obtain protection as well as increase the likelihood of impregnation by a preferred partner (Smuts and Smuts 1993; Stumpf and Boesch 2005). Assuming both males and females benefit from increased grooming during female receptive periods, the effort put into initiating and maintaining grooming bouts by the different sexes may also change. Furthermore, if grooming is used as a strategy to increase reproductive success, the age class of an individual would be expected to have an impact on these grooming relationships.

Chimpanzees exhibit both extensive social grooming and obvious sexual swellings. The menstrual cycle of female chimpanzees is ~ 36 days (Young and Yerkes 1943) and is characterised by changes in the size, shape and colouring of the anogenital region (Wallis 1992). The initial swelling lasts an average of 7.6 days (Young and Yerkes 1943), and maximum swelling for up to 17 days (mean 10-12) (McGinnis 1979), with ovulation taking place during the last one or two days (Graham 1982). The following four days results in a rapid decrease in the size of the swelling (Wallis 1982) and then for the next 14 days the anogenital area remains flat (McGinnis 1979). Females may also experience these swellings during the early stages of pregnancy and it is suggested (Wallis 1982) that any benefits gained by oestrous females will also apply to swollen pregnant females. Females tend to transfer to new communities whilst displaying anogenital swellings, and therefore being swollen whilst pregnant will create an illusion of sexual receptivity and facilitate the increase of genetic diversity between communities.

Adolescent or subadult females also display sexual swellings but may go through approximately 19 menstrual cycles before becoming fertile (Tutin 1980; Boesch and Boesch-Achermann 2000), which has been suggested as a strategy to allow practice of sexual behaviour to ensure insemination with no delay once they become fertile (Short 1976; Turke 1984; Kalkstein 1991). Adult males of many species show an aversion to mating with subadult females (Strum and Western 1982; Smuts 1985; Van Noordwijk 1985; Anderson 1986), so it would be expected that if grooming is used as a strategy to increase copulations, adult males would show a similar aversion to grooming subadult females. Subadult males on the other hand may be physiologically capable of inseminating females, but are generally smaller, weaker, have shorter canines and are subordinate to adult males and therefore less effective at protecting females and infants (Anderson and Bierlet 1994) and therefore should be the less preferred grooming age of sexually receptive adult females.

The aim of this chapter is to describe the relationship between sexual swellings and grooming behaviour between males and females of different age classes within a group of free-living chimpanzees. The main research question that will be addressed in this chapter is: How does the presence of sexual swellings influence grooming interactions between males and females of different age classes? Taking into account the number of females present at any one time during the study period and whether they had either no swelling or swelling, It is hypothesised that:

1. If males are the instigators for reproductive advantages then it would be expected that males give more grooming to females during this time;
2. If females are using grooming of preferred males to protect themselves then it would be expected that more grooming by females to adult males would occur.

Following these it was predicted that:

1. Oestrous females give and receive more grooming bouts to and from males than do anoestrous females
2. Oestrous females allocate more of their grooming time to males than anoestrous females
3. The oestrous state of a female influences which sex initiates a grooming interaction, with males initiating more often with oestrous than anoestrous females
4. The oestrous state of a female influences which sex terminates a grooming interaction, with males terminating less often with oestrous than with anoestrous females

3.2 Study area and methods

3.2.1 Study area

The Budongo Forest Reserve is made up of 793 km² of moist semi-deciduous forest and grassland, and is situated at a mean altitude of 1100m on the edge of the western Rift Valley in western Uganda (Eggeling 1947; Plumptre 1996). The average annual rainfall of the region is approximately 1400 mm, with a dry season between December and February. Daily mean temperatures range between 14ºC and 28ºC (Eggeling 1947).

The Sonso region (1º44' N, 31º33 E') in which this study was carried out lies well within the forest and is named after the river flowing through the area. Although most of the forest was selectively logged in the past, the logging industry halted operations within the study area between 1947 and 1952 (Plumptre 1996). This, together with forest dynamics, has resulted in the Sonso region of the forest being made up of various forest types, including mixed forest, colonizing forest, swamp forest and ironwood forest (Eggeling 1947; Reynolds 1992). The study site was established in 1990 and is maintained by the Budongo Forest Project (Reynolds 1992; Plumptre et al. 1997). A system of trails covering an area of approximately 31km² aids travel through the study area, allowing researchers relatively easy access to the forest.

3.2.2 Study group

Between 1990 and 1994 with the effort of Nick Newton-Fisher and field assistants Geresomu Muhumuza and Zephyr T. Kiwede the chimpanzees were followed and eventually allowed observers to follow them at close quarters throughout the day. Individual chimpanzees of the Sonso group have subsequently been habituated, sexed and identified, and have all been given a two-letter identification code. The chimpanzees spend most of their time within an area of about $7km^2$ with each individual having its own 'core' area (Newton-Fisher 2000).

During the period of this study, the Sonso group consisted of between 36 and 54 individuals (Table 3.1). Eleven of the Sonso chimpanzees had injured limbs as a result of being caught in snares, set by the local people to catch duiker and forest pigs (Waller and Reynolds 2001). Four other groups of chimpanzees are known to occur within the forest, two (Busingiro and Kaniyo-Pabidi groups) of which are currently being habituated for tourism purposes. The other two groups (The Nature Reserve and Waisoke groups) have not yet been habituated or studied but both share boundaries with the study group.

Table 3.1 The number of individuals within each age-sex class from which grooming interactions were recorded during the five and a half year study period.

Age-sex class	1995/96	1996/97	1997/98	1998/99	1999/2000	2000/2001
Adult males (AM)	12	13	11	12	10	10
Adult females (AF)	10	12	10	15	13	11
Subadult males (SM)	1	2	4	4	3	1
Subadult females (SF)	5	5	5	3	3	2
Juvenile males (JM)	4	4	3	4	4	1
Juvenile females (JF)	0	4	6	7	5	0
Infant males (IM)	4	5	5	4	1	0
Infant females (IF)	5	3	2	5	1	1
Total	**41**	**48**	**46**	**54**	**40**	**26**

3.2.3 Data collection

Data were collected continuously between September 1995 and April 2001 as part of a long-term study on the behaviour and ecology of the Sonso chimpanzees. Eleven field assistants (a mean of four at any given time) employed by the Budongo Forest Project conducted sampling, daily (weather permitting) between 07:30 and 13:00 and then again between 14:00 and 16:00 on an *ad libitum* basis (Altmann 1974) whilst following the chimpanzees. Each sample recorded the identities of individuals present, interactions between individuals (grooming, playing, aggression, copulations etc) initiators and terminators of interactions, duration of interactions (recorded to nearest minute) and female anogenital swellings. Subadult and adult females were allocated a score depending on the size of their sexual swelling. The following scores were allocated by observers: 0 – no swelling, 1 - ¼ swelling, 2 - ½ swelling, 3 - ¾ swelling and 4 – full swelling. The following abbreviations will be used throughout the remainder of the chapter to refer to different age-sex classes: AM – adult males, AF - adult females, SM – subadult males and SF – subadult females.

3.2.4 Analysis

Allocation of scores to females by observers was subjective and may have varied between observers. To minimize this variation, scores of 1 and 2 were pooled, as were scores of 3 and 4. This resulted in three categories, with the following scores: 0 – no swelling, 1 – intermediate swelling and 4 – full swelling. After this adjustment there were very few grooming interactions recorded for females with intermediate swellings, so intermediate and full swelling scores were pooled. Thus, for the purpose of analysis two categories were created with the following scores: 0 – no swelling (anoestrous) and 1 – swelling (oestrous). I acknowledge that different stages of swellings may influence access to copulations as well as the fact females may display swellings during early stages of pregnancy. These data were however, not available so were not included in the study reported here. All grooming interactions involving infants, juveniles, maternal siblings and mother-offspring were removed so as to eliminate the influence of these classes on grooming interactions. This resulted in a total of 1445 grooming bouts being used for analysis.

Grooming bouts were separated into the following combinations: AF0 and AM; AF0 and SM; AF1 and AM; AF1 and SM; SF0 and AM; SF1 and AM; SF0 and SM; SF1 and SM. Within these combinations, grooming bouts involving the same two individuals were converted into dyads, which then formed the basis for further analysis. Using these dyads the following was calculated:

1. The number (frequency) of grooming bouts that occurred between each of the above age-sex class groups
2. The percentage of each female's grooming time (minutes) that she gave to, and received from males.
3. The number of approaches by either males or females that resulted in grooming interactions (for the remainder of this chapter the term 'approaches' will be referred to as 'initiations')
4. The number of terminations from grooming bouts that were made by either males or females.

The influence of male rank on grooming relationships was not investigated during this study, but has been investigated for this group of chimpanzees by Arnold & Whiten (2003).

A Chi-square goodness of fit test (Zar 1999) was used to determine whether the observed frequencies of grooming bouts between anoestrous or oestrous females and males differed significantly from expected frequencies (calculated by dividing the proportion of available oestrous females at any one time during the study period by the total number of bouts). The proportion of available oestrous females at any one time was the mean number of oestrous females at any one time during the study period. Bonferroni confidence intervals (Miller 1966; Neu et al.1974) were performed for those chi-square tests that revealed significant differences to determine preference for or avoidance of different age-oestrous classes. Wilcoxon rank sum tests were used to determine whether anoestrous and oestrous females distributed their grooming time between different age-sex classes differently. Chi-square tests were used to determine whether sexual swellings influenced which sex initiated or terminated heterosexual grooming bouts. The binomial hypothesis post hoc test was used to indicate where any significant differences were. Significance for all tests was set at 0.05.

3.3 Results

3.3.1 Frequency of grooming given by anoestrous and oestrous females to males

Bonferroni confidence intervals (Table 3.2) indicate that AF0 and SF0 gave significantly less grooming to AM than expected. Conversely, AF1 and SF1 gave significantly more grooming to AM than was expected. Both AF0 and AF1 gave significantly less grooming to SM whereas SF0 and SF1 gave significantly more grooming bouts to SM than was expected.

3.3.2 Frequency of grooming received by anoestrous and oestrous females from males

Bonferroni confidence intervals (Table 3.3) indicate that AF0 and SF0 received significantly less grooming from AM than expected. Conversely, AF1 and SF1 received significantly more grooming from AM than was expected. Both AF0 and AF1 females received significantly less grooming from SM whereas SF0 and SF1 received significantly more grooming bouts from SM than was expected.

Table 3.2 Bonferroni confidence intervals for the number of grooming bouts that anoestrous and oestrous females gave to males. AF0 – anoestrous adult female, AF1 – oestrous adult female, SF0-anoestrous subadult female, SF1-oestrous subadult female, AM-adult male, SM-subadult male. * = All results significant at $p < 0.05$

Grooming partnership	Availability of females at any one time during study period	Proportion[2] of availability of females (*pi*◦)	Number of grooming bouts observed	Proportion observed in each category (*pi*)	Expected[3] number of grooming bouts	Confidence interval (95%) on observed proportion of occurrence (*pi*)[4]	More / less than expected.
AF0 and AM	13	0.542	209	0.441	257	$0.438 \leq p \leq 0.444$	Less*
AF1 and AM	4	0.167	95	0.200	79	$0.198 \leq p \leq 0.203$	More*
SF0 and AM	5	0.208	67	0.141	99	$0.140 \leq p \leq 0.143$	Less*
SF1 and AM	2	0.083	103	0.217	39	$0.215 \leq p \leq 0.219$	More*
AF0 and SM	13	0.542	45	0.249	98	$0.243 \leq p \leq 0.255$	Less*
AF1 and SM	4	0.167	26	0.144	30	$0.139 \leq p \leq 0.148$	Less*
SF0 and SM	5	0.20	47	0.260	38	$0.254 \leq p \leq 0.266$	More*
SF1 and SM	2	0.083	63	0.348	15	$0.341 \leq p \leq 0.355$	More*

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[2] Proportion expected in each category represent expected grooming bout observations if grooming occurred between each category in exact proportion to availability of females.

[3] Calculated by multiplying proportion *pi*◦ x n; 0.542 x 474 = 257

[4] *pi* represents theoretical proportion of occurrence and is compared to corresponding *pi*◦ to determine if hypothesis of proportional use is accepted or rejected, i.e., *pi* = *pi*◦

Table 3.3 Bonferroni confidence intervals for the number of grooming bouts that anoestrus and oestrus females received from males. AF0 – anoestrous adult female, AF1 – oestrous adult female, SF0-anoestrous subadult female, SF1-oestrous subadult female, AM-adult male, SM-subadult male. * = All results significant at $p < 0.05$

Grooming partnership	Availability of females at any one time during study period	Proportion[5] of availability of females ($pi\circ$)	Number of grooming bouts observed	Proportion observed in each category(pi)	Expected[6] number of grooming bouts	Confidence interval (95%) on observed proportion of occurrence(pi)[7]	More or less than expected.
AF0 and AM	13	0.542	206	0.334	334	$0.332 \le p \le 0.336$	Less*
AF1 and AM	4	0.167	162	0.263	103	$0.261 \le p \le 0.264$	More*
SF0 and AM	5	0.208	97	0.157	129	$0.156 \le p \le 0.159$	Less*
SF1 and AM	2	0.083	152	0.246	51	$0.245 \le p \le 0.248$	More*
AF0 and SM	13	0.542	47	0.2701	94	$0.264 \le p \le 0.277$	Less*
AF1 and SM	4	0.167	23	0.1322	29	$0.127 \le p \le 0.137$	Less*
SF0 and SM	5	0.208	40	0.2299	36	$0.224 \le p \le 0.234$	More*
SF1 and SM	2	0.083	64	0.3676	15	$0.361 \le p \le 0.375$	More*

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[5] Proportion expected in each category represent expected grooming bout observations if grooming occurred between each category in exact proportion to availability.

[6] Calculated by multiplying proportion $pi\circ$ x n; 0.542 x 474 = 334

[7] pi represents theoretical proportion of occurrence and is compared to corresponding $pi\circ$ to determine if hypothesis of proportional use is accepted or rejected, i.e., $pi = pi\circ$

3.3.3 Duration of grooming bouts between anoestrous and oestrous females

Oestrous females allocate their grooming time differently to that of anoestrous females in terms of the different age-sex classes available to them for grooming. Oestrous adult females allocated slightly more of their grooming time to AM than did AF0 ($z = 1.971$; $p = 0.05$) (Figure 3.1) but received significantly more grooming time from AM than did AF0 ($z = 4.028$; $p = 0.0001$) (Figure 3.2). Although AF1 gave and received slightly more grooming to and from SM than AF0, the differences were not significant. Oestrous subadult females gave both AM and SM more grooming than did SF0, although only AM were given significantly more ($z = 2.649$; $p = 0.008$) (Figure 3.3). Oestrous subadult females received more grooming from AM than did SF0, although the difference was not significant (Figure 3.4). Both SF0 and SF1 received more or less equivalent amounts of grooming time from SM.

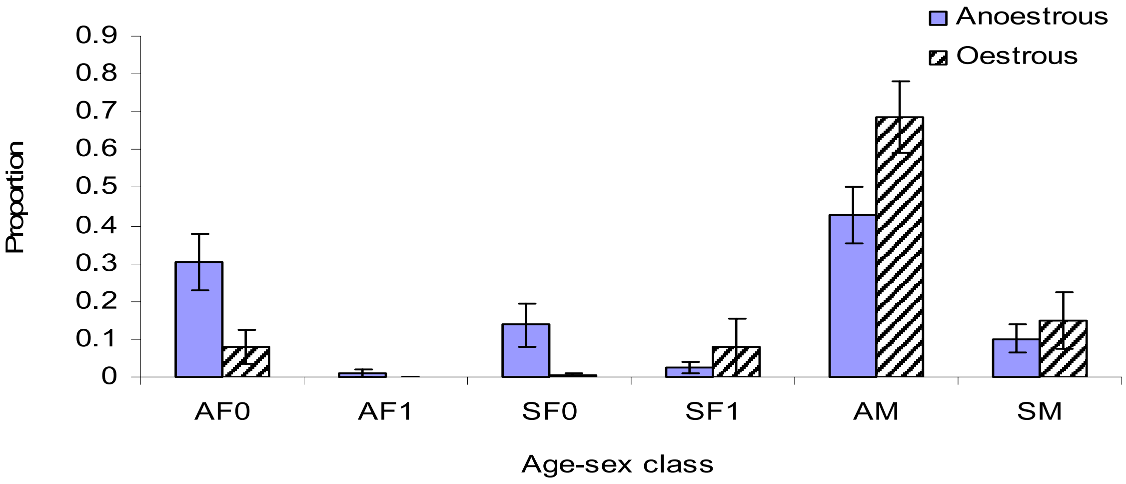

Figure 3.1 The proportion of grooming time (minutes) that adult females gave to different age-sex classes. A-adult, S-subadult, F-female, M-male, 0-anoestrous, 1-oestrous.

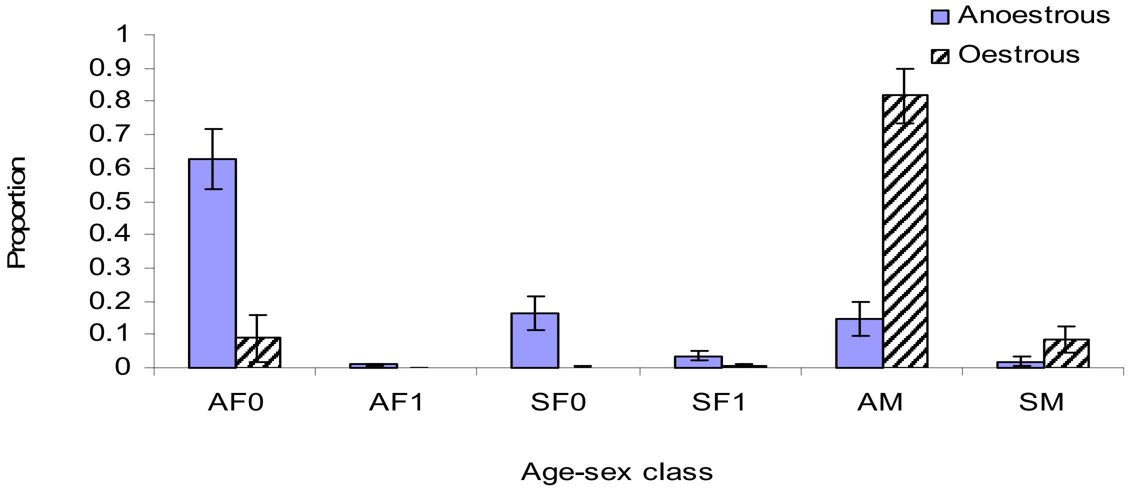

Figure 3.2 The proportion of grooming time (minutes) that adult females received from different age-sex classes. A-adult, S-subadult, F-female, M-male, 0-anoestrous, 1-oestrous**.**

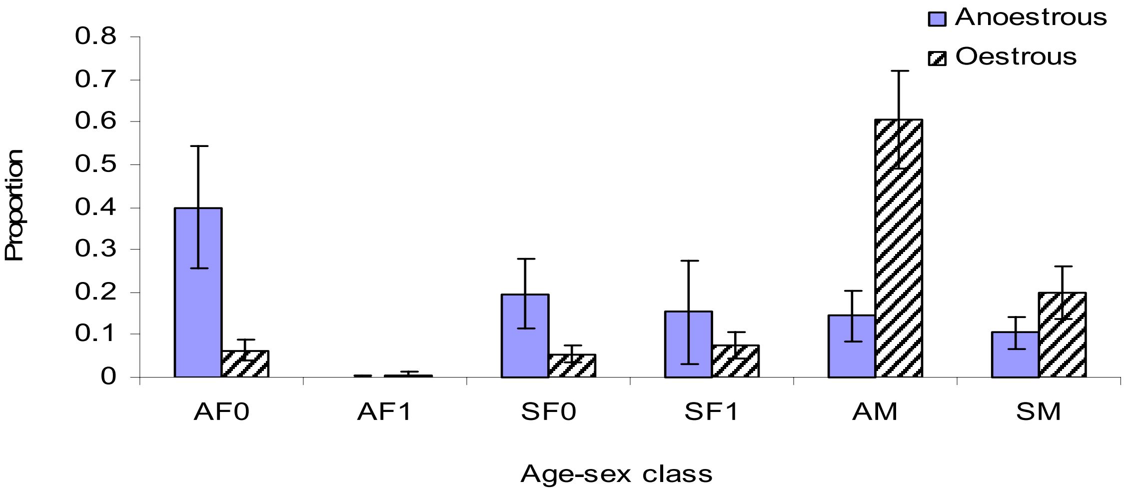

Figure 3.3 The proportion of grooming time (minutes) that subadult females gave to different age-sex classes. A-adult, S-subadult, F-female, M-male, 0-anoestrous, 1-oestrous.

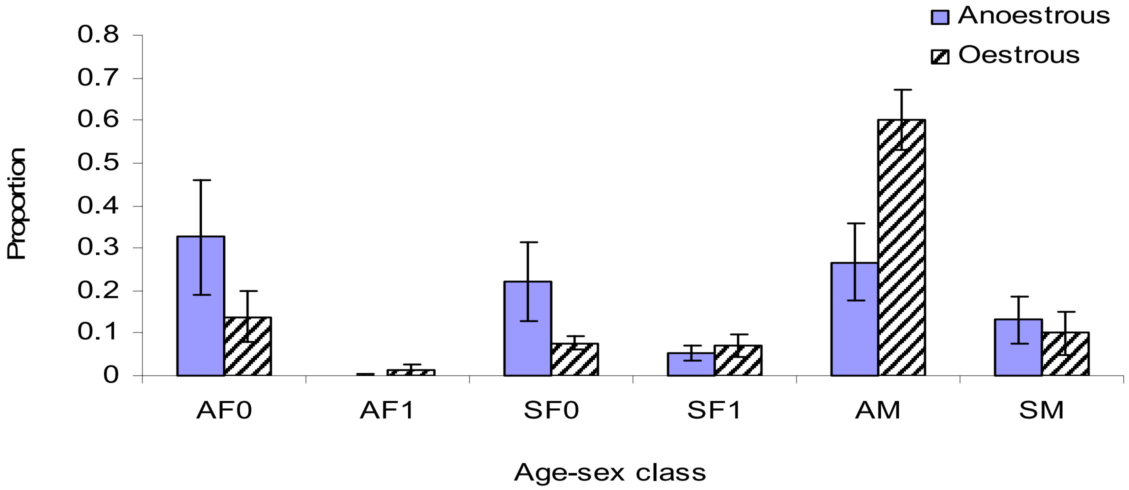

Figure 3.4 The proportion of grooming time (minutes) that subadult females received from different age-sex classes. A-adult, S-subadult, F-female, M-male, 0-anoestrous, 1-oestrous.

3.3.4 Initiation of grooming interactions between males and females

Results from the binomial test (Table 3.4) show that grooming interactions between AM and AF1 were initiated significantly more by the males than by the females (z = -4.087). Grooming interactions between SF0 and AM were initiated significantly more frequently by the females (z = 3.283). Although no other significant differences were found, both AF0 and SF1 were more likely to initiate grooming interactions with AM. Both AF0 and AF1 were less likely to initiate grooming interactions with SM than were the males, however both SF0 and SF1 initiated more grooming interactions with SM than did males.

3.3.5 Termination of grooming interactions between males and females

The only significant difference found was that AM were significantly more likely to terminate grooming interactions than AF1 (Table 3.5).The trend does however, indicate that when involved in grooming bouts with oestrous females, males are more likely than females to terminate grooming interactions.

Table 3.4 Binomial test comparison of the number of initiations by either males or females that resulted in grooming interactions. * indicates where chi-square significance lies. A-adult, S-subadult, M-male, F-female, 0 – anoestrous, 1 – oestrous.

Age-sex class grooming partnership	Grooming bouts (N)	Female initiations (N)	Male initiations (N)	Binomial test (z value)
AF0 and AM	415	316	272	1.815
AF1 and AM	257	123	196	-4.087*
SF0 and AM	164	126	79	3.283*
SF1 and AM	255	208	182	1.317
AF0 and SM	92	54	60	-0.680
AF1 and SM	49	31	34	-0.493
SF0 and SM	87	50	47	0.280
SF1 and SM	127	101	89	0.509

Table 3.5 Binomial test comparison of the number of terminations from grooming interactions made by either males or females. * indicates where chi-square significance lies. A-adult, S-subadult, F-female, M-male, 0 – anoestrous, 1 – oestrous.

Age-sex class grooming partnership	Grooming bouts (N)	Female terminations (N)	Male terminations (N)	Binomial test (z value)
AF0 and AM	415	301	337	-1.425
AF1 and AM	257	131	194	-3.495*
SF0 and AM	164	118	109	0.597
SF1 and AM	255	178	181	-0.158
AF0 and SM	92	72	58	1.228
AF1 and SM	49	30	34	-0.500
SF0 and SM	87	63	68	-0.437
SF1 and SM	127	98	94	0.289

3.4 Discussion

The results of this study confirm earlier reports that sexual swellings influence grooming interactions between chimpanzees (Goodall 1986; Hemelrijk et al. 1992) which supports suggestions that associations of males with females may be a pre-mating component of male reproductive effort (Seyfarth 1978; Smuts 1985). By investing time and effort in grooming interactions with potentially reproductive females, males increase their own chances of siring offspring in the future. Females on the other hand may prefer to form strong social bonds with AM so that when they do display sexual swellings, they minimize the likelihood of being harassed (Anderson and Bierlet 1994).

Grooming patterns between AM and females are found, as predicted, to increase during oestrous periods, whereas grooming patterns involving AF-SM and AM-SF support other primate studies which found that grooming between these age-sex classes is generally either avoided or occurs between low ranking or older AF and SM, which AM will not compete for (Strum and Western 1982; Smuts 1985; Van Noordwijk 1985; Anderson 1986). Both SF0 and SF1 initiated grooming with SM more frequently, suggesting that SF could be using grooming as a means of gaining protection and reinforcing relationships or alternatively these grooming interactions could be association between similar age classes (Mitani et al. 2002)

Oestrous females showed a clear preference for grooming interactions with AM, which is in accordance with the observations by Goodall (1986) as well as studies on captive chimpanzees (Hemelrijk et al. 1992); Barbary macaques (*Macaca sylvanus*) (Wallner et al. 1999) and savanna baboons (Rowell 1968). Adult females showed a tendency to avoid grooming interactions with SM. Although subadults may prefer to associate with adults, they find it is easier to develop and reinforce social bonds with each other for future benefits than risk injury by competing with older and stronger adults. It must also be remembered that there is no clear-cut point at which an individual changes from being a subadult to an adult, and therefore individuals that were classified as subadults by human observers, may have been viewed as young adults by other chimpanzees, which may explain grooming interactions occurring between adults and subadults that coincidently became adults during the study period.

Due to the preference of AM for grooming interactions with AF, it is not surprising that grooming interactions between SF and AM are more likely to be initiated by the SF. These AM may be low-ranking, older males or they may simply recognize the future reproductive potential of these females. Females are subject to more aggression from males whilst displaying sexual swellings (Matsumoto-Oda and Oda 1998), and SF respond to aggression by SM by engaging in grooming interactions with them. Adult females are less likely to initiate grooming interactions with SM despite their reproductive ability, possibly in response to aggression by AM.

To reduce harassment and ensure ‘good’ genes for their offspring, it would be preferable for reproductive females to choose a fully grown, experienced and possibly high-ranking male rather than a smaller, less experienced SM. However, low-ranking AF may have to compete with higher-ranking females for access to high-ranking AM and would possibly rather receive no grooming than risk injury from either the harassing SM or higher-ranking individuals. (Smuts and Smuts 1993). Females also show resistance to copulations with less preferred males during their periovulatory periods when conception is most likely, but are more promiscuous and less selective of copulatory partners during non-periovulatory periods (Stumpf and Boesch 2005).

As hypothesized, males tend to initiate grooming bouts with AF1, whereas when anoestrous, females are more likely to initiate grooming bouts with AM, which supports findings of Wallis (1992). As previously discussed, other benefits of allogrooming may govern grooming interactions during anoestrous periods and as a result social bonds are reinforced, making the occurrence of reproductive opportunities more likely later. The willingness of males to invest increased grooming in females when they come into oestrous may be the final deciding factor for females. Adult females will try and keep preferred males close by for as long as possible, which would explain the increased likelihood of AM terminating grooming with AF1. Grooming could also be terminated due to the arrival of another higher-ranking or older male, which would explain why SM are more likely than AF1 to terminate grooming interactions (Smuts and Smuts 1993).

In conclusion, both age and oestrus swellings have an influence on grooming interactions between chimpanzees. This study further confirms that grooming may be one of the strategies used by males to increase their access to copulation opportunities and by females to increase protection from harassment during swollen periods and possibly increase the opportunity to choose with whom they copulate.

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-Chapter 4-

Grooming distributions and copulations

Abstract

Allogrooming among primates has been suggested as a strategy for enhancing reproductive success, by allowing males to enhance their proximity to oestrous females, or by influencing female choice through the development of affiliative relationships with males. Female chimpanzees have swollen anogenital regions signalling sexual receptivity and by adapting their grooming investment accordingly, males could increase their copulatory success whilst females may increase chances of copulations with preferred males. Five and a half years of data from chimpanzees in the Budongo Forest, Uganda, were examined to test the hypothesis that age class and grooming influence copulatory success in chimpanzees.

Based on the availability of oestrous females at any given time, copulations between males and adult females occurred significantly less than expected, whereas copulations between males and subadult females occurred significantly more frequently than expected. Adult males copulated with both adult and subadult females with equal frequency, although if young adult males were removed from the analysis, adult males copulated with adult females more frequently than subadult females. Adult males copulated with females more frequently than subadult males, suggesting females prefer adult males. A positive relationship between grooming given by males to females and copulatory success was found. The relationships developed during grooming interactions therefore seem to result in a copulatory advantage to males.

Keywords: primate mate choice, courtship, Budongo Forest, grooming

Running title: The influence of age class and grooming on copulation frequency in chimpanzees of the Budongo Forest, Uganda

4.1 Introduction

Grooming behaviour in non-human primates has been well documented with numerous suggestions as to the benefits associated with grooming other individuals (see chapter 1). One of these suggestions is that grooming may be used by individuals to increase their own reproductive success (Weingrill 2000). By using grooming to strengthen social bonds, chances of copulating may also be increased. It may, therefore, be in a male's best interest to invest time and effort in grooming potentially reproductive females rather than non-reproductive ones, whereas females may benefit by developing grooming relationships with strong healthy adult males rather than generally smaller, weaker adolescent males (Anderson and Bierlet 1994).

Energetic investment in the production of offspring is lower for males than it is for females, as more energy is used in the production of eggs than of sperm cells (Trivers 1972). Therefore, the potential for reproductive success is higher for males and is generally directed towards producing quantity whereas for females quality is more important (Anderson 1994). Females are consequently more selective as to who they mate with and, as a result, are a limiting resource for males (Trivers 1972). The reproductive success of males depends largely on their ability to compete with other males for access to reproductive females. Several methods of inter-male competition have been recognised (Anderson 1994), with the importance of different strategies being dependant on various factors relating to individual species as well as ecological factors.

Mating strategies that have been identified in male primates include:

1. Opportunistic – non-competitive, where females are mated by all males (Tutin 1979)
2. Mate guarding – A male actively prevents all other males from mating with a particular female (Tutin 1979; Kummer 1984; Smuts and Smuts 1993; Engelhardt et al. 2004)
3. Consortship – A male and female pair leave the group for a few hours, days or weeks actively avoiding other group members (Tutin 1979; Hrdy and Whitten 1987)
4. Males groom females in exchange for mating opportunities (Soltis 1999)
5. Forced copulations where a male uses speed or strength to catch and physically restrain a female while he copulates her (Clutton-Brock and Parker 1995)
6. Displacement of males whilst copulating by older or higher-ranking males (Tutin 1975)
7. Sperm competition in species where females are copulated by several males resulting in sperm from different males competing within the female's reproductive tract (Dixson 1998)
8. Sneak copulations by low-ranking and non-group individuals (Dunbar 1984; Ohsawa et al. 1993; Berard et al. 1994) including at night time (Goodall 1986; Paul et al. 1993).

Male reproductive success may be further influenced by females choosing who they will allow copulations from (Darwin 1871), thereby further influencing male behaviour around the time of ovulation. Females may be attracted to males by different stimuli such as long courtship, bright colours, 'gifts' or displays (see Anderson 1994 for detailed discussion). Given the evidence for the influence of female choice in animal species (Anderson 1994), female mate choice could be the second major factor interacting with male-male competition to generate mating success in primates (Small 1989), by exhibiting their own mating preferences (Manson 1995). For example, females may accept copulations from certain males during periods of ovulation, whilst during non-fertile periods allow copulations from less preferred but insistent males (Nishida 1997; Nunn 1999; Stumpf and Boesch 2005) thereby reducing harassment.

Suggestions as to why females may copulate with more than one male during an oestrous period include:

1. Sperm competition (Clutton-Brock and Harvey 1976; Hrdy and Whitten 1987; Dixson 1998)
2. Confusion of paternity (Hrdy 1981), which may lead to increased paternal care of offspring (Taub 1980) and reduced chances of infanticide (Hrdy 1979).

Some studies have shown that females may actively choose dominant males (e.g. brown capuchin monkeys*,* Jansen 1984; Welker et al. 1990; vervet monkeys Keddy 1986), prefer copulating with adult males (Grey-cheeked mangabey C*ercocebus albigena* Wallis 1983; orangutans, Schurmann 1982) and actively refuse copulations with younger males (orangutans: Galdikas 1985; Mitani 1985). Females may use grooming behaviour to assess the willingness of males to invest effort in females, and hereby assess the ‘quality’ of males before allowing copulations.

In chimpanzees, which live in multimale-multifemale groups, sexual dimorphism is present which suggests competition between males may contribute to male reproductive success (Plavcan 1999). Through the development of a dominance hierarchy, dominant males are able to exert choice by threatening subordinate males and preventing their mating attempts (Nunn 1999). Whilst several studies have suggested that dominant males have a higher mating success rate than do subordinate individuals (Nishida 1983; Reynolds 2005), others have failed to confirm this (Boesch and Boesch-Achermann 2000). Furthermore, few studies have been able to show a relationship between rank and paternity (Takenaka et al. 1993; Reynolds 2005), suggesting that male dominance rank does not explain all the variance in reproductive success in chimpanzees.

Female chimpanzees have a prolonged period of sexual receptivity as indicated by the presence of anogenital swellings in relation to the time of ovulation, and it is possible that female selection of male partners may be more pronounced than previously thought. A number of studies have shown preferences for certain mating partners (Tutin 1975, 1979; Coe et al. 1979; McGinnis 1979) irrespective of the number of available mating partners (Matsumoto-Oda 1999). Males may therefore have to work harder to gain acceptance from females rather than only compete between each other.

Chimpanzees exhibit both sexually receptive periods through the presence of anogenital swellings (Tutin 1980) and extensive social grooming. DescOestrous (anogenitally swollen) females are groomed more frequently than anoestrous females (Goodall 1986; Hemelrijk et al. 1992; Chapter 3) and therefore grooming may be used by males to gain access to females for copulation. If so, then it would be expected that a positive correlation between the frequency of males grooming oestrous females and copulations would exist. Females may therefore use grooming behaviour to assess the willingness of males to invest effort in females, whereas males may use grooming of oestrous females to increase chances of copulations.

Furthermore, if grooming is used as a strategy to increase reproductive success, the age class of an individual would be expected to have an impact on grooming relationships. Adolescent or subadult females also display sexual swellings but may go through approximately 19 menstrual cycles before becoming fertile (Tutin 1980; Boesch and Boesch-Achermann 2000), which could be a strategy allowing practice of sexual behaviour to ensure insemination with no delay once females become fertile (Short 1976; Turke 1984; Kalkstein 1991). Adult males of some nonhuman primate species show an aversion to mating with subadult females, (Dunbar 1977; Strum and Western 1982; Smuts 1985; Van Noordwijk 1985; Anderson 1986). Possible reasons for this are that subadult females are less likely to conceive, have a successful pregnancy or raise an individual successfully to term (Anderson 1986). Consequently, if grooming is used as a strategy to increase copulations, adult males would show a similar aversion to grooming and copulating with subadult females. Subadult males, on the other hand, may be physiologically capable of inseminating females but are generally smaller, weaker, have shorter canines and are subordinate to adult males and are therefore less effective at protecting females and infants (Anderson and Bierlet 1994). Subadult males should therefore be the less preferred grooming and copulatory age of oestrous adult females.

The aim of this chapter is to determine whether grooming females could be one of the strategies used by males to increase their chances of copulating with receptive females. The main research question that will be addressed in this chapter is: How does the grooming of sexually receptive females by males influence copulations between males and females of different age classes?

Following this the following specific research questions will be answered:

1. How are copulations distributed across different age-sex class combinations?
2. Is there a difference in the number of copulations between males and females of different age classes?
3. Do copulations take place more frequently between adults than between subadults?
4. Are males more likely to obtain copulations from those females that they groomed?

4.2 Study area and methods

4.2.1 Study area

The Budongo Forest Reserve is made up of 793 km² of moist, semi-deciduous forest and grassland, and is situated at a mean altitude of 1100m on the edge of the western Rift Valley in western Uganda (Eggeling 1947; Plumptre 1996). The average annual rainfall of the region is approximately 1400 mm, with a dry season between December and February. Daily mean temperatures ranging between 14ºC and 28ºC (Eggeling 1947).

The Sonso region (1º44' N, 31º33 E'), in which this study was carried out, lies well within the forest and is named after the river flowing through the area. Although most of the forest was selectively logged in the past, the logging industry halted operations within the study area between 1947 and 1952 (Plumptre 1996). This, together with forest dynamics, has resulted in the establishment of various forest types including mixed forest, colonizing forest, swamp forest and ironwood forest in the Sonso region (Eggeling 1947, Reynolds 1992). The study site was established in 1990 and is maintained by the Budongo Forest Project (Reynolds 1992; Plumptre et al. 1997). A system of trails covering an area of approximately 31km² aids travel through the study area, allowing researchers relatively easy access to the forest.

4.2.2 Study group

Between 1990 and 1994 with the effort of Nick Newton-Fisher and field assistants Geresomu Muhumuza and Zephyr T. Kiwede the chimpanzees were followed and eventually allowed observers to follow them at close quarters throughout the day. Individual chimpanzees of the Sonso group have subsequently been habituated, sexed and identified and have all been given a two-letter identification code. The chimpanzees spend most of their time within an area of about 7km² with each individual having its own 'core' area (Newton-Fisher 2000).

During the period of this study, the Sonso group consisted of between 26 and 54 individuals (Table 4.1). Eleven of the Sonso chimpanzees had injured limbs as a result of being caught in snares, set by the local people to catch duiker and forest pigs (Waller and Reynolds 2001). Four other groups of chimpanzees are known to occur within the forest, two (Busingiro and Kaniyo-Pabidi groups) of which are currently being habituated for tourism purposes. The other two groups (The Nature Reserve and Waisoke groups) have not yet been habituated or studied but both share boundaries with the study group. The following abbreviations will be used throughout the remainder of the chapter to refer to different age-sex classes: AM - adult males, AF - adult females, SM - subadult males, SF - subadult females, JM - juvenile males, JF - juvenile females, IM - infant males and IF - infant females.

Table 4.1 The number of individuals within each age-sex class from which grooming interactions were recorded during the five and a half year study period.

Age-sex class	1995/96	1996/97	1997/98	1998/99	1999/2000	2000/2001
Adult males (AM)	12	13	11	12	10	10
Adult females (AF)	10	12	10	15	13	11
Subadult males (SM)	1	2	4	4	3	1
Subadult females (SF)	5	5	5	3	3	2
Juvenile males (JM)	4	4	3	4	4	1
Juvenile females (JF)	0	4	6	7	5	0
Infant males (IM)	4	5	5	4	1	0
Infant females (IF)	5	3	2	5	1	1
Total	**41**	**48**	**46**	**54**	**40**	**26**

4.2.3 Data collection

Data were collected continuously between September 1995 and April 2001 as part of a long-term study on the behaviour and ecology of the Sonso chimpanzees. Eleven field assistants (mean of four at any given time) employed by the Budongo Forest Project conducted sampling daily (weather permitting) between 07h30 and 13h00 and then again between 14h00 and 16h30 on an *ad libitum* basis (Altmann 1974) whilst following the chimpanzees. Each sample recorded the identities of individuals present, interactions between individuals (grooming, playing, aggression, copulations etc) initiators and terminators of interactions, duration of interactions (recorded to nearest minute) and female anogenital swellings.

4.2.4 Analysis

A total of 888 copulations and 666 grooming bouts given by males to females were extracted for analysis. Allocation of scores to females by observers was subjective and may have varied between observers. To minimize this variation, scores of 1 and 2 were pooled, as were scores of 3 and 4. This resulted in three categories, with the following scores: 0 – no swelling, 1 – intermediate swelling and 4 – full swelling. After this adjustment there were very few grooming interactions recorded for females with intermediate swellings, so intermediate and full swelling scores were pooled. Thus, for the purpose of analysis two categories were created with the following scores: 0 – no swelling (anoestrous) and 1 – swelling (oestrous). All grooming interactions involving infants, juveniles, maternal siblings and between mother and offspring were removed so as to eliminate the influence of these classes on grooming interactions.

With the exception of one occurrence (Reynolds 2005), copulations were only observed with females that displayed sexual swellings. It is however, possible that copulations did take place during non-swollen periods since not all individuals were observed all the time, and such behaviour has been observed in other studies (Wallis 1982). Therefore, only grooming data involving swollen females and males were extracted from the data set, along with the copulation data. I acknowledge that different stages of swellings may influence access to copulations as well as the fact that females may display swellings during early stages of pregnancy. These data were however, not available so were not included in the study reported here. The influence of male rank on grooming relationships was not investigated during this study, but has been investigated for this group of chimpanzees by Arnold & Whiten (2003).

A chi-square goodness of fit test (Zar 1999) was used to determine if the observed frequencies of copulations between males and females differed significantly from expected frequencies based on the availability of oestrous females (calculated as the mean number of oestrous females) at any one time during the study period. Bonferroni confidence intervals (Miller 1966; Neu et al. 1974) were performed for those chi-square tests that revealed significant differences to determine preference for or avoidance of different age-sex classes.

As chimpanzees are group-living and because of the problems associated with dependency in an analysis at a dyadic level (Hemelrijk 1990b), this study was conducted at the group level. According to the actor-receiver model, ‘relative’ male-female interchange (Hemelrijk 1990a) occurs when each male directs beneficial acts more often to those females with whom he copulates more frequently. Due to any given dyad being recorded more than once, samples become statistically dependant. Sampling distributions for grooming interactions are not specifiable *a priori* (Schnell et al. 1985) and therefore matrix permutation methods were used to avoid these problems by using observed values to generate a sampling distribution against which to assess the significance of a sample correlation statistic (Hemelrijk 1990a). We used Hemelrijk's (1990a) MATRIXTESTER matrix permutation program as it takes into account individual variation in the tendency to direct a particular behaviour (e.g. grooming) to others, and calculates several association indices between an actor-receiver grooming matrix and its inverse, with a copulation matrix to analyse the degree of interchange. The program randomly permutes columns and rows to generate a sampling distribution for the test statistics derived from the original data matrix. The Kr test statistic (a multivariate version of Kendall's S statistic corrected for individual variation) to measure relative interchange (Hemelrijk 1990a), and a Taukr value, which corrects the Kr value for sample size and ties, is also generated. MATRIXTESTER further calculates a multivariate Mantel's Z coefficient and a multivariate R statistic to measure absolute interchange by assessing the symmetry in the matrices being tested. The R coefficient is a nonparametric version of the Z test and is used in conjunction with the Z test to make up for any deficiencies of the Z test. All tests using this program were carried out using 2000 permutations (Daniel 1978).

4.3 Results

Of the 888 copulations recorded, 43% occurred between AM and AF, 42% between AM and SF, 11% between SM and SF, and 4% between SM and AF (Figure 4.1). Based on the availability of oestrous females at any given time, Bonferroni confidence intervals (Table 4.2) indicated that copulations between males (AM and SM) and AF occurred significantly less than was expected, whereas copulations between males (AM and SM) and SF occurred significantly more frequently than was expected. With the exception of SM and SF, a significant positive correlation ($p<0.05$) was found between the frequency of grooming given by males to females and copulations (Table 4.3). In other words, males were more likely to copulate with those females which they had groomed.

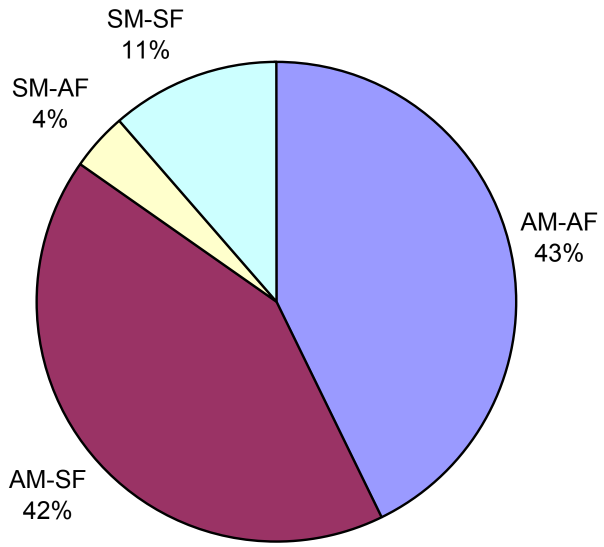

Figure 4.1 The percentage of copulations that each age-sex class combination contributed during the study period. A-adult, S-subadult, M-male, F-female. N= 888 copulations.

Table 4.2 Bonferroni confidence intervals for the number of copulations between oestrous females and males. AF1 – oestrous adult female, SF1 –oestrous subadult female, AM-adult male, SM-subadult male. * = All results are significant at $p<0.05$

Grooming partnership	Availability of oestrus females at any one time during study period	Proportion[8] of availability of oestrous females (*pi◦*)	Number of copulations observed	Proportion observed in each category(*pi*)	Expected[9] number of grooming bouts	Confidence interval (95%) on observed proportion of occurrence(*pi*)[10]	More or less than expected.
AF1 and AM	4	0.667	380	0.505	502	$0.503 \leq p \leq 0.506$	Less*
SF1 and AM	2	0.333	373	0.495	251	$0.494 \leq p \leq 0.497$	More*
AF1 and SM	4	0.667	34	0.259	90	$0.244 \leq p \leq 0.260$	Less*
SF1 and SM	2	0.333	101	0.748	45	$0.740 \leq p \leq 0.756$	More*

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[8] Proportion expected in each category represent expected grooming bout observations if grooming occurred between each category in exact proportion to availability.
[9] Calculated by multiplying proportion *Pi*◦ x n; 0.667 x 753 = 502
[10] *Pi* represents theoretical proportion of occurrence and is compared to corresponding *Pi*◦ to determine if hypothesis of proportional use is accepted or rejected, i.e., *pi* = *pi*◦

Table 4.3 Results of Kr, R and Z tests[‡‡‡] (Hemelrijk 1990a) for correlations between grooming and copulations between males and females of different age classes. All results are based on 2000 permutations. N=16 AM, 13 AF, 6 SM, 5 SF. A – adult, S – subadult, M – male, F – female.

Grooming- copulation partnership	**Taukr**	**P**	**R**	**Z**
AM and AF	0.484	0.0002	2646986.25	1914
AM and SF	0.324	0.0090	157957	2278
SM and AF	0.267	0.0172	127823.5	49
SM and SF	0.230	0.1352	8168.75	594

[‡‡‡] The Kr test statistic (a multivariate version of Kendall's S statistic corrected for individual variation) measures relative interchange, and the Taukr value, corrects the Kr value for sample size and ties. Mantel's Z coefficient multivariate and the R statistic measures absolute interchange by assessing the symmetry in the matrices being tested. The R coefficient is a nonparametric version of the Z test and is used in conjunction with the Z test to make up for any deficiencies of the Z test.

4.4 Discussion

Based on the availability of oestrous SF and AF at any given time during the study period, it was expected that if access to copulations was determined by availability alone, and there being twice the number of available oestrous AF than SF, then males should copulate with AF twice as much as they copulate with SF. However, both AM and SM copulated significantly less frequently with AF and more frequently than was expected with SF which indicates that the availability of oestrous females is not the only factor influencing copulations.

I predicted that males would discriminate between AF and SF in terms of both grooming and copulation since only AF are likely to be reproductive, but we found that males copulated with AF and SF with equal frequency. We suggest two possible reasons for this. Firstly, both display oestrous swellings, and therefore males may not necessarily recognize SF as being potentially sterile. This is, however, unlikely as AM have been found to show a copulatory aversion to adolescents in several species (chimpanzees: Hasegawa and Hiraiwa-Hasegawa 1983; orangutans: Galdikas 1985; captive bonnet macaques: Takahata 1982 and savanna baboons: Rasmussen 1983; Scott 1984). Secondly, AM that are copulating with SF may be low ranking as found in macaques (Takahata 1982; Van Noordwijk 1985; Perry and Manson 1995) or young AM as in Bonnet macaques (Glick 1980) and olive baboons (Scott 1984; Smuts 1985). These young AM may not be able to gain access to AF due to competition with older, higher-ranking males (Boesch and Boesch-Achermann 2000) or resistance by AF themselves but recognize the benefits of developing close social relationships to ensure future reproductive opportunities, once they are older and more experienced. This would also help explain why SF copulated with males more often than expected, as they would be less prone to harassment by higher-ranking males. In a number of species, SF receive the majority of copulations from SM (Anderson 1986), and because they are a less valuable resource, they are less protected by dominant males, therefore inflating the number of copulations. Adult females copulated with both AM and SM less frequently than expected which could be linked to inter-male competition as females would be more likely to move away rather than risk being injured during inter-male fights. Females could prefer males of varying dominance ranks but are intimidated by high-ranking males as in long-tailed macaques (Van Noordwijk 1985), who generally try and prevent females from mating with mid and low ranking males.

Subadult males tend to be displaced or prevented from interacting with oestrous females due to inter-male competition with stronger and more dominant AM, explaining the difference in the number of copulations that SM achieved with SF and AF. This further supports the argument that SF are mating with low-quality males since they are not being defended by the prime males. Adult males, on the other hand, may need the coalitionary support of lower ranking and SM (Reynolds 2005), and therefore would allow these males access to some copulations to ensure this support, further explaining the occurrence of copulations between AF and SM (Vehrencamp 1983). Therefore, females may learn how to behave around males when they are in oestrous in order to increase copulations with preferred males and simultaneously reduce harassment.

It must also be remembered that there is no clear-cut point at which an individual changes from being a subadult to an adult, and therefore individuals that were classified as subadults by human observers may have been viewed as young adults by other chimpanzees, which may explain grooming interactions occurring between adults and subadults that coincidently became adults during the study period. By removing copulations involving individuals recorded as young AM (as defined by observers), 322 copulations took place between AM and AF whilst 270 occurred between AM and SF, thereby making the number of copulations between AM and AF biologically more than that between AM and SF. So, although for purposes of analysis these young AM were initially grouped together with older males, age may influence accessibility to copulations even more noticeably than indicated by the scope of this study.

Oestrous females are more likely to copulate with males that have invested grooming in them than by those males that have not, supporting research on captive chimpanzees (Hemelrijk et al. 1992). Therefore, it appears that grooming could function as a mechanism to enhance reproductive success. However, females are generally groomed more often during oestrous (Chapter 3; Goodall 1986; Hemelrijk et al. 1992) and it may be argued that females might copulate more with their grooming partners because of their proximity during periods of receptivity. This is unlikely since only 223 of the 888 copulations recorded (23%) in this study occurred either, immediately before, during or after a grooming bout between two individuals. The remaining 77% of copulations are therefore not directly associated with grooming interactions or necessarily due to being in association with each other but rather reflects a choice for specific individuals. This indicates that grooming may function to enhance relationships and that female choice may contribute to the observed relationship, rather than males grooming females in order to be proximal and therefore copulate with them. This is further supported by previous primate research which has shown that female chimpanzees and baboons show a preference for males that spend time with them and who engage in high frequencies of affiliative behaviour (Seyfarth 1978; Tutin 1979; Smuts 1985), further explaining why copulations with certain copulation partners were found both in this study and in others (Tutin 1979; Coe et al. 1979; McGinnis 1979).

Although the effect of male rank on copulatory success was not investigated in this study the male 'DN' was alpha throughout the study period and, as would be expected, was recorded to have the most copulations, but tied with another high ranking male (BK) in having the most copulation partners (n = 12). Reynolds (2005) found a significant positive correlation between male rank and copulation rates with older females in this group and also observed that females tend to stimulate competition among the males rather than actively seek out high ranking males. Janie (JN), who at the commencement of the study was classed as a SF and matured into adulthood as the study progressed was observed being copulated on 233 occasions by 15 different males, clearly making her the most promiscuous female, although she was not identified as a high ranking female. Consequently, while there were overall patterns, there were clear individual differences, as expected in primates.

In conclusion, our study found that male chimpanzees appear to increase their chances of copulations by grooming females. Copulations with AF are more beneficial to both AM and SM in terms of reproductive success, but AM are more likely to copulate with AF than SF. If the age class of AM is taken into account, AM will copulate more frequently with AF than SF. If SM and SF are not able to copulate with adults they will copulate with each other, to enhance future reproductive opportunities. Grooming is used as a tactic to enhance reproductive success.

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-Chapter 5-

A comparative analysis of using scan-focal versus *ad libitum* sampling methods in the investigation of grooming behaviour

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Abstract

Scan-focal and *ad libitum* sampling methods were compared to test whether or not they produced the same results during an investigation of the grooming behaviour of free-living chimpanzees. The number of potential grooming dyads recorded between adult males, and between adult males and subadult males were similar for both sampling methods. Both methods found a similar mean number of grooming partners for adult males, but *ad libitum* sampling revealed a higher number of partners for subadult males, adult females and subadult females. Taking the number of individuals of each age-sex class into account and calculating the investment made per adult male, the discrepancy in the percentage of grooming time between the two sampling methods was less than 3%. The slight discrepancies identified between the methods suggest that a*d libitum* sampling methods may be more suitable in studying species which do not move around as a single unit and live in environments where visibility is reduced, therefore increasing the possibility of recording infrequently observed individuals or behaviours, whereas scan-focal sampling may be more suitable in studying species that move around together and occupy habitats offering greater visibility, as it makes it possible to observe all or most group members simultaneously.

Key words: primatology, *Pan troglodytes*, observation methodology

5.1 Introduction.

One concern when dealing with behavioural studies is the reliability of the sampling methods, whether or not the interpretation of the results represents a true reflection of the behaviour being investigated, and whether differences or similarities found between individuals, age-sex classes, behaviours or methods are valid or due to sampling biases (Martin & Bateson 1993). Focal, scan and *ad libitum* sampling methods are some of the common sampling methods used, and although each method has different assumptions and sampling strategies: 1) Focal sampling refers to any sampling method in which all occurrences of specified activities of an individual (s) are recorded during each sample period, or an individual is observed continuously and specified activities recorded; 2) Scan sampling is a technique in which the observer records an individual's or group's activities at predetermined time intervals and 3) *ad libitum* sampling is usually the result of observers recording as much information as possible resulting in behaviours, individuals and duration of activities being recorded on an *ad libitum* basis (see Altmann 1974 for further discussion of these methods).

The human observer however, is an element common to all. This in itself could lead to potential biases in results, as the sex, age and cultural background of the observer may have an influence on data collected: for example, individual animals may react differently to the presence of a female than to a male observer, or may be less likely to flee when only one observer is present than when three are visible (Paterson 2001); male observers tend to overemphasise the importance of the roles of males in the social matrix of a group, whereas female observers tend to overemphasise the roles of females (Altmann 1974); perception varies between observers, although this can be reduced by conducting 'inter-observer reliability' exercises (Paterson 2001); long data collection time periods lead to observer fatigue; in some studies only one observer collects data, whereas in others a number of observers are used and the data collected by the various observers are either analysed separately (Hemelrijk & Ek 1991) or pooled, as occurred during the study reported on here. Other biases that could influence the accuracy of data collected include unequal sampling time due to individual study subjects not all being visible at the same time (Altmann 1974), although this is overcome to some extent when using focal animal sampling (Martin & Bateson 1993). Difficult observation conditions such as thick vegetation or the location of individuals high up in the forest canopy may also lead to potential biases in results (Paterson 2001).

The sampling techniques themselves could also influence the reliability and repeatability of the results, and could influence the conclusions of the study. *Ad libitum* sampling is the least structured technique, and is useful for recording rare but important events, but tends to be biased towards those individuals and behaviours that are most conspicuous. Focal sampling can be difficult under field conditions, as focal animals generally disappear from view at least occasionally. In addition, concentrating on a single animal reduces the number of animals that can be sampled, reflecting the ever-present trade-off between quality and quantity of data. Scan samples enable more individuals to be sampled, but less detail on each individual. Scan sampling also tends to be biased towards conspicuous behaviours. For example, gorillas (*Gorilla gorilla*) tend to be less visible during certain activities (feeding, mating), and so scan samples do not give an accurate representation of the amount of time spent in these activities (Harcourt & Stewart 1984). In order to overcome some of the problems associated with each sampling methods, these methods are frequently combined.

The aim of this chapter was to compare the results of grooming behaviour in free-living chimpanzees using scan-focal (a combination of scan and focal animal sampling) and *ad libitum* sampling methods (Altmann 1974). Two independent data sets were collected by observing the same group of free-living chimpanzees (*Pan troglodytes)* over the same time period. The first data set was collected by one observer using scan-focal sampling (Arnold & Whiten 2003), while the second data set was collected by four observers using the *ad libitum* method.

5.2 Study area and methods

5.2.1 Study area

The Budongo Forest Reserve is made up of 793 km² of moist, semi-deciduous forest and grassland, at a mean altitude of 1100m situated on the edge of the western Rift Valley in western Uganda (Eggeling 1947; Plumptre 1996). The average annual rainfall of the region is approximately 1400 mm with a dry season between December and February. Daily mean temperatures ranging between 14ºC and 28ºC (Eggeling 1947).

The Sonso region (1º44' N, 31º33 E') in which this study was carried out lies well within the forest and is named after the river flowing through the area. Although most of the forest was selectively logged in the past, the logging industry halted operations within the study area between 1947 and 1952 (Plumptre 1996). This, together, with forest dynamics has resulted in the establishment of various forest types including mixed forest, colonizing forest, swamp forest and ironwood forest in the Sonso region (Eggeling 1947; Reynolds 1992). The study site was established in 1990 and is maintained by the Budongo Forest Project (Reynolds 1992, Plumptre *et al.* 1997). A system of trails covering an area of approximately 31km² aids travel through the study area allowing researchers relatively easy access to the forest.

5.2.2 Study group

Between 1990 and 1994 with the effort of Nick Newton-Fisher and field assistants Geresomu Muhumuza and Zephyr T. Kiwede the chimpanzees were followed and eventually allowed observers to follow them at close quarters throughout the day. Individual chimpanzees of the Sonso group have subsequently been habituated, sexed and identified and have all been given a two-letter identification code. The chimpanzees spend most of their time within an area of about 7km² with each individual having it's own 'core' area (Newton-Fisher 2000).

During the time of the data collection for this chapter, the Sonso group consisted of between 50 and 51 individuals: 9-11 adult males, 11-12 adult females, 3-4 subadult males, 4-5 subadult females, 4-5 juvenile males, 6 juvenile females, 4 infant males and 5-9 female infants. The following abbreviations will be used throughout the remainder of the chapter to refer to different age-sex classes: AM – adult males, AF – adult females, SF – subadult females and SM – subadult males.

Eleven of the chimpanzees had injured limbs as a result of being caught in snares, set by the local people to catch duiker and forest pigs (Waller and Reynolds 2001). Four other groups of chimpanzees are known to occur within the forest, two (Busingiro and Kaniyo-Pabidi groups) of which are currently being habituated for tourism purposes. The other two groups (The Nature

Reserve and Waisoke groups) have not yet been habituated or studied but both share boundaries with the study group.

5.2.3 Data collection

Arnold & Whiten's (2003) data on grooming interactions were drawn from 1841 scan samples collected every 15 minutes whilst observing male-only (N=228) and mixed sex parties (N=1089). Focal samples of 30 minute duration (total = 323 hrs) were also collected for all adult and adolescent males and one independent juvenile male, in order to ascertain grooming durations and the frequency of grooming bouts. The data for the *ad libitum* was made up of 1559 bouts and 558 hours. Both sets of data were collected between September 1998 and October 1999. Four field assistants employed by the Budongo Forest Project collected the *ad libitum* data whilst the scan-focal samples were collected by Kate Arnold (Arnold & Whiten 2003). A*d libitum* data were collected by the field assistants daily (weather permitting) between 07:30 and 13:00 and then again between 14h00 and 16h30 whilst following the chimpanzees. Each sample recorded the identities of individuals present, interactions between individuals (grooming, playing, aggression, copulations etc) initiators and terminators of interactions, duration of interactions (recorded to nearest minute) and female anogenital swellings, if present.

5.2.4 Analysis

Analyses used by Arnold and Whiten (2003) were applied to the *ad libitum* data to compare results. The percentage of potential grooming dyads (the possibility that each individual had at least one grooming interaction with every other individual of the group) that performed grooming interactions and the number of grooming partners within age-sex classes were compared descriptively. Wilcoxon signed rank tests were applied to both data sets to determine if AM gave to and received from other AM the same amount of grooming as they gave to and received from other age-sex classes.

5.3 Results

Both the scan-focal and *ad libitum* data indicated that grooming interactions were not evenly distributed throughout the group (Fig. 5.1). However, some differences between the results obtained by means of the two sampling methods were found. Only four of the possible 16 dyads (25%) between SM and SF were recorded by means of scan-focal sampling, whereas 12 of the potential 16 (75%) were recorded by means of *ad libitum* sampling. Ten of the potential 48 dyads (20.5%) between AM and SF were recorded by means of scan-focal sampling and 22 of the potential 48 (45.5%) were recorded by means of *ad libitum* sampling. One of the potential six dyads (16.7%) between SM was recorded by means of scan – focal sampling and four (67%) by means of *ad libitum* sampling. Grooming bouts between 16 of the potential 132 dyads (12.5%) involving AM and AF were recorded by means of scan sampling, whereas 29 (22%) of the potential 132 were recorded by means of *ad libitum* sampling. Differences between the remaining age-sex combinations were relatively small (<7.5% difference).

Although a similar mean number of grooming partners was found using both sampling methods (Table 5.1), *ad libitum* sampling data indicated a wider range of grooming partners for AF, SM and SF, whereas the scan-focal samples indicated slightly wider ranges for AM. Comparison of grooming time that AM gave to or received from different age-sex classes revealed that there was less than an 11% difference between the results achieved by scan-focal and *ad libitum* sampling methods (Table 5.2). When the number of individuals of each age-sex class was taken into account and the investment made per AM (% of individuals grooming time) was calculated, the differences between the results achieved by scan-focal and *ad libitum* sampling methods decreased to less than 3% (Table 5.3). Wilcoxon signed rank tests revealed that both sampling methods indicated that AM gave and received (Table 5.4) significantly more grooming to and from AM than to and from AF and SM, but only the *ad libitum* data revealed that AM gave and received significantly more grooming to and from AM than to and from SF.

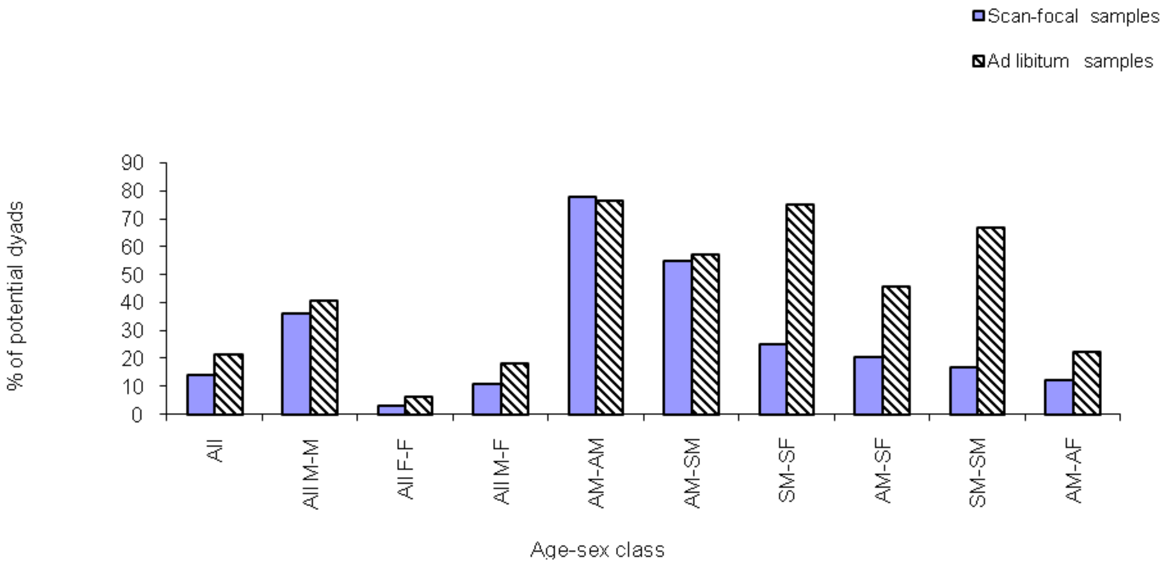

Fig.5. 1. Comparison of scan-focal and *ad libitum* sampling methods with regard to the percentage of dyads in each age-sex class that had grooming interactions. A – adult, S – subadult, M – male, F – female.

Table 5.1 Comparison of scan-focal and *ad libitum* sampling methods with regard to the mean number of grooming partners of different age-sex classes. AM – adult males, AF – adult females, SM – subadult males, SF – subadult females

	Mean number of partners	
	Scan samples	***Ad libitum* samples**
AM and all age-sex classes	13 (range 6-16)	14 (range 1-9)
AF and all age-sex classes	2 (range 2-6)	7.4(range 0-19)
SM and all age-sex classes	7 (range 6-16)	7 (range 0-15)
SF and all age-sex classes	5.5 (range 3-6)	6.4 (range 1-8)
AM and AM	7.5 (range 2-9)	7 (range 4-9)
AM and AF	1.3 (range 0-4)	2.4 (range 1-5)
AM and SF	4(range 0-5)	6.7 (range 5-8)
AF and AF	0.17 (range 0-1)	2.5 (range 1-4)

Table 5.2 Comparison of scan-focal and *ad libitum* sampling methods with regards to the overall percentage of grooming time that adult males (AM) gave to or received from different age - sex classes. AM – adult males, AF – adult females, SM – subadult males, SF – subadult females

	Age-sex class	**Scan (%)**	***Ad libitum* (%)**	**Difference (%)**
AM gave grooming to:	AM	61.6	70.82	9.22
	AF	15.6	7.72	7.88
	SM	4.3	8.91	4.61
	SF	18.6	10.32	8.28
AM received grooming from:	AM	57.4	67.11	9.71
	AF	15.3	12.43	2.87
	SM	9.5	15.34	5.84
	SF	17.8	7.36S	10.44

Table 5.3 Comparison of scan-focal and *ad libitum* sampling methods with regards to the overall percentage of grooming time that adult males (AM) gave to and received from different age-sex classes, taking into account the number of members of each age-sex class. AM – adult males, AF – adult females, SM – subadult males, SF – subadult females

	Age-sex class	**Scan (% per male)**	***Ad libitum* (% per male)**	**Difference (% per male)**
AM gave grooming to:	AM	6.15	6.44	0.29
	AF	1.1	0.58	0.52
	SM	1.4	1.82	0.42
	SF	5.1	2.6	2.5
AM received grooming from:	AM	6.4	6.10	0.3
	AF	0.9	1.04	0.14
	SM	2.9	3.84	0.94
	SF	4.5	1.84	2.66

Table 5.4 Results of Wilcoxon signed rank tests for both scan-focal and a*d libitum* methods with regards to the amount of grooming given and received by adult males (AM) to and from other AM compared to other age-sex classes. AM – adult males, AF – adult females, SM – subadult males, SF – subadult females

	Age-sex class	**Scan (N)**	**T+**	**p**	***Ad libitum* (N)**	**T+**	**p**
Grooming given by AM to:	AM vs AF	10	54	0.002	11	65	0.001
	AM vs SF	10	54	ns	11	55	0.03
	AM vs SM	10	34.5	0.002	10	50	0.01
Grooming received by AM from:	AM vs AF	10	54	0.002	7	27	0.02
	AM vs SF	10	27	ns	11	53	0.04
	AM vs SM	10	52	0.005	9	42	0.01

*significance set at $p<0.05$, ns = not significant

5.4 Discussion

Comparisons of scan-focal and *ad libitum* sampling methods revealed both similarities and differences in results. Both sampling methods confirmed that AM within the Sonso group do in fact groom other AM more than any other age-sex class, supporting other studies that have found chimpanzee groups to be male bonded (Gombe: Goodall 1986; Mahale: Takahata 1990; Kibale: Watts 2000; Taï: Boesch & Boesch-Achermann 2000).

Differences in the percentage of potential partnerships being recorded in grooming interactions by means of scan-focal and *ad libitum* sampling methods are due to some grooming partnerships not being recorded during the scan-focal sampling. These grooming interactions often involved individuals that rarely engaged in grooming interactions with each other, and therefore had more chance of being recorded during the *ad libitum* sampling period. This is to be expected, as *ad libitum* sampling records interactions when they are observed rather than only when they occur within the scan-focal period. Since most grooming in chimpanzees occurs between AM, the possibility of recording these interactions is high when using both methods. This can explain the similarities observed for grooming dyads involving AM and other AM and SM, as well as the similar mean number of grooming partners for different age-sex classes, but differences in the range of number of partners.

The negligible differences (<3%) identified with regard to the percentage of grooming time given and received per AM to and from different age-sex classes indicate that there are no differences in the results obtained, and therefore both scan-focal sampling and *ad libitum* sampling produced similar results with regard to distribution of grooming effort.

Results of the Wilcoxon signed rank tests were similar for both scan-focal and *ad libitum* sampling methods for AM giving and receiving grooming to and from other AM in relation to other age-sex classes, except that analysis of *ad libitum* samples indicated that AM gave and received significantly more grooming to and from other AM than to and from SF, whereas the scan-focal sample analysis did not. However, the pattern of grooming distribution is the same for both methods, which is probably more important than total amounts.

Despite some differences in the comparison of scan-focal and *ad libitum* sampling methods, overall these differences are small and do not seem to affect the overall patterns of grooming of this group of chimpanzees. From the above comparison it can be concluded that:

1. When grooming interactions between individuals occur frequently, such as between AM, both scan-focal and *ad libitum* sampling methods produce similar results.
2. Interactions that do not occur frequently or that involve individuals not often observed may be better represented through *ad libitum* sampling.

From the findings of this study it is suggested that *ad libitum* sampling methods may be beneficial for species such as chimpanzees, which do not move around as a single unit and live in forest environments where visibility is reduced, therefore increasing the possibility of recording rarely seen individuals or behaviours, whereas scan-focal sampling may give optimal results in studies of species that move around together, such as baboons (*Papio spp)*, and occupy habitats which have greater visibility, allowing all or most group members and frequent behaviours to be observed simultaneously. It is therefore possible that the sampling technique used depends on the species biology, habitat type and questions being addressed. This however, needs further investigation. In addition it would be advantageous to have *ad libitum* and scan-focal sampling conducted on the same animals at the same time.

5.5 References

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-Chapter 6-

Synopsis and conclusion

The Budongo Forest in Uganda has been researched since the 1940's when W.J. Eggeling conducted an extensive study into the forest types. During 1962 Vernon and Frankie Reynolds initiated a study on the forest's chimpanzees whilst at Gombe in Tanzania, Jane Goodall was starting her study of chimpanzees. From the mid to late 1960's Yukimaru Sugiyama and Akira Suzuki continued to study the Budongo chimpanzees. Due to civil unrest in Uganda, research in the forest came to a stand still and it was only in 1990 when the Budongo Forest Project (BFP) was set up, did studying the chimpanzees continue. The goal of the BFP has been to gain an understanding of the dynamics of the forest as well as the impact of human activity, both in the form of logging practices and use of forest products by the local community on the flora and fauna of the forest. The outcome of the project is to develop management strategies which allow for both conservation and utilisation.

The Budongo chimpanzees are well habituated to observers and thus offer an ideal opportunity to study and increase the base line knowledge of chimpanzees, whilst also presenting future opportunities for studies of free-living chimpanzees. This study allowed the opportunity to investigate grooming behaviour of one of the few habituated free-living populations of chimpanzees. Numerous other populations have been extensively studied over a period of 42 years (Mitani et al. 2002) and although studies of the Budongo chimpanzees occurred in 1962, it was not until 1995 that the chimpanzees had been habituated to human observers and full-time field assistants were employed to collect long-term data and it is only through the dedication and persistence of these assistants over the years that this study was made possible.

The Budongo chimpanzees, like other populations of free-living chimpanzees consist of a fission-fusion social system (Sugiyama 1968), dominated by male groupings. Using a data set collected over a five and a half year period, the present study was able to investigate grooming behaviour of these chimpanzees. Data collection did not concentrate on a specific age or sex class and therefore allowed for a more general description and comparison of grooming interactions within and between different age-sex classes (chapter 2). As predicted, the distribution of grooming across different age-sex classes was found to be uneven thus confirming that motivations for grooming other individuals is influenced by age and sex. Adults form the foundation of chimpanzee social dynamics and continuously need to reinforce their positioning within the group's social network system. Adults utilise grooming to reinforce social affiliations thereby increasing access to resources, coalitionary support from other group members and opportunities for reproductive success (Hemelrijk 1990; Barton and Whiten 1993; De Waal 1997; Weingrill 2000; Henzi and Barrett 2002). Within the social dynamics of chimpanzees, adult males form the 'core' of social networks explaining why the majority of grooming takes place between them in not only this study but also in others (Goodall 1968; Nishida 1968; Simpson 1973; Wrangham 1986; Nishida and Hiraiwa-Hasegawa 1987; Watts 2000). Based on the social structure of chimpanzees, adult males will have the most benefits or resources to offer other individuals in exchange for grooming. This is reinforced by the finding and confirmation from other studies (Gombe: Goodall 1968, Mahale: Nishida 1979; Nishida and Hosaka 1996; Kanyawara in Kibale: Wrangham et al. 1992; Tai: Boesch and Boesch-Achermann 2000; Ngogo: Watts 2000) that both adults and subadults whether male or female not only allocate most of their grooming time to adult males but also have the majority of their grooming partners as adult males.

Social interactions between adult males and females are generally regarded as being stronger than between adult females, which is confirmed by this study through a similar pattern being observed for grooming relationships. Subadults will be motivated to establish grooming partnerships with adults and subadults for the establishment of future reproductive (Tutin 1979) and coalition opportunities (Bygott 1979), explaining the majority of subadults grooming time being allocated to adult males and then other subadults.

Juveniles and infants are dependant on their mothers and will not establish themselves within the group's social network until they become less independent on their mothers as they reach subadulthood (Reynolds & Reynolds 1965, Pusey 1983). Grooming behaviour is learned through the observation of other, older individuals and would have no or very little direct social significance in these age classes, but rather a more hygienic significance in terms of being cleaned by their mother. Due to the increased importance of grooming in a social context as individuals mature, the number of partners, frequency and duration of grooming bouts increases accordingly and moves from a context of copying or learning to a functional socially significant 'bargaining or resource exchange' tool.

Grooming interactions were generally unidirectional and reciprocated, (although not always immediately), indicating that individuals were more likely to be groomed by those individuals they themselves had groomed supporting other studies (Hemelrijk and Ek 1991; Watts 2000; Arnold and Whiten 2003).

The prevalence of unidirectional grooming bouts could indicate a resource interchange system (Noë and Hammerstein 1995) which suggests that grooming may be exchanged for resources other than grooming or alternatively because overall reciprocation of grooming was found (although not necessarily immediately), grooming may exchanged for grooming, and if the social bonds between individuals is relatively stable, grooming may not to have to be immediately reciprocated (Barrett et al.1999).

Having a multi-male, multi-female social system, competition for access to reproductive partners occurs between both males and females. The presence of anogenital swellings during female sexually receptive periods resulted in grooming interactions between males and females (both adult and subadult) to increase (chapter 3). With there being a higher number of anoestrous females compared to that of oestrous females at any given time during the study period, it was expected that if grooming was based on the availability alone, there would be more grooming bouts between males and anoestrous females. However, both anoestrous adult and subadult females gave and received less grooming from adult males than was expected, whereas they gave and received more than expected when in oestrous. Both anoestrous and oestrous adult females gave and received significantly less grooming from subadult males than expected, whereas anoestrous and oestrous subadult females gave and received more, clearly indicating that adult females whether anoestrous or not did not prefer grooming interactions with subadult males. This clearly shows that availability of potential partners is not the only factor determining the occurrence of grooming interactions.

Grooming interactions between adult males and oestrous adult females were more likely to be both initiated and terminated by males, showing that males were attracted to oestrous females, groomed them to show willingness to invest time and effort in them and then terminated the grooming interaction either by choice or possibly intimidation by another male, whereas females were probably less likely to terminate as the presence of a potentially high ranking male would reduce harassment from other males. Anoestrous females were more likely to initiate grooming interactions with adult males.

Based on the number of oestrous adult and subadult females at any given time, it was expected that if access to copulations was determined by availability alone, then there would be twice the number of copulations with adult females than with subadult females. This was however, not found to occur in this study. Adult females copulated with both adult and subadult males less frequently than expected whereas subadult females copulated with these males more than expected. This clearly indicates that factors are present which reduce the amount of expected copulations for adult females and increase them for subadult females. Because adult females are the preferred copulation sex of adult males, there will be more competition between males for access to females, thereby decreasing the potential availability of these adult females, whereas the less preferred subadult females will be somewhat more available, especially to low ranking or young adult males.

The low number of copulations that took place between subadults reflects the lack of sexual maturity within this age class. Although physiologically capable of insemination, subadult males will be outranked by older or high ranking males for access to adult females. Subadult females although likely to be infertile despite the presence of anogenital swellings, will use these swellings to their advantage and gain access to adult males, albeit only the younger or low ranking adult males. As mentioned in earlier chapters adult males may show a general aversion to copulating with subadult females. Initially this does not appear to be the case in this study. However, it may be that older or high ranking adult males show an aversion to subadult females, whereas young or low ranking adult males being unable to access copulations with adult females, may then copulate with subadult females as investment in potential future reproductive opportunities. Adult females clearly either avoid or are prevented by adult males from copulating with subadult males. As mentioned earlier, adult females may allow copulations from insistent younger males during the early stages of anogenital swellings (Nishida 1997; Stumpf and Boesch 2005), but as their cycle progresses towards ovulation they then become more selective as to whom they will allow copulatory access.

Although copulations didn't necessarily occur immediately before, during or after grooming, males were more likely to obtain copulations with females that they groomed. Firstly, this confirms that grooming and therefore copulation does not necessarily occur due to the mere proximity of two individuals but that an actual preference or choice between members does occur. Secondly, this also confirms that grooming is not only a short term beneficiary tool, but is used over the long term to build and reinforce affiliative relationships between males and females. Grooming is therefore one of the strategies used by males to develop familiarity or 'friendships' with females thereby increasing their chances of copulations.

In chapter 5 of this study, data collected using *ad libitum* and scan-focal sampling methods were compared to establish if different sampling methods yielded different results. This study found that overall the two sampling methods revealed similar results, and discrepancies that were found, were either very small and could be attributed to the scan-focal samples not recording as many grooming partnerships as the *ad libitum* method. The *ad libitum* data revealed a higher number of grooming dyads and in some cases a wider variety of grooming partners, but both sampling methods revealed very similar results in terms of grooming investment made by males to different age-sex classes. Scan-focal sampling may therefore, be beneficial in species which move around together as a single unit such as baboons, in habitats that do not restrict visibility too much, whereas *ad libitum* sampling may be more suited for species such as chimpanzees which do not move around as a single unit and inhabit habitats such as forests which greatly restricts visibility. Furthermore, the results in this study not only validate that the generally not recommended *ad libitum* sampling method does in fact give similar results to that of the more generally accepted scan or focal sampling methods, but also confirms that the overall patterns and determinants of grooming relationships in the Budongo Forest chimpanzees are similar to those of other chimpanzee populations.

Variations that did occur, for example, that mostly unidirectional bouts were recorded but in Pusey's 1990 study of Gombe chimpanzees and Boesch and Boesch-Achermann's 2000 study in Tai, mainly mutual bouts were observed could be influenced amongst other factors by differences in age-sex class ratios as well as differences in resource bases (Barrett et al. 1999). These variables would however, need to be investigated in greater detail in order to tease apart the influences of them on grooming behaviour within free-living chimpanzees.

Overall this study has not only increased the general knowledge base of the sociobiology of chimpanzees but has also supported the hypotheses and questions that were investigated. The information gained from this study can be used to compare results from studies in the future of both the Budongo chimpanzees and other free-living populations of chimpanzees. If the Budongo forest and its chimpanzees are able to survive the encroachment of human development, it would be interesting to see how and if the age and sex ratio composition of the group changes and if these changes influence the patterns and dynamics of grooming behaviour found in the five and a half years of this study. This study therefore forms the basis for future comparative studies for this group of chimpanzees.

6.1 References

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