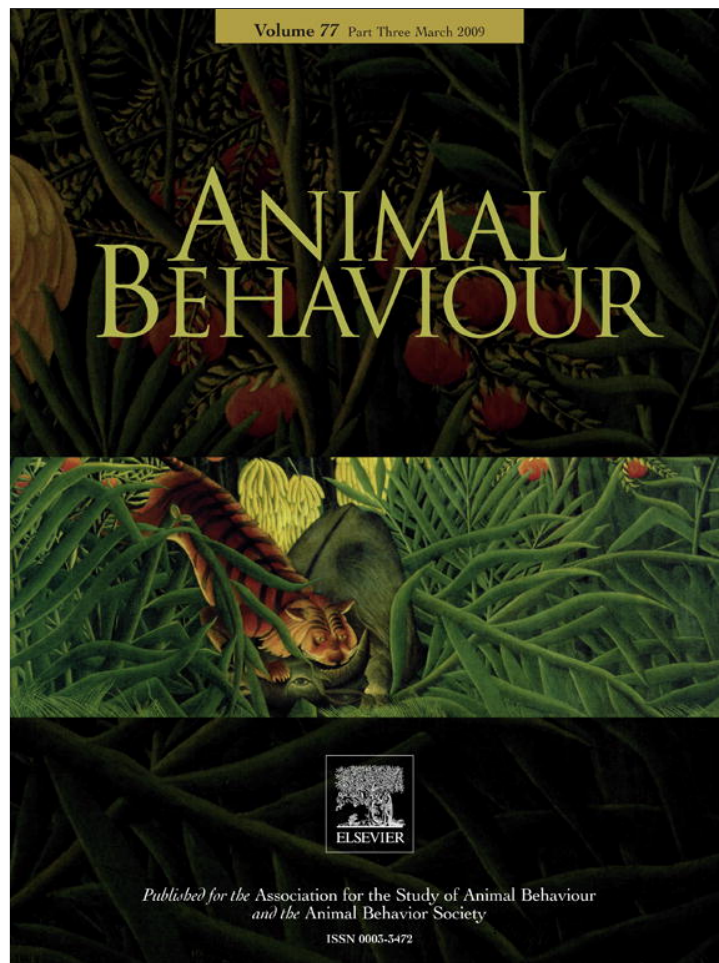


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Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe

Male chimpanzees form enduring and equitable social bonds

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ARTICLE INFO

Article history:

Received 29 September 2008

Initial acceptance 28 October 2008

Final acceptance 18 November 2008

Published online 20 January 2009

MS. number: A08-00627R

Keywords:

chimpanzee

Pan troglodytes

social behaviour

social relationship

Controversy exists regarding the nature of primate social relationships. While individual primates are frequently hypothesized to form enduring social bonds with conspecifics, recent studies suggest that relationships are labile, with animals interacting only over short periods to satisfy their immediate needs. Here I use data collected over 10 years on a community of chimpanzees, *Pan troglodytes*, at Ngogo, Kibale National Park, Uganda, to investigate whether male chimpanzees establish long-term social relationships and to determine the factors that affect variation in relationship quality and the stability of social bonds. Kinship and dominance rank influenced the quality of relationships. Maternal brothers and males of the same dominance rank class groomed each other more equitably than did unrelated males and males that were dissimilar in rank. In addition, males that formed strong social bonds groomed more equitably than did males that displayed weaker bonds. Social bonds were stable over time, with relationships in one year predicting those in subsequent years. Kinship and the quality of social relationships affected bond stability. Maternal half siblings and males that groomed each other equitably maintained longer-lasting bonds than did nonkin and males that groomed each other unevenly. Virtually all of the males established at least one enduring relationship with another individual. The most enduring bonds formed between a few pairs of maternal brothers and dyads that maintained balanced grooming interactions. These results indicate that male chimpanzees maintain long-lasting and equitable social bonds whose formation is affected by maternal kinship and the quality of social relationships.

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Primates are unusually gregarious mammals, which typically interact repeatedly with individually recognizable conspecifics in relatively stable social groups (Smuts et al. 1987). As a result, their social relationships have been subject of intensive study for over a generation (Hinde 1983; Cheney et al. 1986; Silk 2007). Adopting an influential framework developed by Hinde (1979), early fieldwork described primate social relationships with regard to what individuals do with each other, how they do it, and how often interactions occur. These studies provided data on the content, quality, relative frequency and patterning of interactions between individuals (e.g. Seyfarth 1976; Harcourt 1979; Dunbar 1983). Additional research suggested that kin and unrelated individuals cultivate relationships to obtain adaptive benefits (Kummer 1978). For example, maternally related females in many Old World monkey species form long-term alliances to acquire and maintain their dominance rank (Kapsalis 2004). High rank in turn correlates positively with several indirect measures of fitness (Harcourt 1987). Recent observations now indicate that female baboons that form strong social bonds with others reproduce more than do females that develop weaker bonds (Silk et al. 2003). Similarly, female

baboons derive fitness benefits including protection against infanticide and conspecific aggression by establishing long-term friendships with unrelated males (Smuts 1985; Palombit et al. 1997). As a result of this long history of research, primate social relationships are frequently depicted as differentiated and enduring, and as having important reproductive consequences (Hinde 1983; Cheney et al. 1986; Silk 2007).

Recently, this canonical view of primate social relationships has been challenged. In a series of thought-provoking papers, Barrett and colleagues (Henzi & Barrett 1999, 2007; Barrett & Henzi 2002; Barrett et al. 2007) have argued that primates typically do not form long-term relationships with conspecifics. Instead, they suggest that primate social relationships '... need not, and probably do not, take the long-term, temporally consistent form that has been attributed to them ...' and that '... short-term contingent response to current need, may provide a more satisfactory evolutionary account of ... coexistence ...' (Henzi & Barrett 2007, page 73). To support this claim, they furnish observations of female chacma baboons that displayed unstable grooming and proximity relationships over a 4-year period (Barrett & Henzi 2002). Citing this as evidence, they conclude that primates are short-term '... "business partners", not friends' (page 274).

Resolving these different views is difficult because surprisingly few data exist regarding the stability of primate social relationships

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(but see Silk et al. 2006). Chimpanzees, *Pan troglodytes*, provide a model system to investigate whether primates form enduring social bonds. Male chimpanzees in particular are extremely gregarious and engage in a variety of affiliative and cooperative behaviours, including association, grooming, proximity, coalitions, meat sharing and territorial boundary patrols (reviews in: Mitani et al. 2002a; Muller & Mitani 2005). They have been described to form strong social bonds to achieve strategic short- and long-term goals (DeWaal 1982; Nishida 1983; Goodall 1986; Nishida & Hosaka 1996; Mitani & Watts 2001). Male chimpanzees are thus ideal subjects to investigate the stability of primate social relationships.

In this paper, I use data collected over 10 years on an unusually large community of chimpanzees at Ngogo, Kibale National Park, Uganda, to examine whether male chimpanzees establish and maintain long-term social relationships. I begin by evaluating variation in the quality of relationships between male dyads. I then ask whether this and other factors, including kinship, age and dominance rank, affect the stability of social bonds. I conclude by assessing whether male chimpanzees at Ngogo consistently maintain long-term relationships.

METHODS

Study Site and Subjects

I conducted behavioural observations of chimpanzees at Ngogo in the Kibale National Park, Uganda over 10 years from 1998 to 2007. The Ngogo study site lies close to the centre of the 766 km² Kibale Park and near the equator (0°29'53"N, 30°5'0"E) at an altitude of about 1400 m above sea level. The study area is covered with moist, evergreen forest interspersed with patches of *Pennisetum purpureum* grassland. Mean \pm SD annual rainfall at Ngogo is 1397 \pm 174 mm ($N = 10$ years, 1998–2007), with the site experiencing two dry seasons during January–February and June–July. Mean \pm SD minimum and maximum temperatures during 1998–2007 were 16.7 \pm 0.29 °C and 24.7 \pm 0.79 °C, respectively. Struhsaker (1997) provides a detailed description of the Ngogo study site.

Chimpanzees live in communities whose members fission and fuse to form temporary parties that vary in size and composition (Muller & Mitani 2005). The Ngogo chimpanzee community is considerably larger than others that have been studied elsewhere, and at the time of this study, contained approximately 150 individuals, including 24–30 adult males ($\bar{X} \pm SD = 27.2 \pm 2.3$; Mitani 2006a).

Behavioural Observations

I observed adult male chimpanzees for 36 months during the 10-year study period. Observations in 8 of the 10 years were made in 3 months between June and August. In 2 years, 1998 and 2005, data were collected during 6 months between January and June. To obtain data on social behaviour, I followed males during hour-long focal samples and conducted scan samples at 10 min intervals, recording others that were in proximity (≤ 5 m) to or grooming the target subject. Focal males were scored as giving or receiving grooming. Some males died while others reached adulthood during the study period, and as a consequence, all individuals were not observed the same amount of time. Males were followed 1–10 years ($\bar{X} \pm SD = 7.3 \pm 3.4$ years, $N = 35$ males), with the following analyses based on 5410 h of observations (median = 195 h/male, $N = 35$ males).

Kinship, Dominance Rank and Age

Genetic data furnished a means to ascertain the kin relationships between adult males in the Ngogo community. Langergraber

et al. (2007) provide thorough descriptions of the sampling protocol in the field, and laboratory methods, and genetic analyses. Briefly, faecal samples were collected noninvasively from males and stored dry with silica gel after being immersed in ethanol for 24–36 h (Nsubuga et al. 2004). DNA was subsequently extracted and amplified in the laboratory (Bradley et al. 2000; Morin et al. 2001). Individuals were genotyped at 44 autosomal, 13 X-linked, and 13 Y-linked microsatellite loci. Additionally, a 473 base-pair segment of the first hypervariable portion of the mitochondrial DNA control region was sequenced. Likelihood-based parentage and KINSHIP analyses were used to identify maternal and paternal sibling relationships (Marshall et al. 1998; Goodnight & Queller 1999). These analyses showed that there were nine pairs of maternal half siblings and 22 pairs of paternal half siblings among the 35 males in the sample (Langergraber et al. 2007). Recent research indicates that it is extremely difficult to ascertain sibships in natural populations of animals using only autosomal microsatellite genotypes (Csillery et al. 2006; van Horn et al. 2008). The use of a large number of microsatellite loci with three other types of markers with unique sex-specific inheritance patterns facilitated determining sibships with a high degree of confidence.

I used the direction of pant grunts, a formal signal of submission given by low-ranking chimpanzees to higher-ranking individuals, to evaluate the dominance ranks of males (Bygott 1979; Hayaki et al. 1989). I used the MatMan software package (Version 1.0; deVries et al. 1993) to assign ranks to males in each year of the study. MatMan tests the linearity of a dominance hierarchy based on Landau's (1951) index and implements an iterative procedure to rank individuals in a way to minimize the number and strength of inconsistencies between them (deVries 1995, 1998). I averaged the yearly ranks of each male, ordering them from highest to lowest. I then split this ordered list into thirds to classify males as high, medium or low ranking. Males were assigned to the same or a different rank class on this basis.

In the wild, male chimpanzees are conventionally categorized as adults when they reach physical and social maturity at 16 years of age (Goodall 1986). I have studied the Ngogo chimpanzees since 1995, and as a result, the ages of all of the adult males are not known. I used standard morphological and behavioural criteria to estimate male ages (Goodall 1986), and then classified pairs of males as belonging to the same (≤ 5 years age difference) or a different (> 5 years age difference) age class (cf. Mitani et al. 2002b; Langergraber et al. 2007).

Strength of Social Relationships

I used observations of proximity between males to assess the strength of social bonds. Male chimpanzees spend considerable time in close proximity to some members of their communities (Goodall 1986). The maintenance of proximity to conspecifics is a conspicuous aspect of male chimpanzee social behaviour and is correlated with other affiliative and cooperative behaviours displayed by them (Mitani et al. 2000, 2002b). This variable thus furnishes a biologically relevant assay of social relationships in this species.

I computed pairwise affinity indexes between male dyads to determine whether individuals preferentially maintained proximity to each other. Numerically this index is:

$$\frac{I_{ab} \times \sum s_i (s_i - 1)}{\sum a_i (s_i - 1) \times \sum b_i (s_i - 1)}$$

where I_{ab} is the number of appearances of a and b together, a_i is the number of appearances of a , b_i is the number of appearances of b , and s_i is the size of group i (Pepper et al. 1999). I compared observed

pairwise affinity values to a frequency distribution of expected values generated via a group randomization method (Pepper et al. 1999). Here 'groups' are defined in terms of pairs of males that maintained proximity to each other. This procedure repeatedly reshuffles the membership of observed groups, while retaining both the observed number of appearances of each individual and the observed distribution of group sizes. After each randomization, the pairwise affinity index was calculated for each dyad. The ratio of observed to expected values indicates the magnitude of any deviation from expectation. I performed 10 000 randomizations to generate expected values and determined pairs of males that displayed significantly high or low indexes by comparing observed values to the 2.5% tails of the distribution of randomized values. This procedure has several advantages. First, it represents an objective means to evaluate the social preferences of chimpanzees. Second, it controls for each individual's general tendency to interact through implementation of the pairwise affinity index. Third, unlike some other commonly used methods, it provides a way to make statistical inferences about partner preferences.

Some males joined the sample as they matured, while others disappeared as a result of death. Because of this, males were not always together as adults throughout the 10-year sampling period. As a consequence, I used average values of pairwise affinity indexes in some of the following analyses.

Quality of Social Bonds

Grooming represents a major component of a male chimpanzee's social activity budget (Simpson 1973; Nishida & Hosaka 1996; Muller & Mitani 2005) and is generally considered a meaningful measure of social relationships in nonhuman primates (Cords 1997). I therefore used data on grooming behaviour to assay the quality of social bonds between individuals. Specifically, I used observations of grooming given and received to assess whether grooming between pairs of males was balanced or skewed (cf. Silk et al. 2006). For two males, a and b, I calculated the proportion of grooming that b gave to a and subtracted this from the proportion of grooming that a gave to b. I then took the absolute difference of this quantity and subtracted it from 1 as follows:

$$1 - \left| \frac{g_a \rightarrow g_b - g_b \rightarrow g_a}{g_a \leftrightarrow g_b - g_a \leftrightarrow g_b} \right|$$

where $g_a \rightarrow g_b$ is the amount of grooming that male a gave to male b, $g_b \rightarrow g_a$ is the amount of grooming that male b gave to male a, and $g_a \leftrightarrow g_b$ is the total amount of grooming between males a and b. The resulting grooming index ranges from 0 to 1. Zero values indicate situations when grooming is entirely skewed and performed by only male a of the pair, while values of 1 reflect dyads that groom completely equitably. I computed grooming equality values for pairs of males that I observed grooming in 10 or more bouts and limited analyses to these dyads.

Stability of Social Bonds

I adapted a procedure implemented by Silk et al. (2006) to evaluate how long males maintained strong social bonds. I began by identifying males that displayed proximity pairwise affinity indexes that were greater than expected by chance in each year of the study (see above). For each male, I then counted the number of successive years that he maintained these significantly high indexes with others, allowing a gap of 1 year between successive years. For example, if male a had significantly high pairwise affinity indexes with male b during 5 consecutive years, I considered that they formed a strong social bond for 5 years. If pairwise affinity

indexes between males a and b exceeded chance expectations in 1998, 1999 and 2001, but not in 2000, I concluded that they had a strong social bond for 4 years.

Statistical Analyses

Social relationships between pairs of males were the focus of this study, and individuals thus appeared more than once in the following analyses. Because samples were not independent, conventional statistical tests were not used. Instead I used resampling statistical procedures to circumvent the problem created by nonindependence (Manly 1997). In these analyses, I used the difference between the mean values of the categories being compared as test statistics (e.g. grooming equality values or the duration of social bonds between maternal and paternal kin or between males that belonged to the same or different rank and age classes). I evaluated test statistics relative to expected frequency distributions generated by resampling the values in the original data. To produce these expected distributions, I reshuffled observed values in the categories being compared, ensuring that resampled categories included the same number of observations as in the original data. I then computed the means of both categories in the resampled data, using the difference between these two values as a single data point. I iterated this process 10 000 times to produce expected frequency distributions. Comparing test statistics to expected distributions furnished a means to make statistical inferences regarding null hypotheses.

In some of the following analyses, I asked whether one factor affected another variable while controlling for a third, potential confound. In these cases, I used restricted randomization two-factor ANOVAs (Edgington 1995). This procedure is similar to the resampling tests outlined above but reshuffles values within the category being controlled to create expected frequency distributions.

To investigate the stability of social bonds, I asked whether social bonds between pairs of males in one year predicted their bonds in subsequent years. Here I performed K_r matrix correlation tests using pairwise affinity indexes in one year and comparing them with indexes computed in the following year (Hemelrijk 1990a). Only males present in both years could be used in these tests, with nine tests conducted over the 10-year sample period. To reduce the probability of committing type I errors when making these nine comparisons, I adjusted the criteria of significance downward using the sequential Bonferroni technique (Holm 1979). I conducted an additional series of τ K_r partial correlation analyses (Hemelrijk 1990b) to eliminate the possibility that relationships between years were due to maternal kinship, a potential confound.

I examined the relationship between the quality of male social relationships as assayed by grooming equality values and the duration of male social bonds using a Pearson r statistic, and I used a randomization test to evaluate the significance of the correlation coefficient (Manly 1997). I eliminated dyads that were maternal half siblings and performed a similar analysis to test the hypothesis that the relationship between these two variables was influenced by maternal kinship.

I conducted a final analysis to investigate whether males formed long-term social bonds with specific individuals. In this, I limited the sample to males that had the potential to form such bonds. This included 28 of the 35 chimpanzees that were observed a minimum of 5 years. I used the procedure outlined above to determine how long males maintained strong social bonds (see 'Stability of Social Bonds'). I then calculated the maximum number of years that each male maintained a strong bond with another individual. To assess whether the observed maximum durations of bonds formed by

each of the 28 males were long, I created confidence intervals by bootstrapping the observed number of years that males maintained strong bonds with others. Bootstrapped samples included 28 pairs and were replicated 10 000 times. I then compared the upper limit generated by these bootstrapped samples to the durations of the longest bonds formed by the 28 males. Because several males were involved in these comparisons, I adjusted the upper confidence limit higher, with maximum bond durations assessed against an upper limit of 99.91% ($=\frac{1}{2}$ of 0.05/28).

RESULTS

Effects of Kinship, Rank and Age on the Quality of Social Relationships

Male chimpanzees typically display nonrandom patterns of grooming and do not groom all members in their own community (Nishida & Hosaka 1996; Watts 2000; Arnold & Whiten 2003). Grooming data were thus available for only a subset (343) of the 595 male dyads in the sample. Kinship affected the quality of grooming interactions as maternal half siblings groomed more equitably than did male pairs that were unrelated (resampling test: $P < 0.025$; Fig. 1). Dominance rank also influenced grooming relationships. Unrelated males that belonged to the same dominance rank class groomed each other more equitably than did males that were dissimilar in rank (resampling test: $P < 0.01$; Fig. 1). In contrast, paternal relatedness and male age did not affect the quality of grooming interactions. Grooming equality values did not differ between paternal half siblings and unrelated individuals or between unrelated peers and nonpeers (resampling tests: $P > 0.50$ for both comparisons; Fig. 1).

Social bonds also affected grooming equality. Some pairs of males showed strong social bonds by maintaining close proximity to each other. These dyads displayed observed proximity pairwise affinity indexes that exceeded those expected on the basis of chance. Alternatively, males that were weakly bonded showed observed values that were less than expected values. Males that

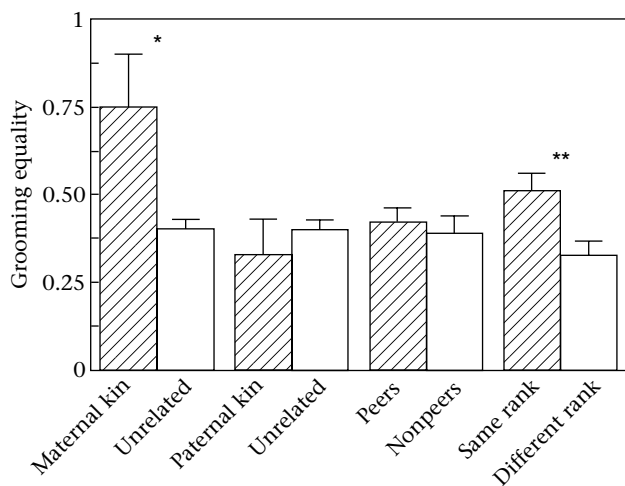


Figure 1. Effects of maternal kinship, paternal kinship, age and dominance rank on grooming equality. Grooming equality assays the degree to which grooming between males is balanced or skewed. Values of 1 indicate situations where males spend equal amounts of time grooming each other, while zeros represent pairs where only one male grooms the other. Means \pm 1 SE are shown for maternal half siblings ($N = 9$ dyads), paternal siblings ($N = 7$ dyads), unrelated males ($N = 94$ dyads), unrelated peers ($N = 53$ dyads), unrelated nonpeers ($N = 41$ dyads), unrelated males that belonged to the same rank class ($N = 39$ dyads), and unrelated males that belonged to different rank classes ($N = 55$ dyads). * $P < 0.03$; ** $P < 0.01$.

had strong social bonds defined in this way groomed more equitably than did males with weaker bonds (resampling test: $P < 0.02$; Fig. 2). Maternal kinship and dominance rank represent two potential confounds since both variables affect the strength of social bonds and grooming equality (see above and Mitani et al. 2002b). Additional analyses, however, revealed that the strength of social bonds continued to predict grooming equality after controlling for the effects of kinship and rank (resampling tests: $P < 0.02$ for both analyses).

Stability of Social Bonds

Six of the 35 males in the sample died during the 10 years of observations included in these analyses. Thirteen others were included in the sample only after they attained adulthood sometime during the 10 years covered here. Thus, there was considerable variation in the number of years that pairs of males were co-resident. Some males did not co-reside with each other as adults, while others did so during the entire 10-year study period. Males co-resided an average \pm SD of 5.4 ± 3.6 years ($N = 595$ dyads). Over half of all pairs lived together as adults for at least 5 years ($56\% = 336/595$), with 23% (136/595) co-residing during the entire 10 years of observation.

The likelihood that social bonds endured over time varied. To compute these probabilities, I divided the number of dyads that maintained strong social bonds for a given number of years by the total number of pairs that lived together for the same number of years (cf. Silk et al. 2006). Fifty six per cent of all pairs of maternal kin, 68% of paternal kin, 66% of unrelated peers and 48% of unrelated nonpeers maintained strong social bonds that lasted at least 1 year (Fig. 3). In general, kin maintained strong social bonds longer than did unrelated males (Fig. 3).

Social bonds between pairs of males were stable across years. Matrix correlation tests revealed that social bonds in one year predicted those in subsequent years ($Tau K_r$ tests: $P <$ sequential Bonferroni criterion for all 9 comparisons). Kinship represents a potential confound because maternal kinship affected the formation of social bonds (see above). Social bonds in one year nevertheless continued to predict those in following years after controlling for kinship effects (partial $Tau K_r$ tests: $P <$ sequential Bonferroni criterion for all 9 comparisons).

I investigated the effects of kinship, age and dominance rank on the stability of strong social bonds. Because males did not co-reside

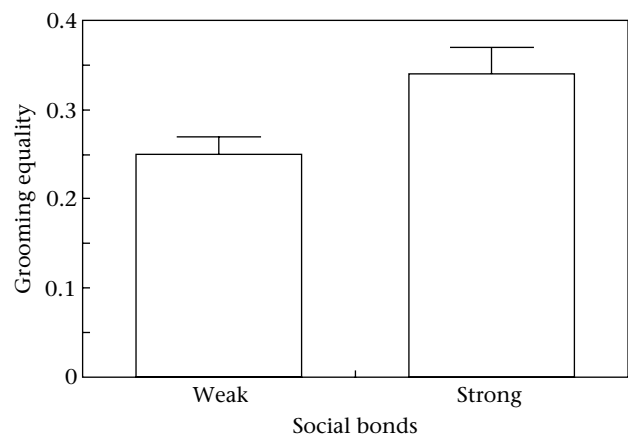


Figure 2. Effect of the strength of social bonds on grooming equality. Strong social bonds were formed by males that displayed observed proximity pairwise affinity indexes that were greater than those expected by chance ($N = 179$ dyads). Weak bonds were formed between pairs whose observed indexes were less than chance expectation ($N = 148$ dyads). Mean values \pm 1 SE are shown.

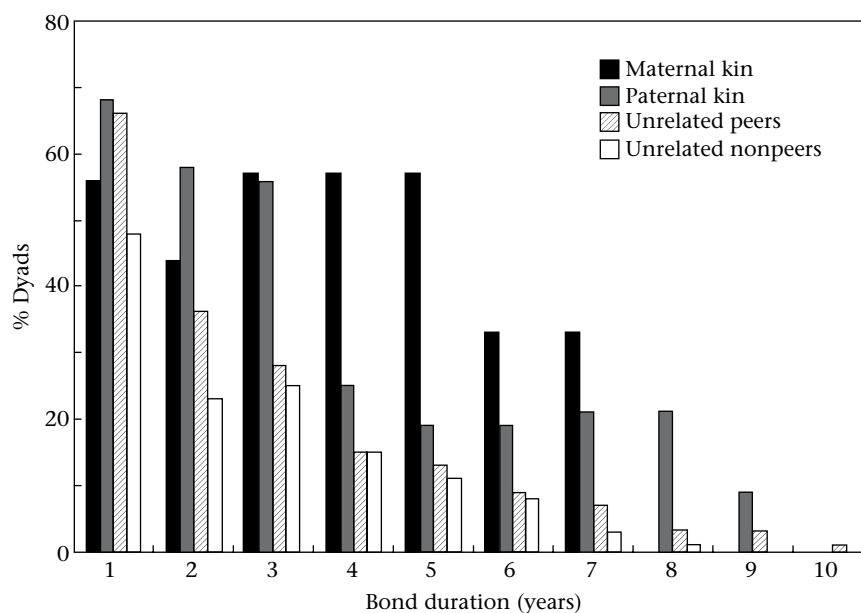


Figure 3. Durations of strong social bonds formed between maternal half siblings, paternal half siblings, unrelated peers and unrelated nonpeers. The percentage of dyads that maintained strong social bonds over time is shown. Values were computed by dividing the number of dyads that maintained strong social bonds at least x years by the total number of dyads that lived together x or more years. See text for further explanation.

the same amount of time, co-residence time represented an obvious confound (see above). In the following analyses, I controlled for variation in the length of time that pairs lived together by splitting the sample into dyads that co-resided a short (≤ 5 years) or long time (≥ 6 years). Maternal brothers formed bonds that lasted longer than did those between unrelated individuals (resampling test: $P < 0.03$; Fig. 4). In contrast, paternal kinship, male age and dominance rank did not influence the stability of social bonds. Paternal half siblings maintained social bonds longer than did unrelated individuals, but this difference was only marginally significant (resampling test: $P = 0.08$; Fig. 4). Bonds between unrelated males that were close in age did not last any

longer than those formed between unrelated males that were dissimilar in age (resampling test: $P > 0.70$; Fig. 4). Similarly, males that differed in rank maintained social bonds for periods that lasted as long as those between males that belonged to the same rank class (resampling test: $P > 0.50$; Fig. 4).

The quality of male social relationships affected the stability of social bonds. Males that groomed each other equitably had the most enduring bonds. Grooming equality between dyads was positively related to the number of years that male displayed strong social bonds (Pearson correlation: $r_{325} = 0.28$, $P = 0.0002$; Fig. 5). Maternal half brothers groomed each other more equitably than did unrelated pairs of males (Fig. 1) and also formed bonds that lasted longer than those between nonkin (Fig. 4). Because of this, maternal kinship was a potential confound that may have led to a spurious relationship between grooming equality and the duration of bonds. This possibility can be ruled out because the positive

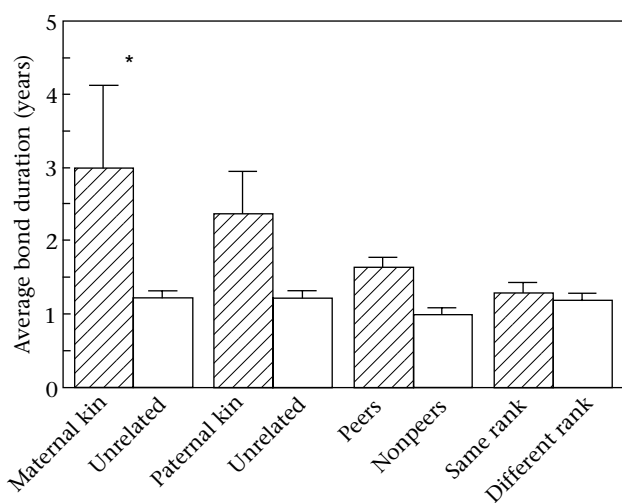


Figure 4. Effects of maternal kinship, paternal kinship, age and dominance rank on the duration of social bonds. Means ± 1 SE are shown for maternal half siblings ($N = 9$ dyads), paternal half siblings ($N = 22$ dyads), unrelated males ($N = 510$ dyads), unrelated peers ($N = 192$ dyads), unrelated nonpeers ($N = 318$ dyads), unrelated males that belonged to the same rank class ($N = 170$ dyads) and unrelated males that belonged to different rank classes ($N = 340$ dyads). * $P < 0.03$.

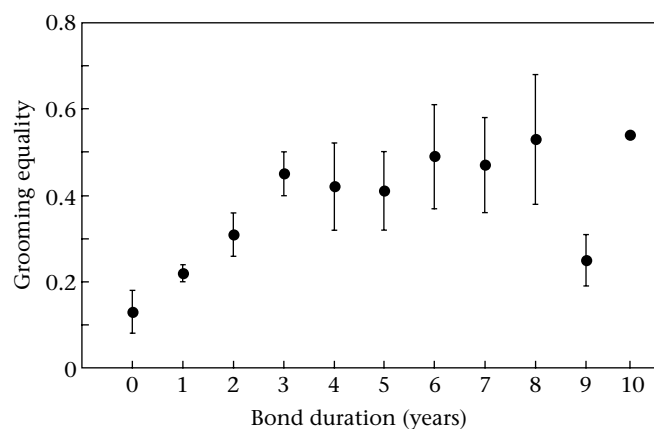


Figure 5. Relationship between grooming equality and the duration of social bonds. Bond duration is the number of consecutive years that males displayed proximity pairwise affinity indexes that were greater than those expected by chance. Grooming equality values of dyads that displayed strong social bonds over different lengths of time are plotted. Means ± 1 SE are shown.

association between these two variables persisted after eliminating maternal half siblings from the analysis ($r_{325} = 0.27$, $P = 0.0002$).

Long-term Social Bonds between Specific Pairs of Males

The 28 males that were observed 5 or more years formed strong social bonds with others that varied from 1 to 10 years ($\bar{X} \pm SD = 1.8 \pm 0.7$ years, $N = 28$ males). Each male typically formed at least one enduring relationship with another individual, with the maximum durations of these averaging 7.1 years ($SD = 2.0$, $N = 28$ males). Twenty five per cent of all of the males in the sample (7/28) maintained a strong social bond with another male during the entire time that they were observed. One pair remained strongly bonded over the 10-year study period, while another individual maintained a strong bond during the 9 years that he was followed. Three males were observed over 5 years and an additional male was followed for 6 years, during which time they each formed a consistently strong bond with others. The 21 other males in the sample formed strong bonds that typically spanned relatively long periods. With the exception of two males, each maintained at least one bond that that lasted well over half of the time that he was observed ($\bar{X} = 75\%$ of observation time, $N = 21$ males).

Bootstrapping the observed durations of bonds between all dyads confirmed that virtually all of the males formed one relationship that lasted a considerable amount of time. Only two males failed to establish an enduring bond with others. The 26 other males maintained bonds that fell outside the upper confidence limit generated by the bootstrap (Fig. 6a).

Neither age nor dominance rank influenced the maintenance of the longest social bonds formed between males. The most enduring social bonds occurred between members of the same age and rank class less than half of the time (age: 39% = 11/28 pairs; rank: 29% = 8/28 pairs). In contrast, maternal kinship and the quality of social relationships affected the formation of extremely long bonds. Four pairs of maternal half siblings lived together as adults 5 or more years. These dyads formed social bonds that lasted 7, 7, 7 and 5 years ($\bar{X} \pm SD = 6.5 \pm 1.0$ years). The 7-year-long bonds manifest by three of these pairs occurred during most of the time that they were observed; two dyads were sampled together over 8 years, while data for the other pair were collected during 9 years. Finally, males that formed the longest social bonds groomed more equitably than males that formed shorter bonds (resampling test: $P < 0.03$; Fig. 6b). Despite the strong effect of maternal kinship, these males were often unrelated. Twenty-two of the 28 males in the sample formed their longest bond with an unrelated individual. Six of the seven males that formed strong bonds during the entire time that they were observed (see above), maintained these relationships with nonkin. The one remaining male maintained a strong bond with his paternal half sibling.

DISCUSSION

The preceding analyses indicate that adult male chimpanzees at Ngogo form equitable and long-lasting social bonds. Kinship and dominance rank influenced the quality of relationships. Maternal brothers and males of the same dominance rank class groomed each other more equitably than did unrelated males and males that were dissimilar in rank. In addition, males that formed strong social bonds groomed more equitably than did males that displayed weaker bonds. Social bonds were stable across years, with relationships in one year predicting those in subsequent years. Kinship and the quality of social relationships affected the stability of these bonds. Maternal half siblings and males that groomed each other equitably maintained longer-lasting bonds than did nonkin and males that groomed each other unevenly. Finally, virtually all of the

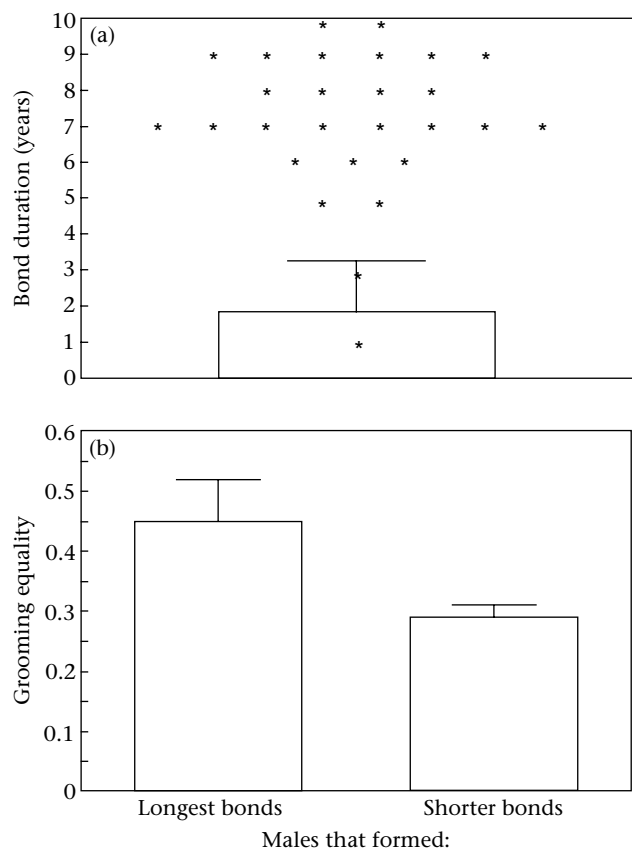


Figure 6. Enduring social bonds between male chimpanzees. (a) Mean + 99.91% confidence limit of the durations of social bonds between males. Asterisks (*) indicate the longest bond maintained by each male in the sample. These show that 26 of 28 males maintained extremely long social bonds with others. (b) Effect of grooming equality on the longest bonds formed by males. Grooming equality values between pairs of males that formed especially long bonds in Fig. 6a ($N = 26$ dyads) are compared with values of other males that maintained bonds over shorter periods ($N = 295$ dyads).

males in the community established at least one enduring relationship with another individual. The most enduring bonds formed between a few pairs of maternal brothers and dyads that maintained balanced grooming interactions. In summary, these results indicate that maternal kinship and the quality of social relationships affected the formation of equitable and enduring bonds between male chimpanzees.

The results presented here bear on two major issues in the study of primate behaviour. First, current controversy exists over the nature of primate social relationships. Although primates are frequently portrayed as forming long-lasting social bonds with conspecifics (Hinde 1983; Cheney et al. 1986; Silk 2007), remarkably few studies have actually shown this to be the case. Field observations conducted over relatively short periods typically reveal that primates bias their behaviour towards kin and age-mates (e.g. Silk et al. 1999; Mitani et al. 2002b). As a consequence, long-lasting social bonds will inevitably emerge whenever these individuals co-reside in the same social group for several years. The characteristic sex bias in dispersal found in many primate species is likely to generate such situations frequently (Pusey & Packer 1987), and consistent with this logic, recent research indicates that female yellow baboons, *Papio cynocephalus*, invest in long-term relationships with maternal kin, age-mates and individuals that are close in dominance rank (Silk et al. 2006). Another study, however, suggests that female chacma baboons, *Papio ursinus*, develop relatively

weak, short-term bonds between themselves (Barrett & Henzi 2002). In general, the paucity of data has made it impossible to formulate general statements about the stability of primate social relationships. In this context, male chimpanzees provide an apt test case as they maintain strong bonds that are commonly assumed to endure over long periods (e.g. Goodall 1986; Muller & Mitani 2005). The preceding findings furnish the first empirical demonstration that they do so, with some relationships lasting up to 10 years. Although male chimpanzees interact with others in a contingent manner to satisfy their current needs, the enduring social bonds established between some pairs go well beyond the short-term 'business partnerships' hypothesized to typify the behaviour of other primates (Barrett & Henzi 2002; Henzi & Barrett 2007).

The long-term social bonds maintained by male chimpanzees bear a striking resemblance to those that have recently been documented in female yellow baboons (Silk et al. 2006). In both male chimpanzees and female baboons, kinship and dominance rank similarity influence the strength of social bonds, with pairs that form strong bonds displaying the most egalitarian grooming relationships. Dyads with the most egalitarian grooming relationships in turn maintain the longest-lasting bonds, sometimes over substantial periods. These parallels across taxa are particularly notable and provide compelling evidence that primate social relationships are stable and continuous over time. The similarities between male chimpanzees and female baboons draw specific attention to how the quality of relationships may influence their maintenance and stability. Additional data from a wider range of primate taxa are needed to determine the extent to which these findings can be applied more broadly across the primate order.

Kin selection theory predicts that animals will bias their behaviour towards their close relatives to obtain indirect fitness benefits (Hamilton 1964). Because female primates maintain enduring bonds with their offspring and males often disperse from their natal groups (Nicholson 1987; Pusey & Packer 1987), it is frequently hypothesized that primates will cooperate with and aid maternal kin, a hypothesis consistently validated by empirical observations (Kapsalis 2004; Silk 2006). Alternatively, internal fertilization coupled with multiple mating by females makes it difficult to ascertain paternity, and thus, to determine whether primates bias their behaviour towards paternal relatives. Nevertheless, observations now suggest that female monkeys preferentially associate with their paternal sisters and that male baboons selectively aid their own infants (Widdig et al. 2001; Smith et al. 2003; Buchan et al. 2003). The long-term data presented here accord with findings derived from prior cross-sectional analyses and confirm that maternal kinship influences the behaviour of male chimpanzees in important ways (Langergraber et al. 2007). Maternal half siblings form equitable and long-lasting social bonds with each other. Additional results show that male chimpanzees do not alter their behaviour with their paternal relatives. Paternal kinship does not affect the quality or duration of male chimpanzee social relationships. These data are consistent with those from previous work showing that male chimpanzees neither discriminate nor interact differentially with paternal kin (Langergraber et al. 2007). These results are in sharp contrast to the additional finding of the current study that maternal kinship influences male behaviour. Male chimpanzees, however, do not always have close maternal relatives throughout their lives. As a consequence and as shown here, long-lasting relationships form between kin and nonkin alike, a result that corroborates our earlier finding that male chimpanzees cooperate frequently with nonrelatives as well as relatives (Langergraber et al. 2007).

A significant, unanswered question that emerges from this study concerns the cognitive mechanisms that male chimpanzees use to maintain their long-term relationships. The hypothesis that

primates fail to develop enduring relationships is based in part on the assumption that they do not possess the requisite cognitive skills to do so (Barrett & Henzi 2002; Henzi & Barrett 2007; Barrett et al. 2007). That such relationships do in fact form belies this idea, but leaves unanswered how bonds are formed and maintained and the mechanisms that male chimpanzees use during the process. Further study will be necessary to investigate these issues. Additional research is also required to clarify the selective benefits that males derive by forming long-term social relationships. Male chimpanzees are well known for cooperating with others, trading goods and services that are both similar and different in kind over the short term. For example, males share meat, a scarce and valuable resource, nonrandomly and reciprocally with others, and also exchange it for coalitionary support (Mitani & Watts 2001). Coalitionary support is reciprocated between pairs (Mitani 2006b) and has important effects on dominance rank relationships. Individual males typically achieve alpha status via the coalitionary support provided by others (Nishida 1983; Nishida & Hosaka 1996). High-ranking males in turn do better reproductively than do lower-ranking males (Constable et al. 2001; Boesch et al. 2006). As these examples suggest, male chimpanzees are likely to obtain several short- and long-term fitness benefits by developing and maintaining enduring social bonds with both kin and unrelated individuals. The exact nature of these awaits future study examining how long-lasting social bonds influence the reproduction and survival of males that form them.

Acknowledgments

My fieldwork has been sponsored by the Ugandan National Parks, Uganda National Council for Science and Technology and the Makerere University. I am grateful to G. I. Basuta, J. Kasenene and the staff of the Makerere University Biological Field Station for logistic support. J. Lwanga, A. Magoba, G. Mbabazi, L. Ndagizi, A. Tumusiime and D. Watts provided assistance in the field. I thank J. Silk for inspiration and comments on the manuscript. My research has been supported by grants from the Detroit Zoological Institute, L.S.B. Leakey Foundation, National Geographic Society, the U.S. National Science Foundation (SBR-9253590, BCS-0215622, IOB-0516644), University of Michigan and Wenner-Gren Foundation for Anthropological Research. This research was approved by the University Committee on the Use and Care of Animals (UCUCA), University of Michigan under UCUCA Research Applications 6793A (3 June 1997), 7472 (20 May 1999), 8436 (20 May 2002) and 9035 (25 April 2005). I dedicate this paper to Barbara Smuts for her collegiality, friendship and long-term social support.

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