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9 • Relationships of male chimpanzees in the Budongo Forest, Uganda

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INTRODUCTION

Relationships between individuals are essentially the product of individual efforts to cope with environmentally imposed selection pressures in a social context. They emerge from repeated interactions between individuals, providing the social structure within which the individuals operate (Hinde 1976). In chimpanzees (*Pan troglodytes*), this structure is especially fluid (Goodall 1965; Reynolds & Reynolds 1965; Nishida 1979). The relationships that an adult male chimpanzee has with other males within his community appear to be both key components in the struggle for high social status within a community, and crucial for successful inter-community territorial encounters (Bygott 1979; Wrangham & Smuts 1980; Wrangham 1986; Nishida & Hosaka 1996; Boesch & Boesch-Achermann 2000). High social status is thought to increase the ability of males to monopolise females and so achieve higher mating success (Sugiyama & Koman 1979; Tutin 1979; Hasegawa & Hiraiwa-Hasegawa 1983). In social situations where a single male may not be able to monopolise access, a pair of males may be able to do so, providing a direct mating benefit to the cooperating males (Goldberg & Wrangham 1997; Watts 1998). Relationships may also provide proximate benefits beyond support in agonistic confrontations, which may, in turn, lead to higher social status, and serve to reduce both social tension and individual stress (Kawanaka 1990; de Waal 1996).

Despite the value of cooperative relationships to male chimpanzees, they appear to show little long-term loyalty to one another and can be extremely fickle in their allegiances (Nishida 1983; Uehara *et al.* 1994; Nishida & Hosaka 1996). Resident for their entire lives within their natal community (unless their mother transfers while they are still young and dependent upon her) adult males will share a long history of interactions and, ultimately, of unreliable relationships. Social status is relative, and there can be only one alpha male. In a fission–fusion society in which the composition of any one grouping is ephemeral and unpredictable (Chapman *et al.* 1993), the shifting sands of male relationships are likely to produce social tension with males vying with one another to build and maintain supportive relationships with individuals they cannot trust because they themselves are pursuing their own selfish interests.

Each relationship that a male has with the other males of his community may at any one time be affiliative, neutral, or antagonistic, and this may change repeatedly. Keeping a relationship affiliative, and thus supportive in some sense, means investing time and energy in that relationship. Grooming of one individual by another is an obvious indication of a willingness to make such an investment, as both time and energy are limited. When there are many possible partners and little time, individuals may be forced to invest disproportionately, focusing on the particular relationships that are currently or potentially more important (Dunbar 1988; Watts 2000b). The pattern of this investment is likely to be demonstrated by the interactions between individuals and will reflect the current, and possibly influence the future, state of relationships.

Male chimpanzees typically spend more time grooming than do females, and more time grooming each other (Wrangham 1986; Nishida & Hiraiwa-Hasegawa 1987). If particular males are desirable and the number of supportive relationships any individual can form is limited, there may be competition for these partners. Males holding high social status may be attractive grooming partners for other male chimpanzees, as high status individuals may be more able to provide support during agonistic encounters. In support of this idea, grooming between males appears (sometimes, but not always) to be directed 'up the hierarchy' (Simpson 1973; Takahata 1990; Hemelrijk & Ek 1991; Nishida & Hosaka 1996; Watts 2000b).

Where grooming does not conform to this pattern, it may be that other characteristics are more important in determining which individuals will be most desired (e.g. age: Bygott 1979), or that high status males need to develop relationships that buffer them from challenges to their status (Nishida & Hosaka 1996). If grooming is a behaviour that is used tactically – with flexibility to increase the future success of the actor most effectively – as it has been described (de Waal 1982; Nishida 1983; Koyama & Dunbar 1996; Nishida & Hosaka 1996), then the way it is distributed may appear more idiosyncratic and not be directly influenced by existing positions in a status hierarchy. Any effect of status may only be apparent when many males are present in a community (cf. Sambrook *et al.* 1995; Watts 2000b): with only a few males, each may be a valuable ally irrespective of his status.

For direct interactions, such as grooming and those that lead to establishment of social status, to take place, individuals must first associate with each other. Under a fission–fusion social system, male chimpanzees may have considerable freedom to alter these association patterns. If chimpanzee parties – the fluid subgroups that make up the social environment – are not passive aggregations of individuals drawn independently to the same resource patches, but the result of active behaviour aimed at altering the make-up of that social environment, then their composition will be a compromise between the optimal mix for each individual (Newton-Fisher 1999). Males may, for example, limit their association with individuals who might interfere with their grooming, or tend to associate with individuals with whom they could engage in grooming (Watts 2000b).

If this is the case, then association patterns themselves may well be an expression of male relationships, and a similar logic applies to the spatial positioning of individuals within parties. Although close proximity is an obvious prerequisite to grooming it may also allow for future possibilities of grooming, perhaps by simply providing an easy choice of grooming partner, or possibly by attempting to exclude others from approaching: a 'zone of control' approach, as seems to work for males who are mate-guarding females (personal observation). Greater distances between individuals, if a regular occurrence, may indicate a degree of avoidance between males who find themselves in the same party. An individual consistently on the periphery of parties may be suffering from some form of social exclusion.

This chapter examines the expression of male relationships for chimpanzees from the Sonso community in the Budongo Forest, Uganda. Data are drawn from the first behavioural study of chimpanzees from this community (Newton-Fisher 1997), which was the first in Budongo since the 1960s (Reynolds & Reynolds 1965; Sugiyama 1968; Suzuki 1971). In particular, this chapter addresses the extent to which observed patterns of association and proximity are indicative of male relationships, and the extent to which the expression of male relationships is governed by social status. The study took place during a period of social instability, with a change in alpha male, and this chapter examines changes in association, proximity, and grooming and their relationship to concurrent changes in social status.

METHODS

Study site

Male chimpanzees of the Sonso community in the Budongo Forest were studied intensively between August 1994 and December 1995. The forest, covering some 428 km^2 in western Uganda, is classified as moist, semi-deciduous, tropical forest and has a history of selective logging (Eggeling 1947; Synnott 1985; Plumptre 1996). The Sonso region (1°44′N, 31°33′E) lies close to the centre of the forest. Members of the study community were individually recognised, named and assigned a two-letter identification code. During this study period, the community contained 12 adult males (DN, VN, BK, MG, KK, MA, BY, MU, TK, CH, JM, NJ) and three adolescent males (ZT, AY, ZF). In addition, there were 14 adult females, and with births and immigrations, the total community size increased to 46 by the end of the study.

Data collection

Focal animal and scan sampling techniques (Altmann 1974) were used to record systematically behaviour and interactions of the 15 subjects between October 1994 and December 1995. During this period, individual males were sufficiently habituated to human observation so that they could be followed at close quarters on the ground, although they were noticeably nervous when unfamiliar observers attempted to follow them.

Scan sampling recorded the identity of each chimpanzee present. These data were used to determine patterns of association. A total of 5117 scan samples, collected every 15 minutes during systematic observation, were collected on parties containing at least one of the adult or adolescent males.

Individual males were subjects of 30-minute focal samples, during which a continuous, timed, record of the behaviour of both the focal and of his nearest neighbour was made. Behaviours relevant to these analyses were: grooming, pant-grunt vocalisations and agonistic acts (detailed below). The 30-minute sampling duration was chosen during initial observations as the maximum length of time for which subjects could be kept under continuous observation with intense data collection. Focal subjects were rotated according to a randomised list, and a minimum time interval of 15 minutes separated consecutive focal samples. Sampling of individual focal subjects was distributed across daylight hours. A total of 1023 30-minute focal samples were collected.

At the start of each focal sample, an instantaneous scan sample of the relative locations of all individuals within a 10-m radius of the focal male was taken. These were used to determine measures of within-party proximity. All proximity scans were separated by at least 45 minutes. The 10-m limit was imposed by habitat-related visibility constraints. A record of the movements of individuals within this area was maintained during the focal sample.

Data analysis

Association was defined as membership of the same party. To associate, or to be an associate, was to be in the same party. Any pair of subjects, whether or not in association, was regarded as a specific dyad. The tendency of males to associate was calculated using a standard twice-weight association index, which was then expressed as a Z-score. Details of the analysis technique and method used to reduce dependency between consecutive samples are presented elsewhere (Newton-Fisher 1999).

To measure positioning of individuals within parties, three Indices, expressed as Z-scores, were derived from proximity scans, after discarding records where no male was within 10 m of the focal. These Indices were (1) the frequency of each dyad existing as 'focal–nearest neighbour'; (2) this frequency weighted by the reciprocal of the distance (estimated by eye to the nearest 0.5 metre) separating the individuals; and (3) the frequency with which an individual was nearest, or second-nearest, neighbour to the focal. In generating Index 2, physical contact was arbitrarily assigned a distance of 0.5 m. Visual estimation of distance was as accurate as using a range finder (≤25 m: $t_s = 1.08$, df = 19, $p = 0.29$; ≤10 m: $t_s = 0.35$, df = 6, $p = 0.74$). Using reciprocal distance attached greater importance to close proximity. As with association, a standard index formed the basis of these measures:

$$P_{AB} = (N_{AB} + N_{BA}) \;/\; (F_A + F_B) \qquad (9.1)$$

[N_{AB}, number of observations with B as nearest neighbour to A; N_{BA}, number of observations with A as nearest neighbour to B; F_A, as number of focal samples of A; F_B, number of focal samples of B.]

Frequencies of grooming were extracted from the focal animal samples, recording which individual was performing the grooming, and which was being groomed. Breaks in grooming in excess of 1 minute were used to mark the end of individual bouts. Frequencies of grooming were corrected for different levels of association by dividing grooming frequency by the frequency of association for each particular dyad. To examine how dyads differed in their grooming, these frequencies were converted into Z-scores, which give a measure of grooming relative to the average level across all male dyads.

A cardinal index of social status was constructed by combining observations of pant-grunt vocalisations and agonistic acts. These were primarily from focal samples, but included relevant ad libitum observations. Five behaviour patterns were lumped together as 'agonistic': threats, displacements/supplants, displays, attacks and chases. Frequencies of interactions were corrected for different observation times of individuals, and ratios based on win/loss (agonistic) and received/given (pant-grunts) criteria were calculated (Fournier & Festa-Bianchet 1995). For each individual these were summed, such that pant-grunts received were combined with agonistic acts performed, and that sum transformed using natural logarithms of square-rooted data. This transformation normalised the data, and the resultant measure was a cardinal index of social status (Newton-Fisher 1997). The broad applicability of this method has been confirmed with data from the Mahale M-group (unpublished results). Individuals who cooperated repeatedly in agonistic interactions were defined as alliance partners. Only one such partnership could be clearly identified: DN & VN, who performed joint displays. A second partnership, between MG & BY, was thought by observers to exist but could not be unambiguously confirmed.

These indices, constructed from data collected throughout the 15-month study period, were used to investigate whether association, proximity and grooming could be regarded as expressions of the relationships between males, and what produced the variation in these behaviour patterns between individual males. Grooming was examined both at the group level and at the dyadic level using observations of grooming-partner choice. These were recorded during focal sampling. The choosing individual was the male that moved into close proximity to a second (the chosen individual); whichever male started to groom first was regarded as initiating the grooming bout.

Table 9.1. *Social status of males in the Sonso community*

	Full study				
Identity	Ordinal rank	Status level	Status index	Jan–Jun 1995 Status index	Jul–Dec 1995 Status index
DN	1	Alpha	2.64	2.15	2.80
VN	2	Beta	2.50	2.15	2.62
BK	3	High	1.12	0.33	1.27
MG	4	High	0.94	1.13	0.87
MA	5	High	0.66	0.62	0.38
CH	6	High	0.43	0.34	0.23
JM	7	High	0.27	−0.32	0.33
BY	8	Mid	−0.18	0.22	−1.28
KK	9	Mid	−0.27	−0.16	−0.36
NJ	10	Mid	−0.55	−0.92	−1.07
MU	11	Mid	−0.65	−1.23	−0.11
ZF	12	Low	−1.20	—	−1.25
TK	12	Low	−1.20	−0.92	−1.18
ZT	14	Low	−1.41	−1.41	−1.02
AY	15	Low	−1.47	−1.92	−1.56

Note:
Indices of social status are given for the full 15-month study period, and for each of the two 6-month blocks in 1995.

The analyses focused particularly on investigating the degree to which social status influenced variation in the way male relationships were expressed. Since this study took place while the alpha male was being replaced, data collected over the 12 months of 1995 were partitioned into two 6-month time blocks, which were then compared to investigate the impact of changing social status on the expression of male relationships.

Parametric statistics were used when the data appeared not to violate underlying assumptions; where these were violated non-parametric methods were used. Extensive use was made of matrix correlation procedures (Hemelrijk 1990) and Mantel regressions (Smouse *et al.* 1986) to avoid problems stemming from possible dependencies in the data. These tests determine significance by generating repeated permutations of the data matrices to produce a distribution of the test statistic against which its probability can be assessed (Adams & Anthony 1996). Matrix correlations are expressed as Kendall's τ values to make the strength of the correlation intuitively obvious (Dietz 1983; Hemelrijk 1990).

RESULTS

Status

In common with male chimpanzees elsewhere, the Budongo males showed clear dominance components in their relationships. While each male could be assigned a unique social status, these clustered into at least four distinct groups: low status (four males), mid-status (four males), high status (five males) and an alpha/beta alliance partnership (Table 9.1).

Patterns of association

For all adult and adolescent males, the average (median) number of associates was either seven or eight. With the exception of the old and disabled TK, all of the adult males spent similar amounts of time associating with other males, and were with at least one other adult male for over 90% of the time (mean percentage time as only male in party = 7.89 ± 4.44%).

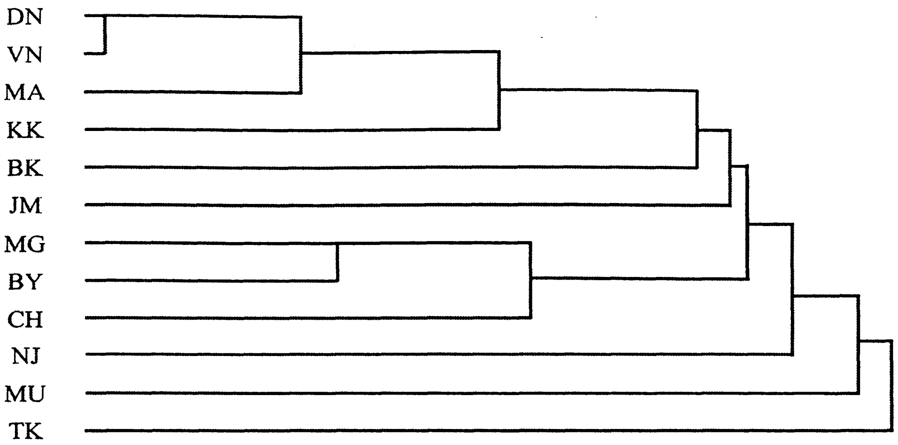

Fig. 9.1. Spatial proximity. Patterns of proximity for the 12 adult males in the study community. Dendrogram produced from UPMGA cluster analysis of weighted proximity indices.

WHAT INFLUENCED ASSOCIATION?

There was a large degree of variation in the tendency males had to associate with others; some dyads were more frequently together than others. Association indices for all 105 dyads varied from -0.88 to $+3.87$ (Z-scores, 15 individuals, calculated over 15 months). The presence of swollen 'oestrus' females increased association between males (Kruskal–Wallis $H = 492.11$, $df = 4$, $p < 0.0001$), but this effect was asymptotic, with the average number of males remaining stable at around four while numbers of 'oestrus' females increased to two and above. Association patterns of male chimpanzees were apparently dominated by preferential association with particular other males. Males preferred to associate in small parties (Newton-Fisher 1999), and showed stronger association with higher status males ($K_r = 609$, $\tau = 0.45$, $p < 0.01$).

Proximity

The average (median) distance between nearest adult males within a party was 1 m (inter-quartile range 0.5–3 m, $n = 72$ dyads).

WAS PROXIMITY AN INCIDENTAL RESULT OF ASSOCIATION?

The frequency with which males were nearest neighbours varied between dyads (-1.83 to $+3.72$; Figure 9.1). Much of this variation was due to variation in association (Mantel regression: $Z = 105$, $p < 0.0001$; $r^2 = 0.65$). As might be expected, the proximity index based on nearest and second nearest neighbours was even more the product of association ($Z = 110$, $p < 0.0001$; $r^2 = 0.72$.). However, some dyads were frequently nearest neighbours within a party, but rarely close to each other, while others were infrequently nearest neighbours but, when they were, the distance between them was short. Known (DN & VN) and presumed (MG & BY) alliance partners, for example, had high positive values for proximity, greater than would be predicted on the basis of their positive association tendencies.

Variation in association explained far less of the variance in proximity when this was weighted by the reciprocal distance separating nearest neighbours (Mantel regression: $Z = 82$, $p < 0.05$; $r^2 = 0.40$), supporting the intuitive idea that distance between nearest neighbours was an important measure, and that spatial positioning within parties was an expression of male relationships beyond that demonstrated by association.

WHAT WAS THE EFFECT OF SOCIAL STATUS?

Relationships between high status males (excluding the alpha and beta males) influenced their proximity. Dyads consisting of two of these males had significantly greater values for weighted proximity than dyads containing only one, or none, of these males (Table 9.2: $F_{2,63} = 6.86$, $p < 0.01$; post hoc Scheffé test). This difference did not exist when the (unweighted) frequency of proximity was used ($F_{2,63} = 0.83$, ns). While many of these dyads had close to average levels of association and proximity, when they were nearest neighbours, inter-individual distances were particularly short.

Male chimpanzees showed no apparent preference for individuals of similar status as nearest neighbours, instead demonstrating a preference for nearest neighbours who

Table 9.2. *Proximity of high status males*

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

Note:
Mean residuals (± standard deviation) from regressions of unweighted and weighted frequencies of dyadic proximity against dyadic association, grouped by the number of high status (excluding alpha and beta) males comprising the dyad.

Table 9.3. *Status and nearest neighbour preference*

	Proximity measured by		
	Nearest male		
Hypothesis Preference for:	Frequency	Weighted frequency	Nearest/ second nearest frequency
Same status level	0.06	0.09	0.03
Other status level	−0.04	−0.09	−0.01
Higher status level	0.16[b]	0.27[a]	0.23[a]
Lower status level	−0.17	−0.19	−0.25[a]

Notes:
Results of K_r tests (matrix correlations) are presented as τ values.
[a] Indicates significant results at $\alpha = 0.05$; [b] indicates an apparent trend (i.e. just not significant at $\alpha = 0.05$).

were of higher status and an avoidance of being one of the nearest two males to lower status males (Table 9.3).

Grooming frequencies

WHAT WAS THE EXTENT OF INDIVIDUAL VARIATION?

The frequency at which males groomed one another varied between dyads, even once grooming frequencies were corrected for differing levels of association. Some males groomed more frequently than others, showing marked preferences for particular partners (Figure 9.2). Whether or not males groomed often was indicated by the deviation in grooming frequency from an average level across all males, and variation in this measure within an individual across potential partners provided an indication of preference. The maximum (most positive) deviation for individual males varied from −0.33 to 3.25. The lowest of these (−0.33) was for the late adolescent male ZT, who showed extremely low levels of grooming other males. This may have been related to his age, but may also have been symptomatic of a problem which culminated in his death at the hands of other males in the community in 1998 (Fawcett & Muhumuza 2000).

WAS THIS VARIATION DUE TO ASSOCIATION PATTERNS?

Association patterns appeared to have little impact on grooming frequencies at a group level (Mantel regression: $Z = 108.14$, $p < 0.01$, $r^2 = 0.07$), although individual males groomed other males in a way that was related to their level of dyadic association ($K_r = 466$, $\tau = 0.37$, $n = 15$, $p < 0.01$) and received grooming similarly ($K_r = 323$, $\tau = 0.27$, $n = 15$, $p < 0.01$). Dyads with higher than average levels of association had higher than average levels of grooming. This pattern was apparent despite correcting the grooming frequencies for differing degrees of association. However, the seven dyads with grooming frequencies far greater than the average (Z-score >1.96) were not the same pairs of males who showed similarly high levels of association (six dyads), and while 18 dyads (grooming) and 15 dyads (association) showed frequencies greater than one standard deviation above average, only eight dyads showed these levels of both grooming and association.

WAS THIS VARIATION DUE TO PROXIMITY PATTERNS?

As might be expected, there were strong correlations between grooming and proximity. Males groomed individuals with whom they were in frequent proximity (frequency: $K_r = 220$, $\tau = 0.34$, $n = 12$, $p < 0.001$; weighted frequency: $K_r = 363$, $\tau = 0.56$, $n = 12$, $p < 0.001$), and received grooming similarly (frequency: $K_r = 170$, $\tau = 0.27$, $n = 12$, $p < 0.01$; weighted frequency: $K_r = 275$, $\tau = 0.43$, $n = 12$, $p < 0.001$). As grooming requires close proximity, investigating whether males simply groomed those that were nearby requires looking directly at the choice of grooming partners (below).

WAS THIS VARIATION INFLUENCED BY SOCIAL STATUS?

Higher status males appeared to groom more frequently ($K_r = 533$, $\tau = 0.43$, $n = 15$, $p < 0.001$) and also to be groomed

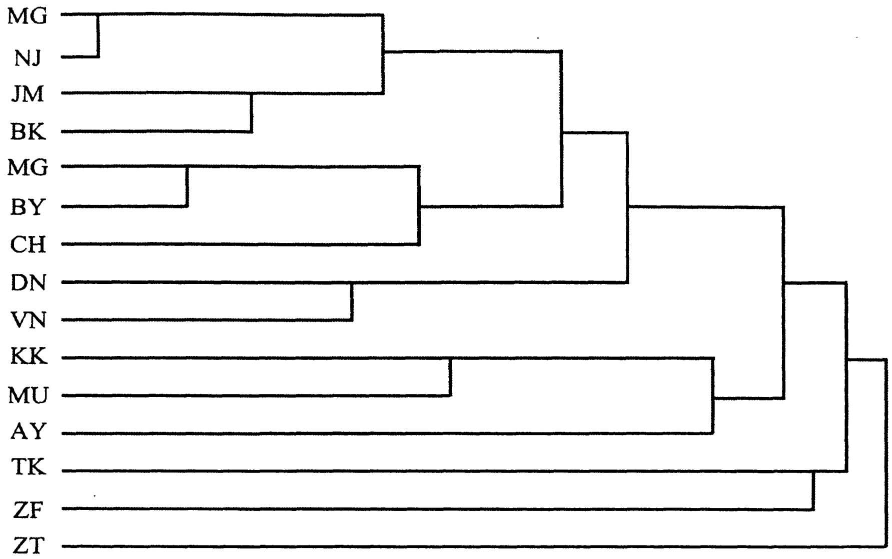

Fig. 9.2. Grooming. Patterns of grooming for the 15 adult and adolescent males in the study community. Dendrogram produced from UPMGA cluster analysis of grooming indices combining grooming performed and received.

more frequently, although this was a weaker effect ($K_r = 251$, $\tau = 0.21$, $n = 15$, $p < 0.05$). The relationship between social status and grooming was curvilinear (grooming: $r^2 = 0.51$, $F_{2,12} = 8.15$, $p < 0.01$; groomed: $r^2 = 0.71$, $F_{2,12} = 18.23$, $p < 0.001$), with the high, but not highest, status males performing most of the grooming. This pattern probably accounted for the reciprocation of grooming, both at the 'relative' level (a rank order distribution of grooming: $K_r = 694$, $\tau = 0.61$, $n = 15$, $p < 0.001$) and at the 'absolute' level (a distribution of grooming in proportion to that received: Mantel $Z = 39544$, $n = 15$, $p < 0.001$).

Choice of grooming partners

Males were observed selecting a grooming partner from two or more potential partners on 81 occasions. In 41 cases the choice was between two males, in 40 cases between three to six males. In 74 cases (91.4%) the choosing individual was responsible for initiating grooming.

DID PROXIMITY AFFECT GROOMING CHOICE?

The distance between individuals appeared to have only minimal impact on the choice of grooming partner. In 31 cases (38%) at least one rejected potential partner was as close to the choosing male as was the selected partner. In the remaining 50 cases, the nearest individual was chosen in 24 cases, a more distant individual in 26 cases. The average (median) distance to the chosen individual was less than to rejected potential partners (Mann–Whitney $U = 5235.5$, $n_{\text{selected}} = 81$, $n_{\text{rejected}} = 155$, $p < 0.05$), but when selecting one of only two possible partners there were no significant differences in the distance between the choosing individual and the selected and rejected partners (Wilcoxon sign ranks test: $z = -0.99$, ns).

WERE HIGHER STATUS MALES MORE ATTRACTIVE GROOMING PARTNERS?

The average (median) status of chosen individuals was higher than those rejected (Mann–Whitney $U = 464$, $n = 36,36$, $p < 0.05$). The number of potential grooming partners was correlated with the status of the choosing individual ($r_s = 0.25$, $n = 79$, $p < 0.05$). This presumably was the result of the preference for higher status individuals as proximity partners, giving higher status males a slightly wider range of potential grooming partners. High status individuals were also approached more rapidly than low status individuals ($r = -0.026$, $n = 60$, $p < 0.05$). The response of the groomed individual (mutual grooming, reversal of grooming, terminating grooming bout) was not related to either the status difference between the individuals (Kruskal–Wallis: $H = 5.6$, df = 3, ns) or the status of the selecting individual ($H = 1.52$, df = 3, ns), although there was a trend for higher status individuals to terminate without returning the

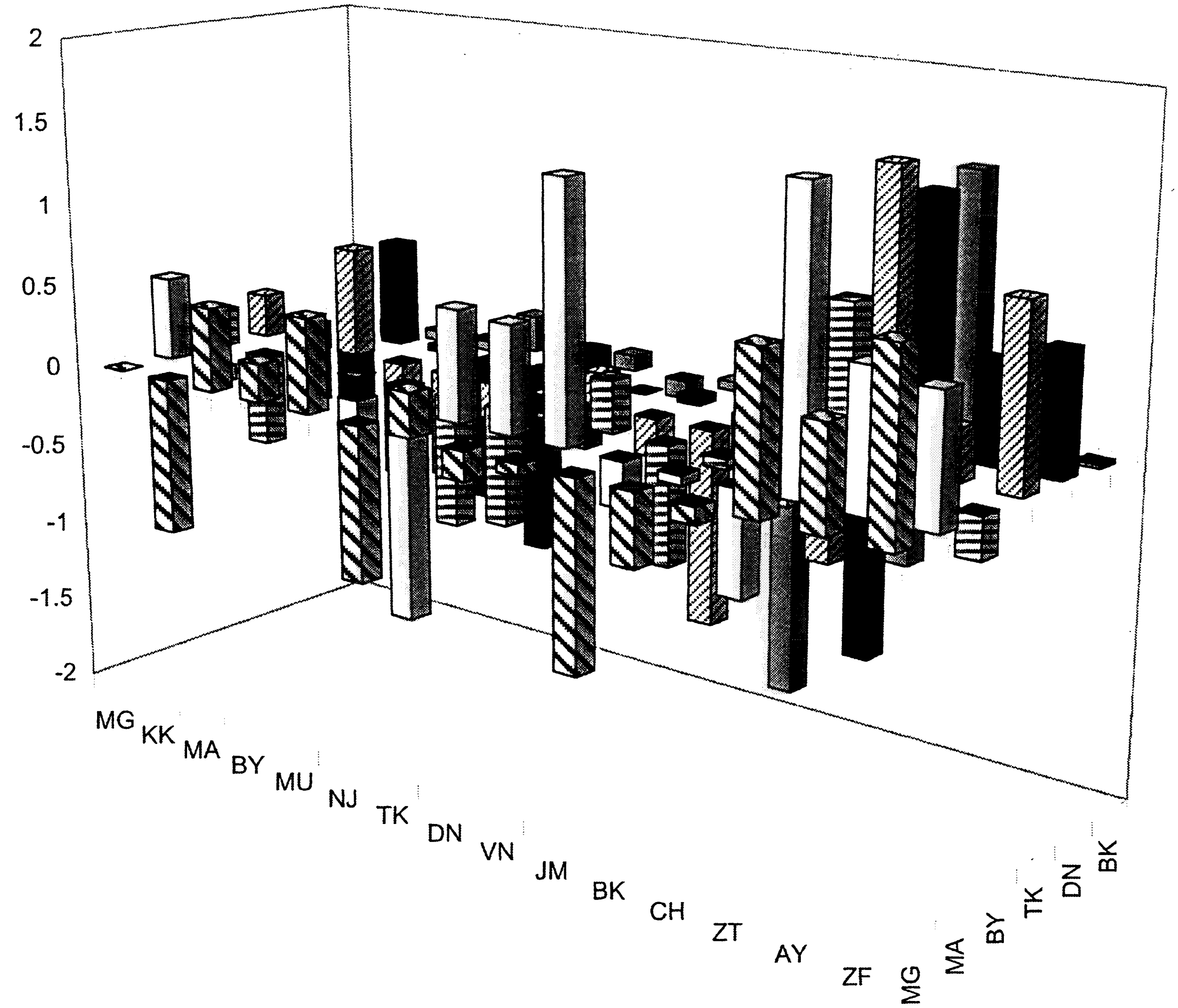

Fig. 9.3. Associations. Changes in association indices (change in Z scores) from the first 6 months in 1995 to the second 6 months. Association changes shown for six males (MG, MA, BY, TK, DN, BK) discussed in the text.

grooming, and for lower status individuals to return grooming ($H = 7.21$, df $= 3$, $p = 0.065$).

WHAT DETERMINED GROOMING CHOICE?

Association patterns appeared to influence the choice of grooming partner. For the choices between two possible partners, dyadic association was the only significant predictor of choice in a stepwise logistic regression ($\chi^2 = 7.98$, df $=$ 1, $p < 0.01$) that included relative measures of distance, status, dyadic association and dyadic proximity and absolute measures of status. Of the two possible options, males chose to groom the individual with whom they more commonly associated.

Relationship dynamics

DID CHANGING SOCIAL STATUS EXERT AN EFFECT ON EXPRESSION OF MALE RELATIONSHIPS?

Relationships between adult males changed over the course of the study. Social status increased for some males and decreased for others. Patterns of association, proximity and grooming all changed. An increase in grooming was associated with an increase in proximity ($K_r = 222$, $\tau = 0.34$, $p < 0.001$), but changing patterns of association were not linked to changes in grooming ($K_r = -31$, ns) and proximity

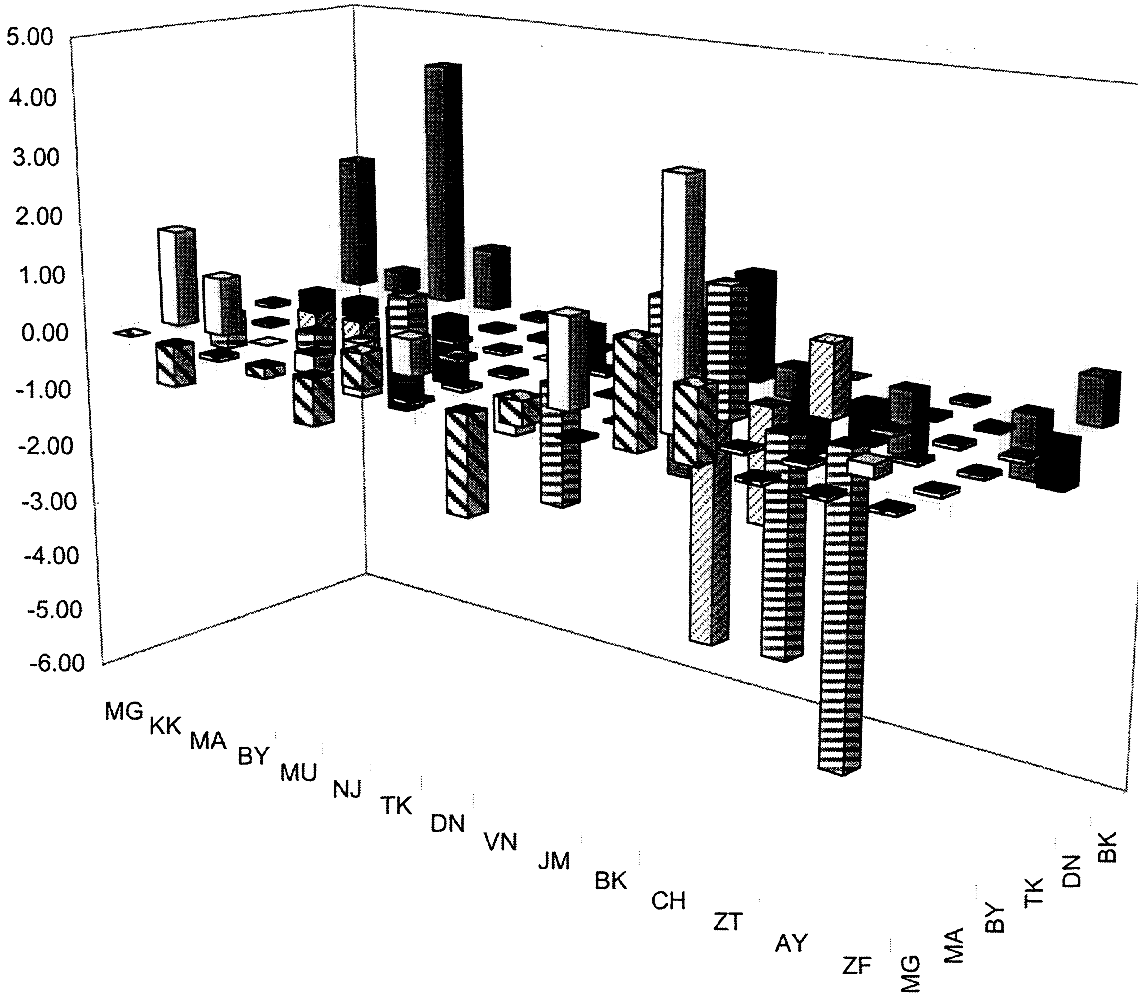

Fig. 9.4. Variation in grooming. Changes in grooming indices (change in Z scores) from the first 6 months in 1995 to the second 6 months. Changes in the amount of grooming performed shown for six males (MG, MA, BY, TK, DN, BK) discussed in the text.

($K_r = 96$, ns). Interestingly, the changes in association (Figure 9.3), proximity and grooming (Figure 9.4) were not related to changes in social status, whether males became more or less similar in status from the first 6-month period to the second, at least when looked at across all subjects (association: $K_r = -27$, ns; proximity: $K_r = -78$, ns; grooming: $K_r = -11$, ns).

WHAT CHANGES WERE SHOWN?

The deposed alpha male (MG) showed a reduction in association with seven of the twelve adult males, increasing association only with MA, MU, BY, and TK (an old, asocial male). MG and BY had absolutely high levels of association (Z-scores: Jan–Jun: +1.83, Jul–Dec: +2.06) and grooming (MG grooming BY: Jan–Jun: +1.71, Jul–Dec: +1.54; BY grooming MG: Jan–Jun: +2.60, Jul–Dec: +2.00), and both fell in status through 1995. BY provided coalitional support for MG and they may have been allies, although this was unconfirmed.

MG changed grooming patterns during 1995, particularly showing more frequent grooming of BK who was rapidly rising in status (MG grooming BK: Jan–Jun: −0.66, Jul–Dec: +1.01). MG received much of his grooming from BK, and also from MA who was one of the most prolific in his grooming of other males. MG showed slightly reduced levels of association (Jan–Jun: +1.89, Jul–Dec: +1.71), and was involved in fewer grooming interactions, with the new alpha male (DN) in the second half of 1995 (MG grooming DN: Jan–Jun: +1.74, Jul–Dec: +0.11; DN grooming MG: Jan–Jun: +0.87, Jul–Dec: +0.32). BY and BK also decreased the grooming they gave the new alpha male. BK changing grooming patterns, including a decrease in grooming DN (Jan–Jun: +1.82, Jul–Dec: −0.43), may have been part of a strategy to increase in social status. Over the course of 1995, BK moved from somewhere in the middle of the high status males (ranked 6 out of 15 males) to an unambiguous gamma male (3rd ranked) position. He used agonistic acts more frequently than all except the alpha and beta males, and was only seen pant-grunting to DN, never to the beta male VN.

The new alpha male maintained high levels of association with five of the adult males, and showed levels of association less than average only with TK and the adolescent males. The only large changes were an increase in association with MA (Jan–Jun: +2.40, Jul–Dec: +3.03) and a decrease in association with CH (Jan–Jun: +0.75, Jul–Dec: −0.53). The frequency with which DN groomed other males went down or remained unchanged, except for an increase in grooming his alliance partner VN (Jan–Jun: +0.69, Jul–Dec: +1.60) and the infrequent associate JM (Jan–Jun: −0.66, Jul–Dec: +1.06). These males both increased the frequency with which they groomed the alpha male (VN: Jan–Jun: +0.35, Jul–Dec: +2.06; JM: Jan–Jun: −0.66, Jul–Dec: +1.51).

DISCUSSION

In the general character of their interactions, as well as in their relationships, males from the Sonso community showed great similarities with male chimpanzees in other communities (Goodall 1986; Nishida & Hosaka 1996; Goldberg & Wrangham 1997; Mitani *et al.* 2000; Boesch & Boesch-Achermann 2000).

In the Sonso community, males with higher social status were preferred as associates and nearest neighbours, but only to a limited extent as grooming partners. However, higher status may have led to a wider choice of potential grooming partners and possibly allowed males to receive grooming without being obliged to reciprocate grooming within a particular bout: they still received grooming despite an apparent trend towards terminating bouts without reciprocation. Across bouts, however, grooming was strongly reciprocal. Males in this community distributed their grooming in proportion to the amount of grooming received. Such absolute reciprocation in chimpanzee grooming (in contrast to a simple rank-order response – relative reciprocation) was first demonstrated in captivity (Hemelrijk 1990) and subsequently in the wild for three communities (Newton-Fisher 1997; Watts 2000a). This reciprocation suggests that chimpanzees attach great importance to the allocation of grooming effort, which supports the idea that grooming is used as a social tactic (de Waal 1982; Nishida & Hosaka 1996), as does the existence of marked preferences for certain grooming partners.

Frequent associates were often, but not always, the preferred grooming partners for individual males, and the stronger the association between males, the greater the preference and the smaller the size of the parties in which they would come together. This would make sense if grooming were related to the current and future state of relationships between males. Smaller parties would provide an environment with fewer disturbances, reducing the probability that grooming would be disrupted by other males. Such separating interventions (de Waal 1982), whereby a male scatters a group of individuals grooming or resting in close proximity, have been observed in the Sonso community (unpublished data).

The use of separating interventions to scatter individuals in close proximity, but not otherwise interacting, suggests that proximity alone may be a component of male relationships and neither simply a precursor to grooming or a by-product of association. Some dyads, particularly of higher status males, were found in close proximity when nearest neighbours within a party although their frequencies of association and proximity were close to average. These males may have been those most likely to need or exploit supportive relationships: above them in the status hierarchy was the well-established alliance between alpha and beta males, below them the young and old, unlikely to challenge for status. Any fickleness in relationships would most likely be occurring amongst these higher status males. Indeed it was these males who were responsible for most of the observed grooming, which is consistent with the idea that they are attempting to modify or maintain their relationships with each other. This contrasts with the established alpha-beta alliance. Although each was the other's most frequent grooming partner, neither showed particularly high levels of grooming.

Changes in social status did not appear to account for changes in the observed patterns of association, proximity, and grooming during the study. This appears to conflict with the observations that social status had an important influence on these behavior patterns. This conflict might be resolved by considering the time-scale of the study, and the changes in social status themselves. The change in alpha male was already underway at the beginning of 1995, with the alliance between DN & VN apparently well established. DN was not clearly alpha male until the second half of the year, and may have continued to strengthen his position thereafter; he remains alpha male in 2001 (V. Reynolds, personal communication).

The changes in association, proximity and grooming may have been the result of males opportunistically shifting the investment they made in each of their relationships during this period of social instability. Each male is likely to have attempted to strengthen supportive relationships while neglecting others. Most – if not all – of the males may have been attempting to do this with the same range of partners at the same time. Such opportunism, possibly compounded by individual personality (Murray, 1995) and relationship history, may have produced the apparently idiosyncratic variation showing no systematic relationship to status changes. A longer time frame, covering periods of stability and instability, may be required to examine properly the impact of social status on the dynamics of relationships.

These analyses support, or are least consistent with, a view of male chimpanzee sociality in which the observed grouping and interaction patterns are products of the relationships between individuals, with association and proximity being the direct, rather than incidental, result of male behaviour. The idiosyncratic variation across individuals and over time, the link between stronger association and smaller party size (Newton-Fisher 1999), and the relationships between association, proximity and grooming all support this view.

The availability of reproductive opportunities in the form of females showing sexual swellings is a factor influencing party size in Sonso, as in other communities (Gombe: Goodall 1986; Stanford *et al.* 1994; Taï: Boesch & Boesch-Achermann, 2000). These females are attractive to males, and their presence seems likely to increase not only party size but also the number of males in the party. However, the pattern seen in this study was more complex than this.

The presence of females with sexual swellings did increase the number of males but only on average from two males to four males, even if more than one swollen female was present. Sexual swellings last for around 9–12 days in chimpanzee females, with ovulation occurring in the last 2 or 3 days of maximum swelling (Tutin & McGinnis 1981; Goodall 1986; Nishida & Hiraiwa-Hasegawa 1987; Takahata *et al.* 1996; Boesch & Boesch-Achermann 2000). Parties, in contrast, can change in composition from moment to moment; average duration for unchanging party composition varies between communities, but is on the scale of minutes, not days (Boesch & Boesch-Achermann 2000, Table 5.1). For the Sonso community, average duration was 14 minutes (V. Reynolds, personal communication).

Male associations could, therefore, change repeatedly without compromising access to swollen females, particularly if sexual swellings were not entirely reliable as indicators of ovulation and males could rely on sperm competition. For most males monopolising access to swollen females may not be a feasible option. Only males of highest social status appear to be successful at monopolising access, even where mate-guarding is conducted cooperatively (Watts 1998). For the rest, their time may be more profitably spent cultivating relationships with an eye to the future, and grabbing copulations when they can.

If the presence of swollen females increases tension and aggression between males (de Waal 1986; Shefferly & Fritz 1992), then males may attempt to avoid such tension by altering their associations. For individual males, the size of the party may be less important than the number of other males, and the number of males may be less important than the identities of those other males. Associating with preferred individuals while avoiding others may provide a male with greater flexibility in forming, maintaining and modifying relationships, although this flexibility will inevitably be constrained by the association patterns of the other individuals in the community.

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