



Mutual grooming among adult male chimpanzees: the immediate investment hypothesis



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Unidirectional grooming is a low-cost behaviour for which the groomer is repaid via kin selection or reciprocity. Return benefits can come in the form of increased probability of being groomed or social benefits such as coalitionary support. By contrast, the reasons for mutual grooming, which occurs when two individuals simultaneously groom each other, are not understood. In this study, we test three hypotheses regarding the function of mutual grooming among wild male chimpanzees, using 16 years of data. The social bonding hypothesis posits that mutual grooming promotes a return benefit by serving to strengthen and maintain social bonds, whereas the immediate investment hypothesis states that it functions as a signal to indicate willingness to invest in (continue) the grooming bout. The switching hypothesis states that mutual grooming results from overlap created when the direction of the grooming interaction is switched. The social bonding hypothesis was not supported: measures of association were not correlated with the probability of mutual grooming. We also found no support for the switching hypothesis, as mutual grooming was equally likely to occur without a switch in the direction of grooming as when a switch occurred. The immediate investment hypothesis was supported by our finding that bouts with mutual grooming (1) were longer, (2) contained a more equitable distribution of unidirectional grooming and (3) had more unidirectional grooming switches than bouts without mutual grooming. We conclude that male chimpanzees use mutual grooming to obtain short-term benefits in the form of prolonging a grooming bout, and suggest that mutual grooming thus represents a form of overlapping parcelling.

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Allogrooming (the grooming of the hair or skin of another individual) is one of the most frequently observed social behaviours among nonhuman primates. While grooming provides tangible benefits in terms of parasite removal (Akinyi et al., 2013; Hart, 1992; Hutchins & Barash, 1976), many aspects of the behaviour suggest that grooming serves more than just a hygienic function (Dunbar, 1988). For example, individuals increase grooming time after agonistic interactions and during periods of social instability, but they do not reduce grooming time during periods of food stress (Dunbar, 1988; Dunbar & Sharman, 1984; Goosen, 1987; Henzi & Barrett, 1999). This suggests that grooming has a social function that is important enough to conserve even at the expense of increased feeding time (Cords, 1997; DiBitetti, 1997; Dunbar, 1988, 1991; Seyfarth, 1977). Individuals are choosy of whom they groom (Schino & Aureli, 2009) and often support frequent grooming partners in agonistic interactions (Seyfarth & Cheney, 1984). As such, grooming can be viewed as a long-term investment in a social bond; the groomer incurs costs that are paid back at a later time

(Henzi & Barrett, 1999). Grooming may also grant access to an immediate rather than a delayed benefit, such as a monopolizable food source (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999) or a desirable infant (Henzi & Barrett, 2002).

To date, most studies have explored the functions and patterns of unidirectional grooming (A grooms B while B is engaged in any activity other than grooming A). In contrast, very few have addressed the function of mutual grooming (A grooms B while B grooms A). This oversight is surprising. Unidirectional and mutual grooming have distinct payoff structures that differ in the timing with which the benefits and costs accrue. In unidirectional grooming, the groomer incurs a cost while the recipient receives a benefit: the longer a bout, the greater the discrepancy. If the recipient does not reciprocate, then the groomer has incurred a net cost. In mutual grooming, the costs and benefits to both participants accrue simultaneously: neither becomes 'indebted' to the other, reducing the opportunity for one individual to defect. This suggests that the two grooming types serve different functions, and that mutual grooming should be more widespread than unidirectional grooming. However, across mammals, patterns of mutual grooming appear to be highly variable. For example, while grooming in equine taxa is almost always mutual (Camargue

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horses, *Equus caballus*: [Feh & Demazieres, 1993](#); [Feist & McCullough, 1976](#); Cape zebra, *Equus zebra zebra*: [Penzhorn, 1984](#)), mutual grooming in vampire bats, *Desmodus rotundus*, is less common (approximately 8% of all grooming time in roosts; [Wilkinson, 1986](#)) and appears to be nonexistent, or at best, rare among cercopithecine primates ([Cooper & Bernstein, 2000](#); [Matheson & Bernstein, 2000](#); [Rowell, Wilson, & Cords, 1991](#)). Patterns of mutual grooming also vary within species. A study of captive coatis, *Nasua nasua*, demonstrated that subunits of individuals within a single group displayed similar frequencies of unidirectional grooming, but significantly different frequencies of mutual grooming. Furthermore, even among species that exhibit mutual grooming exclusively, such as Camargue horses, individuals differ in the amount of time spent grooming and their choice of grooming partner ([Crowell-Davis, Houpt, & Carini, 1986](#)).

Among primates, patterns of mutual grooming are difficult to characterize as many studies do not distinguish between different types of grooming behaviour ([Nakamura, 2000](#)). Grooming is often defined simply as interactions between two individual that involve giving or receiving grooming (e.g. [DiBitetti, 1997](#); [Parr, Matheson, Bernstein, & de Waal, 1997](#)) and it is not often clear the extent to which mutual grooming occurs or if it occurs at all. Furthermore, mutual grooming is not always defined in studies, even though it is distinguished from other forms of grooming and may refer to simultaneously grooming by two individuals or reciprocated unidirectional grooming within a bout (siamangs, *Hylobates syndactylus*: [Geissmann & Orgeldinger, 2000](#); Japanese macaques, *Macaca fuscata*: [Muroyama, 1991](#); ringtailed lemurs, *Lemur catta*: [Taylor & Sussman, 1985](#)). In some cases, it is clear that individuals engage in simultaneous mutual grooming, but the actual frequencies of mutual grooming are never explicitly given (e.g. Milne-Edwards' sifaka, *Propithecus diadema edwardsi*: [Pochron et al., 2003](#)). Patterns of grooming among cercopithecine primates are better understood, and it is clear that mutual grooming is entirely absent or extremely rare among these species, although gelada baboons, *Theropithecus gelada*, are a notable exception ([Dunbar, 1983](#); [Fedurek & Dunbar, 2009](#)). Simultaneous mutual grooming occurred in 45 of 5397 (0.8%) social grooming episodes in a study of Assamese macaques, *Macaca assamensis* ([Cooper & Bernstein, 2000](#)), and it was never observed in studies of rhesus macaques, *Macaca mulatta* ([Matheson & Bernstein, 2000](#)) or blue monkeys, *Cercopithecus mitis stuhlmanni* ([Rowell et al., 1991](#)). Similarly, mutual grooming was virtually absent among white-handed gibbons, *Hylobates lar*, and siamangs ([Palombit, 1996](#)).

In this study, we examine the function of mutual grooming among male chimpanzees, *Pan troglodytes schweinfurthii*. Chimpanzees are an ideal study species because grooming is frequent and characterized by a diversity of interactions (including mutual and polyadic grooming) in a number of contexts ([McGrew & Tutin, 1978](#); [Nakamura, 2000](#)). Grooming patterns, including those of mutual grooming, exhibit variation both within and among chimpanzee populations. Across four study sites, rates and proportions of mutual grooming have been reported to be as low as 9% and as high as 73%, although these studies measured mutual grooming using different methods, and among different age/sex classes and contexts (Mahale, 9% of grooming time for adult male dyads: [Kawanaka, 1990](#); [Takahata, 1990](#); Gombe, 16–21% for grooming during greetings between adult male dyads: [Bygott, 1974](#); [Goodall, 1986](#); Budongo, 28.6 ± 9.4% of adult male grooming time with all age/sex classes: [Arnold & Whiten, 2003](#); Tai, 40–73% of adult male grooming time: [Boesch & Boesch-Achermann, 2000](#); 25% grooming time for all adult dyads: [Gomes, Mundry, & Boesch, 2009](#)). In addition, there appears to be considerable variability within and between individuals, although few studies have explicitly addressed this. Among captive chimpanzees at the

Chester Zoo, U.K. ([Fedurek & Dunbar, 2009](#)), approximately 70% of alpha male grooming bouts became mutual, compared to less than 5% for the fifth-ranking male. [Foster et al. \(2009\)](#) found that rates of mutual grooming by three males at Gombe differed considerably but did not change when the males achieved or lost alpha status.

Understanding the function of mutual grooming will help to explain this variation within and among individuals and communities. Furthermore, by studying the function of mutual grooming in chimpanzees, we may also be able explain the variation in the behaviour across primate and mammal species. We use 16 years of long-term data from the Kanyawara community (Kibale National Park, Uganda) to test three hypotheses regarding the function of mutual grooming among adult male chimpanzees.

The Social Bonding Hypothesis

The social bonding hypothesis posits that mutual grooming facilitates the maintenance of a strong dyadic social bond. Male chimpanzees strategically use grooming to gain social partners who offer benefits. Therefore, grooming is often used to measure affiliative bonds between males ([Mitani, 2009](#); [Muller & Mitani, 2005](#); [Newton-Fisher, 2002](#); [Watts, 2002](#)). It has been suggested that mutual grooming is an especially good indicator of a strong social bond because, unlike unidirectional grooming, both individuals must actively participate and both experience the cost of engaging in grooming rather than another activity ([Fedurek & Dunbar, 2009](#); [Palombit, 1996](#)). In this way, mutual grooming serves as a test of the strength of a dyadic relationship. Similarly, [Boesch and Boesch-Achermann \(2000\)](#) argue that mutual grooming in chimpanzees is related to the maintenance of strong and cooperative social bonds since high rates of mutual grooming at Tai correlate with high rates of patrolling and intercommunity violence. That is, mutual grooming in particular strengthens the male social bonds in order to support the amount of cooperation needed for aggressive between-community interactions ([Boesch & Boesch-Achermann, 2000](#)). Despite this assertion, the connection between mutual grooming and bond strength has never been tested among wild chimpanzees. In one study of captive individuals, related dyads engaged in more mutual grooming than unrelated dyads and rates of mutual grooming (but not unidirectional grooming) were positively related to dyadic proximity scores ([Fedurek & Dunbar, 2009](#)). Thus, according to the social bonding hypothesis, mutual grooming serves as an investment in a bond that may result in increased cooperative behaviour between a dyad at a later time.

The social bonding hypothesis generates two specific predictions (summarized in [Table 1](#), see [Results](#)). First, if mutual grooming is important for maintaining a social bond, then dyads that frequently associate are expected to spend a greater proportion of their grooming time engaged in mutual grooming than dyads that rarely associate. Therefore, the proportion of grooming that is mutual should be positively correlated with association rate. Second, dyads that exhibit an increase in association frequency from one period to another will exhibit a concomitant increase in the proportion of mutual grooming. Hence, any change in dyadic proportions of mutual grooming between subsequent periods should be positively correlated with changes in association rate.

Immediate Investment Hypothesis

Mutual grooming may also reflect a strategy by which chimpanzees seek to maximize short-term rather than long-term social benefits. We propose that mutual grooming serves as a signal of willingness to invest in the grooming bout. If the recipient of

unidirectional grooming initiates a mutual grooming episode (by turning and grooming his partner before he stops), he is indicating his intention to prolong the bout. For clarification, a grooming episode occurs when two individuals engage in grooming (either unidirectional or mutual) and ends when the grooming stops or when the direction of grooming changes. A grooming bout contains one or more grooming episodes between the same two individuals that are uninterrupted by any other nongrooming behaviour. For example, if individual A grooms B and then individual B grooms A, the grooming bout would consist of two unidirectional grooming episodes. Similarly, if individual A grooms B, then A stops grooming to feed, and then individual B starts grooming A, we would consider this as two separate grooming bouts consisting of one grooming episode each.

The immediate investment hypothesis is similar to the parcelling model of reciprocity whereby an individual provides a small amount of grooming and will not continue giving this resource until the partner reciprocates (Connor, 1995; Hart & Hart, 1992; Manson, Navarrete, Silk, & Perry, 2004; Mooring & Hart, 1997; Stopka & Graciasova, 2001). Since grooming is given in small packages, neither individual owes a large debt to the other if one fails to reciprocate, thereby resulting in more equitable grooming bouts. Among chimpanzees, we suggest that mutual grooming may represent a form of overlapping parcelling in which a grooming recipient starts to reciprocate while their partner is still grooming. Similar to parcelling, this results in longer and more equitable grooming bouts between individuals. In contrast to the social bonding hypothesis, the immediate investment hypothesis involves benefits that accrue immediately within the same grooming bout.

We test three predictions of this hypothesis (summarized in Table 1, see Results). First, if mutual grooming signals willingness to invest in the grooming bout, then grooming bouts that include mutual grooming episodes should be longer than purely unidirectional bouts, even after subtracting the amount of mutual grooming time. Second, if mutual grooming is similar to parcelling, we predict that bouts that include mutual grooming episodes should be more equitable than purely unidirectional bouts. Consequently, when considering only the unidirectional grooming within a bout, we predict that the degree of equitability should be correlated with the proportion of mutual grooming. Third, mutual grooming episodes within bouts should encourage switches in the direction of unidirectional grooming, and the duration of unidirectional grooming episodes should therefore be shorter when immediately followed by mutual grooming.

Switching Hypothesis

The simplest explanation for mutual grooming is that it serves no obvious function (delayed or immediate) but simply occurs as the result of overlap between two unidirectional grooming episodes. Individual A grooms B, B starts to groom A, and then A stops grooming shortly afterwards. This hypothesis generates two predictions (summarized in Table 1, see Results). First, individuals should rarely start grooming bouts with a mutual grooming episode. Second, mutual grooming should be more likely to occur between unidirectional grooming episodes in the opposite direction ($A \rightarrow B$, $A \leftrightarrow B$, $B \rightarrow A$) than between unidirectional episodes with no change in direction ($A \rightarrow B$, $A \leftrightarrow B$, $A \rightarrow B$).

The social bonding and the immediate investment hypotheses are not mutually exclusive. They differ in the timing of the benefits of grooming, but do not preclude one another. The switching hypothesis is exclusive since it states that mutual grooming serves no function and is simply a by-product of the structure of the grooming bout.

METHODS

Study Site and Data Collection

We conducted this study using long-term data from the Kanyawara chimpanzee community living in Kibale National Park, Uganda. These chimpanzees have been continuously studied since 1988, and all adult males have been habituated to human observers since January 1990. Every day, two or more trained Ugandan field assistants (FAs) of the Kibale Chimpanzee Project located a party of chimpanzees and followed them for as long as possible, ideally until the party nested for the night. The FAs worked in pairs with one individual using scan sampling (Altmann, 1974) to record party composition at 15 min intervals and taking long-hand notes of all major behavioural events during the interval. If at least one individual in the party was feeding at the time of the 15 min scan, one FA recorded the species and part (e.g. ripe fruit, leaf) being consumed. The other FA used focal sampling (Altmann, 1974) to record the behaviour of specific individuals. From 1993 to July 2009, focal observations took the form of 10 min focal follows (TMFs) in which the FA randomly selected a target chimpanzee and recorded the activity of that individual at 2 min intervals until 10 min had elapsed. On each scan he also recorded the identity of all individuals within 5 m of the focal, and the identity of the focal's nearest neighbour. If the focal was grooming, then the observer recorded the identity of the partner and the direction of the interaction (give, receive, mutual). After 10 min, the FA selected a new focal until all individuals in the party were sampled. To reduce potential bias introduced by observers inadvertently choosing focal individuals that were engaged in 'interesting' behaviours, we only used the last scan of each TMF in our analyses. Since August 2009, FAs have conducted full-day focal follows (FDFs). If possible, they tried to follow every adult in the community at least once per month and chose a new focal animal at the beginning of the day. If a new focal animal was not present in the party, then the observers chose an individual that had not been the subject of a recent focal follow. During the day, the FA recorded the activity of the focal at 1 min intervals. If the individual was grooming, then the observer recorded the partner ID as well as the direction. At 15 min intervals, the FAs recorded the focal chimpanzee's nearest neighbours and those within 5 m.

R. Wrangham carefully trained the FAs, who averaged over 95% accuracy in interobserver reliability tests (Kibale Chimpanzee Project, n.d.). All data, including detailed demographic records, are digitized and stored in a relational database at Harvard University. The Institutional Animal Use and Care Committee of Harvard University approved this research (IACUC protocol number 96-03).

Data Analysis

For this study, we analysed party composition data collected between January 1995 and April 2011. We analysed all FDF data that were available (August 2009–April 2011). We divided the TMF data (January 1995–December 2008) into seven 2-year periods (see Results, Table 2). We chose 2-year periods because this interval yields a large enough sample of observations, yet is short enough to capture changes in dyadic association patterns (Gilby & Wrangham, 2008; Machanda, Gilby, & Wrangham, 2013). Data from Kanyawara indicate that dyadic association patterns between males are stable over at least three consecutive 2-year periods (Gilby & Wrangham, 2008; Machanda, 2009). As our study subjects, we used males that were at least 15 years old ('adult', hereafter) at the start of a given 2-year interval, and still alive at the end. This generated a sample of 13 adult males during the entire study period (Table 2), resulting in 45 male–male dyads in 1995–1996 and 36 male–male dyads in each

subsequent 2-year period from the TMF data set and for the duration of the FDF data set.

Grooming

From the TMF data, we identified all grooming scans between adult males, noting the direction (give, receive, mutual). Then, we calculated a mutual grooming index (MGI), which measured the proportion of grooming scans that were mutual:

$$MGI_{AB} = \frac{A_{Focal} B_{MutGrm} + B_{Focal} A_{MutGrm}}{A_{Focal} B_{Grm} + B_{Focal} A_{Grm}}, \quad (1)$$

where $A_{Focal} B_{Grm}$ is the number of instances individual A was the TMF focal and was grooming with individual B (any direction), $B_{Focal} A_{Grm}$ is the number of instances B was the TMF focal and was grooming with A (any direction), $A_{Focal} B_{MutGrm}$ is number of instances A was the TMF focal and was mutually grooming with B, and $B_{Focal} A_{MutGrm}$ is number of instances B was the TMF focal and was mutually grooming with A. A value of 1 indicates that all grooming observed between individuals A and B was mutual. We calculated this mutual grooming index for every adult male–male dyad in each 2-year period. We restricted all analyses to dyads that groomed at least 10 times during a given period. This cutoff was chosen because when the number of grooming observations for each dyad was plotted, the distribution was continuous until just below 10 observations in the majority of 2-year periods.

To compare patterns of association with those of unidirectional grooming, we calculated a unidirectional grooming index by summing the number of unidirectional scans for each dyad in each 2-year period and dividing by the number of TMF scans that members of the dyad were within 5 m of one another. The dyad members had to be observed within 5 m of one another for at least 10 scans in each 2-year period.

From FDF data, we identified every grooming bout between adult males by looking for sequential and uninterrupted 1 min grooming scans between the same adult males. We calculated the total duration of each grooming bout as well as the duration of unidirectional and mutual grooming episodes within grooming bouts, to the nearest minute, by summing the number of 1 min scans, then calculating the proportion of each grooming bout where the partners groomed mutually. For both types of focal data, we considered hand-clasp grooming (when individuals groom each other while clasping their hands above their heads) to be a form of mutual grooming. Excluding hand-clasp grooming did not change the results.

To measure how evenly each dyad distributed their unidirectional grooming, we calculated a unidirectional grooming equitability (UDG_{eq}) index following Mitani (2009):

$$UDG_{eq} = 1 - \left| \left(\frac{(A \rightarrow B)}{(A \leftrightarrow B)} \right) - \left(\frac{(B \rightarrow A)}{(A \leftrightarrow B)} \right) \right| \quad (2)$$

$A \rightarrow B$ equals the number of scans (TMF data) or the duration (FDF) that A groomed B (when either A or B was the target of a focal). Similarly, $B \rightarrow A$ is the number of scans or duration of time when B groomed A, and $A \leftrightarrow B$ is the total number of scans or total duration of time of unidirectional grooming between A and B. This index represents the difference in the proportional contribution of each individual to all of a dyad's unidirectional grooming. A value of 1 indicates that both individuals contributed exactly the same amount of grooming, and a value of 0 indicates that all unidirectional grooming was performed by one individual only.

From the FDFs, we also identified the number of times within a bout that the participants switched the direction of unidirectional grooming. Switches in direction of grooming occurred when A

groomed B and then B groomed A in the next 1 min scan, or when A groomed B, A and B groomed mutually and then B groomed A. Since our FDF data consists of 1 min behavioural scans rather than continuous data collection through the grooming bout, the number of switches in the direction of grooming is actually a measure of the minimum number of switches in the grooming bout. However, the mean duration of grooming episodes among wild chimpanzees has been reported to be over 1 min (Kaburu & Newton-Fisher, 2013); hence, we expect the minimum number of switches in a bout to be representative of the actual number switches. In this data set, we also noted when mutual grooming occurred between the switch in unidirectional grooming.

Association frequency

Following Gilby and Wrangham (2008), we calculated three indices of dyadic association for each 2-year period. The first, time spent in the same party, was a measure of temporal association. We used a version of the simple ratio index (Cairns & Schwager, 1987), which measures the proportion of total sightings of both individuals when together in the same party. The second index measured the frequency with which two individuals were observed within 5 m of one another, given that both were present in the same party and one was the target of a focal scan. The third measured the frequency with which two individuals were seen as nearest neighbours, given that one was the focal and the other was within 5 m. See Gilby and Wrangham (2008) for more detail on these indices. As with the grooming data, we limited our analyses to indices with a denominator of at least 10.

It is critical to emphasize that these indices provide three independent measures of association. For example, because the within 5 m index controls for the number of times that the two individuals are seen in the same party, dyads that are frequently within 5 m of one another do not necessarily have a high party-level association index. Similarly, the within 5 m index is also independent of the unidirectional grooming index. Therefore, we assume that a dyad with a high score in all three indices has a stronger tendency to associate than a dyad with a high score in just one. To quantify such variation, we used the methods developed by Gilby and Wrangham (2008), briefly described below.

Our first technique for capturing a dyad's overall tendency to associate was to create a 'combined association index' (CAI), which measures a dyad's average deviation from the mean across the three indices described above (for more detail, see Gilby & Wrangham, 2008). Briefly, we standardized each index value by dividing by the mean of all dyads in that period. Therefore, a value greater than 1 indicated that a dyad had a higher index than the average male–male dyad during a particular period. The CAI takes the mean of this observed/expected ratio across the three indices. A dyad with above-average values in all three indices will therefore have a higher CAI than one whose members are often in the same party but are rarely recorded as nearest neighbours.

As noted by Gilby and Wrangham (2008), the CAI does not distinguish between dyads that have a mutual tendency to associate and those in which one member has a strong affinity for the other but not vice versa. Therefore, we also used a second measure of association that identified dyads with a mutual attraction to each other. For each index, we identified dyads for which the value was more than one-half of a standard deviation greater than the means of both individuals. We designated members of a dyad as 'preferred social partners' if they met these criteria for at least two of the three independent indices (Gilby & Wrangham, 2008). Similarly, we identified 'mutual avoiders' as dyads with at least two association indices that were less than one-half of a standard deviation below the means for each of them. We classified dyads that did not qualify as either 'preferred social partners' or 'mutual avoiders' as 'tolerant'.

Dominance rank

We calculated male dominance ranks for each year from 1995 to 2011 using data on the direction of pant-grunts (a vocalization given by subordinate individuals to dominant individuals), as well as the outcomes of decided, dyadic agonistic interactions. We calculated Landau's index of linearity (H') using the MatMan software package (version 1.1, Noldus Information Technology; de Vries, Netto, & Hanegraaf, 1993), which orders males into a hierarchy while minimizing the number of inconsistencies and accounting for absent data between dyads. We used a two-step randomization procedure with 10 000 iterations (de Vries, 1995) to determine that the male dominance hierarchy in each year was significantly linear. For each period, we calculated dyadic rank differences as the absolute value of the difference between the ranks of male A and male B. Rank distances ranged from 1 to 9, with 1 representing dyads with adjacent ranks. We then created three categories of rank difference: small (1–3), medium (4–6) and large (7–9). We ran all models with both absolute rank differences and categorical rank differences and there was no difference in the results. We present the results of the models with categorical rank differences in this paper.

Statistics

We used generalized linear mixed models (GLMM) in SAS 9.2 (SAS Institute, Cary, NC) for all analyses of the social bonding and immediate investment hypotheses. To account for multiple sampling of dyads, we included dyad ID as a random effect in all models. When the response variable was categorical, we used the logit link function. For simplicity, we describe the specifics of each model in the results. To test the switching hypotheses, we used a binomial test to determine whether mutual grooming occurred as the first episode less often than expected by chance. In this case, the expected distribution was the average proportion of minutes of mutual grooming in grooming bouts that had at least one episode of mutual grooming. We also used nonparametric binomial tests to determine whether mutual grooming occurred more often between unidirectional episodes of different direction ($A \rightarrow B$, $B \rightarrow A$) than episodes of the same direction ($A \rightarrow B$, $A \rightarrow B$) than expected by chance (set at 50% in the binomial test). For the binomial tests, we first combined the data for all males but then ran each test for individual adult males to ensure there were no individual effects.

RESULTS

Between January 1995 and July 2009, there were 16 031 last scans from the 10 min focal (TMF) data when the focal chimpanzee was an adult male and there was at least one other adult male in the party (Table 2). The focal male was grooming with another adult male in 2148 (13.4%) of these scans, of which 163 (7.6%) were mutual. Between August 2009 and April 2011, there were 273 days in the full-day focal (FDF) data when an adult male was followed. In this data set, mutual grooming accounted for 10.7% of grooming time between adult males (897 of 8388 grooming minutes in 1139 dyadic grooming bouts). Table 2 lists the totals per 2-year period. Of the 1139 dyadic grooming bouts, 316 (27.8%) contained at least one mutual grooming episode, and of these bouts, 26.6% of the grooming bout was mutual.

We first ran a GLMM of mutual grooming (Y/N) versus categorical rank difference and adult male party size. From TMF data, there was a negative association between rank difference and the probability of mutual grooming: as the rank difference between a dyad increased, the probability of mutual grooming decreased (rank difference: large versus small: odds ratio = 0.39, $\chi^2_1 = 9.9$, $P = 0.002$; large versus medium: odds ratio = 0.40, $\chi^2_1 = 7.53$, $P = 0.006$). There was also a negative association between adult male party size

Table 1
Summary of predictions

Hypothesis	Predictions	Outcome
Social bonding	(1) Mutual grooming probability increases with association rate	Minimal support
	(2) Changes in mutual grooming frequency are positively correlated with changes in association rate	No support
Immediate investment	(1) Unidirectional grooming time within bouts is greater for bouts with mutual grooming	Supported
	(2) Unidirectional grooming events are shorter if followed by mutual grooming and more switches in grooming direction occur within bouts with mutual grooming	Supported
	(3) Equitability of unidirectional grooming is positively correlated with the proportion of mutual grooming within bouts	Supported
Switching	(1) Grooming bouts begin with episodes of mutual grooming less often than expected by chance	Supported
	(2) Mutual grooming episodes are more likely to occur between switches in the direction of unidirectional grooming	No support

and the probability of mutual grooming: as male party size increased, the probability of mutual grooming decreased (odds ratio = 0.93, $\chi^2_1 = 5.71$, $P = 0.02$). Therefore, to control for these correlations, we included rank difference and adult male party size as main factors in all subsequent analyses using TMF data. We then ran a similar analysis examining the effects of categorical rank difference and adult male party size on the proportion of mutual grooming within a bout using the FDF data. We found a significant negative effect of adult male party size on the proportion of mutual grooming ($\chi^2_1 = 21.79$, $P < 0.0001$) but no effect of categorical rank distance ($\chi^2_1 = 4.84$, $P = 0.09$). Therefore in subsequent analyses of the FDF data, we control only for adult male party size.

Association Patterns and Grooming

To test the relationship between mutual grooming and male association patterns, we ran a GLMM of mutual grooming (Y/N) versus the combined association index (CAI) measure of association with categorical rank difference and adult male party size as main factors and dyad ID as a random effect. There was no relationship between the probability that grooming was mutual and a dyad's CAI (TMF data: $\chi^2_1 = 0.005$, $P = 0.94$). Similarly, when the model was run on the FDF data, there was no association between the proportion of mutual grooming within the bout and the CAI ($t_{1101} = 0.82$, $P = 0.41$). We also used a more conservative categorical indicator of association ('preferred social partners', 'mutual avoiders' or 'tolerant'; see Methods). The number of male–male dyads classified as preferred social partners in each 2-year period was as follows: 5 of 45 in 1995–1996; 3 of 36 in 1997–1998; 5 of 36 in 1999–2000; 6 of 36 in 2001–2002; 6 of 36 in 2003–2004; 9 of 36 in 2005–2006; 7 of 36 in 2007–2008; 6 of 36 for the duration of the FDF data set (August 2009–April 2011). The number of male–male dyads classified as mutual avoiders in each 2-year period was as follows: 1 in 1995–1996; 3 in 1997–1998; 2 in 1999–2000; 8 in 2001–2002; 5 in 2003–2004; 7 in 2005–2006; 7 in 2007–2008; 6 for the duration of the FDF data set. All remaining dyads were classified as tolerant. We found a nonsignificant relationship between association category and probability of mutual grooming (TMF data: $\chi^2_2 = 5.73$, $P = 0.06$; Fig. 1). This pattern arose because mutual avoiders were less likely to groom mutually than either preferred social partners (odds ratio = 0.16, $\chi^2_1 = 5.41$, $P = 0.02$) or tolerant dyads (odds ratio = 0.16, $\chi^2_1 = 5.70$, $P = 0.02$; Fig. 1). There was no significant

Table 2
Summary of 10 min focal (TMF) and full-day focal (FDF) data

Focal data		AJ	BB	BF	KK	LB	LK	MS	PG	SL	ST	SY	TU	YB	Totals
TMF															
1995–1996	TMFs	188	186	101		156		188		68	193	139	94	172	1485
	Grooming	20	45	15		22		25		3	24	21	10	12	197 (13.3%)
	Mutual grooming	0	2	0		4		1		0	0	1	3	1	12 (6.1%)
1997–1998	TMFs	260	215			211		291		91	252	201	116	262	1899
	Grooming	18	38			30		34		1	32	18	19	20	210 (11.1%)
	Mutual grooming	1	4			2		5		0	2	1	1	3	19 (9.0%)
1999–2000	TMFs	129	106			138	172	217		56	149		114	193	1274
	Grooming	15	24			13	13	30		4	20		15	24	158 (12.4%)
	Mutual grooming	0	4			0	0	3		0	1		0	1	9 (5.7%)
2001–2002	TMFs	171	118		150		189	222		71	155		128	173	1377
	Grooming	22	22		11		22	35		4	23		23	35	197 (14.3%)
	Mutual grooming	2	1		1		1	1		0	0		0	3	9 (4.6%)
2003–2004	TMFs	185	186		245		225	258		84	195		185	203	1766
	Grooming	27	26		24		20	28		8	31		21	15	200 (11.3%)
	Mutual grooming	2	3		2		1	1		0	1		2	0	12 (6.0%)
2005–2006	TMFs	218	203		522		521	390	348		217		170	407	2996
	Grooming	51	38		38		55	48	14		30		29	59	362 (12.1%)
	Mutual grooming	4	4		3		8	6	1		1		3	2	32 (8.8%)
2007–2008	TMFs	687	331		906		888	463	603		413		480	463	5234
	Grooming	146	80		111		140	102	28		67		89	61	824 (15.7%)
	Mutual grooming	11	14		9		8	5	7		5		9	2	70 (8.5%)
All TMF data	TMFs	1838	1345	101	1823	505	1995	2029	951	370	1574	340	1287	1873	16031
	Grooming	299	273	15	184	65	250	302	42	20	227	39	206	226	2148 (13.4%)
	Mutual grooming	20	32	0	15	6	18	22	8	0	10	2	18	12	163 (7.6%)
FDF															
Aug 2009–Apr 2011	FDFs	10398	10565		17649		17142	4757	12986		12227		7639	15529	108892
	Grooming	1220	1171		1232		1374	650	525		766		578	872	8388 (7.7%)
	Mutual grooming	77	122		130		160	42	67		119		99	81	897 (10.7%)

TMF: includes the total number of last scans with each adult male as the focal individual as well as the number of scans during which the focal was grooming and mutually grooming another adult male; FDF: includes the duration of focal observation time (in minutes) as well as the time (in minutes) that the focal was observed grooming and mutually grooming another adult male.

difference between preferred social partners and tolerant dyads in the probability of mutual grooming ($\chi^2_1 = 0.07$, $P = 0.80$). The FDF data showed no association between the proportion of mutual grooming within bouts and association category ($\chi^2_1 = 1.21$, $P = 0.30$).

Similarly, changes in dyadic CAI values between 2-year periods did not predict changes in the mutual grooming index (MGI, equation (1): $F_{1,13} = 0.2$, $P = 0.67$). In addition, dyads that became preferred social partners from one period to the next ($N = 11$ dyads) were equally likely to exhibit an increase in mutual grooming as were dyads that ceased to be preferred social partners ($\chi^2_1 = 0.38$, $N = 12$ dyads, $P = 0.53$). No dyad ever switched from being preferred social partners to mutual avoiders in consecutive 2-year periods, or vice versa. Since we limited our calculations of the MGI to dyads that groomed at least 10 times in a given period, we did not have an adequate sample size to test whether dyads that became mutual avoiders experienced a decrease in mutual grooming rate compared to dyads that ceased to be mutual avoiders because they were so rarely seen together.

Finally, to determine whether unidirectional grooming was related to patterns of male association, we first ran a GLMM with the unidirectional grooming index as a continuous response variable and the within 5 m index as the predictor with categorical rank difference as a main factor and dyad ID as a random effect. We found a positive relationship between these variables such that dyads that exhibited high within 5 m index values also exhibited high unidirectional grooming values ($\chi^2_1 = 12.03$, $P = 0.001$). We then ran the model against association category and found that preferred social partners were significantly more likely to exhibit high unidirectional grooming values ($\chi^2_2 = 9.7$, $P = 0.008$). However, since the unidirectional grooming index and the nearest-neighbour index (a determinant of the association category) are

not independent of one another, it is difficult to evaluate the meaning of this pattern.

Duration of Grooming, Unidirectional Switches and Equitability

We used the FDF data to examine the effect of mutual grooming on grooming bout duration. We ran a GLMM looking at the effect of the occurrence of mutual grooming (Y/N) in a bout versus the length of the bout, with adult male party size as a main factor and

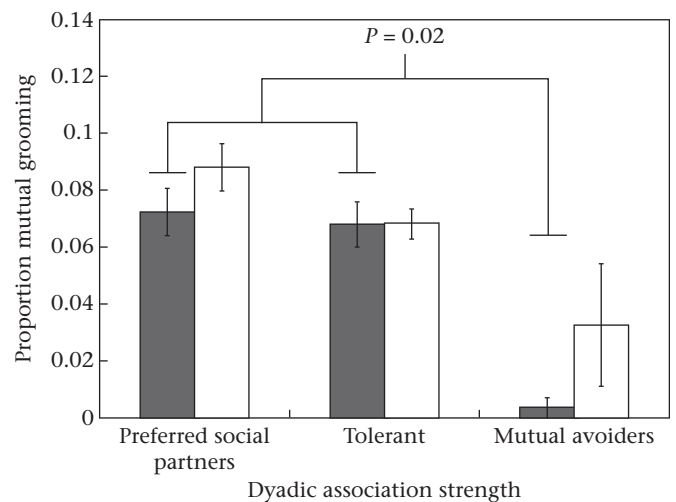


Figure 1. Mean \pm SE proportion of mutual grooming by association category in chimpanzees. The 10 min focal scan data (TMF, solid bars) are averages over the 2-year periods; the full-day focal data (FDF, white bars) were taken between August 2009 and April 2011. These data represent raw indices and not those predicted from the GLMM.

dyad ID as a random effect. Bouts that included any mutual grooming episodes were significantly longer than bouts without mutual grooming (parameter estimate = 6.59, $t_{1099} = 13.42$, $P < 0.001$). This relationship remained significant even when we excluded the time spent mutually grooming in calculating total grooming bout duration (parameter estimate = 7.32, $t_{1099} = 14.80$, $P < 0.001$; Fig. 2). In other words, the occurrence of a mutual grooming episode increased the amount of unidirectional grooming within a grooming bout. One possible explanation for this pattern is that there is a fixed probability of mutual grooming in any bout; thus, the chances of mutual grooming are greater in longer bouts. However, when mutual grooming was observed in a grooming bout, it occurred on average 4.06 min after the bout started (based on 356 grooming bouts with mutual grooming), while the average length of grooming bouts without mutual grooming was 4.58 min. This suggests that unidirectional grooming bouts were, on average, long enough for mutual grooming to occur.

Next, we examined the effect of mutual grooming on switches in the direction of grooming within bouts by running a GLMM of the presence of mutual grooming in a bout (Y/N) versus the rate of switching (number of switches/duration of bout), with adult male party size as a main factor and dyad ID as a random effect. Bouts that included at least one mutual grooming episode had more unidirectional grooming switches than bouts without mutual grooming (parameter estimate = 0.032, $t_{1099} = 4.67$, $P < 0.001$). In addition, unidirectional grooming episodes within a bout were shorter if they were followed by a mutual grooming episode (A grooming B, followed by A and B mutually grooming) than if they were followed by a switch in the grooming direction (i.e. A grooming B followed by B grooming A, parameter estimate = -0.595, $t_{914} = -2.48$, $P = 0.01$). Mutual grooming, therefore, served to encourage more back-and-forth grooming between the giver and the receiver.

Next, we examined the role that mutual grooming played in equality of the grooming relationship. Using TMF data, we found that the probability that a grooming scan was mutual was positively associated with dyad's unidirectional grooming equitability index (UDG_{eq} , equation (2)) in the 2-year period in which the grooming scan occurred (parameter estimate = 0.67, $Z = 2.40$, $P = 0.02$). As expected, dyads with a large rank difference were significantly less likely to have equitable unidirectional grooming relationships than were dyads with small rank differences ($\chi^2_1 = 5.24$, $P = 0.02$). Using the FDF data, we ran a GLMM of the occurrence of mutual grooming

in a bout (Y/N) versus the unidirectional grooming equitability index within a bout, with adult male party size as a main factor and dyad ID as a random effect. We found that bouts with any mutual grooming episodes also showed more equitability in unidirectional grooming than bouts without mutual grooming episodes (parameter estimate = 0.48, $t_{1099} = 25.4$, $P < 0.001$; Fig. 3). Furthermore, the unidirectional equitability index was positively correlated with the proportion of mutual grooming in the bout (parameter estimate = 1.15, $t_{1099} = 20.59$, $P < 0.001$). Therefore, although long-term patterns exist between the probabilities of mutual grooming and dyadic equitability, this may be due to similar short-term patterns of equitability and mutual grooming within bouts.

Finally, to test the switching hypothesis, we examined how often grooming bouts would start with episodes of mutual grooming and found this to be the case in only 66 of 316 (20.9%) of the grooming bouts that had at least one mutual grooming episode. Using a nonparametric binomial test, this was significantly less ($P = 0.013$) than the expected distribution of 26.6% based on the average proportion of time spent mutually grooming within bouts that had at least one mutual grooming episode. To ensure that this result was not being affected by any individual male, we ran the binomial test separately for each adult male and used the average proportion of time that mutual grooming occurred in bouts involving that male and that had at least one episode of mutual grooming as the expected distribution. When we looked at individual males, six out of nine males showed no significant difference from the expected distribution. We then examined whether mutual grooming was more likely to occur between switches in the direction of unidirectional grooming compared to when no switch in the direction of grooming occurred. We ran a nonparametric binomial test on the 310 episodes of mutual grooming from the FDF data set that occurred between two episodes of unidirectional grooming. In 165 episodes (53.2%), mutual grooming occurred between episodes of unidirectional grooming in the opposite direction (i.e. A grooms B, A and B mutually groom, B grooms A). This did not differ significantly from the expected distribution of 50% ($P = 0.255$). When we ran the binomial test separately for each individual male, all nine males showed a nonsignificant difference from the expected 50% distribution.

DISCUSSION

We found little support for the predictions of the social bonding hypothesis, which proposes that mutual grooming functions to

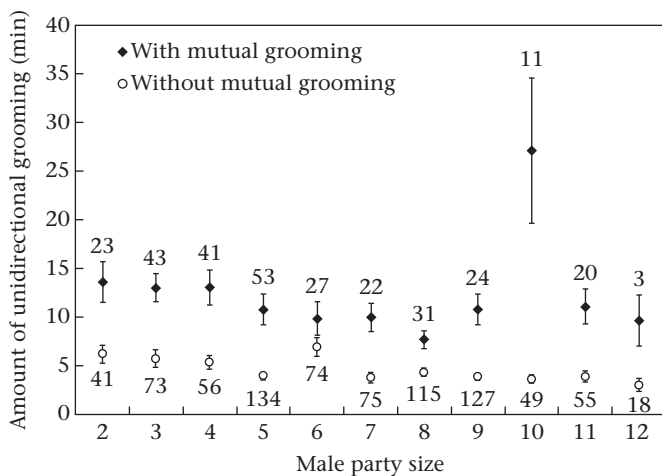


Figure 2. Mean ± SE duration of unidirectional grooming in bouts with mutual grooming (solid diamonds) compared to purely unidirectional bouts (white circles) in chimpanzees. Numbers indicate the number of bouts of each type observed. These data represent raw indices and not those predicted from the GLMM.

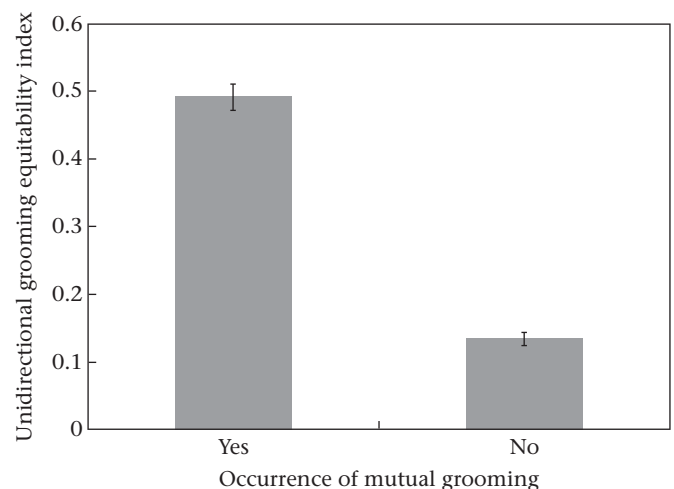


Figure 3. Mean ± SE unidirectional grooming equitability index for grooming bouts with and without mutual grooming in chimpanzees. These data represent raw indices and not those predicted from the GLMM.

maintain strong social bonds among male chimpanzees. The frequency of mutual grooming was not related to association strength, and preferred social partners did not groom significantly more than tolerant dyads. In addition, dyads that became or ceased to be preferred social partners in subsequent periods did not exhibit corresponding changes in their rates of mutual grooming with one another. The only support for the social bonding hypothesis was that dyads classified as mutual avoiders were less likely than other dyads to engage in mutual grooming behaviour. Therefore, while mutual grooming might not strengthen social bonds, it is a particularly rare behaviour in dyads with weak social bonds. Interestingly, a unidirectional grooming index, which measured the frequency with which dyad members engaged in unidirectional grooming bouts given that they were within 5 m of one another, was significantly related to an independent measure of association within 5 m and was higher in dyads that were preferred social partners, suggesting that, in this population, unidirectional grooming may be important in maintaining social bonds.

Our results contrast with the only other direct study of the function of mutual grooming among chimpanzees, which found evidence supporting the social bonding hypothesis (Fedurek & Dunbar, 2009). In their captive study, Fedurek and Dunbar (2009) found a significant positive correlation between face-to-face mutual grooming and time spent in proximity. Furthermore, unlike our study, they found no significant relationship between unidirectional grooming and proximity. This result, however, was driven by both male–female and female–female dyads. In wild populations, although a few of these dyads exhibit strong bonds, average association patterns indicate that these bonds are weaker than those of male–male dyads (Gilby & Wrangham, 2008; Langergraber, Mitani, & Vigilant, 2009; Machanda et al., 2013). Fedurek and Dunbar (2009) found no relationship between proximity and rates of mutual grooming among male–male dyads. While this result may be due to a small sample size (5 males), it does raise the possibility that conditions imposed by captivity alter the natural bonding tendencies in chimpanzees because individuals do not have the option (or the need) to join and leave parties. In the wild, female chimpanzees are less gregarious than males (particularly when high-quality food resources are scarce; Wrangham, 2000), whereas females are known to form stronger bonds in captivity than in the wild (de Waal, 1984). As such, females may use mutual grooming to maintain their social bonds when they are able (or have no alternative) to associate with one another. In addition, because chimpanzees in the wild may be in parties of different composition, their grooming decisions might be mediated by the presence or absence of other individuals, especially other preferred social partners. For example, individuals may be more likely to engage in mutual grooming with nonpreferred social partners if their preferred social partners are not present. Future work is needed to test patterns of mutual grooming for females in the wild and to understand how party composition may affect grooming decisions for individuals.

An alternative function of mutual grooming is that it signals an individual's willingness to invest in prolonging the current grooming bout, thereby increasing his immediate payoff. This 'immediate investment' hypothesis was inspired by the parcelling model of reciprocity (Connor, 1995) whereby individuals swap short (unidirectional) grooming bouts with one another to minimize their loss if the partner fails to reciprocate. The immediate investment hypothesis represents a form of overlapping parcelling in which a grooming recipient starts to reciprocate while his partner is still grooming him. We found strong support for this hypothesis. Grooming bouts with mutual grooming episodes were longer than purely unidirectional bouts, even when the time spent engaged in mutual grooming was removed. Mutual grooming

was associated with more switches in grooming direction per unit time, and unidirectional grooming episodes within a bout were shorter if followed by a mutual grooming episode. Finally, the amount of mutual grooming within a bout was significantly correlated with the equitability of unidirectional grooming between the dyad.

We found no support for the predictions of the switching hypothesis, which suggests that mutual grooming occurs when individuals switch the direction of the interaction, resulting in a period of simultaneous grooming. When mutual grooming occurred between unidirectional grooming episodes, it was just as likely to be in between a switch in the direction of grooming as not. We found some support for one prediction of this hypothesis as mutual grooming occurred at the beginning of grooming bouts less often than expected by the average proportion of time spent mutually grooming within bouts. However, when we looked at individual males, this pattern was only true in three of nine males, and for most males, grooming bouts began with mutual grooming episodes in the same proportion as the time that was spent mutually grooming within the bout.

Our results suggest that chimpanzees are interested in maximizing short-term benefits and that mutual grooming allows individuals to garner the immediate payoff of longer and more equitable grooming bouts. Interestingly, in our study, purely unidirectional grooming bouts lasted 4.58 min on average, shortly after mutual grooming should have started (at 4 min, on average). Thus, we propose that unidirectional grooming bouts tended to end when it became clear that the other partner was unlikely to extend the bout.

In a study of grooming reciprocity conducted among the chimpanzees from the Tai community in West Africa by Gomes et al. (2009), grooming (with and without mutual grooming) between two individuals within bouts and within days exhibited low levels of reciprocity. However, over a longer 22-month period, grooming was reciprocated. This would suggest that individuals are able to remember interactions over the long-term and have multiple opportunities to pay off grooming debts. It seems puzzling then, if individuals are capable of delayed long-term reciprocity, that Kanyawara chimpanzees should use mutual grooming to signal investment in and maintain equitability within an individual grooming bout. However, the Gomes et al. (2009) study is the only one of wild chimpanzees to show this pattern. Among chimpanzees of Ngogo (also in Kibale National Park, Uganda; Mitani, 2009) and Sonso (Budongo Forest Reserve, Uganda; Newton-Fisher & Lee, 2011), individuals exchanged grooming reciprocally in both short-term as well as long-term contexts, suggesting that immediate reciprocity may be important for chimpanzees. These studies and communities differ in three ways that may help explain the different patterns. First, Gomes et al. (2009) included both males and females in their analysis while the other studies included only adult male dyads (Mitani, 2009; Newton-Fisher & Lee, 2011). Across chimpanzee field sites, male–male dyads tend to exhibit stronger bonds and different patterns of association than female–female and male–female dyads (Gilby & Wrangham, 2008; Langergraber et al., 2009; Langergraber, Mitani, Watts, & Vigilant, 2013; Lehmann & Boesch, 2005; Machanda et al., 2013; Mitani, 2009; Newton-Fisher, 2002), suggesting that males and females negotiate and maintain relationships in different ways. Second, because the Tai community has undergone a dramatic decline in community size due to disease epidemics (Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2005), the Gomes et al. (2009) study included only three to five adult males. In comparison, Ngogo is the largest community ever studied and included 20–30 adult males at the time of Mitani's (2009) study. Tai chimpanzees also exhibit a higher degree of overlap of individual core areas compared to East

African study sites, meaning that individuals there are more likely to be found in the same areas (Lehmann & Boesch, 2005). Access to fewer available grooming partners and an increased probability of association at Tai may reduce the need for these individuals to reciprocate grooming in short-term periods. Furthermore, unlike Kanyawara, it is possible that mutual grooming at Tai functions to maintain long-term social bonds, especially during periods of increased intercommunity aggression, as has been suggested by Boesch and Boesch-Achermann (2000). This could explain why proportions of mutual grooming at Tai are reported to be high but reciprocity within bouts is low. Further studies are necessary to determine the frequency and variation in patterns of immediate and delayed reciprocity among wild chimpanzee communities.

Individuals within a group may use different strategies with respect to grooming and reciprocity. Dyads with particularly strong bonds may not seek out immediate benefits because of the increased probability of future encounters (Manson et al., 2004; Trivers, 1971). This should lead to strongly bonded dyads exhibiting less mutual grooming, but this was not supported by our results. However, the majority of dyads in our study were neither preferred social partners, nor mutual avoiders, but tolerant of one another (e.g. 39 of 45 dyads in 1995–1996). Therefore, it is possible that mutual grooming serves a more immediate benefit for individuals with a moderate level of affiliation who make up of the majority of dyads in the community.

This study also sheds light on the variation in patterns of mutual grooming across primates. Male chimpanzees are philopatric and high rates of male–male cooperation are generally believed to be the result of males being more closely related to each other than are females (Gilby & Wrangham, 2008). Surprisingly, however, maternal kinship among males plays only a limited role in patterning cooperative behaviours (including grooming) and most cooperative behaviours involve unrelated dyads (Langergraber, Mitani, & Vigilant, 2007). In contrast, among many cercopithecine primates, cooperative behaviours including grooming are concentrated among matrilineal kin (Chapais, 2001; Silk, 2002, 2006). Therefore, reciprocation within bouts, in the form of mutual grooming, may be unnecessary for these species as long as grooming offers an indirect fitness benefit (Gouzoules & Gouzoules, 1987; Manson et al., 2004; Schino, 2001). Our study included only one pair of maternal brothers, and a larger data set would be necessary to test whether mutual grooming rates differed between closely related pairs among chimpanzees. In addition, chimpanzees exhibit a fission–fusion social system (Sugiyama, 1968) and this creates a situation where individuals may not interact with one another for hours, days or even months. In comparison to other primates that exhibit reduced fission–fusion dynamics (Aureli et al., 2008), chimpanzees may be less confident about future interactions and use mutual grooming to take advantage of the immediate benefits offered by the current party structure (Newton-Fisher & Lee, 2011).

Our study raises several other questions for future research. Although our full-day focal follows allowed us to examine grooming bouts in detail, we are still missing data on how mutual grooming is actually initiated. For example, do individuals who are grooming give a particular signal that they are about to terminate the bout unless there is reciprocation? It is also possible that individuals may engage in mutual grooming when individuals reunite after a long separation or during periods of high social stress. In addition, our analyses included hand-clasp grooming as a form of mutual grooming, but hand-clasp grooming might have yet another function. Studies have suggested that differences in hand-clasp grooming show patterns of cultural differentiation (van Leeuwen, Cronin, Haun, Mundry, & Bodamer, 2012; McGrew, Marchant, Nakamura, & Nishida, 2001), and it is unclear whether

differences in mutual grooming between study sites might be the result of the same phenomenon.

Other studies of chimpanzees have shown that it is important to consider both short- and long-term benefits of cooperative behaviour. For example, a study on meat sharing in chimpanzees by Gilby (2006) found that individuals are more likely to share food with ‘harassers’ more consistently than they are with frequent grooming partners. The immediate benefit in this case is that harassers leave once they receive some meat, allowing the sharer to increase its own rate of meat intake. Our results on mutual grooming exhibit a similar pattern, with little support for investment in long-term social bonds but an indication that mutual grooming increases immediate benefits within grooming bouts. Our results provide further support for the notion that in studies of cooperation, immediate benefits must also be examined when assessing individual motivation. We are not suggesting that chimpanzee behaviour is best explained by cognitively simple mechanisms. Across study sites, chimpanzees are known to use grooming in general to maintain long-term social bonds (Arnold & Whiten, 2003; Mitani, 2006; Muller & Mitani, 2005; Newton-Fisher, 2002). At Kanyawara, it appears that unidirectional grooming may also serve this purpose, but that mutual grooming is used as a means to obtain immediate benefits. Therefore, chimpanzees strategically use their grooming behaviour in ways that maximize these benefits over both short- and long-term periods. This ability to manipulate social dynamics as well as the diversity of grooming behaviours used by chimpanzees may only be possible because of increased cognitive complexity in this species (Nakamura, 2000), highlighting the importance of understanding multiple explanations of cooperative behaviours.

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