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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.

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; Taï, 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 Taï 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