

Third-party grooming in a captive chimpanzee group

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Abstract Social grooming is ubiquitous among the captive chimpanzees at Chester Zoo. Seven individuals were chosen here for a study of third-party social dynamics. The grooming decisions of five adult males were analysed, but only insofar as they directed attention to a mother–daughter pair. Uniquely, the daughter was an unpopular and physically disabled subadult whose congenital motor impairments prevented her from grooming others effectively. The impetus for this study was the observation that some males increased their grooming towards the disabled daughter during days when the mother had a tumescent anogenital swelling (sexually attractive to males) compared to days when the mother was not tumescent (less attractive). Apparently, males were grooming the daughter with no possibility of payback (because the daughter could never “return the favour”). A “grooming rate” (avg. grooming time/hour) was calculated that showed the grooming efforts of all five males towards both mother and daughter. These rates were compared on days when (1) the mother’s anogenital swelling was tumescent, and (2) days when the swelling was not tumescent. Each male showed a different pattern of behaviour. Two males groomed the daughter significantly more when the mother was tumescent. Results for all males were graphed against the quality of the social relationship between each male and the mother.

Apparently, only males that had a weaker relationship to the mother groomed the daughter more when the mother was tumescent. This pattern did not exist for males with a stronger relationship to the mother. Possibly, the insecure males were using the disabled daughter as a way to curry favour with the attractive mother. If this is confirmed, then this type of triadic situation is a possible setting for indirect reciprocity to occur.

Keywords Chimpanzee · Grooming · Oestrus · Disability · Indirect reciprocity

Introduction

When one primate grooms another, it not only provides good hygiene for the recipient (Hutchins and Barash 1976; Tanaka and Takefushi 1993), but it also provides hedonic value (pleasure) from beta-endorphins (Keverne et al. 1989). For the giver of grooming, the benefits are likely more political than hedonic (Dunbar 1991; Pérez and Vea 1998; de Waal 1997; Barrett et al. 2000). However, primate social interactions do not occur in isolation. Most animals inhabit social spheres where communicative signals are easily observed by multiple uninvolved bystanders (McGregor 2005). This leads to questions about the causes of grooming events: does individual A start grooming B solely due to dyadic factors (e.g. B groomed A earlier), or might there also be an influence from a third party? This study revolved around a mother–daughter pair. The daughter was Kiki (KI), a subadult whose congenital motor disability deprived her of the manual dexterity to groom others. Therefore, she could never adequately reciprocate any grooming. As a grooming partner, she was the least popular animal in the group, with a strong grooming

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relationship to her mother and nobody else (Russell 2007). However, it was conspicuous that KI received more grooming from adult males on days when her mother Halfpenny (HP) was in full oestrous. Chimpanzee oestrous swellings follow a 35-day cycle during which the anogenital region swells gradually, reaches maximum tumescence (7–10 days), and then deflates (Yerkes and Elder 1936). This is sexually attractive to male chimpanzees (Nishida 1997; Deschner et al. 2004). There were three aims in this study: (1) to confirm that males were differentially grooming KI according to HPs swellings, (2) to investigate how male behaviour might vary according to the strength of the male's social bond to the mother, and (3) to ascertain whether HP was present and what she was doing while her daughter was being groomed.

Methods

The chimpanzees (*Pan troglodytes*) were housed at Chester Zoo, UK, in a single group of 26 members. There were five adult males and fifteen adult females. The outdoor area was 2000 m², and the cone-roofed indoor enclosure was 13 m in diameter (along the bottom) and 12 m high. There were seven focal individuals in this study. KI (age 7) was conjectured (but not confirmed) to be afflicted with cerebral palsy (S. Hill, Chester Zoo, pers. comm.). She routinely attempted to groom others, but only managed a crude patting technique. The mother Halfpenny (HP, age 28) was above average in popularity (Russell 2007). The males were Boris (BO, age 37), Wilson (WI, age 35), Nicky (NI, age 34), Friday (FR, age 27), and Dylan (DL, age 15). During the previous year, DL had supplanted BO as the alpha male (C. Caws, pers. comm.). As part of a larger study (see Russell 2007), the group was observed for 82 days (402.5 h) in 2003–2004. The investigator scanned groups continuously and recorded all individuals and grooming cliques (identity of groomers, direction of grooming) within 10 m, and noted the start and end times of each clique to the nearest second. For analysis, he divided the data into minute-by-minute blocks (grooming yes/no). A research assistant was trained to collect data simultaneously, which helped to establish an *occurrence reliability* score (Hopkins and Herman 1977) of 84.86%.

The independent variable was HP's swelling, recorded daily as "swollen" or "not swollen". The analysis was day-by-day: comparing grooming on "swollen" versus "not swollen" days. The dependent variables were: (1) male grooming towards HP, and (2) towards KI. Data were partitioned along the five males. "Grooming rate" was the sum of the grooming minutes *per dyad* divided by the number of hours that the individuals in the relevant dyad

were observed in proximity to each other (within 10 m). If the members of a dyad were observed in proximity for <1 h, than that day was excluded from analysis (mean co-observed days per dyad: 71.8, SD = 3.6). Grooming rate was an appropriate measure because there was some extent of species-typical fission–fusion sociality (where individuals are "repeatedly congregating and dispersing freely", Itani and Suzuki 1967, p. 365), since the chimpanzees were usually free to go outside.

Results

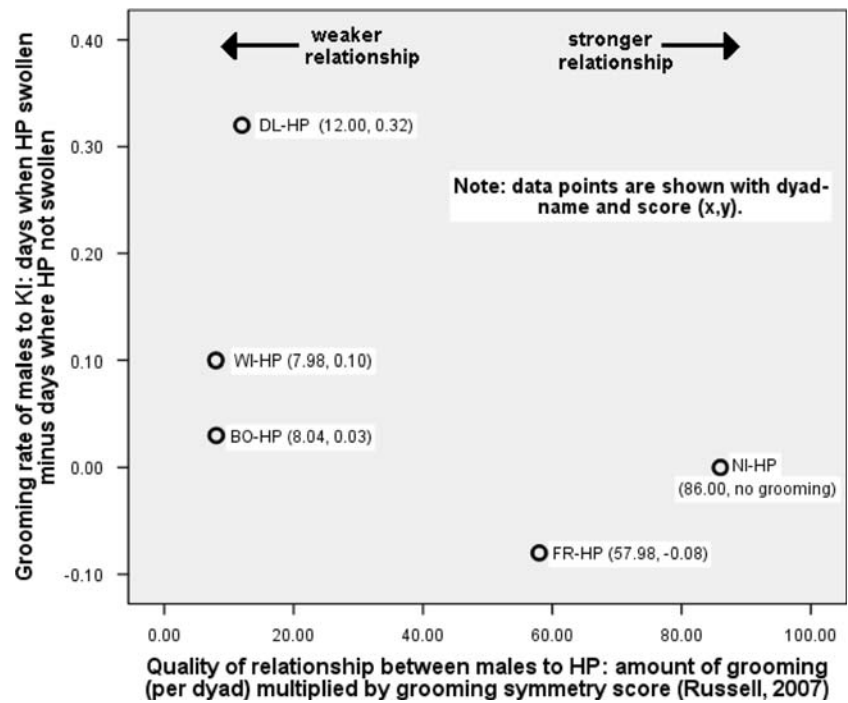
The left side of Table 1 shows the grooming rates by all five males towards mother (HP) and daughter (KI). Two males, DL and WI, groomed KI significantly more when HP was tumescent (DL–KI: Kruskal–Wallis $\chi^2 = 6.329$, $p = 0.012$; WI–KI: $\chi^2 = 8.980$, $p = 0.003$). BO appeared to show the same pattern, but the difference was not significant ($\chi^2 = 1.107$, $p = 0.293$). FR showed no difference ($\chi^2 = 0.217$, $p = 0.641$) and NI never groomed KI. Did the males differentially groom the mother according to her oestrus swelling? Only WI groomed HP more when she was tumescent ($\chi^2 = 18.636$, $p < 0.001$). Two other males—BO and DL—groomed HP less when she was tumescent. This difference was significant for BO ($\chi^2 = 3.872$, $p = 0.049$) but not for DL ($\chi^2 = 2.209$, $p = 0.137$). For the remaining two males, there was no significant difference (FR–HP: $\chi^2 = 1.835$, $p = 0.176$; NI–HP: $\chi^2 = 0.176$, $p = 0.706$). The right side of Table 1 shows HP's behaviour at the beginning of KI being groomed. As shown, HP was present for almost all of KI's grooming events—but was usually not involved in grooming during these events.

In Fig. 1, the male's differential grooming rate is graphed against the quality of that male's social relationship to the mother. The y-axis shows the male grooming rate towards KI on her mother's tumescent days minus the rate on nontumescent days. A positive number indicates that there was more grooming during tumescence. The x-axis is the total amount of "grooming minutes per dyad" multiplied by the "grooming symmetry score" per dyad. The latter was calculated by Russell (2007) for all grooming cliques during the same period (scale 0–1 where 1 is complete symmetry). This refers to the extent to which individuals in a dyad evenly matched their grooming efforts (scores: DL–HP 0.923, FR–HP 0.892, NI–HP 0.988, BO–HP 0.473, WI–HP 0.145). These numbers indicate that HP tended to match the grooming efforts from DL, FR, and NI, that she groomed BO more than BO groomed her, and that she almost completely ignored the grooming efforts of WI.

Table 1 Grooming rates from five adult males (BO, DL, FR, NI, WI) towards the mother–daughter dyad (HP/KI) according to the mother’s oestrous status (swollen/not swollen), and the mother’s (HP) behaviour during the daughter’s (KI) grooming events

Dyad (days counted swollen/not swollen)	Grooming rate		Behaviour of HP while KI is groomed		
	HP swollen mean (SD)	HP not swollen mean (SD)	% time HP was present	% time HP was present and being groomed	% time HP was present and grooming another individual
BO–HP (33/36)	0.82 (2.61)	1.10 (2.29)	100 (9/9)	11.11 (1/9)	22.22 (2/9)
BO–KI (38/38)	0.06 (0.20)	0.03 (0.10)			
DL–HP (32/36)	0.47 (0.88)	1.15 (1.81)	92.64 (63/68)	17.46 (10/63)	15.88 (11/63)
DL–KI (36/39)	0.58 (0.72)	0.26 (0.53)			
FR–HP (33/36)	1.49 (1.76)	1.33 (2.03)	100 (11/11)	14.29 (1/7)	25.57 (2/7)
FR–KI (38/38)	0.05 (0.18)	0.13 (0.42)			
NI–HP (33/36)	2.04 (3.47)	1.69 (3.08)	Not applicable		
NI–KI (n/a)	0	0			
WI–HP (33/36)	2.16 (2.79)	0.25 (0.68)	100 (11/11)	60 (3/5)	60 (3/5)
WI–KI (37/38)	0.10 (0.25)	0			

Fig. 1 Graph of the differential grooming rates of five adult males (BO, DL, FR, NI, WI) towards the daughter (KI) plotted against the quality of the male’s relationship to the mother (HP)



Discussion

Five triadic relationships were examined here (DL–KI–HP, BO–KI–HP, FR–KI–HP, NI–KI–HP, WI–KI–HP), each with a different dynamic. The pre-existing social relationship to HP seemed to be a very important influence on how the males behaved. Two in five males groomed KI significantly more on days when her mother (HP) had a tumescent (sexually attractive) anogenital swelling (despite the fact that KI could not reciprocate their grooming). The clearest pattern was from WI, who significantly groomed both mother and daughter more when HP was tumescent. For two other males—DL and BO—there was

an interesting pattern: during tumescence, both showed reduced interactions with the mother (but the differences were not significant) and increased interactions with the daughter (significant only for DL). The results for DL, BO, and WI all appear on the left side of Fig. 1. These are the “weak” relationships (low frequency). Notably, these males each display a score above zero (indicating that each groomed KI more during HP’s tumescence). In contrast, results for FR and NI appear on the right side of Fig. 1. These are the “strong” relationships, and here the pattern disappears completely. An intriguing possibility is that being nice towards KI functioned as a type of contingency for “weak” relationships only—whereas a “strong”

relationship mitigated against this pattern (they had no need to displace their grooming efforts onto the daughter because they had direct access to the mother). As shown in Table 1, HP was usually present when the males groomed her daughter. Therefore, she was able to observe the males when they groomed KI. Interestingly, HP was not usually involved in grooming when this happened (although WI's case is an exception). Therefore, the males were not displacing onto KI because HP was “too busy” (and even if she was, this should not be a barrier either, as chimpanzees routinely interrupt grooming bouts among others; see Russell 2007).

Why did the males choose to groom the daughter in full view of the mother when she was tumescent? One possibility is that it was a means to be close to HP. The males presumably had a desire to stay in proximity to HP due to her oestrus swelling (cf. Nishida 1997). Close exposure to the swelling may have been a reward in itself (cf. Aharon et al. 2001, who show that reward centres in the male human brain are activated in response to a pretty female face). Another possibility is that the males were trying to curry favour with HP within a reward–punishment system. Koyama et al. (2006)—studying the same group—found evidence that individuals give grooming to encourage the recipient to support them in conflicts, withhold grooming to punish nonsupport, and use grooming to repair weakened relationships. If that mechanism is operating here, then this might be a background for “indirect reciprocity” (e.g. “if A sees B grooming C, then A will groom B”; cf. Hammerstein 2003). If so, then the males would achieve some kind of reward from HP as a result of being kind to her daughter. Whatever the case, these kinds of triadic effects are worth further study. Primatologists who possess large samples of primate social grooming data should scan their datasets for similar effects.

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