'Friendship' for fitness in chimpanzees?

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It has been repeatedly suggested that primates trade social services for fitness benefits in their relationships with the opposite sex. We tested this proposal in a colony of captive chimpanzees, *Pan troglodytes*, by examining behavioural data on grooming, agonistic support and food sharing in relation to genetically established paternity. We found no support for the notion of trade. First, males did not sire more offspring with females that they actively groomed more frequently, that they supported more often or with which they shared food more frequently. Correspondingly, females did not give birth to more offspring sired by males from which they received more services. Second, males that showed more affiliative behaviour towards females in general did not sire more progeny. Furthermore, females did not bear more offspring sired by males to which they themselves directed more sociopositive behaviour. Results from this captive colony are compatible with those reported for chimpanzees under natural conditions.

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Interest in potential trading of social services for sex in chimpanzees, *Pan troglodytes*, has been pronounced. It addresses questions regarding precursors of human trade and psychological mechanisms of bargaining. From an ultimate perspective, it directs attention to possible fitness benefits of intersexual exchange relationships, and that is the focus of this paper.

Central to evolutionary theories about sexual exchange relationships is asymmetry between males and females for investment in offspring. The larger investment by females makes them a limiting resource to males and allows females to exercise choice (Trivers 1972). Accordingly, male social services to females have been interpreted as reproductive strategies (e.g. see Tutin 1980; Galdikas & Teleki 1981; Goodall 1986; Stanford 1996). Such strategies may become effective in two ways: by enhancing the frequency of mating and by increasing the probability of fertilization per mating.

Increased mating opportunities have been suggested for male chimpanzees that share meat with females (e.g. Galdikas & Teleki 1981; Stanford 1998). Tutin (1980) reported that a wild chimpanzee male sometimes builds up a cooperative relationship with a particular female in order to consort with her. Compared with other males, such males groom oestrous females more often and share food more frequently with females in general. However, after a detailed statistical analysis, Hemelrijk et al. (1992) found only marginal evidence for the exchange of social

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services for matings in a colony of captive chimpanzees. In their long-term study on grooming, support in conflicts and food sharing, there was no evidence that mating partners had long-term affiliative relationships. Although males mated more often with those females that they groomed more frequently, they did so only during the oestrous period of the female. Grooming may thus function directly to facilitate mating by suppressing aggression in males and the tendency to flee in females and seems to be part of the sexual repertoire rather than being exchanged for matings.

However, a DNA-typing study conducted on the same colony showed that copulation frequency was not significantly correlated with number of offspring (our unpublished data) and therefore cannot be used as a fitness measure. As suggested above, exchange of social services for fitness could still occur via an enhanced chance of fertilization per copulation, such as through some postcopulatory choice mechanism exercised by females (Martin 1992). Our aim in this study was to establish whether services are exchanged directly for fitness benefits instead of copulations.

We combined behavioural data for those chimpanzees used by Hemelrijk et al. (1992) with paternity inferences based on microsatellite analyses (unpublished data). Since male reproductive strategies are effective only if they coincide with female preferences, intersexual exchange should hold from both male and female perspectives. We therefore tested (at a group level; see Hemelrijk 1990b) whether males sire more offspring with females that they actively groom or support more often,

or with which they share food more frequently. From the female point of view, we examined in the same way whether females conceive more offspring sired by those males from which they acquire more services.

Male services to females may be effective at a more general level than that of specific exchange relationships. For instance, males that show more affiliative behaviour to females in general may be more 'popular' among all females and thus sire more progeny. For this reason, we also tested whether a correlation exists between the number of offspring of males and the services they render to all females.

As an aside, we investigated whether females direct more sociopositive behaviour towards those males that sire more of their live offspring.

METHODS

Study Colony

Behavioural observations were carried out at Burgers' Zoo in Arnhem, the Netherlands. Here, we confine ourselves to observations conducted during the summer in 1985–1989 when the chimpanzees lived in an open-air enclosure of about 0.7 ha (in winter they lived in a much smaller, indoor enclosure). The open-air enclosure consists of a meadow with trees, some of which the chimpanzees can climb. In this enclosure the chimpanzees are sometimes provided with vegetables and fruits and with mixtures of, for example, peanuts, sunflower seeds and brewed linseed. In the mornings and evenings the chimpanzees are fed on fruits, vegetables and monkey chow in their night cages in which they are confined in small groups. In cases of illness or birth, the chimpanzees were sometimes kept inside (in these night cages or in a heated hall of 21 × 18 m) during the day. For further details on the colony, see van Hooff (1973) and Adang et al. (1987).

The behavioural analyses in this study are restricted to mature individuals (i.e. males of 7 years and older and females after menarche; see Goodall 1986) and involve four males and 10 females (for actual numbers per year, see the tables). During the study period, the colony varied between about 20 and 30 individuals.

Observational Methods

Per summer at least 100 observational hours of behavioural data were collected by C.K.H. with the help of a changing team of students. Grooming behaviour, aggressive interactions and agonistic interventions (referred to as 'support' by de Waal 1978) were recorded on a tape recorder by two observers simultaneously during sessions that lasted 30 min or a multiple thereof.

An individual was recorded as a supporter if she/he initiated a new agonistic dyad with one (and only one) of the two individuals already involved in an agonistic dyad (de Waal 1978). Agonistic behaviour was registered by 'all-occurrence' sampling, grooming behaviour by scans at intervals of 10 min (Altmann 1974). To collect data on food sharing, the group was provided in the open-air

enclosure about once a week with about eight branches of trees with leaves, each roughly 2 m in length. The main form of food sharing consisted of feeding from another's branch: while individual A held a branch, B settled nearby and fed from it together with A. We recorded any instances of food sharing once every 5 min per dyad. In each experiment, observations lasted half an hour, or less if all the food had already been eaten. Other, less frequent forms of food sharing are not considered here.

Data Treatment

We subdivided the data into separate summer periods, because group composition and dominance ranks changed and because a different team of students took part in data collection each summer. As it happened, during all periods examined here the position of the alpha male was unclear, that is, he did not receive the submissive rapid-oh-oh vocalization from all adult males or received aggression more often than submission from other males (de Waal 1984).

With respect to male behaviour, for each period the total frequencies of grooming and support and the frequency with which each male allowed females to feed from his branch were counted separately according to whether females were in oestrus. Data were summed in rectangular matrices, in which rows represent males and columns represent oestrous or anoestrous females. We corrected frequencies of grooming and feeding from another's branch for the total period of time during which males were present. Frequencies of support were divided by the number of opportunities for an individual to give support. Individual A's opportunity to support B was defined as the number of conflicts B had with individuals other than A when A was present in the group. When the female perspective was taken, we made similar corrections, with rows representing females and columns males. (To give an impression of the amount of data, the correlations in Table 1 (males) are based on 107 acts of grooming, 13 of support and 375 of food sharing.)

For investigation of correlations with paternity, for each period the number of offspring for each male–female pair was summed in rectangular matrices.

Paternity and Genetic Analyses

From 72 chimpanzees that were in the colony between 1971 and 1996, 34 blood or muscle samples were available for genetic analyses. Muscle samples were taken only from chimps that died. In 1990 chimpanzees were anaesthetized (with Ketalar) to obtain blood samples (10 ml) for this study. We did not observe any adverse effects of the procedure. After blood extraction (following the protocol of the QIAamp Blood and Tissue Kit, 'QIAGEN'), six nuclear loci with dinucleotide repeats (D6S271, D6S311, D7S505, D13S159, D16S420, D17S791) were amplified by the polymerase chain reaction (PCR) methods described by von Segesser et al. (1999), but with the following slightly modified PCR cycling conditions: 3 min of denaturation at 94°C was followed by seven cycles

Table 1. Paternity and social services

Services		1985	1986	1987	1988	1989
Male perspective						
Males grooming females						
Nonoestrous	N_m	2	1	2	2	2
	N_f	6	3	7	5	3
	τ_{Kr}	−0.3	1	−0.4	0.33	0
	P_r	1	0.33	1	0.25	0.65
Oestrous	N_m	2	1	2	2	2
	N_f	6	3	7	5	3
	τ_{Kr}	0.75	−0.5	0.1	−0.38	−0.5
	P_r	0.15	1	0.44	1	1
Males supporting females						
Nonoestrous	N_m	2	—	2	2	2
	N_f	6		7	5	3
	τ_{Kr}	−0.2		0.3	−0.25	−0.5
	P_r	1		0.18	1	1
Oestrous	N_m	—	—	2	—	—
	N_f			7		
	τ_{Kr}			−0.17		
	P_r			1		
Males allowing females to feed from a branch						
Total	N_m	2	1	2	2	2
	N_f	6	3	7	5	3
	τ_{Kr}	−0.2	−0.82	0	−0.16	0.41
	P_r	1	1	0.6	0.81	0.33
Female perspective						
Females being groomed by males						
Nonoestrous	N_f	2	1	2	2	—
	N_m	6	3	3	4	
	τ_{Kr}	−0.3	0.5	−0.5	0.68	
	P_r	1	0.66	1	0.086	
Oestrous	N_f	2	—	2	2	2
	N_m	6		3	4	4
	τ_{Kr}	0.22		−0.5	−0.77	−0.33
	P_r	0.327		1	1	1
Females receiving support from males						
Nonoestrous	N_f	—	—	2	2	2
	N_m			3	4	4
	τ_{Kr}			1	−0.58	−0.33
	P_r			0.33	1	1
Oestrous	N_f	—	—	2	2	2
	N_m			3		
	τ_{Kr}			−0.33		
	P_r			1		
Females feeding from a male's branch						
Total	N_f	2	1	2	2	2
	N_m	6	3	3	4	4
	τ_{Kr}	−0.2	−0.5	−0.82	0.24	0.71
	P_r	1	1	1	0.32	0.09

Male perspective: τ_{Kr} correlation between the number of offspring a male has from each female, on the one hand, and the frequency with which he grooms, supports and shares food with the female, on the other. Female perspective: τ_{Kr} correlation between the number of offspring sired by male partners and services received from them. N_m: Number of males; N_f: number of females; P_r: one-tailed probability in the right tail of the permutation distribution. Combined probability values are nonsignificant. Data for the first correlation are presented in Table 2.

each consisting of (1) 30 s of denaturation at 94°C, (2) annealing for 1 min at 50°C and (3) 90 s of elongation at 72°C. This was followed by a further 30 cycles in which the annealing temperature was adjusted to 54°C. All apparently homozygous loci or loci that were difficult to read were amplified a second time to increase the reliability of the results. The number of alleles for each locus appeared to range from 5 to 10 and allele heterozygosity

from 0.77 to 0.91. All mother–infant pairs shared a common allele at all loci. To be considered the sire of a specific infant, a male had to satisfy three criteria simultaneously. First, he had to be at least 7 years old at the time of conception. To this end, we estimated a range of possible conception dates by subtracting 232 days from the date of birth and adding the complete month before and after this date (to account approximately for

Table 2. Data for matrix correlation between the frequency with which males groomed females and the number of offspring males sired with them

| | Females | | | | | |
Males	G	J	S	T	H	Mo
Fo	0	0	1.4	0*	0	0.9
Ta	0	0.5	0*	4.5	0	0

Fo and Ta are abbreviations of names, column heads represent nonoestrous females. Numbers represent grooming frequencies (corrected for opportunities) in 1985. Asterisks indicate offspring sired in the same year. $\tau_{Kr} = -0.3$, NS (see first correlation in Table 1).

variation in the duration of gestation; Wallis & Lemmon 1986; Martin 1992). Second, he had to show a common allele with the possible offspring at all of the six loci. Third, he had to be the only one satisfying these criteria and the rest of the males had to be excluded at least at two loci. If this were the case, but there were additional potential fathers among those from whom samples were lacking, then the male was considered as the actual father only if all other males could be excluded as fathers with a probability higher than 95%. The paternity exclusion probability was calculated on the allele frequencies of the complete group after Morin et al. (1994). In this way, we inferred with reasonable confidence the fathers of 10 infants that are used in the behavioural analyses in this paper.

Statistical Analysis

All correlations with social services concern sociopositive behaviour observed during the summer period of supposed conception.

Because chimpanzees are group living, but dyads in matrices of social interactions are statistically dependent, we studied social behaviour at a group level using the methods described by Hemelrijk (1990a, b). In this approach, 'relative' male–female interchange (under the actor–receiver model; Hemelrijk 1990b) is said to occur when each male directs beneficial acts more often to those females with which he sires more offspring. The corresponding 'relative' female–male interchange takes place if each female receives more beneficial acts from those males with which she conceives more offspring. To study these hypotheses, we investigated the correlation within rows between two rectangular matrices by means of the τ_{Kr} statistic, that is, Kendall's statistic S was calculated for each row and summed over all rows and this so-called Kr statistic was corrected for sample size and the number of ties. By correlating within rows, the τ_{Kr} test takes individual variation into account. Rows including only zeros were omitted. We calculated the probability of the observed value by using a permutation procedure in which complete rows and columns (i.e. the dependent units) were randomly shuffled. For the τ_{Kr} test to show significance, matrices with at least four columns are required. As an example, the grooming matrix and paternity indications for the first correlation of Table 1 are given in Table 2.

Because observers, group composition and dominance ranks changed between summers, the same correlations had to be tested for each year separately. The more correlations are performed, however, the larger the risk of obtaining significance by chance alone. To reduce this problem, we combined probability values obtained in separate seasons using the improved Bonferroni method (Hochberg 1988).

RESULTS

Independent of the oestrous state of the females, males did not sire more offspring with those females that they groomed, supported or shared food with more often during the period of inferred conception (Table 1). In line with this, females did not conceive offspring more frequently with those males by which they were groomed or supported more often or from which they obtained more food (Table 1). Thus, there was no evidence of effective exchange of sociopositive behaviour for reproductive benefits. We also found no correlation between the number of offspring of each male in a season and the frequency with which he was seen grooming or supporting or sharing food with females in general, independent of the female's identity (Table 3). Results obtained from data pooled to include both oestrous and anoestrous periods were similar. Females did not bear more offspring sired by males that they groomed, supported or shared food with more often (Table 4).

DISCUSSION

Our results indicate that directing sociopositive behaviour to individuals of the opposite sex in a captive colony of chimpanzees does not bring reproductive benefits. This agrees with the lack of indications for exchange at a behavioural level in the same colony (Hemelrijk et al. 1992).

A possible shortcoming of our study is that the colony was small and captive. As regards the sample size, the number of individuals in this study is the same as that in the only study on social positive behaviour and genetic relatedness in wild chimpanzees by Goldberg & Wrangham (1997). There are several reasons why exchange relations are not to be expected under natural conditions either. For example, consortship (where there is ample opportunity for sociopositive behaviour within a

Table 3. Kendall rank correlations between number of offspring per male and the degree of sociopositive behaviour he directs to all females

Males	Year				
	1985	1986	1987	1988	1989
Grooming females					
Nonoestrous					
N_m	3	3	3	4	4
τ	0.82	0.5	0.5	0.82	0
P_r	0.34	0.67	0.66	0.17	0.66
Oestrous					
N_m	3	3	3	4	4
τ	−0.82	0.82	0	0.41	0.89
P_r	1	0.33	0.68	0.31	0.1117
Supporting females					
Nonoestrous					
N_m	3	—	3	4	4
τ	0.5		0.82	0	−0.58
P_r	0.64		0.35	0.83	1
Oestrous					
N_m	—	—	3	4	—
τ			0.82	−1	
P_r			0.32	1	
Food sharing with females					
N_m	3	3	3	4	4
τ	−0.82	−0.82	−0.82	0.82	0.41
P_r	1	1	1	0.17	0.34
Supported by females					
N_m	—	—	—	4	4
τ				0.58	−0.58
P_r				0.51	1
Groomed by females					
N_m	3	—	3	4	4
τ	0		−0.58	0.89	−0.82
P_r	0.68		1	0.17	1

N_m: Number of males; P_r: one-tailed probability in the right tail of the probability distribution. Combined probability values are nonsignificant.

Table 4. τ_{Kr} correlations between the number of offspring a female bore to each male and the frequency with which she directed sociopositive behaviour to him

Male paternity	Year				
	1985	1986	1987	1988	1989
Females grooming males					
N_f	2	—	2	2	2
N_m	6		3	4	4
τ_{Kr}	−0.2		−0.5	0.41	−0.52
P_r	0.8		1	0.17	1
Females supporting males					
N_f	2	—	—	2	2
N_m	6			4	4
τ_{Kr}	−0.2			−0.33	−0.33
P_r	1			1	1
Females food sharing with males					
N_f	—	1	2	2	2
N_m		3	3	4	4
τ_{Kr}		−0.5	−0.5	0.33	0.58
P_r		1	1	0.4	0.49

N_f: Number of females; N_m: number of males; P_r: one-tailed probability in the right tail of the permutation distribution. Combined probability values are nonsignificant.

particular male and female dyad) among chimpanzees in the Tai forest seldom led to paternity (Gagneux et al. 1997, 1999). Males from other communities in the Tai forest sired many infants although the females apparently had no social relationship with them at all. Furthermore, wild chimpanzees are described as highly promiscuous (e.g. Goodall 1986; Morin 1993; Wallis 1997) and there is no long-term bonding between mating partners (Nishida & Hiraiwa-Hasegawa 1987).

This absence of demonstrable fitness benefits highlights the general lack of empirical support for sociobiological hypotheses regarding affiliative acts in primates. For example, DNA studies have shown that sociopositive relationships between adult males and infants in Barbary macaques, *Macaca sylvanus*, do not reflect relatedness, either in captive (Paul et al. 1992) or in wild populations (Ménard et al. 1992). In a further example, an earlier onset of paternal care could not be interpreted as a reproductive strategy that accelerates the female's post-partum ovulation in Goeldi's monkeys, *Callimico goeldii* (Jurke et al. 1995). In yet another study using DNA typing in a wild community of chimpanzees in Kibale, Goldberg & Wrangham (1997) were unable to confirm the received view that matrilineal relatedness underlies cooperative relationships among male chimpanzees.

In line with Gould (1989) and Gould & Lewontin (1979), we conclude that not every behaviour pattern reflects a separate adaptation with specific fitness benefits. Therefore, it is our belief that the specifics of social relationships may often be better understood as contextual and historical consequences of entanglement between behaviour, ecology and physiology (te Boekhorst & Hogeweg 1994; Hemelrijk 1996, 1997, 1999; Thierry 1997; Hemelrijk & Luteijn 1998).

Acknowledgments

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