

Sexual exchange relationships in captive chimpanzees?

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Summary. In a group of captive chimpanzees (*Pan troglodytes*), we studied whether females received more social benefits from males when they were in oestrus than at other times and whether males distributed their beneficial acts especially to females with whom they mated more frequently. When in oestrus, females were groomed more frequently by males than at other times. There was an indication that females were groomed especially by those males with whom they mated more often. From the male point of view, the relationship between active grooming and copulation frequency held only in interactions with oestrous females. No difference was found in the male's tendency to share food with females in oestrous or anoestrous condition. Further, clear disadvantages were associated with being in oestrus: females received support from males less frequently and were more often involved in conflicts with males than in their anoestrous period. Higher ranking males did not mate more often. No relationship was found between the frequency with which a male copulated with a given female and her dominance rank, age or parity, nor did he support her or share food more often with her.

Introduction

Due to greater energy expenditure in eggs compared to sperm cells, females invest more in offspring than males do; as a consequence of this, receptive females become a limiting resource for males (Bateman 1948; Trivers 1972) and females, by exercising female choice (Darwin 1871), may influence male behavior.

In this line of thought, the sexual swelling in female chimpanzees, which marks the ovulation period, is considered by Goodall (1986, pp 484–485) as a “sexual bargaining” point. Though the swelling causes some minor discomfort during sitting and in conflicts is easily ripped

open, Goodall states that it is associated with a variety of “privileges”: swollen females are groomed more often by males and are more successful when begging males for food. Similar results had been obtained by Yerkes (1939, 1940) in a competitive food-acquisition experiment with male-female pairs. When sexual swelling was in the maximum phase females obtained food much more often than at other times. However, Goodall's observations were anecdotal and Yerkes' experiments were confined to an artificial pair situation. The first aim of this study was a quantitative examination of social advantages to oestrous females, other than copulations, that could be ascribed to the sexual swelling, in a captive group of chimpanzees.

Male chimpanzees compete for females. This can be inferred from their increased levels of aggression when oestrous females are present (Nishida 1983). Tutin (1979) described several sexual strategies in wild chimpanzees. Firstly, a male may try to mate whenever a noncompetitive situation occurs. Secondly, male chimpanzees may compete for a higher dominance rank to be able to chase away rivals and thus monopolise oestrous females. Thirdly, males may build up a cooperative relationship with a female in order to consort with her; they also spend more time in a group with oestrous females, groom them more often in between matings and share food more frequently with females in general. However, it is unknown whether these males mate with the same females to whom they direct their seemingly altruistic behavior, as has been established in, among others, baboons (Seyfarth 1978a, b; Smuts 1983a, b, 1985; Noë and Sluifster 1990). In baboons, there are long-term relationships between some males and females that extend into the anoestrous period of the female: males appear to groom and support these “special” females more often than others (Seyfarth 1978b).

The second aim of this study is therefore to examine, from the male point of view, whether male copulation frequencies are associated with male dominance rank, and whether males obtained more copulations from those females they groomed and supported more fre-

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quently and with whom they shared food more often. Males of some primate species show low sexual interest in nulliparous females (e.g. chimpanzees: Hasegawa and Hiraiwa-Hasegawa 1983) and a mating preference for high-ranking females (cited by Smuts 1987, p 397). We investigated whether such preferences also occurred in the study group.

Since stability of male dominance relationships may influence mating strategies (Tutin 1979) and social relationships (de Waal 1984; Hemelrijk and Ek 1991), we analyzed separately periods when the alpha-male position was clear and unclear.

Methods

Study site and subjects. The study was carried out at Burgers' Zoo in Arnhem, the Netherlands. In summer, the chimpanzees live in an open-air enclosure of about 0.7 h, while in winter the animals are kept indoors in one or two heated halls measuring 21 by 18 m. They are fed and sleep in separate night cages and, in cases of illness or birth, are sometimes kept inside during the day. For details on the colony, we refer to van Hooff (1973) and Adang et al. (1987).

This study concerns only mature individuals (i.e. males at least 7 years old and females after menarche; see van Lawick-Goodall 1968). We do not analyze sexual behavior of adult and adolescent males separately, since all are capable of fertilizing females (see also Cowlshaw and Dunbar 1991, pp 1045–1046). During the study period (1976–1989), the colony size fluctuated between about 20 and 30 individuals. For the number of males and oestrous females studied per year, see Table 1.

Observation methods. Data were collected by three different researchers: F.B.M. de Waal (1976–1980), O.M.J. Adang (1981–1984) and the first author (1985–1989) with the help of a changing team of students. Sexual interactions, grooming behaviour, conflicts and agonistic interventions in conflicts (termed "support" by de Waal 1978) were observed by the following standardized observation procedure from 1976 to 1989. Data were recorded by two observers simultaneously using tape-recorders. Each session lasted 30 min or a multiple of 30 min. The behavioral elements that were observed are described by van Hooff (1974).

An individual was considered to be a supporter if he/she was the initiator of a new "agonistic dyad" (de Waal 1978) with one (and only one) of two individuals already involved in an agonistic dyad. The new agonistic dyad had to start during the initial dyad or just after the initial dyad ended (i.e. within 30 s). An "agonistic interaction" or conflict refers to a confrontation during which at least one 'strictly agonistic' element [defined by de Waal (1978) and based on van Hooff's (1974) analyses] occurs. Sexual and aggressive interactions and agonistic interventions occurred infrequently and were therefore recorded using the 'all-occurrence' sampling technique (Altmann 1974). Grooming behavior was recorded by two observers simultaneously by means of the scan-sample technique (Altmann 1974). From 1985 onwards data on food sharing were also collected (see Table 1). To study food sharing, we provided the group once a week with about eight branches each about 2 m. Forms of food sharing were defined as follows:

1. "Feeding from another's branch": A holds a branch, B settles nearby and feeds from it together with A.
2. "Taking away food": A holds a branch, B approaches and tries to take away the whole branch or tear off part of it. As inferred from A's body movements, A may or may not "hinder" B and B may or may not be successful in obtaining some food.

Feeding from another's branch was recorded once per 5 min per dyad, whereas taking away food was noted whenever it occurred. Per experiment, observations lasted half an hour, or less if all food had already been eaten.

Table 1. The data

Periods	Clear/ unclear	No. of males	No. of oestrous females	Copula- tion frequency	Data
1976A	C	4	4	43	G - -
1976B	U	4	4	34	G - -
1976C	C	4	3	22	G - -
1977A	C	4	5	26	G S -
1977B	U	4	7	23	G S -
1978A	U	4	8	31	G S -
1978B	C	4	8	11	G S -
1979	C	4	6	49	G S -
1980A	C	4	4	19	G S -
1980B	U	4	7	20	G S -
1980C	U	3	3	7	G S -
1981	C	4	4	19	G S -
1982	C	5	3	9	G S -
1983	U	6	6	56	G S -
1984	U	7	3	24	G S -
1985	U	7	7	62	G ^a S F
1986	U	3	5	17	G S F
1987	U	3	7	65	G S F
1988	U	4	6	133	G S F
1989	U	4	5	91	G S F

C = Periods in which the position of the alpha-male is clear; U = The alpha-position is unclear; G, S, F = periods from which respectively, grooming, support and food sharing data are analysed in this paper.

^a Grooming data were available for all years, but could only be split for oestrous and anoestrous conditions in years indicated by G

Dominance rank. Dominance rank was inferred from the "rapid-oh-oh" vocalization which, according to Noë et al. (1980) occurs unidirectionally. Since this vocalization was seldom heard, particularly among females, some females were considered to have an equal dominance rank. Data on rapid-oh-oh vocalizations were recorded ad libitum.

Subdivision into periods (Table 1). Observations were made during the summer only. Each summer, a different team of students took part in the collection of data. Therefore, each summer was considered as a separate "period". These periods were further subdivided whenever a new alpha-male took over or stability changed. Following to the definition of de Waal (1984), a period was said to be stable when (1) the alpha-male received the rapid-oh-oh vocalization from all other mature males and (2) when these males displayed this submissive behavior more often to the alpha-male than they undertook agonistic actions against him or displayed bluff (i.e. 'stamp', 'stamp-trot', 'arm-sway' and 'sway-walk' accompanied by hair erection, see van Hooff 1974) towards him. Goodall (1986, pp 424–425) refers to such periods as periods with a clear-cut or obvious alpha-male. We accordingly refer to these periods as periods with an "clear" in contrast to a "unclear" alpha-male position.

Opportunities to interact. In order to compare behavioral acts received by the same female when she was in oestrus and when she was not, data had to be corrected for opportunity of interaction. Frequencies of grooming and feeding from another's branch were divided by the time a female was observed in each condition. The frequency of support received was corrected for the number of conflicts in which a female might have received support. Being tolerated (i.e. not being hindered when taking food from others)

was calculated per condition as a percentage of the total number of times a female tried to take food away from another chimpanzee.

With respect to male behavior, for each period we counted the total frequencies of copulation, grooming, support and the frequency with which each male received females that fed from his branch. Data were summed in rectangular matrices, in which rows represent males and columns represent females. The frequency with which each male copulated with each female was divided by the observation time during which both partners were present in the group. Frequencies of grooming and feeding from another's branch were corrected for the absence of individuals. For example, if one of a pair was present for only half of the observation time and the other was never absent, data for this dyad were multiplied by two. Frequencies of support were divided by the number of opportunities for an individual to give support. Individual A's opportunity to support individual B was defined as the number of conflicts B had with individuals other than A when A was present in the group. Being-groomed and feeding from another's branch was studied in rectangular matrices from the female viewpoint also (Table 2a). In this case rows represent females, columns represent males.

Statistical analysis. Social relationships can be studied at a group level or at dyadic level. Since chimpanzees are group-living, and because of the problems of dependency in an analysis at dyadic level, as described by Hemelrijk (1990b), we will confine ourselves to a study at a group level.

According to the actor-receiver model, "relative" male-female interchange (Hemelrijk 1990a) is said to occur when each male directs beneficial acts more often to those females with whom he copulates more frequently. Conversely, "relative" female-male interchange takes place when each female receives more beneficial acts from those males she copulates with more often. To study this, the correlation within rows between two rectangular matrices is investigated by means of the K , statistic (i.e. Kendall's statistic S calculated for each row and summed over all rows; Hemelrijk 1990a). The probability of the observed value is calculated using a specially adapted version of Mantel's (1967) permutation procedure. For each correlation, 4000 permutations were performed. By correlating within rows, the K , test takes individual variation into account. With the same methods, we studied whether males copulated more often with those females the higher their rank or the older they were, or whether they mated with multiparous females more frequently than with nulliparous ones. For this we reflected dominance rank, age and parity (the latter in yes/no form) of the females in the rows of so-called hypothesis matrices (see Fig. 8 in Hemelrijk 1990a) and analyzed their associations with the matrix of copulation frequencies as explained above.

Although the data were obtained from one and the same colony, its composition, the dominance ranks of its members and the team of observers changed over successive periods. Therefore, we tested correlations for each year separately and combined the probability values afterwards. Since samples of subsequent years were partly dependent, and there is no suitable combination test to deal with this, we compared results of three combination tests: (1) a test for dependent samples (the improved Bonferroni method, Hochberg 1988); (2) a test for independent samples, the Fisher combination test (Sokal and Rohlf 1981) and (3) a conservative version of the Fisher combination test. The latter was applied as follows: in sample sizes smaller than five, correlations were combined only when these were all of the same sign. In larger samples, probability values of similar-signed correlations were combined only when more correlations than expected by chance (as inferred from a binomial test, $\alpha=0.05$ two-tailed) were in the same direction.

For the K , tests, matrices with at least four columns are required; furthermore, rows that included only zeroes in both matrices were left out (Hemelrijk 1990a, p 1026). To summarize, when at least one behavioural act was observed in each matrix and matrices contained four columns or more, the K , test was used.

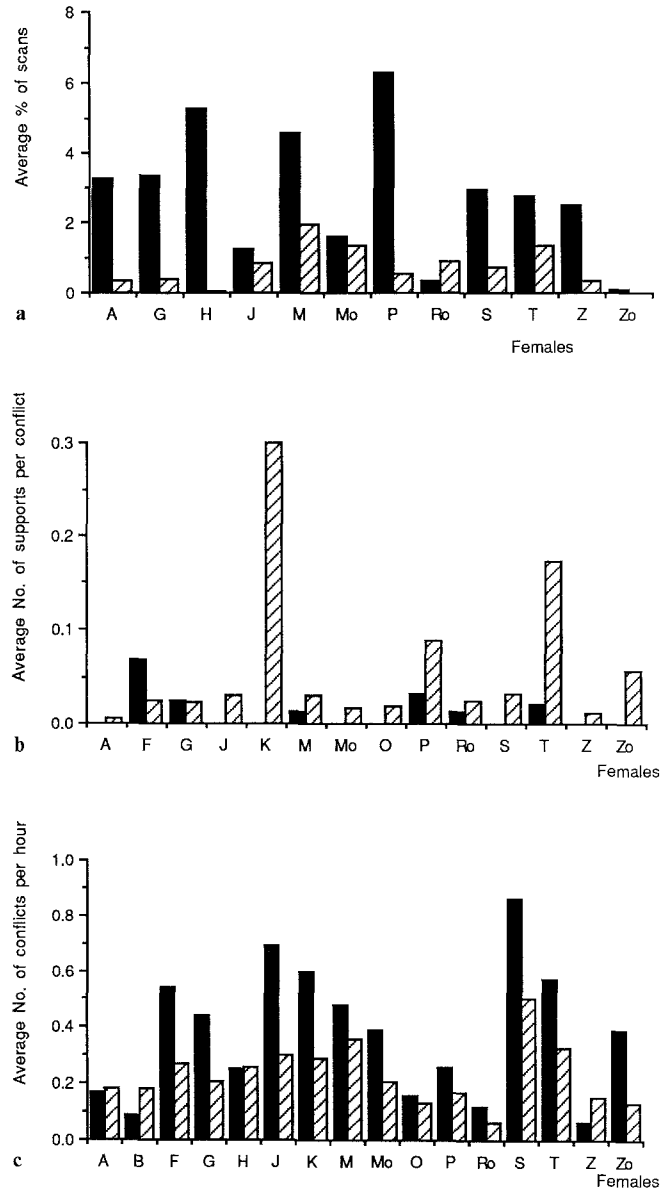


Fig. 1a Average percentage of scans with which females were groomed by males, when these females were in oestrus (*black columns*) and at other times (*hatched columns*). **b** Average number of supports received from males by females in oestrus (*black columns*) or at other times (*hatched columns*). The value for female K is truncated. **c** Average number of conflicts with males of females in oestrus (*black columns*) or not (*hatched columns*)

Results

Social privileges for oestrous females?

Females with sexual swellings were groomed more often by males than when anoestrous (Fig. 1A; Wilcoxon matched-pairs signed-ranks test $n=12$, $T=4$, $P \ll 0.0046$ one-tailed). Although oestrous females were groomed by those males with whom they mated more often, this was nonsignificant (Table 2a). Using the larger data set on grooming, in which data could not be split for the oestrous and anoestrous condition, in combination with

Table 2a. K_r correlations between the frequencies with which, on the one hand, females mate with males and, on the other hand, are groomed by them and feed from a male's branch

Social acts		Years ^a		
		85	88	89
<i>Females being groomed by males</i>				
Oestrous	Nf	7	6	5
	Nm	7	4	4
	K_r	11	5	6
	P_r	0.13	0.25	0.16
Anoestrous	Nf	6	6	5
	Nm	7	4	4
	K_r	6	-3	-4
	P_r	0.30	0.63	0.67
<i>Females feeding from a male's branch</i>				
Oestrous	Nf	5	6	5
	Nm	7	4	4
	K_r	4	-8	0
	P_r	0.29	0.80	0.52
Anoestrous	Nf	5	6	5
	Nm	7	4	4
	K_r	-7	-18	-6
	P_r	0.88	0.95	0.78

Nm = Number of males, Nf = Number of females
 P_r = one-tailed probability value in the right tail of the permutation distribution
 Outcomes of all three combination tests used on these results are nonsignificant
^a In 1986 and 1987 the number of males was insufficient ($n=3$) for a statistical test

Table 2b. K_r correlations between the frequency with which males copulate females, groom them and allow the females to feed from their branch when the females are in oestrus or not

Social acts		Years				
		85	86	87	88	89
<i>Males grooming females</i>						
Oestrous	Nm	7	3	3	4	4
	Nf	7	4	7	6	5
	K_r	9	2	27	-1	-2
	P_r^a	0.18	0.36	0.00	0.57	0.53
Anoestrous	Nm	7	3	3	4	4
	Nf	7	4	7	6	5
	K_r	10	1	4	0	-3
	P_r	0.18	0.48	0.34	0.52	0.68
<i>Males receiving females feeding from the male's branch:</i>						
Oestrous	Nm	7	3	3	4	4
	Nf	5	3	7	6	5
	K_r	1		-8	6	3
	P_r	0.49		0.84	0.25	0.34
Anoestrous	Nm	7	3	3	4	4
	Nf	5	3	7	6	5
	K_r	-4		7	-12	-3
	P_r	0.78		0.22	0.91	0.70

For abbreviations see legend of Table 2a
^a Fisher combination test $df=10$, $\chi^2=18.72$, $P<0.05$ one-tailed
 Conservative Fisher combination test: NS; improved Bonferroni method: $P<0.05$ (due to 1987)
 Outcomes of all three combination tests used on the rest of the results are nonsignificant

Table 2c. K_r correlations between the frequency with which males copulate and support females

Social acts		Years ^a									
		77	78	79	80	81	83	85	87	88	89
Support Oestrus	Nm	4	4	- ^b	-	-	-	-	3	4	4
	Nf	7	10						7	6	5
	K_r	5	13						1	2	-4
	P_r	0.24	0.12						0.49	0.38	1.0
Anoestrus	Nm	4	4	4	4	3	6	7	3	4	4
	Nf	7	10	6	7	4	6	7	7	6	5
	K_r	5	5	0	-7	-7	-8	-11	3	-8	8
	P_r	0.28	0.39	0.50	0.94	0.99	0.85	0.91	0.36	0.95	0.07

For abbreviations see Table 2a
 Outcomes of all three combination tests used on the results are nonsignificant

^a 1982, 1984, 1986: insufficient number of females
^b Males did not support oestrous females in 1979, 1980, 1981, 1983, 1985, 1986

the conservative Fisher combination test, we found that females received grooming significantly more often from those males with whom they mated more frequently ($df=22$, $\chi^2=35.05$, $P<0.05$ one-tailed). However, using the other two combination methods this result was not significant.

No difference was found between oestrous and anoestrous periods in feeding from a male's branch (Wilcoxon

matched-pairs signed-ranks test $n=12$, $T=41$, $P>0.10$ one-tailed), nor for taking away a male's food ($n=8$, $T=8$, $P>0.10$ one-tailed). Contrary to our expectations, oestrous females received support significantly less frequently from males than when not in oestrus (Fig. 1B; $n=14$, $T=11$, $P<0.004$ one-tailed). This result remained for situations in which a female was in conflict with a male ($n=10$, $T=10$, $P<0.04$ one-tailed), but not when

Table 3a. Kendall rank correlation between copulation frequency of a male and his dominance rank

Social acts		Years													
		76ab	76c	77	78	79	80a	80b	81	82	83	84	85	88	89
Dom.	<i>N</i>	4	4	4	4	4	4	4	5	5	6	7	7	4	4
rank	<i>S</i>	5	-1	1	1	4	2	-6	2	-3	-3	5	10*	4	-2

In these correlations, higher ranks are reflected by higher numbers. Outcomes of all three combination tests used on the results are nonsignificant

* $P_R < 0.05$ one-tailed

Table 3b. K_r correlations between copulation frequency and the age, parity and dominance rank of the female partner

Acts		Years ^a													
		76	77	78	79	80	81	83	84	85	86	87	88	89	
<i>Age:</i>															
Fem. part.	Nm	4	4	4	4	4	3	6		7	3	3	4	4	
	Nf	5	7	10	6	7	4	6	3	7	4	7	6	5	
	K_r	-14	25	-21	-11	-21	-1	-12		0	4	-3	-6	-18	
	P_r	0.88	0.08	0.73	0.75	0.94	0.87	0.77		0.52	0.26	0.71	0.84	0.95	
<i>Parity:</i>															
Fem. part.	Nm	-	4	4	4	4	3	6		7		3	4	4	
	Nf		7	10	6	7	4	6	3	7	3	7	6	5	
	K_r		11	23	-4	-5	-1	4		-6		3	-4	-11	
	P_r		0.25	0.16	0.54	0.86	0.82	0.51		0.85		0.44	0.6	0.90	
<i>Dominance rank:</i>															
Fem. part.	Nm	4	4	4	4	4	2	6		3	3	3	4	4	
	Nf	5	7	10	6	7	4	6	3	7	4	7	6	5	
	K_r	-20	5	-21	-17	-16	-6	-12		1	5	-4	-5	-2	
	P_r	0.96	0.4	0.78	0.84	0.87	0.99	0.74		0.5	0.12	0.73	0.77	0.66	

Fem. part. = Female partner. For other abbreviations see legend of Table 2a

Outcomes of all three combination tests used on the rest of the results are nonsignificant

^a In 1982 an insufficient number of females ($n=3$) was in oestrus

she was in conflict with another female (Sign test $n=5$, $x=1$, $P < 0.19$). Furthermore, when in oestrus, females appeared to have more conflicts with males than at other times (Fig. 1C; $n=16$, $T=15$, $P < 0.009$ two-tailed). Although females, when they were in oestrus, thus experienced a higher absolute frequency of conflicts with males, the relative frequency of these conflicts (i.e. the number of conflicts with males as a percentage of their total number of conflicts), did not increase significantly (Wilcoxon matched-pairs signed-ranks test $n=15$, $T=43.5$, $P > 0.05$ one-tailed). Therefore, we have no evidence for the idea that males were less supportive to oestrus females because it might bring them into conflict relatively more often with dangerous opponents, i.e. other males.

Distribution of beneficial acts between females

Since no differences in the distribution of intersexual social acts between clear and unclear periods were found, we left out this distinction.

Males more often groomed those oestrous females with whom they copulated more frequently. However, this relationship was absent when females were not in oestrus (Table 2b). Besides, males neither supported (Table 2c) nor shared food with (Table 2b) those females with whom they mated more frequently. Neither did females feed more from branches of those males with whom they mated more often (Table 2a) (in fact the opposite trend was found). Retesting these correlations after lumping the data from oestrous and anoestrous periods did not change the results.

Dominance rank, age and parity

The copulation frequency of a male was not correlated with his dominance rank (Table 3a). Also, a male's mating frequency was not correlated with the dominance rank of his partner or her age (Table 3b). Besides, males did not appear to mate with nulliparous females more or less frequently than with multiparous ones.

Discussion

Few of the expected correlations were significant in this study. This may be because we analyzed all copulations during tumescence, whereas only those in the last 4 days of maximal tumescence (peri-ovulatory period, Goodall 1986) may lead to conception. Reanalysis for the peri-ovulatory period only did not change the picture, but this may be due to the smaller sample size.

The absence of a correlation between the copulation frequency of a male and his dominance rank is in agreement with findings of Hasegawa and Hiraiwa-Hasegawa (1983, p 78; 1990, p 116) and Takahata (1990, p 145), but in contrast to those of de Waal (1982) and Nishida (1979, 1983). According to Cowlshaw and Dunbar (1991), the lack of such a correlation may be caused by difficulties of high-ranking males in monopolising oestrous females. Indeed, during the observation period more than one female was in oestrus at the same time on half of the occasions.

In accordance with the suggestion of Goodall (1986), females were groomed more often by males when they were in oestrus than at other times. We also found that females were more often groomed by those males with whom they mated more frequently. This relationship is probably due to the oestrous condition, because (1) most of the grooming was received by females when they were in oestrus and (2) the same trend was already found in the oestrous condition only (smaller dataset). In turn, males also groomed more often those oestrous females with whom they mated more frequently. We suggest that male grooming of females may simply have a direct function in suppressing aggressive tendencies in the male and the tendency to flee in the female. Since grooming may therefore be directly advantageous to the male, it is not necessary to think of it as altruism. Also, as long as obvious explanations such as these cannot be ruled out, we feel it is premature to use loaded terms such as "bargaining" or "trading".

Statistically (but not necessarily mentally) these relationships reflect a kind of exchange, but in contrast to baboons (Seyfarth 1978b) seem to be confined to the oestrous period of the female. Thus, there is no indication of long-term bonds between mating partners in our captive group. In captivity, males interfere in each others' interactions with females (O.M.J. Adang, unpublished). Whether this is the cause of the absence of long-term affiliative relationships with females in our group, we do not know. However, also in the natural situation, no evidence has been found for such relationships (Nishida and Hiraiwa-Hasegawa 1987) either.

In agreement with the observations of Boesch and Boesch (1989) on meat sharing in free-living chimpanzees, but in contrast to reports of Goodall (1986) and Yerkes (1939, 1940), males did not share food with females more often when these were in oestrus.

Besides, females experienced more conflicts with males when they were in oestrus than when they were not. Goodall (1986) describes several contexts in which males behave aggressively to oestrous females. Although we have no detailed data concerning the contexts of

agonistic behavior, we did not have the impression that conflicts with oestrous females had anything to do with forced copulations. Rather we think that they resulted from intra-male competition in which oestrous females *volens volens* get involved.

Furthermore, contrary to our expectations, oestrous females received support significantly less often from males. We have no indication that males support oestrous females less to avoid conflicts with other males. However, we suggest that conflicts over oestrous females are perhaps more fierce and therefore males might avoid serious conflicts with other males.

Female baboons in oestrus were more likely to receive support from males in female-female conflicts than when they were not in oestrus (Seyfarth 1978a, p 222), but also in this respect our chimpanzees tended to show the reverse pattern. In summary, we suggest that apart from the stimulus to mating, the social disadvantages of the oestrous swelling seem to outweigh the privileges.

Male-female interchange relationships of support and food sharing for mating were absent as was exchange of grooming between sexual partners in their anoestrous period. This might be caused by the inclusion of the alpha-male; because of his monopolizing power, the alpha-male does not need social exchanges to induce female cooperation (cf. Tutin 1979). After leaving out the alpha-male, however, results remained similar.

Because the correlations were performed at group level, there may yet be incidental male-female pairs in which males exchange support or food for copulations. However, to analyze social relationships at a dyadic level in group-living animals is more difficult than appears at first sight, as I have explained elsewhere (Hemelrijk 1990b). It requires another kind of analysis and new definitions and models and this is outside the scope of this paper.

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