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Influence of feeding and short-term crowding on the sexual repertoire of captive bonobos (*Pan paniscus*)

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Socio-sexuality has been described in bonobos as a mechanism reducing social tension. We studied a captive group of bonobos (Apenheul colony) and tested the influence of feeding sessions on various sexual patterns to functionally differentiate them. Non-reproductive sexual interactions (mounting, GG-rubbing) peaked during the feeding period, whereas copulations did not. During short-term crowding, aggression, self-grooming and copulation rates did not change, however, non-reproductive sexuality and grooming intensified. We suggest that during feeding bonobos may selectively use non-reproductive sex to reduce tension, and that during short-term crowding they may employ both grooming and non-procreative sexuality to avoid a potential raise in tension.

Introduction

Socio-sexuality has been described as a mechanism reducing social tension (Hanby 1977) and several authors described in bonobos (*Pan paniscus*) the occurrence of sexual behaviour in strict association with excitement and tension (Kano & Mulavwa 1984, Kuroda 1984, Thompson-Handler *et al*. 1984, de Waal 1987, 1992, Blount 1990, Kano 1992). The same finding has been recently observed in *Macaca arctoides*, in which socio-sexual behaviours are often used indiscriminately by any pair of opponents as a buffering mechanism to prevent immediate reoccurrence of aggression (Call *et al*. 1999).

In bonobos, both homo- and hetero-sexual interactions have so far been interpreted as means of tension reduction or as exchange items in order to gain access to food resources (Kano 1980, de Waal 1987, 1990). Furthermore, sexual interactions have also been interpreted as a way to assess social bonding (Wrangham 1993, Hohmann & Fruth 2000, Palagi *et al*. 2004, Paoli *et al*. 2006). Studies carried out on wild and captive bonobos showed the presence of a large variety of sexual patterns, including masturbation and genital inspection, involving individuals of all sex and age classes (Kano 1980).

De Waal (1987) described in the San Diego bonobos the use of sex for tension reduction during feeding sessions. The author suggested that while certain types of socio-sexual behaviour (e.g. GG-rubbing between females and mounting between males) may be effective in reducing tension, others may not. However, he did not test the sexual patterns independently, though he suggested that this might have been important. In fact, in that study there were not enough data to analyze each behaviour separately. Accordingly, an additional investigation seems necessary to functionally differentiate the various sexual patterns.

Another condition where tension may arise is spatial crowding. The density/aggression model predicts a substantial increase in aggression rates under crowded conditions (as it occurs in rats and baboons; Calhoun 1962, Elton & Anderson 1977). But research on spatial crowding in captive primates showed contrasting results: a density increase may produce no changes in aggression (Dazey *et al.* 1977, McGuire *et al.* 1978, Demaria & Thierry 1989) or even a decrease in aggression (Eaton *et al.* 1981, Novak & Drewsen 1989, Bercovitch & Lebron 1991), thus de Waal (1989) suggested that primates have evolved effective behavioral mechanisms to keep aggression and violence under control (coping model). According to this model several primates are able to control aggressiveness by increasing some affinitive behaviors (e.g. grooming): this hypothesis has been confirmed during long-term crowding (de Waal 1989) when animals had time to adjust their behavioral habits to the new challenging conditions (Nieuwenhuijsen & de Waal 1982 for *Pan troglodytes*; Novak *et al.* 1992 for *Macaca mulatta*). Alternatively, in case of short-term environmental constraints (from a few hours to a few days) the coping model has not been corroborated and different behavioral strategies seem to function, such as the reduction of the overall level of social activity and aggressive interactions (Judge & de Waal 1993, Aureli & de Waal 1997, Caws & Aureli 2003).

In captive bonobos, medium-term spatial crowding was found to increase grooming and aggressiveness (van Dijck *et al.* 2003, Sannen *et al.* 2004). Nevertheless, Sannen *et al.* (2004) argued that the increase in aggression was relatively small in relation to the space reduction, suggesting that bonobos may cope with the stress created by crowding using grooming as a tension-reduction strategy. Up to now no studies on short-term crowding in bonobos exist.

The goals of this study are twofold. First, we aim at clarifying the possible selective use of sexual interactions during feeding time. Second, we investigate whether a short-term crowding increases anxiety as measured by self-grooming levels (Troisi & Schino 1987, Schino 1988, Aureli & de Waal 1997, Kutsukake 2003) and verify if short-term space reduction affects aggressive, affinitive, and/or socio-sexual behaviours.

Material and methods

We collected behavioral data during 4 observation seasons totaling approximately 12 months on a group of *Pan paniscus* housed in the Apenheul Primate Park (Apeldoorn, The Netherlands), first established in 1998. We observed subjects during six-hour sessions, encompassing both the morning and the afternoon.

The composition of the colony changed over time: in session 1 (July–October 2000) there were 11 individuals (5 mature females, 3 mature males and 3 infants). In session 2 (April–July 2002) there were 9 individuals (4 mature females, 2 mature males, 1 juvenile and 2 infants). In session 3 (September–December 2002) there were 7 individuals (3 mature females, 2 mature males, 1 juvenile and 1 infant) and in session 4 (March–June 2003) there were 8 individuals (one more newborn) (*see* Table 1 for details).

The wild-caught animals came from a Rescue Centre located in the Democratic Republic of Congo and have been rescued from different sites in different periods, therefore we can be fairly confident that they are unrelated. The animals were housed in an enclosure with indoor and outdoor facilities (about 230 m^2 and 5000 m^2, respectively). Since the animals were not always in sight in the indoor facilities, we stopped the observations when more than one animal was out of sight.

The animals were able to move freely from the indoor to the outdoor enclosure after the first feeding session (at 8:45) and received food (milk enriched by vitamins and proteins, monkey chow, vegetables, and fruit) four times a day at about 8:45, 12:30, 14:30 and 16:30. Most of the food items were scattered on the floor. Water was available *ad libitum* and environmental enrichment was provided in the form of fresh branches, rice and nuts broadcasted in the grass to encourage foraging activity, and facilitating renewal of the equipment in the indoor facility. Sometimes a wooden block with holes filled with honey or yoghurt was provided. No stereotypic or aberrant behaviour characterized the study group.

Behavioral data on the whole group were collected using scan sampling at 5-min intervals and focal animal sampling (Altmann 1974) throughout the four observation periods. We accumulated 16 212 scans (session 1: 4224, session 2: 4272, session 3: 3744, session 4: 3972) and 1694 hours of focal sampling (session 1: about 41 h per individual, session 2: about 56 h per individual, session 3: about 52 h per individual, session 4: about 52 h per individual). We also recorded all occurrences of copulations, mountings and GG-rubbings in periods 2–4 (1275 h of group follows). Mountings and copulations were distinguished on the basis of evident intromission.

To investigate if the presence of food affected sexual behaviour, by preliminary observations we distinguished four periods:

- Pre-feeding: the last 30-min block before food provisioning,
- Feeding: the 30-min block starting from food provisioning,
- Post-feeding: the 30-min block following feeding time, and
- Baseline: the 30-min block farthest from feeding times, when animals showed high activity levels (baseline group activity).

The parameter for delimiting the three periods linked to feeding activity was the usual time span necessary for complete food consumption (i.e. 30 minutes). The analyses were carried out on the 12:30 and the 14:30 feedings.

Though observation sessions 2–4 were close in time, there was a two-year interval between sessions 1 and 2. To test for continuity in social relationships over this gap, we used Matman 1.0 by Noldus to compare social interaction (grooming and contact sitting) matrices constructed from session I and II observations. When pooling data, we used mean hourly frequencies of behaviours per dyad, excluding the 2 individuals who died between sessions. Matman's row-wise correlation tool was used with a number of 10 000 permutations (to check for inter-individual variability), employing the one-tailed Kr test (a two-tailed test was not used because a negative correlation would be meaningless in this case). The one-tailed Kr test showed that both distributions of affinitive contacts were significantly correlated between session 1 and 2 (contact sitting: Kr = 33, $\tau_{rw} = 0.56$, $p < 0.05$; grooming: Kr = 20, $\tau_{rw} = 0.34$, $P < 0.05$), thus allowing us to fairly pool data from different observation sessions.

Table 1. The *Pan paniscus* colony in the Apenheul Primate Park (Apeldoorn, The Netherlands). Animals marked with an asterisk (*) died after the first session of observations (July–October 2000). Those labelled with an octothorp (#) died after session II (April–July 2002). All the animals from DRC (Democratic Republic of Congo) were previously housed in a Rescue Centre and came from different collection sites.

Subject	Sex	Class	Year and place of birth	Origin and arrival year
Hani*	M	Adult	1989, wild	DRC, 1998
Mobikisi	M	Adult	1981, wild	Antwerp,1996
Mwindu	M	Adult	1985, wild	DRC,1998
Jill	F	Adult	1985, captivity	SanDiego,1997
Rosie*	F	Adult	1989, wild	DRC,1998
Molaso#	F	Adult	1985, wild	DRC,1998
Zuani	F	Adult	1990, wild	DRC,1998
Lomela	F	Adult	1992, captivity	Frankfurt,1998
Liboso	F	Juvenile	1997, captivity (Zuani's daughter)	DRC,1998
Tarishi#	M	Infant	1998, captivity (Jill's son)	Apenheul
Kumbuka	F	Infant	1999, captivity (Molaso's daughter)	Apenheul

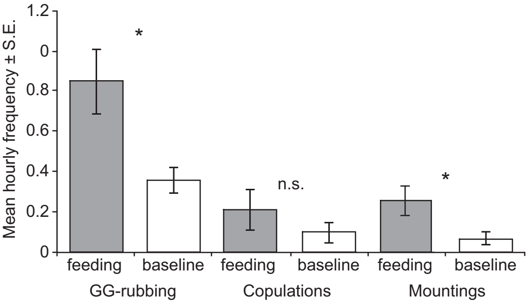

Fig. 1. Distribution of GG-rubbing, copulations and mountings during Feeding (grey) and Baseline (white) among the Apenheul bonobos. (*$p < 0.05$; n.s. = not significant).

When testing for an overall influence of food on sexual behaviour, we calculated the mean hourly frequency of sexual interactions (all occurences) during Pre-feeding, Feeding, Post-feeding and Baseline. Subsequently, we tested for differences across Pre-feeding, Feeding and Post-feeding using Friedman's two way analysis of variance (note: even if this test is more powerful with a sample size of $N > 6$, it is nevertheless sufficiently sensitive with $N = 5$ to single out significant differences). For this analysis, we used data from two subsequent collection periods (3 and 4) as feeding times were more precisely determined during these two sessions. In case of significant difference among the three stages, we used the multiple comparisons test suggested by Siegel and Castellan (1988) to determine what pairs of combinations differed significantly.

We used all-occurrence data on sexual interactions from periods 3 and 4 to test for an overall influence of space availability on sexual behaviour. We took into account a short-term crowding: animals were sometimes and randomly shut in a small space for a few hours to a few days due to bad weather conditions or other reasons.

The mean hourly frequency of sexual interactions was calculated for each subject in two space conditions: (1) large: only outside facility or outside facility + inside facility (animals free to move through the facilities) (about 5000 m^2), and (2) small: only inside facility (about 230 m^2).

Subsequently, we tested for differences between these two conditions using Wilcoxon's matched-pairs signed-rank test. All the analyses were two-tailed and the level of significance was set at 5%. Statistical analyses were performed using Microsoft Excel® and SPSS 12.0®.

Results

GG-rubbing interactions (Fig. 1) among females were significantly more frequent during Feeding than during Post-feeding (Friedman: $\chi^2 = 9.58$, $n = 5$, df = 2, $p < 0.01$; multiple comparisons test: Feeding *vs*. Post-feeding: $p < 0.05$). When comparing each period with Baseline (Wilcoxon's test) we found significant ($p < 0.05$) differences for Feeding *vs*. Baseline ($T = 0$, $n = 5$, ties = 0, with higher rates during Feeding), and for Post-feeding *vs*. Baseline ($T = 0$, $n = 5$, ties = 0, with higher rates during Baseline).

Copulations among adults (Fig. 1) were significantly more frequent during Feeding than during Post-feeding (Friedman: $\chi^2 = 7.11$, $n = 5$, df = 2, $p < 0.05$; multiple comparisons test: Feeding *vs*. Post-feeding $p < 0.05$). We found no significant differences when comparing each period with Baseline (Wilcoxon's test).

Mountings (Fig. 1) were significantly more frequent during Feeding than during Post-feeding (Friedman: $\chi^2 = 14.0$, $n = 7$, df = 2, $p < 0.001$; multiple comparisons test: Feeding *vs*. Post-feeding $p < 0.05$). When comparing each period with Baseline (Wilcoxon's test) we found significant ($p < 0.05$) differences for Pre-feeding *vs*. Baseline ($T = 0$, $n = 7$, ties = 0, with higher rates during Pre-feeding), and for Feeding *vs*. Baseline ($T = 0$, $n = 7$, ties = 0, with higher rates during Feeding).

Grooming interactions (Fig. 2) were not equally distributed across Pre-feeding, Feeding and Post-feeding (Friedman: $\chi^2 = 14.00$, $n = 7$, df = 2, $p < 0.001$). Using the multiple comparisons test we found that grooming frequencies were significantly ($p < 0.05$) higher during Post-feeding than during Feeding. When comparing each period with Baseline (Wilcoxon's test) we found significant ($p < 0.05$) differences for Feeding *vs*. Baseline ($T = 0$, $n = 7$, ties = 0, with higher rates during Baseline), and Post-feeding *vs*. Baseline ($T = 2$, $n = 7$, ties = 0, with higher rates during Post-feeding).

Contact-sitting interactions (Fig. 2) were not equally distributed across Pre-feeding, Feeding

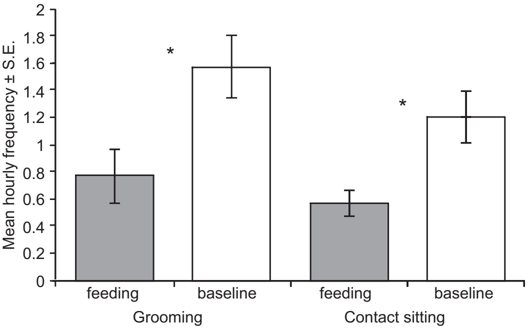

Fig. 2. Distribution of grooming and contact sitting in Feeding (grey) and Baseline (white) among the Apenheul bonobos. (*$p < 0.05$).

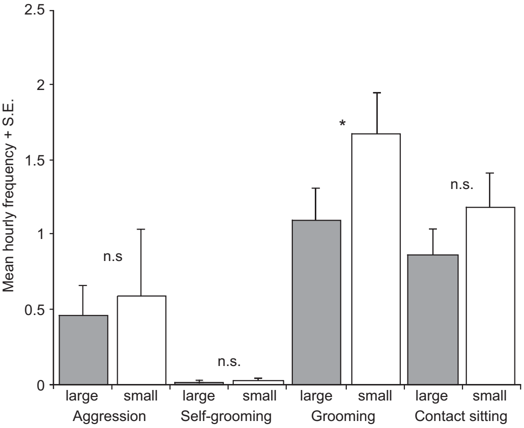

Fig. 3. Distribution of aggressive, self-grooming, grooming and contact sitting rates in large (grey) and small (white) space conditions among the Apenheul bonobos. (*$p < 0.05$; n.s. = not significant).

and Post-feeding (Friedman: $\chi^2 = 11.14$, $n = 7$, df $= 2$, $p < 0.01$). Using the multiple comparisons test we found that contact-sitting frequencies were significantly ($p < 0.05$) higher during Pre-feeding and Post-feeding than during Feeding. When comparing each period with the Baseline (Wilcoxon's test) we found a significant ($p < 0.05$) difference for Feeding *vs.* Baseline ($T = 0$, $n = 7$, ties = 0, with higher rates during Baseline).

Aggressive interactions did not differ significantly in large or small space conditions (Fig. 3). The rates of self-grooming were found to be comparable in the two different space conditions (Fig. 3).

Considering affinitive interactions, the frequency of contact sitting was comparable in the two different space conditions, whereas grooming rates were found to be significantly higher in the small-space condition (Wilcoxon: $T = 0$, $n = 7$, ties = 0, $p < 0.05$; Fig. 3).

Considering sexual interactions, copulatory rates were found to be comparable in large- and small-space conditions (Fig. 4). Non-reproductive sexual interactions were found to be significantly ($p < 0.05$) more frequent in small- than in large-space conditions (Wilcoxon: mountings: $T = 1$, $n = 7$, ties = 0; GG-rubbing: $T = 0$, $n = 5$, ties = 0; Fig. 4).

Discussion

Following the hypothesis by de Waal (1987) that bonobos use sexual behaviour as means to reduce the tension due to the presence of food, we analysed sexual patterns separately and we found that GG-rubbing was significantly more frequent during Feeding than during Post-feeding. This increase in the GG-rubbing rate during Feeding was also confirmed when comparing it with that during Baseline. Even mountings were found to be significantly more frequent during Feeding than during Post-feeding, and more frequent during Feeding than during Baseline.

As for copulatory rates among adults, even if they were found to be significantly higher during Feeding as compared with those during Post-feeding, none of Pre-feeding, Feeding and Post-feeding rates were significantly different from those during Baseline. In light of these findings it seems that sexual behaviour without any reproductive immediate benefit (GG-rubbing and mounting) was used during Feeding in a more selective manner as compared with copulations. In fact, if sexual interactions observed during Feeding are simple effects of the excitement due to the presence of food (in agreement with the arousal-transformation hypothesis; *see* de Waal 1987) each sexual pattern should show a significant increase when compared with the situation during Baseline. Thus, our data support de Waal's (1987) conclusion that sexual patterns may be used selectively for tension reduction.

As for affinitive interactions, both grooming and contact-sitting rates showed a significant decrease during Feeding. If the decrease

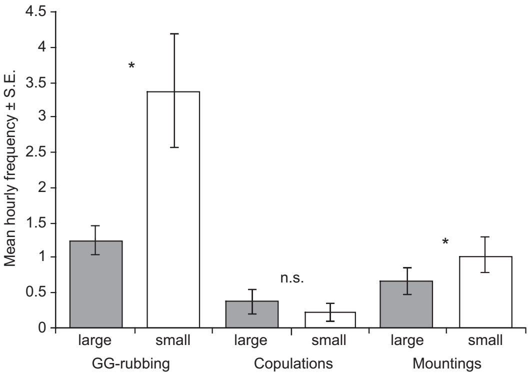

Fig. 4. Distribution of GG-rubbing, copulations and mountings in large (grey) and small (white) space conditions among the Apenheul bonobos. (*$p < 0.05$; n.s. = not significant).

in grooming can be interpreted as an effect of animals being engaged in the feeding activity, the decrease in contact sitting is probably caused by the presence of food resulting in decrease of tolerance levels among animals.

As a whole, these findings on social behaviour around feeding time suggest that when excitement arises when food is present (de Waal 1987), socio-sexual interactions (GG-rubbings and mountings) may serve to dissipate such excitement. Particularly, the high rates of GG-rubbing observed among bonobo females during the feeding time may be a strategy to maintain and strengthen their alliances. In fact, bonobo females probably have priority access to food over males thanks to their strong alliances (Parish 1994, 1996, Vervaecke *et al.* 2000), which may be weakened by the conspicuous intra-sexual competition occurring around food.

Aureli and de Waal (1997) found that during temporary confinement (short-term crowding) into smaller than usual areas, Yerkes chimpanzees showed elevated rates of behavioural indicators of stress (e.g. self-grooming), but a general decrease in aggression rates. In addition, the overall level of group activity was markedly reduced (including allo-grooming) and according to the authors this "social inhibition" may decrease the possibility of social interactions, thereby reducing the probability of aggressive encounters, even though this strategy is probably effective only in the short run as the social tension is not dissipated.

Our results show that in the Apenheul bonobo group, aggression rates were comparable during high- and low-density conditions. In addition, self-grooming frequencies (considered as behavioural indicators of stress) did not differ between the two spatial conditions. Accordingly, we suggest that short-term spatial crowding does not determine tension in this bonobo colony. Nevertheless, we found interesting data when examining the rates of social and sexual behaviours in the two density conditions. Grooming and non-reproductive sexual interactions (mountings and GG-rubbings) were significantly more frequent during the crowded condition. On the other hand, contact sitting rates did not differ as a function of the space available.

In addition, copulation rates were independent of the density condition. In this view, we suggest that there is a selective use of some behaviours in order to avoid an increase in tension. Specifically, grooming and socio-sexual interactions (mountings and GG-rubbings) may serve to circumvent the negative effects of crowding. It is intriguing to note that only sexual behaviours without any immediate reproductive benefit peaked in the high density condition, and these behaviours are significantly more frequent during feeding time, another period in which tension may arise. Therefore, it appears that bonobos selectively use socio-sexual behaviour to cope with short-term high density in a different way than chimpanzees.

Sannen *et al* (2004), studying medium-term crowding in Planckendael bonobos, found that high density resulted in increased aggressiveness and Van Dijck *et al.* (2003) found that grooming increased under such circumstances in the same colony. Of course, our study mainly differs in the duration of crowding. Nevertheless, we found an increase in grooming under high density, which confirms the occurrence of a coping strategy in bonobos. Yet, both previous studies lack data on socio-sexual behaviours that we suggest may be an additional strategy for coping with spatial crowding.

In conclusion, our results support and expand previous data on the use of sexual behaviours during feeding, suggesting a selective use of non-reproductive patterns by bonobos. In addition, we also show the first evidence of the bonobo coping strategy under short-term high density conditions, which includes the use of non-procreative sexual behaviours and grooming to avoid a potential raise of tension.

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