



Use and function of genital contacts among female bonobos

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Female bonobos, *Pan paniscus*, show a mounting behaviour that differs physically from that in other primate species. They embrace each other ventroventrally and rub their genital swellings against each other. We investigated five hypotheses on the function of ventroventral mounting (genital contacts) that derive from previous studies of both primate and nonprimate species: (1) reconciliation; (2) mate attraction; (3) tension regulation; (4) expression of social status; and (5) social bonding. We collected data in six field seasons (1993–1998) from members of a habituated, unprovisioned community of wild bonobos at Lomako, Democratic Republic of Congo. No single hypothesis could account for the use of genital contacts, which appeared to be multifunctional. We found support for hypotheses 1 and 3. Rates of postconflict genital contacts exceeded preconflict rates suggesting that the display is used in the context of reconciliation. Rates of genital contacts were high when food could be monopolized and tension was high. However, genital contacts also occurred independently of agonistic encounters. Our study shows rank-related asymmetries in initiation and performance of genital contacts supporting the social status hypothesis: low-ranking females solicited genital contacts more often than high-ranking females while the latter were more often mounter than mounTEE. Although subordinates took more initiative to achieve genital contact, dominants mostly responded to the solicitation (ventral presentation) with mounting, indicating that the performance benefits both individuals. We suggest that genital contacts can be used to investigate both quality and dynamics of dyadic social relationships among female bonobos.

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Recent approaches to explain variation in social systems in nonhuman primates in an adaptive way are based on the socioecological paradigm which implies that relations among females are set by ecological conditions while relations among males are related to mating opportunities (Wrangham 1980; van Schaik 1989; Sterck et al. 1997). van Schaik (1989) proposed that social relations among females are determined by the nature of resource competition. If the distribution of resources allows control of access, competition will be direct by contest, differences in social status are likely to affect accessibility and behaviours signalling dominance become advantageous. In contrast, if access to resources is not limited, competition will be indirect by scramble, differences in social status are less likely to affect accessibility and signals of dominance become less beneficial. In the latest version of the model, female–female relations are evaluated on top of these ecological factors along three interrelated social dimensions (Sterck et al. 1997): (1) intergroup transfer (female exogamy versus female

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philopatry); (2) structure of dominance relations (despotic versus egalitarian); and (3) execution of dominance (tolerance versus intolerance). Hence, understanding social relations requires correct interpretation of the significance of behaviours. In some cases, it is relatively simple to detect the nature of a given behaviour. Grooming, play and close spatial proximity are generally considered to reflect affiliative relations while agonistic relations are characterized by frequent displacements, formal displays of dominance and physical aggression. In other cases, the significance of behavioural interactions is ambiguous. One example of the latter is female–female mounting.

Mounting between females is known from insects (Mika 1959; Loher & Huber 1964); birds (Jamieson & Craig 1987; Heg & van Treuren 1999) and mammals (Young 1961; Beach 1968; Parker & Pearson 1976). Interpretations concerning its function range from signalling dominance (Zuckerman 1932; Wickler 1967) to the expression of affiliative relations (Rowell 1966; Chevalier-Skolnikoff 1976; Hausfater & Takacs 1987). In some species, mounting among females may stimulate male–male competition and enhance (or suppress) female

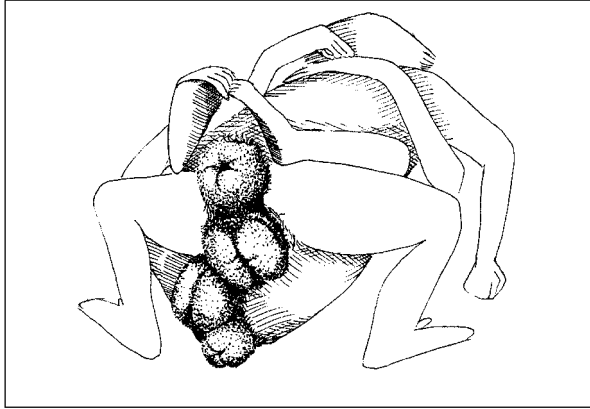


Figure 1. Two females performing a genital contact in a horizontal position.

proceptivity (Parker & Pearson 1976; Tyler 1984; Srivastava et al. 1991).

Female bonobos, *Pan paniscus*, show a behaviour that differs from female–female mounting in other primate species. Participants embrace each other ventroventrally and rub their genital swellings laterally against each other (Fig. 1). Initially observed in captivity, this behaviour is known to occur regularly in nature (Kano 1980; Thompson-Handler et al. 1984) and is often referred to as genitogenital rubbing, a term introduced by Kuroda (1980). Studies on two captive groups (San Diego) suggest that ventral mounting may be used in the context of reconciliation between former opponents (de Waal 1987). After agonistic encounters, de Waal (1987) noticed an overall increase in sociosexual behaviours but did not specify to what degree different behavioural elements were involved. Data from another captive group (Stuttgart) indicate that performance of genital contacts may enhance access to preferred food patches (Parish 1994). Field observations suggest various functions including tension regulation (Kuroda 1984; Furuichi 1989), social integration (Idani 1991), affiliation (White & Lanjouw 1992; Takahata et al. 1996) and proceptivity (Thompson-Handler 1990). Taken together, the information from previous work suggests that genital contacts may serve different functions. However, none of the proposed functions has been tested and interpretations are ambiguous and need clarification.

Our goal in this paper is to explore possible functions of genital contacts among female bonobos. We tested five hypotheses, generated by information on female–female mounting from both primate and nonprimate species, with data collected during a long-term field study on members of a bonobo community at Lomako, Democratic Republic of Congo.

HYPOTHESES AND PREDICTIONS

Hypothesis 1: Reconciliation

After agonistic encounters, primates and other social mammals may exchange friendly behaviours to restore relations between former opponents. The key criterion

used to identify reconciliation is a relative increase in affiliative behaviours between former opponents (de Waal 1987; Kappeler & van Schaik 1992; Silk 1998). The exchange of affiliative behaviours may not be restricted to opponents but may also involve a third individual (Das et al. 1997). Evidence from various primate species suggests that the frequency of reconciliation is positively related to both kinship and close social ties (reviewed by Kappeler & van Schaik 1992). Using this information, we made the following predictions: (1) genital contacts occur frequently in association with agonistic interactions; (2) rates should increase after agonism; and (3) relatives or individuals with close social ties are more likely to have genital contacts than individuals with distant relations.

Hypothesis 2: Mate Attraction

Mounting behaviour between females is assumed to mimic male mating patterns and, thus, may be an effective way to attract males (Ford & Beach 1952; Parker & Pearson 1976). Females may attract mates when males and females are separated for long periods or if females who live in multimale groups want to attract the attention of a certain (e.g. high-ranking) male (Parker & Pearson 1976). In wild bonobos, copulations are tuned to the phase of tumescence (Furuichi 1987) and one would expect genital contacts that are performed to enhance copulations to occur more often during this phase. Accordingly, we predicted the following: (1) the rate of genital contacts should be higher in mixed-sex than all-female parties; (2) genital contacts are closely followed by copulations; (3) females with detumescent swellings perform genital contacts less often than tumescent females; and (4) copulations closely preceded by genital contacts are more likely to involve tumescent females than those that are independent of genital contacts.

Hypothesis 3: Tension Regulation

Hanby (1977) proposed that the major function of sociosexual behaviours in nonhuman primates is the reduction of social tension. Ideally, assessments of social tension would involve physiological data (Sapolsky 1982; Aureli et al. 1999). However, tension is also inferred from certain behaviours such as self-scratching (Schino et al. 1988) or grooming (McKenna 1978). Studies on captive primates suggest that, when living space is reduced, rates of agonistic behaviour decrease while social tension increases (de Waal 1987, 1989; Aureli & de Waal, in press; Judge & de Waal, in press). Under natural conditions, bonobo communities regularly split up into subgroups, called parties, of different size and composition. Proximity between individuals may change with party size as well as with size and quality of food patches. We predicted that the rate of genital contacts should (1) be higher if a food patch can be monopolized and (2) increase with party size. The frequent performance of genital contacts in the presence of food has led to the assumption that the behaviour may be a substitute for aggression (Kuroda 1984; Thompson-Handler 1990).

Thus, we predicted that (3) in a given situation, genital contacts and agonistic encounters do not necessarily involve the same individuals.

Hypothesis 4: Expression of Social Status

Relations between two individuals are the result of differences in social status and they are characterized by the quality of their social interactions (Seyfarth 1977; Moss & Poole 1983; Smuts 1985). High social status may be expressed by agonistic behaviours which evoke submissive behaviour. Alternatively, in a number of species subordinate individuals show displays of submission towards dominants independent of agonistic displays (East et al. 1993 and references therein). Signals of submission may involve genital displays and/or incorporate elements of mating behaviour (Kummer et al. 1974; Fox & Cohen 1977 and references therein) and asymmetries in performance may reflect differences in relative status (Rowell 1966; Bygott 1979; Colmenares 1990). If genital contacts serve to signal differences in social status, one would predict (1) rank-related asymmetries in initiation. If genital contacts serve to demonstrate superiority, one would predict high-ranking individuals to initiate the behaviour more often than low-ranking ones. If the behaviour signals active submission, subordinate individuals should initiate the behaviour more often than dominants. Following the assumption that mounting is an expression of dominance (Wickler 1967; Maestripieri 1996), one would also predict that (2) dominant females are more often in the top position than subordinates.

Hypothesis 5: Social Bonding

It has been proposed that bonobos use sociosexual behaviour to communicate about their social relations (Wrangham 1993; de Waal 1995). More precisely, genital contacts are considered to be a friendly and affiliative behaviour (Kano 1980; Kuroda 1984; White & Lanjouw 1992; Parish 1994). If the frequent exchange of genital contacts reflects close affiliative ties one would predict a high frequency of genital contacts among (1) kin or (2) individuals who associate closely with each other, and (3) positive correlations between genital contacts and other affiliative behaviours such as grooming.

METHODS

Data Collection

We collected behavioural data during six field seasons (1993–1998) lasting between 2 and 7 months (total 27 months). The study involved members of the Eyengo community inhabiting the eastern part of the Lomako study site (Badrian & Badrian 1984). Some earlier studies referred to this community as ‘Rangers’ (e.g. White 1988). Community members were identified by phenotypic traits (disfigured limbs, shape of sexual swellings, pigmentation). We estimated the age of animals born before this study by physical traits such as body size, body

proportions, condition of teeth, length of the mamillae and genital swelling pattern. The number of coresident adult and adolescent females ranged from 11 to 15. Six resident females disappeared, one joined the community, two adolescent females became adult, and two juvenile females became adolescent during the study. More details on demographic changes are published elsewhere (Fruth 1995; Hohmann et al. 1999).

Data collection involved ad libitum, focal animal and event sampling (Altmann 1974). Focal sampling involved 17 individuals. Since females differed in their tolerance towards human observers, records are biased towards certain individuals. Because of frequent day-to-day variation in party attendance, focal females were randomly chosen among those actually attending a given party. Females involved in genital contacts and agonistic encounters during ad libitum observation became focal animals for the following 15 min.

If not stated otherwise we analysed records collected during the entire period of field work (1993–1998). Analyses restricted to certain parts of the complete data set are mentioned below.

Terminology

Genital contact: ventroventral mounting with physical contact of genital swellings. The term is synonymous with genitogenital rubbing or ggr (sensu Kuroda 1980).

Copulation: genital contact between male and female with intromission and pelvic thrusts. Copulation was performed in two positions: dorsoventrally (male mounts female) or ventroventrally (either sex can be the mounter/mountee). Mounts without intromission were not included.

Agonism: resolved and unresolved conflicts between two or more individuals. Participants showed aggressive and submissive behaviours (agonistic displays not addressed to a particular individual were excluded).

Solicitor: individual that tried to initiate a genital contact by presenting ventrally to another individual.

Target: individual that was the target of a solicitation.

Rank

Assessments of rank were based on the outcome of agonistic interactions and nonagonistic displacements (approach–retreat) and were made separately for each field season. Only dyadic relations are considered here. An individual winning more often than it lost against another individual was considered to be dominant within this dyad. From these data, two classes emerged: class 1 (high rank) consisted of females that displaced others more often than they were supplanted; class 2 (low rank) females were displaced more often than they supplanted others.

Rank-related Asymmetry

Analyses are based on behavioural scores from individuals with unequivocal dominance relations. The key

criterion for initiation was presenting ventrally towards another individual. We excluded cases of mutual presentation and when solicitation failed to induce a genital contact. Obvious asymmetries in performance occurred when genital contacts were conducted in a horizontal position. Two positions are distinguished: top (mounter) and bottom (mountee).

Female–Female Agonism and Reconciliation

We evaluated the frequency of temporal relations between the two types of behaviour based on the absolute number of cases scored in relation to the number of cases where genital contacts occurred independent of agonistic encounters. To assess the significance of genital contacts in the context of reconciliation, we investigated whether the behaviour occurred more frequently in the 15-min interval that followed an agonistic conflict than in the 15 min preceding the conflict. First we assessed the distribution of genital contacts in relation to agonism by scoring the number of 15-min intervals with at least one genital contact. For this part of the study we used all samples of preconflict and postconflict intervals available. Second, for each female, raw data obtained from agonistic encounters were pooled and converted into individual rates (genital contacts per 15 min) using only corresponding intervals (pre- and postconflict were related to the same agonistic event).

Mating

In the context of mating, primates may use a variety of behaviours. Here, we used copulations as an indication of mating activity. Investigation of the temporal relation between genital contacts and copulations was restricted to samples from parties containing at least one mature male and two mature females. Although copulations take place throughout the year, external factors may cause seasonal fluctuations of sexual activity (Fogden 1972; Butynski 1988; Wallis 1995). To avoid sampling at times of reduced sexual activity, we restricted this analysis to days when at least one genital contact and one copulation were scored, independent of the order of the two events. To assess whether genital contacts induced copulation, we corrected data for party size and compared the intervals between genital contact and copulation with intervals between other sexual interactions (genital contact followed by genital contact, copulation followed by genital contact, copulation followed by genital contact). All intervals refer to behavioural events that occurred on the same day.

Social Relations

Differences in the social relations between females refer to three aspects: kinship, spatial association and social grooming. Data on genetic relations are available from a previous study on members of this community (Gerloff et al. 1999). Close genetic ties between resident females were restricted to mothers and their immature daughters.

Here we compared frequencies of genital contacts between immature females and adults (mother versus unrelated adult females).

Spatial association

Data were available from four field seasons (1993–1996). They refer to party attendance and involve 774 records of party counts when all members were positively identified. To make data points independent, we used only one record per day, resulting in a reduced data set of 255 party counts. Records collected within the same field season were pooled and analysed separately from records of other field seasons.

We calculated the frequency of party attendance of a certain individual, p_i , by dividing the number of records when the individual was present, n_i , by the total number of records of party size (N). The expected frequency (p_{ij} exp) of two given individuals (i and j) attending the same party was calculated by multiplication of the observed attendance of both individuals ($p_i \times p_j$). To decide whether the observed values of dyadic association deviated from the expected values, we used a randomization test written by Lamprecht & Hofer using a RAN2 generator (Lamprecht 1985; Press et al. 1992). Values of random associations (RA) were computed by running 1000 random, uniformly distributed trials for each individual of a given dyad. The simulation showed how often an observed association (OA) can be expected by chance. Using statistically significant deviations ($P < 0.05$, two-tailed), we assigned dyads to one of three classes: close associates ($OA > RA$), random associates ($OA = RA$) and nonassociates ($OA < RA$).

Social grooming

Comparison of the frequency of genital contacts and social grooming between two given individuals includes data from two field seasons (1993–1994) and 18 adult and adolescent females. The data were from focal observations during all-day follows when contact ranged from 8 to 12.5 h. For this analysis we considered only days when female party members engaged in both behaviours (social grooming and genital contacts) at least once, independent of their identity. The majority of the 153 female dyads had to be excluded from this analysis because they did not engage in either of the two behaviours or because they were lost before interacting again. Seventeen dyads had scores for both behaviours or (one case) were seen long enough for us to be confident that the distribution of the two behaviours was unlikely to be the result of incomplete sampling. To test whether the exchange of social grooming corresponded with the performance of genital contacts, we compared the distribution of both behaviours for each focal female and her partner using a Spearman rank correlation.

Party Size and Composition

Size and composition of parties were recorded opportunistically several times a day. We attempted to conduct counts in 60-min intervals, but we often had to abandon

this schedule because of poor visibility. When consecutive counts produced identical results, we assumed that the party had not changed during the two counts. To assess the relationship between party size and genital contacts we calculated rates of genital contacts/h of observation and compared these with party size. Using the same data set, we also assessed the rate of genital contacts per mature female party member by dividing the hourly rates by the number of mature female party members.

To reduce the possible impact of variability of metric dimensions of food patches, we selected a subsample of records collected during one season (1993) from *Polyalthia* sp. This species was chosen because it varies little in size (tree height: $\bar{X} \pm \text{SD} = 23.14 \pm 6.31$ m; diameter at breast height: 22.40 ± 9.06 cm; crown height: 9.44 ± 3.11 m, $N=50$). To control for differences in feeding time, we counted genital contacts during the first 10 min after occupation of an individual tree. Analyses consider both the number of mature females and total size of the party (all mature individuals).

Two types of parties were distinguished here: (1) mixed parties consisting of mature individuals of both sexes and (2) all-female parties consisting of mature females and their immature offspring. For the comparison of genital contacts with party composition we scored a party as being all-female only if females travelled without males for the entire day (usually from nest to nest).

Genital Swellings

Records on changing patterns of genital swellings were available from four field seasons (1995–1998). Ratings considered two criteria: firmness and skin surface structure. Four stages were distinguished: (1) tissue flaccid, swelling wobbly, skin dry with deep wrinkles; (2) tissue viscous, swelling wobbly, skin wrinkled; (3) tissue firm, swelling elastic, skin soft with no or reduced wrinkles; and (4) tissue swollen, swelling sturdy during locomotion, skin shiny. Labial occlusion (sensu Dahl 1986), moist skin and vaginal secretion were used as additional characteristics to distinguish stage 4 from stage 3. However, because some older females did not always develop stage 4, and because differentiation between stages 1 and 2 was sometimes difficult we pooled records of different stages in some analyses (see below). Expected values for the distribution of genital contacts across different swelling stages were based on the number of days each female displayed signs of one of the different stages.

Access to Food

Records were from three field seasons (1993, 1995, 1997). To investigate the possible relationship between genital contacts and differences in accessibility to food, we analysed data from two species of feeding trees: *Irvingia gabonensis* and *Treculia africana*. *Irvingia* is a large tree (diameter at breast height: $\bar{X} \pm \text{SD} = 113 \pm 37$ cm, $N=6$). Fruits were of medium size ($\bar{X} \pm \text{SD} = 94 \pm 22$ g, $N=33$) and eaten from the ground. Horizontal crown size is large ($\bar{X} \pm \text{SD} = 1342 \pm 411$ m², $N=6$) and we estimated

the number of fruits available at one time from 500 to 5000 ($N=13$). Trees were revisited many times before they were depleted. *Treculia* is also a large tree (diameter at breast height: $\bar{X} = 92.4$ cm, $N=2$). Although it produces many fruits only one or two are available at the same time. The average weight of a single fruit $\pm \text{SD}$ was 7.6 ± 6.6 kg ($N=25$). As for *Irvingia*, fruits were eaten on the ground. In most cases they were held by one individual (owner). Other individuals (bystanders) try to gain some of the food by actively taking or begging (Hohmann & Fruth 1996). Collective consumption of a single fruit could last for more than 2 h ($\bar{X} \pm \text{SD} = 62.4 \pm 35.9$ min, $N=20$).

We analysed feeding episodes for which the following information was available: (1) beginning and end of feeding on a particular patch or item; (2) composition and size of the party during that time; (3) number of genital contacts; and (4) identity of individuals involved in genital contacts. Observations of larger parties were often incomplete and the restriction caused a bias to records obtained from smaller parties. However, it seems unlikely that this bias would affect the relative number of interactions in the two feeding situations. The time bonobos spent feeding at food patches of both trees was similar (Mann–Whitney test: $Z = -1.238$, $N_{Irvingia} = 23$, $N_{Treculia} = 22$, $P = 0.216$) but the number of females per party differed (Mann–Whitney test: $Z = -3.087$, $P = 0.002$). To control for this difference we calculated rates of genital contacts per female by dividing the number of all females present in a given party by the number of genital contacts.

To explore whether the exchange of genital contacts was related to a discrepancy in access to a food source, we distinguished genital contacts between two bystanders from those involving a bystander and the 'owner' of food. To avoid biases from repeated genital contacts of the same individuals, each female–female dyad was counted only once per feeding session, unless their roles changed (e.g. bystander became the owner of food or vice versa).

Statistics

All statistical analyses are nonparametric and two tailed. The following programs were used: SPSS for Windows, SsS by Rubisoft and the Fortran version of a randomization program written by Lamprecht & Hofer.

RESULTS

General Description

Of 484 genital contacts, 466 were performed by females, two by males and 15 by mixed-sex dyads. In one case information on sex was missing. All adult and adolescent females of the Eyengo community were seen to engage in genital contacts (Table 1). The behaviour occurred in two positions, vertically ($N=32$) or horizontally ($N=371$). Genital contacts were silent ($N=305$) or accompanied by vocalizations ($N=92$) produced by one or both individuals. The average rate of genital contacts (number/h) $\pm \text{SD} = 0.29 \pm 0.59$ ($N=1674$ h, 349 days).

Table 1. Individual differences in number and frequency of genital contacts

Female	Field season*	Days seen†	Genital contacts‡	Contacts/day§	Position**	
					Top	Bottom
Amy	2	42	25	0.60	7	12
Bhagmati	6	165	109	0.66	26	32
Geraldine	4	116	27	0.23	17	6
Gina	6	192	89	0.46	19	41
Kamba	6	177	51	0.29	26	12
Lolema	1	49	12	0.24	10	0
Lorle	6	108	52	0.48	12	18
Luna	6	169	63	0.37	13	27
Merit	4	85	15	0.18	6	3
Mona Lisa	6	155	45	0.29	25	11
Ndunge	6	133	34	0.26	10	16
Senufo	4	76	19	0.25	13	5
Thabita	6	140	60	0.43	12	27
Vanessa	4	66	11	0.17	5	1
Viola	6	148	26	0.18	15	5
Zora	6	177	43	0.24	29	0

*Number of field seasons a given female was present in the community.

†Total number of days a given individual was seen.

‡Number of genital contacts.

§Number of genital contacts/day.

**Number of genital contacts when the female was in the top or bottom position.

Genital contacts were usually initiated by one individual. Targets responded to solicitations either by mounting ($N=299$) or by moving away ($N=33$). When attempts to initiate a genital contact failed, solicitors showed signs of frustration (e.g. body rocking, pout face, whimpering) and sometimes directed aggression against another individual. Occasionally (27 times) genital contacts appeared to be enforced by the dominant.

Of the 484 genital contacts, 385 occurred in the context of feeding (including contest for food) and 34 were not related to food (rest, travel, play). In the remaining cases ($N=65$) classification was not possible because of an overlap of different context categories.

Hypothesis 1: Reconciliation

Prediction 1: genital contacts follow agonistic interactions

Of 466 genital contacts between mature females, 30 were preceded by agonistic encounters involving one or more females. In 376 cases, no agonistic encounter occurred in the 15-min interval preceding the genital contact. In 60 cases, information was incomplete.

Prediction 2: rates increase after agonism

Comparison of 105 preconflict intervals and 108 postconflict intervals showed that genital contacts occurred more often after than before agonistic encounters (22 versus 7%; Wilcoxon test: $Z = -3.162$, $N=105$, $P=0.002$). Considering all cases for which information on the preconflict and the corresponding postconflict interval was complete ($N=67$), we found that the average rate of preconflict genital contacts was four times lower (0.07) than that of postconflict genital contacts (0.29). However, of the 15 females contributing to the data set, six were

involved in agonistic encounters with other females only once or twice (Table 2). Considering only females with higher scores (more than two agonistic interactions), the overall difference between preconflict and postconflict rates of genital contacts was significant (Wilcoxon signed-ranks test: $T=0$, $N=8$, $P=0.017$).

Of 26 postconflict genital contacts, 15 involved both former opponents, one a female and the mother of her

Table 2. Frequency and rate of genital contacts before and after agonistic conflicts

Female	No. of conflicts	Genital contacts			
		Number		Rate	
		Before	After	Before	After
Amy	2	0	0	0	0
Bhagmati	25	3	7	0.12	0.28
Geraldine	2	0	2	0	1.00
Gina	10	1	2	0.10	0.20
Kamba	10	1	1	0.10	0.10
Lolema	2	0	0	0	0
Lorle	10	1	9	0.10	0.90
Luna	19	3	7	0.16	0.37
Merit	1	0	0	0	0
Mona Lisa	12	0	1	0	0.08
Senufo	1	0	0	0	0
Thabita	6	0	1	0	0.17
Vanessa	1	0	0	0	0
Viola	6	0	0	0	0
Zora	12	0	2	0	0.17

The frequency (absolute number of scores of genital contacts) and rate of genital contacts (number of genital contacts/number of conflicts) during a 15-min interval before and after an agonistic conflict are shown.

former opponent and four one of the opponents and a female that was not involved in the conflict. In six cases information was incomplete.

Prediction 3: close associates reconcile more than individuals with distant relations

Females accounted for 22.7% of all records of agonistic behaviour ($N=348$ events). Fifty-nine events of female–female agonism involved individuals for which we had sufficient information to calculate values of dyadic spatial association. The low frequency of agonistic encounters did not permit separate calculations for each field season. Overall, the distribution of agonistic encounters among the three classes did not differ from values one would expect from the average number of dyads of each association class (Kruskal–Wallis test: $H_2=4.571$, $N_{\text{close associates}}=6$, $N_{\text{nonassociates}}=2$, $N_{\text{random associates}}=51$, NS). The 26 cases of postconflict genital contacts among females involved 13 individuals and 14 different dyads. One dyad consisted of females that were close associates. In all other cases the females were random associates. Nonassociates were never seen to use genital contacts to reconcile their agonistic conflicts.

Summary

Rates of genital contacts of some but not all females increased after agonistic encounters. However, the performance of postagonistic genital contacts appeared to be independent of association patterns and a large proportion of genital contacts occurred independently of agonistic encounters.

Hypothesis 2: Mate Attraction

Prediction 1: rate of genital contacts is higher in mixed-sex than in all-female parties

As in other species with a fission–fusion social organization, bonobo parties vary in size and composition. Previous studies showed that 76% of the parties consisted of adults of both sexes while all-female parties made up 20% of the total sample ($N=485$ parties; Fruth 1995). In our study, mixed-sex parties had more female members than all-female parties ($\bar{X} \pm \text{SD}=4.77 \pm 2.07$, $N=264$ versus 3.26 ± 1.34 , $N=46$; Mann–Whitney test: $Z= -5.579$, $P<0.0001$). To control for this difference, we divided the hourly rate of genital contacts by the number of mature female party members. Females of mixed-sex parties performed genital contacts at higher rates ($0.06 \pm 0.1/\text{h}$, range 0–2, $N=261$) than members of all-female parties ($0.03 \pm 0.08/\text{h}$, range 0–0.4, $N=45$; Mann–Whitney test: $Z= -2.109$, $P=0.035$).

Prediction 2: genital contacts are followed by copulation

To test the possible effect of genital contacts on the behaviour of males, we investigated the temporal association of, and the participation by mature females in, genital contacts and copulations with mature males. Sexual interactions (copulations and genital contacts) among mature community members were scored on 140

Table 3. Intervals between sex events and pairwise comparison of intervals

Interval	$\bar{X} \pm \text{SD}$ (min)	Median	N	Pairwise χ^2		
				C–G	G–C	G–G
C–C	341±679	37	64	NS	NS	*
C–G	558±887	120.5	58	—	NS	*
G–C	401±899	60	49	—	—	*
G–G	210±553	12	92	—	—	—

C: copulation; G: genital contact.

* $P<0.001$.

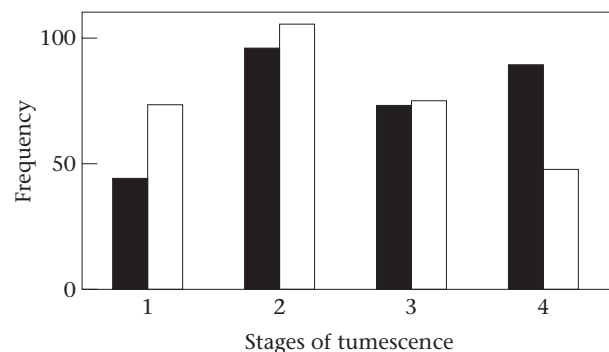


Figure 2. Observed (■) and expected (□) relative frequencies (%) of genital contacts during four stages of tumescence. Expected values are based on mean values obtained from 10 females.

days. On 77 days only one type of sexual interaction occurred. Sixty-three days produced scores of both copulations ($N=101$) and genital contacts ($N=181$). Considering this subsample, 74 of all copulations occurred independently of a genital contact, while 26 of the copulations involved one female from a preceding genital contact. The average interval between genital contact and copulation $\pm \text{SD}$ was 73.4 ± 137.5 min (median 15 min, range 0–585 min, $N=181$). Comparison of the intervals from sequences of genital contact–copulation ($N=49$) with intervals of the other three combinations of sexual interaction ($N_{\text{copulation–copulation}}=64$, $N_{\text{copulation–genital contact}}=58$, $N_{\text{genital contact–genital contact}}=92$) showed no difference in length of interval ($\chi^2_3=3.28$, $P=0.351$). Pairwise comparison of the different types of sexual behaviour revealed that intervals between two genital contacts were significantly shorter than intervals in other combinations of sexual behaviour (Table 3).

Prediction 3: rates depend on phase of tumescence

For 181 scores of participants of genital contacts, the degree of tumescence of genital swellings was available. Of these, 128 showed signs of tumescence (swelling stages 3 and 4) while 53 did not (swelling stages 1 and 2). Overall, the distribution of females performing genital contacts across the four stages of tumescence deviated significantly from an equal distribution ($\chi^2_3=42.59$, $P<0.001$; Fig. 2). However, since length of cycles and duration of the different swelling stages are known to vary (Dahl 1986; Vervaeke et al. 1999), we calculated the

Table 4. Distribution of genital contacts in relation to four stages of tumescence

	Days with rating	No. of genital contacts	1		2		3		4	
			O	E	O	E	O	E	O	E
Bhagmati	70	58	5	4.1	29	19.9	9	19.9	15	14.0
Gina	76	27	6	6.4	4	8.1	10	9.2	7	3.2
Kamba	116	25	11	8.6	12	10.3	0	3.0	2	3.0
Lorle	56	34	4	10.3	17	11.5	0	4.3	13	7.9
Luna	74	35	9	7.1	7	6.6	18	18.4	1	2.8
Mona Lisa	79	26	2	9.2	3	6.3	7	7.6	14	2.9
Ndunge	41	22	1	1.6	5	8.6	4	6.9	12	4.8
Tabita	63	28	2	7.1	3	6.2	12	8.4	11	6.2
Viola	86	18	1	3.1	7	7.9	5	3.1	5	3.8
Zora	137	29	3	7.8	9	13.5	8	3.8	9	3.8

Stages of tumescence: 1: minimum; 4: maximum. O: observed; E: expected.

frequency of genital contacts during different swelling stages using only data from complete cycles. Individuals varied considerably but there was a general tendency for fewer than expected contacts during detumescence (stages 1 and 2) and more during tumescence (stages 3 and 4; Table 4). However, only at stage 4 (maximum tumescence) did this deviation reach significance (Wilcoxon signed-ranks test: $T=4.5$, $N=10$, $P<0.02$).

Prediction 4: enhanced copulations involve primarily females at maximum tumescence

Copulation between mature individuals was seen 166 times. For 67 copulations we knew the swelling stages of females involved. To test whether fertile females used genital contacts to enhance copulation, we compared swelling stages of females involved in copulations without genital contacts ($N=50$) with those that mated after genital contacts ($N=17$). The proportion of detumescent females involved in copulations that were preceded by genital contacts was not different from that occurring independently of genital contacts ($\chi^2_1=0.457$, NS). The same result was obtained when the stage of maximum tumescence (4) was compared with the three stages of reduced tumescence ($\chi^2_1=0.120$, NS).

Summary

Females performed genital contacts more often when travelling together with males and more often during the stage of maximum tumescence. However, the temporal relation between genital contacts and copulations was weak and participation by females in copulations closely preceded by genital contacts appeared to be independent of their swelling stage.

Hypothesis 3: Tension Regulation

Prediction 1: rate of genital contacts is higher if food can be monopolized

We compared the rates of genital contacts and agonistic encounters when food was accessible to most or all party members (*Irvingia*, $N=23$ visits) with those when access was limited to a few individuals (*Treculia*, $N=22$

visits). At a *Treculia* food patch, the average rate of genital contacts was significantly higher than at *Irvingia* food patches ($\bar{X} \pm SD=2.83 \pm 3.53$ versus 0.35 ± 0.78 genital contacts/h; Mann-Whitney test: $Z=-4.903$, $N_1=22$, $N_2=23$, $P<0.0001$). Moreover, the rate of genital contacts per female party member was also higher for *Treculia* than *Irvingia* ($\bar{X} \pm SD=0.52 \pm 0.36$ versus 0.12 ± 0.25 genital contacts per female party member; Mann-Whitney test: $Z=-4.556$, $N_1=22$, $N_2=23$, $P<0.0001$).

Prediction 2: rates increase with party size

To test the impact of party size on the rate of genital contacts, we compared the rate of genital contacts/h with party size. Data from 315 parties of known size and composition showed that both the rate of genital contacts/h as well as the rate of genital contacts/h per female party member increased with party size (Spearman rank correlation: overall rate of genital contacts/h: $r_s=0.34$, $N=315$, $P<0.0001$; rate of genital contacts/h per female party member: $r_s=0.27$, $N=315$, $P<0.0001$). Since differences in party size are likely to reflect differences in the size and abundance of food patches, we investigated the relation between party size and rate of genital contacts with a data set obtained during feeding in *Polyalthia* sp., a tree species with comparatively homogeneous dimensions in crown size. Between two and seven females were seen to feed within the same tree ($\bar{X} \pm SD=3.42 \pm 1.37$, $N=64$). Females performed genital contacts 13 times in the first 10 min after entering a food tree. The average number of genital contacts/tree was 0.42/10 min (range 0–5, $N=64$) and the rate of genital contacts appeared to be independent of the number of females feeding in the same tree ($\chi^2_5=5.269$, $P=0.384$).

Prediction 3: genital contacts occur more often between owners and bystanders than between bystanders

Data for this part of the study were obtained when bonobos were feeding on *Treculia*. Of 57 genital contacts, 40 occurred between a bystander and an owner while 17 involved two bystanders ($\chi^2_1=8.491$, $P<0.01$). Bystanders and owners initiated 27 genital contacts each while three times initiation was unknown. During the same sampling

period, females were involved in 16 agonistic encounters, 14 involved bystanders and two one bystander and the owner ($\chi^2_1=7.563, P<0.01$).

Summary

Rates of genital contacts were high when food could be monopolized and rates increased with party size. However, in a data set collected from a type of food patch with homogeneous dimensions the positive correlation between party size and frequency of genital contacts disappeared. Data collected in a specific food context showed that dyads performing genital contacts were different from those involved in agonistic encounters.

Hypothesis 4: Expression of Social Status

Prediction 1: initiation of genital contacts shows status-dependent asymmetries

Ventral presentation was the key criterion to decide which of the two females had initiated a genital contact. This information was available for 149 records. In 52 cases the two females belonged to the same rank category and in 97 to different rank categories. In the latter, low-ranking individuals initiated genital contacts more often than high-ranking individuals (89 versus 8 times; Wilcoxon signed-ranks test: $T=44, N=97, P<0.001$).

Prediction 2: individual spatial position shows status-dependent asymmetries

Differences in spatial position were scored when genital contacts were performed in a horizontal position ($N=371$). Information on both spatial position and rank of the female participants was available for 191 of all records. The majority of females were seen in both spatial positions during genital contacts (Table 1). Only the top-ranking female (Zora) and an old female (Lolema), who was thought to be of high rank, were always in top position. In 63 cases, the two females involved belonged to the same rank category. The majority of dyads of the same rank ($N=13$) performed genital contacts only once or twice during the entire period of data collection. In the eight dyads with higher scores ($>2; N=43$), the two individuals often performed genital contacts in sequence ($N=28$), in the top position in some genital contacts, and on the bottom in others. When females differed in rank (128 times), high-ranking individuals were more often in the top position than low-ranking individuals (84 versus 44 times; Wilcoxon signed-ranks test: $T=8, N=128, P<0.0001$).

Summary

Asymmetries in initiation and performance of genital contacts were related to rank. Low-ranking females solicited genital contacts more often; high-ranking females were more often mounter than mountee.

Hypothesis 5: Social Bonding

Prediction 1: high frequency of genital contacts among kin

Genital contacts between four immature females and mature resident females occurred 34 times. Of these, 30

involved unrelated females and four involved a mother and her daughter. Considering the average number of mature female party members ($\bar{X} \pm SD=4.74 \pm 2.05, N=310$), genital contacts with unrelated females occurred more often than expected by chance (goodness-of-fit test: $G_1=22.178, P<0.001$).

Prediction 2: high frequency of genital contacts among close spatial associates

The proportion of genital contacts corresponded well with that of dyads of each association class (Fig. 3). Applying mean values of association classes and genital contacts of the four field seasons to a Kruskal–Wallis test, we found that females of different association classes did not differ in their frequency of performance of genital contact ($H_2=4.571, N=3, P=0.06$).

Prediction 3: genital contacts are positively related to grooming

It is widely assumed that differences in social grooming reflect differences in affiliative relations. Previous analyses of data from the same community revealed a positive correlation between grooming and close spatial associations (Hohmann et al. 1999). We compared frequencies of grooming with frequencies of genital contacts within a dyad (Table 5). Four dyads showed a positive relation between both behaviours, that is, dyads with scores of grooming also performed genital contacts. Thirteen dyads had a negative relation, that is, dyads engaging in grooming did not perform genital contacts and vice versa. Overall, comparison of the r_s values of the relation of both behaviours in each dyad revealed a significant negative relationship between genital contacts and grooming (Wilcoxon signed-ranks test: $T=33.5, N=17, P<0.05$; Fig. 4).

Summary

Neither kinship nor close spatial association increased the performance of genital contacts. Moreover, the data indicated a negative relationship between social grooming and genital contacts.

DISCUSSION

Table 6 summarizes our results in the light of the hypotheses proposed above. It appears that no single hypothesis can account for the varied ways in which genital contacts are used. Instead, genital contacts seem to serve a number of functions. Table 6 also shows that in some cases the data used to test a given hypothesis produced inconsistent results. However, the different predictions for each hypothesis vary in their magnitude. For example, the crucial test for the reconciliation hypothesis is whether rates of genital contacts rise after agonistic encounters. The finding that the majority of genital contacts occurred independently of agonistic encounters does not necessarily conflict with the former result but suggests that the behaviour has a function beyond the context of conflict resolution. Thus, we conclude that reconciliation is one function of genital contacts.

Table 5. Relationship between grooming and genital contacts for 17 female–female dyads

Dyad	N	Grooming	Genital contacts	Grooming plus genital contacts	r_s^*	P
Amy–Merit	13	2	8	3	+0.541	NS
Bhagmati–Zora	13	1	5	7	+0.478	NS
Geraldine–Lolema	12	5	6	1	–0.739	0.003
Gina–Mona Lisa	13	1	5	7	+0.303	NS
Kamba–Bhagmati	13	4	7	2	–0.443	NS
Lea–Amy	5	2	3	0	–1.000	<0.001
Lolema–Bhagmati	7	1	4	2	–0.161	NS
Lorle–Kamba	8	2	5	1	–0.079	NS
Luna–Bhagmati	12	3	8	1	–0.755	0.005
Merit–Luna	8	2	6	0	–0.864	0.006
Mona Lisa–Zora	7	1	5	1	–0.100	NS
Ndunge–Kamba	6	2	0	4	–0.174	NS
Senufo–Gina	5	1	1	3	+0.318	NS
Tabita–Lorle	8	1	2	5	–0.265	NS
Vanessa–Ndunge	2	0	0	2	–1.000	<0.001
Viola–Senufo	5	0	5	0	–0.471	NS
Zora–Tabita	11	4	4	3	–0.700	0.008

N is the number of days a dyad was scored for either grooming, genital contacts or both. The number of days when a dyad was engaged only in grooming, only in genital contacts, or both, is shown.

*Spearman rank correlation coefficient.

Comparative data on the use of genital contacts for reconciliation from other groups of bonobos are not yet available. Although the overall increase of sociosexual behaviour after agonistic conflicts found by de Waal

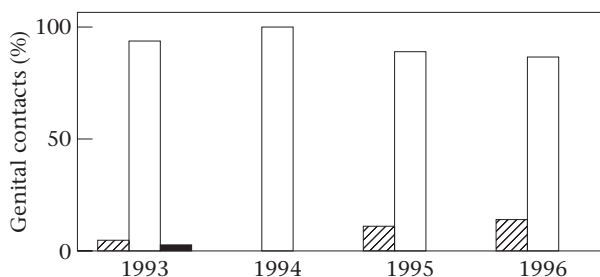


Figure 3. Relative frequency of genital contacts in the three classes of dyadic association for each field season. ▨: Close association; □: random association; ■: no association.

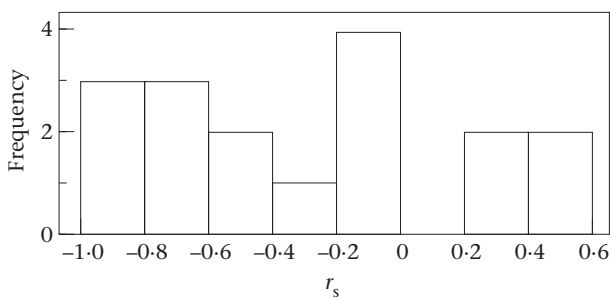


Figure 4. Relationship between relative frequencies of social grooming and genital contacts of 17 female dyads. Spearman rank correlation coefficients (r_s) indicate whether the relationship between behaviours was positive (high or low scores for both behaviours, respectively) or negative (high grooming scores correspond with low scores of genital contacts or vice versa). Numbers on the Y axis show the number of dyads falling in each category.

(1987, 1995) may have included genital contacts, their actual number before and after the conflict was not specified. Data from another captive group (Parish 1994; Manson et al. 1997) and from a long-term field study (Furuichi 1989; Kano 1989) show that genital contacts were related to social tension rather than agonistic conflicts. In mountain gorillas, *Gorilla gorilla beringei*, opponents tend to avoid close contact by travelling further apart (Watts 1995) and the fission–fusion system of wild bonobos enables contestants to separate. Under such circumstances, immediate reconciliation may be less beneficial than when group members are forced to remain in proximity (e.g. captivity). Moreover, there is evidence that reconciliation is most likely to occur among close kin (reviewed by Kappeler & van Schaik 1992). In captivity it is not uncommon for groups to consist of related individuals. For example, all adult females studied by de Waal (1987) at San Diego were full siblings. This is different from the wild where close genetic ties among resident females are absent (Hashimoto et al. 1996; Gerloff et al. 1999).

Table 6. Results of predictions of hypotheses tested in this study

Hypothesis	Prediction			
	1	2	3	4
Reconciliation	–	+	–	None
Mate attraction	+	–	+	–
Tension regulation	+	+/–	+	None
Expression of social status	+	+	None	None
Social bonding	–	–	–	None

+ : Prediction supported; – : prediction not supported. See text for details of predictions.

Testing the mate attraction hypothesis, we found that genital contacts were performed more often in the presence of males. Moreover, considering the conditions of genital swellings of females participating in genital contacts, stage 4 (maximum tumescence) occurred more often than the other three swelling stages. However, there was no evidence that copulation was affected by the performance of genital contacts, making it unlikely that genital contacts serve to attract mates. Comparison of different party types showed that mixed-sex parties were larger than all-female parties (see above). Moreover, previous studies at Lomako revealed seasonal variation in party size which was assumed to be related to differences in food availability (Fruth 1995). Thus, party size rather than party composition may explain the high rates of genital contacts in mixed parties.

For the tension regulation hypothesis, two out of three predictions were supported by our data. Our results agree with findings from a study in which rates of genital contacts were high when access to food was limited (Parish 1994). However, they contrast with those from another study conducted at the same field site by White & Lanjouw (1992) who reported that genital contacts were frequent when food was abundant and rare when food was limited. The study distinguished two categories of food patch quality using one metric dimension (crown size) of food trees and ignored other variables such as type and intensity of feeding competition or distribution and quality of food.

The lack of a positive correlation between party size and rate of genital contacts in trees of *Polyalthia* sp. suggests that differences in social tension are not only a function of party size but may also depend on other factors such as the quality of food, accessibility and differences in the type of competition.

For the social status hypothesis we made two predictions, both of which were supported by our data. Genital contacts were characterized by rank-related asymmetries and subordinate females initiated the behaviour more often than dominants. Rates of genital contacts were particularly high when access to food was limited and contested. Under these circumstances, ambiguities about social status are most likely to lead to agonistic conflicts and subordinates may derive immediate benefits from displays of submission. In one study of captive bonobos by Parish (1994, 1996) dominant females were more often the target than subordinates. In another captive group de Waal (1987) found that the dominant female was more often the mounter (top position) than the mountee. Similar rank-related asymmetries in spatial position have been reported from stump-tailed macaques, *Macaca arctoides* (Goldfoot et al. 1980). Mounting occurred when females were placed in the same observation cage and it was the most dominant individual that mounted another subordinate female.

The social-bonding hypothesis was not supported by our data. Furuichi (1989) proposed that immigrants use genital contacts to form close associations with residents. However, the data required to show that genital contacts affect social relations between two individuals in a predictable way are not yet available. Moreover, the

hypothesis does not explain why high-ranking resident females that are well integrated into the social network of the community engage in such a behaviour. Another question mark follows from the observation that the behaviour occurs almost exclusively in the context of feeding. Woolly spider monkeys, *Brachyteles arachnoides*, do embrace each other in tense situations (e.g. intergroup encounters) but also during their long resting periods (Strier 1992). Spotted hyenas, *Crocuta crocuta*, perform greeting ceremonies not only when they feed but also when they meet at the communal den (East et al. 1993). Male squirrel monkeys, *Saimiri sciureus*, engage in coalitionary genital displays in a number of different situations (Mitchell 1994). If the major function of genital contacts were to develop or maintain affiliative ties, they should also occur outside the context of feeding.

Recent research on the regulation of conflicts among primates is biased towards the restoration of individual relationships after agonistic encounters, an issue that needs to be separated from other types of conflict resolution (Hofer & East, in press). Conflicts arise out of ambiguities about access to resources and are likely to be followed by agonistic disputes. Reconciliation implies that an agonistic interaction has taken place before the exchange of friendly behaviours (de Waal & van Roosmalen 1979). Tension regulation does not necessarily require the emergence of agonistic behaviour. Bonobos provide an example of the difference between the two types of conflict resolution. When feeding on fruits of *Treculia* the majority of agonistic interactions occurred between those individuals competing for access to food (bystander) whereas genital contacts were almost exclusively exchanged between a bystander and a possessor of food (owner).

In our study lower-ranking females took more initiatives in initiation and performance. Although genital contacts were sometimes enforced by dominants we assume that subordinate females were highly motivated to solicit a genital contact. However, the fact that most targets responded to presentations with ventral mounts indicates that both females are likely to benefit. This raises questions concerning the advantages of genital contacts that the data currently available are not sufficient to answer. However, some of the ideas outlined below may help to develop testable predictions for future studies.

Advantages for the Target

First, assuming that individuals associate mounting with high status, acceptance of a solicitation provides an opportunity to demonstrate superiority at low costs. Second, by accepting an invitation in a tense situation, the target may reduce the probability that the solicitor will behave aggressively. Anecdotal evidence for the latter assumption comes from observations when targets appeared to ignore a ventral presentation. In some cases solicitors had temper tantrums and directed aggression against third individuals. Third, the observation that targets may ignore the solicitation from another female suggests that the payoffs from this behaviour are not

equally distributed. Experimental studies could make a major contribution to determine when targets submit and when they ignore a solicitation.

Advantages for the Solicitor

We found that within the same period of time, genital contacts occurred six times as often as agonistic female–female encounters (79 agonistic interactions versus 466 genital contacts). However, whether the low rate of agonism was causally related to frequent displays of subordination remains open. Agonistic interactions are likely to cause physiological stress which in turn may have negative long-term effects on lifetime reproductive success (Sapolsky 1985; Packer et al. 1995). Exchange of friendly behaviour, on the other hand, may reduce syndromes of socially induced stress (Gust et al. 1996). If the stress-induced effects known to exist in other social mammals (baboons, *Papio cynocephalus*: Altmann et al. 1995; mongooses, *Helogale parvula*: Creel et al. 1996) are similar in bonobos, subordinate females would obtain higher benefits from tension reduction than high-ranking individuals.

Within a given food patch, high-ranking females are likely to occupy better places than low-ranking females. Since genital contact requires physical contact, a female that presents to another is likely to come close to food. Indeed, females that had performed genital contacts were found to feed closer than other females (Furuichi 1989; unpublished data). However, quantitative data that would allow one to test the effect of genital contacts on food intake are not yet available.

Are bonobos the only great ape to have developed such an elaborate display to signal differences in social status? In chimpanzees, *Pan troglodytes*, and mountain gorillas females use vocal signals of submission (grumble calls in mountain gorillas: Watts 1994; pant grunts in chimpanzees: Goodall 1986; Nishida 1989). However, in conflict situations female chimpanzees embrace each other and may insert a finger into the vagina of a subordinate (Wrangham et al. 1992) or touch the other's genitals (R. Wittig, personal communication). This indicates that female chimpanzees use behavioural elements such as stimulation of genitals and embracing which are constituents of genital contacts of bonobos. Why females of the two *Pan* species differ in their displays of social status remains a challenge for future research. The finding that bonobos perform this behaviour so regularly indicates that social status is an important issue for the females of this species. Because of their frequent use, dyadic performance, spatial variability and behavioural plasticity, we suggest that genital contacts can be used to investigate the quality and dynamics of social relationships among female bonobos.

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