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RESEARCH ARTICLE

Perineal Swelling, Intermenstrual Cycle, and Female Sexual Behavior in Bonobos (*Pan paniscus*)

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Many reports have claimed that the duration of the swelling cycle in female bonobos (*Pan paniscus*) is longer than that of chimpanzees, and that the bonobo maximum swelling phase is markedly prolonged. Field data on intermenstrual intervals (IMIs) in female bonobos are limited and restricted to interswelling intervals (ISIs), which are assumed to reflect the IMI, though a direct comparison between the duration of ISIs and IMIs is still lacking. Reports on bonobo sexual activity as a function of the swelling phase are often contradictory. Moreover, the function of female homosexual interactions (genito-genital (GG) rubbing) is still debated. This study examines the reliability of the ISI as an approximation of the IMI, and the attractivity of female sexual swellings for other individuals. An analysis of 51 ISI-IMI pairs showed that ISIs are a fair representation of the reproductive cycle. The cycle length was 35.6 ± 1.1 SE days relying on the ISI, whereas it was 35.0 ± 1.1 SE days considering the IMI. This result is similar to the cycle length reported for chimpanzees. Female homosexual interactions and copulatory rates were higher during maximum tumescence, suggesting that the sexual swelling may be attractive for both males and other females. Furthermore, the GG-rubbing was performed free of a hierarchical postural imposition, and was not correlated with affinitive interactions. We suggest that GG-rubbing, which is generally the most frequent female sexual interaction, is a tool for social assessments among females. Am. J. Primatol. 67:333–347, 2006.

Key words: sexual swellings; cycle length; GG-rubbing; copulations; bonobos

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INTRODUCTION

In some primates the most obvious morphological cue of impending ovulation is the sexual swelling of females. The sexual skin around the perineum starts to swell and/or redden during the follicular phase of the ovulatory cycle, and it usually shows a conspicuous maximum tumescence around the presumed time of ovulation [Dixson, 1983; Girolami & Bielert, 1987; Hrdy & Whitten, 1987; Reichert et al., 2002]. These cyclic changes in the appearance of the sexual skin should reflect cyclic fluctuations in the secretion of ovarian hormones during the female cycle, thereby influencing the attractivity [Beach, 1976] of females to males [Dixson, 1983; Reichert et al., 2002]. The size of sexual swellings has been related to female fitness in olive baboons [Domb & Pagel, 2001; but see Zinner et al., 2002] and to cycle quality in chimpanzees [Deschner et al., 2004; Emery & Whitten, 2003], and graded changes in swelling size within cycles may signal the proximity of ovulation [Deschner et al., 2004; Nunn, 1999].

Many reports have claimed that the duration of the swelling cycle is longer in female bonobos than in chimpanzees [Dahl, 1986; Furuichi, 1987], and that the duration of the maximum swelling phase is markedly prolonged in bonobos [Blount, 1990; Dahl, 1986; Furuichi, 1987; Kano, 1992; Thompson-Handler et al., 1984]. The presence of a prolonged perineal tumescence has been related to extended female attractivity [Furuichi & Hashimoto, 2004; Kano, 1989; Stanford, 1998] and the consequent hypersexuality [de Waal, 1987; Wrangham, 1993]. Yet, as previously mentioned by Vervaecke et al. [1999], because it is difficult to observe menstruation in wild primates, field data on the intermenstrual intervals (IMIs) in female bonobos are still limited and restricted to the interswelling intervals (ISIs, sometimes ''measured between the last days of successive periods of maximum swelling'' [Furuichi, 1987]), which are assumed to reflect the IMI. Some studies showed a similarity between the IMIs of female bonobos and chimpanzees (IMI = 36 days [Savage-Rumbaugh & Wilkerson, 1978], 36 days [Thompson-Handler, 1990], and 34 days [Vervaecke et al., 1999]). On the other hand, other studies showed the presence of a longer IMI (or ISI for field studies) in female bonobos compared to chimpanzees (IMI = 44 [Neugebauer, 1980], 49 [Dahl, 1986], and 42 days [Furuichi, 1987]; see Table I for a comparative review). A comparison between the two *Pan* species is relevant because of their phylogenetic closeness, and because their differences in social and reproductive behaviors have been related to different patterns of swelling cycles [Kano, 1992; Kuroda, 1980; Stanford, 1998; Thompson-Handler et al., 1984]. Moreover, the picture that is currently emerging is that sexual behaviors differ less between the two species than was initially thought [Furuichi & Hashimoto, 2002; Takahata et al., 1996].

In this paper we compare perineal swelling cycle lengths with IMIs to determine how closely anatomical fluctuations in bonobo females reflect underlying physiological changes. Moreover, we also investigate the influence of genital swelling on the sexual behavior of male and female bonobos. First, we address via behavioral data the significance of swellings as a reproductive cue to males, and relate these findings to our data on cycle and swelling durations. Hamilton [1984] first proposed that sexual swellings were used to pinpoint ovulation. However, Heistermann et al. [1996] and Reichert et al. [2002] found that the pattern of sexual swelling is not a reliable indicator of ovulation in bonobos, reinforcing the idea of a ''concealed'' ovulation (sexual swelling as a dishonest indicator of the female physiological condition [Pawlowski, 1999]). Although bonobo males may also use other cues (e.g., olfactory cues) to detect ovulation, previous data on

TABLE I. Comparative Data on Inter-menstrual (IMI) and Inter-swelling (ISI) Intervals in *Pan paniscus*

Study	IMI/ISI	Max swelling phase	Condition	Number of females
Savage-Rumbaugh and Wilkerson [1978]	IMI = 36 days	15.3 days	Captivity	1
Neugebauer [1980]	IMI = 44 days	–	Captivity	2
Dahl in Thompson-Handler [1984][a]	IMI = 46 days	22.4 days	Captivity	3
Dahl [1986]	IMI = 49 days	–	Captivity	3
Furuichi [1987]	ISI = 42 days	14.6 days	Wild	3
Thompson-Handler [1990]	IMI = 36 days	–	Captivity	10
Vervaecke et al. [1999]	IMI = 3.82 days	–	Captivity	6

[a] Preliminary results of data reported in Dahl [1986].

pheromone perception in humans and some related primates showed contrasting evidence [Del Punta et al., 2002; Rodriguez et al., 2000; Zhang & Webb, 2003]. Furthermore, a previous study on bonobos [Reichert et al., 2002] showed that males do not appear to use other (non-morphological) cues, apart from sexual swelling, to determine their mating activity. Nevertheless, some authors found a higher copulatory rate in the period of maximum tumescence [Furuichi, 1987; Kano, 1980, 1989, 1992], whereas others stated that this rate is fairly constant regardless of the swelling phase [Savage-Rumbaugh & Wilkerson, 1978; Thompson-Handler et al., 1984]. In the light of this contrasting evidence, we present an additional investigation of the influence of sexual swelling on the copulatory rate.

Second, we focus on the role of swellings in female–female sexual behavior. Bonobo females show a characteristic homosexual behavior (genito-genital (GG) rubbing) in which two participants hold each other and swing their hips laterally while keeping the front tips of their vulvae, where the clitorises protrude, in contact [Kano, 1992]. Some studies in the wild found that females were more likely to perform GG-rubbing during maximum tumescence [Kano, 1992; Kuroda, 1980]; however, Furuichi [1992] stated that there was no correlation between frequency of GG-rubbing and swelling phase in the same wild bonobo population. In this paper we investigate the influence of the sexual swelling on GG-rubbing rates. Furthermore, we also try to clarify the social role of GG-rubbing. Several hypotheses have been proposed to elucidate the biological meaning of GG-rubbing, such as signaling social status, expressing relationship quality, regulating social tension, and indicating female proceptivity (for an extensive review see Hohmann and Fruth [2000]). Here we address the reliability of GG-rubbing as 1) an indicator of social status, and 2) a type of affiliative behavior.

MATERIALS AND METHODS

Study Group

We collected behavioral data during four observation seasons, for a total of approximately 12 months, from a group of *Pan paniscus* housed in the Apenheul Primate Park (Apeldoorn, The Netherlands). The colony was first established in

TABLE II. The Apenheul Bonobo Colony

Subject	Sex	Class	Date of Birth	Origin, arrival date
Hani[a]	M	Adult	1989, wild	DRC, 1998
Mobikisi	M	Adult	1981, wild	Antwerpen, 1996
Mwindu	M	Adult	1985, wild	DRC, 1998
Jill	F	Adult	1985, captivity	San Diego, 1997
Rosie[a]	F	Adult	1989, wild	DRC, 1998
Molasa[b]	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[b]	M	Infant	1998, captivity, Jill's son	Apenheul
Kumbuka	F	Infant	1999, captivity, Molaso's daughter	Apenheul

[a]Animals that died after the first session of observations (July–October 2000).
[b]Animal that died after session II (April–July 2002).

1998. We observed the subjects during 6-hr sessions, encompassing both the morning and the afternoon.

The composition of the colony changed over time: During session 1 (July–October 2000) there were 11 individuals (five mature females, three mature males, and three infants). In session 2 (April–July 2002) there were nine individuals (four mature females, two mature males, one juvenile, and two infants). In session 3 (September–December 2002) there were seven individuals (three mature females, two mature males, one juvenile, and one infant), and in the last session (session 4, March–June 2003) there were eight individuals (one more newborn; see Table II for details).

The wild-caught animals came from a rescue center located in the Democratic Republic of Congo. They were collected from different sites in different periods, and therefore we can be fairly confident that they were unrelated. The group was established from some wild animals for conservation purposes. The animals were housed in an enclosure with both an indoor and an outdoor facility (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 0845 hr) and received food (milk enriched by vitamins and proteins, monkey chow, vegetables, and fruit) four times a day at about 0845, 1230, 1430, and 1630 hr. 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 broadcast over the grass to encourage foraging activity, and regular renewal of the equipment in the indoor facility. Sometimes a wooden block with holes filled with honey or yogurt was provided. No stereotypic or aberrant behavior characterized the study group.

Data Collection

Daily observations of perineal swellings and menstruation were carried out with the help of the Apenheul bonobo keepers over a period of $3\frac{1}{2}$ years (January 2000–June 2003).

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: 4,224; session 2: 4,272; session 3: 3,744; session 4: 3,972) and 1,694 hours of focal sampling (session 1: about 41 hr per individual; session 2: about 56 hr per individual; session 3: about 52 hr per individual; session 4: about 52 hr per individual). We also recorded all-occurrences of copulations and GG-rubbings in periods 2–4 (1,275 hr of group follows).

We used the following operational definitions:

1. ISI: Days between the onset of subsequent maximum swelling tumescence. We used this calculation for ISI following the method of Emery Thompson (personal communication), who found that in chimpanzees the mean cycle length calculated this way is more consistent with previous calculations based on menstruation or endocrine landmarks.
2. Swelling stage: Daily appearance of sexual swellings recorded according to a rating system ranging from 1 (deep wrinkles in the ano-genital area, maximum detumescence) to 3 (maximum tumescence and firmness, no wrinkles, and shiny skin) [Dahl, 1986].
3. IMI: The period between two subsequent menstruations (from the day following the first day of menstruation until the first day of the subsequent menstruation). Menstruation was assessed via direct observation of bleeding.

Mountings and copulations were distinguished on the basis of evident penal intromission.

Statistical Analyses

Though observation sessions 2–4 were closely proximate, there was a 2-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 observations made during sessions 1 and 2. When we pooled the data, we used the mean hourly frequencies of behaviors per dyad and normalized the frequencies to the time each individual was observed, excluding the two individuals that died between sessions. Matman's row-wise correlation tool was used with 10,000 permutations (to check for interindividual variability) and a 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 sessions 1 and 2 (contact-sitting: $Kr = 33$, $tau_{rw} = 0.56$, $P < 0.05$; grooming: $Kr = 20$, $tau_{rw} = 0.34$, $P < 0.05$). This allowed us to pool data from different observation sessions.

To check the data for normality we used the Shapiro-Wilk test when $n < 50$, and the Kolmogorov-Smirnov test when $n > 50$. If the assumption of normality held, we used the paired *t*-test to compare the frequency of a given behavior in a matched pair (i.e. copulation rates in two conditions: max swelling, detumescence). In the case of non-normality, we used the Wilcoxon signed-ranks test to perform the paired analysis. We pooled focal data from periods 1–4 and checked for normality of the female rates of GG-rubbing and copulations, which were not found to violate the normality assumption. When we compared the durations of ISIs and IMIs, we contrasted the IMI that began with one menses with the ISI that commenced just after menstruation, across all female cycles. We chose this procedure because a given ovulation that characterizes an IMI is comprised of the

ISI that commences immediately after the beginning of that IMI (note: this is true if the ISI is defined as days between the onset of subsequent maximum swelling tumescence). Only four females were included in this analysis because one subject (Molaso) was experiencing postpartum lactational amenorrhea (yet, Molaso constantly showed a series of complete perineal cycles; see Table III for details on the reproductive history of each female).

Moreover, we used only those ISIs in which menstruation was clearly observed. The Kruskal-Wallis one-way analysis of variance (ANOVA) was used to test for differences between the cycle length among females. If the null hypothesis was rejected by the Kruskal-Wallis test, we used the multiple-comparisons test suggested by Siegel and Castellan [1988] to determine which pairs of samples differed significantly.

The binomial test was employed when the variable of interest was a dichotomy whose two values were mutually exclusive and exhaustive for all cases (i.e., mounter and mountee in a GG-rubbing interaction inside a given dyad: in this case a binomial test was applied to each dyad to label it as symmetric (0) or asymmetric (1), and then an overall binomial test on symmetry/asymmetry was performed).

All-occurrences data on sexual interactions from sessions 2-4 were pooled, and Matman's row-wise correlation tool was used to check for correlations between GG-rubbing and grooming/contact-sitting frequencies, since the latter generally express the extent of close affinitive ties inside a given dyad of individuals [Muroyama & Sugiyama, 1994; Preuschoft et al., 2002].

All of the analyses were two-tailed and the level of significance was set at 5%. Probabilities between 5% and 10% are reported as trends. We made use of exact tests according to the threshold values suggested by Mundry and Fischer [1998]. Statistical analyses were performed using SPSS 12.0®.

RESULTS

The weighted mean for ISI was $X \pm SE = 35.6 \pm 1.1$ days ($n = 57$, range = 22–66 days), while the weighted mean for IMI was $X \pm SE = 35.0 \pm 1.1$ days ($n = 51$, range = 17–65 days), excluding IMIs characterized by suspect (very long) durations and comprising more ISIs inside them. When we included all IMIs, the average was slightly higher: $X \pm SE = 37.7 \pm 1.8$ days ($n = 55$ cycles, range = 17–94 days). Paired IMI and ISI durations were not significantly different (Wilcoxon signed-ranks test: $Z = -0.153$, $n = 51$, *NS*; Fig. 1).

Individual differences in cycle length were observed for both IMIs and ISIs (IMI: Kruskal-Wallis test, $H = 31.84$, $df = 3$, $P < 0.001$; ISI: $H = 29.79$, $df = 3$, $P < 0.001$). In both cases, post-hoc comparisons revealed that the only significant difference was between Rosie (nulliparous female) and Zuani (parous female) (ISI mean value: Rosie $X \pm SD = 29.9 \pm 4.7$ days, $n = 22$, range = 22–37; Zuani $X \pm SD = 40.5 \pm 7.3$ days, $n = 29$, range = 33–66; IMI mean value: Rosie $X \pm SD = 33.7 \pm 16.2$ days, $n = 18$, range = 17–33; Zuani $X \pm SD = 41.2 \pm 11.2$ days, $n = 27$, range = 31–65).

A maximum swelling was present for 37.6% of the ISIs across the four females (mean value for maximum swelling duration $X \pm SE = 13.4 \pm 0.7$ days, $n = 57$, range = 2–24). Individual differences in the maximum swelling length were observed (Kruskal-Wallis test, $H = 38.99$, $df = 3$, $P < 0.001$), and post hoc comparisons revealed that the only significant difference was between Rosie and Zuani (Rosie $X \pm SD = 8.1 \pm 2.7$ days, $n = 22$, range = 2–13; Zuani $X \pm SD = 17.2 \pm 3.5$ days, $n = 29$, range = 10–24).

TABLE III. Reproductive History of Apenheul Females

Name	Reproductive state during collection of data on cycles	2000	2001	2002	2003
Jill	Parous	Swelling cycle with postpartum amenorrhea	Swelling cycle with postpartum amenorrhea	Swelling cycle with menses	Swelling cycle with menses/pregnancy
Lomela	Nulliparous	Swelling cycle without menses/menarche	Swelling cycle with menses	Swelling cycle with menses/pregnancy	Postpartum amenorrhea without swelling cycle
Molaso	Parous	Swelling cycle with postpartum amenorrhea	Swelling cycle with postpartum amenorrhea	Swelling cycle with postpartum amenorrhea - died	–
Rosie	Nulliparous	Swelling cycle with menses	Swelling cycle with menses	Swelling cycle with menses - died	–
Zuani	Parous	Swelling cycle with menses	Swelling cycle with menses	Swelling cycle with menses	Swelling cycle with menses

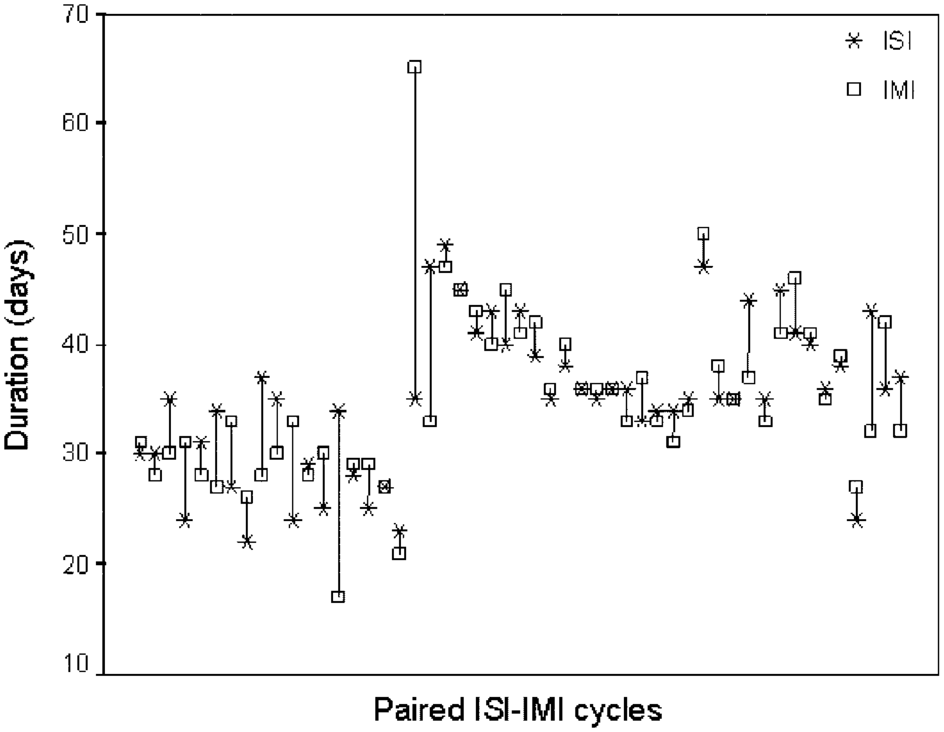

Fig. 1. Duration of paired IMI and ISI cycles across all of the study females.

Although copulations occurred at higher rates in the maximum swelling phase than in non-maximum swelling/detumescence in four of the five females, the observed difference failed to reach statistical significance (paired *t*-test: $t = 1.425$, n = 5, *NS*; Fig. 2a). A significant statistical difference was observed for more GG-rubbing interactions in the maximum swelling phase compared to non-maximum/detumescence phases (paired *t*-test: $t = 3.074$, n = 5, $P < 0.05$; Fig. 2b).

Females participated in GG-rubbing at higher rates than they participated in heterosexual copulations, regardless of swelling status, though one female (Zuani) showed similar rates of both behaviors (maximum swelling phase: paired *t*-test: $t = 2.863$, n = 5, $P < 0.05$; non-maximum swelling and detumescence: paired *t*-test: $t = 2.582$, n = 5, trend).

During GG-rubbing interactions among all female dyads (all occurences data from sessions 2–4; mother–daughter pairs excluded, immature individuals included), no difference was observed between the mounter and the mountee at an overall level, though in some dyads there was an asymmetry (seven dyads showed asymmetry, and four dyads showed symmetry; binomial test, n = 11, *NS*), (Fig. 3). Moreover, no asymmetry was observed in invitations to GG-rubbing (three dyads showed asymmetry, and six dyads showed symmetry; binomial test, n = 9, *NS*).

We also compared the correlation between GG-rubbing and grooming and contact-sitting frequencies in all female dyads (including immature individuals). The *Kr* test showed that neither grooming nor contact-sitting interactions (estimated by scan sampling) were significantly correlated with GG-rubbing rates

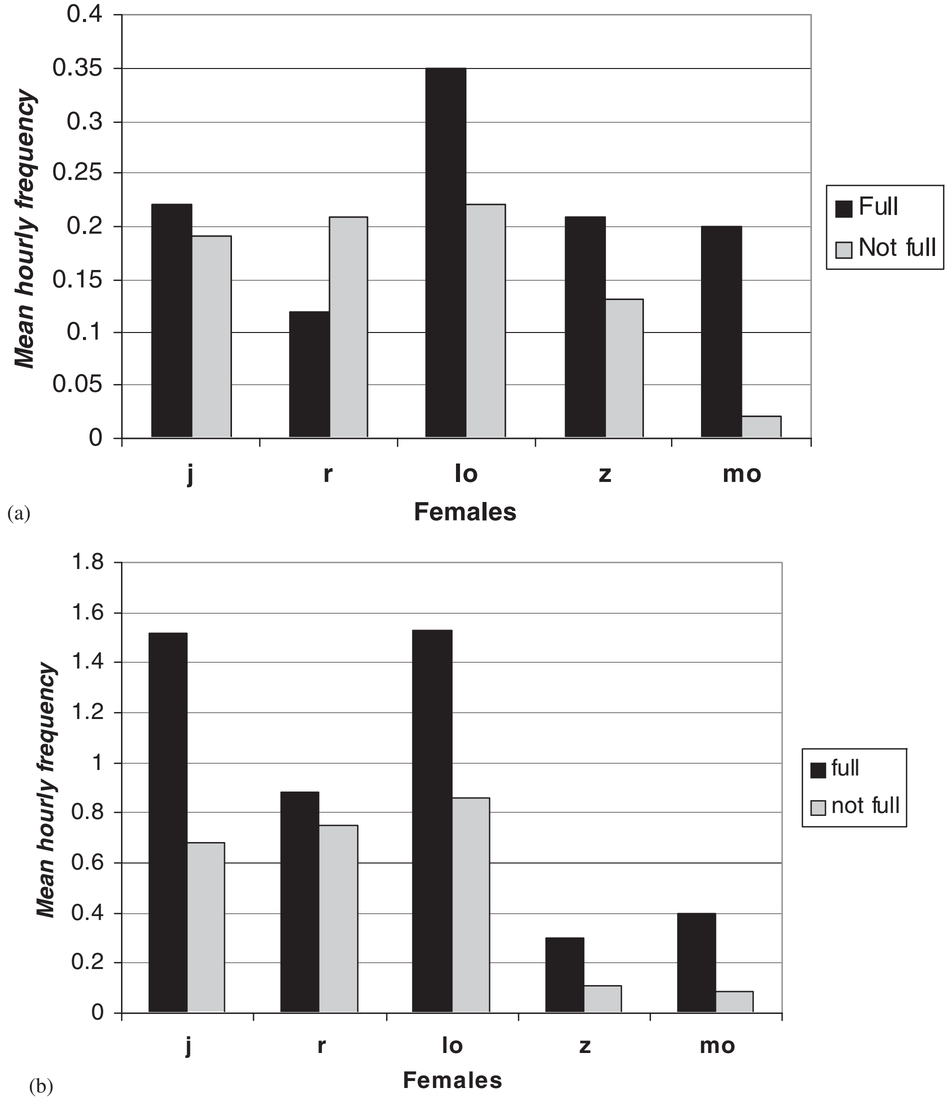

Fig. 2. **a:** Female rates of copulations during maximum swelling phase (full, black bars) and non-maximum swelling/detumescence (not full, gray bars). **b:** Female rates of GG-rubbing during maximum swelling phase (full, black bars) and non-maximum swelling/detumescence (not full, gray bars).

(contact-sitting and GGR: $Kr = 1$, $tau_{rw} = 0.017$, *NS*; grooming and GGR: $Kr = -4$, $tau_{rw} = -0.068$, *NS*).

On the other hand, grooming and contact-sitting frequencies were positively correlated ($Kr = 41$, $tau_{rw} = 0.69$, $P < 0.01$).

DISCUSSION

We found a mean ISI of 35.6 days, whereas the mean IMI was 35.0 days. To our knowledge no one has yet been able to directly compare ISIs and IMIs;

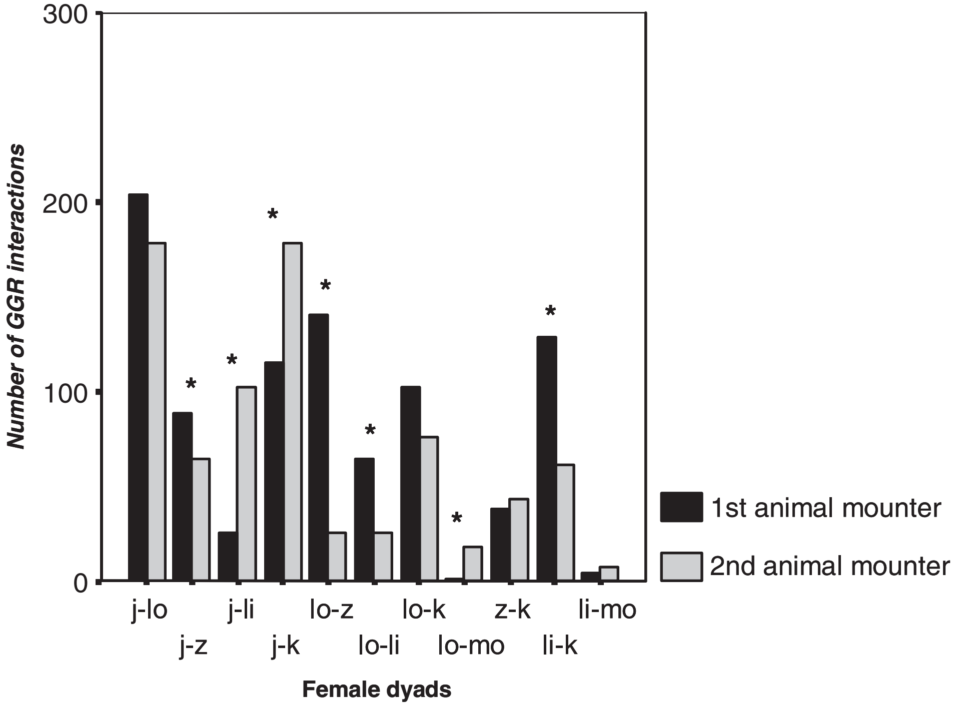

Fig. 3. Score of GG-rubbing interactions with the first animal of a given dyad as the mounter and mountee across all female dyads (mother–daughter dyads excluded). An asterisk marks the dyads that show a significant asymmetry ($^{*}P < 0.05$).

therefore, our results pairing ISIs and IMIs that show comparable lengths may be valuable for field workers. Thus, an ISI defined as "days between the onset of subsequent maximum swelling tumescence" seems to be an optimal and fair estimate of the female bonobo ovarian cycle (i.e., the IMI). In addition, we would like to emphasize that the cycle length is very often reported with no explanation as to how it is calculated. In wild conditions, the appearance of the sexual skin is often the only sign of female reproductive physiology [Vervaecke et al., 1999], but studies that rely only on ISIs may be biased by swellings that occur during postpartum amenorrhea. Such cases may cause a bias in the interpretation of menstrual cycle length in bonobos. That is why we excluded Molaso from the analysis of ISI duration in this study. For each female we considered only ISIs accompanied by menses. Our results appear to be in line with most reports on captive groups [Savage-Rumbaugh & Wilkerson, 1978; Thompson-Handler, 1990; Vervaecke et al., 1999], in which cycles were calculated as intervals between subsequent menses. In particular, the IMI value found for Apenheul females is very similar to that reported by Thompson-Handler [1990] in her study of the largest sample of bonobo females (204 cycles in 10 females) across European and U.S. captive groups (see Table I). On the other hand, there appears to be a noticeable discrepancy between the current results and previous studies by Neugebauer [1980] and Dahl [1986]. This may be due to the small number of females and/or the reduced number of cycles analyzed in the previous studies (two females and five cycles for Neugebauer; three females and 23 cycles for Dahl), or more likely to a peculiar cycle duration for the females in those studies. In fact, a considerable degree of interindividual variability was previously reported by Vervaecke et al. [1999], and our findings confirm this variability, with Rosie (nulliparous female) showing the shortest cycle and maximum swelling duration, and Zuani (parous female) showing the longest ones. A considerable degree of interindividual variability is also not unusual in human females [Bartlematz, 1953; Treloar et al., 1967].

We found that the mean value for maximum swelling duration was 13.4 days (37.6% of the perineal cycle). This finding on maximum swelling duration is reasonably in line with other reports (15.3 days [Savage-Rumbaugh & Wilkerson, 1978] and 14.6 days [Furuichi, 1987]), although it is noticeably shorter than the 22.4 days reported by Dahl (cited in Thompson-Handler et al. [1984]). Nevertheless, our finding supports to some extent the idea that the mean maximum swelling phase of bonobos is prolonged in comparison to that of chimpanzees, which is generally estimated to be shorter (10.4 days [Yerkes and Elder, 1936], 9.6 days [Tutin, 1979], 12.5 days [Hasegawa & Hiraiwa-Hasegawa, 1983], 11.9 days [Wallis, 1992], 10.9 days [Matsumoto-Oda & Oda, 1998], 10.9 days [Deschner et al., 2003], and 11.5 days [Emery & Whitten, 2003]). However, our results also indicate that the widespread view that bonobo females have a prolonged maximum swelling phase compared to chimpanzees should at least be tempered, since the discrepancy is likely only 1–3 days [Furuichi & Hashimoto, 2002].

In addition, the mean intermenstrual cycle of the Apenheul female bonobos was very similar to that of chimpanzee females (about 36 days; for an extensive review see Wrangham [1993]). Reichert et al. [2002] found that bonobo females showed ovulation outside the period of maximum tumescence in 30% of ovulatory cycles. Thus, although bonobo swellings outwardly resemble those of chimpanzees, the presence of a ''prolonged'' maximum swelling phase suggests that bonobo females may display a more misleading or imprecise anatomical sign.

The difference between female rates of copulations during the maximum swelling phase and during non-maximum swelling/detumescence failed to reach statistical significance; however, for four out of five females, copulations were more frequent in the maximum swelling phase. The presence of a higher rate of copulations during maximum tumescence is in line with reports by Kano [1980, 1989, 1992] and Furuichi [1987], and contrasts with the results of Savage-Rumbaugh and Wilkerson [1978] and Thompson-Handler et al. [1984]. Specifically, a higher rate of copulations during maximum tumescence is often reported for wild populations, whereas constant copulation throughout swelling cycles is often reported for captive groups. In any case, copulation rates should be affected by the peculiar history of a given group (e.g., this colony consists largely of wild-born individuals that may be housed in more naturalistic conditions than other captive groups) and by individual temperament—a factor that cannot be ignored in great apes. The atypical pattern observed in Rosie (''r'' in Fig. 2a) may be interpreted from this perspective, as no other clear explanation emerged.

As for the female homosexual behavior, we found that GG-rubbings occurred more frequently (statistically) when the focal females were in the maximum swelling phase compared to non-maximum swelling/detumescence, in agreement with Hohmann and Fruth [2000]. This finding is consistent with the natural scenario in which females that reach sexual maturity migrate to neighboring groups when they experience a maximum swelling [Furuichi, 1989; Idani, 1991]. While this is also the case for female chimpanzees (which are accepted more easily by resident males during maximum tumescence [Wallis, 1982]), in bonobos the maximum swelling may also be used as a means of attractivity among females (i.e., a "social passport" tool) in order to enhance social integration. Dahl [1986] observed that the occurrence of swelling shifts the location of the clitoris to a more ventral position, and this finding is consistent with the hypothesis of Takahata et al. [1996, p. 153] that "female bonobos may show maximal swelling in order to exchange GG-rubbing with other females, rather than to copulate with males." Our data appear to support this paradigm.

Asymmetries in the initiation [Parish, 1994] and performance of genital contact were described by de Waal [1987] and Hohmann and Fruth [2000], with high-ranking females observed more often as the mounter than the mountee. This does not appear to be the case for Apenheul female bonobos. During GG-rubbing no significant difference was observed between the mounter and the mountee at an overall level, though in some dyads there was an asymmetry (Fig. 3). Moreover, the alpha female, Jill (for data on social rank in the Apenheul group, see Paoli et al. [in press]), was found to perform GG-rubbing as the mounter or mountee in relation to different partners (Fig. 3), without any emerging status-dependent pattern. Furthermore, no overall asymmetry was observed in the invitation to GG-rubbing. Therefore, this behavior seems to be performed free of a hierarchical postural imposition or a hierarchical directional request. In view of this, the idea that GG-rubbing signals social status [Hohmann & Fruth, 2000; Wickler, 1967; Zuckerman, 1932] does not seem to be reliable, at least for this group. Moreover, our current finding is in line with results reported by Furuichi [1989]. Once more, it has to be stressed that the particular life history of a social group, as well as individual temperaments, may influence the patterns of a given behavior to a great extent. For example, all of the adult females studied by de Waal [1987] at the San Diego Zoo were full siblings, whereas in this study only unrelated females were taken into account for analyses of GG-rubbing.

Finally, no correlation was found between GG-rubbing and grooming and contact-sitting rates. Hohmann and Fruth [2000] found that social grooming and female genital contacts were negatively correlated. Two possible interpretations arise. First, GG-rubbing may not express the relationship quality, as suggested by some authors [Chevalier-Skolnikoff, 1976; Hausfater & Takacs, 1987; Rowell, 1966; Takahata et al., 1996; White & Lanjouw, 1992], and it may more likely be a tool for social assessment [Furuichi, 1989; Idani, 1991]. In fact, GG-rubbing is an immediate and intense means of testing the willingness of an animal to interact "fairly" by exposing a vulnerable part of the body [Wrangham, 1993]. Second, GG-rubbing may complement affinitive interactions. In fact, when forming intimacy, an individual may selectively perform GG-rubbing with some individuals and grooming/contact-sitting with others.

In conclusion, we argue that although in female bonobos the duration of the ISI is a fair depiction of the reproductive cycle, the exaggerated and "prolonged" sexual swelling in this species may also be a means of attractivity among females, elaborated to function in GG-rubbing, which appears to be a powerful tool for social assessment.

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