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What Females Tell Males About Their Reproductive Status: Are Morphological and Behavioural Cues Reliable Signals of Ovulation in Bonobos (*Pan paniscus*)?

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Abstract

In many Old World primate species, female attractivity increases during the tumescent phase of the sexual swelling for a period that lasts considerably longer than oestrus-related attractivity in other mammals. We examined the reliability of the swelling as an indicator of ovulation in captive bonobos, a species with a long and variable phase of maximum tumescence. Using a combined approach of (1) observations of sexual behaviour, (2) visual scoring of the sexual swelling and (3) analysis of faecal progestin to assess the timing of ovulation during 23 ovulatory cycles of eight adult females, we found that in 30% of these cycles the presumed day of ovulation did not fall within the period of maximum tumescence. When ovulation did occur during maximum swelling, it was more closely related to the end rather than the onset of the maximum swelling period. However, the pattern of sexual swelling was not a reliable indicator of ovulation. In addition, sexual behaviour of both sexes increased in frequency with the degree of the swelling but not around the time of ovulation. We conclude that swellings in bonobos provide honest information on the probability of ovulation, but not its exact timing, and that therefore the 'obvious ovulation'-hypothesis cannot explain the function of sexual swellings in bonobos.

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Introduction

In many mammalian species, mating activity is restricted to the so-called 'oestrus' period, that coincides with the fertile phase of the female ovulatory cycle (Heape 1900). Apart from behaviour, the patterns of olfactory or morphological cues displayed by a female may also change during 'oestrus' (Dixson 1998). For males, who are not able to detect ovulation itself, these cues can serve as indirect signals of the fertile phase. As sexual behaviour in monkeys and apes is less strictly controlled by hormones than in other mammals, the term 'oestrus' has often been considered inappropriate for these species (Rowell 1972; Dixson 1983a). Although, in general, signalling their readiness to mate lasts much longer than the fertile phase and is more variable in Anthropoid primates than in other mammals (Martin 1992), the variety of female cues that can stimulate male mating activity remains the same.

One of the most obvious morphological cues of impending ovulation are the sexual swellings of many Old World primates. Here, the sexual skin around the perineum begins to swell or redden during the follicular phase of the ovulatory cycle, showing a conspicuous maximum around the presumed time of ovulation (Dixson 1983b; Hrdy and Whitten 1986; Girolami and Bielert 1987). These cyclic changes in the appearance of the sexual skin which usually reflect cyclic fluctuations in the secretion of ovarian hormones during the female cycle (Rowell 1972; Clutton-Brock and Harvey 1976; Dixson 1983b, 1998) markedly influence the attractivity of females to males (Bielert and Girolami 1986). Although moderate changes in the external genitalia can be observed in many non-primate mammals and prosimians during the periovulatory phase (Dixson 1998), the occurrence of exaggerated sexual swellings is mainly restricted to Old World primate species with multi-male mating systems (Clutton-Brock and Harvey 1976; Dixson 1983a; Hrdy and Whitten 1986). The duration of tumescence and of maximum tumescence of the swelling varies considerably between species, the latter ranging from 3 to more than 20 d (Wildt et al. 1977; Mc Arthur et al. 1981; Nadler et al. 1985; Goodall 1986, p. 444; Furuichi 1987; Aujard et al. 1998).

The functional significance of sexual swellings has been the subject of much discussion and several hypotheses have been suggested. (1) Sexual swellings have evolved as honest signals of ovulation that increase paternity confidence for a high-ranking male and thus allocate paternal care (obvious ovulation: Hamilton 1984). (2) They increase male–male mating competition and therefore a female's chances to mate with a superior male. Consequently, she gains profit from the male's superior quality either for herself or for her offspring (best male: Clutton-Brock and Harvey 1976). (3) Swellings enable females to mate with many males and therefore confuse paternity and probably minimize the risk of infanticide (many males: Hrdy 1979, 1981). (4) They are a graded signal (Martin 1992) that allows females to follow a mixed strategy of biasing and confusing paternity by mating with the dominant male at peak swelling and with multiple males outside peak swelling (bias and confuse: Nunn 1999; van Schaik et al. 2000). (5) Sexual swellings conceal ovulation and force males into long-lasting consortships (concealed ovulation: Turke 1984). (6) Sexual swellings inform males about female quality (Pagel 1994). (7) Sexual swellings serve as a social passport during inter-group transfer (Pusey 1979; Nishida et al. 1985; Goodall 1986, p. 483). While hypotheses 6 and 7 do not explain why swellings evolved originally, hypotheses 1–5 focus on the question of whether sexual swellings actually serve to advertise or confuse ovulation.

To shed light on the advertising-confusing dichotomy it is important to investigate mating patterns in relation to sexual swellings, including information about the female's reproductive state and especially the timing of ovulation. Unfortunately, with only some exceptions (e.g. Lindburg and Harvey 1996; Aujard et al. 1998), most studies so far have either analysed mating behaviour without considering information on the precise timing of ovulation (Wallis 1992; Oi 1996), or investigated hormone-swelling interactions without considering behaviour (Mc Arthur et al. 1981; Nadler et al. 1985; Heistermann et al. 1996).

Analyses of endocrine, morphological and behavioural changes across the ovarian cycle of Tonkean macaques suggest that their sexual swellings are a reliable indicator of the periovulatory phase (Aujard et al. 1998). Compared with this species and also to chimpanzees, sexual swellings in bonobos (*Pan paniscus*) are characterized by a longer and more variable duration [duration of maximum tumescence in Tonkean macaques: 6–15 d (Aujard et al. 1998), chimpanzees: 7–17 d (Tutin and Mc Ginnis 1981), bonobos: 6–24 d (Dahl 1986)]. In bonobos, mating activity was found to peak at maximum tumescence (Furuichi 1987, 1992; Kano 1989), but females also mate when tumescence is below maximum (Kano 1992; White 1992). Thus, it has been concluded that sexual swellings do not allow male bonobos to assess the time of ovulation reliably (Furuichi 1987). Heistermann et al. (1996) investigated the timing of ovulation with respect to maximum swelling and concluded that sexual swellings are a poor predictor of ovulation in bonobos. However, as no data on sexual behaviour were collected, this study could not explain whether or not ovulation actually affects the mating behaviour of either sex.

Therefore, the aims of this study were to further investigate the value of sexual swellings as a signal of ovulation in captive bonobos by (1) assessing the temporal relationship between sexual swelling and ovulation and (2) analysing whether mating activity is influenced only by the degree of sexual swelling or whether it shows further changes around the time of ovulation. Specifically, we have used a combined approach of behavioural and morphological observations together with non-invasive faecal hormone analysis to determine the day of ovulation to test the following predictions. (1) If sexual swellings advertise ovulation reliably in bonobos, ovulation should be predictable from the onset of maximum tumescence. Nonetheless, based on the knowledge of the hormonal regulation of sexual swellings (Dixson 1983a), ovulation is expected to take place closer to the end rather than the onset of maximum tumescence and the beginning of detumescence should signal that ovulation has already occurred. (2) The degree of tumescence of the sexual swelling should influence the frequency of sexual interactions and sexual interactions should be most frequent around the time of ovulation.

Methods

Animals

Data on four different captive groups were collected between Oct. 1996 and Mar. 1999. Social composition of the study groups and observation periods are given in Table 1.

Of the 11 adult females present in these groups, eight showed regular ovarian cycles and were therefore included in the analysis. For details on female age, relatedness, reproductive history and reproductive state during the study see Table 2. Two of the study females conceived during the study period and gave birth after 230 and 237 d, respectively.

In three of the four groups, only one adult male was present at a time (the two males of the Stuttgart group never joined the females simultaneously). The two adult males of the Cologne group were father and adult son with the mother also being present in the group. No sexual interactions were observed in this mother–son dyad.

Table 1: Observation regime and group composition of each group observed. Group composition: adult males/adult females/juveniles + infants

Group	Observation period	Observation time (h)	Group composition
Cologne	Oct.1996–Feb.1997	443	2/2/1
Twycross	May–Jun.1997	293	1/2/2
Stuttgart	Aug.–Nov.1997	506	2/3/3
Frankfurt	Aug.1998–Mar.1999	820	1/4/3

Table 2: Identity and characteristics of study females. Age was determined at the beginning of each observation period. C = ovulatory cycles, C(l) = ovulatory cycles during lactation, conc = conception cycle, P = pregnant, LA = lactational amenorrhoea. Females contributing to the data set are marked (°)

Group	Identity	Age (yr)	Relatedness	Reproductive history	Reproductive state
Cologne	Bon°	20	–	Multiparous	C
	Kam°	9	–	Nulliparous	C
Twycross	Dia	20	Mother of Kic	Multiparous	P
	Kic°	8	Daughter of Dia	Nulliparous	C
Stuttgart	Kom°	31	–	Multiparous	Conc
	Dan	29	–	Multiparous	LA
	Lin	12	–	Nulliparous	P
Frankfurt	Mar°	47	Mother of Sal	Multiparous	C
	Nat°	29	Mother of Uke	Multiparous	C(l)
	Sal°	25	Daughter of Mar	Multiparous	C(l) + conc + P
	Uke°	13	Daughter of Nat	Primiparous	C(l)

During observation, the animals had access to 1–3 inside enclosures, with a total cage size of 59 to approx. 100 m^2. At Twycross, Stuttgart and Frankfurt zoo access to outside enclosures of 69 to approx. 450 m^2 was possible when temperatures exceeded 10°C or on days without rain. The animals were fed four to seven times daily with fruits and vegetables, but twigs, seeds, and sometimes mash enriched with vitamins or minerals, etc. were also provided.

Collection of behavioural data

Behavioural data were collected during 6 d/wk from the groups in Cologne, Twycross and Stuttgart by the first author alone, and on a daily basis for the Frankfurt group by the first author with the help of a student assistant. Data on sexual interactions were recorded using continuous recording during focal observations of adult females and ad libitum recording of interactions among non-focal individuals (Altmann 1974) and categorized according to female proceptivity, attractivity and receptivity (Beach 1976).

Proceptivity

– *Female solicitation:* presentation of genitalia to the male (Patterson 1979).

Attractivity

– *Male solicitation:* ventral presentation of erected penis to the female (Patterson 1979).

– *Male genital inspection:* visual inspection of female genitalia (distance max. 30 cm), sometimes incl. touching or sniffing (Nishida 1997).

– *Successful female solicitation:* female presentation that results in copulation.

– *Copulation:* mount with intromission and pelvic thrusts (Furuichi 1992; Nishida 1997).

Receptivity

– *Successful male solicitation:* male presentation that results in copulation

Copulation duration was measured with a digital watch and was defined as the time between the onset of pelvic thrusting after intromission and withdrawal of either participant. The occurrence of ejaculation as inferred from the presence of seminal fluid visible on the female or male genitalia after copulation could be recorded reliably only for the Frankfurt group.

Scoring of sexual swelling

Details of the appearance of wrinkles, turgidity, shine and colour of the genital and the perianal area as well as the presence or absence of labial occlusion

(Dahl 1986) and menstrual bleeding were recorded at the beginning and end of each observation day.

Collection of faecal samples

To assess the female reproductive state and provide information on the occurrence of ovulation, faecal samples were collected four to seven times per week. Samples were frozen within 4 h after defecation and stored at −20°C until analysis for concentrations of immunoreactive pregnanediol (iPd) which has been shown to represent a reliable indicator of luteal function and timing of ovulation in bonobos (Heistermann et al. 1996).

Data Analysis

Behaviour

Only interactions among adult individuals were included into the analysis. Rates per dyad, day and hour were calculated for all observed interactions. The influence of sexual swelling and fertile phase on the frequency of sexual interactions was tested by comparing mean rates per dyad. Mean values are given with their standard deviation. As not all animals or dyads showed all behaviours investigated (e.g. the two females of the Cologne group were not observed to copulate), sample numbers can be smaller than the total number of possible female–male dyads.

Assessing copulation frequency is only one way to investigate the influence of sexual swelling on mating behaviour, another parameter would be the probability of ejaculation. Mounts with intromission may also serve social functions (de Waal 1987; Thompson-Handler 1990) and in many primate species repeated mounts are required to achieve ejaculation (e.g. Lindburg and Harvey 1996). As there is no hint yet that bonobos are ‘repeated mounters’, we assumed that males need a certain number of pelvic thrusts to achieve ejaculation (Goodall 1986; Dixson 1998) or, as an indirect measure, a certain copulation duration. Accordingly, copulations were divided into three classes regarding their duration (1–7, 8–14, 15–21 s) and the distribution of ejaculations across these classes was tested (only Frankfurt group).

Sexual swelling

When trying to use a similar scale as Dahl (1986) to score the sexual swelling, not all females reached all swelling stages. Therefore, we used a rating system ranging from 1 (non-tumescence: deep wrinkles in sexual skin) to 3 (maximum tumescence: no wrinkles, maximum firmness, shiny surface) (Furuichi 1987) so that all swelling stages were reached in every menstrual cycle. Thus, a high degree of objectivity and inter-animal comparability in rating swelling changes was provided.

As morning and evening scores of sexual swelling were highly related (Cramer coefficients of association 0.9–1.0 for each female), only morning data were used for further analysis. The period of maximum swelling was defined as the period from the first day of its occurrence to the last day it was seen in a given swelling cycle.

Hormone analysis

Faecal samples ($n = 1040$) were lyophilized, pulverized, and after removal of undigested material 0.1 g aliquots of the resulting powder were extracted using 5 ml 40% methanol. Following appropriate dilution in assay buffer (0.04 M PBS containing 0.1% BSA, pH 7.2) extracts were measured for concentrations of iPd using validated microtiterplate enzyme-immunoassays as described by Heistermann et al. (1996). Inter-assay coefficients of variation were 15.0% ($n = 63$) at 30% binding and 16.6% ($n = 63$) at 70% binding, intra-assay coefficients were 6.1% ($n = 15$) and 14.1% ($n = 17$), respectively. Mean (± SD) extraction efficiency determined from the recovery of tritiated progesterone added to the first 10 faecal samples of each extraction series was $60.5 \pm 3.6\%$ ($n = 15$ series).

Timing of ovulation and the fertile phase

In bonobos, as in other primate species (e.g. Carosi et al. 1999; Fujita et al. 2001), excretion of oestrogens into faeces shows a high day-to-day variability which usually renders the detection of a clear preovulatory oestrogen peak more difficult (Heistermann et al. 1996; Jurke et al. 2000; K. E. Reichert, pers. obs.). In this study, assessment of the time of ovulation was thus solely based on the pattern of faecal progestin excretion, a procedure which has been shown to be reliable for assessing female reproductive status and timing of ovulation in a variety of other primate species (e.g. Strier and Ziegler 1997; Carosi et al. 1999; Heistermann et al. 2001). Specifically, for each ovarian cycle, the sustained rise in faecal iPd levels above a threshold of the $\bar{x} + 2$ SD of five preceding baseline values was used to indicate the onset of the postovulatory phase of the ovarian cycle (Royston 1983; Heistermann et al. 1995; Thierry et al. 1995; Carosi et al. 1999). The presumed day of ovulation was then assessed as the day of the defined faecal iPd increase corrected for a time lag of 3 d as inferred from a previous study on captive bonobos (Fig. 1; Heistermann et al. 1996; see also Heistermann et al. 2001). Because of the possible variability in the temporal relationship between ovulation and the postovulatory faecal progestin increase, data on timing of ovulation can be expected to include an error of ±1 d.

Copulations can lead to conception in a window of time spanning the functional life of the spermatozoa and the ruptured egg (France 1981; Gomendio and Roldan 1993a,b). We defined the fertile phase of an ovarian cycle to comprise the day of ovulation plus the three preceding days (Fig. 1) that have been

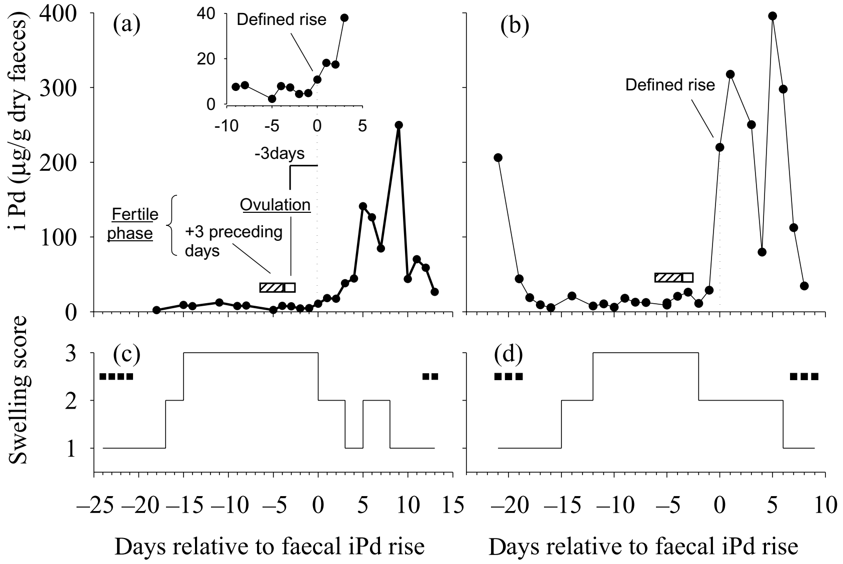

Fig. 1: Pattern of faecal immunoreactive pregnanediol (iPd) excretion (a, b), sexual swelling scores (c, d) and calculation of the respective fertile phases during two menstrual cycles of one female. (a) The days directly before and after the defined iPd rise (above a threshold of $\bar{x} + 2$ SD of five preceding samples) are shown enlarged in the inserted figure, (b) shows only the defined iPd rise and the presumed fertile phase. (c, d) The pattern of sexual swelling is represented by the step lines: 1 = non-tumescence, 2 = tumescence, 3 = maximum tumescence. ■ = menstrual bleeding

suggested to represent the functional life span of human sperm (France 1981) as comparable data are missing for apes. While sperm cells might be motile for more than 3 d (Baker and Bellis 1995), their fertility will decrease with time (France 1981) resulting in a reduced competitiveness against sperm from more recent copulations.

In total, data on 23 periods of maximum swelling were collected. All swelling periods were associated with ovulatory cycles as indicated by faecal progestin analysis. For 17 swelling cycles, the iPd increase was based on daily samples during the phase of the progestin increase. In the remaining six cases, one sample was missing between the last baseline and first elevated (above threshold) progestin level. For those cases, we determined the first sample with elevated iPd level to represent the day of the significant hormone increase.

Statistics

Only non-parametric statistical tests were used [Statistica, StatSoft Inc. (1999), Tulsa, USA], the α-level of significance was 0.05 (two-tailed). Because of the relatively small sample size, all p values given resemble exact probabilities (Siegel and Castellan 1988; Mundry 1998).

Results

Sexual Swelling and Timing of Ovulation

To assess how reliably sexual swellings advertise ovulation, we analysed the variability of the duration of maximum swelling and the timing of ovulation relative to this phase. Females were tumescent (scores 2 and 3) during 38–75% of the menstrual cycle (range 13–38 d in 26–65 d cycles, n = 23). Within this period, the duration of maximum tumescence lasted on average 16.0 ± 6.8 d (range 3–30 d, Fig. 2) and was highly variable both within and between individuals. Detumescence lasted 1-21 d ($\bar{x}$ 5.9 ± 2.4 d).

Hormone analysis showed that ovulation never occurred in the first half of the maximum swelling period. In 16 of 23 cases (69.6%) it took place in the second half of maximum swelling and in the remaining seven cases after the onset of detumescence (30.4%, in five of eight females; Fig. 2). The occurrence of ovulation after maximum swelling was not related to those six cycles where one faecal sample was missing during the period of the progestin rise. Maximum swelling began 3–27 d before ovulation ($\bar{x}$ 14.3 ± 6.5 d) and ended on average 0.7 ± 5.1 d thereafter (range −16 to +6 d). In two cases, more than 10 d passed between the end of maximum swelling and ovulation (Fig. 2). In all cases where

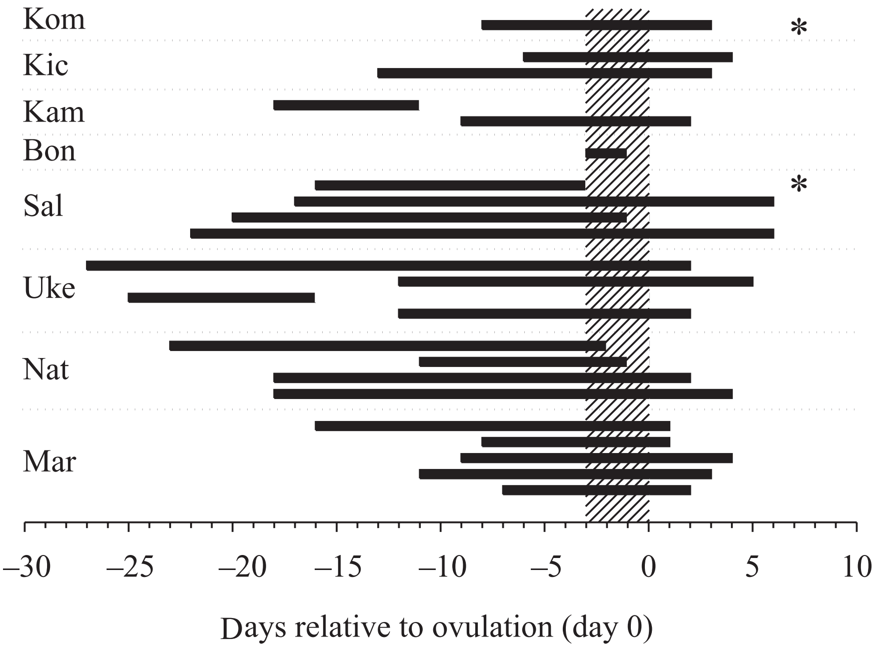

Fig. 2: Duration and timing of maximum swelling relative to the day of ovulation (day 0). Horizontal bars represent the period of maximum swelling and are ordered chronologically with each female's latest swelling cycle being on top. The shaded area highlights the fertile phase. * = conception cycles

ovulation occurred after maximum swelling, the swelling was still in the stage of detumescence.

Patterns of Sexual Swelling and Sexual Behaviour

Influence of the swelling phase on copulations

In total, 411 copulations were analysed with respect to the phase of swelling or menstrual cycle. Copulation frequencies differed significantly between swelling stages (Friedman ANOVA, $F_r = 12$; $n = 6$; $p < 0.01$; Fig. 3, all copulations). Although the mean copulation rate increased more than fivefold with advancing tumescence, multiple post-hoc comparison analysis revealed that only the increase from non-tumescence to maximum tumescence was significant ($z = 2.394$; $n = 6$; $p < 0.05$).

Ejaculations were observed less frequently in short copulations (≤ 7 s) and more frequently in longer copulations (> 7 s) than would be expected by chance (chi-square test, $\chi^2 = 25.58$; $df = 2$; $p < 0.001$; Table 3). On this basis, we separated short from long copulations and compared the influence of the swelling stage on the frequencies of both copulation types in all groups (Fig. 3). The frequencies of both short and long copulations were found to differ significantly between swelling stages (Friedman ANOVA, $n = 6$; short copulations: $F_r = 8.43$; $p < 0.05$; long copulations: $F_r = 9.33$; $p < 0.01$), with a significant increase being seen between non-tumescence and maximum tumescence for both types (Friedman post hoc comparisons; $z = 2.394$; $n = 6$; both $p < 0.05$). The increase in copulation frequency, however, was much more pronounced in long copulations than in short ones (factor 9.6 vs. 3.7; Fig. 3). When comparing the frequency of short and long copulations during the three swelling stages, their rates did not

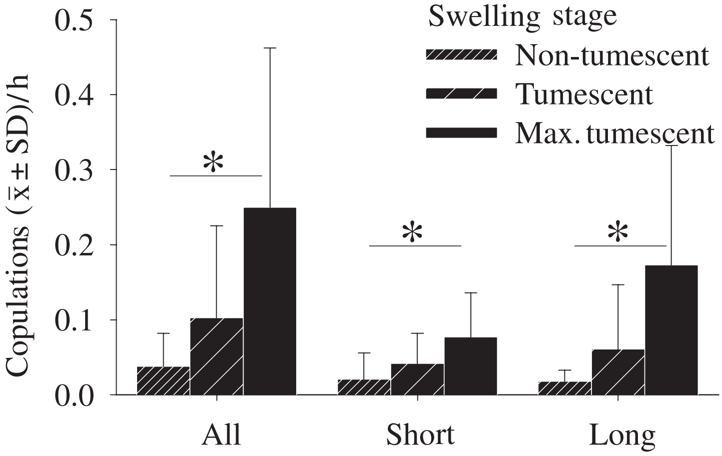

Fig. 3: Mean rates (± SD) of all copulations, short copulations (≤ 7 s) and long copulations (> 7 s) per hour in relation to stages of sexual swelling. * = Friedman ANOVA, $p < 0.05$

Table 3: Distribution of copulations with ejaculation among classes of different copulation duration. Data from Frankfurt group only

Copulation duration (s)	Copulations with ejaculation	All copulations observed
1–7	2	137
8–14	15	84
14–21	16	65
Sum	33	286

differ when the swelling was non-tumescent or tumescent (Wilcoxon Matched Pairs Signed Rank test, non-tumescent: n = 5; T = 10; tumescent: n = 6; T = 12; both ns). Yet during maximum tumescence, long copulations occurred at a significantly higher frequency than short copulations (n = 6; T = 21; $p < 0.05$).

Influence of the swelling phase on sexual solicitations and genital inspections

The degree of sexual swelling did not significantly alter the frequency of total female solicitations (Friedman-ANOVA, n = 8; $F_r = 2.89$; ns) nor did it influence the rate of successful female solicitations (Friedman-ANOVA, n = 6; $F_r = 5.2$; ns; Fig. 4). Male sexual behaviour increased tendentiously with advancing swelling. While this increase was not significant for male solicitations (Friedman-ANOVA, n = 8; $F_r = 5.87$; $p < 0.10$), the rate of successful male solicitations changed significantly across swelling cycles (Friedman-ANOVA, n = 6; $F_r = 8.33$; $p < 0.05$;

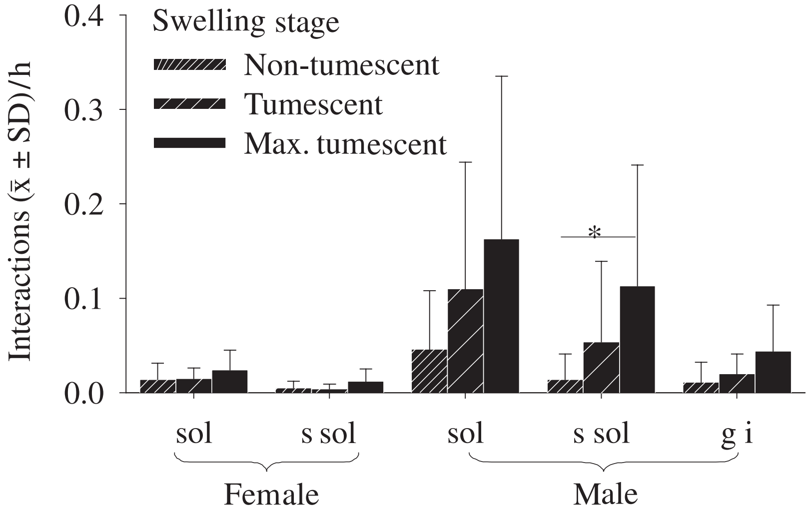

Fig. 4: Mean rates (± SD) of sexual interactions per hour in relation to stages of sexual swelling. sol = solicitation, s sol = successful solicitation, g i = genital inspection. * = Friedman ANOVA, $p < 0.05$

Fig. 4). Male solicitations were accepted by females significantly more often during maximum tumescence than during non-tumescence (Friedman multiple post-hoc comparison, $z = 2.394$; $n = 6$; $p < 0.05$).

In general, males solicited females at a significantly higher rate than females solicited males (Mann-Whitney U test; male solicitations: 0.11 ± 0.04; $n = 8$; female solicitations: 0.02 ± 0.01; $n = 8$; $W_x = 43$; $p < 0.01$).

Although males inspected female genitals more frequently at higher swelling stages, this did not reach statistical significance (Friedman-ANOVA, $n = 9$; $F_r = 4.47$; ns; Fig. 4).

Sexual Behaviour and the Fertile Phase

It was investigated whether the frequency of sexual interactions during maximum tumescence is influenced by female reproductive status, i.e. the fertile phase of the ovarian cycle. For all sexual interactions recorded, frequencies (shown during maximum tumescence) did not differ significantly between the non-fertile and the fertile phase of the ovarian cycle although there seemed to be a tendentious rise in some cases (Fig. 5, Wilcoxon Matched Pairs Signed Rank test, all results ns; all copulations: $n = 5$, $T = 13$; short copulations: $n = 5$, $T = 11$; long copulations: $n = 5$, $T = 14$; female solicitations: $n = 6$, $T = 18$; female successful solicitations: $n = 5$, $T = 12$; male solicitations: $n = 6$, $T = 14$; male successful solicitations: $n = 5$, $T = 12$; male genital inspections: $n = 6$, $T = 20$). Long copulations were significantly more frequent than short copulations both in

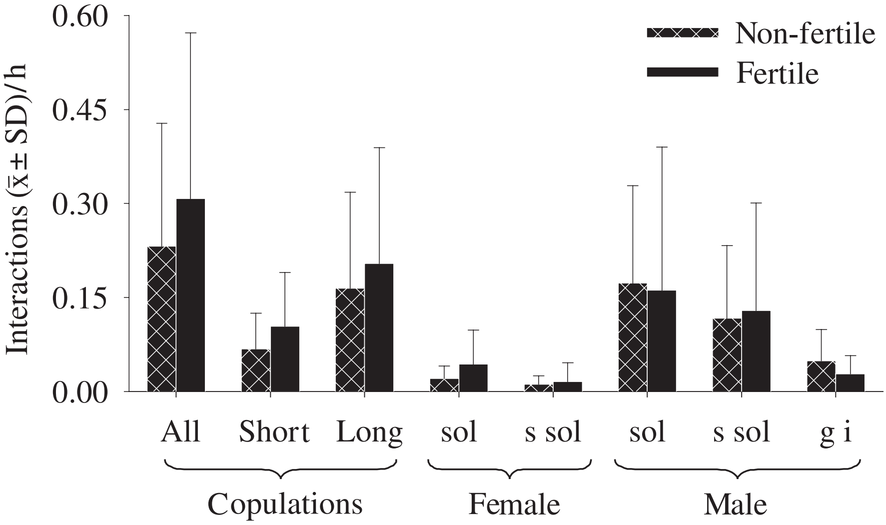

Fig. 5: Mean rates (± SD) of sexual interactions per hour in the non-fertile and the fertile phase during maximum tumescence. Abbreviations see legend Fig. 4. Friedman ANOVA, ns

the non-fertile and the fertile phase (Wilcoxon Matched Pairs Signed Rank test, non-fertile: $n = 6$, $T = 21$; fertile: $n = 5$, $T = 15$; both $p < 0.05$).

Discussion

The aims of this study were (1) to investigate whether the pattern of sexual swelling in bonobos is a reliable signal of ovulation and (2) to determine whether mating activity and other sexual interactions are solely influenced by the stage of female sexual swelling or also by the reproductive status, specifically the fertile phase of the cycle. We have shown that the pattern of sexual swelling is a poor predictor of ovulation in bonobos. Our results further indicate that female attractivity and receptivity are significantly influenced by the stage of the sexual swelling, but not by the fertile phase of the menstrual cycle. Female proceptivity changed neither with advancing degree of sexual swelling nor during the fertile phase.

Our data show that the phase of maximum tumescence in the bonobo is markedly long, covering on average a period of 31.2% of the menstrual cycle. In addition, the duration of the swelling stages shows high variation both within and between individuals. These findings are in line with other data on wild and captive bonobos (Dahl 1986; Furuichi 1992; Heistermann et al. 1996) as well as with reports of other primate species [maximum tumescence in macaques: 3–37 d, baboons: 3–20 d, chimpanzees: 7–17 d (Tutin 1979; Shaikh et al. 1982; Lindburg and Harvey 1996)].

The timing of ovulation in relation to the onset as well as the end of maximum tumescence of the sexual swelling was found to be highly variable. Furthermore, one-third of ovulations occurred when the swelling had already started to deflate (but see Heistermann et al. 1996). Although this proportion could be overestimated given that our timing of the day of ovulation might include an error of ±1 d, the phenomenon was observed in several of the study females and does not seem to indicate infertile cycles, as one individual conceived during such a cycle and gave birth after a normal gestation length of 230 d (cf. Dahl 1986; Heistermann et al. 1996). This suggests that, in bonobos, detumescence is not as reliable as in other primate species in indicating that ovulation has occurred (cf. baboons: Shaikh et al. 1982; chimpanzees: Nadler et al. 1985). Furthermore, only 57% of ovulations (baboons: 93%, Shaikh et al. 1982) actually occurred during the last 4 d of maximum tumescence, a period which is generally assumed to represent the fertile phase in chimpanzees (Hasegawa and Hiraiwa-Hasegawa 1983; Goodall 1986, p. 444 ; Wallis 1992; Nishida 1997). This indicates also that inferring ovulation retrospectively from the onset of detumescence may lead to erroneous results for bonobos. Additionally, it underscores the importance of hormonal data whenever accurate information on female reproductive status and timing of ovulation is needed.

Apart from sexual swelling, males could use other cues to detect ovulation, e.g. olfactory cues from genital inspections or urine sniffing. However, data on pheromones in Old World primates are rare and inconclusive (Gould and Martin

1981; Fox 1982; reviews: Hrdy and Whitten 1986; Zeller 1987; Dixson 1998). Although olfactory communication has not yet been investigated in bonobos, the fact that rates of sexual interactions did not statistically differ between the non-fertile and the fertile phase of the ovarian cycle suggests that male bonobos do not use other, non-morphological cues for assessing ovulation. Note that the results remain the same when only those copulations with a high probability of ejaculation are considered. Although the sample size on which these findings are based is relatively small, we are confident that it did not affect the statistical outcome of our results given that a significant influence of the sexual swelling on sexual interactions was found in the same data set. As well, copulations with a higher probability of ejaculation were more frequent than those with a low probability already in the non-fertile phase of peak swelling.

With respect to the influence of the swelling on mating behaviour, our results are in line with previous data on wild bonobos where it has been reported that copulation rates are the highest at stages of maximum tumescence (Furuichi 1987) and that copulations are more often initiated by males than by females (Takahata et al. 1996). In contrast to bonobos, in which sexual behaviour thus appears to be mainly influenced by the swelling size, mating behaviour in chimpanzees shows a further peak during the last 4 d of maximum swelling that are suggested to represent the fertile phase (Goodall 1986).

Regarding the function of sexual swellings in bonobos, the unreliability of the sexual swelling as a signal for the precise time of ovulation and the lack of increased mating activity during the fertile phase as found in this study suggest that the 'obvious ovulation'-hypothesis (Hamilton 1984) cannot explain the function of sexual swellings in *Pan paniscus*. Unfortunately, the limited number of males in our study groups did not allow to test the alternative hypotheses on the function of sexual swellings in a straightforward way. However, female bonobos are known to mate promiscuously during the menstrual cycle in captivity and in the wild (Furuichi 1992; Takahata et al. 1999; Vervaecke and van Elsacker 2000). This would favour the 'many males'- rather than the 'best male'-hypothesis (Clutton-Brock and Harvey 1976; Hrdy 1979). Additionally, by not advertising the fertile phase reliably, as has been shown in this study, females should have more chances to mate with multiple males. Otherwise, increased intra-sexual competition among males could limit female choice.

Our finding that male bonobos appear to be unable to detect the time of ovulation would partly support the 'concealed ovulation'-hypothesis proposed by Turke (1984). However, no trend towards ovulatory or swelling synchrony was detected in the study females (data not shown) and consortships do not play an important role in bonobos (Kano 1992; Takahata et al. 1999). Therefore, this hypothesis still cannot be favoured.

It has been recently proposed that sexual swellings allow female primates to follow a mixed strategy of confusing and biasing paternity, among others as a mechanism to reduce infanticide risk (Nunn 1999; van Schaik et al. 2000). Assuming that the swelling is a graded signal that advertises the probability of ovulation (Martin 1992), females could mate promiscuously during stages of moderate swelling, but mainly with high ranking males during the fertile period of the cycle. In the present study, we found that up to 70% of ovulations fell within the period of maximum swelling and, moreover, that 57% of ovulations occurred during the last 4 d of maximum tumescence, with a decreasing probability of ovulation with increasing temporal distance from the onset of detumescence. This clearly suggests that swelling in bonobos is an honest signal of the probability of ovulation sensu Martin (1992) and Nunn (1999), but not for its exact timing. By advertising the likelihood of ovulation but concealing its precise timing from the males, the swellings may thus help female bonobos to bias and confuse paternity. The adaptive significance of such a function in bonobos, however, is not clear because infanticide risk is probably lower in bonobos compared with other primate species (van Schaik et al. 2000). However, to test whether the 'bias and confuse'-hypothesis is the best explanation for the function of sexual swellings in bonobos, further studies carried out in multi-male groups are required to examine whether female mating preferences actually change during the swelling and the course of the ovarian cycle, and how this is related to paternity outcome.

In summary, our data suggest that sexual swellings of bonobos do not reliably advertise the fertile phase. Female behavioural cues do not advertise this phase either and males are therefore not able to precisely detect impending ovulation. Nevertheless, sexual swellings of bonobos appear to be 'honest enough' to stimulate male arousal and mating, but probably leave room for females to influence male reproductive success and exert their own reproductive strategies. We conclude therefore, that the 'obvious ovulation'-hypothesis cannot explain the function of sexual swellings in bonobos. Further studies are needed to assess direct and indirect mate choice of female bonobos during the menstrual cycle and to test whether other hypotheses better explain the function of sexual swellings in this species.

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