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Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*

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Females of many catharrine primates show a periodic and often pronounced swelling of the perineum, the functional significance of which is unclear. Several hypotheses that exist to explain the function of this conspicuous trait are based on assumptions about the temporal relation between the period of maximum swelling and ovulation, and remain largely untested. We examined this relation in free-living chimpanzees of the Taï National Park, Côte d'Ivoire, and assessed the reliability of perineal swelling as an indicator of ovulation in this species. We used noninvasive urinary progestogen analysis of female reproductive status, together with observational data on swelling characteristics, to determine the variability of timing of ovulation within the maximum swelling phase in 36 cycles from 12 females. The period of maximum swelling was highly variable, lasting from 6 to 18 days. Although ovulation was virtually restricted to the second half of the period of maximum tumescence, its timing varied considerably in relation to both the onset and the end of the maximum tumescence phase. Probability of ovulation, however, was not random, but peaked on day 7 after the onset of the maximum swelling phase, and was almost 60% between days 7 and 9. Thus, in wild chimpanzees perineal swelling indicates the probability of ovulation, but does not provide sufficient information to deduce its exact timing. Given the temporal variability of ovulation relative to the last day of maximum tumescence, field workers should try to include hormonal analysis if information on timing of ovulation is required for interpretation of observational data.

In animal species in which sperm cannot be stored for long periods, copulation has to take place within a narrow time window around ovulation if fertilization is to result. Since males are unable to detect ovulation itself, females have developed a variety of signals, such as proceptive behaviour (primates: Carosi et al. 1999), vocal cues (primates: Aich et al. 1990; Gust et al. 1990; African elephants, *Loxodonta africana*: Poole et al. 1988; chipmunks: Callahan 1981; birds: Montgomerie & Thornhill 1989; Arvidsson 1992), olfactory cues (insects: Greenfield 1981; Hölldobler & Wilson 1990; fish: Stacey et al. 1986; primates: Ziegler et al. 1993) or morphological signs (reptiles: Cooper & Crews 1987) to indicate the periovulatory period to males. In primate species, one conspicuous morphological cue, which is assumed to have evolved in the context of ovulation advertisement, is the swelling of the female's perineum (sexual swelling). This morphological trait has evolved independently at least five times during catarrhine evolution (Dixson 1998) and is presently found in cercopithecids, Asian and African colobids, hylobatids and the genus *Pan*.

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Although it is known that sexual swellings generally increase female attractiveness and stimulate male sexual arousal (Girolami & Bielert 1987), the exact functional significance of this trait, particularly with respect to its influence on mating patterns (and thus male and female reproductive success), remains unclear. A number of hypotheses exist to explain the function of sexual swellings in primates (see review in Dixson 1998; Nunn 1999; Stallmann & Froehlich 2000), the most prominent of which are the best-male hypothesis (Clutton-Brock & Harvey 1976), the many males hypothesis (Hrdy 1981; Hrdy & Whitten 1987), the obvious-ovulation hypothesis (Hamilton 1984), the distant-male hypothesis (Dixson 1983), the reliable-quality indicator hypothesis (Pagel 1994), and the graded-signal hypothesis (Nunn 1999).

The reliable-quality indicator hypothesis not only assumes that swellings indicate receptivity but also proposes that swelling size provides honest information on overall female quality; the other hypotheses mainly focus

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on the existence of a relation between swelling/swelling stage and female reproductive status. Two hypotheses (best-male and distant-male hypotheses) regard the swelling as a rough indicator of female reproductive condition; the other three depend on a more precise temporal relation between swelling stage and ovulation. According to the many males hypothesis, females use the attraction of males to the swellings to mate with many males, which may help them to confuse paternity and thereby reduce the risk of infanticide. Thus, ovulation should be randomly distributed over the period of tumescence so that males cannot use swelling patterns as a means of predicting its timing. In contrast, the obvious-ovulation hypothesis suggests that swellings provide precise information on the timing of ovulation and thereby help to assure paternity to the dominant male and in turn secure his services in protecting the offspring. This hypothesis predicts a tight link between swelling stage and ovulation, leading to low variability in timing of ovulation relative to the onset of maximum tumescence. Finally, the graded-signal hypothesis proposes that swellings indicate a certain probability of ovulation according to their size. In this way, the dominant male can monopolize the female on the days when her swellings are largest and the probability of ovulation is highest. Lower-ranking males, however, would have a small but significant chance of paternity on days when swellings are smaller and probability of ovulation is lower and the female is not monopolized by the dominant male. A probabilistic relation between swelling and ovulation should therefore exist, with highest probability values when the swelling is biggest and lower values towards the beginning and the end of the swelling period. Each of these hypotheses, however, makes assumptions about the timing of ovulation in relation to maximum swelling, which have been difficult to verify.

One species with a well-pronounced sexual swelling is the common chimpanzee. Because of its close relatedness to humans, chimpanzees have been used as a model for human reproduction for many years and thus many data exist on menstrual cycle characteristics. Collectively, these indicate a mean cycle length of about 36 days (Yerkes & Elder 1936; Young & Yerkes 1943; Tutin 1979; Wallis 1982) and an average duration of the maximum tumescence phase of about 10 days (Tutin 1979; Hasegawa & Hiraiwa-Hasegawa 1983). These studies, however, also report a considerable variation in maximum swelling duration, ranging from 2 to 17 days in captive housed females (Elder 1938; Nadler et al. 1985) and 7 to 19 days in those living in the wild (Tutin & McGinnis 1981; Hasegawa & Hiraiwa-Hasegawa 1983; Matsumoto-Oda & Oda 1998).

Thus, although perineal swellings in chimpanzees have been well characterized, the functional significance of this trait, particularly in terms of its value in signalling the female's fertile phase, remains unclear. On the one hand, studies in captive animals have yielded contradictory results on the relation between swelling stage and timing of ovulation, with some studies indicating a strong link (Graham et al. 1973; Steinetz et al. 1992), and others a weak one (Nadler et al. 1985). Furthermore, the relevance of data derived from individual cycles from relatively few animals living under laboratory conditions is questionable in terms of understanding the functional significance of swellings in natural social groups. On the other hand, extensive data on swelling characteristics exist for free-ranging chimpanzees, but information on underlying physiological parameters is not available. To test the validity of the different hypotheses on the reliability of swelling with respect to signalling ovulation, a combination of both parameters is required.

Our aim in this study was therefore to combine non-invasive hormone analysis for assessing female reproductive status with measurements of swelling changes to examine the temporal relation between sexual swelling and ovulation in free-ranging chimpanzees. Our specific objectives were: (1) to characterize the patterns of perineal swelling and describe their variability between and within females; (2) to determine the time of ovulation based on progestin measurements in urine samples collected in the wild; (3) to assess the variability of timing of ovulation within the period of maximum tumescence; and (4) to use these data to test the assumptions underlying the various hypotheses on the functional significance of perineal swelling in the common chimpanzee. Since in the absence of hormonal information, fieldworkers studying chimpanzees usually refer to the last day of maximum tumescence as the day of ovulation (based on the results for captive chimpanzees, Graham 1981), our final aim was to test whether this assumption is correct and, if not, to propose a more precise way of estimating the fertile period in wild chimpanzees.

METHODS

Study Animals and Study Site

We studied a group of wild West African chimpanzees inhabiting an evergreen forest in the Taï National Park, Côte d'Ivoire. Data were collected during three field periods (October 1998–April 1999, October 1999–May 2000, and December 2000–June 2001) on the 'South Group' of the Taï chimpanzee project (Herbinger et al. 2001; Vigilant et al. 2001). The group has been habituated since 1990, and demographic data for the group have been available since 1995. During the period of data collection, the study group comprised 51–53 individuals, including three adult males and 19–20 adult females, the rest being juveniles and infants. The animals were not provisioned with food, during either the habituation process or the study period.

Of the 20 adult females in the group, data were collected from 14 (42 cycles, 1–8 cycles/female). Three females were lactating throughout the study period and did not show any signs of swelling; three further females were not sufficiently well habituated to permit frequent sample collection. Of the 42 cycles, data are presented from 36 (12 females) in which frequency of urine sampling was sufficiently high (sampling gaps not more than

Table 1. Demographic data, reproductive history and number of cycles studied in Taï female chimpanzees

Female	Estimated age (years)*	Age of dependent infant* (years/months)	Parity†	Cycles analysed
Atra	17	3/6; 1/4	P/M	3
Duna	24	—	P/M‡	7
Eva	33	4/9	M	3
Isha	28	4/1	M	2
Kabisha	24	4/7	M	3
Mandy	34	5/0	M	2
Margot	24	4/6	M	3
Olivia	28	2/1	M	1
Sumatra	36	4/9	M	3
Tita	23	6/0	M	3
Yucca	30	4/6	M	2
Zora	44	4/6	M	4

*At beginning of sample collection.
†P: primiparous; M: multiparous.
‡At beginning of habituation phase female was seen with presumed adolescent daughter, but thereafter did not conceive despite showing regular swellings.

1 day during the periovulatory period) to allow reliable determination of the day of ovulation (Table 1).

Sample Collection and Scoring of Swelling

Regular urine samples were collected by T.D. and three field assistants. Directly after a chimpanzee had been observed urinating, the urine was collected by aspiration from the ground or vegetation using disposable plastic pipettes (Knott 1997). Only samples that were not contaminated with faeces were taken. Samples were transferred into 2-ml polypropylene tubes and upon return to camp (same day) were frozen at − 20°C until shipment to the laboratory. Sample collection from individual animals was timed to begin as soon as possible after the onset of perineal swelling until 5 days after the start of detumescence, to cover the presumed periovulatory period. For the cycles for which data are presented, samples were collected either daily or (occasionally) every second day. Although the majority of samples were collected before midday, in some cases the period of collection was extended to 1800 hours. Where samples could be collected twice a day from the same individual, there was no significant difference in hormone concentration between samples collected in the morning and in the afternoon (paired *t* test: pregnanediol glucuronide: $t_{10}=-0.145$, $P=0.89$; oestrone conjugates: $t_{10}=0.016$, $P=0.99$).

We recorded sexual skin swelling characteristics every morning by visual inspection of the perineal area. In some cases, nontarget females seen with maximum swellings in the morning might have started detumescence later the same day. On these occasions, onset of detumescence on that day would have gone unnoticed and would have been first recorded as on the following day. To avoid this element of imprecision, data throughout this paper refer to the last day of maximum tumescence. Since a distance of at least 5 m was maintained between observer and subject (to reduce disturbance and risk of disease transmission), we used Furuichi's (1987) method, which is based on degree of wrinkling, as the main parameter for ranking swelling stage, and not labial occlusion (Dahl et al. 1991). Accordingly, we defined three major stages of tumescence: (1) no swelling: minimal size and maximal degree of wrinkling; (2) partial swelling: relative increase/decrease in size and loss/appearance of wrinkles compared with stage 1 or 3; (3) maximum swelling: maximum size with no wrinkles and tight appearance, that is, the period of maximum turgidity. Using this approach, we obtained a high degree of objectivity and interanimal comparability in rating perineal swelling changes (see also Heistermann et al. 1996; Reichert et al. 2002).

Sample Preparation and Hormone Assays

We analysed urine samples for immunoreactive oestrone conjugates (E1C) and pregnanediol glucuronide (PdG) (major urinary metabolites of oestradiol and progesterone known accurately to reflect ovarian function in the chimpanzee, e.g. McArthur et al. 1981; Steinetz et al. 1992), using enzyme immunoassay procedures (Heistermann et al. 1996). In brief, urine samples were diluted in assay buffer (0.04 M PBS, pH 7.2, dilutions 1:10–1:1200 for E1C and 1:10–1:6000 for PdG, depending on the reproductive status) and duplicate 50-μl aliquots taken to assay along with 50-μl aliquots of reference standard in doubling dilutions over the ranges of 15.6–1250 pg/well for E1C and 12.5–1600 pg/well for PdG. The sensitivities of the assays at 90% binding were 28 pg for E1C and 12.5 pg for PdG. Serial dilutions of urine samples of the follicular and luteal phase gave displacement curves parallel to those obtained with the appropriate standards. Intra- and interassay coefficients of variation,

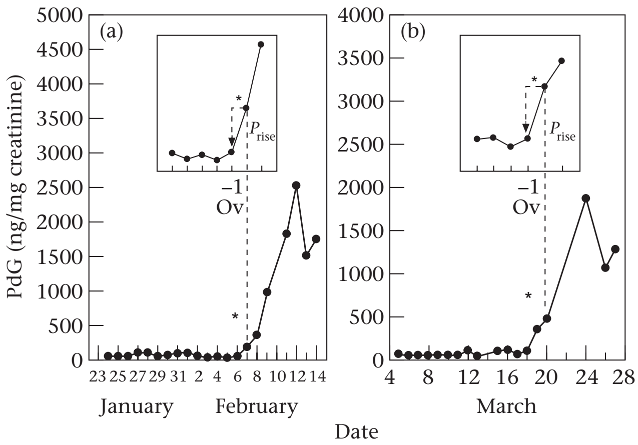

Figure 1. Urinary immunoreactive pregnanediol glucuronide (PdG) profiles throughout individual ovarian cycles in two female chimpanzees in 2001. (a) Kabisha and (b) Mandy. The timing of ovulation (Ov) is deduced by identifying the day on which urinary PdG levels increase above a defined threshold value (P_{rise}, indicated by asterisks) and correcting for a time lag of 1 day (inserts; see Methods).

calculated from replicate determinations of high- and low-value quality controls, gave values between 5.6 and 10.4%, and 6.5 and 13.2%, respectively.

To compensate for variations in the volume and concentration of the voided urine, we measured creatinine (Cr) concentrations in each urine sample (Bahr et al. 2000) and we express all hormone values as mass/mg creatinine. In four of 36 cycles (11.1%) creatinine concentrations could not be determined for all samples; in these cases we corrected for variation in urine concentration by calculating the PdG/E1C and E1C/PdG ratios (Baird et al. 1991). Hormone profiles in which both creatinine indexing and progestin/oestrogen ratio were used were highly correlated (Pearson correlation: $r_{492}=0.89$, $t=44.18$, $P<0.001$), and provided similar results in terms of timing of the postovulatory progestin rise (see below); the average difference ± SD was 0.10 ± 0.72 days.

Interpretation of Hormone Profiles

We used patterns of urinary hormones to determine the occurrence of ovulatory cycles and the timing of ovulation and conception. Since a clear preovulatory oestrogen peak was not discernible in all cycles, we based timing of ovulation on PdG excretion profiles. In this respect, we used the sustained rise in urinary PdG levels above a defined threshold value (two standard deviations above the mean of the preceding three to five baseline values, Jeffcoate 1983) to indicate the onset of the postovulatory (luteal) phase of each ovarian cycle (Fig. 1; see also Carosi et al. 1999; Heistermann et al. 2001). Based on the finding that the PdG rise in urine occurs 1–3 days after the serum luteinizing hormone peak (Munro et al. 1991; Steinetz et al. 1992), we defined the day of ovulation as the day before the day of the postovulatory PdG rise. This may, however, include an error of 1 day. We also used the defined PdG rise to calculate the length of the ovarian cycle and to assess the temporal relation between onset and end of maximum perineal swelling and ovulation. Cycle length was defined as the time between successive PdG rises in consecutive cycles. Since in most cases it was not possible to detect menstruation, and urine samples were not collected during the entire cycle, data on the lengths of the follicular and luteal phases are not available.

Ovulation and Fertility

We estimated the probability of ovulation for each day of the maximum tumescence period (*T*) by dividing the number of observed ovulations on each day of maximum tumescence (counted from the beginning) by the overall number of ovulatory cycles examined. This is represented by the formula:

$$P(T=t)=\frac{n_t}{n},\ t=1,2,3\ldots,$$

where *t* is a specific day within the maximum tumescence period, n_t is the number of cycles in which ovulation occurred on day *t*, and *n* is the overall number of ovulatory cycles.

The fertile phase is a function of the fertile life spans of the ovulated egg and ejaculated sperm within the female's reproductive tract. Although the life span of the human ovum is generally agreed to be not more than 24 h (France 1981; Gomendio & Roldan 1993a, b), the fertile life span of ejaculated sperm is not clear. While some authors calculate this to be 6 days and more (Baker & Bellis 1995), others use a more conservative estimate of 33.6 h (Gomendio et al. 1998). Based on the data of Wilcox et al. (1995) showing that only 6% of human pregnancies result from sperm older than 3 days, we defined the fertile phase as the day of ovulation and the 3 preceding days.

To calculate a day-specific probability of fertility we took the fertile phase for each cycle and assumed as a first approximation that probability of fertilization remains the same for all 4 days. We attributed to each of the 4 days of the fertile phase of a particular cycle a probability of fertilization of 1, whereas outside this phase the probability is zero. To estimate the average likelihood of fertility on any given day of the maximum tumescence period (*f*), we added the scores of probability of ovulation for day *f* and the following 3 days. This probability is given by:

$$P(X(f)=1)=\sum_{t=f}^{f+3}P(T=t),$$

where $\{X(f)=1\}$ is the event of a fertile day and $P(T=t)$ from above.

Data Analysis

Because of missing samples and observations, not all cycles could be included in all analyses. Composite hormone profiles (see Fig. 3 in the Results) included only

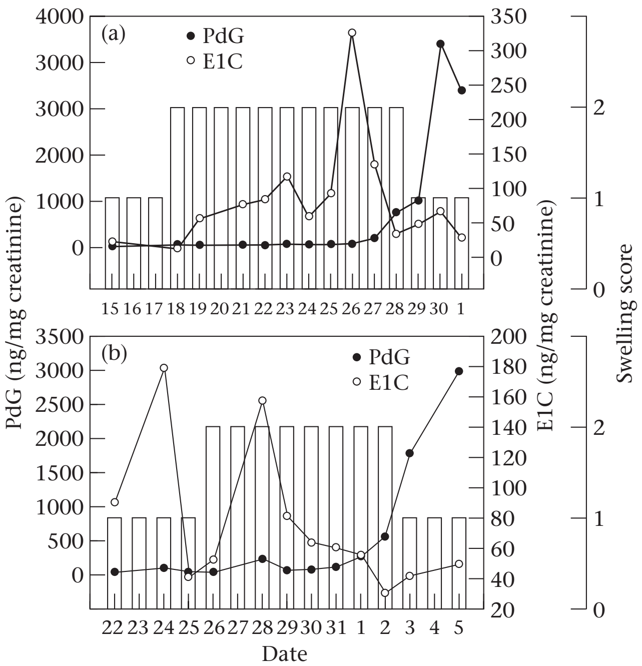

Figure 2. Profiles of immunoreactive urinary oestrone conjugates (E1C) and pregnanediol glucuronide (PdG) in relation to changes in perineal swelling size throughout individual nonconception cycles in two female chimpanzees, (a) Margot November 1999 and (b) Duna March/April 2001.

those cycles where hormone concentrations could be indexed by creatinine (*N*=32). Data shown in Fig. 5 in the Results also include cycles where PdG/E1C ratios were used to time ovulation and in which both the beginning and the end of maximum tumescence were known with a maximum error of 1 day. In three out of 33 cycles, maximum swelling duration could be determined only with an error margin of 1 day (see Fig. 4 in the Results). In these cases, the shorter estimate for maximum swelling duration was taken for analysis, thus potentially representing an underestimation of 1 day.

Data were checked for equal variances and normal distribution. Before calculating the day of the PdG rise, we log transformed hormonal values to meet the assumptions of parametric tests. Hypotheses were tested with either a *t* test for dependent samples or one-way ANOVAs (Zar 1999). All statistical tests are two tailed.

RESULTS

Figure 2 shows representative profiles of immunoreactive urinary E1C and PdG in relation to the pattern of perineal swelling during two individual nonconception cycles in two females. Both profiles show a well-defined pattern of PdG excretion characterized by consistently low levels during the follicular phase and markedly elevated levels in the presumed luteal phase. While this general pattern of PdG excretion was similar in all cycles, profiles of E1C were more variable between both cycles and females (Fig. 2). Nevertheless, a gradual increase in E1C levels during the maximum swelling period, reaching a discernible peak 1–3 days before the defined postovulatory PdG rise was seen in 74% of cycles (Fig. 2a).

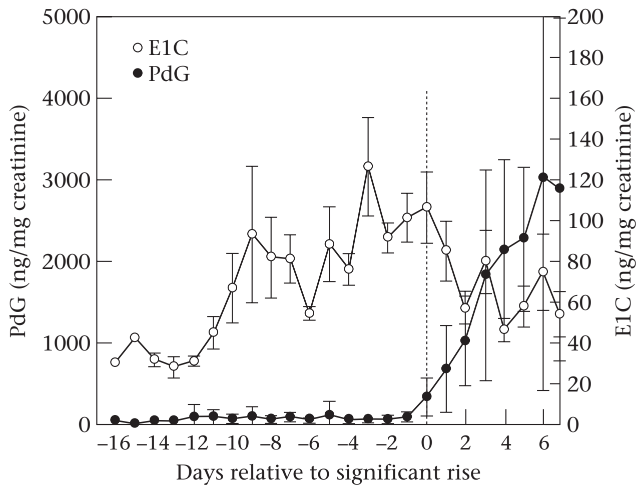

Figure 3. Composite profiles of immunoreactive urinary oestrone conjugates (E1C) and pregnanediol glucuronide (PdG) derived from 32 ovarian cycles of 11 females. Values are presented as means±SD. The data are aligned to the day of the defined postovulatory rise in PdG, indicating the onset of the luteal phase (day 0, vertical line).

Figure 3 shows the composite profiles of urinary oestrogen and progestin excretion calculated from 32 cycles (11 females). Mean E1C levels gradually increased from a baseline of 20–30 ng/mg Cr on days −11 to −14 (early follicular phase) to an initial small peak on day −9 followed by a further rise to maximum levels of 120–140 ng/mg Cr 3 days before the PdG rise. Mean E1C levels during the period of maximum tumescence were significantly higher than those during the nontumescent period of the follicular phase (paired *t* test: $t_{13}=-4.9$, $P<0.001$). PdG concentrations were consistently low (50–100 ng/mg Cr) during the phase of rising oestrogens, but increased rapidly after the oestrogen peak to reach levels of 2500–3000 ng/mg Cr around day +7. Based on the interval between successive PdG rises (16 cycles, 10 females), mean cycle length was 40.3 ± 5.7 days (range 34–54 days).

The maximum swelling period lasted 6–18 days ($\bar{X}\pm\text{SD}=10.9\pm3.2$ days, *N*=33; Fig. 4). Maximum swelling duration varied between individuals (ANOVA: $F_{11,21}=4.183$, $P=0.002$) and between cycles of individual females (Fig. 5). There was no difference in maximum swelling duration between conception and nonconception cycles (paired *t* test: $t_5=-0.25$, $P=0.813$). Furthermore, there was no consistent relation between female age and maximum swelling duration (Pearson correlation: $r_{10}=0.021$, $P=0.949$).

Figure 5 shows the period of maximum tumescence in relation to the day of ovulation and fertile phase for 33 individual cycles. In all cases, ovulation occurred within the period of maximum swelling and, with one exception (cycle of Zora in January 2001), during the second half of this period. Nevertheless, timing of ovulation in relation to both the onset and end of maximum swelling varied

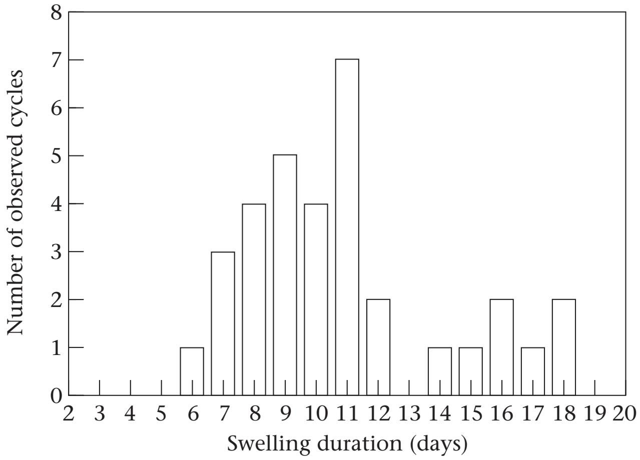

Figure 4. Frequency distribution of maximum swelling duration (cycles N=33; females N=12)

considerably between females and cycles. Time from onset of maximum swelling to ovulation was 1–13 days ($\bar{X} \pm SD = 7.3 \pm 2.4$ days, N=33). Maximum swelling duration prior to ovulation differed significantly between females (ANOVA: $F_{9,21}=4.323$, $P=0.003$), but not between conception and nonconception cycles (paired t test: $t_5=-0.131$, $P=0.901$). Time from ovulation to the last day of maximum tumescence was 0–6 days ($\bar{X} \pm SD = 2.5 \pm 1.4$ days, N=33). There was no difference in the length of the postovulatory maximum swelling phase either within females (ANOVA: $F_{9,21}=2.152$, $P=0.071$) or between conception and nonconception cycles (paired t test: $t_5=0.504$, $P=0.636$).

There was a well-defined peak in ovulation probability within the period of maximum swelling, with the highest probability of ovulation occurring on day 7 (0.27; Fig. 6a). The combined probability of ovulation occurring within the 3-day period of days 7–9 was 0.57. Nevertheless, ovulation could occur anywhere from day 2 to day 14. Probability of fertility was highest (0.64) on days 6 and 7 of maximum tumescence (Fig. 6a). Fertilization was possible over a period of 15 days from 2 days before to day 13 of maximum tumescence. If cycles were adjusted to the last day of maximum tumescence and this day was taken as day zero, probability of ovulation was highest on days −1 and −2 (0.25 each; Fig. 6b), although ovulation could occur over a period of 7 days from day −6 to day 0. Probability of fertility was highest between days −5 and −2 (Fig. 6b).

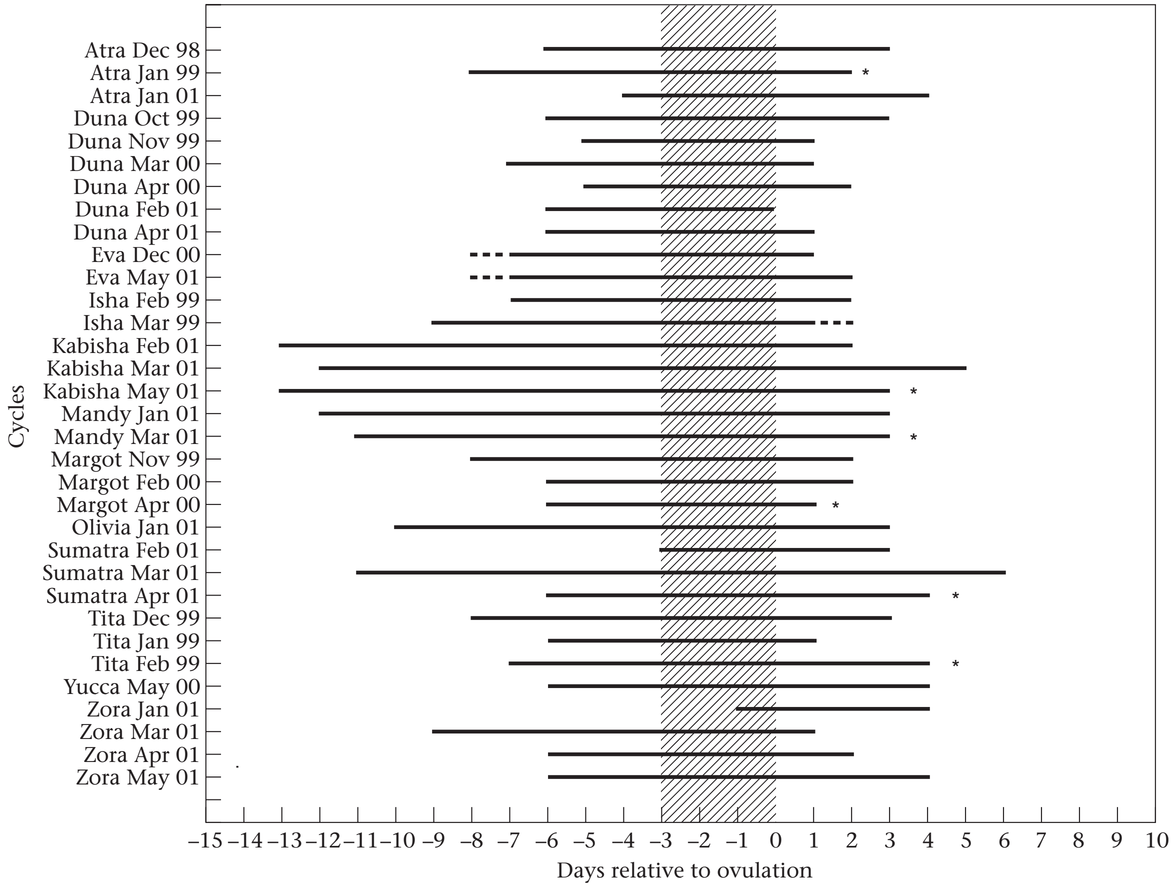

Figure 5. Duration and timing of maximum swelling relative to the day of ovulation (day 0). Horizontal bars represent the period of maximum swelling of the various female cycles (names and dates are shown on the Y axis). – – –: Cycles where the beginning or end of the maximum swelling period could be only detected with an error of 1 day because of missing observational data; *conception cycles. The shaded area indicates the fertile phase.

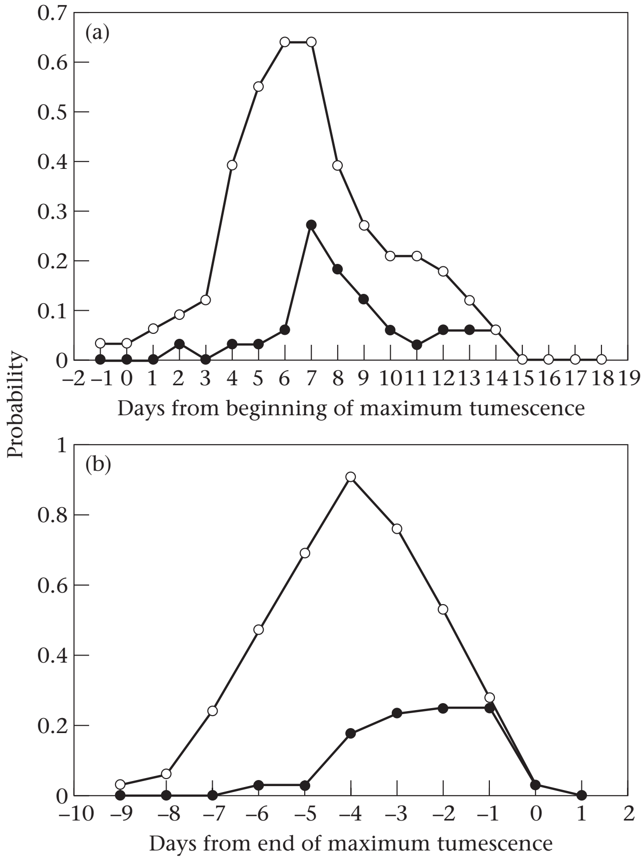

Figure 6. Probability of ovulation (○) and fertility (●) relative to (a) the first day of maximum tumescence (see Methods) and (b) the last day of maximum tumescence (*N*=34).

DISCUSSION

By using noninvasive endocrine methodologies to examine the temporal relation between sex skin swelling and timing of ovulation in wild chimpanzees, we have shown that perineal swellings in chimpanzees do not provide precise information about the time of ovulation. On the other hand, the skew in the distribution of ovulation around days 7–9 of the maximum swelling period shows that ovulation does not occur randomly within this period and that therefore sex skin swellings in the common chimpanzee provide more than general information on the reproductive status of the female. On a more practical level, our results indicate that in the vast majority of cycles ovulation took place earlier than on the last day of maximum tumescence, as normally assumed by field researchers when approximating the periovulatory period. The results therefore not only help improve our understanding of the function of sex skin swellings in chimpanzees, but also have implications for behavioural studies relying on sex skin swelling data to interpret the reproductive significance of mating events.

The profiles of E1C and PdG excretion in our study females are similar in terms of both absolute values and relative changes to those reported for captive-housed animals (Graham et al. 1972; Dahl et al. 1991; Steinetz et al. 1992), indicating that the measurement of these urinary hormones also provides reliable information on ovarian function in wild chimpanzees. Although the average cycle length of the study females (40 days) was slightly longer than the 34–36-day cycles reported for captive chimpanzees (Savage-Rumbaugh & Wilkerson 1978; Nadler et al. 1985; Dahl et al. 1991; Wallis 1997) and in a wild East African population at Gombe (Tutin & McGinnis 1981), individual cycle lengths in our study were well within the ranges reported by others. Since our period of data collection for most females included the period immediately after lactational amenorrhoea, it is possible that the slightly longer cycles recorded for the free-ranging females in Taï might have been influenced by recent lactation, as has also been suggested for captive bonobos, *Pan paniscus* (Heistermann et al. 1996).

The duration of maximum swelling for the Taï chimpanzees is similar to those reported for captive populations (e.g. Yerkes & Elder 1936; Dahl et al. 1991) and other populations of wild chimpanzees at Gombe (9.6 days, range 7–17 days: Tutin & McGinnis 1981) and Mahale (12.5 days, range 8–19 days: Hasegawa & Hiraiwa-Hasegawa 1983; 11.3 days, range 5–14 days: Matsumoto-Oda 1999) in Tanzania. The source of the pronounced individual variation in maximum swelling duration is not clear, since studies examining factors influencing sex skin swelling patterns have not been systematically carried out. We tested age and the influence of conception and Wallis (1997) tested parity but none of these factors was related to the length of the maximum swelling phase. Owing to the limited number of observed cycles per female, we could not test statistically whether at least part of the within-subject variation in maximum swelling duration was related to the number of cycles a female had experienced since the end of lactational anovulation before conception.

The finding that ovulation almost always happened within the second half of the maximum swelling phase compares well with data on captive animals in which the preovulatory luteinizing hormone peak (McArthur et al. 1981; Nadler et al. 1985) or ovulation (Graham et al. 1973), or both, are generally associated with the late stages of the maximum swelling period. Thus, ovulation in chimpanzees seems to be linked more tightly to sexual swelling patterns than in captive bonobos, in which about one-third of ovulations are reported to occur outside the phase of maximum swelling and occasionally even up to 10 days after the onset of detumescence (Reichert et al. 2002).

Taking into account the variability in overall maximum swelling duration (6–18 days), as well as the variability of preovulatory maximum swelling duration (2–13 days), it is clear that swelling patterns alone do not provide precise information about the timing of ovulation. Thus, our findings in wild female Taï chimpanzees do not support the obvious-ovulation hypothesis for the function of sexual swellings (Hamilton 1984). However, ovulation was also not completely randomly distributed throughout the period of maximum tumescence either, as would be required by the many males hypothesis. We therefore conclude that this hypothesis, at least in as far as it predicts that sexual swellings function as a method of paternity confusion, cannot explain swelling patterns in Taï female chimpanzees. On the other hand, our finding that sexual swellings indicate a certain probability of ovulation supports the predictions of the graded-signal hypothesis (Nunn 1999). By extending the duration of maximum swelling, a female effectively makes it difficult and costly for the dominant (or any other) male to monopolize her for the whole period during which ovulation might occur. Since swelling patterns indicate a certain probability of ovulation, they should enable the dominant male to monopolize the female during days when ovulation is most likely to occur, but allow her sufficient freedom to mate with other males during periods when ovulation is less likely. The extent to which Taï chimpanzees allocate their mating behaviour in relation to swelling patterns and the timing of ovulation is unclear, since data on patterns of male monopolization and matings in relation to the female reproductive status are not yet available.

Comparable data relating the onset of maximum tumescence to timing of ovulation in other primates species are relatively rare. Using data on bonobos (Reichert et al. 2002) and Tonkean macaques, *Macaca tonkeana* (Aujard et al. 1998), and the same methods as in the present study, we have estimated a ‘minimum 50% ovulation probability window’ for these two species. While this window was 5 days for Tonkean macaques and therefore similar to the 3-day window reported here for chimpanzees, it was 10 days for bonobos. Thus, to achieve a similar probability of paternity, a bonobo male would have to mate-guard and monopolize a female more than three times longer than a chimpanzee male. Sexual swelling patterns in bonobos might thus fit more closely to the predictions of the many males hypothesis, than do those of chimpanzees. The fact that possessive mating and consortships are frequently observed in chimpanzees (Tutin & McGinnis 1981; Hasegawa & Hiraiwa-Hasegawa 1983) but are absent in bonobos (Takahata et al. 1999) further supports this line of reasoning. Since species differences are to be expected, further comparative data will be essential to our understanding of the functional significance of sexual swellings in primates. Furthermore, whether males do indeed use the information content of sexual swellings and adjust their reproductive strategies accordingly can be shown only by the inclusion of behavioural data in the analysis.

In addition to their function in influencing mating outcome, perineal swellings could also provide information on female quality in general as proposed by the so-called reliable-quality indicator hypothesis (Pagel 1994). Domb & Pagel (2001) showed that female lifetime reproductive success is positively correlated with swelling size in baboons, *Papio cynocephalus anubis*, and that males compete more over females with bigger swellings. Although the validity of the data analysis used in that study has been questioned (Zinner et al. 2002), the reliable-quality indicator hypothesis nevertheless remains a candidate to explain aspects of the evolution and function of female sexual swellings in chimpanzees.

Many studies on reproductive strategies of chimpanzees have assumed that ovulation takes place on the last day of maximum tumescence (Tutin & McGinnis 1981; Hasegawa & Hiraiwa-Hasegawa 1983; Matsumoto-Oda 1999). Our results show that although ovulation took place most frequently on days -1 to -3 relative to the last day of maximum tumescence (day 0), the overall range in timing was 7 days and in only one cycle did ovulation take place on the last day of the maximum swelling phase. We therefore recommend that researchers studying chimpanzee reproductive strategies include endocrine markers for ovulation in individual cycles in their data collection. If this is not feasible one should use an earlier window from days -2 to -5 to indicate the periovulatory period.

Although the assumptions underlying the estimation of the probability of fertility still need to be refined with more data on age-dependent sperm fertilization capacity, a comparison with the distribution of probability of ovulation (Fig. 6) is of considerable heuristic value. The distribution of fertility has a less pronounced peak but a broader base which is slightly shifted to earlier days. From a male’s point of view, this means that if there are competitors for fertilization, copulations on days before the day of highest probability of ovulation gain, and those on the following days lose, in value. For monopolization of females to be effective, it has to be applied over a period of several days. Furthermore, if sperm from copulations on days considerably earlier than ovulation has a high chance of fertilization, then any signal that is close in time to ovulation loses in importance in favour of earlier signals, even if these signals are less tightly linked to ovulation. Against the background of the evolution of sexual swellings, this means that as soon as the number of male competitors within a group rose above zero, males became inclined to react to more and more distant signals of future ovulation at the expense of reliability of that signal. Females in their turn could have profited from this need by offering more temporally removed and less reliable signals of ovulation and in this way meet the demands of their own reproductive strategies. Differences in variation of maximum swelling duration and the timing of ovulation within and around this period between chimpanzees and bonobos might therefore just mark a different stage in the arms race of intra- and intersexual competition.

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