

Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees

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Abstract

Conspicuous swellings of the perineal skin can be observed in females of many catharrine primate species particularly during the middle stages of the ovarian cycle. The functional significance of this trait remains poorly understood. Recently, two hypotheses, the “reliable indicator” hypothesis and the “graded signal” hypothesis that take into account not only the pattern but also the exaggerated size of sexual swellings, have gained attention. Here we test several predictions made by these hypotheses by combining (i) direct size measures (from video captures) of female sexual swellings with (ii) urinary hormone data to indicate timing of ovulation through enzyme immunoassay measurements of estrone conjugates and pregnanediol glucuronide (PdG) and (iii) behavioral observations of male mating efforts throughout 36 ovulatory cycles in 12 wild chimpanzees. We are able to show that (i) even within the traditionally defined maximum swelling period, further slight increases in swelling size indicate approaching ovulation, and (ii) that male mating interest changes according to the changes in swelling size. Furthermore, absolute swelling size during the periovulatory period increases and the alpha male associates more with females as the number of cycles to conception decreases. Finally, when having the choice between several “maximally” tumescent females, the alpha male prefers the female that is in the fertile phase of her cycle rather than that with the biggest swelling at that time. Thus, most of our findings are in line with the predictions of the graded signal hypothesis while none of them would support the reliable indicator hypothesis. © 2004 Elsevier Inc. All rights reserved.

Keywords: Sexual swelling; Sexual selection; Chimpanzee; Male mate choice; Ovulation; Estrogen; Progesterone

Introduction

Sexual selection has led to the evolution of a variety of conspicuous secondary sex traits in numerous animal species (Andersson, 1994; Darwin, 1871). Conspicuous swellings of the perineal skin found around the time of ovulation in females of many old world primate are considered to be a sexually selected character (Darwin, 1871). Changes in swelling of female sexual skin reflect changes in estrogen and progesterone secretion during the menstrual cycle (Dixon, 1983), and sexual swellings increase female attractiveness and stimulate male sexual arousal (Girolami and Bielert, 1987).

Although there is consensus that sexual swellings have evolved in the context of sexual selection, disagreement exists on their functional significance, which is reflected in the existence of a number of hypotheses (for a review, see Stallmann and Froehlich, 2000; Zinner et al., 2004). In recent years, two new hypotheses on the functional significance of sexual swellings, the “reliable indicator” hypothesis (Pagel, 1994) and the graded signal hypothesis (Nunn, 1999), that take into account the exaggerated size of sexual swellings have gained increasing attention. The “reliable indicator” hypothesis (Pagel, 1994) proposes that in multimale–multifemale primate groups, females compete with each other for matings with high-quality males while males are choosy in the selection of their mating partners. In this context, the size of sexual swellings honestly advertises female fitness, enabling her to attract the best males to mate with and thereby maximize the genetic quality of her offspring. One major prediction that results from this hypothesis is that males, having the choice between more than one female at a given

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time, should prefer the one with the biggest swelling. Results of a study on olive baboons at Gombe (Domb and Pagel, 2001) seem to support this prediction since males competed more for females with bigger swellings and vertical swelling length was positively correlated with female reproductive fitness. However, the validity of the data analysis used in this study has been recently questioned (Zinner et al., 2002).

In addition to signaling overall female quality as proposed in Pagel's (1994) reliable indicator hypothesis, it has also been suggested that swelling size could signal cycle-to-cycle variability in the probability of conception (Zinner et al., 2002). Support for this idea comes from a recent study on captive chimpanzees, where Emery and Whitten (2003) found that cycle quality as indicated by patterns of ovarian hormones correlates with swelling size. Furthermore, in chacma baboons, Weingrill et al. (2003) found that older males with a long tenure, and who have known individual females for a long time, consorted females more often in their conceptive cycle compared to their nearest nonconceptive cycle. If cyclic variation in sexual swelling size indeed signals variability in probability of conception, several predictions can be postulated. First, sexual swelling size should become bigger from cycle to cycle, as the number of cycles to conception decreases. Second, reproductively relevant hormone levels should become higher, as the number of cycles to conception decreases. And third, males should increase their mating interest as the number of cycles to conception decreases.

The second main hypothesis, the graded signal hypothesis (Nunn, 1999), proposes that changes in sexual swelling size indicate the probability of ovulation. Dominant males could thereby monopolize a female during the time when probability of fertility is highest, while less dominant males could still achieve copulations during periods of lower (but nonzero) probability of fertility. This enables females to balance the benefits of confusing paternity to reduce the risk of infanticide on the one hand and to bias paternity towards the dominant male to increase paternal care and the probability of obtaining good genes for their offspring on the other hand (Nunn, 1999). According to this hypothesis therefore, sexual selection would work through intersexual conflict over the control of reproduction so that male manipulation efforts resulting in reduced female mate choice (such as monopolization, sexual harassment, and infanticide) are countered by females through the evolution of traits that enables them to resist these manipulations (Holland and Rice, 1998, 1999). Several predictions result from this hypothesis. First, sexual swellings should change in size over the course of the cycle and should be biggest during the time when fertilization is possible. Second, if swelling size indeed indicates the probability of ovulation, the dominant male should try to monopolize the female at times when the swelling is biggest, while other males should place their mating efforts around the period of high fertilization probability.

One species, in which females exhibit prominent sexual swellings, is the common chimpanzee (*Pan troglodytes*).

Chimpanzees live in large multimale–multifemale communities (Boesch, 1996; Goodall, 1986; Nishida, 1979). Although competition among males over parous females has been frequently observed, females generally mate with several males during a swelling period (Boesch and Boesch-Achermann, 2000; Hasegawa and Hiraiwa-Hasegawa, 1983; Goodall, 1986; Matsumoto-Oda, 1999; Watts, 1998). Females have a mean cycle length of about 36 days (Deschner et al., 2003; Wallis, 1982; Yerkes and Elder, 1936) and an average duration of the maximum tumescence phase of the swelling of about 10 days (Deschner et al., 2003; Matsumoto-Oda and Oda, 1998; Tutin, 1979). A recent study on captive chimpanzees showed that the size of sexual swelling is correlated to several sex hormone parameters, which suggests that it indicates probability of conception and may convey information to competing males about the fecundity of a potential mate (Emery and Whitten, 2003). Since conceptions were prevented in the study of Emery and Whitten (2003), and moreover data on male–male competition and male mate choice in relation to female sexual swelling size and timing of ovulation are not available, it remains to be tested how males respond to differences in swelling size and if they prefer females with bigger swellings as mating partners. Previous studies on male sexual behavior in wild chimpanzees showed that male interest in females and male competition over access to females increases towards the end of the maximum swelling phase (Hasegawa and Hiraiwa-Hasegawa, 1990; Tutin and McGinnis, 1981) when probability of ovulation is highest (Deschner et al., 2003). However, since no size measurements of the swelling have been performed, and moreover no hormonal data on timing of the fertile phase were collected in these studies, it remains unclear whether males respond to subtle size changes in female swelling and/or to changes in female reproductive status.

The overall aim of this study therefore is to clarify the temporal relationship between changes in swelling size during the maximum tumescence period and the fertile period and male mating efforts in a naturally reproducing group of free-ranging chimpanzees. By doing so, we also test the predictions on the function of sexual swellings set by the reliable indicator and the graded signal hypothesis. Specifically, by incorporating three data sets, size of sexual swelling, timing of ovulation, and male mating effort into our analysis, we want to explore the following questions:

Do swellings change in size within the period of maximum tumescence, and if so do those changes correspond to the fertile period? Do males adjust their mating efforts according to changes in maximum sexual swelling size and/or timing of the female's fertile period? Does average swelling size change among cycles of an individual female with approaching conception? Does male preference for females rise as the number of cycles to conception decreases? Do males prefer females with bigger swellings, when they can choose between more than one maximally swollen female at the same time?

Material and methods

Animals and study site

The study was conducted on a group of wild West African chimpanzees, *Pan troglodytes verus*, inhabiting an evergreen forest in the Taï National Park, Côte d'Ivoire. Endocrinological data and data on swelling size and duration were collected during three field research periods (October 1998 to April 1999, October 1999 to May 2000, and December 2000 to June 2001) on the "South group" of the Taï chimpanzee project (Deschner et al., 2003; Herbinger et al., 2001; Vigilant et al., 2001). In addition, during the field research in 1999/2000 and 2000/2001, behavioral data were collected from the group. During the period of data collection, the study group composed 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. Out of the 20 adult females in the group, data were collected from 14 (42 cycles, 1–8 cycles per 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 to allow reliable determination of the day of ovulation (sampling gaps not more than 1 day during the periovulatory period; Table 1).

Table 1
Demographic data, reproductive history, and number of cycles studied in Taï chimpanzee females

| Female | Estimated age (years) ^a | Age of dependent infant ^b (years/months) | Parity ^b | Cycles analyzed (swelling size) | Cycles analyzed (behavior) |
|---------|------------------------------------|---|--------------------------|---------------------------------|----------------------------|
| Atra | 17 | 3/6; 1/4 | prim/multip | 2 | 1 |
| Coco | 21 | 5/4 | multiparous | 1 | 0 |
| Duna | 24 | – | prim/multip ^c | 6 | 5 |
| Eva | 33 | 4/9 | multiparous | 2 | 2 |
| Isha | 28 | 4/1 | multiparous | 2 | 0 |
| Kabisha | 24 | 4/7 | multiparous | 3 | 3 |
| Mandy | 34 | 5/0 | multiparous | 2 | 2 |
| Margot | 24 | 4/6 | multiparous | 3 | 3 |
| Olivia | 28 | 2/1 | multiparous | 1 | 1 |
| Sumatra | 36 | 4/9 | multiparous | 2 | 3 |
| Tita | 23 | 6/0 | multiparous | 2 | 0 |
| Yucca | 30 | 4/6 | multiparous | 0 | 2 |
| Zora | 44 | 4/6 | multiparous | 3 | 4 |

^a At the beginning of sample collection.

^b Prim = primiparous; multp = multiparous.

^c At the beginning of habituation phase, female was seen with presumed adolescent daughter but thereafter did not conceive despite showing regular swellings.

Behavioral observations

Behavioral data on adult males and maximally swollen females were collected by the first author, and two field assistants, Camille Bolé and Nicaise Oulaï Daurid, on 26 cycles from 10 of the 12 females (Table 1). The study group was followed from dawn to dusk and focus females were followed for a complete day using the focal animal sampling method (Altmann, 1974). In some cases, the group could not be found immediately after leaving the nests or a focus animal was lost during the day. Therefore, only data of days when the animal was observed for more than 4 h were used in the analysis. A total of 180 focal days of 10 females resulting in 1765 h of observation and 19 focal days of the alpha male resulting in 198 h of observation were used in the analysis. Three behavioral categories were analyzed to determine male interest into maximal tumescent females: (i) association time with the female, (ii) frequency of copulations, and (iii) interventions into other males' copulation attempts. Since it is known that male chimpanzees compete over females and try to prevent others from access to females, the observed mating patterns might not represent true male interest. According to the priority of access model (Altmann, 1962), we considered the alpha male to have the highest degree of freedom in his mating decisions while freedom of choice of other males might be increasingly limited with decreasing rank. Therefore, for most tests of male interest, we limited the analysis to the alpha male behavior. Association rate was defined as the time a male was seen in proximity (visual contact) with the focus female on a given day divided by the overall observation time of the focus female of this day. This equals the index of association proposed by Nishida (1968) where $I = Nab / (Na + Nb + Nab)$, with Nab being the time the two individuals were seen together, Na and Nb being the time where one individual was seen without the other. Since for any single analysis in this study only focal data of one sex was used, Nb = 0 and Na and Nab adds up to the overall observation time of the focus animal leading to $I = Nab / \text{overall observation time}$. A copulation was defined as a heterosexual mating that included at least one intromission, and successive intromissions occurring within 15 min were considered to belong to the same copulation (Hasegawa and Hiraiwa-Hasegawa, 1983; Matsumoto-Oda, 1999; Tutin, 1979).

Intervention rate was defined as the number of copulations of other males than the alpha male that were interrupted by interventions of the alpha male by either interposing himself between the female and other males, displaying at the female or other males, or charging at other males divided by the overall number of copulations with all males including the alpha male of the focus female on a given day. For determining male mate preferences between females, we used focal data of the alpha male and calculated copulation rates for every female with a maximum tumescent swelling when there were more than one female with a maximum tumescent swelling in the group.

Average interobserver reliability for these three categories was 95.2% for association time with the female, 97.4% for copulations with adult males, and 72.2% for interventions into other males' copulation attempts.

Collection of urine samples, hormone analysis, and assessment of the fertile phase

To determine a female's cycle stage and the time of ovulation we collected regular urine samples, which were analyzed by enzyme immunoassay for immunoreactive estrone conjugates (E1C) and pregnanediol glucuronide (PdG), as previously validated and described in detail by Deschner et al. (2003). The E1C EIA used an antibody raised in a rabbit against estrone-3-glucuronide-BSA. With estrone-3-glucuronide as a standard (100%), the antiserum showed the following cross-reactivities: estrone 71%, estrone-3-sulfate 17%, estradiol-17 β 0.9%, estradiol-3-sulfate 0.2%, and <0.1% for all other steroids tested. In the PdG assay, an antiserum raised in a rabbit against pregnanediol-3-glucuronide-BSA was used. Relative to PdG (100%), the antiserum showed the following cross-reactivities: 20 α -hydroxyprogesterone 32%, pregnanediol 22%, 5 α -pregnane-20 α -ol-3-one 14%, progesterone 0.5%, and <0.1% for all other steroids tested. The sensitivities of the assays determined at 90% binding were 28 pg/well for E1C and 12.5 pg/well for PdG. Intra- and interassay coefficients of variation, calculated from replicate determinations of high- and low-value quality controls measured within and between assays, gave values between 5.6% and 10.4%, and 6.5% and 13.2%, respectively.

Based on the defined postovulatory rise in PdG levels, we determined for each cycle the presumed day of ovulation as the day preceding the day of the PdG increase (Deschner et al., 2003). Based on human data on survival time of the ovum and sperm, the fertile period (POP) was defined as the day of ovulation plus the three preceding days as described in Deschner et al. (2003). In addition, a prefertile period (pre-POP) and postfertile period (post-POP) were defined as

the period of maximum tumescence preceding and following POP, respectively (Fig. 1).

Scoring of perineal swelling and measurements of swelling size

Sexual skin swelling characteristics were recorded every morning by visual inspection of the perineal area. Relative swelling size was rated on a scale of 1–3 as described in Deschner et al. (2003), with the period of maximum tumescence (MS) covering all days on which a score of 3 was recorded. In addition, the absolute size of the swelling was repeatedly measured during the maximum tumescent phase. For this, video captures were taken of fully swollen females, both from the side and the back. Size of swelling was defined by the area of hairless or pink tissue. For images from the back, the considered area of the swelling was taken as all the pink colored tissue; while for images from the side, the considered area of the swelling was taken as all swollen hairless tissue (Fig. 2). Lengths and area were measured in dimensionless units. Since the video images give only a relative size of the swelling, we had to calibrate our units. For calibration of the swelling size, we used the lengths of the hind leg of the respective females. Its length was determined from the sole to the upper limit of the ischial callosity by taking video images while a female stood straight legged and still. Once the female moved off, a meter stick was placed at the location of the leg by an assistant and then filmed from the same location that was used to film the leg. Leg length was then measured dimensionless and calibrated by using the meter stick, with the help of the software program "didger" (Golden Software, Inc.). By measuring the leg length (LL) and a marked known length (60 cm) on the meter stick with this program, leg length in cm was calculated as:

$$LL[\text{cm}] = \frac{LL[\text{units}] \times \text{sticklength}[\text{cm}]}{\text{sticklength}[\text{units}]}$$

On average 3.5 measures of the hind leg were taken and the average variation among the mean was $\pm 4.4\%$

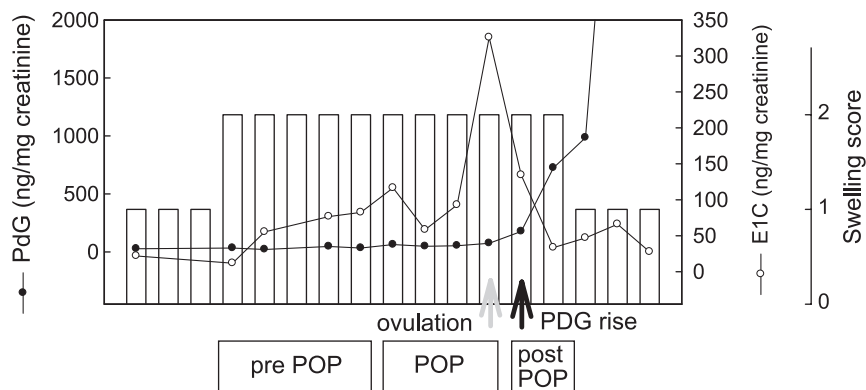


Fig. 1. Profiles of urinary estrogens (E1C), progestogens (PdG), and perineal swelling in an individual female chimpanzee (MARGOT) during November 1999. POP: periovulatory period including the day of ovulation and the three preceding days. Pre-POP: period of maximum tumescence preceding the POP. Post-POP: period of maximum tumescence following the POP.

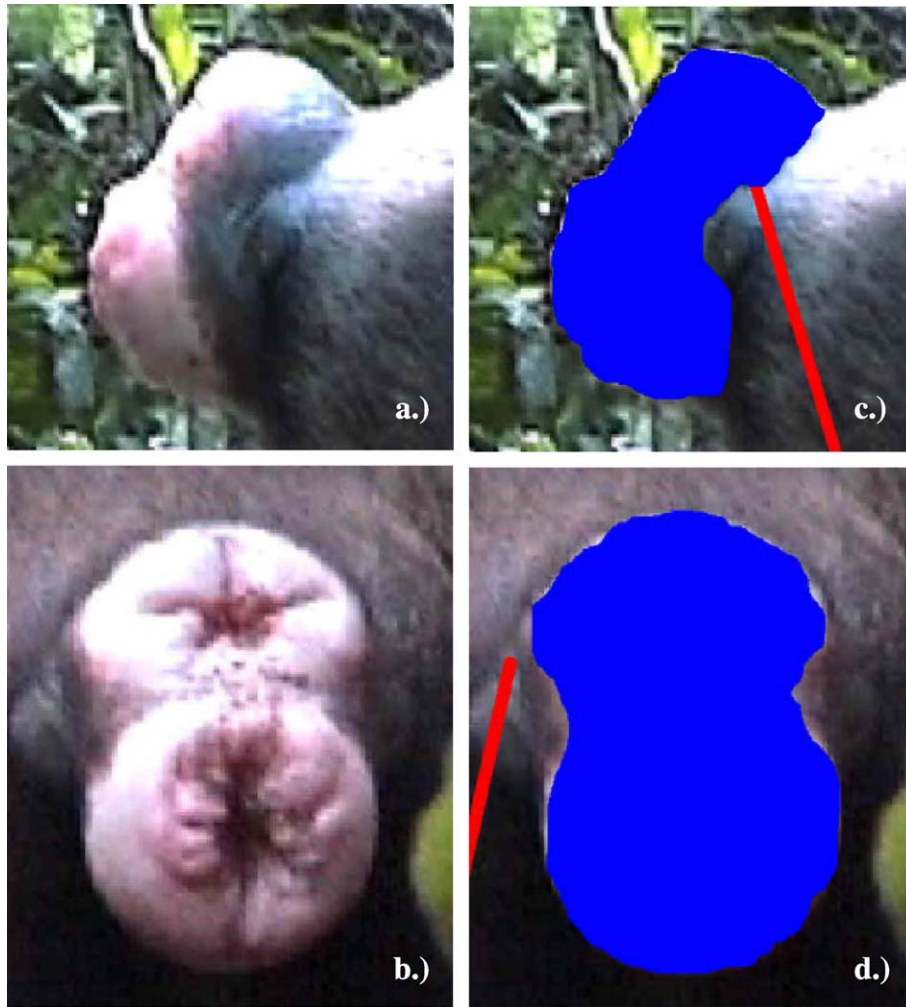


Fig. 2. Video images of a maximum swelling taken from (a) the side and (b) the back of an individual female and swelling areas as measured from these images (c and d). For details of measurement see Materials and methods.

for images taken from the back and $\pm 2.2\%$ for images taken from the side. Once the length of a female's hind leg was determined, swelling size as the two-dimensional area (a) of the swelling on a given image was calculated as:

$$a[\text{cm}^2] = \frac{(\text{LL}[\text{cm}])^2 \times a[\text{units}^2]}{(\text{LL}[\text{units}])^2}$$

If more than one image was taken of a female on a given day, swelling size was calculated as the mean size of all images. Average variation among the mean for images taken on the same day were $\pm 5.1\%$ for images taken from the back and $\pm 9.5\%$ for images taken from the side. Numbers of swelling images per day and female ranged from 1 to 6. In total, 996 images of 217 days contributed to the analysis. Reliability was estimated by having an independent assistant measuring 50 swelling images. The mean difference of measurements of swelling size was 4.6% for

images taken from the back and 7.3% for images taken from the side.

Statistical analysis

We used general linear mixed models (GLMMs) to analyze the effect of categorical variables (reproductive cycle phase) and continuous variables (cycles to conception) on a dependent continuous variable (e.g., swelling size). A GLMM is an extension of the general linear model, which allows to account for repeated observations of the same subjects by including subject (female individuality) as a random factor in the model (Coté and Festa-Bianchet, 2001; Pinheiro and Bates, 2000). As a covariance structure for the random factor, we selected compound symmetry. We used restricted maximum likelihood methods to estimate the models and Satterthwaites F tests to test for fixed parameter effects (Paper, 2002). These methods are robust against unequal sample sizes and against violation of the assumption of multisperecity (Keselman et al., 2001). Because

Satterthwaites F tests do not have exact F distributions, the denominator degrees of freedom are not integer. GLMM analyses were done using SPSS 11.5 (SPSS Inc.).

Following a significant fixed effect of a categorical variable, differences between the categories were tested using contrasts. We used AIC model selection to choose between models with and without interactions between the independent categorical variable and the random factor “females” (Pinheiro and Bates, 2000). In all analyses, models without interactions were chosen.

We conducted an exact binary logistic regression for stratified data using the program “LogXact” (Cytel Software Company) to identify influences on the alpha male’s mate preference (copulation or association preference) between two or more females with maximum tumescent swellings (Cytel, 2000; Tabachnick and Fidell, 2001). The stratum was alpha male observation days when more than one female had a maximum tumescent swelling. Females within a stratum were therefore treated as a matched set. To minimize dependency of data, we restricted the analysis on days with different females exhibiting maximum tumescent swellings or when the same females were in different phases of the MS (pre-POP, POP, and post-POP). We used exact likelihood ratio tests to identify significance of the model and parameters.

Independent variables were the categories absolute swelling size, female age, cycles to conception, and cycle phase. Each category was divided into two levels so that the female with the biggest swelling, the highest age, the closest to conception, and the cycle phase closer to ovulation (POP and post-POP vs. pre-POP) were classified as level 1 and the rest of the females as level 0. The binary dependent variable was

either male mated most/male mated less or male associated most/male associated less with the respective female.

Results

Swelling size changes within the maximum swelling phase (MS)

Fig. 3 illustrates the changes in the mean size of the perineal swelling (relative to the average POP size) during the period of the maximal swelling. Data are side views and are aligned to the presumed day of ovulation. Despite a high degree of interindividual variation, there was a gradual increase in size from the onset of the maximum swelling phase until the day of ovulation. Although swelling size decreased slightly thereafter, it remained clearly elevated above pre-POP values.

Swelling size measured from the side differed significantly between the phases [GLMM: $F(2,65.2) = 9.77$; $P < 0.001$]. Post hoc comparisons revealed significant differences between pre-POP and POP ($P < 0.001$) and between pre-POP and post-POP ($P = 0.006$) (Fig. 4a). Swelling size measured from the back was also significantly different between phases [GLMM: $F(2,66.1) = 15.35$; $P < 0.001$], with post hoc comparisons revealing significant differences between pre-POP and POP ($P < 0.001$) and pre-POP and post-POP ($P < 0.001$) (Fig. 4b).

Male behavior changes within MS

Alpha male copulation rate was low during the initial days of the pre-POP period, although, as with average

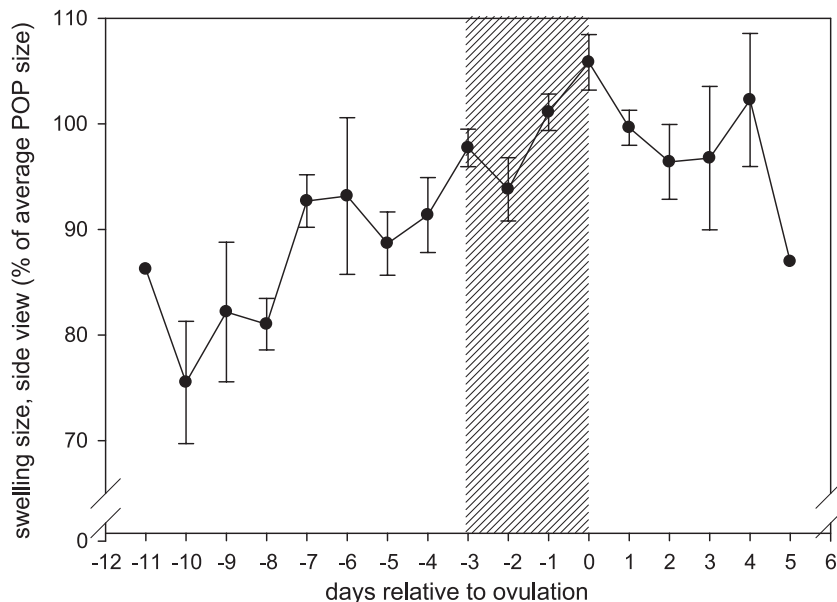


Fig. 3. Composite profile of relative swelling size (side view) during the maximum swelling period in 12 females aligned to the day of ovulation (day 0). The shaded area indicates the fertile phase (POP). Data are plotted as mean \pm SEM for the total number of cycles available ($n = 29$ around ovulation, decreasing outwards according to the lengths of individual maximum swelling periods).

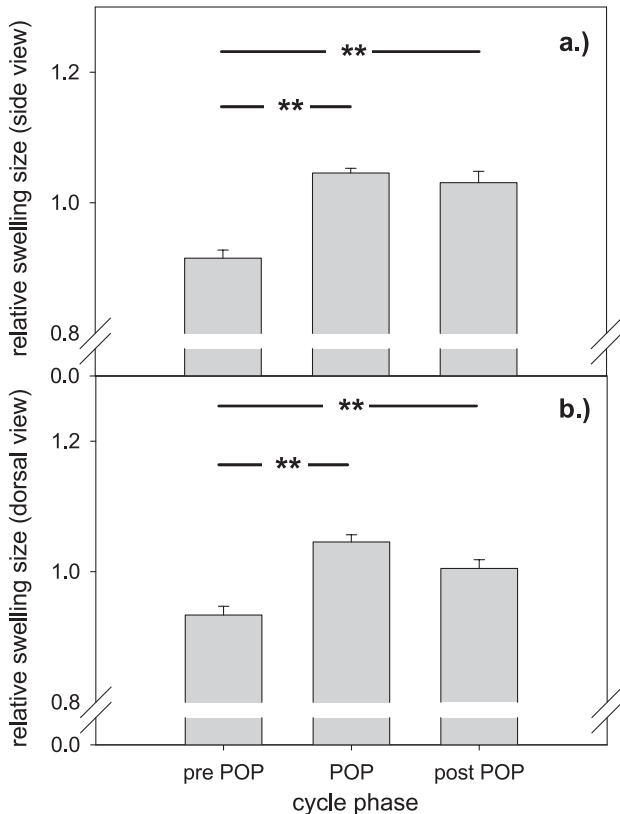


Fig. 4. Bar chart showing changes in relative swelling size (mean + SEM) as determined from (a) dorsal view and (b) side view between the three different reproductive phases of the maximum swelling period (cycles $n = 29$; females $n = 12$; $**P < 0.01$). Because of large interindividual variation in swelling size, for illustration purposes, relative swelling size is shown in this graph. It is calculated as the average absolute swelling size of each reproductive phase (pre-POP, POP, and post-POP) of each cycle, divided by the mean value of the three phases of each cycle.

relative swelling size, there was a high degree of variation for any given day (Fig. 5). The mean copulation rate showed a clear rise (about fourfold) on the day preceding POP and copulation frequency remained at this elevated level until the day after ovulation. Copulation rate gradually decreased thereafter until day 3 following ovulation, after which no more copulations were seen. As expected from the pattern seen in Fig. 5, copulation rate of the alpha male differed significantly between reproductive phases [GLMM: $F(2,57.5) = 7.48$; $P = 0.001$] (Fig. 6a). Copulation rate was significantly higher during POP ($P = 0.002$) and post-POP ($P = 0.001$) than during pre-POP.

Association and intervention rates of the alpha male differed in the same way as copulation rate between the phases [association rate: GLMM: $F(2,54.3) = 5.1$; $P = 0.009$; intervention rate: GLMM: $F(2,31.2) = 5.67$; $P = 0.008$] (Figs. 6b and c). Association rate was higher during POP ($P = 0.017$) and post-POP ($P = 0.004$) than during pre-POP.

Similarly, intervention rates were higher during POP ($P = 0.041$) and post-POP ($P = 0.002$) than during pre-POP, when almost no interventions occurred.

The association behavior of the beta male followed the same pattern (data not shown). His association rate also differed significantly between the phases [GLMM: $F(2,58,3) = 4.81$; $P = 0.01$], and he was more often in association with a female during POP ($P = 0.032$) and post-POP ($P = 0.004$) than during pre-POP. In contrast to the alpha-male, however, the copulation rate of the beta male did not differ significantly between the three phases.

Association rate of the gamma male also differed significantly between the phases [GLMM: $F(2,59.9) = 3.33$; $P = 0.042$]. In contrast to the two higher ranking males, however, the gamma male associated more often with maximally tumescent females during post-POP than during pre-POP ($P = 0.013$), but no significant difference was found between pre-POP and POP and between POP and post-POP. As seen for the beta male, gamma male's copulation rate did not differ significantly between the three phases.

Swelling size, estrogen levels, and male behavior between cycles

As a post hoc measure, we determined the conception cycle through hormonal analysis and pregnancy tests and then numbered individual cycles according to their distance to conception. There was a significant increase in mean maximum swelling size between cycles of individual females as the number of cycles to conception decreased, and this was reflected in both images taken from the back [GLMM: $F(1,11.7) = 28.71$; $P < 0.001$] and from the side [GLMM: $F(1,8.1) = 56.50$; $P < 0.001$]. The same result was obtained when only swelling size during POP was taken into consideration [back: GLMM: $F(1,14.2) = 15.32$; $P = 0.002$; side: GLMM: $F(1,11.2) = 21.45$; $P = 0.001$; Fig. 7]. Furthermore, mean estrogen

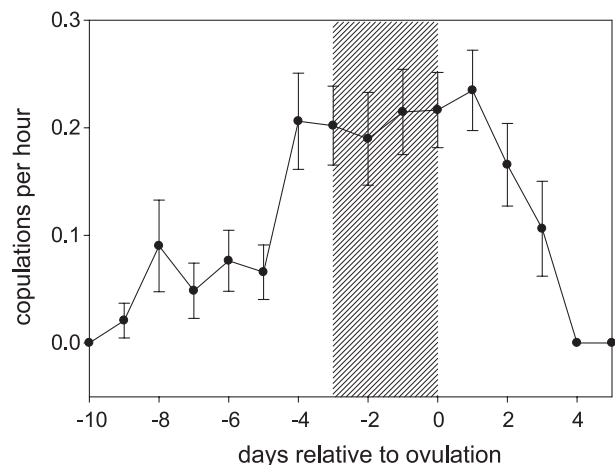


Fig. 5. Alpha male copulation rate during the phase of maximum tumescence (cycles: $n = 26$; females: $n = 10$, decreasing outwards according to the lengths of individual maximum swelling periods). Data are aligned to the day of ovulation (day 0) and present means \pm SD. The shaded area indicates the fertile phase (POP).

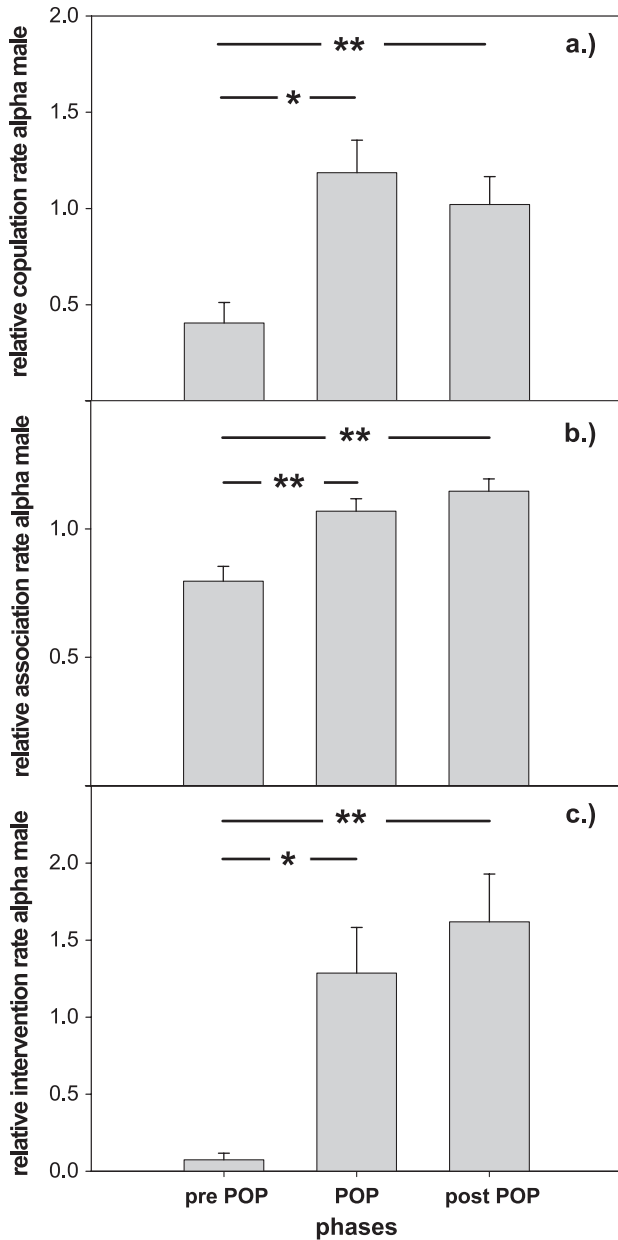


Fig. 6. Bar chart showing relative alpha male (a) copulation, (b) association, and (c) intervention rates (mean + SEM) for the three different reproductive phases of the maximum tumescence period (cycles: $n = 26$; females: $n = 10$); * $P < 0.05$, ** $P < 0.01$.

levels during POP increased significantly as the number of cycles to conception decreased [GLMM: $F(1,12) = 4.75$; $P = 0.05$], although there was a high interanimal variability in estrogen levels during each cycle (Fig. 8). The alpha males association rate during the periovulatory period rose as well significantly as the number of cycles to conception decreased [GLMM: $F(1,7) = 6.14$; $P = 0.042$]. There was also a tendency for the alpha male to copulate more frequently during POP as the number of cycles to conception decreased [GLMM: $F(1,6.4) = 3.80$; $P = 0.096$].

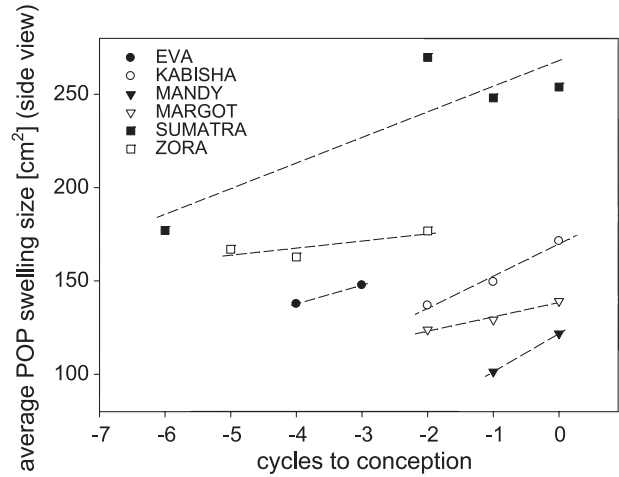


Fig. 7. Absolute perineal swelling size (side view) in consecutive cycles of individual females aligned to the cycle in which conception occurred (0). Dashed lines represent individual regression lines.

Swelling size and male mate preferences

We calculated the average swelling size using images of all days a female was seen with a maximum tumescent swelling of 13 different females based on images taken from the back (Fig. 9). Although several females had overlapping swelling sizes, for a considerable part of females, swelling size did not or only slightly overlap. Average swelling size ranged from 111.0 cm² (COCO) to 327.6 cm² (SUMATRA) with an average for all females of 187.2 cm². We tested for criteria of alpha male mate choice by calculating his copulation and association rates for every female with a maximum tumescent swelling when there was at least one other maximally swollen female in the group. The preferred female was defined as the one the alpha male associated or copulated with the most on that given day. Preference for a female calculated

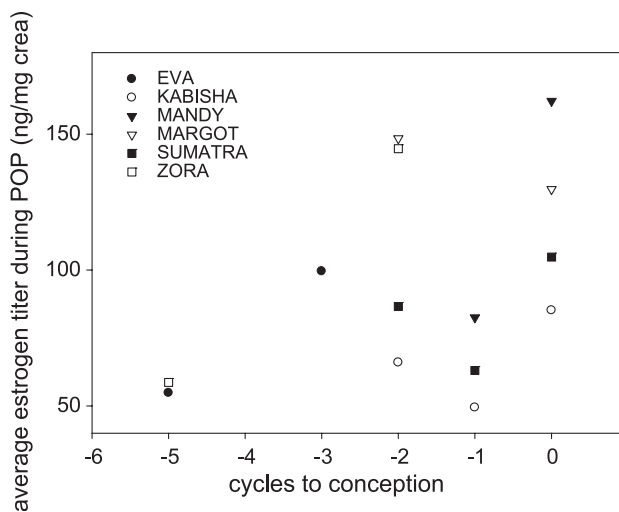


Fig. 8. Mean estrogen titer during the fertile phase (POP) in consecutive cycles aligned to the cycle in which conception occurred (0).

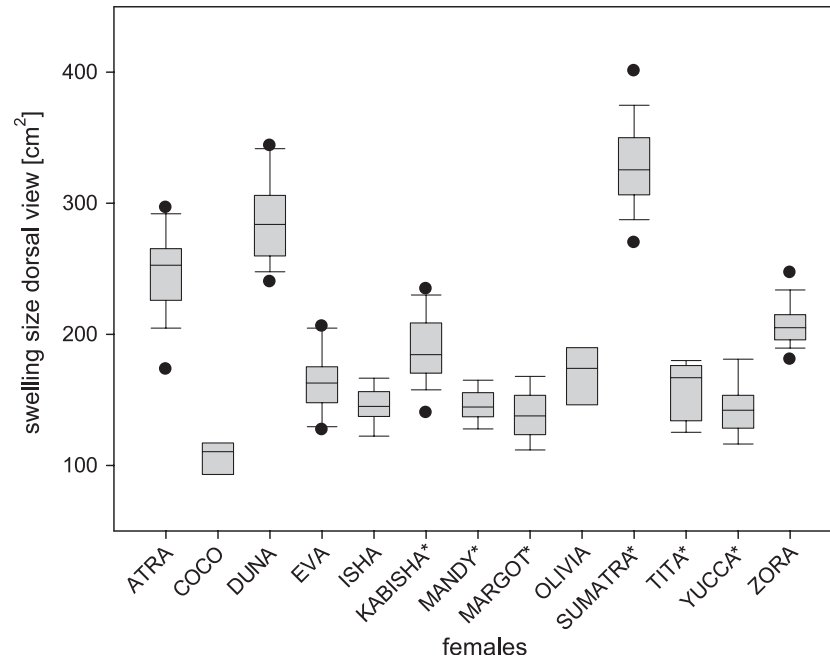


Fig. 9. Box plot chart of perineal swelling sizes (dorsal view) in the study females. For females marked with an asterisk, the data include the conception cycle. The top, middle, and lower horizontal lines show the 75th, 50th, and 25th percentiles, respectively.

on either factor (association or copulation) was always in agreement; however, on 2 days, the alpha male was not seen copulating at all; therefore, these 2 days had to be excluded for the analysis of preference based on copulation rate. A stratified logistic regression showed that of all categories tested (female age, absolute swelling size, cycles to conception, and cycle phase), only cycle phase had a significant influence on the alpha male's mate choice if association was taken as an indicator of preference (exact LR test: $\chi^2 = 18.67$; $P = 0.026$; phase: $e^\beta = 4.6$; $P = 0.049$; all other factors $P > 0.5$). The alpha male was 4.6 times more likely to associate more with a female being in her POP or post-POP phase than a female being in her pre-POP phase. The model showed significant differences as well when copulation was taken as an indicator of preference (exact LR test: $\chi^2 = 16.16$; $P = 0.049$) and an analysis of the categories revealed an almost significant effect only for "cycle phase": $e^\beta = 4.3$; $P = 0.058$. After removing the three nonsignificant categories age, absolute swelling size, and cycles to conception, the model with the category "cycle phase" became highly significant (exact LR test: $\chi^2 = 15.02$; $e^\beta = 11.0$; $P < 0.01$). The alpha male was 11 times more likely to copulate most with a female during her POP or post-POP phase than a female during her pre-POP phase.

Discussion

By combining direct size measures (video captures) of female sexual swellings with noninvasive endocrine methods to determine the fertile phase and behavioral indicators of male interest in the female, the present study provides

evidence that in free-ranging female chimpanzees swelling size conveys information that males can use to assess female reproductive value and to adjust their mating efforts accordingly. Specifically, we have shown that within the maximum tumescent period, further increases in sexual swelling size occur as the time of ovulation approaches. Furthermore, male interest (alpha and beta male) in the female as indicated by association, copulations, and intervention rates closely matched these subtle changes in swelling size. Our data also show that swelling size in individual females increases from cycle to cycle with approaching conception, paralleled by an increase in mean urinary estrogen concentrations during the periovulatory period. The alpha male associated significantly more often with females the closer they came to conception, and there was a tendency for copulation rates to increase as well. Finally, our data demonstrate that alpha male mate choice between maximally tumescent females was based on the actual cycle stage of the female but was not influenced by the female's absolute swelling size, her age, or the closeness to conception.

Changes in swelling size

Based on roughly the same definition of maximum tumescence, previous studies in chimpanzees consistently reported similar values for range (7–19 days) and mean length (10 days) of the maximum tumescent period (Deschner et al., 2003; Hasegawa and Hiraiwa-Hasegawa, 1983; Matsumoto-Oda and Oda, 1998; Tutin, 1979). This long period with no obviously visible changes in swelling appearance suggested that ovulation might not be reliably advertised by the swelling pattern. Our finding that signifi-

cant quantitative changes, representing a 15–20% increase in swelling size, still occur within the traditionally defined maximum tumescent period and that the periovulatory phase is associated with the biggest swelling size however clearly indicates that chimpanzee swelling patterns advertise the fertile period more precisely than previously thought. Chimpanzee swelling patterns might therefore resemble more closely the swelling patterns of other primate species living in multimale multifemale groups, such as baboons (e.g., Wildt et al., 1977) or Tonkean macaques (Aujard et al., 1998), where ovulation tends to occur at peak swelling. In contrast to the latter species, however, in chimpanzees this increased swelling size usually persists for up to 4 days after ovulation, indicating that “peak” swelling (e.g., $\pm 5\%$ of the maximum value) is still longer in chimpanzees than in baboons and macaques.

Our data also strongly suggest that swelling size does not only carry information on how close a female is to ovulation, but that it may also convey information on female fecundity since mean POP swelling size increased from one cycle to the next with approaching conception. This contention is supported by our finding of increasing mean estrogen levels during POP the closer a given cycle is to conception. It is known in humans that elevated midfollicular (Lipson and Ellison, 1996) and periovulatory estrogen levels (Li et al., 2001) correlate with fecundity and this has also been recently proposed for chimpanzees (Emery and Whitten, 2003). The data thus clearly suggest that changes in swelling size between consecutive cycles might serve as an indicator of a female’s proximate reproductive quality (Emery and Whitten, 2003; Zinner et al., 2002). Absolute swelling size, however, does not appear to provide information on between-female reproductive quality as there was not only a high variability in interindividual swelling size (see Fig. 9), but more importantly swelling sizes in conception cycles also differed markedly between females (see Fig. 7). In this respect, our data strongly suggest that swelling size on a given day is a poor predictor of relative fertility between females. For judging on an individual female’s fertility in a given cycle, a male would have to use size estimates of previous cycles. Old male chacma baboons with long tenure consort more with females during their conception cycle, while young dominant males, recently immigrated into the group, consort more with females during nonconception cycles (Weingrill et al., 2003). The temporal change in swelling size with approaching conception found in this study could explain such a pattern, so that males that know females for a long time can estimate their fertility by monitoring cycle to cycle changes in swelling size while newly immigrated males still lack this ability. Taï female chimpanzees and bonobos seem to have a considerably higher number of cycles to conception than East African chimpanzees (Boesch and Boesch-Achermann, 2000; Wrangham, 2002). Whether these nonconceptive cycles are nonfertile cycles and which factors influence the number of cycles to conception needs further investigation.

Male interest, swelling size, and ovulation

For all three behavioral categories, association, copulation, and intervention, interest shown by the alpha male (and except for interventions also beta male) in the female increased from pre-POP to POP, clearly indicating a change in female attractiveness between these phases. The data furthermore strongly suggest that the alpha male is capable of allocating his mating efforts in a way that increases his chances for successful reproduction. Since the changes in the male’s behavior matched changes in the female’s swelling size, our data provide circumstantial evidence that at least high-ranking males might use subtle changes in female swelling size as a basis for their mating decisions. Moreover, since the interest of the males in the females remained elevated during the post-POP period (and thus at a time when fertilization is no longer possible) when peak swelling size persists, it is reasonable to assume that the males indeed respond to the female’s swelling rather than to cues temporally more strictly related to the event of ovulation (e.g., pheromones). However, since specific female proceptive behavior patterns were not recorded, we cannot exclude the possibility that changes in female proceptivity or receptivity paralleled the changes in swelling size, and if so that males might either exclusively or in part also use changes in female behavior to adjust their sexual interest and mating efforts. Studies in chacma baboons, however, have shown that males use swellings as an indicator for conception probabilities (Bielert and Anderson, 1985; Bielert and van der Walt, 1982; Girolami and Bielert, 1987). Irrespective of which cue(s) the males relies on, however, it appears that they are obviously not capable of precisely detecting the time of ovulation, as otherwise rates of association and copulation with a female as well as intermale competition would not be expected to extend beyond the fertile period given the potential costs, such as increased energy expenses and risk of being injured involved in the display of these behaviors (e.g., Alberts et al., 1996).

From the female’s point of view, keeping swelling size (and/or proceptivity or receptivity) high after ovulation might increase her chances of mating with additional males (Hrdy, 1981; Hrdy and Whitten, 1987). This can be achieved in two ways: (i) by increasing the likelihood that the alpha male overstretches his capability to monopolize and becomes exhausted, and (ii) by increasing the probability of an overlap in the maximum tumescence period occurring with other female(s), thus making monopolization by the alpha male more difficult. In this way, the female could benefit either by confusing paternity and thus reducing the risk of infanticide (Hrdy, 1981; 1988; Van Schaik et al., 1999, 2000) or by profiting from having her offspring sired by the male who is most successful in sperm competition (Harvey and May, 1989).

As expected, male behavioral responses to changes in swelling size became less and less pronounced with decreasing rank. This might be due to several reasons. Firstly, the mere presence of the alpha male might discourage other

males from associating with an estrous female. Secondly, mating efforts by nonalpha males might be low due to fear of aggressive attacks from the alpha male or, thirdly (as shown in the present study), their copulation attempts may be interrupted by the alpha male. Generally, our results are in accordance with the priority of access model (Altmann, 1962) by suggesting that in a chimpanzee group with a limited number of males, only the alpha male is free in his mating decisions while the other males have to adapt their strategies according to the alpha males monopolization efforts. Genetic studies confirm this pattern by showing that alpha males indeed sire the majority of offspring and that this effect is stronger the fewer males are resident in the group (Boesch et al., in preparation).

Several other studies on free ranging chimpanzees have explored sexual behavior in relation to sex skin swelling patterns (Hasegawa and Hiraiwa-Hasegawa, 1990; Matsumoto-Oda and Oda, 1999; Tutin, 1979; Tutin and McGinnis, 1981; Watts, 1998). All found that male interest in the female increases towards the end of the maximum tumescent period. Depending on the study, this was expressed through possessive male behavior (Hasegawa and Hiraiwa-Hasegawa, 1990; Tutin and McGinnis, 1981), coalitionary mate guarding (Watts, 1998), female mating frequency and number of mating partners, or the proportion of adult male matings (Matsumoto-Oda, 1999). These findings correspond well with the results of our study in that firstly, adult males in general are more interested in females towards the end of the maximum tumescence period, and secondly, especially highest ranking males are successful in mating with females during the later stages of the maximum tumescence period. However, with additional data on swelling size and ovulation, we have shown that although the alpha male's behavior closely follows the changes in female swelling size, it is not in complete accordance with the female reproductive endocrinology.

Hypotheses to the function of sex skin swellings in primates

Several results obtained in this study are in accordance with predictions about the functional significance of swellings drawn from the graded signal hypothesis proposed by Nunn (1999). Firstly, within a cycle, chimpanzee sexual swellings are indeed graded signals since they become gradually bigger with approaching ovulation. However, since the swelling size does not decrease immediately after ovulation, a degree of imprecision in indicating timing of the fertile period remains. Secondly, male behavior matched the pattern predicted by the graded signal hypothesis: The alpha male showed the highest interest in the female during times when her swelling was biggest and the probability of fertility highest, whereas mating rates of the lower ranking males were considerably lower (but still higher than zero). In this way, the female has the possibility of both confusing paternity to some extent, but at the same time biasing it towards the alpha male as is also suggested by Nunn's hypothesis.

When more than one female shows a maximum tumescent swelling at the same time, the alpha male did not prefer the female with the biggest swelling as would be predicted by the reliable indicator hypothesis proposed by Pagel (1994). Instead, we found a significant preference of the alpha male for the female in her POP or post-POP phase (high probability of fertility), even though she does not necessarily have the biggest swelling in the group at that time.

Our finding that average swelling size and midcycle estrogen concentrations increased with approaching conception could be interpreted as signaling of female quality as predicted by the reliable indicator hypothesis. However, as also suggested by Emery and Whitten (2003), these differences do not indicate overall female quality but rather reflect differences in ovarian function during consecutive cycles and are therefore an indicator of the proximate reproductive quality of the cycle in which the swelling is displayed.

In conclusion, sexual swellings in wild female Tai chimpanzees therefore do not seem to be reliable indicators of overall female quality that have evolved through female–female competition over access to high-quality males. It rather seems that by offering males a graded signal of probability of fertility and thereby altering the costs and benefits of mating, females succeed in manipulating male behavior and achieving their own reproductive goals (Nunn, 1999; Zinner et al., 2004). Sexual conflict, where one sex evolves traits to resist the manipulative attempts of the other sex, seems therefore to have played a significant role in the evolution of this conspicuous trait in chimpanzee females.

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