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Sexual swellings in wild white-handed gibbon females (*Hylobates lar*) indicate the probability of ovulation

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Abstract

Conspicuous sexual swellings in the females of some primate species have been a focus of scientific interest since Darwin first wrote about them in 1871. To understand these visual signals, research focused on exaggerated sexual swellings of Old World primates. However, some primate species develop much smaller sexual swellings and it is as yet unclear if these smaller swellings can serve similar functions as those proposed for exaggerated swellings, i.e. advertising fertility to attract mates. We studied the temporal patterns of sexual swellings, timing of ovulation and female reproductive status in wild white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand, where this species has a variable social organization. We established fecal progestogen profiles in fifteen cycles of eight cycling females and, to detect swellings outside the menstrual cycle, five pregnant and six lactating females. In 80% of menstrual cycles, ovulation and maximum swelling phase (duration: ∅ 9.3 days; 42.8% of cycle length), overlapped tightly. The probability of ovulation peaked on day 3 of the maximum swelling period. Nevertheless, the temporal relationship between maximum swelling and probability of ovulation varied from day −1 to day 13 of the swelling period and three times ovulations fell outside the maximum swelling phase. The different swellings phases occurred in similar proportions in cycling and pregnant, but not lactating females, which were rarely swollen. Despite their smaller size, gibbons' sexual swellings probably serve functions similar to those suggested for exaggerated swellings by the graded-signal hypothesis, which predicts that sexual swellings indicate the probability of ovulation, without allowing males to pinpoint its exact time.

Keywords: Genital sexual swelling; Gibbons; *Hylobates lar*; Ovulation; Fecal progestogen; Fertility; Graded-signal hypothesis; Paternity confusion; Monogamy; Polyandry

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Introduction

In some animal species (e. g. keeled earless lizard, *Holbrookia propinqua*: Cooper and Crews, 1987; Ferguson, 1976; alpine accentor, *Prunella collaris*: Davies et al., 1996), and perhaps in humans (Roberts et al., 2004), females temporally develop specific visual signals to advertise their fertility. Such signals commonly increase a female's attractiveness to male partners and encourage copulation to achieve conception. In a number of female mammals, including most primates (Dixson, 1983, 1998; Hrdy and Whitten, 1987; Campbell, 2006), changes in coloration and/or swelling of the skin of the external genitalia evolved as morphological signals of fertility, which are triggered by accompanying changes in estrogen and progesterone secretion (e. g. in *Papio ursinus*: Saayman, 1973; *Miopithecus talapoin*: Dixson and Herbert, 1977). Recent studies have distinguished changes in external genitalia mainly with regard to the anatomical features involved and their absolute sizes (Dixson, 1998). Primates have been classified as either (i) exhibiting no obvious visual signals around ovulation, (ii) showing "ordinary" swellings or (iii) producing "exaggerated" swellings (Nunn, 1999; Sillén-Tullberg and Møller, 1993).

Over the last 30 years most effort has focused on studying exaggerated swellings (see review in Zinner et al., 2004), which are prominent in size (representing up to 17% of a female's

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body mass; Dixson, 1983) and extend beyond genital areas to the circumanal, subcaudal and paracallosal regions (Dixson, 1983). These swellings occur in all species of *Cercocebus*, *Mandrillus*, *Theropithecus*, *Papio* and *Pan* (Dixson, 1983), in most, but not all, macaques (Anderson and Bielert, 1994), as well as some colobines and guenons (Dixson, 1998; Oates et al., 1994). In contrast, small ("ordinary") swellings are characterized by a moderate size and pinkness of vulval and clitoral areas and have been observed in prosimians (van Horn and Eaton, 1979; Wright et al., 1986), some New World and Old World monkeys (Dixson, 1983; Glander, 1980; Rowell and Chalmers, 1970; Sicchar and Heymann, 1992; Struhsaker and Leland, 1979; Tenaza, 1989) and in gibbons (Chivers, 1974, 1978; Dahl and Nadler, 1992a,b).

To explain the evolution and the function of large sexual swellings, most of the hypotheses proposed in the past treat sexual swellings as honest signals indicating female quality or timing of ovulation in order to attract males and ensure fertilization (Dixson, 1998; Nunn, 1999; Stallmann and Froehlich, 2000). Although for a number of primate species the day of ovulation coincides with maximum sexual swelling size, recent studies indicate considerable variation in the relation between timing of ovulation and swelling patterns, both within and between females (Aranda et al., 2006; Deschner et al., 2003; Engelhardt et al., 2005; Möhle et al., 2005). Moreover, in some species, swellings occur outside the menstrual cycle when ovulation is impossible or unlikely, for example during pregnancy or when females nurse small infants (*Macaca nemestrina*, *Mandrillus sphinx*, *Mandrillus leucophaeus*: Hadidian and Bernstein, 1979; *Pan troglodytes*: Wallis, 1982; *Cercocebus atys*: Gordon et al., 1991). One plausible functional explanation for this pattern is that swellings under certain circumstances may serve to confuse paternity in order to solicit paternal care (Taub, 1980) or to reduce the risk of infanticide (*Papio h. hamadryas*: Zinner and Deschner, 2000) by signalling sexual attractiveness to males. Furthermore, since the absence of swellings has been mainly noticed in monogamous species and exaggerated swellings among polygamous species, in which females mate promiscuously, current hypotheses on the function of sexual swellings, emphasize a correlation between sexual swelling size and mating system.

In this study we investigate the occurrence of sexual swellings in a predominantly monogamous primate, the white-handed gibbon. Among gibbons (family Hylobatidae), sexual swellings have been reported for white-handed gibbons (*Hylobates lar*: Carpenter, 1941; Breznock et al., 1977; Dahl and Nadler, 1992a,b), agile and müller gibbons (*Hylobates agilis* and *Hylobates muelleri*: Cheyne and Chivers, 2006) and for wild siamangs (*Symphalangus syndactylus*: Chivers, 1974, 1978). Although smaller in size than swellings of some Old World monkeys or apes of the genus *Pan*, swellings in gibbons are clearly recognizable and larger than in other species living in one-male units, such as the gorilla (*Gorilla gorilla*: Nadler, 1975). Given their predominantly pair-living social organization, sexual swellings in gibbons are unexpectedly large. To understand the physiology and possible functions of sexual swellings in wild gibbons, it is important to identify at what age swelling cyclicity emerges, the pattern of swellings during the menstrual cycle and whether they can be displayed outside the menstrual cycle (e.g. during pregnancy or lactation).

In captive white-handed gibbons, Dahl and Nadler (1992a,b) found that the duration of the swollen phase was relatively long and correlated to concentrations of estrogens, while detumescence was associated with increasing concentrations of progesterone (Nadler et al., 1993). These results indicated that swellings in gibbons are mediated by the same hormonal conditions as those found in other female primates (Dixson, 1983) and that they might therefore indicate ovulation. However, how closely sexual swelling cycle is tied to ovulation and the fertile phase has not been examined in gibbons.

The objectives of this study are to provide information on endocrine characteristics of the ovarian cycle, pregnancy and lactation in wild gibbon females and to clarify the relationship between sexual swellings and female reproductive status, in particular timing of ovulation, in a free ranging population. By doing so, we hope to move towards a better understanding of the possible functions of small swellings in primates which have received far less attention than exaggerated swellings. Specific aims are: (1) to determine the pattern of genital swelling in cycling and non-fertile (sub-adult, pregnant, lactating) females and assess their inter-individual variability; (2) to describe ovarian cycle characteristics (lengths of cycle and component phases, timing of ovulation) in wild female gibbons based on fecal progestogen profiles; (3) to investigate the temporal relationship between swelling changes and the timing of ovulation; and (4) to compare sexual swelling characteristics across species to assess whether characteristics of exaggerated swellings also characterize species with smaller swellings.

Methods

Study site and animals

The study was carried out in Khao Yai National Park, situated in central Thailand (2169 km^2; 101°22′E, 14°26′N; 130 aerial km northeast of Bangkok), in a seasonally wet, evergreen rain forest interspersed with few, small patches of mature secondary growth at an elevation of 730–870 m. Data on female reproductive biology and endocrinology were collected over three field seasons (July–December 2003, February–August 2004 and October 2004–March 2005) on twelve social groups in an area named Mo Singto-Klong E-Tau (Reichard, 2003), which hosts a high density of 15.9 individuals of white-handed gibbons per km^2. Seven of the study groups consisted of a single adult female, one adult male and up to four were immature, reflecting a pair-living social organization (cf. Kappeler and van Schaik, 2002), whereas the remaining five groups each comprised a second adult male that was unrelated to the female of the group. These social units are best characterised as multimale or socially polyandrous. Members of all groups had been well habituated for at least 6 months prior to the beginning of the study and for most of the groups data on reproductive histories were available since 1992 (Brockelman et al., 1998).

Data were collected on twelve multiparous adult and three sub-adult females, who had not yet achieved adult body size (for age-classes see Reichard, 2003), and were daughters of the adult females of groups D, H, and R (Table 1). Each adult female was followed during one or more reproductive stages (i. e., cycling, pregnant and lactating) to obtain fecal samples for hormone analysis and data on swelling characteristics. In total, data were available for 8 cycling individuals (15 cycles in total, 7 females with 2 cycles, 1 female with 1 cycle), 5

Table 1
Demographic data and reproductive stages of data collection in study females

Group	Female	Age (year/month)[a]	Collection during pregnancy	Collection during lactation	Collection during cycling period	Parities (lost infant)[a]
A	Andromeda	>33	–	–	+	5
B	Bridget	>33	–	–	PR	3
C	Cassandra	30	–	+	+	6 (1)
D	Daow	24	+	+	+	4 (2)
H	Hannah	26	+	–	+	5
J	Jenna	18	++	+	+	2 (2)
N	Natasha	>33	–	–	+	4
NOS	Nasima	19	–	–	+	4
R	Brit	21	–	+	+	3 (1)
S	Sofi	28	–	–	†	6
T	Brenda	15	–	+	–	1 (1)
W	Wolga	23	+	+	–	5
D	Dara (SA)	10/9	–	–	–	N
H	Hima (SA)	10/3	–	–	–	N
R	Rung (SA)	9/4	–	–	–	N

SA: subadult; N: nulliparous; PR: post reproductive, excluded from analysis. †: Abnormal cycle, excluded from analyses; +: Occurrence of collection; ++: Female was collected twice (during 2003 and 2004).

[a] At December 2005.

pregnancies and 6 lactating females (Table 1). The female Jenna was collected during two gestation periods, because after losing her 7-month-old infant she immediately started cycling and conceived again.

Gibbon observations and fecal sample collection were conducted without contact or interaction with individuals and under permission of the Thai National Research Council and the Royal Forest Department of Thailand.

Age calculation

Individual ages were known for three sub-adult females (see Table 1). Minimum ages of the remaining females were calculated from the females' long-term birth records. Birth records in the population indicated a minimum age of 10 years for a female to first experience parturition. For each birth we added 3 years to a female's age, because 3 years was the average birth interval observed in Khao Yai gibbon females (Reichard, 2003). When a female lost her infant before weaning, we added only 2 years to her age, as 2 years was the average interbirth interval in our population after a suckling infant was lost ($n=6$; range: 11 months to 2 years and 9 months; U.R., unpublished data). Since age was calculated in December 2005, in cases of infants born between 2004 and 2005, we only added another year to a female's age if the baby was born before June 2005. Three females were considered older than 33 years of age, because they were well known individually since the early 1980s (Raemaekers and Raemaekers, 1985; Brockelman et al., 1998).

To test the effect of old age on female reproductive physiology we divided our sample in a subset of females that were younger than 25 years of age (<25 years) and a subset of females that were 25 years and older (≥25 years).

Sexual swellings

Based on anatomical reports on the structures of external genitalia in *H. lar* (Dahl and Nadler, 1992a,b; Nadler et al., 1993), the degree of wrinkling of the labia minora, urethral eminence and dorsal lining of the vaginal wall, were taken as main parameters for evaluating changes in sexual swellings. Visual inspections of genital swellings were carried out daily at a distance of approximately 10 m with Leica 10 × 42 binoculars. Qualitative characteristics of the appearance of the vulva (shape, tumescence, and color) were systematically recorded on a pre-designed check sheet with multiple choices to mark. The size of the genital swelling was assessed intra-individually in comparison to the size of the ischial callosities (Fig. 1), which are a constant body part, measuring approximately 4 × 5 cm (Matthews, 1946). Qualitative characteristics and genital size were later converted to a defined score. Due to difficulties in applying the 7-point swelling scale of Dahl and Nadler (1992b) under natural conditions and to allow comparison with available data on rating genital swellings in other primates (e. g. Deschner et al., 2003; Heistermann et al., 1996; Reichert et al., 2002), three swelling stages were defined:

1. *No swelling:* minimum size of outer genital structures. When the vulva is almost invisible or appears as a pink mass of less than 2 cm (approximately 1/4 of one ischial callous) in length (compares to stages 0 and 1 of Dahl and Nadler's (1992b) scale).
2. *Partial swelling:* any intermediate stage between no swelling and maximum swelling. The vulval lobes are smooth and protrusions of lobes are visible.
3. *Maximum swelling:* All genital structures are maximally protruded and present both maximum size and tumescence. Vulval dimensions approximate 3–4 cm (approximately 3/4 of one ischial callous) in length (compares to stages 4 to 7 of Dahl and Nadler's scale).

Inter-observer reliability of genital swelling scores between C.B. and three field assistants revealed good to excellent agreement with Cohen's κ values (Siegel and Castellan, 1988) calculated on 20% of the total of observation days per cycling female were 0.74 ($n=28$ days) for Assistant 1, 0.83 ($n=34$ days) for Assistant 2 and 0.92 ($n=42$ days) for Assistant 3 (all $P<0.001$).

Fecal sample collection and hormone analysis

Fecal samples were collected systematically by C.B. and five field assistants. Fecal samples of females potentially showing cyclic ovarian activity, defined as all females not carrying an infant, were collected daily, whereas feces of pregnant and lactating females were collected weekly to bi-weekly. Feces of each potentially cycling female and each lactating female were sampled over a period of 3 months. On average, one sample was obtained every 1.09 days (range 1–4 days) in cycling females, every 1.93 days (range 1–8 days) in pregnant females and every 6.93 days (range 1–25 days) in lactating females. Samples were, with few exceptions, collected immediately after defecation under the night-tree or during the first three activity hours. Following homogenization of the sample, a urine-uncontaminated aliquot of feces was placed in a polypropylene tube containing 10 ml of 95% ethanol (Ziegler et al., 2000). Samples were stored at 4–5°C within 10 h of collection. In addition, signs of menstruation were checked daily on drops of urine samples collected

Fig. 1. Photograph of a wild gibbon female's sexual swelling (SS) showing protruded genital structures, maximum size and tumescence, in comparison to the ischial callosities (IC).

from leaves and branches using a urine-stick-test kit (Combur-3-Test E, Roche Diagnostics Mannheim, Germany).

Prior to hormone measurement, samples were homogenized in their original ethanol solvent and subsequently extracted twice as described by Ziegler et al. (2000) with the modification that samples were vortexed twice for 10 min on a multitube vortexer instead of shaking overnight. Efficiency of the extraction procedure, determined by monitoring the recovery of ^{3}H-progesterone added to a subset of samples prior to homogenization was 85.7±5.8% (mean±SD, n=20). Following extraction, the remaining fecal pellets were dried in a vacuum oven and the dry weight of the samples was determined. All hormone concentrations are expressed as mass per gram of dry weight.

Fecal extracts were measured for levels of immunoreactive 5α-reduced 20-oxo pregnanes (5-P-3OH) which have been identified as quantitatively abundant fecal metabolites of progesterone following a radiometabolism study in the white-handed gibbon (Nadler, personal communication). Moreover, in a pilot study on captive-housed animals, we have shown that the measurement of 5-P-3OH, as in various other primate species (e.g. Heistermann et al., 2001; Möhle et al., 2005; Ostner and Heistermann, 2003), accurately reflects female reproductive status, including ovarian function, in the study species (Barelli and Heistermann, in press). 5-P-3OH was determined using a microtiterplate enzyme immunoassay which has been described in detail by Hodges et al. (1997) and validated for white-handed gibbons by Barelli and Heistermann (in press). Cross-reactivity of the antibody relative to 5α-pregnane-3α-ol-20-one (100%) was 66.7% for 5α-dihydroprogesterone, 47.3% for progesterone and <2% for all other steroids tested. Prior to assay, depending on female reproductive status, samples were diluted 1:20 to 1:100 in assay buffer. Serial dilutions of fecal extracts from samples of females of different reproductive conditions gave displacement curves that were parallel to the standard curve. Recovery of known amounts (5 doses) of 5α-pregnane-3α-ol-20-one (5-P-3OH) added in quadruplicate to fecal extracts containing low levels of endogenous 5-P-3OH levels was 110.6±6.7% (mean±SD) with a correlation coefficient between added and recovered amounts of 0.99. Sensitivity of the assay at 90% binding was 15 pg. Intra- and interassay coefficients of variation, calculated from replicated measurements of high- and low-value quality controls, were 7.2% (n=16) and 11.9% (n=60) (high) and 8.1% (n=16) and 15.0% (n=60) (low), respectively.

Timing of ovulation and the fertile phase

Fecal progestogen (5-P-3OH) profiles were used to determine the lengths of the follicular and luteal phases of the menstrual cycles, the presumed day of ovulation and the timing of the fertile phase. In this respect, and according to Heistermann et al. (2001), the sustained rise in fecal 5-P-3OH levels above a threshold of the mean plus two standard deviations of 4 to 5 preceding baseline values was used to determine the onset of the post-ovulatory (luteal) phase of each ovarian cycle. Only cycles in which no more than one sample was missing around the significant 5-P-3OH rise, and in which progestogen levels remained elevated for at least 3 consecutive days were included in the analysis. A radiometabolism study of injected ^{3}H-progesterone in two female white-handed gibbons indicated that the majority of radioactivity was excreted into feces with a clear peak on day 3 after injection in both animals (Nadler et al., unpublished data). Based on these data, the presumed day of ovulation was assessed as the day of the defined fecal 5-P-3OH increase corrected for a time lag of 3 days. Due to a possible variability in the temporal relationship between ovulation and fecal progestogen rise, as well as missing sampling days in a few cycles, timing of ovulation may, however, include an error of 1 day.

Based on this definition, the length of the follicular phase was defined as the interval between the first day of menstruation and the day of ovulation, whereas the luteal phase comprised the interval between the day after ovulation and the day before subsequent menstruation. For determination of overall cycle length, we have used both intervals between successive menstruations and intervals between successive 5-P-3OH rises, because for three of the eight cycling females, the occurrence of menstruation could not accurately be detected. The fertile phase of an ovarian cycle was defined as a period of 5 days. This period comprises the day of ovulation, plus 1 day to account for a possible error in timing ovulation (see above), and 3 days preceding the day of ovulation to account for the functional life span of sperm (France, 1981; Wilcox et al., 1995; data from humans).

To examine the relationship between genital swelling stage and timing of ovulation in gibbons, we estimated probabilities of ovulation and fertility as reported in Deschner et al. (2003) and Zinner et al. (2004). The probability of ovulation has been computed for each day of the maximum swelling period (T) by dividing the number of observed ovulations on each day of maximum swelling (counted from the beginning) by the overall number of ovulatory cycles considered. This corresponds to the formula:

$$P(T=t)=\frac{n_t}{n},$$

where t represents a specific day, i.e. day 1, day 2, day 3,..., within the maximum swelling period, n_t is the number of cycles in which ovulation occurred on day t, and n is the overall number of ovulatory cycles. Assuming that probability of fertilization remains constant for the 5 fertile days, we attributed a probability of fertilization of 1 to each of the 5 days, whereas outside this phase the probability was assumed to be zero. The probability of fertility on any given day of the maximum swelling period (f), was calculated by averaging the scores of probability of ovulation for day f across the females.

Data analysis

Hypotheses were tested either with standard non-parametric tests (Siegel and Castellan, 1988), one-way ANOVAs (Zar, 1999), mixed linear models (SPSS 14.0.0; repeated factor: reproductive stage; repeated covariance type: compound symmetry) or by using the related samples with missing values test while maintaining the position of the missing values and running 10,000 permutations (Mundry, 1999). Non-parametric tests were exact tests if sample size was small (Siegel and Castellan, 1988; Mundry and Fischer, 1998). In cases of multiple pair-wise post-hoc comparisons we used LSD statistics provided with the mixed linear model. All statistical tests are two-tailed.

Results

Sexual swelling scores and hormone profiles in cycling females

Representative profiles of immunoreactive fecal 5-P-3OH of two females are shown in Fig. 2 in relation to the pattern of genital swelling over 2 complete menstrual cycles each. The fecal progestogen profiles followed a clear cyclic pattern in which the follicular (consistently low progestogen levels) and luteal phases (elevated progestogen levels) of the cycles can be clearly distinguished. As expected, in each cycle menstruation occurred with declining progestogen levels, indicating the onset of a new cycle. Although 5-P-3OH levels in both the follicular and luteal phase varied between cycles and females, mean 5-P-3OH levels in the luteal phase (6.0±3.1 μg/g) were three times higher than in the follicular phase (2.0±0.89 μg/g; Wilcoxon test: T=15, n=5 females, P=0.063). With average values of 10.6 and 10.1 days, follicular and luteal phases were similar in length, although both component cycle phases showed high inter-individual variability. The inter-menstrual interval was 21.1 days and resembled, in length, the intervals between successive fecal 5-P-3OH rises (20.7 days; Table 2).

In accordance with cyclic changes at the ovarian level, cycling females also showed changes in swelling size and degree of wrinkling of the labia minora (Fig. 2). With respect to ovarian cycle stages, maximum swelling (regarding tumescence and size) was confined to the follicular and early luteal phases, with a gradual decrease observed within 4–5 days following the

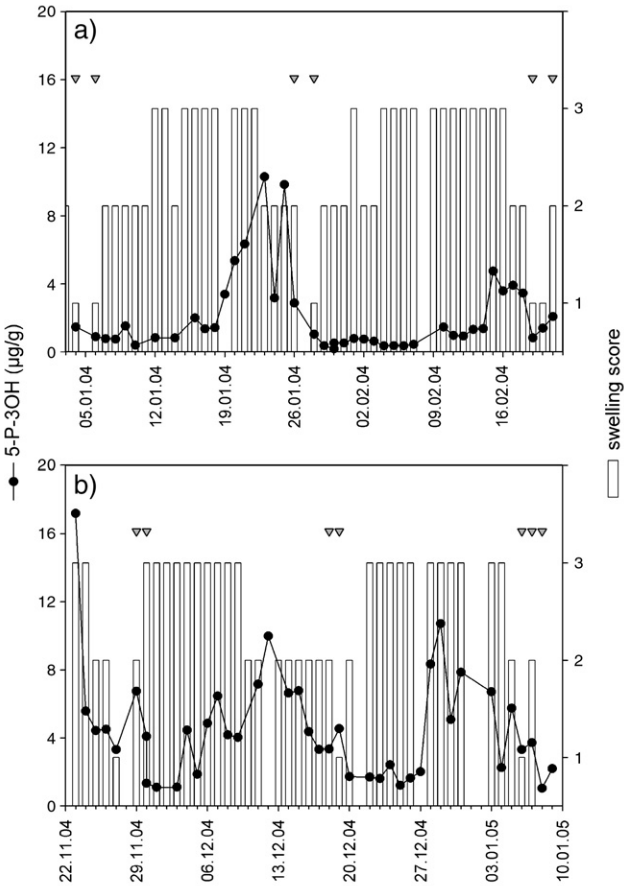

Fig. 2. Profiles of fecal immunoreactive progestogen (5-P-3OH) excretion in relation to changes in sexual swelling score (white bars) of two consecutive cycles in females Daow (a) and Brit (b). Missing bars indicate days with missing values on swelling score. Grey triangles indicate menstruation occurrence.

Table 2
Menstrual cycle characteristics of wild white-handed gibbons and duration of maximum swelling phase

Individual	Inter-menstrual interval (days)[a]	Interval between consecutive 5-P-3OH rises[a]	Follicular phase (days)[a]	Luteal phase (days)[a]	Max swelling duration (days)[a]
Andromeda	–	15	–	–	6.5
Brit	20.3	22	6.5	12.5	11.5
Cassandra	21	–	8.5	11.5	9
Daow	21.6	27	15.5	7.5	12
Hannah	21.3	–	10.5	9	8
Jenna	–	23.5	–	–	11
Nasima	–	16	–	–	10
Natasha	21.3	–	12	10	6
Mean ± SD	21.13 ± 0.50	20.7 ± 5.09	10.6 ± 3.44	10.1 ± 1.98	9.3 ± 2.3
Range[b]	19–25	15–27	5–18	6–14	5–13
Total number	15	6	9	9	15

[a] Figures for each female represent mean values if more than one period from the respective female was available for calculation.

[b] Calculated across all individual periods.

defined post-ovulatory 5-P-3OH rise (Fig. 2). Maximum swelling periods lasted usually between 7 and 11 days (11 out of 15 cycles; Table 2). Maximum swelling duration varied significantly between individuals [ANOVA: $F(7,7)=6.491$, $P=0.012$] as well as between cycles of individual females (see Fig. 3). Within-female swelling duration variation appeared unrelated to cycle type, because maximum swelling periods of three conception cycles (11.3 ± 1.5 days) were comparable to non-conception cycle maximum swelling durations of the same females (11 days). However, age markedly affected the duration of the maximum swelling period, with older females (≥ 25 years of age) having significantly shorter maximum swelling phases than younger females (Mann–Whitney U-test, $U=0$, $n_{\mathrm{age}\geq 25}=4$, $n_{\mathrm{age}<25}=4$, $P=0.029$).

Sexual swelling as an indicator of fertility and ovulation

An analysis of the temporal relation of genital swellings, ovulation and females' fertile phase showed that in 12 out of 15 cycles, ovulation occurred within the period of maximum swelling (Fig. 3). In the other three cycles, ovulation occurred twice after the onset of detumescence and once before the onset of maximum tumescence. Maximum swelling began on average 5.3 ± 2.5 days before ovulation (range: −1 to +13 days, $n=15$ cycles) and ended on average 3.1 ± 4.7 days after ovulation (range: −9 to +10 days; Fig. 3). No significant difference in the length of maximum swelling between females was detected, neither from the first day of maximum swelling until the day of ovulation [ANOVA: $F(7,7)=0.723$, $P=0.660$], nor considering the duration from ovulation to the last day of maximum swelling [ANOVA: $F(7,7)=1.750$, $P=0.239$].

Assuming that males could potentially predict the time of ovulation by relating it from the start of the maximum swelling stage, we calculated the peak of ovulation probability within the period of maximum genital swelling. The highest probability of ovulation occurred on day 3 of maximum swelling (0.33; Fig. 4), with 80% of all ovulations occurring within days 3 and 8 of

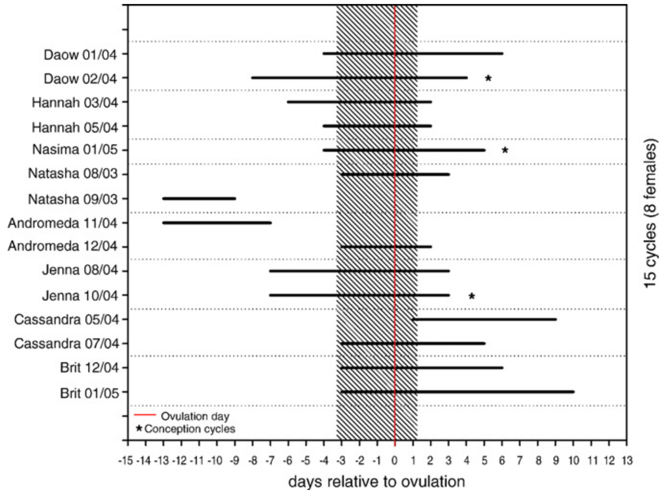

Fig. 3. Maximum swelling duration (days) in relation to ovulation (day 0). The shaded area indicates the presumed fertile period. Numbers behind female names indicate month and year of collection.

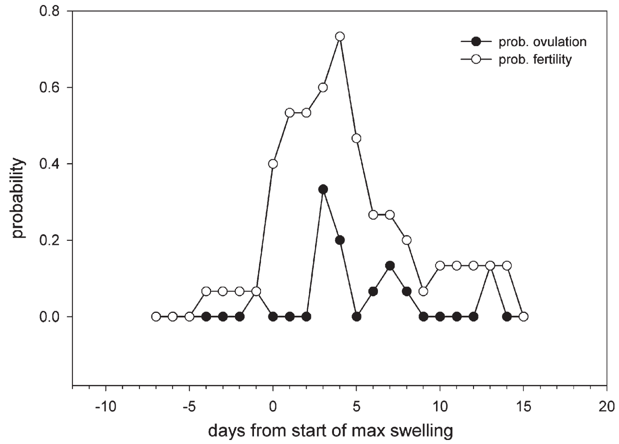

Fig. 4. Probability of ovulation and fertility, relative to the first day of maximum swelling ($n=15$).

the maximum swelling period. Nonetheless, the relationship between maximum swelling and probability of ovulation showed some variation as ovulation occurred from 1 day before the beginning of maximum swelling, to 13 days after the onset of maximum tumescence. Considering fertilization to be possible during 5 days around ovulation, we also calculated the probability of fertility on those days in relation to maximum genital swelling. Fertilization was possible during a period from 4 days before to 14 days after the onset of maximum swelling, with the highest probability of fertility being recorded on day 4 (0.73) of the maximum swelling phase (Fig. 4). Nevertheless, ovulation could take place between 10 days before the last day of maximum swelling and 9 days after the onset of detumescence.

Sexual swelling scores and hormone profiles in sub-adult, pregnant, and lactating females

Sub-adult females

Two sub-adult females displayed their first elongated vulva with a conspicuous mass of pink tissue at approximately 8 years of age (Hima: 8 years and 109 days; Rung: 8 years and 49 days). Variation in swelling size and color were observed thereafter, but none of the three sub-adult females exhibited a clear cyclic swelling pattern before natal dispersal, which happened around 1 year after the first emergence of the sexual swelling (1 year and 42 days for female Hima and 1 year and 24 days for female Rung). Sub-adult females had mean progestogen (5-P-3OH) levels (2.8 ± 0.8 μg/g) that were within the range of cycling adult females. However, none of the sub-adult females showed a cyclic pattern in progestogen levels that would have allowed distinguishing follicular and luteal components of the menstrual cycle and no menarche was detected while they lived in their respective natal groups.

Pregnant and lactating females

Five pregnancies were carried to term and resulted in the birth of healthy offspring. Based on the interval between calculated dates of conception to observed parturition, gestation lengths for two females for which conception dates were available were 184 and 195 days. The relative proportion of the three swelling stages (no, partial, and maximum swelling) differed with reproductive condition [Linear Mixed Model: No Swelling: $F(2,13.77)=95.07$, $P<0.001$; Partial Swelling $F(2,13.61)=7.75$, $P=0.006$; Maximum Swelling: $F(2,14.54)=17.79$, $P<0.001$]. The proportion of swelling stages in lactating females differed significantly from those in cycling and pregnant females (LSD-test: all $P<0.005$), whereas no difference was found between cycling and pregnant females (LSD-test: all $P>0.77$). While lactating females showed no swelling (78.2% of time) during most of the observation period and were barely ever maximally swollen (see Table 3), pregnant females exhibited a maximum swelling 43.3% of the time during the observation period and were not swollen during only 5.2% of gestation. Although overall figures for pregnant females were comparable to figures of cycling females (see Table 3), changes in genital swelling dimensions during gestation did not follow a cyclic pattern. Thus, periods of maximum swelling appeared to occur at random intervals throughout pregnancies with an average duration of 2.7 days, which was considerably shorter than the average of 9.3 days seen in cycling females.

Discussion

In the present study, we combined observational data on sexual swelling morphology with data on female reproductive status based on fecal progestogen analysis to investigate the relationship between swelling changes and female reproductive condition in a population of wild living female white-handed gibbons. Our results indicate that gibbon females exhibit cyclic sexual swelling patterns during the menstrual cycle that are consistent with the theory of advertising fertility, although they do not provide exact information on the precise timing of ovulation. Moreover, changes in genital swellings were not confined to cycling females. Pregnant females displayed sexual swellings in a similar proportion as observed in cycling individuals, but their swelling patterns were not regular. In contrast, sexual swellings were absent in lactating females with the notable exception of one female, whose sexual swelling rapidly increased in size after a male take-over. We conclude that the reproductive biology, sexual swelling patterns, and ovarian changes of wild gibbons most closely resemble patterns and characteristics found in primate species with exaggerated swellings, and suggest that sexual swelling in gibbons has functions similar to those proposed for species with exaggerated sexual swellings.

The emergence of sexual swelling in three young females occurred at approximately 8 years of age. However, even

Table 3
Swelling stages during female reproductive states

Reproductive status	No swelling (%)	Partial swelling (%)	Maximum swelling (%)
Cycling ($n=8$)	6.9	50.9	42.2
Pregnant ($n=5$)	5.2	51.5	43.3
Lactating ($n=6$)	78.3	21	0.7*

* Shown by one female after the group male had changed.

though they showed similar fecal progestogen levels as adult cycling females, their swellings (and progestogen levels) did not show cyclical changes, which might have been due to increased social stress from persistent adult aggression (i.e. chasing from food trees and sleeping areas). Our finding that maximum swelling duration was negatively affected by female age is consistent with data for species with exaggerated swellings (Engelhardt et al., 2005; Nunn et al., 2001), but is in contrast to recent findings in a study on captive-housed gibbon *Hylobates* spp., in which a reverse relationship was found (Cheyne and Chivers, 2006). However, since the latter finding was mainly based on data from juvenile and subadult females of unknown reproductive state (while our data are exclusively based on adult cycling animals) and in which swelling patterns are likely to be irregular (see our study), results of the two studies are not directly comparable and therefore not necessarily contradicting.

Although exaggerated swellings appear strictly associated with mating behavior and competition among males for access to females, the functional significance of this trait remains controversial. Species with exaggerated swellings are found in societies where females mate with multiple males and most functional hypotheses have based their argumentations on this relationship (see review by Zinner et al., 2004). Exaggerated swellings are hypothesized to serve seemingly different purposes for females, e.g. to increase paternity certainty, reliably advertising changes in female reproductive status ("obvious-ovulation hypothesis": Hamilton, 1984) or provide information on female quality ("reliable-quality indicator hypothesis": Pagel, 1994). On the other hand, they are thought to confuse paternity if ovulation does not precisely occur at peak swelling and females mate with multiple males when potentially fertile ("best-male hypothesis": Clutton-Brock and Harvey, 1976; "many-male hypothesis": Hrdy, 1981; Hrdy and Whitten, 1987). The "graded-signal hypothesis" (Nunn, 1999) has reconciled the apparently contradicting functions of sexual swellings in primates. It treats the swelling as a probabilistic signal of females' readiness to conceive and there is empirical support for this interpretation from a number of studies (Reichert et al., 2002; Deschner et al., 2003; Engelhardt et al., 2005). According to this hypothesis, exaggerated swellings indicate the probability of ovulation, without precisely pinpointing it, thus giving females more freedom to manipulate male mating interests. The highest probability of ovulation should occur close to peak swelling, but because of the prolonged duration of receptivity associated with a prolonged display of the sexual signal, females might mate with other males when ovulation is less likely but still possible (Nunn, 1999).

Whether small swellings of primates are compatible with the graded-signal hypothesis has not yet been investigated. In our sample of cycling gibbon females, the majority of ovulations (80%) occurred during maximum swelling, although the timing of ovulation within this period was variable, a finding that resembles the pattern found in many species with exaggerated swellings (Aranda et al., 2006; Deschner et al., 2003; Engelhardt et al., 2005; Möhle et al., 2005). Thus, changes in genital swelling characteristics in white-handed gibbons appear to provide information on the probability of ovulation and the fertile period whilst not allowing males to pinpoint the day of

Table 4
Representative data, ordered by ratio, on swelling parameters and ovarian cycle characteristics across primate species

Species	Cycle length (days)	Maximum swelling duration (days)[a]	Ratio (%)[b]	Range of swelling duration (days)	Swelling type	Mating system
Tarsius bancanus[c]	24±3.2	2.2±0.6	9.17	1–3	O	U-M/U-F
Cercocebus albigena[d]	30	5	16.67	4–6	E	M-M/M-F
Pan troglodytes[e, f]	35.5	10.9±3.2	28.42	6–18	E	M-M/M-F
Macaca tonkeana[g]	35.6±4.5	13±1.3	36.52	6–20	E	M-M/M-F
Hylobates lar[h]	21.1±0.5	9.3±2.3	42.80	5–13	O	U-M/U-F M-M/U-F
Papio papio[i]	29.8±4.1	13.2±2.9	43.69	–	E	M-M/M-F
Pan paniscus[j, k]	33.8±1.4	16±6.8	47.34	3–30	E	M-M/M-F
Macaca fascicularis[l, m]	30.9±4.8	15.1±7.0	48.87	5–25	E	M-M/M-F
Mandrillus sphinx[n]	39.6±10.9[o]	19.5±8.4	49.24	5–46	E	U-M/M-F

O: ordinary swelling; E: exaggerated swelling; U-M: uni-male; U-F: uni-female; M-M: multi-male; M-F: multi-female.

[a] For each species the total number of cycles are more than 10, except for *Tarsius bancanus* (n=10), *Macaca fascicularis* (n=9) and *Macaca tonkeana* (n=6).

[b] Ratio between swelling duration and cycle length.

[c] Wright et al. (1986).

[d] Rowell and Chalmers (1970).

[e] Deschner et al. (2003).

[f] Emery and Whitten (2003).

[g] Thierry et al. (1996).

[h] Present study.

[i] Gauthier (1999).

[j] Heistermann et al. (1996).

[k] Reichert et al. (2002).

[l] Engelhardt et al. (2005).

[m] Dukelow et al. (1979).

[n] Bettinger et al. (1995).

[o] 38 days in semifree-ranging animals: Setchell and Wickings (2004).

ovulation. Furthermore, our data that maximum swelling duration in wild female gibbons is prolonged, covering almost half of the menstrual cycle is similar to the situation found in species with exaggerated swellings (see Table 4), but different to that found in the only other species with small swellings for which comparable data exist (*Tarsius bancanus*; Table 4). Collectively, our data on swelling characteristics in the gibbon are in agreement with the graded-signal hypothesis (Nunn, 1999). The fact that almost half of our study groups were stable polyandrous groups, together with the finding that extra-pair copulations have been reported in several wild gibbon populations (Palombit, 1994; Reichard, 1995; Lappan, 2005), further suggests that gibbon females may have evolved sexual swellings because they are likely to mate with more than one male. Finally, our data on follicular phase length and its degree of variability are consistent with predictions for a species having multiple mating partners as derived from a cross-species comparison carried out by van Schaik et al. (2000).

Because in some primates sexual interaction occurs most frequently when females' genitals are maximally swollen, swellings may assist a male in achieving intromission (Dixson, 1977, 1983) or functions to ensure maximum likelihood of conceptions. Even if sexual swellings in gibbons may have such functions, a recent report that copulations occurred more frequently when a female was swollen (Cheyne and Chivers, 2006) together with our own findings that male mating activities are closely associated with the stage of maximum swelling in both cycling but also pregnant females (82% and 69% of copulations are confined to this period in cycling and pregnant females, respectively; Barelli et al., in preparation) support our interpretation that the small swelling in gibbons attracts male sexual interest analogous to exaggerated swellings of many Old World monkeys and Great Apes.

The graded-signal hypothesis, however, makes no prediction with regard to the occurrence of sexual swellings during non-fertile periods (i.e. pregnancy). It has been suggested that for primate females that face a risk of infanticide continued sexual activity during non-fertile periods may reduce the risk of their infant falling victim of male infanticide (van Noordwijk and van Schaik, 2000). In this respect, developing a swelling during pregnancy, as found in our study females, may help maintain males' sexual interests and mating activity (van Schaik et al., 1999), which in turn can create paternity confusion as a means to reduce infanticide risks (e.g. Engelhardt et al., 2006). Alternatively, but not mutually exclusive, maintaining male sexual interests during non-fertile times may also help a female to ensure the male(s) to stay and to assist with protecting the infant and to defend the territory. Our finding that lactating females exhibit no sexual swelling is not contradicting either explanation.

In conclusion, considering the extended duration of maximum swellings, its variable relationship with timing of ovulation and the common occurrence of swellings during non-fertile periods, the small sexual swellings found in the gibbon appear to be also a sexually selected trait having functions similar to those proposed for exaggerated sexual swellings. From the data available, it appears that the graded-signal hypothesis proposed by Nunn (1999) is in line with characteristics of exaggerated swellings and is also applicable to the less conspicuous swellings, at least in the gibbon, and thus offers to date the most comprehensive explanation for the patterns of sexual swellings found in primates. However, since data on the significance of small swellings are extremely limited, more studies on primates with non-exaggerated sexual swellings and which may differ in their mating system and perhaps other variable factors (e.g. degree of breeding seasonality) are needed to further elucidate the functions of sexual swelling and to unravel the relationships between sexual swellings, social organization and mating systems. In this respect, studies on primate species with small sexual swellings and a variable mating system and a small number of males as found in pair-living and polyandrous primates such as gibbons will be particularly rewarding to investigate whether males use this female trait as a signal to allocate their mating activities and how this in turn affects male–male reproductive competition. Altogether, this approach should substantially improve our understanding not only of the function but also of the evolution of a sexually selected trait that is common amongst female primates.

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