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Mating patterns and sexual swellings in pair-living and multimale groups of wild white-handed gibbons, *Hylobates lar*

CLAUDIA BARELLI*†, MICHAEL HEISTERMANN†, CHRISTOPHE BOESCH* & ULRICH H. REICHARD‡
*Department of Primatology, Max Planck Institute for Evolutionary Anthropology
†Department of Reproductive Biology, German Primate Centre
‡Department of Anthropology, Southern Illinois University, Carbondale

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White-handed gibbons usually live in monogamous pairs, but at Khao Yai National Park, Thailand groups often contain two adult males. We studied mating and sexual behaviour (i.e. proceptivity, receptivity and attractivity) of 12 females in relation to the females' fertile phases as assessed by faecal progestogen analysis. Females' mating activity, in pairs and multimale groups, exceeded the fertile phase and extended well into gestation and, in one exceptional case, into lactation. Whereas copulation frequency was skewed towards one male and peaked during the periovulatory period, no significant difference between fertile and nonfertile phases of the menstrual cycle was detected. Similarly, frequencies of female sexual behaviours, such as proceptivity and receptivity, did not differ across menstrual cycle phases and were common during pregnancy but absent during lactation. However, female attractivity in the form of sexual swellings directly affected copulation frequency, in that copulations were concentrated in the period when females were maximally swollen. Our data suggest that female sexual behaviours do not provide reliable information on the precise timing of the fertile phase to males. Because copulation frequencies were closely associated to sexual swelling stage during both ovarian cycles and pregnancy, we advocate that gibbon females display such visual signals to manipulate male mating behaviour. The results suggest that sexual swellings enable females to mate with multiple males during times when they are not fertile, perhaps to benefit from paternity confusion or to bias copulations towards preferred males when highly fertile to acquire 'good genes'.

Keywords: faecal progestogen; gibbons; *Hylobates lar*; mating behaviour; multimale social system; ovulation; paternity confusion; pregnancy; sexual swellings

In mammals, sexual activity is usually confined to the short fertile phase of the female ovarian cycle, which is the period when copulations can lead to conception (e.g. Idaho ground squirrels, *Spermophilus brunneus*: Sherman 1989; review for mammals: Beach 1947; review for primates: Butler 1974). This temporally restricted window of peak sexual receptivity, generally known as oestrus, is defined as a female's willingness to copulate with males and includes three components: proceptivity, receptivity and attractivity (Beach 1976). With proceptive behaviours, females initiate and maintain sexual interactions with a male. For this, they either use subtle cues such as seeking spatial proximity to a male (Czaja & Bielert 1975; Zehr et al. 2000) or more obvious body postures, gestures, facial expressions, vocalizations or sexual behaviours (e.g. solicitations) to attract male interest in them (e.g. Dixson 1998; tufted capuchins, *Cebus apella*: Carosi et al. 1999). With receptive behaviours, females facilitate intromission and ejaculation while copulation is achieved (Dixson 1998). Attractivity, on the other hand, is often the result of nonbehavioural or passive cues consisting mainly of olfactory (chemical) and visual signals. For example, in many primates, females have evolved visual cues, including coloration and/or size changes of the sexual skin (e.g. sexual swellings), during different phases of their menstrual cycle

Correspondence: C. Barelli, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany (email: barelli@eva.mpg.de). M. Heistermann is at the German Primate Centre, Kellnerweg 4, 37077, Göttingen, Germany. U. H. Reichard is at Southern Illinois University, 4430 Faner Hall, Carbondale, IL 62901-4502, U.S.A.

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which are thought to advertise sexual attractivity (Dixson 1983, 1998; for review see: Zinner et al. 2004).

In contrast to other mammals, in most primates, including humans, female receptivity is prolonged, considerably exceeding the length of the fertile phase (Hrdy & Whitten 1987), and sexual activity can occur at all stages of the reproductive cycle (including pregnancy). Female primates may have evolved extended periods of sexuality as an adaptation to protect their reproductive interests, such as becoming more independent of male coercion (Wrangham 2002). Concealing the timing of ovulation by being receptive for an extended period of time may prevent males from monopolizing access to females during the fertile phase and thus facilitate female choice or polyandrous matings (van Schaik et al. 2000; Hanuman langurs, *Presbytis entellus*: Heistermann et al. 2001; chimpanzees, *Pan troglodytes*: Deschner et al. 2003).

Since most mammal females invest more in offspring than males (Trivers 1972; Emlen & Oring 1977) and the number of young produced during their life span is usually low, females are expected to select their mating and conception partners carefully (e.g. grey mouse lemurs, *Microcebus murinus*: Eberle & Kappeler 2004; pronghorns, *Antilocapra* sp.: Byers & Waits 2006). Generally, females can increase their reproductive success by (1) choosing a specific male to mate with or (2) mating with many males (Keller & Reeve 1995; Jennions & Petrie 2000; Soltis 2002; Hosken & Stockley 2003). By choosing a specific male, females might obtain a combination of both indirect genetic benefits in the form of good genes for their offspring (Hamilton & Zuk 1982; Small 1989; Petrie 1994; Arnqvist & Nilsson 2000) and direct benefits (Davies 1992; Hunter et al. 1993). On the other hand, by mating polyandrously, females might obtain important direct benefits, such as reduced risk of male infanticide through paternity confusion (Hrdy 1979; Cicirello & Wolff 1990; van Schaik et al. 2000; Heistermann et al. 2001; Wolff & Macdonald 2004), increased paternal care (Taub 1980; Burke et al. 1989; Davies 1992; Briskie et al. 1998; Sánchez et al. 1999), improved access to resources (Stanford et al. 1994; Gray 1997), or territorial defence by attracting more males to a group (van Schaik & Hörstermann 1994; Goldizen 2003). Polyandrous mating can lead also to direct genetic benefits if sperm competition occurs (Birkhead & Møller 1998; Dixson 1998; Arnqvist & Kirkpatrick 2005).

In primates, the graded-signal hypothesis (Nunn 1999) further clarified that ovulation concealment, represented by probabilistic cues such as sexual swellings, can allow females to enjoy the benefits of paternity confusion by mating polyandrously (cf. van Schaik & Kappeler 1997) and allowing female choice by being able to bias conception towards a preferred male. The graded-signal hypothesis argues that females living in multimale social systems signal the probability of ovulation rather than its precise timing. By doing so, females mate with the preferred, often dominant, males at the most likely time of ovulation but also mate with other males when conception is less likely. Although studies of some primates have supported this hypothesis (Deschner et al. 2004; Engelhardt et al. 2004; Stumpf & Boesch 2005), empirical data on the degree to which (1) ovulation is successfully concealed from males and (2) female primates are selective across their reproductive cycle are still limited. This information is, however, important to elucidate primate mating strategies and their impact on paternity.

Males might detect female fertility and consequently allocate their copulation activity by using visual cues such as sexual swellings (e.g. chimpanzees: Emery Thompson 2005; baboons, *Papio* sp.: Gesquiere et al. 2007; Barbary macaques, *Macaca sylvanus*: Brauch et al. 2007) and proceptive behaviours (e.g. longtailed macaques, *Macaca fascicularis*: Engelhardt et al. 2005) but also by unclear signals (e.g. capuchins, *Cebus capucinus*: Carnegie et al. 2005; Hanuman langurs: Ostner et al. 2006). Following a recent study of wild gibbons, which revealed that sexual swellings regularly occur in this species but are not strictly confined to the fertile phase (Barelli et al. 2007), we here focus on how female gibbons engage males and express their interest in copulation.

Gibbons (family Hylobatidae) are small apes of east and southeast Asia that are well known for elaborate vocal displays of loud solo songs and complex duets (Geissmann 2002; Clarke et al. 2006). They defend territories of 15−50 ha (Carpenter 1940; Savini et al., in press) against neighbours during regular intergroup encounters (Reichard & Sommer 1997; Bartlett 2003) and were until recently thought to live only in pairs (Fuentes 2000) despite limited information about sexual behaviour and reproductive biology in wild gibbon populations (Reichard 2003; Bartlett 2007).

We studied a population of white-handed gibbons at Khao Yai National Park, Thailand, in which females have an unusually high opportunity for promiscuous matings because 42% of the gibbon groups in our sample contained more than one sexually mature male. By comparison, most gibbon populations consist of monogamous pairs (Carpenter 1940; Ellefson 1974), even though extrapair copulations (EPCs) have been reported in this population (Reichard 1995) and in other populations (Palombit 1994; Lappan 2005). Our main aim was to elucidate possible reasons for multiple mating in this usually pair-living species by investigating patterns of female sexual activity during different reproductive conditions (fertile versus nonfertile) and in different social settings (pair-living versus multimale units). We were also interested in the relationship between female sexual activity and sexual swellings because we have shown recently that the small sexual swellings of gibbons display characteristics similar to the exaggerated swellings of other primates (Barelli et al. 2007). Specifically, we examined behavioural (e.g. proceptivity and receptivity) and nonbehavioural (attractivity, cf. sexual swelling) cues that females might use to achieve copulations and males' responses in allocating their mating effort.

We tested the following predictions. If (1) females copulate only to ensure conception, mating activity will be largely confined to the fertile period. Furthermore, if (2) females copulate primarily to achieve indirect genetic benefits, they will be selective and mate with a preferred male during the fertile period. However, if (3) females are interested mainly in confusing paternity, as a possible direct benefit, they will copulate with more than one male indiscriminately with regard to their stage in the ovarian cycle and when conception is impossible (e.g. during pregnancy or during lactation in case a male take-over occurs). However, a combination of the last two predictions would be in accord with (4) the graded-signal hypothesis. Females will mate with a preferred male when the probability of fertility is high but will still allow other males to copulate when the probability of fertility is low (but not zero). Finally, if (5) females use sexual signals (e.g. specific proceptive behaviours, sexual swellings) to influence male mating activities, males will show increased copulatory activity during days when females display such signals.

To test these predictions we combined faecal hormone analysis with behavioural observations to assess female copulatory activity with males in relation to female reproductive condition and ovarian cycle phase. Moreover, we determined how closely female sexuality (proceptivity, receptivity and attractivity) is linked to the female fertile phase and whether males used potential attractive cues, such as sexual swellings, to allocate their mating effort.

METHODS

Study Site and Animals

The study was carried out in Khao Yai National Park, central Thailand (101°22′E, 14°26′N). The study area consists of a seasonally wet evergreen rain forest with small patches of secondary growth and is at an elevation of 730–870 m. Data were collected from 12 groups, each with a single multiparous female. Seven of the groups were pair-living while five groups contained two adult males that were unrelated to the female. Those five groups are considered to exhibit multimale group structures and/or socially polyandrous mating systems (sensu Kappeler & van Schaik 2002). The number of males included in the analysis was 21, which we divided into two categories. Twelve ‘primary males’ were defined as the single male in pair-living groups ($N = 7$) or males in multimale groups ($N = 5$) who engaged exclusively, or almost exclusively, in singing duets with the adult female. The remaining nine males, defined as ‘secondary males’, were the other adult males in multimale units ($N = 5$), who rarely sang with the female, or males in neighbouring groups which engaged in EPCs during group encounters ($N = 4$).

Behavioural Observations

Behavioural observations were carried out by C. Barelli and three experienced Thai field assistants over three field periods (July–December 2003, February–August 2004 and October 2004–March 2005), with faecal collection and recording of sexual swelling scores being done concurrently. Each observer followed one of the 12 study females from dawn to dusk (average observation time: 8.24 h/day) over a period of 3 months, recording occurrence or absence of copulations using the all-occurrence sampling method (Altmann 1974). Copulations were defined as males achieving intromission and pelvic thrusting for more than 5 s. Ejaculations could not be detected. To rule out days in which copulations were not biologically meaningful, we defined the frequency of copulations as the number of copulations performed by the females divided by the number of days in which copulations had been observed. In addition, to compare the amount of copulations performed in different reproductive stages, we calculated the frequencies of copulations over the total number of hours observed in each reproductive stage. Where not stated otherwise, frequency refers to the first definition. In addition, detailed data on sexual behaviour were collected by C. Barelli for a total of 295 complete days for seven cycling (1402 h, average: 8.43 h/day), six pregnant (773 h, average: 8 h/day) and seven lactating (381 h, average: 8 h/day) females.

One female which appeared to be postreproductive and one presenting abnormal hormone profiles from which the timing of ovulation could not be reliably assessed (see below) were excluded from analysis (Table 1).

Definitions of Female Sexual Behaviours

In line with previous definitions (Beach 1976; Dixson 1998), we classified proceptive behaviours as spontaneous ventral or dorsal presentation of genitalia by a female to a male. Additionally, as a plausible measure to assess female initiative, we recorded female approaches to within a 0.5-m radius around the male. We assessed the frequency of approaches as the total number of entries in which a female was responsible for seeking close proximity (0.5 m) to a male divided by the total time, expressed in hours, in which the dyad was observed for mating and nonmating days. Receptive behaviours included behaviours that facilitated intromission: a female bending forward and lifting her hip and genitals towards the male, grasping and

Table 1. Hormonal and behavioral data collected during different reproductive stages of Khao Yai female gibbons

	Group	Female	Pregnant	Lactating	Cycling
Multimale group					
1	A	AN	—	—	× (2)*
2	D	DA	×	×	× (2)
3	J	JE	××	×	× (2)
4	NOS	NA	×	—	× (1)
5	T	BE	—	×	—
Pair-living group					
6	B	BD	—	—	PR
7	C	CA	—	×	× (2)
8	H	HA	×	×	× (2)
9	N	NT	—	—	× (2)
10	R	BR	—	×	× (2)
11	S	SO	—	—	†
12	W	WO	×	×	—

PR: postreproductive, excluded from analysis; †: abnormal cycle, excluded from analysis; ×: occurrence of collection; ××: Jenna was collected over two gestation periods, first in 2003 and second in 2004 after losing her 7-month-old infant and conceiving again.
*Number of cycles included in the analysis (in parentheses).

pulling the male towards herself while bent and/or using eye contact during intromission. Refusal behaviours were identified as behaviours displayed by the female such as moving away, screaming or responding aggressively to a male's approach and attempt to copulate.

Assessment of Sexual Swelling Stage

To test predictions about the timing of copulations within the female reproductive cycle and whether males respond to visual cues, we collected systematic data on female sexual swellings. Swelling tumescence was scored daily after visual inspection and the size was assessed intraindividually by comparing it to the size of a female's ischial callosities. We distinguished three categories: no swelling, partial swelling and maximum swelling (for details see Barelli et al. 2007).

Faecal Sample Collection, Hormone Analysis and Assessment of the Fertile Phase

All 12 females were followed regularly during one or more reproductive conditions (i.e. cycling, pregnant or lactating; Table 1). To determine a female's reproductive stage, timing of ovulation and fertile phase we regularly collected faecal samples and measured levels of immunoreactive 5α-reduced 20-oxo pregnanes (5-P-3OH) as previously validated and described (Barelli et al. 2007; Barelli & Heistermann, in press). Over the individual 3-month study periods, frequency of faecal sampling varied according to female reproductive condition. Faeces of potentially cycling females (females that did not carry an infant) were collected almost daily, whereas faeces of lactating females were collected weekly to biweekly. When after a 3-month collection of daily samples females did not give birth, we switched to a weekly/biweekly sampling regime because we considered these females to be potentially pregnant. Since a cycling or pregnant status could, however, be identified only post hoc by the female's faecal progestogen profile (see Barelli et al. 2007), samples of pregnant females were available in variable frequencies (from daily to once weekly). Prior to hormone measurements, faecal samples were extracted twice (Barelli et al. 2007) and, depending on female reproductive status, prior to assay, samples were diluted 1:20 to 1:100 in assay buffer. 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.

Hormone profiles were available for eight cycling females (15 cycles in total), six pregnant females and seven lactating females (Table 1). Based on the defined postovulatory (luteal) rise in faecal progestogen levels and taking into account steroid passage time, we determined for each cycle the presumed day of ovulation as 3 days preceding the defined faecal 5-P-3OH increase (Barelli et al. 2007). According to human data on the functional life span of sperm (France 1981; Wilcox et al. 1995) and allowing for possible error in the determination of ovulation, the fertile phase of an ovarian cycle was defined as a period of 5 days, comprising the presumed day of ovulation plus the following day and the 3 days preceding ovulation (Barelli et al. 2007). Days preceding and following the 5-day fertile period were considered the nonfertile phase.

All data collection was carried out in compliance with current Thai laws and permission of the National Research Council of Thailand and the National Park, Wildlife and Plant Conservation Department of Thailand.

Statistical Analyses

Hypotheses were tested with a Wilcoxon test or by using the related samples with missing values test while maintaining the position of missing values and running 10 000 permutations (Mundry 1999). Nonparametric tests were exact tests if samples were small (Siegel & Castellan 1988; Mundry & Fischer 1998). We used binomial tests to compare the number of copulations a female performed with the primary and the secondary male in polyandrous groups. Since such a test was conducted for each female separately, we adjusted P values for multiple testing using a function which can be derived from the Dunn–Šidák equation (Sokal & Rohlf 1995), $P_{ck} = 1 - (1 - \alpha)^k(1/k)$, with P_{ck} = adjusted P value, α = original P value and k = number of tests. Such corrected P values can be interpreted as usual. In some cases we present exact Wilcoxon tests based on sample sizes that are too small to possibly reveal a significant outcome ($N < 6$). We nevertheless felt that indicating such results is useful because, first, with $N = 5$ an exact Wilcoxon test may still reveal a trend ($P < 0.1$) and, second, a large P value would still suggest that there is not a very large effect. All statistical tests were two tailed.

RESULTS

Mating Activity in Relation to Reproductive Conditions and Social System

Mating activity was not confined to specific months or seasons. We observed matings in each month of the year for cycling females and in 11 of 12 months for pregnant females. In total, 442 copulations were recorded (cycling females: 62%, $N_{cop} = 275$; pregnant females: 36%, $N_{cop} = 158$; one lactating female: $N_{cop} = 9$; the lactating female copulated only directly after a male replacement). The frequency of copulations over the total time of observation was similar in cycling (median = 0.12, range = 0.02–0.28, $N = 8$) and pregnant (median = 0.13, range = 0.03–0.39, $N = 6$) females but was markedly lower during lactation (only one of seven females engaged in copulations; Fig. 1).

Two females (one cycling, one pregnant) living in pairs and one (cycling) living in a multimale unit were observed engaging in six EPCs. All five females living in multimale social units engaged in polyandrous mating during either the cycling or the pregnant stage (Table 2). However, copulation with multiple males was highly skewed. Cycling

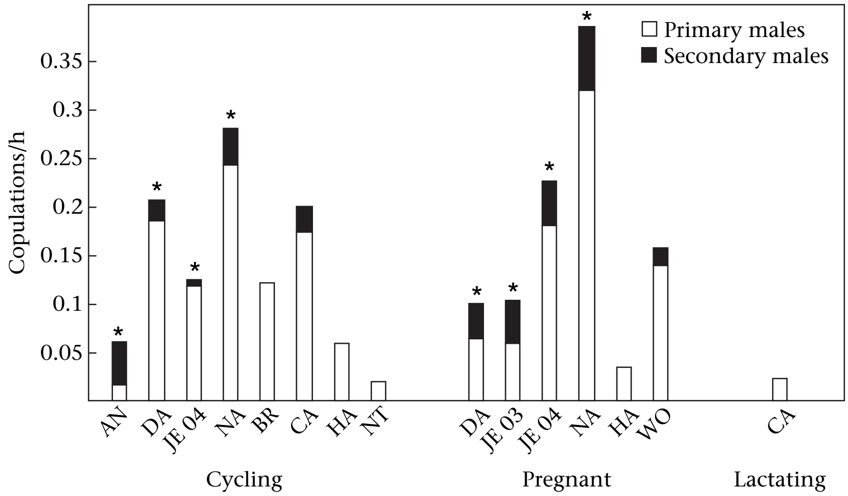

Figure 1. Frequency of copulations (copulations/h observed) performed and proportions performed with primary and secondary males for the three different reproductive conditions (see text for definition of primary and secondary males). *Females living in multimale groups.

females performed significantly more copulations with primary ($N = 244$) than with secondary (EPCs included: $N = 31$) males (four binomial tests: three of four females: $P_{c4} < 0.039$, all $N \geq 6$); similar results were observed for pregnant females, who mated more often with primary ($N = 125$) than with secondary ($N = 33$) males (two of four females: $P_{c4} < 0.001$, all $N \geq 8$; see Fig. 1).

Table 2. Proportion of sexual interactions performed by different females with their primary male, for females living in different social systems and in relation to their reproductive condition

	Cycling stage			Pregnant stage		
Female	Cop	Pro	Rec	Cop	Pro	Rec
Multimale group						
AN	0.27	0.50	0.44			
DA	0.90	nd	nd	0.65	0.88	0.86
JE 03				0.57	0.45	0.63
JE 04*	0.96	1	1	0.80	0.79	0.81
NA	0.86	1	0.80	0.83	0.97	0.80
Pair-living group						
CA†	0.87	0.90	0.73			
HA	1	1	1	1	0	1
NT	1	1	1			
BR	1	1	1			
WO				0.89	1	1
Total average (%)	0.86	0.91	0.85	0.79	0.68	0.85

Cop/Pro/Rec: proportions of total number of copulations/bouts of proceptive behaviours/bouts of receptive behaviours observed with the primary male during cycles considered. Values <1 indicate that females copulated not only with their primary male but also with both the second male in the group and/or the neighbouring males. nd: Data not available.

*JE was collected during two pregnant stages (during 2003 and 2004).

†The only female that, during lactation, after a group male take-over, engaged in copulations ($N = 9$) with the new primary male but did not show any proceptive or receptive behaviour.

Distribution of Copulations in Relation to Timing of Ovulation and Fertile Phase

Figure 2 shows the distribution of copulation frequencies for the two types of males relative to the presumed day of ovulation. Whereas copulations with secondary males remained at a consistently low rate throughout the cycle, copulation frequency with primary males increased progressively from the early/midfollicular phase towards ovulation, with peak values being recorded 2 days after ovulation. Copulation frequency declined rapidly thereafter, reaching nonfertile phase levels by day 5 after ovulation (Fig. 2). With regard to the copulation frequency of females with primary males, no significant difference was found between the fertile and the nonfertile phases (fertile

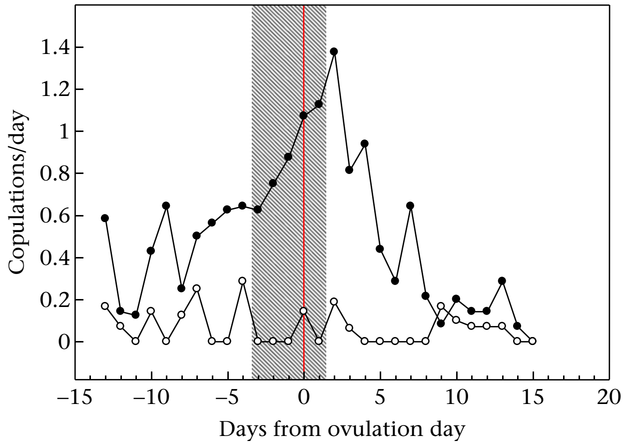

Figure 2. Female copulation frequencies (copulations/day in which copulations occurred) with primary males (●) and secondary males (○) related to the day of ovulation (day 0). Copulation frequency was calculated by taking the average copulation frequency for each female separately and averaging across these individual values to yield a representative composite frequency that equally balanced individual contributions. The shaded area indicates the presumed fertile phase.

phase: median $= 1.54$, range $= 0.5-4.20$; nonfertile phase: median $= 1.42$, range $= 0.2-2.33$; Wilcoxon test: $T^+ = 20$, $N = 8$, $P = 0.844$), whereas copulation frequency tended to be higher during the nonfertile phase for copulations with secondary males (fertile phase: median $= 0$, range $= 0-0.2$; nonfertile phase: median $= 0.33$, range $= 0.08-0.80$; $T^+ = 15$, $N = 5$, $P = 0.063$), presumably because they rarely copulated during the fertile phase (Fig. 2).

Female Sexual Behaviours in Relation to the Fertile Phase

Female proceptive and receptive behaviours occurred in cycling and pregnant stages but not during lactation. Females were proceptive and receptive towards all males in the group (Table 2). The single sexually active lactating female displayed neither proceptive nor receptive behaviours. Cycling females were proceptive towards primary and secondary males during fertile and nonfertile phases of their ovarian cycles with frequencies of behaviour not significantly different between phases (fertile phase: median $= 0.4$, range $= 0-2.2$; nonfertile phase: median $= 0.67$, range $= 0.29-2$; Wilcoxon test: all males: $T^+ = 17$, $N = 7$, $P = 0.69$; primary males: $T^+ = 16$, $N = 7$, $P = 0.81$). Females also approached males similarly often in the fertile and nonfertile phases of the cycle (fertile phase: median $= 0.19$, range $= 0.07-0.21$; nonfertile phase: median $= 0.17$, range $= 0.10-0.35$; Wilcoxon test: primary males: $T^+ = 11$, $N = 5$, $P = 0.44$; for female DA and JE data were not available) and showed receptive behaviour towards both types of males with frequencies not significantly different between cycle phases (fertile phase: median $= 1$, range $= 0-3.67$; nonfertile phase: median $= 0.75$, range $= 0.14-1.80$; Wilcoxon test: all males: $T^+ = 19$, $N = 7$, $P = 0.47$; primary males: $T^+ = 20$, $N = 7$, $P = 0.37$). Finally, female avoidance of male copulation attempts did not differ significantly between the fertile and the nonfertile phases (fertile phase: median $= 0$, range $= 0-0.5$; nonfertile phase: median $= 0.05$, range $= 0-0.33$; Wilcoxon test: primary male: $T^+ = 8$, $N = 5$, $P = 1$; for female DA and JE data were not available), but this behaviour was rare. Because of the small sample sizes, we could not reasonably test female solicitations (proceptivity) and facilitations (receptivity) towards secondary males.

Male Mating Activity in Relation to Female Sexual Swelling Stage

Given that maximum sexual swellings are largely displayed during the female fertile phase but are also well extended outside the 5-day fertile phase of the ovarian cycle (Barelli et al. 2007), we investigated the possible relationships between sexual swelling stage (no, partial and maximum swelling; for definition see Barelli et al. 2007) and male mating behaviour. We found that 72% of all copulations performed by cycling females occurred during maximum swelling stage and with primary males (Fig. 3a). However, when females were maximally swollen, copulation frequencies did not differ significantly between their fertile and their nonfertile phases (Wilcoxon test: primary males: $T^+ = 21$, $N = 7$, $P = 0.281$). Only outside the 5-day fertile phase did primary males copulate significantly more often when females displayed maximum sexual swellings compared to partial swellings (Wilcoxon test: primary males: $T^+ = 32.5$, $N = 8$, $P = 0.047$; Fig. 3a). Secondary males, who copulated mainly during the nonfertile phase, engaged in copulations more indiscriminately with respect to partial and maximum swelling stage (Wilcoxon test: $T^+ = 3$, $N = 4$, $P = 1$; Fig. 3b).

A similar pattern was found for pregnant females: copulation frequencies with primary males were significantly higher when females were maximally swollen compared to partially swollen ($T^+ = 21$, $N = 6$, $P = 0.031$), whereas, when females copulated with secondary males, there were no differences in copulation frequencies for maximum and partial swelling stages (Fig. 4).

DISCUSSION

By combining behavioural and endocrinological data we provide direct evidence of flexible mating behaviour in a wild white-handed gibbon population. Specifically we show that, contrary to earlier descriptions of white-handed gibbon mating behaviour (Carpenter 1940; Ellefson 1974), the majority of females in our sample are polyandrous and not monoandrous. Although females copulated with multiple males (either the social partner and extragroup males or both males in multiple groups), copulation activity was highly skewed towards one male, a primary male. The copulation frequency with primary males increased progressively towards ovulation and remained elevated for some days thereafter, so that copulation frequencies did not differ significantly between fertile and nonfertile phases of the female cycle. Males appeared to mate not in accordance with female fertility but in response to the presence of a maximal sexual swelling. Frequencies of female proceptive and receptive behaviours also did not differ with regard to cycle phase or primary versus secondary males. Sexual activity was, however, linked to female sexual swelling stage. Primary, but not secondary, males copulated significantly more with females who were maximally swollen. We assume that these males cued on the swelling rather than another signal because (1) they also mated with maximally swollen pregnant females and (2) female sexual behaviours did not vary detectably across the menstrual cycle.

Although an extended period of sexual activity is not exceptional in primates (Campbell 2007), a peak in mating is usually observed on days surrounding the fertile phase (e.g. tufted capuchins: Carosi et al. 1999; Japanese macaques, *Macaca fuscata*: O'Neill et al. 2004; longtailed macaques: Engelhardt et al. 2005) and this was also seen in the gibbon females studied here. However, sexual activity was extended far beyond the fertile phase and, moreover, copulations occurred at similar frequencies during cycling and pregnant stages. In both reproductive conditions, females performed multiple matings, achieving a high frequency of copulations with the second male in the group, up to 43% during pregnancy or, in

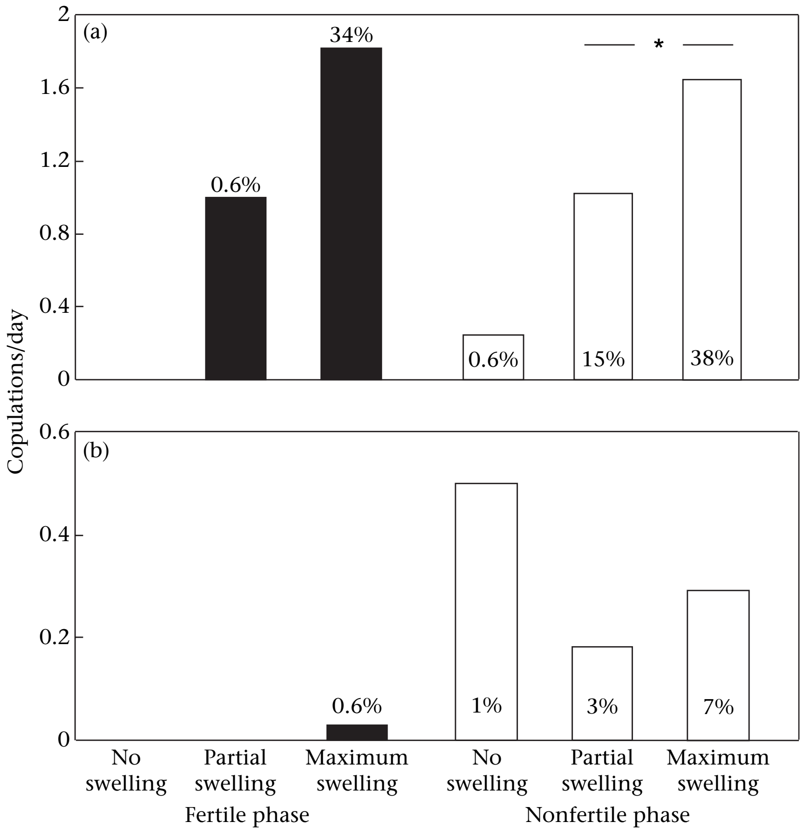

Figure 3. Cycling females' copulation frequencies (copulations/day in which copulations occurred) with (a) primary males and (b) secondary males during fertile (black bars) and nonfertile (white bars) phases in relation to sexual swellings. Percentages indicate the proportion of copulations, in each swelling stage and per type of male, over the total copulations observed during the cycling condition. $^*P < 0.05$ (for details see text).

an exceptional case, up to 73% during cycling stage (Table 2). The latter case might be the reflection of the relatively new trio formation which also influenced the regular singing patterns. This female was seen engaging in duets, simultaneously or separately, with both adult males in the group. These observations of flexible female sexual activity thus beg the question: what benefits could a female gain in mating with more than one male and

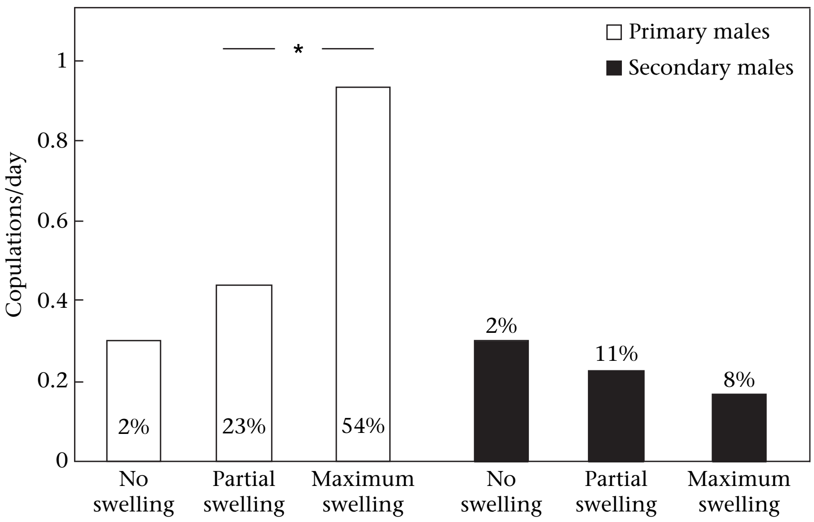

Figure 4. Pregnant females' copulation frequencies (copulations/day in which copulations occurred) with primary and secondary males in relation to the three different sexual swelling stages. Percentages indicate the proportion of copulations, in each swelling stage and per type of male, over the total copulations observed during pregnancy. $^*P < 0.05$ (for details see text).

outside her fertile phase? Females who mate polyandrously when possibly fertile might profit by ensuring conception (van Noordwijk & van Schaik 2000) or having their offspring sired by the male who is most successful in sperm competition (Dixson 1998). If copulations are, however, skewed towards a specific male, as found in this study, a female might also benefit by focusing paternity certainty on a male that is most capable of defending her infant (Borries et al. 1999; van Schaik et al. 1999, 2004) or territory (van Schaik & Hörstermann 1994; callitrichids: Goldizen 2003). Such a strategy would simultaneously, however, also allow for paternity confusion with the benefit of reducing the risk of infanticide (Hrdy 1979; Nunn 1999; van Schaik et al. 2000) because it would be costlier for a male to mistakenly kill his own offspring than to resist killing another male's infant if there is a slight, but nonzero, probability that he is the sire (van Schaik et al. 2004). Moreover, matings during pregnancy, when fertilization is impossible, have also been suggested to confuse paternity and reduce the risk of infanticide in case of a male take-over (van Noordwijk & van Schaik 2000; van Schaik et al. 2000). Interestingly, although speculative, the only lactating female that was sexually active had just experienced a male take-over. Fourteen weeks after the new male's take-over, her infant disappeared following the new male's persistent approaches and a few observed attempts of slapping at the mother–infant pair. Moreover, whether her sexual activity was ultimately linked to the male take-over remains speculative, but her spontaneous development of a sexual swelling and the onset of sexual activity contrasted strongly with other lactating females' behaviour. Perhaps, her sexual activity is best interpreted as part of a tactic to prevent an infanticide by trying to deceptively communicate receptivity to the new male. The case is suggestive because it fulfils three key requirements for the occurrence of sexually selected male infanticide (van Schaik et al. 2000): (1) the new male was unknown in the area and therefore can be assumed to have had a zero or close to zero probability of having fathered the female's current offspring, (2) killing the infant shortened the interval until the female's subsequent conception compared to the expected interval if the current infant had survived, and (3) the new male had an increased chance to father the female's subsequent offspring because he remained paired with the female until her next parturition.

Extended sexual receptivity and absence of reliable signs of ovulation are important prerequisites facilitating paternity confusion (van Schaik et al. 2000). Such a function would be in accordance with our findings that proceptivity and receptivity did not differ in frequency in the fertile and nonfertile phases and thus did not advertise the female gibbons' fertile phases (see also black-handed spider monkeys, *Ateles geoffroyi*: Campbell 2004). Although proceptive and receptive behaviours are displayed in both fertile and nonfertile phases of the female cycles and during pregnancy, the overall amount of data collected on female sexual behaviours was relatively small, which might be an alternative explanation for our deviant results compared to many other primates (e.g. rhesus monkeys, *Macaca mulatta*: Wallen et al. 1984; tufted capuchins: Carosi et al. 1999; longtailed macaques: Engelhardt et al. 2005), in which females clearly signal their fertility via behavioural changes. However, in some primates, female sexual behaviour may obscure rather than clearly advertise fertility (Nunn 1999; Stumpf & Boesch 2005) and, alternatively, males could use nonbehavioural cues such as pheromones from vaginal discharge to assess timing of the fertile phase (Epple 1986; Cerda-Molina et al. 2006). However, data on pheromones in primates, including gibbons, are equivocal and behaviours that would suggest olfactory communication for gibbons have not been reported. Since copulation frequencies did not differ significantly between the fertile and the nonfertile phases of the menstrual cycle, it seems likely that male gibbons are unable to use olfactory cues for assessing female fertility.

Instead, sexual swelling, a nonbehavioural cue, was of key importance in guiding male gibbons' sexual interest and mating behaviour. Studies on several primates have showed that, because the duration of sexual swellings is prolonged over the ovarian cycle, they do not indicate the exact time of ovulation but rather give a crude measure of a period when ovulation will probably occur (e.g. bonobos, *Pan paniscus*: Reichert et al. 2002; chimpanzees: Deschner et al. 2003; Emery & Whitten 2003; longtailed macaques: Engelhardt et al. 2005; Barbary macaques: Möhle et al. 2005); such results were also found in our previous study of this population (Barelli et al. 2007). As predicted by the graded-signal hypothesis (Nunn 1999), copulation frequencies varied in relation to sexual swelling stage, being highest when females were maximally swollen. Thus our data clearly suggest that male gibbons used changes in female swelling stage as a basis for their mating activity, thus resembling chimpanzees (Deschner et al. 2004), bonobos (Reichert et al. 2002), baboons (Gesquiere et al. 2007), and Barbary macaques (Brauch et al. 2007). That males use swellings to allocate their copulations might also explain why the copulation peak in our study females is seen 2 days after ovulation, as on average detumescence occurred 3 days postovulation (Barelli et al. 2007). However, given the imprecise information that swellings provide about the exact timing of ovulation and their presence during pregnancy (Barelli et al. 2007), male gibbons are most likely unable to precisely detect impending ovulation and thus to effectively monopolize a female at the time when fertilization is most likely.

Extending the display of sexual swellings beyond the fertile phase might increase polyandrous mating (Hrdy & Whitten 1987; van Noordwijk & van Schaik 2000). Of nine study females, four lived in multimale social groups with two adult males to whom they directed proceptivity and receptivity and engaged in sexual interactions at similar frequencies during their cycling and pregnant stages. Moreover, five neighbouring males engaged in copulations with either cycling or pregnant females that lived in pairs or multimale groups. Thus, although primary males performed most copulations and had the greatest access to females during the fertile phase, secondary males likewise achieved some copulations at any time and, in one case, even did so during the presumed day of ovulation of a conception cycle (Fig. 2). This suggests that secondary male gibbons are not excluded from achieving paternity. In addition, in the only case of a male take-over observed during the study, a female with a dependent offspring developed sexual swellings during lactation and soon afterwards was observed copulating with the new male, which is consistent with the hypothesis that sexual swellings enhance copulations. Thus, flexible mating behaviour and imprecise sexual swellings in wild gibbon females are consistent with the theory of confusing paternity.

An important finding of our study is that, although gibbon females increased mating with a preferred male during the fertile phase, sexual activity extended into the nonfertile phase of the ovarian cycle, occurred during pregnancy and was performed with multiple males. Even though the reproductive success of the primary males should be sufficiently high to outweigh the costs of the presence of a second male in the group, female white-handed gibbons may have developed an ability to manipulate paternity and thereby safeguard their own reproductive success. Gibbon females appear to be able to attract males through nonbehavioural cues (e.g. sexual swellings), which might reduce the need for high levels of proceptive and receptive behaviours. Finally, the display of imprecise sexual swellings, together with a flexible social organization and variable mating system, shows how sexual behaviour in anthropoid primates, including humans, has been to some degree uncoupled from ovarian activity, thus departing from the usual mammalian pattern.

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