Hormonal correlates of the ovarian cycle in the yellow-cheeked crested gibbon (*Nomascus gabriellae*), and a review of ovarian cycles in gibbons (Hylobatidae)

Thomas Geissmann[1] and Gustl Anzenberger[2]

[1] Anthropological Institute, University Zürich-Irchel,
Winterthurerstr. 190, CH–8057 Zürich, Switzerland
E-mail: thomas.geissmann@aim.uzh.ch

[2] Psychological Institute, Biomathematical Section, University Zürich,
Attenhoferstr. 9, CH-8032 Zürich, Switzerland, and Zoo de Mulhouse,
51 rue jardin zoologique, F-68100 Mulhouse, France

Ovarian cycles were determined for two captive females of the yellow-cheeked crested gibbon (*Nomascus gabriellae*) using urinary sex steroids. The mean cycle length was 21.1±1.2 days ($n = 7$ cycles). The interval between any peak in oestrone concentration and the corresponding oestradiol peak had a range of 0-1 days, and cycle lengths determined with oestrone differed from those determined with oestradiol by 0-2 days. Neither hormone tended to peak earlier than the other. In female 1, menarche probably occurred just before or around the beginning of the colour transition from the black juvenile to the adult yellow fur coloration, whereas the older female 2 apparently began to exhibit regular cycles during this study, years after changing to adult fur colouration. Mean cycle lengths determined in this study for *N. gabriellae* were virtually identical to those for those of other gibbons determined in previous studies applying endocrinological methods (*Hylobates* spp.: 20.0-25.4 days, *N. leucogenys*: 21.9, *Symphalangus syndactylus*: 21.8). These values are, in most cases, similar to intervals determined between peaks of sexual swellings. On the other hand, published cycle lengths based on intervals between menstrual bleedings or between copulations tend to be considerably longer. Because some cycles may easily remain undetected with the latter two methods, the resulting intervals may not be reliable indicators of the duration of menstrual cycles in gibbons. Cycles of gibbons appear to be shorter than those of other primates, apart from some – but not all – New World monkeys.

Introduction

Monitoring ovarian cycles is of considerable importance for managing breeding in captive primates. Most previous publications dealing with endocrinology of reproduction in gibbons (Hylobatidae) have referred to *Hylobates lar* (Barelli *et al.*, 2007; Czekala *et al.*, 1985; Nadler *et al.*, 1993) or other members of the genus *Hylobates*. These gibbons differ from gibbons of other genera in several respects, including body weight (*Hylobates*: c.5 kg, *Nomascus* and *Hoolock*: c.7-8 kg, *Symphalangus*: c.11 kg) (Geissmann, 1993, 1998). Therefore, information on the reproductive endocrinology of *H. lar* may not necessarily apply to gibbons of the other genera.

Crested gibbons (genus *Nomascus*) are all endangered or critically endangered in the wild by the IUCN's Red List assessment (Geissmann, 2007; IUCN, 2008), and captive populations of most species, including the yellow-cheeked crested gibbon (*N. gabriellae*), are very small (Geissmann, 1995a; Lernould, 1993; Moisson and Prieur, 2007). Information on the reproductive biology of this group is of pivotal importance for successful captive breeding.

The aims of the present study were to: (1) characterize the ovarian cycle by urinary sex steroid levels in the yellow-cheeked crested gibbon (*N. gabriellae*); (2) compare these hormonal cycles with those reported in the literature but determined using other methods; and (3) compare the ovarian cycles of the genus *Nomascus* to those of other gibbon genera.

Animals, materials and methods

Animals

Taxonomic treatment of the Hylobatidae follows Geissmann (2007). International Studbook numbers of study animals refer to Lernould (1993).

The following three females were included in this study:

Female 1 ("Robin", International Studbook No. 0122) was born on 15 Jul. 1981 at the Los Angeles Zoo (U.S.A.) (parents 0064 "Koo" x 0065 "Bahmetoo"). The adult female was loaned to Mulhouse Zoo (France) on 10 Jan. 1992, and, during 1993, was intermittedly paired there with an adult male ("Charlot", Fig. 1). By Feb. 1994 (the beginning of urine sampling), the female had been moved to the quarantine quarters of the Zoo Mulhouse waiting for her transfer to the Osnabrück Zoo. During the period of urine sampling, the female was kept singly but adjacent to the also singly housed subadult male "Dorian" (*N. siki*, 0221). On 31 Jan. 1995, the female was transferred to Osnabrück Zoo (Germany), where she was paired with the adult male "Chang", starting on 8 Feb. 1995. Between 2 Jan. 1997 and 15 Oct. 1999, the pair had four offspring at Osnabrück, but none of them was reared. The pair was transferred to the Hannover Zoo (Germany) on 6 Sep. 2001.

Fig. 1. Female 1 ("Robin", right) and male "Charlot" (left) on 3 July 1993 at the Mulhouse Zoo. Photo: Thomas Geissmann. – *Das Weibchen "Robin" (rechts) mit Männchen "Charlot" im Zoo von Mulhouse am 3 Juli 1993*.

Female 2 ("Tsickó" or "Chicho", International Studbook No. 0158) was initially identified as *N. siki* based on unpublished karyological studies using the criteria proposed by Couturier *et al.* (1991) (Lernould, personal communication to TG) and was listed as *N. siki* in the studbook by Moisson and Baudier (2005). However, she is identified here as *N. gabriellae* on the basis of species-specific characteristics of fur coloration (described in Geissmann, 1994, 1995b; Geissmann *et al.* 2000) as documented during various stages of her development. This identification is further supported by the female's song vocalizations tape-recorded in Budapest, Osnabrück and Hannover (Geissmann, unpublished data) and mitochondrial DNA sequences from the control region which clearly group the female with *N. gabriellae* and not with *N. siki* (Geissmann and Kressirer, unpublished data).

Female 2 was kept solitary in adjacent indoor/outdoor cages at the Budapest Zoo (Hungary). Although visual contact was ruled out, the study animal could hear and probably smell another unrelated, solitary female *N. gabriellae* kept in a neighbouring cage (adut female 3 of this study, see below).

Female 2 was wild-born. She was imported from Vietnam and arrived at Budapest Zoo on 4 Nov. 1987. She exhibited a black fur coloration, and, based on photographs, she was estimated to be about 1.3 years old when she arrived in Budapest. By June 1993, her nipples had grown to adult size. After June 1993, the female began to change her fur colouration. At about the time of sexual maturity (at around 5-8 years of age), female gibbons of the genus *Nomascus* are known to lose the black fur colouration typical of juveniles and adopt the yellowish or buff coloration with black cap typical of adult females (Geissmann, 1993). In Oct. 1993, light fur became conspicuous above the study female's ears, in the shoulder area on the back, in the genital region and around the ischial callosities.

During the study (Jan.–May 1994), the female was of adult size, her canines appeared to be fully erupted, and she had an estimated age of 7.5-7.8 years. At the end of this study (on 8 May 1994), the female was about halfway through the transition from juvenile to adult fur colouration: Her back was light yellow-grey, but the ventrum, lower arms and lower legs were still dark grey (Fig. 2a). Her colour change was progressing rapidly (Fig. 2b) and by Sep. 1994, her fur was essentially yellow, only the upper (cranial) part of her ventrum was still dark grey.

After this study, the female was kept as a pair with an adult male *N. leucogenys* and produced several hybrid offspring, the first of which was born on 25 Dec. 1995. On 20 May 1997, the female was transferred to Nyíregyháza Zoo (Hungary), where she died on 30 May 1997.

Female 3 (Júska, International Studbook No. 0168) was wild-born, reportedly circa 1986 in Vietnam (Moisson and Baudier, 2005). She arrived at Moscow Zoo on 18 Feb. 1987 as a black juvenile and was named "Yuyu" there. Photographs made in Nov. 1988 show her with a light grey fur colouration, about halfway through the transition from juvenile to adult fur colouration (Fig. 3a). As this colour change should be expected to occur at a later age than two years, it is likely that her age at arrival in Moscow was underestimated and her birth date may have been closer to 1984 than to 1986. On 16 March 1991, the female was transferred to Budapest Zoo. The female was in the adult yellow coat on arrival in Budapest (Fig. 3b), where she was renamed "Júska" and kept solitary in the cage adjacent to that of female 2 (Tsickó). On 28 June 1994, she was transferred to Bojnice Zoo (Slovakia), on 11 Sep. 1996 to Bratislava Zoo (Slovakia), an on 12 June 2002 back to Bojnice. In Slovakia, the female was renamed "Jozefina" and successively paired with two males. Her only offspring was deadborn prematurely on 16 July 2005. The female suffered from chronic diarrhea and died of Crohn's disease in June 2008 (P. Luptak, personal comm. 30 Apr. 2009).

Fig. 2. Female 2 ("Tsickó") at the Budapest Zoo on 8 May 1994 (a) and in June 1994 (b) showing rapidly progressing change of fur colouration when she was about 7 years old. Photos: Krisztina Vasarhelyi and Janos Tardi. – *Das Weibchen "Tsickó" im Zoo von Budapest durchlief im geschätzten Alter von 7 Jahren einen raschen Wechsel der Fellfärbung: (a) 8. Mai 1994, (b) Juni 1994*.

Fig. 3. Female 3 ("Júska") during her change of fur colouration at the Moscow Zoo in Nov. 1988 (a) and in her adult coat at the Budapest Zoo on 13 June 1993 (b). Photos: Vladimir Spitsin and Krisztina Vasarhelyi. – *Das Weibchen "Júska" (a) während des Wechsels der Fellfärbung im Zoo von Moskau im November 1988 und (b) im gelben Erwachsenenkleid im Zoo von Budapest am 13. Juni 1993*.

During the period when urine sampling took place, study females 2 and 3 were kept in adjacent cages at Budapest Zoo. On 13 June 1993, while female 2 still was in the black juvenile coat, the zoo tried to keep both animals in the same cage. The older female 3 did not exhibit any aggression and appeared to be calm. The younger female, however, immediately fled from the older one, crouched on the cage floor, appeared to be very frightened and continued to produce shrill alarm calls until the females were separated again.

Collection of Urine Samples

Urine samples from female 1 (Robin) at the Mulhouse Zoo were collected in intervals of two to four days from 4 Feb. to 14 June 1994 between 09:00 amd 11:00 h. Samples from females 2 and 3 (Tsickó and Júska) at Budapest Zoo were collected almost daily from 7 Jan. to 8 May 1994 between 07:30 and 07:55 h.

Urine samples were aspirated from the cage floor with disposable glass pipettes. The urine was transferred to 2 ml vials and frozen at –20°C until analysis.

Radioimmunoassay of Urinary Samples

Throughout the analysis, pipetting was done manually using glass constriction pipettes. Steroid conjugates were hydrolyzed by incubation of 100 µl of urine sample in 150 µl of Sörensen buffer (66.7 mM, pH 6.0) with 50 µl of enzyme solution (β-Glucuronidase / Arylsulfatase, EC 3.2.1.31 / EC 3.1.6.1; Boehringer Mannheim, Cat. No. 127.060; working dilution 1:20 in Sörensen buffer) in a water bath at 37°C for 14 hours. Based on pilot studies, 700 µl of PBS-Gel (0.1 % gelatine in 0.14 M NaCl, 0.01 M phosphate buffer, pH 7.0) were added to the original incubate to give 1000 µl of working solution with a final concentration of 100 µl of urine per 1,000 µl of diluents.

Oestradiol-17β was measured with a commercial radioimmunoassay (RIA) kit using an iodinated tracer and DCC-separation (Sorin Biomedica S.p.A., I-13040 Saluggia, Italy; distributed by Sodiag SA, Via Locarno 76, CH-6616 Losone, Switzerland; Cat. No. ER 155). Oestrone was determined with a commercial RIA kit using tritiated oestrone and DCC-separation (Api-Bio-Mérieux, 51 Avenue Blanc, CH-1202 Geneva, Switzerland; Cat. No. 66100).

Creatinine was measured in each urine sample to control for variation in liquid intake and its effects on urinary metabolite concentration, within and between study animals, and concentrations of urinary hormones were expressed as mass mg^{-1} creatinine. A Beckman Creatinine Analysor 2 (Beckman Instruments, Inc, Fullerton, CA) was used. All samples were diluted 1:20 prior to creatinine determination.

Results

Hormonal cycles of *Nomascus gabriellae*

Variations in oestrone and oestradiol levels were monitored over a period of 131 days for female 1 and 122 days for females 2 and 3 (Fig. 4). Only female 1 and 2 exhibited distinct cyclical patterns in the urinary concentrations of oestrone and oestradiol, showing a series of six periods of elevated hormone levels which can reasonably be considered to represent ovarian cycles. Individual peaks are clearly separated from each other by intervening phases of about two weeks with markedly lower hormone levels. No regular cycles were apparent in female 3.

The time interval between a peak in oestrone concentration and the corresponding oestradiol peak had a range of -1 to +1 days, and neither hormone tended to peak first.

The cycle length was calculated from the highest hormone concentration of a cyclical peak to that of the next. Female 1 did not exhibit clear and regular cycles during the first half of the study, but began cycling during the second half. Two cycles lengths could be determined, each of which had a duration of 22 days, independently of whether oestrone or oestradiol peaks were used as markers.

In female 1, peaks in oestrone and oestradiol concentrations coincided exactly, but this may be an artefact of the relatively long time intervals between urinary samples that were collected of this individual.

In female 2, cycle lengths determined with oestrone differed from those determined with oestradiol by a duration of 1-2 days. The mean cycle length for five complete oestrone cycles of female 2 was 20.8±1.3 days (range 19-22 days), and 21.2±1.3 days (range 20-23 days) in the corresponding oestradiol cycles.

If the results from females 1 and 2 are combined, the mean cycle length for seven complete oestrone cycles is 21.1±1.2 days (range 19-22 days), and 21.4±1.1 days (range 20-23 days) in the corresponding oestradiol cycles.

Although female 2 exhibited regular cycles and female 3 did not, oestrone levels of the two neighbouring females were correlated, and the relationship was statistically significant (Pearson correlation $r = 0.322$, $p < 0.005$). High oestrone levels of female 2 were often mirrored by female 3, but not necessarily *vice versa*. Urinary concentrations of two other hormones (oestradiol, testosterone) were not significantly correlated between the two individuals.

Comparison among studies

Table 1 summarizes data collected from various reports on the duration of menstrual cycles in gibbons. Many of the reported cycle lengths are based on observations of more-or-less periodical copulations between mated gibbons, menstrual bleedings, and genital swellings in females. Most of the observations listed in Table 1 refer to white-handed gibbons (*Hylobates lar*), or to other closely related species within the genus *Hylobates* (such as *H. albibarbis*, *H. moloch*, *H. muelleri* and *H. pileatus*). Only limited data are available for gibbon genera other than *Hylobates*.

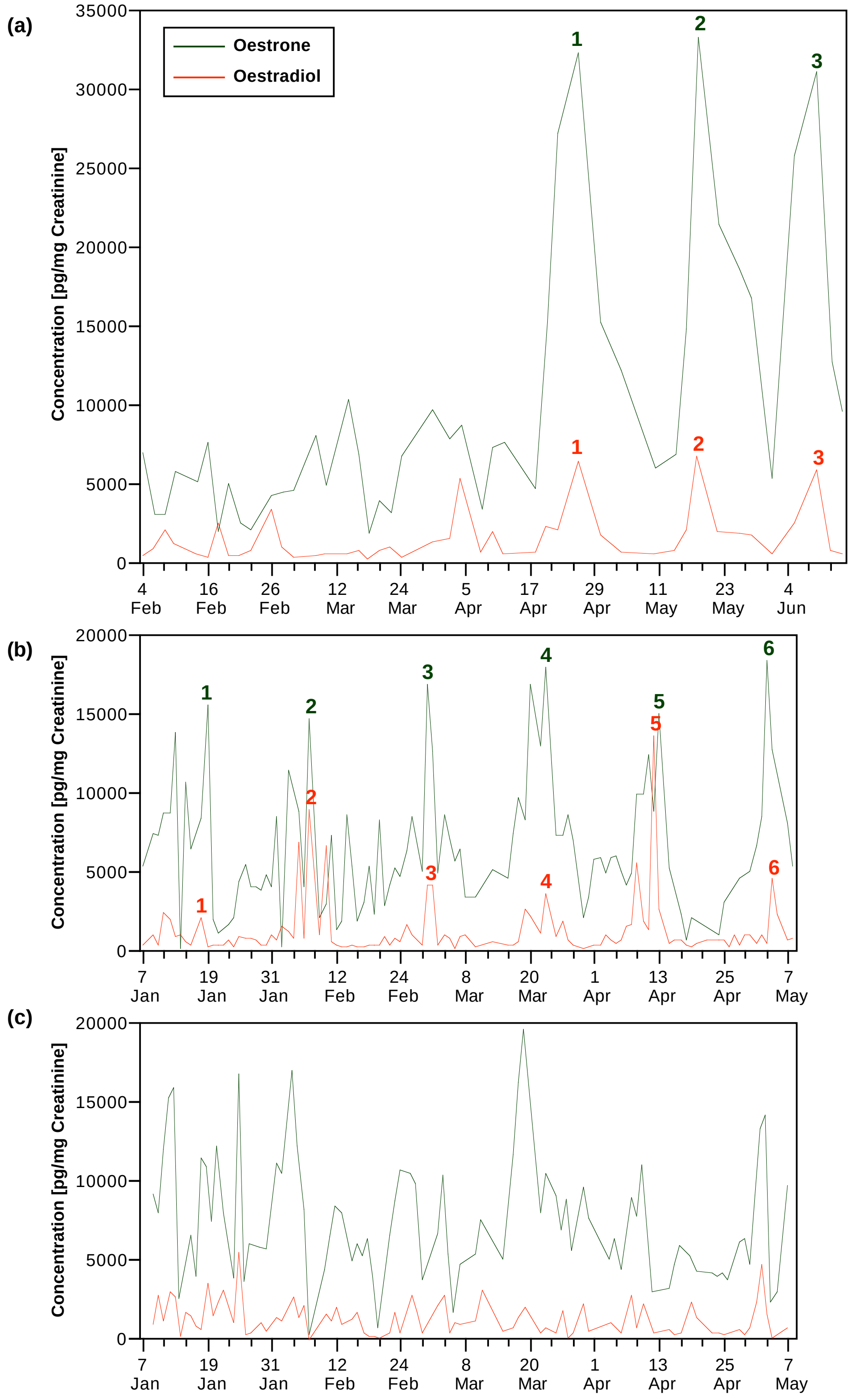

Fig. 4. Oestrone and oestradiol urinary levels in three female yellow-cheeked crested gibbons. Cyclical peaks in hormone concentrations are indicated by numbers. (a) Three consecutive cycles of adult female 1 (“Robin”) during the second half of a period of 131 days. During the first two study months, no clear cycles are evident in this female. (b) Six consecutive cycles of maturing female 2 (“Tsickó”) over a period of 122 days. (c) No regular cycles are apparent in adult female 3 (“Júska”) over a period of 122 days. – *Konzentrationen von Östron- und Östradiol-Metaboliten im Urin bei drei weiblichen Gelbwangen-Schopfgibbons. Regelmässig wiederkehrende Spitzenwerte der Hormonkonzentrationen sind mit Ziffern gekennzeichnet. (a) Drei aufeinander folgende Zyklen des Weibchens “Robin”, über einen Zeitraum von 65 Tagen. Während der ersten zwei Monate sind bei diesem Weibchen keine regelmässigen Zyklen erkennbar. (b) Sechs aufeinander folgende Zyklen des Weibchens “Tsickó”, über einen Zeitraum von 122 Tagen. (c) Beim erwachsenen Weibchen “Júska” sind über einen Zeitraum von 122 Tagen keine regelmässigen Zyklen zu erkennen.*

Table 1. Ovarian cycle duration in gibbon females. – *Dauer des Ovulationszyklus bei Gibbonweibchen*.

	Cycle duration (days)		**Menses duration (days)**	**Sample size (*n*)**		**Moni-tored marker**[1]	**References**
	Mean ±SD	**Range**		**Females**	**Cycles**		
Hoolock							
H. hoolock							
	27.8 ±4.1	20-33	2-4	1	6	B	Matthews (1946)
Hylobates							
H. albibarbis and H. muelleri							
	23.8	–		17	?	S	Cheyne and Chivers (2006)
H. lar							
	29.8 ±4.1	21-43	2-5	2	17	B	Carpenter (1941)
	36.1 ±36.1	3-366	1.8±1.8 (1-26)	32	385	B	AFRIMS study 1968-1974 [2]
	30.0	–		1	1	C	Ellefson (1974, p. 91)
	30.0	22-44	1-3	20	?	B, S	Breznock *et al*. (1977)
	22.0	–		?	?	H	Czekala *et al*. (1985)
	?	23-33		3	12	H, S	Chaiyabutr and Maharrnop (1987)
	21.2–22.0	15-25		4	36	S	Dahl and Nadler (1992b)
	20.2 ±1.6	19-22		4	5	H, B, S	Nadler *et al*. (1993)[3]
	21.0	15-27		5	c.100	S	Dahl *et al*. (cited in Nadler *et al*., 1993)
	19.3 ±3.1	–		3	?	S	Ebert (1999)
	21.1 ±0.5	19-25		5	15	B	Barelli *et al*. (2007)
	20.7 ±5.1	15-27		5	6	H	Barelli *et al*. (2007)
H. moloch							
	?	21-36	3	3	?	H, B, S	Maheshwari (2006), Maheshwari *et al*. (2005)
	25.4 ±8.4	15-38		4	10	H	Hodgkiss (2007)
	26.0 ±10.0	–		7	162	B	Hodgkiss (2007)
	25.4 ±11.9	–		11	234	S	Hodgkiss (2007)
H. muelleri							
	31.0	–		?	?	NS	Brody and Brody (1974)
H. pileatus							
	?	21-30		?	?	B	Badham (1967)
	26.1 ±12.9	6-70	2.1±1.1 (1-5)	1	60	B	AFRIMS study 1968-1974 [2]
	21.1 ±0.8	–		1	7	H	Morikaku *et al*. (2006)
Hylobatidae spp.							
	?	15-47		4	?	B	Muschamp (pers. comm. cited in Chivers, 1978)
Nomascus							
N. concolor							
	25.6	19-72	1-3	1	71	B	Zhen (1989, and pers. comm. to TG)
N. gabriellae							
	21.1 ±1.2	19-22		2	7	H	Geissmann and Anzenberger, this study
N. hainanus							
	c.30.0	–	2-3	1	?	B	Pocock (1905)
N. nasutus							
	30.0	–		?	?	NS	Le (1973, cited in Dao Van Tien, 1993)
	45.0	41-49	3-5	1	2	B	Fischer (1980)
N. leucogenys							
	23.8	16-37		1	19	B	Bachmann and Sodaro (2000)
	21.9 ±2.9	12-27		1	38	H	Lukas *et al*. (2002)
Symphalangus							
S. syndactylus							
	21.8 ±4.4	19-34	1-2	1	12	H, B	Knott (pers. comm. to TG), Knott *et al*. (1993)
	c.28.0	–		?	?	B	Von Hegel (pers. comm. cited in Orgeldinger, 1989, p. 229)
	?	42-49		1		C	Alberts (1983)

[1] B = Menstrual bleeding; H = Hormonal data; C = Copulations; S = Genital swellings; NS = not specified.

[2] Mean and standard deviation were calculated by one of us (TG) from published individual values of of a long-term study carried out at the Armed Forces Research Institute of Medical Sciences, Bangkok, Thailand (AFRIMS). The original data were published in Vick *et al*. (1968), Chaicumpa *et al*. (1969), Johnsen *et al*. (1970), and Tingpalapong *et al*. (1971, 1973, 1974). One individual (B-85) of the study animals was reported to be *H. pileatus*.

[3] Means and standard deviations were calculated from published individual values in Table 1 of Nadler *et al*. (1993).

Table 2. Comparison of mean average ovarian cycle durations in gibbons determined with different markers (summarizing data from Table 1). – *Vergleich der mit verschiedenen Methoden bestimmten durchschnittlichen Dauer des Ovulationszyklus bei Gibbonweibchen (Zusammenfassung der Mittelwerte aus Tabelle 1).*

Monitored marker[1]	**Cycle duration (days)**			**Number of studies**	**References**
	Mean ±SD	**SE**	**Range of means**		
H	21.7 ±1.5	0.5	20.0-25.4	9	Barelli *et al*. (2007); Chaiyabutr and Maharrnop (1987); Czekala *et al*. (1985); Geissmann and Anzenberger (this study); Hodgkiss (2007); Lukas *et al*. (2002); Morikaku *et al*. (2006); Nadler *et al*. (1993); Knott (pers. comm. to TG), Knott *et al*. (1993)
S	23.5 ±3.8	1.6	19.3-30.0	6	Breznock *et al*. (1977), Cheyne and Chivers (2006); Dahl and Nadler (1992b); Dahl *et al*. (cited in Nadler *et al*., 1993); Ebert (1999); Hodgkiss (2007)
C	30.0	–	–	1	Ellefson (1974, p. 91)
B	29.8 ±6.3	1.9	23.8-45.0	10	AFRIMS studies 1968-1974[2], Bachmann and Sodaro (2000); Carpenter (1941); Fischer (1980); Hodgkiss (2007); Matthews (1946); Pocock (1905); Von Hegel (pers. comm. cited in Orgeldinger, 1989, p. 229); Zhen (1989, and pers. comm. to TG)
NS	30.5	–	30.0-31.0	2	Brody and Brody (1974); Le (1973, cited in Dao Van Tien, 1993)

[1] B = Menstrual bleeding; H = Hormonal data; C = Copulations; S = Genital swellings; NS = not specified.

[2] Mean and standard deviation were calculated by one of us (TG) from published individual values of of a long-term study carried out at the Armed Forces Research Institute of Medical Sciences, Bangkok, Thailand (AFRIMS). The original data were published in Vick *et al.* (1968), Chaicumpa *et al*. (1969), Johnsen *et al*. (1970), and Tingpalapong *et al*. (1971, 1973, 1974).

Table 2 summarises average cycle durations in gibbons determined with different markers. Mean values of studies applying endocrinological methods (hormonal data) are lowest, and values based on genital swellings are only slightly higher. Values based on other markers (menstrual bleeding or copulations) are much higher. A statistical comparison of all studies listed in Table 2 using ANOVA revealed statistically significant differences among the markers ($df = 4$, $p = 0.004$). A *post-hoc* test revealed a significant difference between the markers menstrual bleedings and hormone data (Bonferroni-Dunn, $p = 0.0006$). A simple comparison between mean values based on hormone concentrations and all other mean values also found a significant difference (Mann-Whitney *U*-test, $p = 0.007$).

Discussion

This study presents the first data on the ovarian cycle of the yellow-cheeked crested gibbon (*Nomascus gabriellae*). Most previous publications on menstrual cycles in crested gibbons (genus *Nomascus*) either determined cycle length by using intervals between menstrual bleedings (Fischer, 1980; Pocock, 1905; Zhen, 1989) or did not mention the method by which cycle length was assessed (Le, 1973, cited in Dao Van Tien, 1993). In these publications, average cycle duration was reported to be 25.6 or 30 days (Le, 1973, cited in Dao Van Tien, 1993; Pocock, 1905; Zhen, 1989) or ranging from 41 to 49 days (Fischer, 1980). In the only previous study on the hormonal cycle length of *Nomascus* (Lukas *et al*., 2002), a duration of 21.9±2.9 was determined for one white-cheeked crested gibbon (*N. leucogenys*). A virtually identical hormonal cycle length of 21.1±1.2 days was determined for two females of *N. gabriellae* in the present study, suggesting that the ovarian cycle of the genus *Nomascus* is much shorter than indicated by earlier studies using markers other than endocrinological values.

Similar to the situation in crested gibbons (genus *Nomascus*), previously published data on the duration of menstrual cycles in other gibbon genera show a broad range (Table 1). Although most values range between 20 and 40 days, maximum values of up to 49 days have been reported. It is noteworthy that most mean values greater than 22 days are based either on observations of menstrual bleedings or on copulations. The only study that found longer hormonal cycles in a gibbon species reported an average of 25.4±8.4 days for four females of the Javan silvery gibbon (*Hylobates moloch*), including some unusually long cycles of up to 38 days (Hodgkiss, 2007) which seem to be outliers and need further explanantion.

A statistical comparison reveals that cycles based on hormonal data are significantly shorter than the pooled cycle data based on other markers and shorter than cycles based on menstrual bleedings. The reason for this discrepancy is that monitoring of menstrual bleedings or copulations may not yield sufficiently reliable estimates of cycle length.

Monitoring gibbon copulations is particularly problematic: copulations are short and easily escape detection if a pair is not under daily observation from dawn to dusk. Furthermore, the possibility remains that some copulations may even occur during the night. This may explain why very long cycles may be determined when using this marker.

If menstrual bleedings are monitored, some cycles may also remain undetected: Breznock *et al.* (1977) reported that the character of menstrual flow, lasting 24-72 hours in *H. lar*, was very variable and “ranged from an overt flow of blood to an amount visualized only with the aid of a cotton swab”. After having monitored over 20 individuals of *H. lar*, Tingpalapong *et al.* (1971) noted that “the degree of variation in the length of the menstrual cycle … confirms previous observations that regularity in the gibbon is a yet to be discovered exception to the rule that the gibbon has a completely irregular menstrual cycle.” After another year of daily observation and vaginal swabbing of 11 of these gibbons, Tingpalapong *et al.* (1973) wrote that “in nearly all animals, periods of amenorrhea two or three months in duration or longer were noted”. In *H. albibarbis* and *H. muelleri*, menstrual bleeding was observed only rarely (1% of observations) (Cheyne and Chivers, 2006). In a study of the ovarian cycle of *H. moloch*, Hodgkiss (2007) determined the cycle length based on sexual swellings in all 11 study animals, but only in seven of them could cycle length be determined based on menstrual bleeding – in the remaining four individuals, this marker was not observed at all or was not observed regularly enough. In order to limit the high variability of their results when using genital swellings or menstrual bleedings as markers, Hodgkiss (2007, p. 19) ignored all intervals that were shorter than seven days or longer than 60 days.

Gibbons have been reported to exhibit cyclical swellings of vulval tissues. Although the degree of these genital swellings shows considerable individual variation, the average pattern indicates a significant level of swelling for 6.3 days on average (range 4–8 days) (Cheyne and Chivers, 2006; see also Barelli *et al.*, 2007; Breznock *et al.*, 1977; Carpenter, 1941; Dahl and Nadler, 1992a, b; Kollias and Kawakami, 1981; Nadler *et al.*, 1993). In two studies on *H. lar*, genital swellings were found to reach their maxima in association with mid-cycle peaks in oestrogens and with ovulation, and appeared to be a useful marker for monitoring progress of the menstrual cycle (Barelli *et al.*, 2007; Nadler *et al.*, 1993). In a study of *H. moloch*, however, the sexual swellings of four females did not coincide with the fertile periods (Hodgkiss, 2007, p. 50).

In summary, ovarian cycles determined with hormonal data appear to produce more homogenous results than cycles based on other markers. Results of the present study, combined with those of Lukas *et al.* (2002) suggest an ovarian cycle in crested gibbons (genus *Nomascus*) of 20-22 days on average ($n = 3$ individuals). A study on hormonal cycles of one siamang female (*Symphalangus syndactylus*) also found an average cycle length of about 22 days (Knott *et al.*, 1993; Knott, personal communication to TG). Most endocrinological studies on gibbon ovarian cycles have been conducted on the genus *Hylobates*. In *H. lar* ($n = 10+$ females), average cycles lengths were reported to range from 19-25, with a mean of 21 days (Barelli *et al.*, 2007; Czekala *et al.*, 1985; Nadler *et al.*, 1993). The hormonal cycle length of one *H. pileatus* was found to be 21.1 days on average (Morikaku *et al.*, 2006). Only the results for *H. moloch* appear to be less uniform. Maheshwari (2006) found averages of 21-24 ($n = 3$ females), which appears to conform to the results of the other studies discussed here, but the results of a second study (Hodgkiss, 2007) exhibit a surprisingly wide range (15-38 days) with a relatively high average of 25.4 days ($n = 4$ females). In general, however, hormonal cycles in gibbons appear to average around 20-22 days.

Interestingly, the cycles of gibbons are apparently shorter than those of other Old World monkeys and great apes, which reportedly range from 25-40 days. They are also shorter than those of many other primates including most strepsirrhines (29-50 days) and tarsiers (24 days). Only some – but not all – New World monkeys (7-36 days) appear to have cycles which are as short as, or distinctly shorter than, those of gibbons (Barelli *et al.*, 2007; Dixson, 1998; Hrdy and Whitten, 1987; Martin, 1990; Robinson and Goy, 1986; van Schaik *et al.*, 1999).

Although the adaptive significance of this finding is poorly understood, the duration of the follicular phase has been reported to be the main source of variability and diversity of ovarian cycle length among catarrhine primates (Old World monkeys and apes) (van Schaik *et al.*, 2000). It has also been suggested, that long follicular phases in primates may be a female adaptation to confuse paternity and thus reduce the risk of infanticide (van Schaik *et al.*, 2000). This would be particularly adaptive in those primates where females have a high need for paternity manipulation, i.e. in females that live in groups with several males and that are subject to high sexual coercion. Sexual coercion is particularly high in species with high sexual dimorphism in body weights and canine dimensions (van Schaik *et al.*, 2000). None of these criteria apply to gibbons, where both sexes are almost identical in body weights and canine dimensions, where the mean number of mates per cycle is very low, and where females have total control over their mating behaviour. As a result, there should be little need for paternity confusion in gibbons, and their follicular phase – and thus their ovarian cycle – should be expected to be shorter than that of other catarrhine primates, which is exactly what we find.

Although the paternity confusion hypothesis described above provides a plausible explanation for why the ovarian cycles of gibbons are shorter than those of other catarrhine primates, the explanation does not appear to be comprehensive. According to the hypothesis, the shortness of the gibbon cycle results from the short duration of the follicular phase, whereas the luteal phase should be similar to that of other catarrhines. However, in a comparison of female reproductive hormone patterns among hominoids (apes and humans), Czekala *et al.* (1988) noticed that the duration of the luteal phase is similar in most species with the exception of the gibbon, in which it is abbreviated. In catarrhines, the average duration of the follicular and luteal phases are 14.99±3.37 days and 14.94±1.58 days, respectively (van Schaik *et al.*, 2000, p. 374). Based on previously published data (Barelli *et al.*, 2007, Czekala *et al.*, 1985; Hodges *et al.*, cited in van Schaik *et al.*, 2000, p. 382, and Hodgkiss, 2007), we calculate an average duration of the follicular phase in gibbons of 11.91±4.02 days, and of the luteal phase of 9.48±2.01 days (Table 3). A comparison reveals that the average follicular phase in gibbons is about 3.1 days shorter, and the luteal phase is 5.5 days shorter than the respective values of catarrhines. Whereas the difference in the follicular phase is predicted by the paternity confusion hypothesis, the apparently more pronounced difference in the luteal phase is not. We conclude that the paternity confusion hypothesis does not fully explain the shortness of the gibbon ovarian cycle. Other (as yet unidentified) factors appear to be involved.

Table 3. Published durations of the follicular and luteal phases in gibbon ovarian cycles. For comparison, average values for catarrhine primates are provided in the last row. – *Literaturwerte für die Dauer der follikulären und der lutealen Phase in den Ovulationszyklen von Gibbons. Vergleichswerte für catarrhine Primate (Altweltaffen und Menschenaffen) sind in der letzten Tabellenzeile eingetragen*.

Species	**Follicular phase (days)**			**Luteal phase (days)**			**Sample size (*n*) cycles/ females**	**Reference**
	Mean	SD	Range	Mean	SD	Range		
Unknown species	8.4							Hodges *et al.*, cited in van Schaik *et al*. (2000, p. 382)
Unknown species			11-14			10-11	10/1	Lasley *et al*. (1984), cited in Hayssen *et al*. (1993, p. 222)
Hylobates lar	13.0			9.0				Czekala *et al*. (1985)
H. lar						9-10	12/3	Chaiyabutr and Maharrnop (1987)
H. lar	9.2	2.4	7-13	11.8	3.1	8-15	6/4	Nadler *et al*. (1993)[1]
H. lar	10.6	3.44	5-18	10.1	1.98	6-14	9/5	Barelli *et al*. (2007)
H. moloch			11-18			8-48	?/3	Maheshwari *et al*. (2005)
H. moloch	18.4	7.09	9-28	7.0	1.89	4-10	10/4	Hodgkiss (2007)
Hylobatidae mean	11.91	4.02		9.48	2.01			
Catarrhines mean	14.99	3.37		14.94	1.58			Hodges *et al.*, cited in van Schaik *et al*. (2000, p. 374)

[1] Means and standard deviations were calculated by one of us (TG) from published individual values in Table 1 of Nadler *et al*. (1993, p. 452).

It may be interesting to note that the three females of this study considerably differed in the expression of the ovarian cycles. Female 1 (12.4 years old at the beginning of this study) exhibited regular hormonal cycles only during the second half of this study. Female 2, the youngest of the study animals and estimated here to be about 7.5 years old at the beginning of this study, exhibited regular hormonal cycles throughout the study period. Female 3, estimated here to be about 10 years old at the beginning of the study, did not exhibit a regular cyclic pattern in her urinary hormone concentrations during the study period. As female 3 was clearly dominant over female 2, it is unlikely that her cycles were somehow suppressed by the presence of female 2 in the neighbouring cage. In any case, it appears that the age at which cycling begins in crested gibbons may exhibit considerable variability, and the reasons for this may be manifold. At the same time, a female might cease ovarian activity even after having undergone the normal process of menarche during ontogeny.

At the age of about 5-8 years, females of the genus *Nomascus* change their fur coloration from black to light yellow or buff and adopt the coloration typical of adult females (Geissmann, 1993; Geissmann *et al*., 2000). These colour changes have been equated with the onset of sexual maturity by Delacour (1951), but were also found to be very variable by Deputte and Leclerc-Cassan (1981). The variability of the onset and the duration of colour transition still remain to be documented in females whose ages are known precisely. It is therefore interesting to note that female 2 of this study exhibited constant cycles, although she had not fully completed her colour change at the end of the study, suggesting that menarche probably set in before or near the beginning of the colour transition. The opposite order of events seems to have occurred in female 1. The exact timing of her colour change is not known, but she was already in her adult coat when she arrived at Mulhouse Zoo (i.e. more than two years before the observed onset of her regular hormonal cycles).

The oestrone levels of females 2 and 3 (kept in neighbouring cages) show a statistically significant correlation, although only one of the two females exhibited clear cycles. It is tempting to speculate that gibbon females living in close proximity may influence each other's ovarian cycles, but much better data would be required to test such a hypothesis. Ovarian cycle synchrony among group-living females has been reported in several mammalian species, especially primates (McClintock, 1971, 1984; Wallis, 1985) and has been suggested to be mediated by female-female olfactory signalling (McClintock, 1978, 1984; Russell *et al*., 1980). However, re-examination the evidence for synchrony revealed that many reports of synchrony were spurious, resulting from systematic methodological errors and biases in the measurement and statistical analyses of synchrony (Schank, 2001; Yang and Schank, 2006).

Conclusions

1. The mean cycle lengths for seven complete oestrone cycles in two female *N. gabriellae* are 21.1±1.2 days (range 19-22 days).

2. The time interval between a peak in oestrone concentration and the corresponding oestradiol peak had a range of 0-1 days, and cycle lengths determined with oestrone differed from those determined with oestradiol by a duration of 0-2 days. Neither hormone tended to peak earlier than the other.

3. In study female 2, menarche must have set in at or before the beginning of the colour transition from the black juvenile to the adult light fur coloration, whereas the opposite order may have occurred in study female 1.

4. The average hormonal cycle lengths of *N. gabriellae* (21 days, this study) are nearly identical with most hormonal cycle lengths determined for other gibbons (including one *N. leucogenys*, one *S. syndactylus*, and individuals of several species of the genus *Hylobates*). The typical average duration of ovarian cycles in gibbons appears to be 20-22 days.

5. Cycle lengths based on sexual swellings are usually similar to those based on sex hormone concentrations.

6. Cycle lengths based on hormonal data are often considerably shorter than those based on intervals between menstrual bleedings or between copulations. The latter two may not be reliable indicators of menstrual cycle duration, because some cycles may easily remain undetected with these methods.

7. Gibbon cycles are apparently shorter than those of other primates, with the exception of some – but not all – New World monkeys.

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Zusammenfassung

Hormonelle Korrelate zum Ovulationszyklus von Gelbwangen-Schopfgibbon (*Nomascus gabriellae*), und eine Übersicht der Ovulationszyklen bei Gibbons (Hylobatidae)

Ovulationszyklen wurden bei zwei zoo-lebenden Gelbwangen-Schopfgibbons (*Nomascus gabriellae*) anhand urinärer Steroidmetaboliten bestimmt. Die durchschnittliche Zyklusdauer betrug 21.1±1.2 Tage ($n = 7$ Zyklen). Der zeitliche Abstand zwischen Maximalwerten der Östron-Konzentration und den entsprechenden Östradiol-Maxima betrug 0–1 Tage, und die mit Östron bestimmten Zyklusdauern unterschieden sich von den mit Östradiol bestimmten um 0–2 Tage. Keines der beiden Hormone erreichte die Maxima konsistent früher als das andere. Beim ersten Weibchen begann die Geschlechtsreife (regelmässige Ovulationszyklen) vor oder während der Umfärbung vom schwarzen Juvenilkleid zum gelben Adultkleid, während das ältere zweite Weibchen anscheinend erst im Verlauf dieser Studie begann, regelmässige Zyklen zu zeigen, also Jahre nach ihrer Umfärbung zum Adultkleid. Die in dieser Studie bestimmte durchschnittliche Zyklus-Dauer für *N. gabriellae* ist praktisch identisch mit den auf Hormondaten basierenden Ovulationszyklen, die in früheren Studien bei anderen Gibbons bestimmt wurden (*Hylobates* spp.: 20.0-25.4 Tage, *N. leucogenys*: 21.9, *Symphalangus syndactylus*: 21.8). Diese Werte stimmen meistens auch ziemlich gut mit den Zyklusdauern, die mit Hilfe der Sexualschwellungen bestimmt wurden, überein. Sie sind dagegen meist deutlich kürzer als Zyklusdauern, die auf Menstruationsblutungen oder der Häufigkeit von Paarungen basieren. Das dürfte daran liegen, dass mit den letzteren beiden Methoden oft einzelne Zyklen übersehen werden und dass die so bestimmten Zyklen keine verlässlichen Indikatoren für den Ovulationszyklus bei Gibbons darstellen. Zyklen von Gibbons scheinen kürzer zu sein als die von anderen Primaten, mit Ausnahme einiger – wenn auch nicht aller – Neuweltaffen.