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RESEARCH ARTICLE

Female Reproductive Parameters in the Javan Gibbon (*Hylobates moloch*)

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Javan gibbons (*Hylobates moloch*) are one of the most endangered gibbon species in the world. Data on the reproductive biology of the species are almost nonexistent, and a general understanding of the female reproductive biology of this species is important for both ex situ and in situ conservation. Using 18 years of data from 11 captive individuals, we provide new information on the reproductive biology of Javan gibbons based on sexual swelling and menstrual bleeding, including reproductive development, interbirth intervals, and ovarian cycle lengths. Menarche and the onset of sexual swelling occurred at 6.2 and 6.5 years respectively, followed by a period of adolescent sterility of about 1.5 years. Average age at first birth was 8.8 years, and interbirth intervals were about 2.3 years, decreasing to 1.0 year during cases of infant mortality at or shortly after birth. Ovarian cyclicity was measured through periods between menstrual bleeding and sexual swelling. Menstrual bleeding indicates the start of a new ovarian cycle, while sexual swelling normally occurs near the time of ovulation. Menstrual bleeding intervals gave a cycle length of 25.6 days, while sexual swelling intervals gave a cycle length of 27.3 days. These both correspond closely to cycle lengths in other gibbon species, as well as hormonal studies in Javan gibbons. In particular, observing the presence/absence of swellings was found to be a useful and easy method to monitor female ovarian cycles, and could be a practical noninvasive technique for caretakers and researchers. Zoo Biol 29:449–456, 2010.

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INTRODUCTION

Javan gibbons (*Hylobates moloch*) are one of the most endangered gibbon species in the world, with estimates of as few as 4,100 individuals remaining in the wild [Nijman, 2004]. Because of their dense rainforest habitat, gibbons are difficult to study in the wild, and so only a limited amount of research has been done [Dallmann and Geissmann, 2001; Geissmann and Nijman, 2006; Nijman, 2004]. Data on the reproductive biology of the species are largely nonexistent [Kappeler, 1984; Geissmann and Orgeldinger, 1995; Geissmann, 1991], and many important life-history factors, such as age at sexual maturity, interbirth interval, and ovarian cycle lengths, have only been estimated [Geissmann, 1991].

A general understanding of female reproductive biology of a species is important for establishing successful captive management programs and for in situ conservation [e.g. Seal, 1993; Shimizu, 2005; Lasley and Savage, 2007]. In captivity, the study of reproductive biology of animals is useful for assessing fertility control techniques, diagnosing and treating infertility, and developing husbandry strategies to maximize successful production of offspring [Schwarzenberger, 2007; Shimizu, 2005; Lasley and Savage, 2007]. Conservation tools such as Population and Habitat Viability Analyses are used to evaluate risk of extinction in wild populations, and these analyses rely on basic reproductive data, such as age at reproductive maturity, interbirth interval, and reproductive seasonality [Seal, 1993].

Given the difficulties of collecting data in the wild, captive Javan gibbon populations provide the best alternative to in situ research for long-term studies of reproductive biology. The captive Javan gibbon population is about 130 individuals (Nijman, unpublished data), 53 of which are held in 10 zoological institutions outside of Indonesia [Cocks, 2005; ISIS, 2007]. While a captive management plan for the species has been recommended [Wallis, 1997] and is currently under development (Cocks, personal communication), a recent study by Nijman [2006] suggests that Javan gibbons rarely reproduce in any Indonesian zoos, and only five international institutions that still keep the species have successfully bred them. More information about the reproductive biology of Javan gibbons is required to address these low reproductive rates [Supriatna, 2006], which is a major concern in an endangered species that already has a low reproductive potential because of their monogamous social groups and long interbirth intervals [Palombit, 1994; Wallis, 1997].

Using long-term data from captive individuals, we provide new information on the reproductive biology of the female Javan gibbon, including:

- Reproductive development and age of sexual maturity (age at menarche, first sexual swelling, first conception, and parity);
- Duration of interbirth intervals and the impact of infant mortality;
- Ovarian cycle length.

We also assessed the use of menstrual bleeding and sexual swellings as a practical and noninvasive method for caretakers and researchers to monitor ovarian cycles. Ovarian cycle data allow for the determination of the onset of fertility, pregnancy, and reproductive aging [Dixson, 1998], and can also be indicative of

nutritional and environmental stress and disease in both wild and captive populations [Bercovitch and Strum, 1993; Machatschke et al., 2006; Mor et al., 1997].

METHODS

Study Animals

Study animals were 11 female Javan gibbons housed at Howletts Wild Animal Park in Kent, UK (Table 1). Howletts houses over half of the captive breeding population of Javan gibbons and has had the most successful breeding program in the world, with 26 births in the past two decades, and only four cases of infant mortality (Thetford, personal observation). Of the animals in this study, six were multiparous, two were primiparous, and three were nulliparous.

Data Acquisition

Data on dates of birth and ovulatory cycles were obtained from records collected over 18 years by the animal care staff at Howletts Wild Animal Park (under the supervision of E. Thetford). The presence of sexual swelling and menstrual bleeding were recorded daily, were noninvasive, and were based on visual inspection (Fig. 1). Sexual swellings are less pronounced in gibbons than many other primate species, with edema occurring in the hormonally sensitive tissue of the labia minora, urethral eminence, and a small portion of the vaginal wall [Nadler et al., 1992]. The process is regulated by hormones, with estrogen causing the swelling and progesterone decreasing it, which indicates that maximum swelling should occur at ovulation when estrogen levels are highest [Nadler et al., 1992].

TABLE 1. Demographic data of the female Javan gibbons (*Hylobates moloch*) included in this study

Individual	Birth year	Origin (age arrived at Howletts)	Number of offspring	Age during data collection (years)
Assini	1980	Captive-born Winnipeg (9 years)	9[b]	9–26
Marlene	1978[a]	Wild born (4 years)	8	8–25
Shewok	1988	Captive-born Howletts	1	7–14
Loci	1989[a]	Wild born (3 years)	2[c]	5–13
Yoni	1991	Captive-born Howletts	4	6–15
Kulon	1994	Captive-born Howletts	3	5–13
Salak	1996	Captive-born Howletts	2	6–11
Pangrango	1997	Captive-born Howletts	1[d]	5–7
Kendang	1998	Captive-born Howletts	0	5–9
Reggat	1999	Captive-born Howletts	0	7–8
Simpang	2000	Captive-born Howletts	0	6–7

[a]Values are estimates and were not included in calculations.
[b]Last infant born at Belfast Zoo, Northern Ireland.
[c]Infants (twins) born at St. Martin La Plaine Espace Zoologique, France.
[d]Infant born at Tierpark Hellabrunn, Munich, Germany.

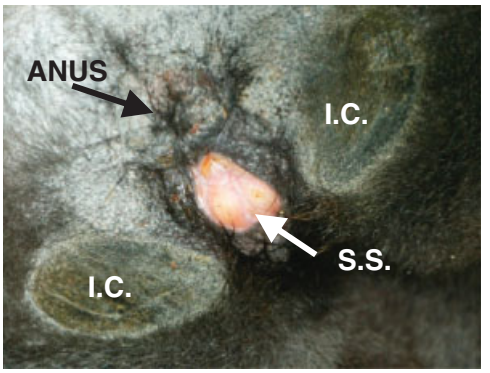

Fig. 1. Photograph showing the relative size of sexual swelling (S.S.) of the genitals compared to that ischial callosities (I.C.). (Photo by E. Thetford.)

Historical records for each individual were used to calculate the interswelling interval (ISI), intermenstrual interval (IMI), and the occurrence of sexual swelling during pregnancy. ISI was defined as the number of days between onset of subsequent swellings, while IMI was defined as the number of days between onset of subsequent menstrual bleeding [Cheyne and Chivers, 2005; Paoli et al., 2006; Vervaecke et al., 1999]. The presence or absence of swelling was used rather than having a scale, as it was not possible to get close enough to the animals to measure accurately the swelling on a daily basis. During certain times, data collection was suspended due to external factors; thus, these periods were excluded from the analyses. If the ISI or IMI was found to be less than seven days it was assumed to be a part of the same cycle. If the ISI or IMI was found to be more than 60 days (equivalent to the mean plus 2.5 standard deviations), it was assumed that swelling or bleeding had been missed, and these data were not included in the final analyses.

Data Analyses

Using a total of 79 years of data, collected over an 18-year period, ISI, IMI, and interbirth intervals were calculated. The age of sexual maturity was determined by calculating the onset of sexual swelling, onset of menstrual bleeding (menarche), and age at first conception. Gestation was estimated to be 210 days [Thetford, unpublished data; Geissmann, 1991], and this was used to calculate age of first conception. Averages were calculated from an equal contribution of data for each individual. Nonparametric statistics were used to analyze results, and significance was accepted at $P<0.05$ in a two-tailed test.

RESULTS

Reproductive Maturity and Interbirth Intervals

A summary of reproductive parameters is shown in Table 2. In captivity, Javan gibbons show the first signs of sexual swelling at about 6.5 ± 0.7 years of age, though this ranges from 5.6 to 7.5 years. On average, menarche occurs slightly earlier at 6.2 ± 1.0 years, with a range of 5.0–7.5 years. The age at first birth was 8.8 ± 0.7 years, with a range of 8.2–9.8 years. Since the average age at first conception was

TABLE 2. Reproductive parameters of female Javan gibbons (*Hylobates moloch*) at Howletts Wild Animal Park

Individual	Age of first sexual swelling (years)	Age at menarche (years)	Ovarian cycle length: sexual swelling[b] (number of cycles)	Ovarian cycle length: menstrual bleeding[b] (number of cycles)	Age at first birth (years)	Interbirth interval (years)
Assini	9.1[a]	9.1[a]	29.0±12.4 (5)	24.0 (1)	9.8	2.07±0.65
Marlene	8.2[a]	8.4[a]	25.9±12.8 (45)	27.7±13.1 (7)	8.4[a]	1.96±0.76
Shewok	6.7	6.8	23.5±10.8 (52)	25.7±9.2 (44)	8.2	–
Loci	5.0[a]	5.0[a]	27.4±13.4 (47)	25.5±11.6 (62)	18[a]	–
Yoni	7.0	5.1	29.3±13.7 (3)	26.5±9.6 (18)	8.4	2.10±0.15
Kulon	7.5	5.9	29.3±11.3 (6)	–	8.3	2.59±0.14
Salak	6.1	5.0	23.8±11.0 (38)	26.9±7.6 (29)	9.4	1.42
Pangrango	5.6	–	28.4±8.7 (5)	–	8.4	–
Kendang	5.6	7.5	22.2±11.5 (22)	–	–	–
Reggat	7.3	6.8	28.3±14.5 (7)	23.0 (1)	–	–
Simpang	6.1	–	32.8±13.0 (4)	–	–	–
Overall average	6.5±0.7	6.2±1.0	27.3±3.1	25.6±1.6	8.8±0.7	2.04±0.42

[a]Values are estimates and were not included in calculations.
[b]Cycle lengths are reported in days.

determined by counting 210 days back from age at first birth, it was not possible to get an accurate number for two females who gave birth to premature infants.

The interbirth interval was calculated for all pregnancies of the five females who gave birth while at Howletts Wild Animal Park (Table 2). Full-term pregnancies with infant survival had an interbirth interval of 2.3±0.4 years, while in cases where the infant died at or died shortly after birth the average interbirth interval was half the length (1.0±0.3 years).

Sexual Swellings and Menstrual Bleeding

The cycles of tumescence and detumescence of sexual swellings were calculated for each of the 11 female Javan gibbons, a total of 234 cycles. The average cycle length across all animals was 27.3±3.1 days. The length of the ovarian cycle was also determined by counting the number of days between menstrual bleeding for 7 of the 11 females. By this measure, the average cycle length was 25.6±1.6 days. In the four individuals not included in the analysis, menstrual bleeding was observed irregularly or not at all.

In three females for which data were available for a total of seven pregnancies, sexual swellings were observed during all 7 months of gestation (Table 3). There was no significant difference in the occurrence of sexual swelling across each month of gestation; therefore, this would not be useful in diagnosing pregnancy (Friedman: $\chi^2 = 11.8$, $n = 7$, df = 6, $P = 0.07$). Most females only had a few days of gestational swelling per month; however, one female had a high number of days each month in her second pregnancy.

TABLE 3. Occurrence of sexual swelling (in days) across each month of pregnancy for three female Javan gibbons (*Hylobates moloch*) at Howletts Wild Animal Park

	Month						
Individual	1st	2nd	3rd	4th	5th	6th	7th
Assini	1	0	1	1	1	0	1
	2	0	1	1	1	1	0
	8	0	2	4	1	0	0
Yoni	1	0	1	1	4	1	2
	1	17	24	22	20	20	22
Salak	17	4	4	5	3	3	2
	3	2	5	1	0	1	15

DISCUSSION

The knowledge about the basic reproductive parameters of the female Javan gibbon is extended in this study. As with other endangered primates, there are limited numbers of Javan gibbons in captivity, making it important to share fragmentary data when available for future compilations of species-level generalizations [Vervaecke et al., 1999].

The results provided here suggest that female reproductive parameters in the Javan gibbon are consistent with other members of the family Hylobatidae [Geissmann, 1991; Nadler et al., 1992; Bartlett, 2003; Cheyne and Chivers, 2005; Barelli et al., 2007]. The average age of menarche was 6.2 years, which closely corresponded to the age when sexual swelling was first observed at 6.5 years. Menarche and the appearance of sexual swellings were followed by an average period of adolescent sterility of 1.5 years before first conception, which is consistent with many haplorhine species, as early menstrual cycles are not ovulatory and rarely result in conception [Wallen and Zehr, 2004]. The average age at first birth ranged from about 8 to 10 years, slightly higher than the range of 6–8 years for captive gibbons suggested by Geissmann [1991]. The captive management plan at Howletts leaves females in their natal group until about seven years of age before they are paired with a mate. This ensures that they witness the birth of up to three younger siblings, and observe maternal care of the infants.

When pregnancies resulted in live birth followed by lactation, the interbirth interval was about 2.3 years. If infants died at or shortly after birth, the interbirth interval was halved, as would be expected due to lack of lactational amenorrhea. Interbirth intervals in wild white-handed gibbons are about 3 years [Bartlett, 2003], and about 1–2 years in captive gibbons [Geissmann, 1991].

The two methods of calculation used to determine the length of the ovarian cycle in Javan gibbons gave an average cycle length of 27.3 days (sexual swelling) and 25.6 days (menstrual bleeding). This is consistent with cycle lengths based on fecal hormonal analyses in this species [Hodgkiss, 2007]. Studies on white-handed gibbons have shown a cycle length of 19–22 days using urinary hormone analyses [Nadler et al., 1992], and 21 days using fecal hormone analyses [Barelli et al., 2007]. An average cycle length of 24 days was seen in Bornean white-bearded and Müller gibbons by measuring ISI [Cheyne and Chivers, 2005].

Although the cycle length as determined by IMI was very close to those obtained by other methods, fewer IMIs were observed in the same time period as ISIs (IMI: $n = 162$; ISI: $n = 234$). Many menstrual cycles were not included due to large amounts of

time between observed bleeding (>60 days), indicating that some bleeding cycles had not been observed. This could lead to overestimated figures of the average IMI if this was not taken into account [Thierry et al., 1996]. In one study on sexual swellings in gibbons, menstrual bleeding was only recorded in 1% of observations [Cheyne and Chivers, 2005].

Although sexual swelling is not as conspicuous in gibbons as in many other primate species, there is a visible change in color and size of the vulva during the ovarian cycle. Sexual swellings increase following menstruation to a mid-cycle peak, and then decline before the subsequent menstruation [Nadler et al., 1992; Cheyne and Chivers, 2005]. This is a simple noninvasive method for animal care staff to monitor whether female gibbons are approaching reproductive maturity and if they are experiencing regular cycles.

During one particular observation period, two young females showed sexual swelling for almost 3 months continuously. In many primate species, adolescent females undergo a phase of exaggeration of sexual signals [e.g., Barbary macaques (*Macaca sylvanus*): Anderson and Bielert, 1994]. In this study, females showed these exaggerations at ages 7 and 8. In the wild, female gibbons leave the natal group and search for a mate at about 9 years of age [Bartlett, 2003], and it has been suggested that sexual swelling may assist females in attracting mates during initial pair formation or mate replacement [Cheyne and Chivers, 2005].

Sexual swelling was observed during gestation, which has also been observed in white-handed gibbons, but in both species the swellings do not follow a pattern [Barelli *et al*., 2007]. This has been noted in several primate species [silvered langurs (*Trachypithecus cristatus*): Shelmidine et al., 2007; Barbary macaques (*Macaca sylvanus*): Möhle et al., 2005; chimpanzees (*Pan troglodytes*): Coe et al., 1979]. In most primates with gestational swellings, this occurs in the earlier stages of pregnancy. Since no consistent pattern across gestation was found in this study, it suggests that gestational swellings would not be useful in diagnosing pregnancy.

CONCLUSIONS

(1) The average age at menarche was 6.2 years, which closely corresponded to the first observations of sexual swelling at 6.5 years. This suggests that both may be useful in assessing the age of reproductive maturity in individuals.
(2) Most females gave birth for the first time between 8.2 and 9.8 years, which is consistent with other gibbon species.
(3) The duration of the interbirth interval was about 2.3 years, and infant mortality decreased this by half.
(4) The length of the ovarian cycle as determined by menstrual bleeding was 25.6 days, compared to 27.3 days for sexual swelling, though swellings provided a more observable means of assessment.
(5) Evidence is provided of the applicability of noninvasive methods for collecting data about the reproductive development of Javan gibbons.

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REFERENCES

Anderson C, Bielert C. 1994. Adolescent exaggeration in female catarrhine primates. Primates 35:283–300.

Bartlett T. 2003. Intragroup and intergroup social interactions in white-handed gibbons. Int J Primatol 24:239–259.

Barelli C, Heistermann M, Boesch C, Reichard U. 2007. Sexual swellings in wild white-handed gibbon females (*Hylobates lar*) indicate the probability of ovulation. Horm Behav 51:221–230.

Bercovitch F, Strum S. 1993. Dominance rank, resource availability, and reproductive maturation in female savanna baboons. Behav Ecol Sociobiol 33:313–318.

Cheyne S, Chivers D. 2005. Sexual swellings of female gibbons. Folia Primatologica 77:345–352.

Cocks L. 2005. International studbook for Javan gibbons (*Hylobates moloch*), year 2005. [Online]. Retrieved on November 18, 2006 from: http://www.gibbons.de/main2/index.html.

Coe C, Connolly A, Kraemer H, Levine S. 1979. Reproductive development and behavior of captive female chimpanzees. Primates 20:571–582.

Dallmann R, Geissmann T. 2001. Different levels of variability in the female song of wild silvery gibbons (*Hylobates moloch*). Behaviour 138: 629–648.

Dixson A. 1998. Primate sexuality: comparative studies of the Prosimians, monkeys, apes and human beings. Oxford: Oxford University Press. 560p.

Geissmann T. 1991. Reassessment of age of sexual maturity in gibbons (*Hylobates* spp.). Am J Primatol 23:11–22.

Geissmann T, Nijman V. 2006. Calling in wild silvery gibbons (*Hylobates moloch*) in Java (Indonesia): behavior, phylogeny, and conservation. Am J Primatol 66:1–19.

Geissmann T, Orgeldinger M. 1995. Neonatal weight in gibbons (*Hylobates* spp.). Am J Primatol 37:179–189.

Hodgkiss S. 2007. Characterising the hormonal and physical correlates of the ovarian cycle in female Javan gibbons (*Hylobates moloch*). [Dissertation]. Oxford Brookes University, Oxford.

International Species Information System (2007). Species holding database. [Online]. Retrieved on September 5, 2007 from http://app.isis.org/abstracts/abs.asp.

Kappeler M. 1984. The gibbon in Java. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The Lesser Apes. Evolutionary and behavioural biology. Edinburgh: Edinburgh University Press. p 19–31.

Lasley B, Savage A. 2007. Advances in the understanding of primate reproductive endocrinology. In: Campbell C, Fuentes A, Mackinnon K, Panger M, Bearder S, editors. Primates in perspective. Oxford: Oxford University Press. 720p.

Machatschke I, Wallner B, Dittami J. 2006. Impact of social environment on female chimpanzee reproductive cycles. Horm Behav 50:126–131.

Möhle U, Heistermann M, Dittami J, Reinberg V, Wallner B, Hodges J. 2005. Patterns of anogenital swelling size and their endocrine correlates during ovulatory cycles and early pregnancy in free-ranging barbary macaques (*Macaca sylvanus*) of Gibraltar. Am J Primatol 66:351–368.

Mor A, Yamaguchi N, Watanabe K, Shimizu K. 1997. Sexual maturation of female Japanese macaques under poor nutritional conditions and food-enhanced perineal swelling in the Koshima troop. Int J Primatol 18:553–579.

Nadler R, Dahl J, Collins D. 1992. Serum and urinary concentrations of sex hormones and genital swelling during the menstrual cycle of the gibbon. J Endocrinol 136:447–455.

Nijman V. 2004. Conservation of the Javan gibbon *Hylobates moloch*: population estimates, local extinctions, and conservation priorities. Raffles Bull Zool 52:271–280.

Nijman V. 2006. In-situ and ex-situ status of the Javan gibbon and the role of zoos in conservation of the species. Contrib Zool 75:161–168.

Palombit R. 1994. Dynamic pair bonds in Hylobatids: implications regarding monogamous social systems. Behaviour 128:65–101.

Paoli T, Palagi E, Tacconi G, Tarli S. 2006. Perineal swelling, intermenstrual cycle, and female sexual behavior in bonobos (*Pan paniscus*). Am J Primatol 68:333–347.

Schwarzenberger F. 2007. The many uses of non-invasive faecal steroid monitoring in zoo and wildlife species. Int Zoo Yearb 41:52–74.

Seal U. 1993. Population and habitat viability analysis (PHVA). Apple Valley: Conservation Breeding Specialist Group.

Shelmidine N, Borries C, Koenig A. 2007. Genital swellings in silvered langurs: what do they indicate? Am J Primatol 69:1–14.

Shimizu K. 2005. Studies on reproductive endocrinology in non-human primates: application of non-invasive methods. J Reprod Dev 51: 1–13.

Supriatna J. 2006. Conservation programs for the endangered Javan gibbon (*Hylobates moloch*). Prim Conserv 21:155–162.

Thierry B, Heistermann M, Aujard F, Hodges J. 1996. Long-term data on basic reproductive parameters and evaluation of endocrine, morphological, and behavioral measures for monitoring reproductive status in a group of semifreeranging Tonkean macaques (*Macaca tonkeana*). Am J Primatol 39:47–62.

Vervaecke H, van Elsacker L, Mohle U, Heistermann M, Verheyen R. 1999. Inter-menstrual intervals in captive bonobos (*Pan paniscus*). Primates 40:283–289.

Wallen K, Zehr J. 2004. Hormones and history: the evolution and development of primate female sexuality. J Sex Res 41:101–112.

Wallis J. 1997. Primate conservation: the roles of zoological parks. Chicago: American Society of Primatologists. 252p.