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## A Reassessment of Age of Sexual Maturity in Gibbons (*Hylobates* spp.)

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From studies of both wild and captive animals, gibbons are thought to reach sexual maturity at about 6 to 8 years of age, and the siamang (*Hylobates syndactylus*) at about 8 to 9 years. However, a review of the literature reveals that in most cases the exact age of the maturing animals was not known and had to be estimated. This study presents seven case reports on captive gibbons of known age. Captive males of the white-cheeked crested gibbon (*H. leucogenys leucogenys*) and of the siamang (*H. syndactylus*) can breed at the age of 4 and 4.3 years, respectively. Similarly, hybrid females (*H. lar* x *H. moloch*) and siamang females can breed at 5.1 and 5.2 years, respectively. This finding may help to improve the breeding success of captive gibbon populations. It is not clear whether gibbons reach sexual maturity earlier in captivity or whether sexual maturity is also reached by five years of age in the wild. Possible implications for the interpretation of group size regulation and of reproductive strategies of wild gibbons are discussed.

**Key words:** gibbons, siamang, sexual maturity, *Hylobates syndactylus*, *Hylobates leucogenys leucogenys*, *Hylobates lar* x *H. moloch*

### INTRODUCTION

Field studies on gibbons (*Hylobates* spp.) have suggested that sexual maturity is attained at the age of about 6 years in *H. lar* and *H. klossii* [Ellefson, 1974, p.89; Tilson, 1981, p.263], between 6 and 8 years in *H. hoolock* [Tilson, 1979, p.14], and between 8 and 9 years in *H. syndactylus* [Chivers, 1974, p.234]. Gibbons are thought to be “not fully independent until 7 or 8 years of age” [Gittins & Raemaekers, 1980, p.68].

Reports on captive gibbons seem to be consistent with the field data. Although some indications suggest that captive gibbons may begin to mature sexually before the age of six years [Brody & Brody, 1974; Delacour, 1951], in none of these publications was the exact age of the animals known, and the latter study does not explain what observable change was taken as indicating the onset of sexual maturity (e.g. changes in the color of the fur, first copulation, onset of menstruation, birth of first offspring).

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Times of color changes occurring in subadult females of *H. concolor* [Fischer, 1980; Pocock, 1905], *H. leucogenys* [Delacour, 1951; Deputte & Leclerc-Cassan, 1981; Dittrich, 1979], and *H. hoolock* [McCann, 1933; Peart, 1935], and in subadult males of *H. pileatus* [Brockelman, 1975; Dobroruka, 1979; Gray, 1861; Marshall & Sugardjito, 1986] are sometimes equated with the onset of sexual maturity [e.g. Delacour, 1951; McCann, 1933]. It remains to be demonstrated that this is justifiable. In females of *H. leucogenys leucogenys*, "color change seems to begin some time before sexual maturity, but it may occur afterwards" [Deputte & Leclerc-Cassan, 1981]. Likewise, the onset of sexual activity or the onset of menstruation would seem to be problematic as an indicator of sexual maturity. In captive male baboons (*Papio cynocephalus*) and in female talapoin (*Miopithecus talapoin*), for instance, sexual activity was observed to occur several years earlier than actual reproduction [Lister, 1975; Rowell, 1977]. A period of "adolescent sterility" in females between the onset of menarche and the time of first conception has been reported in many primates [Richard, 1985, p.222], for instance in talapoin [Rowell, 1977] and in chimpanzees (*Pan troglodytes*) [Goodall, 1986]. Rowell [1977, p.285f] considers age at first conception a biologically more relevant index of female reproductive maturity.

This study presents seven case reports as evidence that captive males of the northern white-cheeked crested gibbon (*H. leucogenys leucogenys*), males and females of the siamang (*H. syndactylus*) and female hybrids (*H. lar* x *H. moloch*), at least, can reach sexual maturity well before six years of age. This finding may have some importance for the improvement of the breeding success of captive gibbons. In addition, possible implications for the interpretation of group size regulation and of reproductive strategies of wild gibbons are discussed.

## MATERIAL AND METHODS

Data presented in the case reports were collected from zoological gardens in Czechoslovakia, East Germany, Switzerland, and West Germany in the course of a study on gibbon communication. For animals cited in previous reports [Geissmann, 1986, in press], the same abbreviations of names have been used in order to facilitate cross-references.

As recommended by Rowell [1977], age at first conception was used as an index of sexual maturity. In order to permit direct comparison between data on the age of sexual maturity in gibbons presented in this report and data from the literature, age at birth of the first offspring is also given. The age at attainment of sexual maturity using this method can be calculated by subtracting gestation length from the age at birth of the first offspring.

Comparative data on birth weight in siamangs was needed for the second case report. Little information is available on this [Anonymous, 1976; Eisenberg, 1981; LaMalfa, 1969; Rumbaugh, 1967; Schultz, 1972], and even some of these data are questionable: A handwritten note in the A.H.Schultz-Archive (Anthropological Institute Zürich) documents that the three birth weights published in Schultz [1972] were taken from *preserved* specimens. Eisenberg [1981] published a (mean?) birth weight for the siamang, but does not indicate how many individuals had been weighed. LaMalfa [1969] published weights of four newborn siamangs, but the the lowest weight of 6 oz was a printing error and should have read 16 oz (454g) [LaMalfa, pers. comm. 1988]. Therefore, data for 23 birth weights of individual siamangs were obtained from several zoos in England (Twycross), Germany (Dortmund, Duisburg, Frankfurt, Krefeld), Switzerland (Zürich), and the U.S.A. (Milwaukee). To these were added two individual birth weights from the literature [Anonymous, 1976; Rumbaugh, 1967].

**Table I. Ages of Captive Gibbons at Birth of First Offspring: Data From the Literature**

Species	N (individuals) <sup>a</sup>		Age of individual at birth of 1st offspring (yr) <sup>b</sup>		Reference
	M	F	1	2	
<i>H. leucogenys</i>	1	1		Ca. 7.5	Adler et al. [1988]
<i>H. leucogenys</i>	1	1		9	Dittrich [1979]
<i>H. lar</i>		14		Ca. 6–9	Kawakami and Kollias [1984]
<i>H. lar</i>		1	Ca. 6.6		Schessler and Nash [1977]
<i>H. lar</i>		1	Ca. 7		Kollias and Kawakami [1981]
<i>H. lar</i>		1		Ca. 7+	Sawina and Opachowa [1981]
<i>H. lar</i>	1	1		Ca. 8	Haggard [1965]
<i>H. lar c</i>		1		Ca. 8.8–9.8	Meyer–Holzapfel [1950]; Steiner [1947, 1949]
<i>H. lar</i>		1		Ca. 9	Poglayan–Neuwall [1977]
<i>H. lar</i>		1	9.82		Haggard [1965]
<i>H. muelleri</i>	1			Ca. 6.8	Brody and Brody [1974]
<i>H. muelleri</i>		1		Ca. 7.3	Brody and Brody [1974]
<i>H. pileatus</i> <sup>c</sup>	1			Ca. 8.8–9.8	Meyer–Holzapfel [1950]; Steiner [1947, 1949]
<i>H. syndactylus</i> <sup>d</sup>		1		Ca. 5.3–8.3	Fox [1972, 1977, 1984]; La Malfa [1969]
<i>H. syndactylus</i>	1			Ca. 6.1	Bennett [1976]
<i>H. syndactylus</i>		1		Ca. 7.4	Bennett [1976]
<i>H. syndactylus</i>	1	1		Ca. 8	Bartmann and Brahm [1980]
<i>H. syndactylus</i>		1	8.25		Haimoff [1981]
<i>H. syndactylus</i>	1			Ca. 10	La Malfa [1969]

<sup>a</sup> M = males; F = females.

<sup>b</sup> 1 = age known; 2 = age estimated; y = years.

<sup>c</sup> The gibbon pair studied by Steiner [1947, 1949] and Meyer–Holzapfel [1950] can be identified as a male *H. pileatus* and a female *H. lar*, based on the published photographs. The age of both animals upon their arrival at the zoo was estimated to be 4 years in one report [Steiner, 1949], and 3 years in the other two reports [Meyer–Holzapfel, 1950; Steiner, 1947]. The male was still in the process of colour change when his first offspring was born. Personal observations on maturing pileated gibbons favor use of the younger age estimate.

<sup>d</sup> The age of this siamang female was estimated upon her arrival at the zoo to be 3 or 4 years [see Fox, 1972, 1977, 1984], and 6 years by LaMalfa [1969], hence the large range for this animal in the table. In addition, the reported date of arrival at the zoo differs by 28 days between the two authors.

In this report, black crested gibbons, *H. concolor*, and light-cheeked crested gibbons, *H. leucogenys* are regarded as two distinct species. This view is based on anatomical differences between *H. concolor* and *H. leucogenys* (Ma and Wang, 1986; Ma et al., 1988). In addition, overlapping distribution of *H. concolor* and *H. leucogenys* has been reported for two localities in northern Vietnam (Dao Van Tien, 1983) and for one in southern Yunnan Province in China (Ma and Wang, 1986; Ma et al., 1988).

## RESULTS

Table I summarizes data collected from the literature on the age of gibbons at the birth of first offspring. Data (also collected from the literature) on the duration of gestation in gibbons are listed in Table II. For the sake of brevity, the

TABLE II. Gestation Lengths in Gibbons

Species	N (preg- nancies)	Duration (days)	Reference
<i>H. leucogenys</i>	1	(ca. 7 months)	Rode [1942]
<i>leucogenys(?)</i>			
<i>H. leucogenys siki</i> or <i>H. gabriellae</i> <sup>a</sup>	1	200–212	Olivier [cited in Rode, 1942]
<i>H. lar</i>	1	199 (or less)	Voss [1970]
	1	ca. 205	Poglayen–Neuwall [1977]
	51(?)	210 (R=190–218)	Kollias and Kawakami [1981]
	1	210–217	Ellefson [1974, p. 91f]
	6	ca. 210	Martin et al. [1979]
	1	208–216	Robinson [1925]
	1	215	Crandall [1964, p. 131]
	1	222	Kollias and Kawakami [1981]
	?	225	Eisenberg [1981]
<i>H. muelleri</i>	1	195	Brody and Brody [1974]b
	1	210 (or less)	Linke [1988]c
<i>H. pileatus</i> and <i>H. lar</i> (?)	4	183–221	Breznock et al. [1979]
<i>H. pileatus</i>	2	193	Dr. C.R. Schmidt [pers. comm.], Schmidt–Pfister [1984]
	1	(ca. 7 1/2 months)	Badham [1967]
<i>H. syndactylus</i> <sup>d</sup>	1	199	Dr. C.R. Schmidt [pers. comm.]
	1	189–219	Dr. C.R. Schmidt [pers. comm.]
	1	200 (premature)	La Malfa [1969]
	1	221 (or less)	Dr. C.R. Schmidt [pers. comm.]
	?	223	Eisenberg [1981]
	1	230	Hill [1967], La Malfa [1969]
	1	231	Hill [1967], La Malfa [1969]
	1	235	Hill [1967], La Malfa [1969]
	1	238	La Malfa [1969]
	1	239	La Malfa [1969]

a The gestation length reported by Olivier [cited in Rode, 1942] was observed on the colony of crested gibbons held at Clères Zoo (France). Although these gibbons have been published as *H. leucogenys leucogenys* [Delacour, 1934; Rode, 1942], at least some of them (males and juvenile females) should probably be identified as *H. l. siki*, to judge from the published photographs [Delacour, 1934, pp. 7 and 12; Rode, 1942, fig. 1]. This is a subspecies only later defined by Delacour [1951].

b Brody and Brody [1974] reported that “this gestation period was exactly 210 days, reckoned from the first day of the last menstruation”. As this female's regular estrus averaged 31 days [Brody and Brody, 1974] and as other gibbons have been reported to cycle approximately every 27–30 days [King & Mitchell, 1987], I subtract 15 days and use a gestation of 195 days.

c These gibbons have previously been identified as *H. moloch* [e.g. Linke, 1988; Ritscher & Linke, 1982; Tembrock, 1974]. I visited the breeding male and the two surviving female offspring of the pair. On the basis of vocalizations and fur coloration, the male can be identified as *H. muelleri abbotti*. The breeding female died before my visit. Based on photographs kindly made available to me by Dr. K. Linke, this female can also be identified as *H. muelleri*, possibly *H. muelleri funereus*, certainly not *H. muelleri abbotti*. Based on fur coloration and vocalization, the offspring of the pair can be identified as *H. muelleri*.

d Whereas the gestation lengths provided by Schmidt [pers. comm.] cluster around 210 days, those reported by Hill [1967] and La Malfa [1969] are close to 235 days. It seems unlikely that the two estimates are compatible with each other. The difference between them is close to the suggested cycle length of about 30 days for the siamang [King & Mitchell, 1987]. It is possible that the onset of gestation occurred one cycle length earlier than recorded in the shorter estimates, or otherwise one cycle length later than recorded in the longer estimates. The latter interpretation seems more probable, since at least one of the shorter estimates is based on a pair which was together for only 221 days before giving birth [Schmidt, pers. comm.].

results of the seven case reports of the present study have been summarized in Table III. Additional information on cases No. 2 and 6 can be found in Schmidt [in press] and Merz [1987], respectively.

## DISCUSSION

Table I lists previously published data on the age of gibbons at the birth of first offspring. These data, after subtraction of gestation length (Table II), give information about the age at attainment of sexual maturity in gibbons. Most of the data fit well with the traditional view that gibbons usually become sexually mature somewhere between 6 and 8 years of age, and the siamang (*H. syndactylus*), at about 8 to 9 years. However, in most previously reported cases the exact age of the maturing animals was not known and had to be estimated (see Table I).

Seven case reports are summarized in Table III. These cases show that, under certain circumstances at least, gibbons can reach sexual maturity by 5 years of age in captivity (or even at 4 years in one case). This is much earlier than one would expect from previous data on the onset of fertility in gibbons.

Monogamous mammals and birds frequently exhibit a characteristic pattern of social, behavioral, ecological, and morphological features [e.g. Farabaugh, 1982; Kleiman, 1977; Kunkel, 1974]. Gibbons have been reported to show a similar complex of characteristics [MacKinnon & MacKinnon, 1984; Raemaekers & Chivers, 1980]. However, one characteristic has never been reported for gibbons as yet. It has been suggested that one of the features common to many monogamous species is a long maturation period of the young [Kleiman, 1977] and delayed sexual maturation of juveniles when they remain with the family group: "...inhibition of reproduction after the age of sexual maturity is common in juveniles remaining with the adults in the artificial conditions of captivity" [Kleiman, 1977, p.41]. Inhibition of reproduction in gibbons has not been reported to date, although a few observations have been made suggesting a delay in social maturity of gibbons retained in the natal group [Raemaekers & Chivers, 1980, p.294].

In the wild, the timing of emigration from the natal gibbon group may depend on the availability of space and unmated individuals [Chivers & Raemaekers, 1980], but aggressive parental behavior and the number of younger siblings may also be important determinants. Such factors might also help to explain the differences in the age of sexual maturity observed in gibbons.

Monogamy is a relatively rare social pattern among mammals [e.g. Kleiman, 1977]. Bischof [1972, 1975] proposed two different mechanisms which could maintain reproductive monopoly by the parents: (1) The offspring leave the group at attainment of sexual maturity or are driven away by the parents. (2) The offspring remain with the family group for some time after attainment of sexual maturity, but are excluded from propagation by their parents. Thus, social inhibition of reproduction should be expected to occur in those species following the second type of monogamy, whereas gibbons are thought to typify the first mechanism (e.g. Anzenberger, 1985; Bischof, 1972, 1975).

Although it is uncertain whether or not callitrichids are monogamous [see e.g. review by Goldizen, 1987], social inhibition of reproduction has been found to occur in laboratory groups of several species of callitrichid monkeys, including *Callithrix jacchus*, *Saguinus fuscicollis*, and *S. oedipus*. These studies have demonstrated that social environment influences fertility, sociosexual behavior, and pair bond formation in these species. The presence of the father or of another reproductive male may inhibit mating in a subordinate male [Abbott, 1984; French et al., 1984], while the presence of the mother or of another reproductive female may inhibit sexual behavior in a subordinate female, and even suppress ovulation

Table III. Ages of Captive Gibbons at Birth of First Offspring: Data from the Seven Case Studies of this Report

Case no. Name	Previous history of case individual				Previous history of pair partner				History of first offspring		Age at first reproduction (yr)		Gestation length (days)	Age at first conception (yr)		
	Sex	Birth date	Birth place	Rearing <sup>a</sup>	Paired since	Name	Birth date	Birth place	Rearing <sup>a</sup>	Birth date	Birth place	Survival			Age at first reproduction (yr)	
<i>Hylobates syndactylus</i>																
1	Ta, "Tawar"	m	8/3/1973	Zürich (CH)	h	1/9/1977	Vr	About 1963	Wild born	m	19/2/1979	Studen (CH)	1 day	5.95	189–239	5.30–5.44
2	Da, "Dagobert" <sup>b</sup>	m	4/10/1979	Dortmund (GFR)	h	Aug. 1981	Ch	25/12/1976	Zürich (CH)	h	28/9/1984	Zürich (CH)	0.8 months <sup>c</sup>	4.98	189–239	4.33–4.47
3	Jo, "Josef" <sup>d</sup>	m	11/3/1982	Dresden (GDR)	m	29/8/1985	Ir	13/6/1981	Munich (GFR)	m	22/2/1987	Gottwaldov–Lesná (CSSR)	still alive	4.95	189–239	4.30–4.44
4	Ki, "Kimmy"	m	11/11/1983	Dresden (GDR)	m	Dec. 1986	Ce	31/10/1978	Dortmund (GFR)	h	20/9/1988	Dortmund (GFR)	0 days <sup>f</sup>	4.86	189–239	4.21–5.34 <sup>g</sup>
5	Ir, "Inna" <sup>de</sup>	f	13/6/1981	Munich (GFR)	m	29/8/1985	Jo	11/3/1982	Dresden (GDR)	m	22/2/1987	Gottwaldov–Lesná (CSSR)	still alive	5.70	189–239	5.04–5.18
<i>H. leucogenys leucogenys</i> <sup>h</sup>																
6	Er, "Erich"	m	29/1/1983	Leipzig (GDR)	m	3/9/1987	Mi	About 1967	Wild born	h	3/9/1987	Hannover (GFR)	still alive	4.59	200–212	4.01–4.05
<i>H. lar</i> x <i>H. moloch</i> <sup>i</sup>																
7	Gi, "Gipsy" <sup>ak</sup>	f	2/4/1979	Rheine (GFR)	m	25/11/1984	Jr-II	17/4/1976	Nürnberg (GFR)	?	25/11/1984	Rheine (GFR)	still alive	5.65	190–225 <sup>l</sup>	5.03–5.13

<sup>a</sup> h = hand-reared, m = mother-reared.

<sup>b</sup> From August 1981 until 20 September 1984, this group included two males of comparable age: Da and Fa. The latter (born on 2 June 1979) was the younger brother of the female Ch. Da (and not Fa) is presumed to be the father of the group's offspring (twins), because only he was seen copulating with Ch (on 23 April 1982 and 18 August 1983) [Dr. C.R. Schmidt, pers. comm.].

<sup>c</sup> Twin birth. The second twin was stillborn (weight: 411 g), the first twin died of cachexia on 30 May 1985 (weight: 660 g) [for details, see Schmidt, in press]. The weight of the stillborn twin (411 g) is relatively low compared with a sample of 25 newborn siamangs (mean and standard error = 480±18g, or, if those five animals are omitted which were stillborn or which died during the day of birth: 497±20g). These data on birth weights have been collected from the records of various zoos, and from the literature (see Material and Methods).

<sup>d</sup> Cases No. 3 and 5 concern a male and a female siamang (Jo and Ir) which were kept together as a pair at the Gottwaldov–Lesná Zoo.

<sup>e</sup> Re-named "Tschermula" at the Gottwaldov–Lesná Zoo (CSSR).

<sup>f</sup> Premature male. The infant was completely hairless and had closed auditory canals (Dr. H. Lückner, pers. comm.). It died on the same day.

<sup>g</sup> The male's age at conception of the infant may have been slightly older than calculated, because the infant was prematurely born.

<sup>h</sup> On the basis of the appearance of his white facial markings, I attribute the male white-cheeked crested gibbon Er to the subspecies *H. leucogenys leucogenys*, following the descriptions of Groves [1972] and Schilling [1984]. Photographs of the parents published by Adler [1984, 1986] are likewise consistent with their attribution to *H. l. leucogenys*. At the Hannover Zoo, Er was kept together with a female (Mi) which has previously been identified as *H. l. leucogenys* by Dittrich [1979], on the basis of her juvenile coloration.

<sup>i</sup> The father of the hybrid female Gi can be identified as *H. lar* (pale phase), based on photographs kindly made available to me by Mr. A. Johann. The hybrid's mother (Jr-II), until recently living at the Munich Zoo, can be identified as *H. moloch*, on the basis of coloration and song characteristics (own observations).

<sup>j</sup> Gi was not hand-reared but remained in her natal group, together with her older sister He (born on 17 February 1974). The hybrids' father died on 12 November 1979. In November 1982, the mother was removed from, and an adult male *H. lar* (Jr-II, dark phase) was introduced to, both hybrid females. On 23 October 1983, the younger hybrid female Gi was reported to menstruate, but it is not known whether this was her first menstruation (Mr. A. Johann, pers. comm.). The older hybrid female He gave birth to a baby (5 December 1983). Due to tensions in the group, He was sold on 7 December 1983, leaving only her younger sister Gi with the lar male Jr-II, and on 25 November 1984, Gi gave birth to a healthy male infant (Js).

<sup>k</sup> No data on the gestation length of *H. moloch* or of hybrid gibbons are apparently available at present. A pregnancy of 190 to 225 days (which may be typical of gibbon species closely related to *H. lar*, see Table II) has been used for calculating Gi's age at conception of the infant.

<sup>l</sup> No data on the gestation length of *H. moloch* or of hybrid gibbons are apparently available at present. A pregnancy of 190 to 225 days (which may be typical of gibbon species closely related to *H. lar*, see Table II) has been used for calculating Gi's age at conception of the infant.

[Abbott, 1984; Abbott & Hearn, 1978; Abbott et al., 1981; Epple & Katz, 1984; French et al., 1984; Savage et al., 1988; Tardif, 1984]. Subordinate animals are apparently released from this social suppression or inhibition of sexual behavior (and fertility) when they are removed and housed with an adult animal of the opposite sex. In addition, it has been shown that maturing tamarins (males and females of *Saguinus fuscicollis* and females of *S. oedipus*) can fulfill the behavioral roles of pair bonded adults and also breed at a much earlier age when they live under the influence of an adult sex partner, in comparison with animals cohabiting with a sex partner of their own age [Epple, 1981; Epple & Katz, 1980], or remaining in their family group [Tardif, 1984].

It may, therefore, be significant that four of the gibbons presented in the case reports of this study had been separated from their natal group, and had, at a relatively young age, been brought together with a much older potential mate (case reports 1, 2, 4, 6). However, in one pair of captive siamangs, both animals had been mother-reared, both had been brought together at an early age (before the age of five years), and both became sexually mature well before the age of six years (case reports 3 and 5). The seventh case concerns a young female whose parents had been removed from the natal group, while a strange adult male had been introduced. The male formed a breeding pair with that female's older sister, but as soon the older sister had been removed, the young female started breeding with the same male.

Two different social variables could possibly have influenced the early sexual maturity in the cases presented here: **1.** The disruption of the family unit and removal of parental pressure, and **2.** the appearance of a strange social stimulus.

It has been suggested that chemical stimuli found in the scent secretions produced by the natal family are most likely involved in reproductive suppression in tamarins. This potential role of scent secretions is supported by the observation that scent markings from the natal family have the ability to disrupt reproductive cycles in *Saguinus fuscicollis* [Epple & Katz, 1984] and to delay the onset of ovulations in newly paired females of *S. oedipus* [Savage et al., 1988]. In this context, it may be relevant that the presence of a scent gland has recently been discovered in the siamang (*Hylobates syndactylus*) [Geissmann, 1987a], and macroscopically similar glandular structures seem to be present in (perhaps all) other gibbon species [Geissmann, 1987b; Mootnick et al., 1987].

However, social factors influencing the onset of sexual maturity in gibbons cannot securely be demonstrated from these data. Early sexual maturation in the case studies presented above could also have been the result of a third variable: better nutrition of these animals. In baboons, macaques and chimpanzees, the age at attainment of developmental markers such as the age of first reproduction may occur much earlier in captive or provisioned than in unprovisioned wild animals [e.g. Altmann et al., 1981; Sugiyama & Ohsawa, 1982; Tutin & McGinnis, 1981]. For instance, in yellow baboons (*Papio cynocephalus*), "the ratio of age at attainment of developmental milestones for animals in captivity to that for unprovisioned wild animals was approximately 3.5 to 5" [Altmann & Alberts, 1987].

Thus, three different variables may have influenced the early sexual maturity of the gibbons studied here: early removal from the family group, early confrontation with a suitable mate, and boosted nutrition. The variables could not be experimentally controlled in this purely descriptive study. Therefore, it cannot be decided which of the three variables may have been responsible for the early sexual maturity reported here. Each variable seems plausible to some degree.

If one of these variables (no matter which one) can speed up sexual maturation by about 1 to 3 years in gibbons, this holds some promise for breeding these

animals in captivity. Because of the strictly monogamous social structure of most species, adult gibbons must usually be kept in pairs. In addition, due to their low reproductive potential, "gibbons cannot be perpetuated in significant numbers artificially, despite attempts to do so. Their maximum reproductive rate is low (about one offspring per every 1–2 years), and many individuals will not reproduce in captivity. Even if captive populations could replace themselves (some zoos have had good success), any margin of increase would be extremely low and unsteady" [Brockelman, 1975, p. 149].

Lowering the age at first reproduction would mean not only one additional offspring per breeding pair, but also that the offspring can breed earlier. Hence, a geometrical shift in the pattern of population increase could result. This would represent a significant improvement in the breeding success of the captive gibbon population, thus reducing the demand for animals captured from the fast-diminishing wild populations, some of which have already, or very nearly, reached relict status [Brockelman & Chivers, 1984; Chivers, 1986; MacKinnon, 1986, 1987; MacKinnon & MacKinnon, 1987].

## CONCLUSIONS

1. Virtually without exception, data collected from the literature support the traditional view that gibbons, both in the wild and in captivity, usually become sexually mature somewhere between 6 and 8 years of age, and the siamang (*H. syndactylus*), at about 8 to 9 years. However, in most previously reported cases the exact age of the maturing animals was not known and had to be estimated.

2. This study presents seven case reports on captive gibbons of known age. Captive males of the white-cheeked crested gibbon (*H. leucogenys leucogenys*) and of the siamang (*H. syndactylus*) can breed at the age of 4 and 4.3 years, respectively. Similarly, hybrid females (*H. lar* x *H. moloch*) and siamang females can breed at 5.1 and 5.2 years, respectively. This is much earlier than one would expect from previous data on the onset of fertility in gibbons.

3. It is not known whether gibbons reach sexual maturity earlier in captivity or whether sexual maturity is also reached by five years of age in the wild.

4. Relative to earlier case studies, three different variables could possibly have influenced the age at sexual maturity in the cases presented here: 1) The disruption of the family unit and removal of parental pressure, 2) the appearance of a strange social stimulus, and 3) high quality nutrition.

5. The maximum reproductive rate of gibbon pairs is relatively low (about one offspring per every 1–2 years, but rather 2–3 years in the wild). Lowering the age at first reproduction would not only mean one additional offspring per breeding pair, but that the offspring could also breed earlier, resulting in a geometrical modification of the pattern of population increase. This would represent a significant improvement in the breeding success of the captive gibbon population, thus reducing the demand for animals to be removed from threatened wild populations.

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