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## **Extra-pair Copulations in a Monogamous Gibbon (*Hylobates lar*)**

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### **Abstract**

This study, conducted in a rainforest in Thailand, presents the first evidence for extra-pair copulations in white-handed gibbons – Asian apes that live in monogamous groups. The ratio of in-pair copulations versus extra-pair copulations as observed among three free-ranging, well-habituated groups was 88 versus 12 % and involved one adult paired female and three adult paired males. Extra-pair copulations may be explained as an effort to breed with a partner of superior quality to the current mate and/or may be part of a strategy to forestall infanticide.

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### **Introduction**

Monogamous mating systems are restricted to less than 3 % of mammalian species and, hence, are relatively rare among mammals (KLEIMAN 1977). By contrast, about 90 % of all avian species have traditionally been reported to be monogamous breeders (review: WELTY 1962; LACK 1968). In recent years, however, the number of 'truly' monogamous bird species has decreased as observations of extra-pair copulations (EPC) and evidence for extra-pair fertilizations (EPF) has grown (GLADSTONE 1979; FORD 1983; BIRKHEAD et al. 1987; GIBBS et al. 1990; WESTNEAT et al. 1990; VENIER et al. 1993). The proportion of monogamous primates is relatively high at about 15 % of all species (RUTBERG 1983). Primary examples in this regard can be found among neotropical primates and among the hylobatids (gibbons) which inhabit the tropical and less seasonal parts of the semi-evergreen rain forests in south Asia.

Since the earliest field studies of gibbons (MCCANN 1933; CARPENTER 1940), it has been proposed that these Asian apes form monogamous pairs, live in small

nuclear families with 2–6 members, and are territorial. These assumptions have been reinforced by more detailed research on the nine or so species of the *Hylobatidae* in the past 20 years (TENAZA 1971, 1975; CHIVERS 1974; ELLEFSON 1974; GITTINS 1979; SRIKOSAMATARA 1980; KAPPELER 1981). Bonds between adults are commonly believed to be stable for many reproductive cycles (LEIGHTON 1987), or may even last a lifetime (GITTINS & RAEMAEEKERS 1980). Mating is assumed to occur exclusively between pair-mates (BROCKELMAN & SRIKOSAMATARA 1984), although relatively few actual data are available concerning sexual behavior in wild populations (CARPENTER 1940; ELLEFSON 1974; CHIVERS 1978; CHIVERS & RAEMAEEKERS 1980; REICHARD 1991).

Females give birth approximately every three yr, and, once an infant becomes independent at around 2 yr of age, they will probably cycle several mo before becoming pregnant again (LEIGHTON 1987). However, not much is known about reproductive parameters in females, as field projects have often been too short to cover several complete consecutive receptive cycles of a given group's female. To observe the relatively short matings of these exclusively arboreal apes that dwell high in the canopy is a difficult affair in any case, even though pairs sometimes vocalize during copulation (COOLIDGE 1933; ELLEFSON 1974; HAMILTON & ARROWOOD 1978). Hence, to date, most aspects of gibbon reproductive biology such as mate acquisition, pair-bond maintenance, pair stability, dispersal and pair-formation lack firm quantitative information. Most importantly, during many studies, researchers successfully habituated only one group, which made it difficult, or even impossible, to document in detail encounters between neighboring groups or unfamiliar individuals. Consequently, the prediction of mate fidelity could rarely be tested. Indirect support for the assumption of mating exclusivity came, however, from field play-back experiments, in which territorial intrusion was simulated (MITANI 1984, 1985; RAEMAEEKERS & RAEMAEEKERS 1985). Resident pairs responded mostly agonistically towards strangers' play-back calls. Individuals reacted most strongly to the loud vocalizations of simulated same-sex intruders, although partners usually joined the subsequent behaviors such as approaches and/or duets. It was therefore proposed that aggression between same-sex individuals primarily regulates interactions between neighboring pairs (MITANI 1984).

Elaborations on Darwin's sexual-selection theory have produced several corresponding characteristics concerning the genital morphology and mating behavior of primates living in one-male-one-female social systems (SHORT 1981), e.g. there is no evidence of overt signs of the female ovulatory state, such as perineal swellings and/or sex-skin-color changes during the menstrual cycle (ALEXANDER & NOONAN 1979; SILLÉN-TULLBERG & MØLLER 1993), and males have small testes due to the absence of sperm competition. By contrast, large testes and advertisement of ovulation are found in most multi-female-multi-male primate groups (CLUTTON-BROCK & HARVEY 1976), and are probably linked to mating conditions (HARCOURT et al. 1981).

Gibbons have traditionally been thought to conform to most of these predictions. More detailed recent research on captive individuals, however, has

revealed that gibbon females actually develop relatively complex genital structures (DAHL & NADLER 1992a). Moreover, changes in the turgidity and/or coloration of the anogenital region have been noted occasionally (CARPENTER 1940, 1941; CHIVERS 1974, 1978; BREZNOCK et al. 1977; DAHL & NADLER 1992b), which correspond with hormonal changes during the menstrual cycle (NADLER et al. 1993). These characteristics can be summarized as slight signs of the ovulatory state. Testes are small if compared to those in males of multi-female-multi-male societies such as macaques or chimpanzees, but notably larger than in gorillas or orang utans, which typically reproduce in a one-male mating situation (HARCOURT 1981). Moderate-sized testes, as well as changes in the external genitalia during the menstrual cycle are not per se expected under a strict one-male mating system such as monogamy.

Indeed, extra-pair sexual activity has recently been reported for a female siamang (*Hylobates syndactylus*) that copulated with three males from a neighboring group (PALOMBIT 1994). In this study, intergroup relations of three habituated, neighboring white-handed gibbon groups (*Hylobates lar*) were investigated, and evidence for a mixed (e.g. not exclusively monogamous) reproductive strategy is presented by reporting in detail three cases of extra-pair copulations.

### Material and Methods

The study site, at 730–870 m above sea level, was located inside the primary rain forest of the Khao Yai National Park in Thailand (2168 km<sup>2</sup>; 101°22' E, 14°26' N; 200 km NE of Bangkok). Data on a population of white-handed gibbons were collected by the author in a preliminary study from Oct. 89 to the end of Jan. 90, and, in the main study period, from Jan. 92 to the end of May 93. J. NEUDENBERGER and B. KLAUSEN contributed data during the latter period. The composition of the three main study groups A, B and C is given in Table 1.

Individuals were denoted by a specific name and a three-letter code indicating age, sex, and group (e.g. AFA = adult female group A). Group members were individually known and well habituated. Details on the groups' histories have been provided by RAEMAEEKERS & RAEMAEEKERS (1984), REICHARD (1991), NETTELBECK (1993), and NEUDENBERGER (1993). Observations of EPCs were made by the author while following group A. In this group, focal-animal and instantaneous sampling methods (ALTMANN 1974) were conducted for 3–25 d during each mo of the study period, usually from 0600–1630 h. No observations were made in Aug. 92. The succession of reproductive events, in-pair copulations (IPCs) and EPCs, as described below, is summarized in Table 2.

### Results

In study group A, an infant was born around Oct. 90. Resumption of sexual activity by the pair was first observed in May 1992, when the female was weaning the infant. Frequent matings were recorded from Dec. 92 to Apr. 93, when the infant already appeared to be relatively independent. Over a 10-mo period, 59 IPCs were observed over 31 d. In addition, the female was seen to engage in 7 EPCs with the adult male from neighboring group C (27 Jan. and 11 Mar. 93), and in 1 EPC with the adult male from neighboring group B (25 Apr. 93). The first and last incidents were located in overlap areas of the groups' home ranges. The second incident occurred, however, inside group A's territory, which is an area which is usually not visited by members of neighboring groups (Fig. 1).

Table 1: Age-sex composition of three groups of white-handed gibbons, Khao Yai National Park, Thailand (1992–93)

Group	Sex	Age class	Color	Denotation (age/sex/group)	Name
A	f	adult	buff	AFA	Andromeda
	m	adult	black	AMA	Fearless
	m	juvenile	black	JMA	Amadeus
	m	infant	buff	IMA	Aran
B	f	adult	black	AFB	Bridget
	m	adult	black	AMB	Bard
	f	subadult	black	SFB <sup>1</sup>	Brit
	f	juvenile	buff	JFB	Brenda
	f	infant	black	IFB	Benedetta
C	f	adult	black	AFC	Cassandra
	m	adult	buff	AMC	Cassius
	m	subadult	buff	SMC1	Chet
	m	subadult	black	SMC2	Claude
	m	juvenile	black	JMC	Christopher
	m	infant	buff	IMC	Caleb

<sup>1</sup> Individual left group B around Aug. 1992.

The female gave birth around mid Oct. 93. In white-handed gibbons, the gestation period is estimated to last about 27–32 wk (ARDITO 1976; GEISSMANN 1991). Thus, at least some of the EPCs took place during the period of conception.

A total of 15 IPCs were recorded in study group C over a 12-d period beginning in Nov. 92. This female also carried an infant which was in the process of weaning. However, observations of matings ceased abruptly in Jan. 93, when the female suffered an injury which paralysed her right arm for the subsequent two mo (Table 2). Nevertheless, the female must have conceived around May 93, because she gave birth in Nov. 93 (W. Y. BROCKELMAN pers. comm.).

The adult female of the third study group (B) carried and nursed an infant throughout the observation period. She was not seen to engage in sexual behavior during this study.

Details about the occurrence of EPCs are provided in the following excerpts from field notes.

#### 27 Jan. 93 (EPC between AFA/AMC)

1204 h: After having fed near group C in the same large tree for about 30 min, group A moved toward a little stream, led by AMA. On their way they approached SMC2, who thereupon emitted a short series of low-intensity encounter hoots.

1205 h: AMC emerged from a nearby vine and sat beside SMC2, 10 m away from AMA. The three males stared at each other and uttered encounter hoots.

Table 2: In-pair (IPC) and extra-pair copulations (EPC) in three groups of white-handed gibbons, Khao Yai National Park, Thailand (1992-93)

Group	Date	Event	Individual(s)	No. of copulations	Days with copulations	Female reproductive state (assumed)
A	About Oct. 90	Birth	AFA			lactational amenorrhea
	09 May 92	IPC	AFA/AMA	2	1	lactational amenorrhea
	11 Sep. 92	IPC	AFA/AMA	1	1	lactational amenorrhea
	16/19 Nov. 92	IPC	AFA/AMA	2	2	cycling
	17 Dec. 92-21 Jan. 93	IPC	AFA/AMA	30	15	cycling
	27 Jan. 93	EPC <sup>1</sup>	AFA/AMC	1	1	cycling
	16 Feb. 93-04 Mar. 93	IPC	AFA/AMA	17	7	cycling
	11 Mar. 93	IPC	AFA/AMA	2	1	cycling or pregnant
		EPC <sup>2</sup>	AFA/AMC	6		cycling or pregnant
	24 Mar. 92-14 Apr. 93	IPC	AFA/AMA	5	4	cycling or pregnant
	25 Apr. 93	EPC <sup>3</sup>	AFA/AMB	1		cycling or pregnant
	16 Oct. 93	Birth	AFA		1	pregnant
						lactational amenorrhea
	B	About Nov. 91	Birth	AFB		
Jan. 92-Apr. 93		Carry infant	AFB			lactational amenorrhea
25 Apr. 93		EPC <sup>3</sup>	AFA/AMB	see above		see above
C	About Dec. 90	Birth	AFC			lactational amenorrhea
	03 Nov. 92-01 Jan. 93	IPC	AFC/AMC	15	12	cycling
	19 Jan. 93	Injury observed	AFC			
	27 Jan. 93	EPC <sup>1</sup>	AFA/AMC	see above		see above
	11 Mar. 93	EPC <sup>2</sup>	AFA/AMC	see above		see above
	Nov. 93	Birth	AFC			lactational amenorrhea

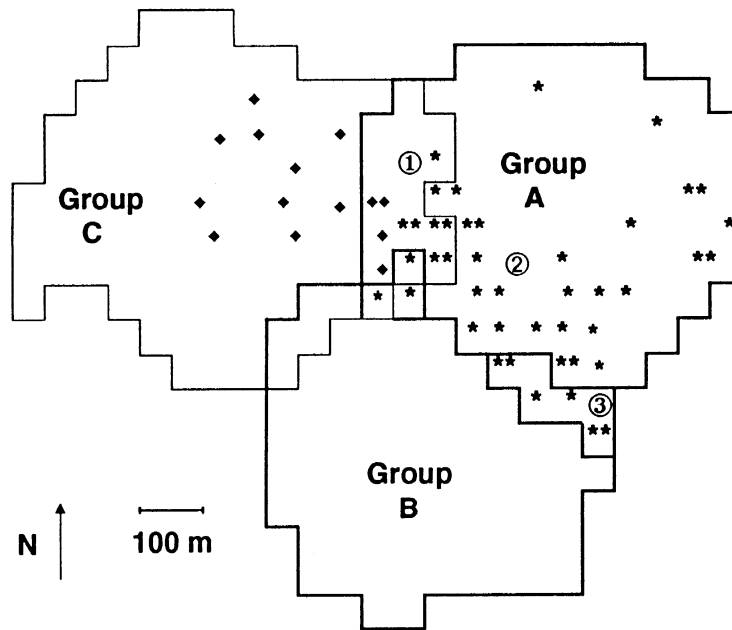


Fig. 1: Home ranges and copulations in three groups of white-handed gibbons, Khao Yai National Park, Thailand (1992–1993).

\* IPC (in-pair copulation) AFA/AMA (May 1992–Apr. 1993); ◆ IPC AFC/AMC (Nov. 1992–Jan. 1993); ① EPC (extra-pair copulation) AFA/AMC (27 Jan. 1993); ② EPC AFA/AMC (11 Mar. 1993); ③ EPC AFA/AMB (25 Apr. 1993)

1206 h: SMC2 retreated toward the remaining members of group C. AMA followed him until they were both out of sight, although their encounter hoots could still be heard. Meanwhile, AMC approached AFA, who rested with her offspring, IMA and JMA, in the lower canopy.

1207 h: AMC moved within arms' reach of AFA, who screamed loudly (as if she had been hit, but probably had not) and dropped 2 m. AMC stared at her, approached closer from behind and attempted to mount her. However, AFA did not cooperate and turned around. AMC approached again from behind and AFA remained still. The male shortly smelled at her genital region and mounted. The subsequent dorso-ventral copulation lasted 46 s and was accompanied by about 23 pelvic thrusts. At about the same time, AMA – who was followed by a second observer – engaged in an agonistic encounter with the subadult males SMC1 and SMC2 of group C, about 25 m away.

1209 h: AMA returned to AFA about 1 min after the EPC had occurred. Upon AMA's arrival, AMC crossed the stream to the opposite direction and disappeared through the canopy toward group C's territory.

1215 h: AFA resumed body contact with AMA for the first time after the EPC.

