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Extra-pair copulations in monogamous wild white-handed gibbons (*Hylobates lar*)

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Ever since the earliest field study of gibbons (CARPENTER 1940) it has been suggested that these Asian apes form monogamous pairs, live in small groups of 2–6 members and are territorial. Pairs are commonly believed to remain together for many reproductive cycles or even for a lifetime (GITTINS and RAEMAEEKERS 1980), and mating is assumed to occur exclusively between pairmates (BROCKELMAN and SRIKOSAMATARA 1984). However, relatively few actual data are available concerning sexual behaviour in wild populations (e.g. ELLEFSON 1974; REICHARD 1991). Hence, most aspects of gibbons' reproductive biology lack firm quantitative information. Most importantly, during many field studies, researchers habituated only one group, which made it difficult or even impossible to document intergroup behaviour and to test the prediction of mate fidelity.

Elaborations of Darwin's sexual selection theory have produced several links concerning genital morphology and mating behaviour of primates living in one-male mating systems (SHORT 1981) including the lack of female anogenital swellings and colour changes during menstrual cycles (HARCOURT 1981), as well as small testes of males (HARCOURT et al. 1981). Gibbons are commonly believed to conform to most of these predictions. Gibbon females, however, develop relatively complex genital structures which sometimes change in turgidity and/or colouration during the menstrual cycle (NADLER et al. 1993). Testes of males are medium-sized compared to chimpanzees and gorillas (HARCOURT et al. 1981) and might therefore be classified as "moderate". Moreover, extra-pair copulations have recently been reported for the siamang (*Hylobates syndactylus*) (PALOMBIT 1994).

The present study was conducted in the primary rain forest of the Khao Yai National Park, Thailand (2.168 km²; 101°22' E, 14°26' N). Data were collected from October 89 through January 90 and from January 92 through May 93. J. NEUDENBERGER and B. KLAUSEN contributed data during the latter period. The composition of the study groups A, B and C were: (A) 1 adult female, 1 adult male, 1 juvenile male, 1 infant male; (B) 1 adult female, 1 adult male, 1 subadult female (which left the group in August 93), 1 juvenile female, 1 infant female; (C) 1 adult female, 1 adult male, 2 subadult males, 1 juvenile male, 1 infant male. Observations of extra-pair copulations (EPC) were made by the author while following group A. In this group, regular observations were conducted for 3–12 days during each month of the study period, usually from 06:00–16:00 hrs. No observations were undertaken during August 92.

In group A, an infant was born around September 90. Resumption of sexual activity of the pair was first noticed in May 92. Frequent matings were recorded from December 92–April 93. Over a 10 month period, 59 in-pair copulations (IPC) were observed on 31 days. In addition, the female was seen to engage in 7 EPCs with the adult male of

group C (27 January and 11 March 93) and in one EPC with the adult male of group B (25 April 93). Hence, 12% of observed copulations of this female were EPCs and they occurred on 9% of the days on which sexual behaviour was recorded. During the last EPC, however, the female was presumably already pregnant, because she gave birth in mid October 93.

EPCs might be an adaptation of gibbon females' to increase the chance of fertilisation by a male of superior genetic qualities (FISHER 1930). They might also increase offspring survival by, e.g., enhancing access to food sources. The study groups' home ranges overlapped substantially. Group encounters in these areas were frequent but not always agonistic (pers. obs.). This tolerance was potentially linked to the occurrence of EPCs. Furthermore, EPCs might lower the risk of infanticide after mate changes (van SCHAIK and DUNBAR 1990). Although, infanticide has not yet been observed in gibbons, evidence is mounting that male replacements and group composition changes are more frequent than has previously been reported (e.g. TREESUCON and RAEMAEEKERS 1984; PALOMBIT 1992).

Gibbon males could benefit from EPCs by leaving more offspring as compared to strictly monogamous males. Even though copulating with several females does not always result in a reproductive pay-off when compared with monogamous mating (DUNN and ROBERTSON 1993). Additionally, a paired male which searches for a chance to copulate with a second female must leave his mate and thus risks her infidelity. Therefore, a male will have to balance the search for EPC opportunities with the need to insure paternity of the offspring of the mate.

The behaviour of gibbon males as observed in the present study support these predictions. Groups were cohesive and individuals spent most of the day in close proximity. Therefore, a female was rarely found without the company of her pair-male. During group encounters, males usually positioned themselves between their mate and the neighbouring male(s) presumably to prevent close proximity through their physical presence. Thus, the circumstantial and behavioural observations illustrate the males' conflicting interests of guarding their mate and searching for additional reproduction opportunities.

In summary, the sexual behaviour of wild white-handed gibbons as described here suggests more reproductive flexibility for these Asian apes than expected from the earlier descriptions of a strictly monogamous mating system.

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