

SHORT COMMUNICATIONS

Extra-pair copulations in a monogamous ape

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Individuals of the nine to 10 species of monogamous gibbons (*Hylobates* spp., Hylobatidae) maintain unambiguous heterosexual pair bonds that are sometimes suggested to be 'life-long' (Gittins & Raemaekers 1980). Fidelity to one's mate has long been considered an implicit behavioural corollary of monogamy in gibbons in particular and animals in general. This is in part because the evolution of extensive, direct paternal investment characterizing many (but by no means all) monogamous species predicts relatively high certainty of paternity (Kleiman & Malcolm 1981), which is most obviously generated by mating exclusivity (but see Parker 1984). Among gibbons, the siamang, *Hylobates syndactylus*, is uniquely characterized by substantial direct paternal care in the form of infant-carrying (Chivers 1974). Trivers (1972) argued, however, that monogamy did not a priori preclude 'mixed' reproductive strategies based on 'extra-marital' consortships. Indeed, recent observations of unexpectedly high rates of extra-pair copulations and fertilization in many 'apparently' monogamous birds have revealed considerable variation in sexual behaviour and thereby challenged the assumption that avian monogamy and mating exclusivity are invariably linked in any functional or proximate sense (e.g. Gowaty & Mock 1985; Birkhead et al. 1986). During a 2.5-year study of wild white-handed gibbon, *Hylobates lar*, and siamang, *H. syndactylus*, at the Ketambe Research Station, northern Sumatra, Indonesia, I observed five episodes of extra-pair copulations involving a pair-bonded adult female siamang of one family group, designated 'C' group, and three other conspecific males of a neighbouring group, referred to as 'P' group.

C group comprised a mated, heterosexual pair and a subadult female at the beginning of the study (August 1985). Besides the extra-pair copulations reported here, the adult male and female of C group

copulated with one another throughout the study. All extra-pair copulations between the C female and other males occurred during or after 'inter-group interactions' in which the members of neighbouring groups meet regularly at their mutual territorial boundaries, exchange aggressive displays, and chase one another. Three copulations involved an immature male of P group, who was judged an older juvenile at the beginning of the study. The first of these (15 February 1986) occurred at the end of an especially long (> 3 h) inter-group interaction. Approximately 10 min after the adult male of C group had left the interaction area and travelled into his group's territory (followed by one observer, while a second observer stayed behind to monitor the remaining individuals), the juvenile male approached and copulated with the adult female of C group (intromission and thrusting observed). It was unlikely that this interaction was visible to the adult male of C group because he was 80–90 m away feeding on fruit and the copulating pair was low (15 m) in the densely foliated main canopy of the forest. Approximately 5 min after the copulation had ended and the juvenile had withdrawn from the female, the adult male of C group ceased feeding, returned to the interaction area, joined his female mate, and then travelled away with her. The C female again had sexual contact with this immature male during a subsequent inter-group interaction (7 August 1986). As the immature male mounted the C group female, her adult male was only a few metres away and immediately brachiated towards the pair whereupon the young male dismounted (only 6 s after observed intromission), screamed, and withdrew quickly. The adult male of C group did not pursue him. This pair copulated a third time on 26 September 1986 (by which time this immature male was considered a subadult) approximately 40 min after an inter-group interaction had concluded

(i.e. after P and C groups had travelled away from each other into their respective territories). The immature male did not follow members of his group at this time, but instead remained near the members of C group. He approached the adult female of C group, mounted, copulated for 31 s (intromission and thrusting observed), then returned to his group. The adult male of C group was approximately 20 m away.

The other two extra-pair copulations were between the C female and two different adult males, which were successive monogamous pairmates of the adult female of P group. One of these copulations (9 April 1986) occurred after the adult male of P group approached the C female during an inter-group interaction (intromission and thrusting were observed). The adult male of C group, who was 50 m away at the time, oriented in the direction of the copulating pair, and brachiated towards them. When the advancing C male came to within 20 m of the copulating pair, the male of P group dismounted and brachiated quickly away. A final extra-pair copulation (9 February 1987) involved this female and another adult male of P group (who had replaced the adult male mentioned above as the mate of the adult female of P group). During an inter-group interaction, this male approached the female of C group and copulated with her (intromission and thrusting observed). The adult male of C group was 30–35 m away at the time.

Although all extra-pair copulations were preceded by approaches of the males involved, the C female also played a role in initiating them by: (1) maintaining proximity to the territorial border where a male from a neighbouring group could gain sexual access to her (which sometimes involved moving towards the male); (2) not avoiding an extra-group male that approached her; and (3) directing the same 'solicitation' gesture at some extra-group males that she had been observed to give prior to her mate's approaches and subsequent copulation with her mate (Palombit 1992).

The timing of extra-pair copulations with respect to the female reproductive cycle is unclear (although the female did not lactate during the study). Extra-pair (as well as intra-pair) copulations involving the C female in 1986 and early 1987, did not result in any pregnancies that progressed long enough for visible indicators (such as abdominal distension) to become apparent. On 21 August 1987, however, the C female gave birth to a male infant that was dead at birth or died immedi-

ately thereafter. Given that this infant was apparently several weeks premature (see Palombit 1992) and that the gestation period is approximately 33–35 weeks (Hill 1967), it is possible that the extra-pair copulation of 9 February (as well as concurrent intra-pair copulations) occurred during the time the C female was ovulating and that she became pregnant at this time. Because the C female did not sustain a pregnancy to full-term at any time during 2.5 years, in spite of copulations with her mate and extra-pair males, it is possible that impaired reproductive functioning of this female or her mate (or both) may have promoted in part her pursuit of extra-pair copulations with other males. Any other deficiency of her mate that might have influenced the likelihood of extra-pair copulations was not manifested in his duetting, territorial defence or intra-pair social interactions (which were similar to other males for which data were available).

More data are needed in order to evaluate the generality and possible significance of extra-pair sexual behaviour in the monogamous gibbons, particularly because it does not necessarily have genetic consequences (Gyllenstein et al. 1990). Low rates of extra-pair copulation can act as a potentially important selective force behind the evolution of social behaviour of monogamous males (e.g. mate guarding). Moreover, the current rarity of sightings of extra-pair copulations does not necessarily indicate that they are of negligible evolutionary importance if only for the reason that observations of sexual behaviour (and of reproduction) in general are extremely limited for wild hylobatids (siamangs: Koyama 1971; Chivers & Raemackers 1980) in part because of the typically long intervals between periods of female receptivity. In captivity at least, the sexual behaviour of paired white-handed gibbons does not strongly suggest rigid mating exclusivity (Palombit 1992). Extra-pair copulations have been reported in one other monogamous primate, the titi monkey, *Callicebus moloch* (Mason 1966), which also exhibits male 'jealousy' behaviour further implicating a potential for extra-pair copulations (Cubicciotti & Mason 1978). Ostensibly monogamous humans in industrialized Western societies also engage in relatively high rates of adultery (Small 1992). The recent revelations of surprisingly widespread extra-pair matings in birds and these preliminary observations of extra-pair copulations in non-human primates argue forcefully for careful study of the sexual behaviour of monogamous primates.

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REFERENCES

- Birkhead, T. R., Atkin, L. & Møller, A. P. 1986. Copulation behaviour of birds. *Behaviour*, **101**, 101-138.
- Chivers, D. J. 1974. The siamang in Malaya: a field study of a primate in a tropical rain forest. *Contrib. Primatol.*, **4**, 1-335.
- Chivers, D. J. & Raemaekers, J. J. 1980. Long-term changes in behaviour. In: *Malayan Forest Primates* (Ed. by D. J. Chivers), pp. 209-258. New York: Plenum.
- Cubiciotti, D. D. III & Mason, W. A. 1978. Comparative studies of social behavior in *Callicebus* and *Saimiri*: heterosexual jealousy behavior. *Behav. Ecol. Sociobiol.*, **3**, 311-322.
- Gittins, S. P. & Raemaekers, J. J. 1980. Siamang, lar, and agile gibbons. In: *Malayan Forest Primates* (Ed. by D. J. Chivers), pp. 63-105. New York: Plenum.
- Gowaty, P. A. & Mock, D. W. Eds. 1985. *Avian Monogamy*. Washington, D.C.: American Ornithologists' Union.
- Gyllenstein, U. B., Jakobsson, S. & Temrin, H. 1990. No evidence for illegitimate young in monogamous and polygynous warblers. *Nature, Lond.*, **343**, 169-170.
- Hill, C. A. 1967. A note on the gestation period of the siamang. *Int. Zoo Yrbk*, **7**, 93-94.
- Kleiman, D. G. & Malcolm, J. R. 1981. The evolution of male parental investment in mammals. In: *Parental Care in Mammals* (Ed. by D. J. Gubernick & P. H. Klopfer), pp. 347-387. New York: Plenum.
- Koyama, N. 1971. Observations of mating behavior of wild siamang gibbons at Fraser's Hill, Malaysia. *Primates*, **12**, 183-189.
- Mason, W. A. 1966. Social organization of the South American monkey, *Callicebus moloch*: a preliminary report. *Tulane Studies in Zool.*, **13**, 23-28.
- Palombit, R. A. 1992. Pair bonds and monogamy in wild siamang (*Hylobates syndactylus*) and white-handed gibbon (*Hylobates lar*) in northern Sumatra. Ph.D. thesis, University of California, Davis.
- Parker, G. A. 1984. Sperm competition and the evolution of animal mating strategies. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 2-61. New York: Academic Press.
- Small, M. F. 1992. The evolution of female sexuality and mate selection in humans. *Human Nat.*, **3**, 133-156.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136-179. Chicago: Aldine.