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Female Capped Gibbon (*Hylobates pileatus* Gray 1891) Sings Male Song

Most gibbons are known as "sexually divocal", i.e. males and females have their own vocal repertoires. For the first time a case is reported where a female capped gibbon (*Hylobates pileatus*) – upon union with a new, timid male – uttered the full typically male vocalizations, although she later again produced the female "great call". This observation bears on questions of the phylogeny of duetting and on functional differences between male and female song parts.

1. Introduction

All known gibbon species live in tropical rain-forest and form monogamous, territorial family groups (Carpenter, 1940; Chivers, 1974; Ellefson, 1974; Gittins, 1980; Tenaza, 1975*a*; Tilson, 1981). Their loud and distinctive vocalizations seem to play a role in territorial advertisement. Species can easily be distinguished by their songs. Song repertoires are remarkably constant in call structure and temporal organization and are therefore assumed to be largely genetically determined (Boutan, 1913; Brockelman, 1978; Marler & Tenaza, 1977). In most species song repertoires of males and females are reported to differ markedly. Mates typically sing together and produce a well patterned duet (Gittins, 1978; Goustard, 1979; Haimoff, 1981; Lamprecht, 1970; Marier & Tenaza, 1977; Marshall & Marshall, 1976; Marshall *et al.*, 1972; Schröpel, 1977; Tembrock, 1974). This is also true for the capped gibbon, *Hylobates pileatus*, occurring in southeastern Thailand and Cambodia west of the Mekong River. Its territorial song – documented with sonagrams by Marshall *et al.* (1972), Marshall & Marshall (1976), and Marler & Tenaza (1977) – has been described as follows:

To my knowledge it has never been reported for a "sexually divocal" gibbon species that one sex sang the other's full repertoire. But I was lucky enough to witness an instance of this at the Zoological Garden in Zürich, Switzerland. The observation can be of some importance in relation to the phylogeny of sexual "divocalism" and to the functional significance of male and female duet parts.

2. Animals and Methods

On 9 March 1981 a *pileatus* male (Blacky) from Opel Zoo in Kronberg (West Germany) arrived in Zürich, and a day later a *pileatus* female (Gray) was imported from the Zoological Garden in East Berlin (Tierpark Berlin-Friedrichsfelde). Both had lived in gibbon groups. The male had sired and raised several hybrid young with a female *Hylobates lar*. The female

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had lived with lar-gibbons, too, but had never been reported pregnant. The male was estimated to be about 20, the female between seven and nine years old.

Upon arrival the animals were kept in separate adjacent sleeping boxes (where they never sang) and were then allowed alternate access to a large cage of about 30 m^2 in the ape house. During this time they could hear but not see each other. From 19 March the animals were let into the cage together.

They were observed at irregular intervals from 9 March 1981 until 26 April 1982, later only occasionally. Vocalizations before, during, and after their first encounter were recorded on tape.

3. Results

In the large cage alone, before the encounter, each animal sang solo. The male produced typical male sequences [Figure 1 (a)] up to several minutes at a time. The female sang single "great calls" [Figure 1 (b)]. No other vocalization and no overlap in the repertoires were heard during this period.

The following is a report of the first encounter between the two gibbons on 19 March: The male had spent the early morning in the large case. At 10:10 h the female was released from her sleeping box into the same cage. They brachiated and moved towards each other within the first minute. A mutual open-mouth threat occurred, they kicked each other and then turned away. Later the female repeatedly tried to get close to the male, who always moved off.

A few minutes after entering the female uttered her first soft and undifferentiated vocalizations which were answered by the male within seconds with his typical male sequence. Then the female uttered a clear full series of male diphasic calls with final trill [Figure 1 (c)]. Both animals now alternated in singing male phrases. Hardly ever did one interrupt the other. Their phrases were equal in quality, but the female sang at a slightly higher pitch and speed. Only typical male calls were produced.

Whenever the female approached, the male took flight and sometimes showed a threat grimace. These approaches seemed to stimulate the male's singing activity.

After 27 minutes of uttering male calls the female gave the first typically female "great call", repeated two minutes later, and again after a further three minutes. In all three instances the male joined in with his phrases so that a typical pileatus duet resulted [Figure 1 (d)]. Five minutes later they sang a last duet. Then the male almost completely stopped singing, and male-type calls produced by the female predominated. Soon after the keepers left the side of the cage singing ceased, after almost 44 minutes.

The two gibbons were left in the cage until 14:30 h and then taken back to their sleeping boxes during cage cleaning. At 15:00 h the male entered the cage again where he brachiated. After entering an hour later the female sat on a high shelf and sung a "great call" to which the male responded perfectly. Then the male sang three more of his phrases, the last vocalizations of that day.

During the following weeks the female's approaches towards the male became less and less frequent. No body contact, mutual grooming, play or sexual behavior, which typically occur in normal gibbon pairs, were ever observed. Regular dueting was their only type of interaction. The male sang his phrases several times a day, while the female on average sang two "great calls" daily, always answered by the male.

Figure 1. (a) Two solo male phrases produced by the male. (b) Solo "great call" from female (three or four of the opening notes are missing in the sonagram). (cl-c3) Continuous sequence of alternating male type phrases produced by both male and female. (d) Typical duet by male and female (although first phrase is normally produced by the male).



No male calls were heard from the female until a year later, on 8 March 1982. The animals again alternated in singing male phrases, but this new occurrence of male calls in the female could not be attributed to any particular circumstances. On 1 April 1982, the curator witnessed a copulation, and on 25 November the female gave birth to a son (Schmidt, pers. comm.).

4. Discussion

Wickler & Seibt (1982) outlined three phylogenetic routes for duetting to be accomplished. Two of them – song-merging and song-splitting – can give rise to duets with partners using different vocalizations. In song merging, individuals with basically different repertoires may combine them in a duet according to rules which may even be pair specific. At no transitional stage along this evolutionary route would one expect a partner to be able to sing the other's repertoire. This is more likely to occur in song-splitting, where a basic song is divided into two subrepertoires, each becoming increasingly confined to one sex. Wickler & Seibt (1982) characterize (and document with examples from bird duets) an intermediate stage 2, where each subrepertoire is typical for one sex but can also on occasions be uttered by the other.

That both typical male and typical female duet parts were sung by one female capped gibbon suggests that song-splitting rather than song-merging occurred during the phylogeny of duetting in this species (and probably in other gibbons too).

Most authors presume multiple functions of gibbon songs, some stressing territorial advertisement as the primary function (e.g. Brockelman, 1975; Chivers, 1975, 1976; Ellefson, 1974; Marshall & Marshall, 1976; Marshall *et al.*, 1972; Tenaza, 1975b), while others mainly discuss possible benefits for the maintenance of pair and family bonds (e.g. Chivers, 1974; Goustard, 1979). It is the song as a whole which is thought to serve these functions. In contrast, Marshall & Marshall (1976) suppose that different selection pressures act on male and female repertoires, and Gittins (1978) postulated different functions for the various song contributions of family members.

It is possible that particular social circumstances induced male song in our capped gibbon female, although we cannot yet specify these circumstances. But if repertoire switching could be tied down to particular external situations, this would be another hint at different selection pressures acting on male and female gibbon song repertoires.

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