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Hand modulation of vocalization in Siamangs

Hylobates syndactylus

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Although hand modulation of vocalization in Siamangs *Hylobates syndactylus* in captivity has been reported in the literature its functional significance within the Hylobatidae has not been thoroughly investigated. One-hundred-and-ten sequences of vocalizations were observed in a pair of Siamangs maintained at the International Center for Gibbon Studies, Santa Clarita. The ♀ used both the palmar aspect of the hand and the distal part of the forelimb to modify vocalizations during di-phasic barking in the 'great-call' duet. Analysis of this behaviour indicates that it occurs independently of intragroup social context. Data collected for 150 gibbons, representing all four subgenera and 11 species, indicate that hand modulation of vocalization is unique to Siamang. Hand-rearing did not effect the development of the behaviour in ♂♂ but did appear to be conducive to its development in ♀♀.

Key-words: gibbon, great call, hand modulation of vocalization, siamang, song duet

Gibbons *Hylobates* spp are recognized as belonging to a single genus, containing four subgenera (Prouty *et al.*, 1983a,b; Marshall & Sugardjito, 1986). Chromosomal comparisons (Couturier & Lernould, 1991) and examination of the mitochondrial cytochrome b gene (Garza & Woodruff, 1992, 1994) of the subgenus *Nomascus* have indicated two additional species, thus the total number of species in the Hylobatidae is 11. Gibbons inhabit tropical and sub-tropical rain forests in south-east Asia and are characterized by long-term pair bonding and territorial defence through interactive vocalization (Carpenter, 1940; Chivers, 1974; Marshall & Marshall, 1978; Srikosamatara & Brockelman, 1983). Studies of gibbon vocalization have focused primarily on

acoustic and functional aspects and there has been little detailed research on the behaviour associated with it (Lamprecht, 1970; Fox, 1972, 1977; Gittins, 1979; Srikosamatara, 1980; Haimoff, 1981; Embury, 1983).

The monotypic Siamangs *Hylobates syndactylus* are classified in the subgenus *Symphalangus.* They can weigh between 8 and 13 kg (Nowak, 1991), more than twice that of other gibbon species, and have broad chests and a stocky build. Siamangs are sexually dimorphic in body size and cranium (Hooijer, 1952; Groves, 1972), and have large throat sacs which produce the loudest and most complex vocalizations of any gibbon species (Marshall & Sugardjito, 1986). Siamangs also have a sternal gland (Geissmann, 1987) and, except for the Kloss' gibbon *Hylobates klossi,* are the only gibbon species with webbing between the second and third toe (Schultz, 1974). During vocalization Siamangs use the palmar aspect of the hand or the distal part of the forelimb to modulate vocalizations. Hand modulation of vocalization may be a behaviour which further differentiates *H. syndactylus* from other gibbons.

Between 1990 and 1993 a study of hand modulation of vocalization in a ♀ Siamang and the behaviour of conspecifics in the same enclosure was carried out at the International Center for Gibbon Studies, Santa Clarita. Data were also collected on gibbons maintained at institutions in North America, Europe, south-east Asia and Australia to determine whether this behaviour is unique to Siamangs and whether there is a correlation between individuals that hand modulate vocalizations and their social and physical environments. Results and possible implications are discussed.

FOCAL SUBJECTS

The ♀ Siamang (stdbk. no. 218) was born at Cheyenne Mountain Zoo, Colorado, in 1983 and mother-reared until 22 months old, after which she was housed alone for 16 months. In 1986 she was paired with a mother-reared ♂ (stdbk. no. 191) (5 years 2 months old) from Miami Monkey Jungle, Florida. At the Center the pair was housed in an outdoor enclosure 9 m × 3 m × 4 m high, which permitted auditory and visual contact with conspecifics, and they produced four offspring. The gibbons were fed three times a day and were observed for a minimum of 5 hours each day.

FOCAL OBSERVATION

From February 1990 to the end of July 1993 data were collected on 110 complete vocalization sequences. The presence of hand modulation was recorded for each sequence as were duration of the behaviour, the position of the ♂ and ♀, both in the enclosure and in relation to each other, and any activities they engaged in during vocalization. Hand modulations were described for each occurrence.

SURVEY SUBJECTS

Data were compiled on all 11 species from interviews with zoo personnel for an additional 95 gibbons at 27 institutions in North American, Europe, Australia and south-east Asia (Table 1). Fifty-three of the gibbons had been maintained at the Center in similar conditions to the focal pair. The conditions of the remaining 95 animals varied by institution. It is difficult to determine the subspecies of Siamangs or Lar gibbons *Hylobates lar* because mitochondrial DNA sequencing for gibbons has not yet been perfected (M. Ruvolo & D. Woodruff, pers. comm.). A combination of skull measurements, height and weight provides an alternative means of determining Siamang subspecies. In our survey, however, most institutions could only provide data on weight, and diet, age, illness or pregnancy all make subspecific determination difficult when using this parameter as the sole criterium. Thus it was not possible to determine whether both subspecies of Siamang were well represented in the study.

DATA

Data were collected for a number of life-history details, including species, subspecies, wild/captive born, rearing condition (hand-reared, mother-reared or mother-reared for 10 months and then hand-reared), presence of hand modulation of vocalization in the study animal and the occurrence of this behaviour in the parents. Subspecies could not be determined for Lar gibbons or Siamangs, except for animals still maintained in the country of origin. Information on the housing conditions of some gibbons and the weights of all Siamangs were obtained but these data were not quantitatively analysed. Information on the parents of Siamangs in North America was based on the North American Siamang studbook (Fiore, unpubl.).

SPECIES	NO. ANIMALS
Western hoolock gibbon	
Hylobates h. hoolock	0.2
Eastern hoolock gibbon	
H. h. leuconedys	1.2
Mountain agile gibbon	
Hylobates a. agilis	7.4
Bornean agile gibbon	
H. a. albibarbis	1.3
Lar gibbon	
Hylobates lar spp	10.10
Silvery or Moloch gibbon	
Hylobates moloch	7.4
Abbott's grey gibbon	
Hylobates muelleri abbotti	1.1
Northern Mueller's gibbon	
H. m. funereus	2.3
Eastern Mueller's gibbon	
H. m. muelleri	2.2
Pileated gibbon	
Hylobates pileatus	6.5
Kloss' gibbon	
Hylobates klossi	1.1
Black gibbon	
Hylobates concolor	1.1
Northern white-cheeked gibbon	
Hylobates l. leucogenys	4.6
Southern white-cheeked gibbon	
H. l. siki	2.2
Buff-cheeked gibbon	
Hylobates gabriellae	4.4
Siamang	
Hylobates syndactylus spp	21.26
Hybrid	
H. agilis × *H. muelleri*	0.3

Table 1. The number of each species and subspecies of *Hylobates* included in a survey on the occurrence of hand modulation of vocalization in gibbons ($n = 150$ at 28 institutions). Classification of the genus *Hylobates* follows Geissmann (1995).

RESULTS

The Siamangs vocalized for *c.* 12–30 minutes, generally between 1000 and 1330 hours, one to five times a week. The ♀ primarily hand modulated during the first two phases of the 'great-call' sequence which was characterized by an accelerated series of booms and barks (Lamprecht, 1970; Tembrock, 1974; Haimoff, 1981; Barkell, 1988). The ♀ placed either the distal part of the forelimb or the palmar aspect of the hand *c.* 5–20 cm from her mouth during barks and lowered the forelimb during booms (Fig. 1). The extent to which the forelimb was lowered during booms appeared to be related to the time between barks and booms; an acceleration of barks and booms, characterizing the second phase of the great-call sequence, was associated with an increase in rapidity of the forelimb motion, coupled with a decrease in the distance of the vertical movement. At the climax of the second phase the forelimb remained nearly stationary in front of the mouth. The conclusion of hand modulation usually corresponded to the onset of the ♂'s 'bi-tonal scream' early in the third phase of the great-call sequence (Fox, 1977; Haimoff, 1981; Barkell, 1988). The duration of hand-modulation bouts ranged from 1 second to *c.* 17 seconds of continuous modulation (mean 6 seconds).

Occasionally the ♀ would cover her mouth with either her fingertips or the distal end of the forelimb so that the fingertips grazed her ear (Fig. 2). Right or left limbs were used with approximately the same frequency and alternation of right and left limbs within a single call sequence was observed when both limbs

Fig. 1. Hand-modulation in Siamang *Hylobates syndactylus*. **During hand-modulated vocalization the fingers and thumbs are relaxed. Three different angles were observed.**

were free. The ♀ and ♂ assumed a variety of positions during the ♀'s hand-modulation bouts, including hanging by one arm or upside down, standing or sitting on the ground, a platform or branch, and facing towards or away from each other. The ♀ would hand modulate vocalizations when alone or while carrying an infant. There was no correlation between the occurrence of hand modulation during vocalization and the distance between the ♂ and ♀ or the position of conspecifics in the enclosure. No relationship was found between the occurrence of modulation and the ♀'s activity (sitting, brachiating, hanging) or the activity of the ♂ or offspring.

Hand modulation of vocalization was reported in 12 (25%) of the 48 Siamangs for which data were available and in none of the other 102 gibbons in the survey. There was no significant difference in the occurrence of this behaviour between captive-born ($n=6$) or wild-born ($n=6$), or paired ($n=8$) or unpaired ($n=4$) animals. Siamangs which hand modulated vocalizations were less likely to have parents that exhibited this behaviour than Siamangs which did not modulate. Hand modulation was observed in more hand-reared ($n=6$) than mother-reared ($n=2$) animals and more ♀♀ ($n=9$) than ♂♂ ($n=3$) exhibited the behaviour.

DISCUSSION

From the survey it would appear that hand-rearing could be a prerequisite for the development of hand modulation ($n=6$). Siamangs which were mother-reared until they were 10 months old and then removed from their natal group were also more likely to exhibit the behaviour

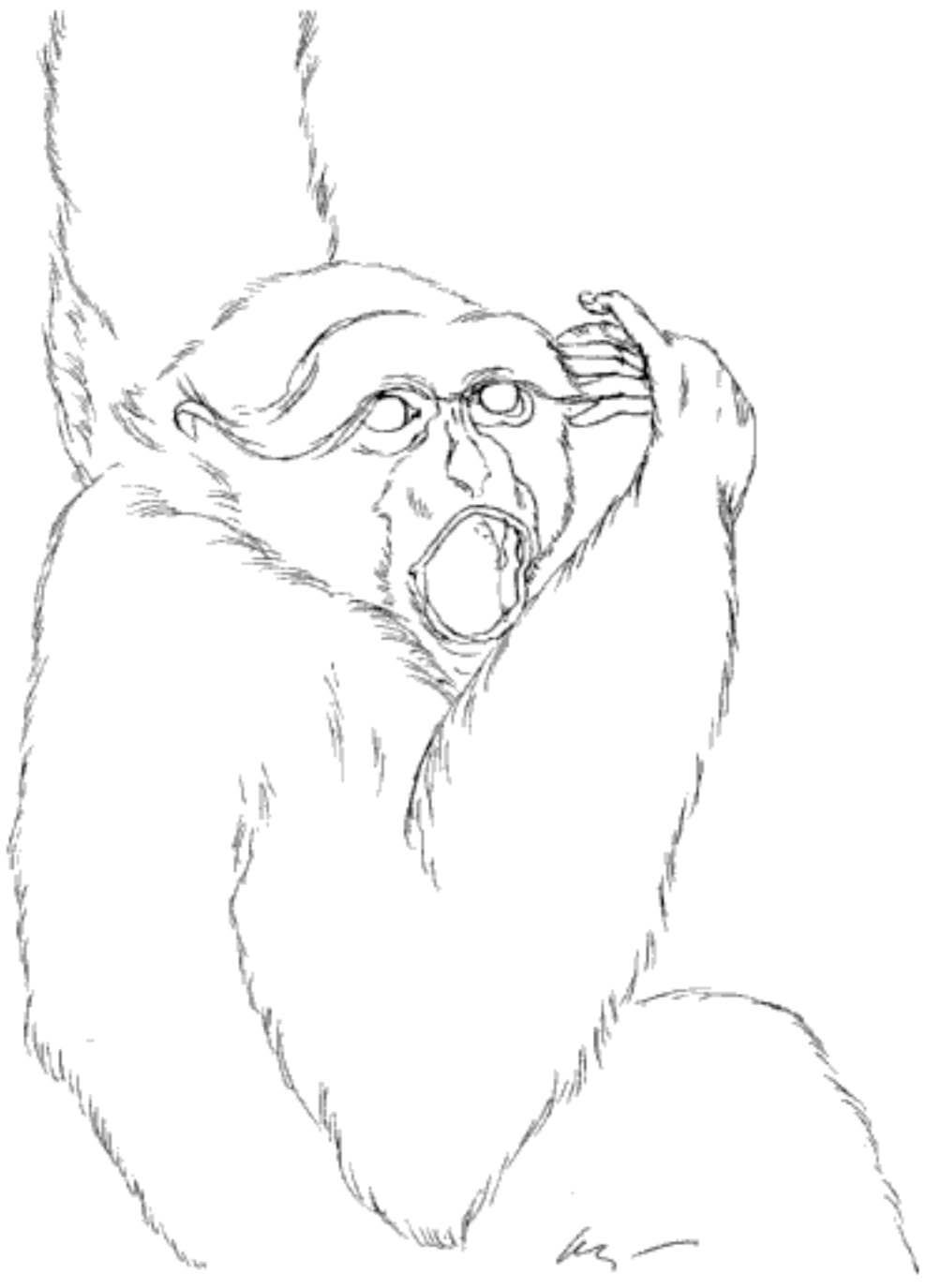

Fig. 2. Occasionally the ♀ Siamang would cover her mouth with the distal end of her forelimb so that the fingertips grazed her ear.

($n=4$), which suggests that it may be associated with early environmental influences. Observations of the focal ♀ also suggest that hand modulation may occur independently of the presence, identity, position or activity of conspecifics in the same or nearby enclosures.

Hand modulation occurred almost exclusively during the high-frequency component of di-phasic barking prior to the ♂'s bi-tonal scream (Lamprecht, 1970; Fox, 1977). In the wild gibbons use vocalization as a means of territorial defence and vocal modulation may be an adaptation to deceive conspecifics as to the size or location of the group or the distance from neighbouring groups (J. T. Marshall, pers. comm.). Lower pitched booms or barks will penetrate several kilometers through the forest canopy and higher-pitched vocalizations tend to be absorbed by the dense foliage (Wilson, 1986). Siamangs in captivity may not be maintained in densely planted enclosures which may mean that vocal modulation can only be accomplished either manually or by utilizing artificial sound-altering media, such as walls and other barriers. Although hand modulation will be used in non-resonating environments, such as chain-link enclosures, solid barriers which deflect sound may encourage the Siamangs to use these media instead.

Hand modulation often occurs in enclosures constructed of glass or concrete which are conducive to the distortion of sound (Fox, 1972). This behaviour may allow Siamangs to overcome the acoustic limitations on transmission of vocalizations in a captive environment (Fox, 1977). A ♂ Siamang (stdbk. no. 125) housed on an island exhibit at New Orleans Zoo was observed vocalizing directly towards a tree stump and when in an indoor enclosure he would sometimes call while facing a cement wall (D. Robinett, pers. comm.). On numerous occasions a ♂ Siamang (stdbk. no. 124) at the Center was observed creating an echo by vocalizing while facing a hill. There are no reports of other gibbon species manipulating vocalization and hand modulation has not been observed in the wild. From the current study the implication is that the development of hand modulation may be associated with captive-rearing but it would seem more probable that free-ranging Siamangs would have greater reason to deceive neighbouring conspecifics. A more recent theory is that Siamangs may use hand modulation to enable them to hear their own vocalizations better by reflecting the sounds they make back towards themselves (B. Merker, pers. comm.).

Hand modulation of vocalization may also be used for maintaining synchronous vocal rhythm. A ♂ Siamang (stdbk. no. 124) at the Center was observed uttering a low series of grunts in synchrony with a vocalizing ♀ Pileated gibbon *Hylobates pileatus* in order to pace his bi-tonal scream. From the survey it was not possible to ascertain whether the animals move their limbs during hand modulation to pace their vocalizations.

Future studies should attempt to determine whether hand modulation or similar behaviour is exhibited by gibbons in the wild. This may be difficult because of the inherent problems of observing *in situ* gibbon behaviour, such as location high in the forest canopy, small body size and rapid locomotion throughout their range. Observing hand modulation of vocalization is considerably easier in captivity and as awareness of this behaviour increases more data should become available for future studies.

Hand modulation of vocalization may be one more characteristic which distinguishes the Siamang from other gibbon species although it cannot be determined whether the behaviour has any functional significance other than the distortion of normal vocalization. Given the high propensity of hand-reared ♀♀ and moderate propensity of both ♂ and ♀ Siamangs mother-reared to 10 months to exhibit this behaviour, future studies could focus on

the developmental aspects of gibbon vocalization and other related behaviours.

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