

## COVARVARIATION IN THE GREAT CALLS OF REHABILITANT AND WILD GIBBONS (*HYLOBATES ALBIBARBIS*)

**Susan M. Cheyne**

*Kalaweit Care Centre, Jalan Pinus No 14, Palangka Raya, Kalimantan Tengah, Indonesia.  
Wildlife Research Group, Department of Anatomy, University of Cambridge, Downing Street,  
Cambridge, CB2 3DY, United Kingdom  
CIMTROP, UNPAR Kampus Tanjung Nyaho, Jalan Yos Sudarso, Palangka Raya 73112,  
Central Kalimantan, Indonesia  
Email: susanchejne76@yahoo.com (Corresponding author)*

**David J. Chivers**

*Wildlife Research Group, Department of Anatomy, University of Cambridge, Downing Street,  
Cambridge, CB2 3DY, United Kingdom*

**Jito Sugardjito**

*Fauna & Flora International-Indonesia Program, Jalan Harsono RM, #1, Pusat Laboratorium Universitas  
Nasional, Ragunan, Jakarta Selatan 12550, Indonesia*

**ABSTRACT.** – Sex- and species-specific singing is an integral part of gibbon behaviour. Young gibbons learn to sing by copying their parents. Analysis of the recorded great calls of wild-born, captive-raised agile gibbons (*Hylobates albibarbis*) from the Kalaweit Gibbon Rehabilitation Project, Central Kalimantan, Indonesia and wild-raised agile female songs in two locations around Kalimantan are presented herein. We found high variance of song characteristics both within and between populations. This result shows that captive-raised gibbon females can learn flexibility in the song pattern in the great call phase. We also demonstrate variation in song patterns between distinct populations, indicating a genetic component to the levels of flexibility in the great call.

There is a clear genetic component, as gibbons raised alone produce the species-specific song and there is a clear level of individuality to the great call component of the song. This distinct individuality supports the hypothesis that the song of gibbons is a mechanism of intra- and inter-specific communication about the status of individual gibbons and pairs e.g. social and physical status. In addition evidence is presented suggesting that separate populations of the same species may have distinct dialects. Implications for rehabilitation and reintroduction of gibbons are discussed.

**KEYWORDS.** – Gibbons, great calls, song, rehabilitation, captive-raised, *Hylobates albibarbis*.

---

### INTRODUCTION

Gibbons are well known for their loud duets, which consist of a coordinated sequence of sex- and species-specific notes, usually repeated (Marshall & Sugardjito, 1986). The female produces a distinctive great call. Male and female each have a sex-specific repertoire that is (at least partially) genetically determined (Brockelman & Schilling, 1984; Geissmann, 1984; Tenaza, 1985). The possible functions of singing, as highlighted by Haimoff & Gittins (1985) all include some form of communication, either inter- or intra-group. The duet likely acts as a spacing mechanism in inter-group communication, informing other groups of each others location. The sex-specific parts of the duet could also serve

as intra-group communication, imparting information about relative strength of the pair bond, how well the pair is established in their territory and/or the physical strength of the pair bond. The duet also provides territorial defence through exclusion of same-sex conspecifics. Possible secondary functions of the duet include group orientation and/or pair-bond reinforcement and maintenance (which may explain why the duetting behaviour is maintained after the pair has formed and throughout the life of the pair (Wachtmeister, 2001) and why older, well-established pairs sing with greater coordination and organisation (Chivers, quoted in Haimoff (1984). Males and females coordinate their song to form the duet (Haimoff, 1981; 1986). A wild-raised gibbon learns to sing by copying its parents, an

experience that has been denied to wild-born, captive-raised gibbons.

All the juvenile, sub-adult and adult gibbons at the Kalaweit Gibbon Rehabilitation Project sing. Gibbons enter the project at varying ages from 1 week – 9 years old. As far as possible, age information is acquired from the previous owners. This information is always substantiated by Kalaweit staff by checking the wear and length of canines (Dirks, 1998; Dirks, 2003). All the Kalaweit gibbons in this study have been with the project for at least 18 months. The important question for rehabilitation and reintroduction is whether the gibbons are singing an unmodified genetic template of their species-specific song or whether they can learn to modify their songs to effectively discriminate between conspecifics? With regard to gibbon biology, the ability to sing the species-specific song does show a small degree of variation (Haraway & Maples, 1998). A uniform song pattern caused by genes so that communication transmission is unambiguous is important if the sole function of singing is for spacing of groups e.g. (Mitani, 1985) but if the function of singing also includes conveying very specific information about a particular individual, then individual variation is desirable.

If the great call is the most genetically similar part of the song, as suggested by Haimoff, (1983, 1985) Geissmann (1984, 2002) and Gittins (1984), then this should be the best place to examine differences. Nine song characteristics were selected and measured in a similar manner to earlier studies (Haimoff & Gittins, 1985; Haimoff & Tilson, 1985; Dallmann & Geissmann, 2001), where these characteristics were selected based on their ability to distinguish between females of the same species. Understanding song development and function in gibbon society will improve gibbon reintroductions. The four objectives were:

- To determine if individuality was present in captive-raised gibbons, *Hylobates albibarbis* (Groves, 2001) as has already been shown in the wild.
- To determine what environmental factors affected the singing of both captive-raised and wild gibbons.
- To determine if the structure of the great call phase changed with the age of the female.
- To determine if the individuality in the great call phase was as high between wild populations as within.

We expect that gibbons in a rehabilitation programme will experience similar levels of variation in the great call to those observed in wild populations. We also expect lower levels of variation between wild populations (not within auditory distance) than within populations.

## MATERIALS AND METHODS

The Kalaweit Gibbon Rehabilitation Project was founded in 1999 to rescue, rehabilitate and reintroduce gibbons confiscated from the illegal pet trade. The Project now has two locations in Kalimantan and Sumatra and houses a combined total of about 300 gibbons and siamangs (*Hylobates syndactylus*). The project has strict animal welfare guidelines and behavioural monitoring of all gibbons both pre- and post-release (Cheyne, 2004; Cheyne et al., 2005).

Analysis of the song structure was carried out using XWaves and Wavesurfer 1.5.5. All calls were analysed using narrowband bandwidth (20Hz), FFT window length was 1,024 points, rate of recording was 1,1025 and the spectrogram was cut at 2,500Hz. Recordings were made of all agile females at Camp Kalaweit (n = 12) who produced full great calls.

Gibbon songs can be heard up to 2 km from the source. Songs herein were recorded using a Sony TCM-40DV Cassette-Corder and Type 1 Normal Audio cassettes (90 min). Calls were recorded from gibbons in the Kalaweit Gibbon Rehabilitation Project and from wild gibbons. All gibbons at the Kalaweit Project were confiscated wild-born, captive-raised gibbons which had been kept as pets.

The first great call from female wild-raised gibbons can be expected from 0430 anytime up to 1200 (Marshall & Marshall, 1976; Tenaza, 1976; Haimoff, 1984) and rarely occurs after 1200, thus only songs sung between the hours of 0400 and 1200 were used. Songs sung after 1200 are often the result of the gibbons meeting other wildlife and are alarm singing (S.M. Cheyne, pers. obs.). Gibbons that sang in the afternoon were noted, though it was only the juveniles that sang after 1200. All recordings were carried out at least 50 m, and at most about 500 m, from the wild-raised gibbons (maximum recording distance was estimated from recording gibbons in cages and walking away until the recorder no longer picked up the song), and always out-of-sight of the captive Kalaweit gibbons, to rule out humans influencing the singing. Since no specialist equipment was used (e.g. directional microphones), there was occasionally a degree of background noise and harmonics in the spectrograms. Thus calls recorded from further than 500 m tended to be too faint to analyse and/or contained too much background noise and were not included in the analysis. Spectrograms were printed using Ghostscript Version 1.1.

The song characteristics measured were: duration of great call, number of notes/great call, frequency range, duration of the climax note, peak frequency of the climax note, lowest frequency, notes/duration, number of post-climax notes and the duration of the post-climax phase.

Camp Kalaweit is the main rehabilitation site of the Kalaweit Gibbon Project located in the Bukit Baka Bukit Raya National Park in Central Kalimantan, Indonesia. Songs were recorded from 13 females. In addition, recordings were made from as many wild agile females as possible from two different locations, the Bukit Baka Bukit Raya National Park (BBBRNP) in Central Kalimantan (n = 9) and Sungai Bahara location in West Kalimantan (n = 9, Fig. 1). Both wild populations are separated by the Schwanner Mountain range and overlap does not occur.

It was necessary to determine if each individual female had any differences in their own song across recording sessions. This was conducted to rule out large variation in the flexibility of each female within each of the three populations affecting the inter-population analysis. The level of flexibility for each

Table 1. Analysis of the song variables within-population from two separate wild populations and the Kalaweit gibbons. Data refer to average values for each population.

Variables	Kalaweit	TNBBBR	Sungai Bahara
Number of gibbons (n)	13	9	9
Total number of great calls analysed	105	20	21
Duration of great call (s)	0.01	0.01	0.01
No. of notes/great call	0.001	0.001	0.01
Frequency range (Hz)	0.01	NS	NS
Duration of climax note (s)	0.01	0.01	0.01
Peak frequency of climax note (Hz)	0.01	0.01	0.05
Lowest frequency (Hz)	NS	NS	NS
Notes/duration (n/d)	0.001	0.001	0.01
Number of post-climax notes	NS	NS	0.01
Duration of post-climax phase (s)	0.01	NS	0.01

female within the different sample populations was first assessed, using the Kruskal-Wallis one-way analysis of variance by ranks, as in Haimoff and Gittins (1985), Haimoff and Tilson (1985) and Dallmann and Geissmann (2001). Following this, an average song of each female from each populations was tested using Kruskal-Wallis to determine variation in individual song characteristics. Kruskal-Wallis indicates that at least one pair of factors is significantly different from each other but does not indicate if all samples are significantly different. To tease out the data, and identify the song variables that were different within each population, a post-hoc Mann-Whitney U-test was carried out on all factors that were significant after the Kruskal-Wallis test, as described in (Dytham, 2003). Spearman Rank tests were used to assess the degree of relationship between variables which were significant after the two previous tests. Bonferonni tests were used to account for the variance in sample size from each population. Chi-squared tests were used to test expected results (from wild gibbons) against those of the Kalaweit gibbons in specific behavioural situations.

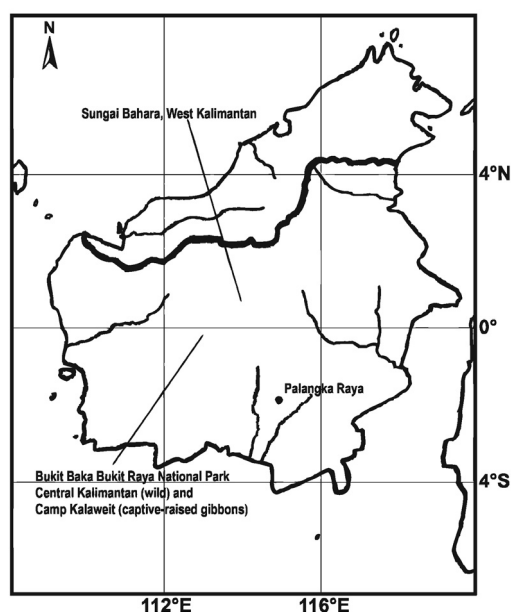


Fig. 1. Map showing the two recording sites.

Weather variables were measured using a maximum/minimum thermometer, and rain gauge (mm). Wind was classified by observers as 0 = no branch moving, 1 = branch moving, 2 = bough moving and 3 = heavy wind (gale). Cloud cover was also estimated by observers 1 = 0–25% of sky covered by cloud, 2 = 26–50% covered, 3 = 51–75% covered and 4 = 76–100% covered.

## RESULTS

Sonogram examples (Fig. 2 a–c) of three females are shown. The lowest notes on the sonograms represent the actual song, other notes are harmonics and were not analysed, as they are not a true representation of the actual song produced by the gibbon, harmonics are not pure tones i.e. the tones are produced by a the vocal chords resonating producing a note at a fraction of the length of the true note (Dr. Sarah Hawkins, Dept. of Linguistics, University of Cambridge, pers. comm.). Wild songs are from two populations separated by mountains, rivers and logging concessions. To determine whether the individual females have distinct calls (12 rehabilitant females and nine wild females from each wild population), nine variables were analysed.

### Individuality

The recorded females did not show any significant difference in song structure within their own songs, when all variables from all recordings for each female were tested against the others (Kruskal-Wallis test,  $p > 0.01$ ). The median values for all song variables (Table 1) were compared within populations (Kalaweit, TNBBBR and Sungai Bahara). All populations showed significant differences in duration of great call, number of notes/great call, duration of climax note, peak frequency of climax note and notes/duration (5/9 characteristics). Neither wild population showed significant differences in frequency range of great call bout and no population showed variation in lowest frequency note.

There was a significant relationship between the number of

Table 2 Kruskal-Wallis tests on song variables against age. Data refer to average values for each age group.

Variables	3–4yrs vs 5–6yrs	5–6yrs vs >7yrs	3–4yrs vs >7yrs
Number of gibbons	4 vs 5	5 vs 4	4 vs 4
Number of samples	38 vs 47	47 vs 49	49 vs 38
Duration of great call (s)	0.001	0.001	0.001
No. of notes/great call	0.001	0.001	0.001
Frequency range (Hz)	0.05	0.05	0.05
Duration of the climax note (s)	0.01	0.01	0.01
Peak frequency of the climax note (Hz)	NS	NS	NS
Lowest frequency (Hz)	05	0.05	0.05
Notes/duration (n/d)	0.01	0.01	0.01
Number of post-climax notes	NS	NS	NS
Duration of post-climax phase (s)	NS	NS	NS

notes in the song and the duration of the great call (Spearman Rank Correlation value 0.754;  $p = 0.001$ ).

Differences in individuality may be related to age and learning. Thus, song characteristics were tested against age (categories are 3–4yrs, 5–6yrs and >7yrs: Table 2). Older gibbons produce a longer, louder and more complex song than younger females. Again, only results that were significant after the Mann-Whitney post-hoc tests are reported. Only Kalaweit gibbons were included in this analysis as more accurate estimates of age could be obtained. All age groups differed significantly in duration and number of notes in the great call. Some variation was present in frequency range, duration of the climax note, lowest frequency reached and the number of notes/duration of song.

There was a highly significant difference in the duration of the call, and the number of notes, that make up the call as the

gibbons get older. Only Kalaweit gibbons are analysed, as accurate ages for the wild gibbons could not be established.

### Between population variation

The values for each individual for each category were compared between the two wild populations. Again, Kruskal-Wallis one-way analysis of variance by ranks was used to account for the high variability within populations (Table 3). Population variation was apparent in several characteristics of the great call. Significant differences were found in all analysed characteristics of the great call phase.

### Environmental influence on singing behaviour

Kalaweit gibbons followed the wild population habit of not singing during wet weather: wild gibbons in the national park surrounding camp did not sing 103/117, 88% of the time. Kalaweit gibbons were more likely to resume singing in the afternoon all following a wet morning, unlike wild gibbons who never sang after 1300 (Table 4). Temperature of days when no singing occurred did not vary significantly from singing days. Cloud cover had no significant effect on the onset time of singing. The association between windiness and days on when there was no singing was significant in the wet season. In the dry season there was very little rain, especially in 2002 and comparatively less wind. At Camp Kalaweit, most of the summer rain occurs in the afternoon and does not affect morning singing bouts (the socialisation cage gibbon's afternoon bouts are not included in the analysis). On mornings when there was rain, the gibbons started to sing much later, between 0900 and 1000 instead of between 0430 and 0600.

### DISCUSSION

The Kalaweit gibbons showed the greatest range in frequency of the great call phase, while the TNBBBR gibbons showed greatest variation in number of notes/great call. Sungai Bahara gibbons had the longest songs.

In order to rehabilitate the gibbons fully, consideration must

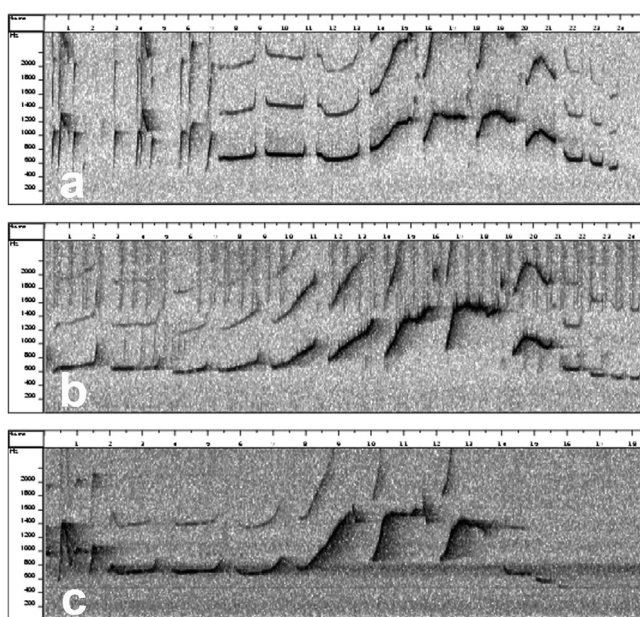


Fig. 2. Example sonograms of rehabilitant, released and wild agile female gibbons: a, rehabilitant; b, released captive-raised; c, wild-raised.



Table 3. Analysis of the song variables between populations of females from two separate wild populations (Kruskal-Wallis analysis).

Variables	TNBBBR vs Sungai Bahara
Number of gibbons	18
Number of samples	214
Duration of great call (s)	0.01
No. of notes/great call	0.001
Frequency range (Hz)	NS
Duration of climax note (s)	0.01
Peak frequency of climax note (Hz)	0.01
Lowest frequency (Hz)	NS
Notes/duration (n/d)	0.001
Number of post-climax notes	0.001
Duration of post-climax phase (s)	0.001

Table 4. Weather characteristics affecting gibbon singing.

Weather variable	$\chi^2$ test statistic	Degrees of freedom	Significance level
Rain	36.85	3	<0.05
Temperature	17.19	4	NS
Cloud cover	14.23	3	NS
Wind	9.00	4	NS

be given to the development of their sex and species-specific songs. The majority of rehabilitant gibbons will not have learned their song by copying the same-sex parent, as wild gibbons would. Thus, a study of captive-raised gibbon songs, compared to those of wild gibbons, will be important in determining how the rehabilitation process affects song development i.e. after a period of at least 12 months in the rehabilitation centre, are the gibbons showing variation in the individual female great calls or are all the females conforming to a uniform song? This study has shown that the Kalaweit females exhibit levels of variation in great call similar to that of both wild populations.

### Individuality

The lack of variation in the great call phase indicates that each female has a particular and individual song structure that did not change regardless of the environmental conditions. The songs of all females show individuality within all study populations (with more than one recorded female) in all variables except duration of the great call. There were differences between the songs of females at Kalaweit and those of females in two of the wild-raised gibbon populations. We would expect the captive-raised gibbons to show marked variability in individual great call structure, since they have probably come from several different locations (i.e. where they were born).

It would appear that the Kalaweit gibbons are basing their songs on a genetic template and possibly some individual aspects 'remembered' from their mothers; otherwise, we

would expect more conformity and for the songs to conform to something more uniform since the gibbons are all housed within auditory distance of each other and could learn to copy other Kalaweit gibbons. Since genes play a role in song development, we would expect there to be some conformity to the songs of the Kalaweit females, as shown by low significance for lowest frequency and duration of post-climax phase. Despite this there is significant variation in seven characteristics of the songs of different Kalaweit females. Juvenile females housed at Kalaweit may be learning song variation from older females within auditory distance. This may be similar to the learning that would occur between mother and daughter in the wild, thus indicates that learning is still a component of the juvenile females songs.

Since the variability between individuals was high (i.e. the significance of the variables was high), this would suggest that the captives are either retaining quite a large part of their mothers' song, or they are developing their own song quickly by learning from older females at Kalaweit. If there were little variance between the Kalaweit gibbons, this could indicate that the females (most presumably from different populations) were converging on a common song template.

Preliminary analysis indicates that there may be distinct dialects between the various wild populations of agile gibbons, and there appears to be high within-population variation in structure of the great call phase and equally high between-population variation. The populations from Bukit Baka Bukit Raya National Park and Sungai Bahara, (West Kalimantan), showed significant differences in song

characteristics. Individuality in the species-specific song of wild gibbons has been noted by several other authors: female *H. agilis* (Haimoff and Gittins, 1985) and male *H. albibarbis* and *H. muelleri* (Mitani, 1987).

Sub-adults give calls that are not substantially different from those of the same-sex adult, whereas juvenile songs are acoustically simpler, lower amplitude versions of the adult (Mitani, 1990). Age was clearly related to complexity of gibbon song. Older females produce longer songs, encompassing a more complex repertoire with more notes, but with slightly narrower frequency range. Though song is genetically programmed (Geissmann, 1984, 2002; Mather, 1992), there is an obvious element of learning and practice that comes with age. Older females, both captive-raised and wild, produce more elaborate and complex songs. It is possible that these females have refined their songs enough that they no longer need to use the wide range of frequencies that they may have done when they were younger i.e. their vocal chords are more honed. These results are consistent with the hypothesis that the great calls advertise an individual's identity as well as their presence in the territory (Tenaza, 1976).

Individuality would be important in territorial defence, as the pair would need to ensure that other groups and floating, non-paired gibbons were well aware of who occupied each space in the forest. So the individual call could involve intra-group communication. Another hypothesis proposed by (Cowlishaw, 1992) is that the female sings to defend the territory (and hence the food resources) and the male sings to defend the female and the offspring. If this were true, then individuality in the gibbon song (supported by this study) would be essential to advertise accurate information to other gibbons. This individuality would be important within populations to aid recognition of conspecifics and exchange information.

As a result, variation between populations that cannot physically meet nor overhear each other would be of less value. Variations of song structure between populations are reported herein, as well as within them (Table 3). Highly significant variation was found in number of notes/great call, notes/duration, number of post-climax notes and duration of post-climax phase. If two populations are not within auditory distance, it is possible that high levels of song variance are indicative of the variance in individual female song within that population. Without more data on dispersal distances and patterns, it is not possible to speculate how far a dispersing female would have to travel to be out of auditory distance from her mother and any relatives who may share song characteristics.

Thus it would appear that there is a species-specific song to which all agile females adhere, within which there are separate dialects in separate areas and each female has a unique call or voice. Thus, while Kalaweit gibbons have not learned from their mother, they are capable of developing a complex song, as has been described in the wild. There was a trend showing that the frequency range that the female exploits decreases with age, thus the song is more controlled.

## Environmental influence on singing behaviour

Other studies have shown that rain inhibits singing behaviour (Whitten, 1982; Mitani, 1985, 1985; Lan et al., 2000). Singing is a costly activity in terms of energy. If the gibbons spent the night and/or morning wet (and possibly cold), they will be more concerned with finding food than duetting, in order to replenish their sugar levels. Due to the high surface area to body volume ratio, gibbons experience heat loss throughout the night, which will be even more pronounced after rain. For the Kalaweit gibbons non-singing days were not significantly colder than singing days, so temperature alone was not a factor that determines if the gibbons sing or not. The temperature fluctuated little and the most likely way of a gibbon getting cold was through getting wet; thus, rain seems to be the main factor determining singing for Kalaweit gibbons, as it is in the wild (Tenaza, 1976; Whitten, 1982).

## ACKNOWLEDGEMENTS

SMC would like to thank Aurélien Brulé (Chanee), the director of the Kalaweit Project, and all staff who helped with data collection. Also to LIPI, the Indonesian Institute of Science for permission to work in Kalimantan. Funding was provided by The Gibbon Foundation, the C.K. Marr Educational Trust and Downing College, University of Cambridge.

## LITERATURE CITED

- Brockelman, W. Y. & D. Schilling, 1984. Inheritance of stereotyped gibbon calls. *Nature*, **312**: 634-636.
- Cheyne, S. M., 2004. Assessing rehabilitation and reintroduction of captive-raised gibbons in Indonesia. Cambridge, University of Cambridge. PhD Thesis.
- Cheyne, S. M., D. J. Chivers, & J. Sugardjito, 2005. Proposed Guidelines for Gibbon Rehabilitation. <http://www.iucnsscrg.org/pages/1/index.htm>, IUCN/SSC Reintroduction Specialist Group. <http://www.iucnsscrg.org/pages/1/index.htm>.
- Cowlishaw, G., 1992. Song function in gibbons. *Behaviour*, **121**(1-2): 131-153.
- Dallmann, R. & T. Geissmann, 2001. Individuality in the female songs of wild silvery gibbons (*Hylobates moloch*) on Java, Indonesia. *Folia Primatologica*, **71**: 220 (abstract).
- Dirks, W., 1998. Histological reconstruction of dental development and age at death of a juvenile gibbon (*Hylobates lar*). *Journal of Human Evolution*, **(35)**: 411-425.
- Dirks, W., 2003. Effect of diet on dental development in four species of Catarrhine primates. *American Journal of Primatology*, **61**: 29-40.
- Dytham, C., 2003. *Choosing and using statistics: A biologists guide*. Blackwell Publishing, London. 264 pp.
- Geissmann, T., 1984. Inheritance of Song Parameters in the Gibbon Song, Analyzed in 2 Hybrid Gibbons (*Hylobates pileatus* X *Hylobates lar*). *Folia Primatologica*, **42**(3-4): 216-235.

- Geissmann, T., 2002. Duet splitting and the evolution of gibbon songs. *Biological Reviews of the Cambridge Philosophical Society*, **77**(1): 57-76.
- Gittins, S. P., 1984. Territorial advertisement and defense in gibbons. In: Preuschoft, H. H., D. J. Chivers, W. Y. Brockelman & N. Creel (eds.), *The Lesser Apes: Evolutionary and Behavioural Biology*. Edinburgh University Press: 420-424.
- Groves, C., 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington D. C. 350 pp.
- Haimoff, E. H., 1981. Video analysis of siamang (*Hylobates syndactylus*) songs. *Behaviour*, **72**: 128-151.
- Haimoff, E. H., 1983. Gibbon songs: an acoustical, organisational and behavioural analysis. Wildlife Research Group. Cambridge, University of Cambridge. PhD Thesis.
- Haimoff, E. H., 1984b. Acoustic and organisational features of gibbon song. In: Preuschoft, H., D. J. Chivers, W. Y. Brockelman & N. Creel (eds.), *The Lesser Apes: Evolutionary and Behavioural Biology*. Edinburgh, University of Edinburgh Press: 333-353.
- Haimoff, E. H., 1985. The organisation of song in Müllers gibbon (*Hylobates muelleri*). *International Journal of Primatology*, **6**(2): 173-192.
- Haimoff, E. H. (1986). Convergence of duetting of monogamous old world primates." *Journal of Human Evolution*, **15**: 51-59.
- Haimoff, E. H. & S. P. Gittins, 1985. Individuality in the songs of wild agile gibbons (*H. agilis*) of Peninsular Malaya. *American Journal of Primatology*, **8**: 239-247.
- Haimoff, E. H. & R. L. Tilson, 1985. Individuality in the female song of wild Kloss' gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *Folia Primatologica*, **44**: 129-137.
- Haraway, M. M. & E. G. Maples, 1998. Flexibility in the species-typical songs of gibbons. *Primates*, **39**(1): 1-12.
- Lan, D., S. Ma, S. Li, S. & G. Guo, 2000. Timing of hoolock gibbon (*Hylobates hoolock*) songs in west Yunnan. *Zoological Research*, **20**(4): 273-277.
- Marshall, J. T. & E. R. Marshall, 1976. Gibbons and their territorial songs. *Science*, **193**: 235-237.
- Marshall, J. T. & J. Sugardjito, 1986. Gibbon Systematics. In: Swindler D. R. & J. Erwin (eds.), *Comparative Primate Biology: Systematics, evolution and anatomy*. **1**: 137-185.
- Mitani, J. C., 1985. Gibbon song duets and interspacing behaviour. *Behaviour*, **92**: 59-96.
- Mitani, J. C., 1985. Responses of gibbons (*H. muelleri*) to self, neighbour and stranger song duets. *International Journal of Primatology*, **6**(2): 193-200.
- Mitani, J. C., 1987. Species discrimination of male song in gibbons." *American Journal of Primatology*, **13**: 413-423.
- Mitani, J. C., 1990. Demography of agile gibbons (*H. agilis*). *International Journal of Primatology*, **11**(5): 411-424.
- Tenaza, R. R., 1976. Songs, choruses and countersinging of Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. *Zeitschrift für Tierpsychologie*, **40**(1): 37-52.
- Tenaza, R. R., 1985. Songs of hybrid gibbons (*H. lar* × *H. muelleri*). *American Journal of Primatology*, **8**: 249-253.
- Wachtmeister, C.-A., 2001. Display in monogamous pairs: a review of empirical data and evolutionary explanations. *Animal Behaviour*, **61**: 861-868.
- Whitten, A. J., 1982. The ecology of singing in Kloss gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *International Journal of Primatology*, **3**(1): 33-51.