

Individuality in the female songs of wild Silvery Gibbons (*Hylobates moloch*) on Java, Indonesia

Robert Dallmann & Thomas Geissmann

Institute of Zoology, Tierärztliche Hochschule Hannover, Germany. E-mail: robert@dallmanns.de

Keywords: *Hylobates moloch*, Silvery Gibbon, song, individuality, vocalization, *Hylobates agilis*, *Hylobates klossii*

Abstract

This is the first study comparing individuality in the songs among several gibbon species. All gibbon species produce loud, long and elaborate song bouts in the early morning. Silvery gibbons (*Hylobates moloch*) differ from other hylobatids, however, in that duet song bouts are absent, male singing appears to be uncommon and most song bouts are female solo songs. Consistent individual differences easily distinguish neighboring females in the field, and it has been suggested that female individuality is particularly high in *H. moloch* in order to compensate for the lack of a family-labeling male song. The aim in this study is to test this hypothesis by quantifying individuality in *H. moloch* and comparing it with data on song individuality in two other gibbon species, *H. agilis* and *H. klossii*, available from earlier studies (Haimoff and Gittins, 1985; Haimoff and Tilson, 1985). The focus in those studies had been on the great call (i.e. the most stereotypical song phrase produced by gibbon females) and individual variation of several variables (such as duration and frequency range of selected great call notes) had been determined. We exactly replicated each of those studies with great calls of *H. moloch*, which were tape-recorded in Ujung Kulon and Gunung Pangrango. According to the working hypotheses, individuality should be highest in *H. moloch*, lower in *H. klossii* (male singing is common) and lowest in *H. agilis* (male singing and duets are common). Results: We found a statistically-significant degree of inter-individual variability in most great call variables of *H. moloch*, which is higher than that of *H. klossii*, but lower than that of *H. agilis*. Our results do not support the hypothesis that *H. moloch* females compensate for the rarity of male song contributions with an elevated degree of individuality in their singing. Instead, we suggest that the amount of great call individuality may be compromised by the amount of a trill component exhibited by various species of the *lar* group of gibbons.

Contents

Introduction	41
Material and methods	42
Study animals	42
Recording and analysis	43
Data collecting	43
Statistics	45
Results	45
Comparison sets A and B	45
Comparison set C	45
Comparison between all three sets	45
Discussion	46
Conclusions	49
Acknowledgements	49
References	49

Introduction

Gibbons are distributed throughout the tropical rain forests of South-east Asia (Chivers, 1977; Geissmann, 1995; Marshall and Sugardjito, 1986) and live in monogamous, territorial family groups typically consisting of an adult pair and 1-3 immature offspring (Chivers, 1977, 1989; Leighton, 1987). All species of gibbons are known to produce elaborate, loud, long and stereotyped patterns of vocalization often referred to as „songs“ (Geissmann, 1993, 1995; Haimoff, 1984; Marshall and Marshall, 1976). These song bouts are preferentially produced in the early morning and have a duration of about 10-30 minutes. In most species, mates typically combine their species-specific and often sex-specific vocalizations to produce well-patterned duets. In the *lar* group of gibbons (e.g. *H. agilis*), mated males

additionally produce solo song bouts. In two species (*H. klossii*, *H. moloch*), males and females produce no duets, but solo songs only (Geissmann, 1993, 1995, in prep.; Geissmann and Nijman, 1999, 2000). The silvery gibbon is even more unusual among hylobatids, because of the rarity of male singing (Geissmann, in prep.; Geissmann and Nijman, 1999, 2000). In this species, adult females appear to be the vocal “‘representative’ of the family” (Kappeler, 1984a, p. 388).

Acoustic differences have repeatedly been reported to exist between vocalizations produced by individual primates, including gibbons (Haimoff and Gittins, 1985; Haimoff and Tilson, 1985; Mitani, 1996; Snowdon, 1986; Waser, 1982). Quantitative data on the individuality of female songs, however, appear to be available only for two gibbon species, *H. agilis* and *H. klossii* (Haimoff and Gittins, 1985; Haimoff and Tilson, 1985). A high degree of individuality has been reported for *H. moloch* (Geissmann and Nijman, 1999, 2000; Kappeler, 1981, 1984a), and it has been suggested that female individuality may be particularly high in this gibbon species, „thus compensating for the lack of a family-labeling male song“ (Marshall and Sugardjito, 1986, p. 157).

If correct, this hypothesis would let us predict that individuality in female songs should be low in those species which produce both duets and male solo songs but no female solo songs (e.g. *H. agilis*), higher in that gibbon species which does not duet but produces separated solo songs of males and females (*H. klossii*), and highest in the species in which duets are absent, males sing only rarely and most of the singing is provided by the females (i.e. *H. moloch*). The aim in our study is to test this hypothesis by quantifying individuality in wild *H. moloch* and comparing it with data on song individuality in *H. agilis* and *H. klossii* available from earlier studies (Haimoff and Gittins, 1985; Haimoff and Tilson, 1985).

Material and methods

Study animals

In order to ensure the comparability of our results with those of the two earlier studies (Haimoff and

Gittins, 1985; Haimoff and Tilson, 1985), we exactly replicated each of them with our study animals. This dictated the whole design of our study. We used the same number of individuals, analysed the same number of great calls of each animal, measured analogous variables and used the same statistical tests as the previous studies. Because the earlier study on *H. agilis* (Haimoff and Gittins, 1985) had included data from two different localities, we also included two localities in our comparison samples of *H. moloch*, and the selected localities (Kalejatan and Gunung Pangrango on Java) were about the same distance apart from each other as those in the earlier study (Sungai Dal and Ulu Muda on peninsular Malaysia). The localities where tape-recordings were made are shown in Fig. 1.

Kalejatan is located near the westernmost tip of Java (Indonesia) in the Ujung Kulon-Gunung Honje Nature Reserve. The gibbons of Kalejatan were tape-recorded during a long term study in 1976 (Kappeler, 1981, 1984a). Songs of 75 great calls of 5 females (referred to as ka5-ka9 in the following) were analysed in this study.

The second locality is situated on the northeastern slopes of the Gunung Pangrango, about 150 km east of Kalejatan. Tape-recordings of 3 females (referred to as pa1-pa3) were made by one of us (TG) in September 1998. A total of 68 great calls from these individuals could be sonographed.

The number of individuals and great calls used for this study are listed in Table 1. Because the Kruskal-Wallis one-way analysis of variance by ranks is quite susceptible to variations in the sample size, we chose an identical number of animals and great calls / individual for statistical analysis as the previous studies (Haimoff and Gittins, 1985; Haimoff and Tilson, 1985). We created 3 comparison sets of data (A, B, and C), one each for comparison with *H. agilis* from Sungai Dal, *H. agilis* from Ulu Muda, and *H. klossii* from Siberut. For comparison with *H. agilis*, we used all 3 specimens from Gunung Pangrango and 5 from Kalejatan (Table 1, comparison set A), thus simulating the 3 *H. agilis* from Ulu Muda and the 5 from Sungai Dal studied by Haimoff and Gittins (1985). Like that study, we choose 5 great calls of each female for comparison with Ulu Muda and 3-10 great calls / female for comparison with Sungai Dal (Table 1, comparison set B).

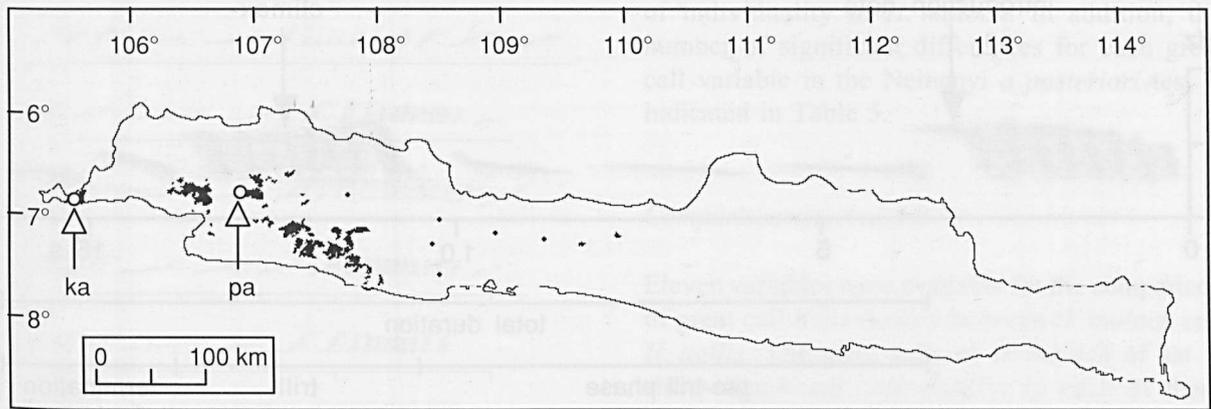


Fig. 1. Map of Java showing the two localities (arrows) where gibbon songs were tape-recorded. Black spots symbolize forests inhabited by gibbons (after Kappeler, 1984b, supplemented). Abbreviations: ka = Kalejatan; pa = Gunung Pangrango.

Table 1. Origin and number of great calls analysed in this study for comparison with those of *H. agilis* and *H. klossii* (Haimoff and Gittins, 1985; Haimoff and Tilson, 1985).

Comparison set	Population of <i>H. moloch</i>	Individuals	Number of great calls / individual	Comparison with previous studies
A	Kalejatan	ka6, ka7, ka8	10	<i>H. agilis</i> from Sungai Dal (Haimoff & Gittins, 1985)
		ka5	5	
		ka9	3	
B	Gunung Pangrango	pa1, pa2, pa3	5	<i>H. agilis</i> from Ulu Muda (Haimoff & Gittins, 1985)
C	Kalejatan	ka6, ka7, ka8	10	<i>H. klossii</i> (Haimoff & Tilson, 1985)
		ka5	8	

In their study on *H. klossii*, Haimoff and Tilson (1985) had analysed 10 great calls each of 3 individuals and 8 great calls of a fourth one. For comparison, we analysed the same numbers of great calls of four gibbons from Kalejatan (Table 1, comparison set C).

Recording and analysis

Songs of silvery gibbons from Ujung Kulon were recorded with a UHER REPORT 4200 tape recorder and a NIVICO IVC directional microphone, those from Gunung Pangrango were made with a SONY WM-D6C cassette recorder and a JVC MZ-707 directional microphone.

The sound material was digitised with a sample rate of 11 kHz and a sample size of 16 bit. Time versus frequency displays (sonagrams) of tape-

recorded vocalizations were generated using the Canary software version 1.2.4 on an Apple personal computer (Power Macintosh G3). The FFT size of the sonagrams was 2048 points with an overlap of 75% and a frame length of 1024 points (Charif et al., 1995).

Data collecting

The female song bout of *H. moloch* consists of 2 different acoustic components: (1) great calls phrases, and (2) single *wa*-notes and phrases of *wa*-notes. In contrast to the more variable organization of *wa*-phrases, great calls are highly stereotypic phrases of the female song. We identify three basic phases in the great calls of *H. moloch* females (Fig. 2): (i) a pre-trill phase, (ii) a trill and (iii) the termination phase. Since females of

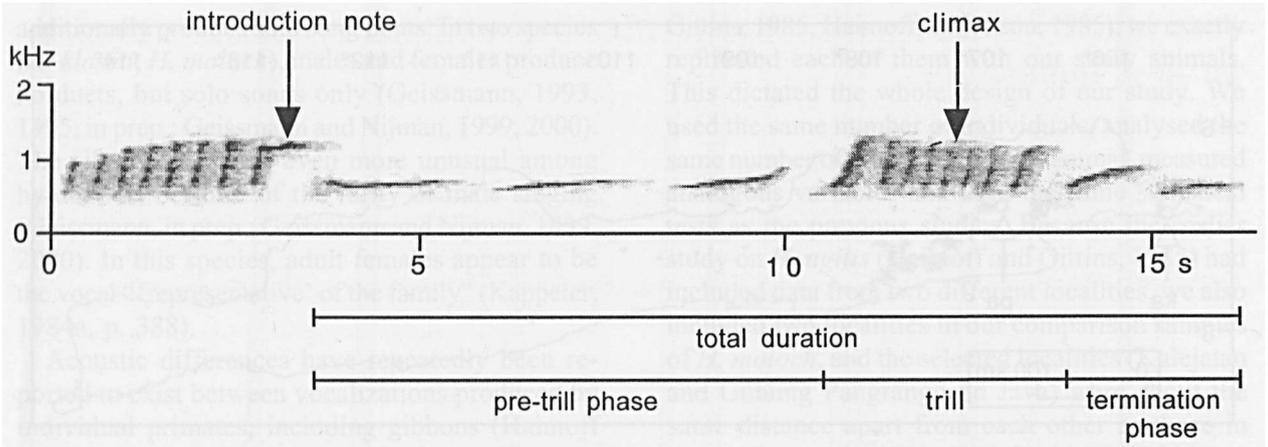


Fig. 2. Sonagram of a great call phrase produced by a female silvery gibbon, illustrating the 3 main phases (i.e. pre-trill phase, trill phase, and termination phase) which are typical features of this species great calls, and the variables measured.

Table 2. Great call variables for *Hylobates moloch* used in the present study and corresponding variables for *H. agilis* and *H. klossii* used in previous studies.

Variable for <i>H. moloch</i> Dallmann & Geissmann (this study)	<i>H. agilis</i> Haimoff & Gittins (1985)	<i>H. klossii</i> Haimoff & Tilson (1985)
1. Total duration of great call (s)	Total duration	Total duration of great calls
2. Frequency range of entire great call (Hz)	Frequency exploitation	Frequency band exploited during great calls
3. Number of pre-trill phase notes	No. of intro. phase notes	Total number of notes before the trill
4. Duration of first note (s)	–	Duration of first note
–	Combined dur. intro. phase notes	–
5. Frequency range of first note (Hz)	–	Frequency modulation of first note
6. Duration of second note (s)	–	Duration of second note
7. Frequency range of second note (Hz)	–	Frequency of second note
8. Duration of pre-trill phase (s)	Duration intro. phase	Total duration before the trill
9. Duration of first note of trill (s)	Duration inflective note	–
10. Frequency range of first note of trill (Hz)	Frequency modulation inflective note	–
11. Max. frequency of first note of trill (Hz)	Peak frequency inflective note	–
12. Min. frequency range in trill (Hz)	Peak frequency climax note	–
13. Duration of the trill (s)	–	Total duration of the trill
14. Number of notes during trill	–	Total number of notes during the trill
15. Number of notes during trill / duration trill (s ⁻¹)	–	Notes per second during the trill
16. Max. note speed in trill (s ⁻¹)	Duration climax note	Notes per second during the climax
17. Number of termination phase notes	No. of post-climax notes	Total number of post-trill notes
18. Duration of termination phase (s)	Duration post-climax phase	Total duration of post-trill period

H. moloch may occasionally abort a great call, a song bout may also contain great call fragments which were not included in the analysis.

Previous studies on individuality of gibbon songs analysed the great call exclusively, because it is the longest and most standardised part of the female’s song repertoire (Haimoff and Tilson, 1985). In the present study, the great calls of

H. moloch females were analysed.

Twenty variables of the great call were quantified and measured in a similar manner as in the earlier studies on *H. agilis* and *H. klossii* (Haimoff and Gittins, 1985; Haimoff and Tilson, 1985). A description of our great call variables and those defined in the earlier studies is presented in Table 2.

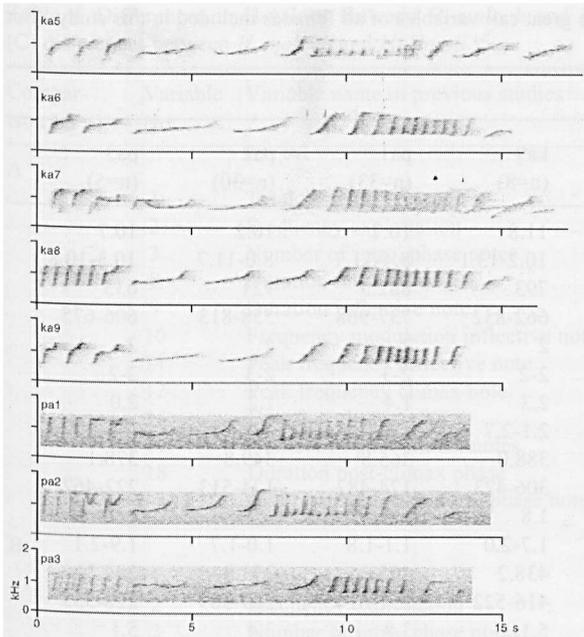


Fig. 3. Representative great calls by the 8 *Hylobates moloch* females from Kalejatan (ka) and Gunung Pangrango (pa) studied here.

Statistics

In order to demonstrate individuality among study animals, we used the Kruskal-Wallis one-way analysis of variance by ranks (Kruskal and Wallis, 1952), as in Haimoff and Gittins (1985) and Haimoff and Tilson (1985). To this we added the Nemenyi *a posteriori* test (Köhler, 1995). This test can only be carried out on variables which are significant in the Kruskal-Wallis test. All tests used were two-tailed, and the null hypothesis was rejected at $p = 0.05$.

Results

Figure 3 shows sonograms of a typical great call of each study animal. Medians and ranges of the various measured great call variables for all available great calls are listed in Table 3.

After having formed three comparison sets of great calls (A, B, C), as described above, we carried out a Kruskal-Wallis one-way analysis of variance by ranks with each set. The results are shown in Table 4. Most variables show a significant degree

of individuality in *H. moloch*. In addition, the number of significant differences for each great call variable in the Nemenyi *a posteriori* test is indicated in Table 5.

Comparison sets A and B

Eleven variables were available for the comparison of great call individuality between *H. moloch* and *H. agilis*. The great calls of *H. moloch* of set A show significant individuality in each of these variables (Kruskal-Wallis test, Table 4A). The great calls of set B are significant in 7 of 11 variables (Table 4B); only variables 3, 9, 11 and 18 are not significant. Only variable 18 is among the three least significant variables in both sets. These results are confirmed in the Nemenyi *a posteriori* test (Table 5). None of the females of data set A could be distinguished in variables 17 and 18.

Comparison set C

As shown in Table 4C, all 14 great call variables show significant individuality except one (variable 18), and 10 of them are highly significant ($p < 0.001$). Similar to the results in data set B, variable 18 is not significant in the Kruskal-Wallis test, and variable 17 shows no significant dyads in the Nemenyi *a posteriori* test (Table 5).

Comparison between all three sets

In order to compare *H. moloch* with *H. agilis* and *H. klossii*, respectively, we determined which species had the higher H-value in the Kruskal-Wallis test for each variable (Table 5). A higher H-value in this nonparametric test indicates a higher degree of inter-individual differences. The H-value differences are plotted in Fig. 4 for all 3 data sets. In the graph, a major difference becomes apparent between data sets A and B on the one hand and data set C on the other. *Hylobates moloch* has lower H-values than *H. agilis* in 8 out of 11 variables (data set A) and in 7 out of 11 variables (data set B). In the comparison with *H. klossii*, the situation

Table 3. Measurements (median and range) from the sonagrams of the great call variables of all females included in this study. (For a description of the variables see Table 2).

Variable No.	Individual							
	ka5 (n=5)	ka6 (n=23)	ka7 (n=27)	ka8 (n=12)	ka9 (n=8)	pa1 (n=33)	pa2 (n=30)	pa3 (n=5)
1	13.7	12.2	12.3	11.0	11.8	10.7	10.2	10.7
	12.6-14.9	9.8-14.1	10.7-13.7	10.0-13.3	10.2-13.1	8.4-11.7	8.0-11.7	10.3-10.8
2	717	769	815.5	731.5	793	862.5	721	633
	687-788	710-852	751-918	698-797	662-832	737-968	558-813	606-675
3	2	2	3	3	2	2	2	2
	2-2	2-3	2-3	3-3	2-2	2-3	2-3	2-2
4	2.0	3.0	2.4	1.9	2.3	1.4	1.2	2.0
	0.9-2.2	2.1-3.4	1.9-3.3	1.6-2.0	2.1-2.7	1.2-1.8	1.0-1.5	1.4-2.0
5	349.3	460.8	450.1	381.0	388.0	365.8	349.8	378.1
	267-520	299-727	316-521	217-471	306-423	174-482	174-513	222-462
6	1.8	1.9	2.0	1.6	1.8	1.5	1.2	2.0
	1.6-2.3	1.6-2.3	1.6-2.4	1.4-1.8	1.7-2.0	1.1-1.8	1.0-1.7	1.9-2.1
7	413.4	413.6	458.2	424.3	438.2	495.1	373.8	292.3
	244-512	335-501	368-581	299-456	416-522	251-614	229-509	228-335
8	4.8	5.9	6.7	5.7	5.1	3.8	3.4	5.1
	4.5-5.0	5.0-7.4	4.8-8.1	5.1-6.3	4.8-5.6	3.4-4.7	2.9-5.1	4.8-5.2
9	0.8	1.2	0.6	0.6	1.1	0.9	0.6	0.8
	0.8-0.9	0.8-1.3	0.4-1.0	0.5-0.9	1.0-1.2	0.4-1.5	0.3-1.0	0.7-1.1
10	658.8	644.7	683.8	616.7	642.5	690.3	618.8	469.4
	636-681	588-729	627-856	572-650	535-706	581-796	229-694	441-539
11	1367.2	1344.4	1372.0	1309.0	1338.5	1474.3	1314.0	1239.0
	1350-1375	1308-1423	1291-1496	1270-1358	1292-1386	1296-1605	881-1347	1228-1265
12	497	475	507.5	495	449.5	617.5	342.5	450
	485-503	401-519	413-587	433-539	365-502	354-700	231-553	400-464
13	4.8	5.3	4.3	4.4	5.3	4.8	4.7	4.0
	4.4-5.4	4.5-6.0	3.0-6.4	3.3-5.6	4.5-5.8	3.1-6.0	3.5-6.2	3.7-4.6
14	10	10.5	11	10	11	13	16	11
	10-10	8-13	8-15	9-13	8-13	10-18	12-20	8-12
15	2.08	1.92	2.57	2.27	2.08	2.72	3.40	2.78
	1.8-2.2	1.2-3.5	2.0-2.9	1.6-3.9	1.4-2.4	1.6-5.7	1.9-5.6	1.7-3.2
16	1.11	0.87	0.88	0.97	0.86	0.90	0.69	0.83
	1.0-1.1	0.8-1.0	0.7-1.0	0.9-1.1	0.7-0.9	0.7-1.1	0.5-1.1	0.7-1.3
17	3	1	1	1.5	1.5	2	2	2
	2-3	1-2	1-2	1-2	1-2	1-3	1-4	1-2
18	4.5	0.8	0.9	1.0	1.4	2.1	1.6	1.7
	1.8-5.1	0.3-1.9	0.5-2.5	0.7-1.8	0.6-2.0	1.0-2.8	0.6-2.6	0.9-2.0

is reversed: *Hylobates moloch* has higher H-values than *H. klossii* in 12 out of 14 tested variables. Only in two variables does *H. klossii* exhibit higher H-values than *H. moloch*, and both these variables refer to the termination phase of the great call (Nos. 17 and 18), which has been described as the most intra-individually variable part in the great call of *H. moloch* (Kappeler, 1984a).

Discussion

Structural variability of the great calls among silvery gibbons (*H. moloch*) was tentatively proposed to occur by Geissmann and Nijman (1999, 2000) and Kappeler (1981, 1984a). The great calls of *H. moloch* are characterized by specific quantifiable variables. These physical features exhibit statistically-significant individuality among the singing females. The evidence of the statistical tests con-

Table 4. Differences in H-values between *H. moloch* and *H. agilis* from (A) Ulu Muda and (B) Sungai Dal (Malaysia), and (C) differences between *H. moloch* and *H. klossii*.¹

Comparison set	Variable No.	Variable name in previous studies	H-values of <i>H. moloch</i>	Published H-values of <i>H. agilis</i>	Difference of H-values	
A	1	Total duration	20.42***	34.49***	-14.07	
	2	Frequency exploitation	21.76***	31.46***	-9.70	
	3	Number of intro. phase notes	20.15***	36.99***	-16.84	
	8	Duration intro. phase	12.50*	34.94***	-22.44	
	9	Duration inflective note	27.56***	22.85***	4.71	
	10	Frequency modulation inflective note	24.38***	18.74***	5.64	
	11	Peak frequency inflective note	21.50***	21.33***	0.17	
	12	Peak frequency climax note	17.87***	30.89***	-13.03	
	16	Duration climax note	24.19***	26.37***	-2.18	
	17	Number of post-climax notes	12.46*	24.64***	-10.46	
	18	Duration post-climax phase	14.18**	24.36***	-14.34	
			Combined duration intro. phase notes	-	34.52***	-
	B	1	Total duration	7.46*	10.30**	-2.84
		2	Frequency exploitation	10.21**	10.05**	0.16
		3	Number of intro. phase notes	0.00	12.99***	-12.99
		8	Duration intro. phase	18.73***	11.83**	6.90
		9	Duration inflective note	5.18	5.39	-0.21
		10	Frequency modulation inflective note	10.50**	11.80**	-1.30
11		Peak frequency inflective note	5.12	11.96**	-6.84	
12		Peak frequency climax note	12.50**	9.38**	3.12	
16		Duration climax note	9.64**	8.49*	1.13	
17		Number of post-climax notes	6.70*	11.25**	-7.23	
18		Duration post-climax phase	4.74	11.82**	-7.08	
			Combined duration intro. phase notes	-	9.36*	-
C		1	Total duration of entire great calls	18.46***	11.92**	6.54
		2	Frequency band exploited during great calls	12.18*	10.80*	1.38
		3	Total number of notes before the trill	27.69***	15.46***	12.23
		4	Duration of first note	27.24***	10.13*	17.11
		5	Frequency modulation of first note	17.71***	2.67	15.04
		6	Duration of second note	30.64***	6.98	23.66
	7	Frequency of second note	18.23***	3.98	14.25	
	8	Total duration before the trill	33.61***	12.29**	21.32	
	13	Total duration of the trill	21.75***	8.15*	13.60	
	14	Total number of notes during the trill	12.89**	10.01*	2.88	
	15	Notes / second during the trill	30.42***	13.40**	17.02	
	16	Notes / second during the climax	23.10***	12.10**	11.00	
	17	Total number of post-trill notes	8.12*	13.20**	-5.08	
	18	Total duration of post-trill period	6.46	14.50**	-8.04	

¹ * = p < 0.05, ** = p < 0.01, *** = p < 0.001

ducted here clearly demonstrates that individuality exists throughout most aspects of the entire female great call.

Most measured variables show a significant degree of differences between great calls of different tested females. Solely variables 17 (“number of termination phase notes”) and 18 (“duration of

termination phase”) show no significances at all in the Nemenyi tests with the three data sets. The extremely high intra-individual variability of this part of the great call has previously been mentioned by Kappeler (1984a) and appears to compromise individuality in this part of the great call.

The termination phase is usually produced with

Table 5. Number of significant differences for each great call variable in the Nemenyi *a posteriori* test. Only variables which were significant in the Kruskal-Wallis test (Table 4) are included.

Comparison set	Comparison with	Number of significant dyads	Variable No.
A	<i>H. agilis</i> , Sungai Dal	0	17, 18
		1	1, 16
		2	3, 11, 12
		3	8, 2
		4	9, 10
B	<i>H. agilis</i> , Ulu Muda	0	–
		1	1, 8, 2, 10, 12
		2	16
C	<i>H. klossii</i>	0	17
		1	2, 5, 7, 13, 15
		2	1, 4, 16
		3	6, 3, 14
		4	8



Fig. 4. Comparison of the H-values (from Table 3) between gibbon species for each great call variable: The horizontal axis shows the difference between the H-value of *H. moloch* minus the corresponding H-value of A) *H. agilis* from Sungai Dal; B) *H. agilis* from Ulu Muda; and C) *H. klossii*. Positive bars indicate a higher individuality in *H. moloch*, whereas negative bars indicate a higher individuality in *H. agilis* and *H. klossii*, respectively. Great call variables (vertical axis) appear in the same order as in Tables 2 and 4.

decreasing amplitude and can only be heard in the singer's immediate vicinity. Because these soft notes are probably inaudible to neighbouring groups, it is less likely that they provide information on who is singing. Selection for individuality in these short-range notes can be expected to be relaxed given the ability of recipients to use other sensory modalities to identify signallers. The same argument was also presented in a study on communication in wild chimpanzees, whose pant hoots (long-distance calls) showed greater within-individual stereotypy and between-individual variability than pant grunts (short-range calls) (Mitani et al., 1996).

In contrast to our findings in *H. moloch*, Kloss's gibbons exhibit significant inter-individual differences at the end of the great call and the highest H-values of all tested variables. *Hylobates agilis*, on the other hand, shows little inter-individual variability in the termination phase. Female agile gibbons appear to exhibit more inter-individual differences in the introduction phase than in the termination phase (Haimoff and Gittins, 1985). These differences between the three species may be related to differences in their great call structure. The great call of *H. klossii* includes a very fast and long central trill which may be more suited to convey information on the singer's stamina than about its identity. The trill is considerable shorter and slower in *H. moloch*, and virtually absent in *H. agilis* (Geissmann, 1993).

A reliable comparison of the degree of individuality in different parts of the great call would require larger samples of individuals and great calls. In addition, more variables would need to be measured, representing a more balanced amount of information on the different parts of the whole great call.

Although we were able to demonstrate individual differences in the great call of *H. moloch* females, it is unknown, whether gibbons can individually distinguish great calls of conspecifics. This could be investigated upon with the help of playback experiments. Furthermore, it is unknown, whether the individual differences remain stable over time.

Among gibbons, only in *H. moloch* is most of the singing provided by females. It has been predicted that female songs of this species would show a greater individuality than female songs of species with frequent male solo songs (such as *H. klossii*

and *H. agilis*) and male duet contributions (such as *H. agilis*) (Marshall and Sugardjito, 1986, p. 157). By using the same methods previously applied to great calls of *H. agilis* and *H. klossii* (Haimoff and Gittins, 1985; Haimoff and Tilson, 1985), we were able to demonstrate that, in contrast to our study hypothesis, *H. moloch* is not showing the highest degree of individuality in its female great calls. We conclude that the lack of male singing has not resulted in an elevated individuality in the female song of *H. moloch*.

This study is the first to compare song individuality among gibbon species. Our results do not indicate that great call individuality is related to either the amount of solo singing or the amount of male singing among the three species under comparison. We offer an alternative hypothesis. Great calls of the *lar* group of gibbons can be grouped into three classes (Geissmann 1993, p. 197; Marshall et al., 1984): Those of the soaring or wailing type (*H. agilis*, *H. lar*) consist of different, frequency-modulated note types which increase and decrease in frequency and are produced at slow speed with only slight variation in rhythm. The other extreme is represented by the bubbling or trilling type (*H. klossii*, *H. muelleri*, *H. pileatus*), mainly consisting of notes of increasing frequency which are produced with a pronounced acceleration in rhythm and which are climaxing in a long and fast bubbling trill. The great call of *H. moloch* is somewhat intermediate between the two extremes, because „it neither soars nor trills“ (Marshall et al., 1984). It consists of notes of mainly increasing frequency uttered with an acceleration in rhythm, but only a short trill of moderate speed is reached. It appears reasonable to assume that species with a long and fast trill may exhibit less individuality because the trill consists of repetitive notes only. This may explain why *H. klossii* exhibits less great call individuality than *H. agilis*, and why *H. moloch* occupies an intermediate position. As suggested by Geissmann (1993, p. 198), the soaring great call type probably represents a derived characteristic within the *lar* group. It is possible that the trill was deleted in *H. agilis* and *H. lar* in order to accommodate more individuality-coding notes in the great call. This hypothesis could be tested by analysing great call individuality in the remaining

species of the *lar* group. If our hypothesis is correct, *H. lar* should exhibit an amount of individuality similar to that of *H. agilis*. *Hylobates muelleri* and *H. pileatus*, on the other hand, should exhibit a much lower amount of individuality, similar to that *H. klossii* or even lower, because their trill makes up the highest proportion of the great call duration among gibbons of the *lar* group.

Conclusions

- 1 We found a statistically-significant individuality in most great call variables of *H. moloch*, similar to the findings of previous studies on *H. agilis* and *H. klossii*.
- 2 The degree of individuality in *H. moloch* is higher than in *H. klossii*, but lower than in *H. agilis*.
- 3 Our results do not support the hypothesis that *H. moloch* females compensate for the rarity of male singing with an elevated degree of individuality in their singing.

Acknowledgements

Additional tape-recordings used in the present study were kindly made available by Dr. Markus Kappeler. We are grateful to Dr. D.J. Chivers and Dr. B. Merker for reading and commenting on this manuscript.

References

- Brockelmann WY, Srikosamatara S. 1984. Maintenance and evolution of social structure in gibbons. In: Preuschoft H, Chivers DJ, Brockelmann WY, Creel N, eds. *The lesser apes. Evolutionary and behavioural biology*. Edinburgh: Edinburgh University Press, 298-323.
- Charif RA, Mitchell S, Clark CW. 1995. *Canary 1.2 user's manual*. New York: Cornell Laboratory of Ornithology, Ithaca.
- Chivers DJ. 1989. The social behavior of the lesser apes. In: Seth PK, Seth S, eds. *Perspectives in primate biology, vol. 3*. New Delhi: Today and Tomorrow's Printers and Publishers, 141-155.
- Chivers DJ. 1977. The lesser apes. In: Prince Rainier III of Monaco, Bourne GH, eds. *Primate conservation*. New York: Academic Press, 539-598.
- Chivers DJ. 1984. Feeding and ranging in gibbons: A sum-

- mary. In: Preuschoft H, Chivers DJ, Brockelmann WY, Creel N, eds. *The lesser apes. Evolutionary and behavioural biology*. Edinburgh: Edinburgh University Press, 267-281.
- Geissmann T. 1993.** *Evolution of communication in gibbons (Hylobatidae)*. PhD thesis, Anthropological Institute, Philosoph. Faculty II, Zürich University.
- Geissmann T. 1995.** Gibbon systematics and species identification. *Int. Zoo News* 42: 467-501.
- Geissmann T. in prep.** Duett-splitting and the evolution of gibbon songs. *Int. J. Primatol.* (Manuscript submitted).
- Geissmann T, Nijman V. 1999.** Singing behavior of the silvery gibbon (*Hylobates moloch*) in Central Java, Indonesia. *Primate Report* 54: 18-19 (Abstract only).
- Geissmann T, Nijman V. 2000.** Do male silvery gibbons have anything to say? – Haben männliche Silbergibbons etwas zu sagen? *Folia Primatol.* 71: 225 (Abstract only).
- Haimoff EH, Tilson RL. 1985.** Individuality in the female songs of wild Kloss' gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *Folia Primatol.* 44: 129-137.
- Haimoff EH, Gittins SP. 1985.** Individuality in the songs of wild agile gibbons (*Hylobates agilis*) of Peninsular Malaysia. *Am. J. Primatol.* 8: 239-247.
- Haimoff EH. 1984.** Acoustic and organizational features of gibbon songs. In: Preuschoft H, Chivers DJ, Brockelmann WY, Creel N, eds. *The lesser apes. Evolutionary and behavioural biology*. Edinburgh: Edinburgh University Press, 333-353..
- Kappeler M. 1981.** *The Javan silvery gibbon (Hylobates lar moloch)*, PhD thesis, Philosophisch-Naturwissenschaftliche Fakultät, Universität Basel.
- Kappeler M. 1984a.** Vocal bouts and territorial maintenance in the moloch gibbon. In: Preuschoft H, Chivers DJ, Brockelmann WY, Creel N, eds. *The lesser apes. Evolutionary and behavioural biology*. Edinburgh: Edinburgh University Press, 376-389.
- Kappeler M. 1984b.** The gibbon in Java. In: Preuschoft H, Chivers DJ, Brockelmann WY, Creel N, eds. *The lesser apes. Evolutionary and behavioural biology*. Edinburgh: Edinburgh University Press, 19-31.
- Köhler W. 1995.** *Biostatistik: Einführung in die Biometrie für Biologen und Agrarwissenschaftler*, 2. Auflage, Berlin: Springer.
- Kruskal WH, Wallis WA. 1952.** Use of ranks in one-criterion variance analysis. *J. Am. Statist. Assoc.* 47: 583-621.
- Leighton DR. 1987.** Gibbons: Territoriality and monogamy. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds. *Primate societies*. Chicago and London: University of Chicago Press, 135-145.
- Marshall JT, Marshall ER. 1976.** Gibbons and their territorial songs. *Science* 193: 235-237.
- Marshall, JT, Sugardjito, J, Markaya, M. 1984.** Gibbons of the lar group: Relationships based on voice. In: Preuschoft H, Chivers DJ, Brockelmann WY, Creel N, eds. *The lesser apes. Evolutionary and behavioural biology*. Edinburgh: Edinburgh University Press, 533-541.
- Marshall, JT, Sugardjito J. 1986.** Gibbon systematics. In: Swindler DR, Erwin J, eds. *Comparative primate biology, vol. 1: Systematics, evolution, and anatomy*. New York: Alan R. Liss, 137-185.
- Mitani JC, Gros-Louis J, Macedonia JM. 1996.** Selection for acoustic individuality within the vocal repertoire of wild chimpanzees. *Int. J. Primatol.* 17: 569-583.
- Snowdon CT. 1986.** Vocal communication. In: Mitchell DR, Erwin J, eds. *Comparative primate biology, vol. 2A: Behavior, conservation, and ecology*. New York: Alan R. Liss, 495-530.
- Waser PM. 1982.** The evolution of male loud calls among manglebeys and baboons. In: Snowdon CT, Brown CH, Petersen MR, eds. *Primate communication*. Cambridge: Cambridge University Press, 117-143.

Received: 3 July 2000