DIFFERENT LEVELS OF VARIABILITY IN THE FEMALE SONG OF WILD SILVERY GIBBONS (HYLOBATES MOLOCH)

by

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Summary

Gibbon songs are known to include species- and sex-specific characteristics. It has been suggested frequently that these songs also exhibit a high degree of individuality, but quantifying individuality has rarely been attempted. Because the statistical methods used in earlier studies were highly dependent on sample size (Kruskal-Wallis one-way analysis of variance by ranks), it was not possible to compare results among studies directly. We introduce a mean pairwise difference (MPD) of scaled variables in order to quantify great-call variability and individuality. Because of its construction as simple normalised difference, the MPD is largely independent of sample size. This makes it possible to compare results directly with those of other studies on other populations or species. Even various levels of variability (intra- vs. inter-individual, intra- vs. inter-population variability) can be determined and compared with this method. In addition, the MPD can be calculated independently for any acoustic variable. This opens up a broad variety of research options in the area of comparative analysis of acoustic communication. For instance, variability in various parts of a phrase, in various parts of a song bout, in various contexts or in various seasons can be compared, and this is possible even if the variables under comparison are not the same. As an example we analysed female great-call phrases of wild silvery gibbons in Java (Indonesia). We found that inter-individual variability is significantly higher than intra-individual variability. This implies that females can be distinguished by their great-calls, although this was not examined during the present study. Additionally, variability of female songs was found to be significantly lower within one population than among any two populations. The various

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sections of the great-call differ in their variability. The first half of the great-call (excluding the introductory note) shows the highest potential for individual recognition.

Keywords: *Hylobates moloch*, silvery gibbon, song, individuality, vocalisation.

Introduction

The gibbons or small apes are distributed throughout the tropical rain forests of south-east Asia (Chivers, 1977; Marshall & Sugardjito, 1986; Geissmann, 1995). They live in monogamous, territorial family groups typically consisting of an adult pair and 1-3 immature offspring (Chivers 1977, 1989; Brockelman & Srikosamatara, 1984; Leighton, 1987). All species of gibbons are known to produce elaborate, loud, long and stereotyped patterns of vocalisation often referred to as 'songs' (Marshall & Marshall, 1976; Haimoff, 1984; Geissmann, 1993, 1995). Preferentially, song bouts are produced in the early morning and have a duration of about 10-30 minutes. In most gibbon species, mated pairs utter their songs in the form of well-coordinated duets. In addition to duet song bouts, gibbon pairs of the *lar* group may also produce male solo songs. Only in two species (*Hylobates klossii* and *H. moloch*), female solo songs are common, whereas duet songs are apparently absent.

Acoustic individuality has been demonstrated to exist in several gibbon species (Haimoff & Gittins, 1985; Haimoff & Tilson, 1985; Dallmann & Geissmann, in press). Unfortunately, the statistical method used in each of these studies (Kruskal-Wallis one-way analysis of variance) has several limitations:

(1) This type of analysis provides information on whether the median values of at least one sub-sample differ from that of the whole sample. It does not quantify which and how many sub-samples differ from each other.

(2) Comparisons among the results of different studies are possible only based on the H-values produced by the Kruskal-Wallis analysis. Because the H-values are strongly influenced by the sample size, this requires that each study uses exactly the same number of samples (individuals, calls/individual, variables *etc.*). How problematic this can be is shown in Dallmann & Geissmann (in press), who had to repeat each of two previously-published studies in every detail in order to get comparable results.

(3) The Kruskal-Wallis analysis does not allow to compare different levels of variation in vocalisations (within and between individuals, within and between populations, comparison of various variables, *etc.*).

In order to circumvent these limitations, we introduce a different method, the mean pairwise difference (MPD) of scaled variables. Our method can be applied in several new contexts, except that this is not a method for individual identification, but a method for quantifying individuality and different levels of variability.

Different levels of variability may have different causes and functions, albeit — at least in gibbons — these causes and functions are a matter of speculation. Inter-individual variability may be used by the receiver for individual recognition. Songs with low intra-individual variability should be particularly suited for individual recognition. Being able to discriminate between neighbours and strangers would be useful in order to react adequately (Brooks & Falls, 1975; Catchpole & Slater, 1995, p. 134; Stoddard, 1996). In addition, individual song characteristics could be important mate choice criteria. For instance, recognition of family-specific song characteristics could be used in order to avoid inbreeding (Catchpole & Slater, 1995, pp. 69 and 206f).

Differences between populations, at least on the species level, are genetically determined in gibbons (Brockelman & Schilling, 1984; Geissmann, 1984, 1993) and may be used for species recognition (Mitani, 1987). It has been suggested that differences should also exist between populations below the species level. Such differences may evolve by random historical events (simple genetical drift, genetical isolation, bottleneck effects, hybridization), environmental determinism, and social adaptation (Payne, 1981; Mather, 1992). To what degree these vocal differences are recognised or even used by the receiver, however, is unknown. If recognisable vocal differences exist, i.e. among subspecies, they would represent an important tool for conservation biologists, because many gibbon subspecies cannot be reliably identified based on traditional characteristics such as morphology or fur colouration (Geissmann, 1995).

Although functions and, therefore, variability of gibbon songs are usually assessed and discussed for the song as a whole, it has also been proposed that different parts of the same individual's song may also differ in function (Goustard, 1985; Geissmann, 2000). If correct, we should expect to find different degrees of (each level of) variability in different parts of the same song.

As an example, we apply our method to the analysis of the female great-call of wild silvery gibbons. The silvery gibbon (*H. moloch*) is particularly unusual among hylobatids because of the rarity of male singing (Geissmann & Nijman, 2000). In this species, mated females appear to be the vocal "'representative' of the family", and the individuals can be easily distinguished in the field by their songs (Kappeler, 1984a, p. 388). We compare great-call variability within and between individuals, within and between populations. In addition, we compare the variability of different sections of the great-call phrase. Because our technique is very robust for effects of sample size, our results can be used as a baseline for future studies on individuality in gibbon songs.

Material and methods

Study animals

We analysed a total of 316 great-calls from 30 different *H. moloch* females. Tape-recordings were carried out by one of us (TG) in September 1998. Additional tape-recordings were made in 1976 and 1978 by Markus Kappeler. Tape-recording localities are shown in Fig. 1, and sample sizes (number of individuals and great-calls) are listed in Table 1. Tape-recordings from 8 different localities were available for this study, covering most of the current distribution area of the silvery gibbon. We divided our sample into 5 distinct populations by pooling localities of the same forest system or reserve.

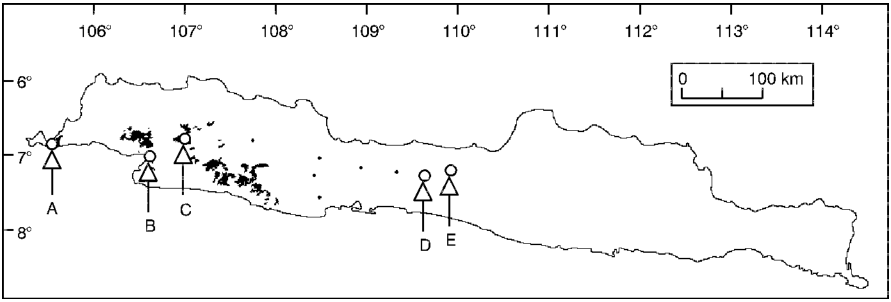


Fig. 1. Map of Java showing the localities (arrows) where gibbon songs were tape-recorded. Black spots symbolise forests inhabited by gibbons (after Kappeler, 1984b, supplemented). Abbreviations of populations: A = Kalejatan and Tereleng; B = Pelabuhanratu; C = Cibodas, and Gunung Pangrango; D = Gunung Lawét; E = Linggo Asri.

TABLE 1. *Origin, abbreviation, number of individuals and great-calls and recording information of the material analysed in this study*

Population	Locality	Abbreviation	Number of individuals	Number of great-calls	Recorded by[a]
A	Kalejatan	ka	9	96	1a
	Tereleng	te	3	12	1a
B	Pelabuhanratu	pe	1	10	1b
C	Cibodas	cb	1	12	1b
	Gunung Pangrango	pa	3	66	2
D	Gunung Lawét	la	1	2	1b
E	Linggo Asri	as	11	116	2
Total:			29	314	

[a] Code to sources of tape-recordings:
(1a) Markus Kappeler (1976);
(1b) Markus Kappeler (1978);
(2) Thomas Geissmann (1998).

Recording and analysis equipment

Gibbon songs were recorded with a Sony WM-D6C cassette recorder and a JVC MZ-707 directional microphone by T. Geissmann and with a UHER REPORT 4200 tape recorder and a NIVICO IVC directional microphone by M. Kappeler.

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 vocalisations 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 (Frequency resolution = 5.433 Hz) (Charif *et al.*, 1995).

Data collecting

The female song bout of *H. moloch* consists mainly of 2 different acoustic components: (1) great-call phrases which are uttered at intervals of about 2 minutes, and (2) single *wa*-notes and phrases of *wa*-notes, which are produced before, after and between the great-calls. In contrast to the more variable organisation of *wa*-phrases, great-calls are highly stereotypic and species-specific phrases of the female song (Haimoff, 1984; Kappeler, 1984b). We identify three basic phases comprising the great-calls of all females of *H. moloch* (Fig. 2): (i) a pre-trill phase with 2 or 3 long soaring notes, (ii) a trill consisting of an accellerando-decellerando of notes and (iii) a very variable termination phase which is closing the great-call. Because females of *H. moloch* may occasionally abort a great-call, a song bout may also contain great-call fragments. These were not included in the analysis.

Similar to most previous studies on songs of female gibbons, we are analysing the great-call exclusively, because it is the longest and most standardised part of the female's song repertoire (Haimoff & Tilson, 1985).

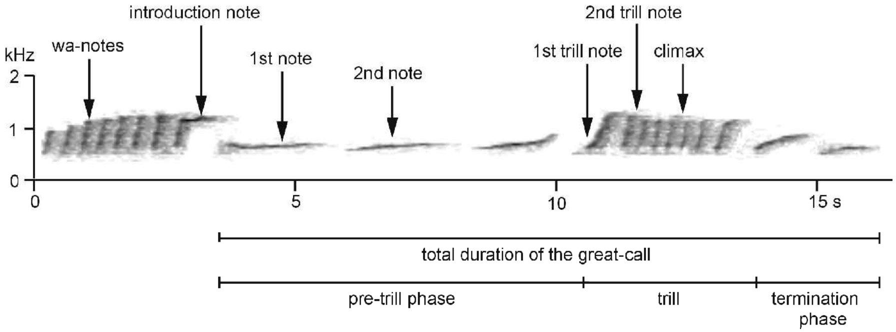


Fig. 2. Sonagram of a great-call phrase produced by a female silvery gibbon, illustrating the 3 main phases (*i.e.* pre-trill phase, trill phase, and termination phase) which are typical great call features of this species, and the variables measured.

A total of 39 great-call variables were defined and measured. A description of these variables is listed in Table 2.

In order to detect variability on different levels of organisation, we built up 2 data sets. The first one included 316 great-calls from all 30 individuals. The intra-individual variability was calculated by randomly selecting two great-calls from each individual out of this data set. One individual was not included here because only one great-call was of suitable quality for analysis. In order to compute the inter-individual variability, we randomly selected the same number of great-call pairs, but this time, each pair included great-calls of two different females. In addition, we made sure that no great-call was used twice in this comparison.

Data set number 2 consists of 3 subsets. Each subset includes 78 great-calls from populations A (6 females), C (4 females) and E (6 females), respectively (A, C, E as defined in Table 1). Samples from populations B and D were to small for inclusion in this part of the study. In order to measure intra-population variability, we randomly picked two great-calls of two different females from the same subset of data set 2. Then, inter-population variability was computed by selecting two great-calls from two randomly-chosen individuals which were not members of the same subset.

We compared the four different levels of variability by determining whether they were correlated among each other.

Finally, we wanted to know how much different components of the great-call contributed to each level of variability. We defined 8 great-call sections, as shown in Fig. 2. The sections and the variables which describe them are the following: introduction phase (variables 12, 13, 14, 15); 1. note (16, 17, 18, 19); 2. note (20, 21, 22, 23); pre-trill phase (10, 11); 1. trill note (24, 25, 26, 27); 2. trill note (28, 29, 30, 31); trill (3, 32, 35, 36, 37); termination phase (38, 39). All variables which are measuring features of more than a single great-call section were summarised under the term ‘others’ (variables 1, 2, 4, 5, 6, 7, 8, 9, 33, 34). We determined the average variability (average MPD, as defined below) of all variables for each great-call section.

Statistics

All data of the same variable were standardised in order to enable a comparison of the variability among variables and individuals. We used a very simple form of standardisation

TABLE 2. *Descriptions of the variables analysed in this study*

No.	Variable (Unit)		Description
1	Total great-call duration (s)		Time interval between start of first note until the end of the last note of the great-call
2	Total great-call duration excluding termination phase (s)		No. 1 minus No. 38
3	Duration of trill (s)		No. 1 minus (No. 11 plus No. 38)
4	Number of notes of entire great-call		Number of notes between first and last note of great-call
5	Frequency range of entire great-call (Hz)		No. 7 minus No. 9
6	Number of note with max. frequency		The number of the note with the highest frequency
7	Maximum frequency (Hz)		The highest frequency in the entire great-call
8	Number of note with min. frequency		The number of the note with the lowest frequency
9	Minimum frequency (Hz)		The lowest frequency in the entire great-call
10	Number of pre-trill phase notes		Number of notes between first note and last note before trill
11	Duration pre-trill phase (s)		Time between start of first note and start of first trill note
12	Introduction note	Duration (s)	Duration of the introduction note
13		Frequency range (Hz)	No. 15 minus No. 14
14		Min. frequency (Hz)	The lowest frequency of the introduction note
15		Max. frequency (Hz)	The highest frequency of the introduction note
16	1. note	Duration (s)	Duration of the first note of the great-call
17		Frequency range (Hz)	No. 19 minus No. 18
18		Min. frequency (Hz)	The lowest frequency of the first note of the great-call
19		Max. frequency (Hz)	The highest frequency of the first note of the great-call
20	2. note	Duration (s)	Duration of the second note of the great-call
21		Frequency range (Hz)	No. 23 minus No. 22
22		Min. frequency (Hz)	The lowest frequency of the second note of the great-call
23		Max. frequency (Hz)	The highest frequency of the second note of the great-call
24	1. trill note	Duration (s)	Duration of the first trill note
25		Frequency range (Hz)	No. 27 minus No. 26
26		Min. frequency (Hz)	The lowest frequency of the first trill note
27		Max. frequency (Hz)	The highest frequency of the first trill note
28	2. trill note	Duration (s)	Duration of the second trill note
29		Frequency range (Hz)	No. 31 minus No. 30

TABLE 2. *(Continued)*

No.	Variable (Unit)	Description
30	Min. frequency (Hz)	The lowest frequency of the second trill note
31	Max. frequency (Hz)	The highest frequency of the second trill note
32	Number of trill notes	No. 4 minus (No. 10 plus No. 39)
33	Number of notes before climax	Number of notes from first note until the climax note (climax note included)
34	Number of notes after climax	No. 33 minus No. 4
35	Min. frequency at end of a trill note (Hz)	The lowest frequency at an end of a trill note
36	Min. frequency range in trill (Hz)	The minimal frequency bandwidth of a trill note
37	Max. note speed in trill (s)	The minimal time needed for three consecutive trill notes
38	Duration of termination phase (s)	The time from start of the first termination phase note until the end of the last termination phase note
39	Number of termination phase notes	The number of notes in the termination phase

referred to as ‘ranging’ (Gower, 1971; see also Sneath & Sokal, 1973, p. 153). In ranging, the smallest value for the variable ($X_{\min}$) is subtracted from each value (X) and the result is divided by the range ($X_{\max} - X_{\min}$):

$$X' = \frac{(X - X_{\min})}{(X_{\max} - X_{\min})}$$

As a result of this procedure, the smallest value of each variable then becomes 0, and the largest value becomes 1.

In order to compare two or more samples, we calculated the pairwise difference between the ranged great-call variables. The mean of all differences for one variable is there defined as mean pairwise difference (MPD) for this variable.

We used the Mann-Whitney U test (Siegel & Castellan, 1988) to compare two independent samples. All tests were two-tailed, and the null hypothesis was rejected at $p = 0.05$. Pearson correlation coefficients among various levels of variability (*e.g.* intra-individual *vs* inter-individual variability) were calculated using StatView 5.0 software on a G3 Power Macintosh.

Results

The variability among great-calls of the same individual (a) and of two different individuals (b) of *H. moloch* is illustrated in Fig. 3. Median, mean values and ranges for the whole sample of great-calls used in this study are listed in Table 3. A complete list of medians, means and ranges of all populations of this study is available from the authors upon request.

We determined the MPD for all measured variables of each of our two data sets. In order to visualise our results, we determined a kind of 'meta' mean pairwise distance, which is the mean of all 39 MPDs calculated for each of the different variability categories. These values are charted in Figs 4 and 5.

The intra-individual variability of *H. moloch* great-calls is lower than the inter-individual variability; the difference is statistically significant ($N = 39$, $p < 0.0001$). Furthermore, intra-individual variability is significantly lower in population A than in populations C and E ($N = 39$, $p = 0.0004$, and $N = 39$, $p = 0.017$, respectively).

The intra-population variability is significantly lower than the inter-population variability ($N = 39$, $p = 0.033$). The various dyads of populations also exhibit different amounts of variability: The inter-population variability of the dyad C & E is significantly higher than that of dyad A & C

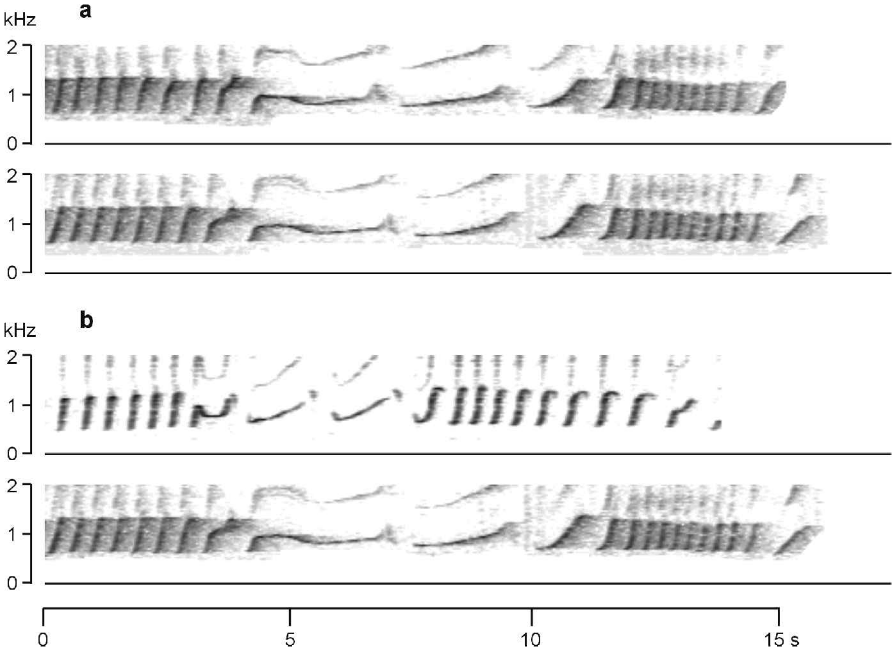


Fig. 3. Two representative *Hylobates moloch* great-calls (a) of the same individual, and (b) of two different individuals.

TABLE 3. *Medians, mean values and ranges for the whole sample of great-calls used in this study ($N = 314$)*

Variable	Mean	Median	Minimum	Maximum
1	10.8	10.8	6.3	15.9
2	9.3	9.2	5.7	14.4
3	4.8	4.8	2.5	7.5
4	14.5	14.0	8	22
5	853	830	558	1167
6	3.5	3.0	2	18
7	1428	1411	1180	1640
8	13.5	14.0	1	21
9	576	578	417	699
10	2.1	2.0	1	5
11	4.5	4.3	1.8	9.9
12	0.7	0.7	0.0	1.5
13	680	676	0	966
14	644	640	0	901
15	1324	1329	0	1675
16	2.0	1.9	0.9	3.6
17	467	459	115	820
18	697	688	505	962
19	1164	1138	736	1546
20	1.2	1.4	0.0	2.5
21	370	420	0	937
22	599	732	0	969
23	969	1170	0	1698
24	0.85	0.87	0.3	1.5
25	702	697	229	1054
26	713	704	460	908
27	1414	1406	881	1640
28	0.5	0.5	0.2	1.9
29	719	717	318	1011
30	661	659	552	821
31	1380	1376	986	1637
32	11.65	11.0	4	20
33	8.00	8.0	5	13
34	6.48	6.0	2	13
35	1164	1158	924	1486
36	478	472	231	890
37	0.9	0.9	0.2	1.8
38	1.5	1.5	0.2	6.1
39	1.9	2.0	1	8

The units of the variables are given in Table 2.

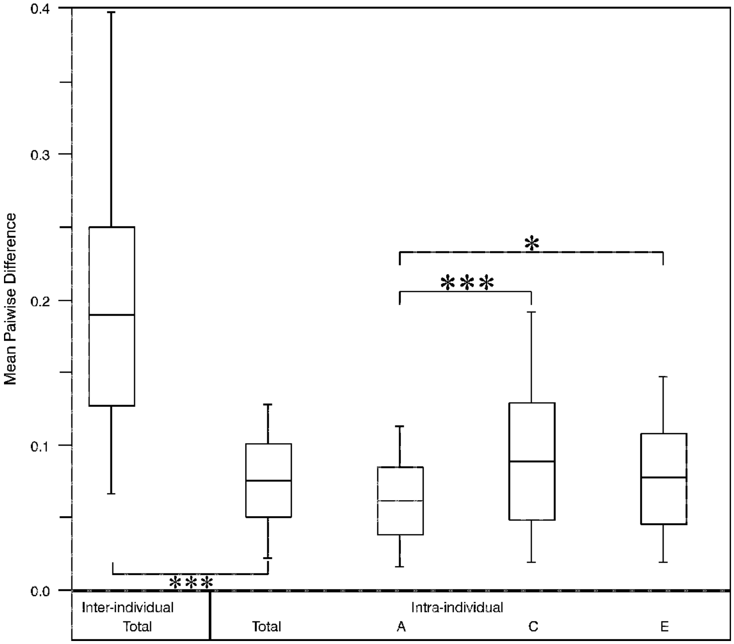


Fig. 4. Plot of the mean pairwise difference (MPD) for individual data, showing mean, range, and standard deviation for each sample (*: $p < 0.05$; ***: $p < 0.001$).

($N = 39$, $p = 0.0004$), and the A & C dyad is significantly less variable than the dyad A & E ($N = 39$, $p = 0.01$).

A pairwise comparison of the four levels of variability revealed a general similarity among three of these levels (Table 4). We found a high correlation between inter-individual and inter-population variability ($N = 39$, $r_P = 0.965$, $p < 0.001$). The correlation coefficient among any of these two and intra-population variability is higher than 0.82 ($N = 39$, $p < 0.001$). Intra-individual variability appears to be the most deviating variability measurement of this study. It shows only a weak correlation with intra-population variability and no significant correlation at all with the other two levels of variability (Table 4).

The mean MPDs for each section of the great-call are shown in Fig. 6. In addition, the shading (white, grey and black) indicates the lowest, intermediate and highest mean MPDs, respectively, and visualises the differences and similarities among the four variability levels.

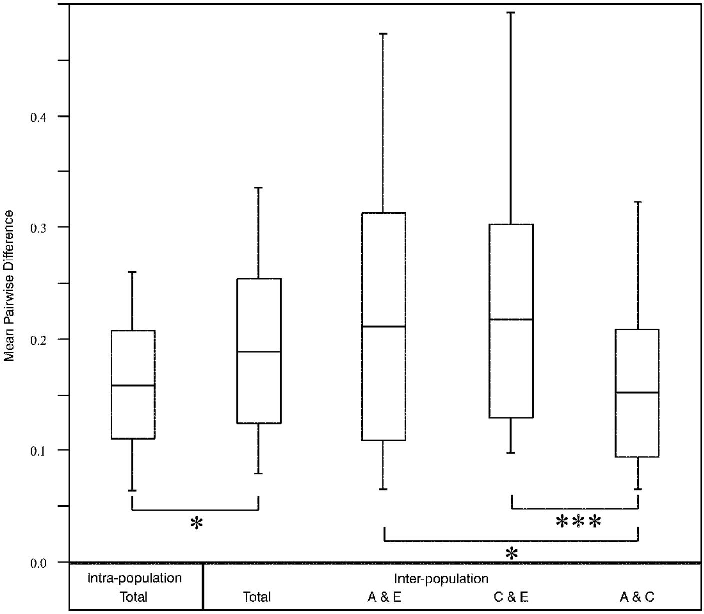


Fig. 5. Plot of the mean pairwise difference (MPD) for population data, showing mean, range, and standard deviation for each sample (*: $p < 0.05$; ***: $p < 0.001$).

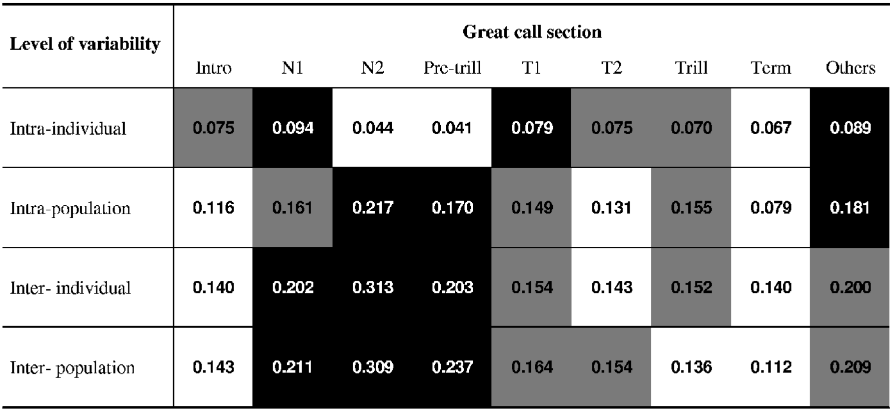
TABLE 4. *Correlation matrix for all 39 variables*

	Intra-individual	Intra-population	Inter-individual	Inter-population
Intra-individual	1	0.328 (0.041)	0.02 (0.889)	0.026 (0.876)
Intra-population		1	0.831 (<0.001)	0.827 (<0.001)
Inter-individual			1	0.965 (<0.001)
Inter-population				1

Values are Pearson correlation coefficients r_p and error probabilities p (in parentheses).

Discussion

Previous studies on vocal variability and individuality in primates have mainly been using three different statistical techniques: (1) simple univariate statistics which provide information on whether two samples (such as individuals or populations) are different (Chivers, 1974, pp. 238-241; Marler & Hobbett, 1975; Waser, 1976; Quris, 1980); (2) the Kruskal-Wallis one-way analysis of variance (or ANOVA) which provides information on whether the median values (or means) of at least one sub-sample differ from that



Level of variability	Great call section								
	Intro	N1	N2	Pre-trill	T1	T2	Trill	Term	Others
Intra-individual	0.075	0.094	0.044	0.041	0.079	0.075	0.070	0.067	0.089
Intra-population	0.116	0.161	0.217	0.170	0.149	0.131	0.155	0.079	0.181
Inter- individual	0.140	0.202	0.313	0.203	0.154	0.143	0.152	0.140	0.200
Inter- population	0.143	0.211	0.309	0.237	0.164	0.154	0.136	0.112	0.209

Fig. 6. Mean variability (MPD) determined for different great-call sections. Abbreviations (and variables used) for great-call sections: Intro = introduction phase (variables 12, 13, 14, 15); N1 = 1. note (16, 17, 18, 19); N2 = 2. note (20, 21, 22, 23); Pre-trill = pre-trill phase (Nos. 10, 11); T1 = 1. trill note (24, 25, 26, 27); T2 = 2. trill note (28, 29, 30, 31); Tr = trill (3, 32, 35, 36, 37); Term = termination phase (38, 39); Others (1, 2, 4, 5, 6, 7, 8, 9, 33, 34). For each level of variability, the cells with the 3 highest mean MPDs are indicated in black, the 3 intermediate values have grey cells, and the 3 lowest values have white cells.

of the whole sample for the comparison of several samples (Chapman & Weary, 1980; Maeda & Masataka, 1987; Mitani *et al.*, 1992; Arcady, 1996; Arcady *et al.*, 1998; Mitani *et al.*, 1999; Dallmann & Geissmann, in press); and (3) multi-variate techniques (such as discriminance analysis or principle components analysis) which provide information on how big the differences between samples are relative to each other (Smith *et al.*, 1982; Zimmermann & Lerch, 1993; Mitani & Brandt, 1994; Mitani & Gros-Louis, 1995; Fischer *et al.*, 1998; Steenbeek & Assink, 1998).

Only the third of these techniques will permit some sort of ranking of variabilities and thus allow comparison of the degree of variability among large numbers of different samples or variables. As a result, multi-variate techniques have become the method of choice among many of the more recent studies on vocal variability and individuality.

Compared to multi-variate techniques, the advantage of our method consists in its simplicity. As another advantage of our method, future studies can be compared very easily with our results without requiring our original data sets. Additionally, it might be useful to calculate MPDs even prior to multi-variate techniques in order to find out which variables are suited for inclusion in the analysis in the first place.

As pointed out in previous studies on *H. agilis*, *H. klossii* and *H. moloch* (Haimoff & Gittins, 1985; Haimoff & Tilson, 1985; Dallmann & Geissmann, in press), great-calls of *H. moloch* are characterised by specific quantifiable variables. Unfortunately, the statistical methods used in earlier studies (Kruskal-Wallis one-way analysis of variance by ranks, Nemenyi *post hoc* test) were highly dependent on sample size. As demonstrated by Dallmann & Geissmann (in press), a quantitative comparison between such results is only possible, if each study is exactly replicated (in this case by using the same number of individuals, the same number great-call phrases/individual, and the same variables).

One advantage of the present report, besides using a much larger sample size than previous studies, consists in the method we use. Thanks to its construction, the mean pairwise difference (MPD) appears to be much less susceptible to different sample sizes and variables. Thus, our results can easily be compared with those of future studies. In addition, the MPD is a useful tool for the comparison of individuality in vocal variables and for the comparison of different levels of variability.

Through the MPD method, we were able to document that inter-individual variability is significantly higher than intra-individual variability. A similar comparison does not appear to have been published for non-human primate vocalisations, and has only rarely been studied in other mammals (*e.g.* Sayigh *et al.*, 1998). In addition, we were able to document that intra-population variability is significantly lower than inter-population variability. Furthermore, the populations do not differ from each other in the same amount of variability. Differences among *H. moloch* females from populations A & C are higher than those between individuals from populations C & E or those from A & E.

Molecular data appear to support a split of *H. moloch* into two distinct populations (possibly subspecies), one in western Java and one in central Java (Andayani *et al.*, 1998; Supriatna *et al.*, 1999). Indeed, the possible existence of two subspecies was previously proposed by Sody (1949), but rejected by Groves (1972) and Kappeler (1981). Gibbon songs provide particularly suitable characteristics for taxonomical classifications (Geissmann, in press; Haimoff *et al.*, 1982). If there were two subspecies on Java, one should expect more pronounced differences in singing behaviour between populations belonging to different subspecies than between populations of the same subspecies. In order to correspond to the molecular findings of Andayani *et al.* (1998), we should find higher vocal differences between A and C than between C and E, but we found exactly the opposite. Our data do not disprove the occurrence of subspecies, but if there were two subspecies in *H. moloch*, the common distribution border between them should be located somewhere between our populations C and E, not between A and C, as indicated by the results of Andayani *et al.* (1998). Further investigations are necessary in order to resolve these contradicting results. A multivariate analysis of our vocal data may provide more reliable information on the affinities among silvery gibbon populations and will be carried out in a future study.

There are significant differences in the amount of intra-individual variability between the populations A (Kalejatan, Tereleng) and C (Cibodas, Ciletu, Gunung Pangrango), and between A and E (Linggo Asri), respectively (Fig. 4). The reason for these differences is not clear. They may be influenced by population density. Possibly, the selective pressures acting on vocal individuality correlate with population density. If there are many neighbours, it may be advantageous to produce more stable great-calls in order to be individually recognisable, whereas fewer individual characteristics may be necessary for individual recognition in a population at low density. Unfortunately, population density estimates for various silvery gibbon populations are so vague and differ so much between authors as to be hardly comparable (*e.g.* Gurmaya *et al.*, 1994; Asquith *et al.*, 1995; Nijman & van Balen, 1998). In addition, it is unknown whether gibbons are able to differentiate between *neighbours* and *strangers* based on the variability of the great-call (or of other song phrases), but a playback study on *H. muelleri* produced a negative result (Mitani, 1985).

The 39 great-call variables of our study show a different range of variability on all four levels of variability used in our study. Additionally, MPD values appear to differ strongly among the various sections of a great-call and among the various levels of variability used in the present study (Fig. 6). For instance, variables describing the second great-call note (N2) and the pre-trill phase of the great-call exhibit very low values in the intra-individual analysis but very high values in all other variability levels. Some great-call sections, however, show less differences among the variability levels. For example, the variables of the first great-call note (N1) and variables covering more than one great-call section (Others) show almost uniformly high

MPDs, whereas variables describing the termination phase (Term) exhibit relatively low MPDs overall.

Mather (1992, p. 55) reported that the termination phase in *H. agilis* and *H. muelleri* was particularly variable and generally of low amplitude, and suggested that this part of the great-call was probably not under strong selective pressure. Haimoff (1983), referring to intra-individual variability, also noted that the termination phase of *H. moloch* great-calls was particularly variable in each individual. Dallmann & Geissmann (in press) found a high variability in the termination phase of *H. moloch*, as well. These authors used the *H*-values resulting from the Kruskal-Wallis one-way analysis of ranks as an estimate of the amount of variability. Their estimate closely corresponds to what is termed intra-population variability here. In the present study, however, the variables describing the termination phase (variables 38 and 39) show low MPDs on all levels (intra- and inter-individual, intra- and inter-population; Fig. 6). This does not correspond to the findings previously presented by Haimoff (1983) and Dallmann & Geissmann (in press).

The contradiction seems to originate in method and sample size. Whereas Haimoff (1983) presented no quantitative data to support his claim that the termination phase was particularly variable, Dallmann & Geissmann (in press) were using a method which is highly dependent on sample size, and their sample size is quite low compared to the number of great-calls and individuals analysed for the present study. These arguments make it reasonable to assume that the termination phase variables are less variable than proposed in earlier studies.

Overall, the great-call of female silvery gibbons appears to show low variability values on all levels during the introduction phase and during the termination phase, whereas the highest variability is exhibited during the first half of the great-call, especially on the first long note of the great-call. The second note and the pre-trill notes also show high variability when individuals are compared (be it from the same or from different populations), but not among great-calls of the same individual. It appears that variables describing the first part of the great-call are the best candidates in order to identify individuals. Whether or not silvery gibbons make use of this information remains to be demonstrated yet.

Our results support the hypothesis that different parts of the same individual's song may differ in their variability and, probably, in their function. As a result, some functions of gibbon singing behaviour could be masked from detection, if the gibbon song is studied as a unit only. Future functional studies may benefit from approaching different song parts separately.

This study also shows that populations of *H. moloch* differ in their great-calls. As a result, statistical analysis of great-call variables may be a valuable tool for conservation biologists. Once the amount of variability typical of different subspecies is established, it could be used to locate previously unrecognised subspecies boundaries in wild gibbons. If it is possible to find vocal key characteristics of various gibbon subspecies, subspecies identification would become easy and reliable. This would resolve one of the major problems in captive breeding of gibbons (Moore, 1986).

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