Chapter 6

Individual and Geographical Variability in the Songs of Wild Silvery Gibbons (*Hylobates Moloch*) on Java, Indonesia

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Introduction

The present study focuses on the great-call phrases of wild female silvery gibbons (*Hylobates moloch*). The aim of this study is to answer the following questions: (1) To what degree is great-call variability within a species useful for both individual and population identification? (2) Do vocal differences among local populations correspond to geographical distances or do they show evidence for genetic isolation among populations? (3) Can vocal data be used to test the validity of subspecific taxon boundaries suggested by previously reported genetic data?

Compared with bird vocalizations, primate vocalizations, in general, and inter-population differences in these vocalizations, in particular, are rarely analyzed (but see Green 1975; Hodun et al. 1981). As Hodun et al. (1981) point out, however, there are several good reasons for studying vocalizations in more than one population of a species. Firstly, vocal differences can be used to assess affiliations among taxa and to reconstruct their phylogenies, similar to the more frequently used morphological and molecular differences (Haimoff et al. 1982; Oates and Trocco 1983; Haimoff et al. 1984; Gautier 1988, 1989; Geissmann 1993; Macedonia and Stanger 1994; Stanger 1995; Geissmann 2002a; Takacs et al. 2005). Secondly, vocal differences can be used to estimate the degree of divergence between populations and the positions of taxonomic and biogeographic boundaries between populations, as suggested by studies on birds, tree frogs, and gibbons (Baker 1974, 1975; Ralin 1977; Konrad and Geissmann 2006). Unfortunately, most studies compare no more than two different samples (e.g., Maeda and Masataka 1987; Mitani et al. 1992; Arcady 1996; Fischer et al. 1998; Hafen 1998;

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Mitani et al. 1999), which makes it difficult to assess the relevance of the vocal differences.

The gibbons or small apes are distributed throughout the tropical rain forests of Southeast Asia (Chivers 1977; Marshall and Sugardjito 1986; Geissmann 1995). They usually live in socially monogamous territorial family groups typically consisting of an adult pair and 1–3 immature offspring (Chivers 1977; Leighton 1987; Chivers 2001). All species of gibbons are known to produce elaborate, loud, long and stereotyped patterns of vocalization often referred to as "songs" (Marshall and Marshall 1976; Haimoff 1984; Geissmann 1993, 1995, 2000). Typically, song bouts are produced in the early morning and last about 10–30 min. In most species, mated pairs utter their songs in the form of well-coordinated duets. In addition to duet song bouts, gibbons of the genus *Hylobates* also produce male solo songs. Female solo songs are common and duet songs are apparently absent in only two species (*Hylobates klossii* and *H. moloch*; Tenaza 1976; Kappeler 1981, 1984a; Geissmann 1993, 2002b; Geissmann and Nijman 2006). Due to the rarity of male singing in *H. moloch* (Kappeler 1981; Geissmann and Nijman 2006), adult females of this species appear to be the vocal "representative of the family" (Kappeler 1984b: 388).

In this study, we focus on the great-call, which has been identified as the most conspicuous and stereotyped phrase of the female song repertoire (Marshall and Marshall 1976; Geissmann 1995). In the silvery gibbon, a typical female song bout consists of several great-calls, which are usually introduced by series of so-called *wa*-phrases and single *wa*-notes (Geissmann 1993, 1995; Geissmann and Nijman 2006). Variability and syntax of the silvery gibbon male song is described elsewhere (Geissmann et al. 2005).

Species-specific song characteristics in gibbons are largely genetically determined (Brockelman and Schilling 1984; Geissmann 1984; Tenaza 1985; Marshall and Sugardjito 1986; Mather 1992; Geissmann 1993, 2000), which makes gibbon song vocalizations particularly suitable for the reconstruction of the phylogenetic relationships among species (Geissmann 2002a). The apparent lack of vocal learning constitutes a fundamental difference to songbirds, where vocal dialects of the song can be learned (Thorpe 1958; Nottebohm 1968; Marler 1970; Mundinger 1982; Slater 1986; Marler and Peters 1987; Catchpole and Slater 1995; Whaling 2000; Tchernichovski et al. 2001; Yamaguchi 2001). To date, there is no evidence that any vocal differences between gibbon populations are learned.

Although gibbon great-calls are remarkably stereotypic, they clearly exhibit some degree of variability, even within the same song bout (Kappeler 1981, 1984b; Dallmann and Geissmann 2001a, b). Although it has been reported that gibbon great-calls exhibit individual-specific characteristics (Kappeler 1981, 1984b; Haimoff and Gittins 1985; Haimoff and Tilson 1985; Mitani 1985), great-call variability has only been quantified for three species (*H. agilis*: Haimoff and Gittins 1985; *H. klossii*: Haimoff and Tilson 1985; *H. moloch*: Dallmann and Geissmann 2001a, b). In earlier studies on *H. moloch*, we demonstrated that inter-individual differences in most great-call variables are statistically significant (Dallmann and Geissmann 2001b). In addition, we found that inter-individual variability of great-calls is significantly higher than intra-individual variability. Furthermore, we demonstrated that variability is significantly lower within one population than among any two populations (Dallmann and Geissmann 2001a).

The silvery gibbon is endemic to Java (and is therefore also called the Javan gibbon). It occurs only in relatively few, isolated forest patches (Fig. 6.1). A viability analysis carried out in 1994 estimated that approximately 400 gibbons were left in Java (Gurmaya et al. 1994). In their most recent report, the IUCN Species Survival Commission (IUCN 2008) recognized the species as Endangered. Although we know now that the gibbon population in Java is much larger than 400 individuals (Asquith et al. 1995; Nijman 2004), the species is in any case more endangered than any species of great ape (Geissmann 2002c).

Although the silvery gibbon has traditionally been regarded as a monotypic species (Groves 1972; Marshall and Sugardjito 1986; Geissmann 1995; Groves 2001), a few recent publications recognize two distinct taxa: a western subspecies (*H. moloch moloch*) and a Central Javan subspecies (*H. moloch pongoalsoni*; Hilton-Taylor 2000; Supriatna and Wahyono 2000). Evidence for pronounced differences in great-call characteristics between any two of our sample sites could help to locate a possible subspecies boundary and thus be of importance in population management and conservation strategies for this species.

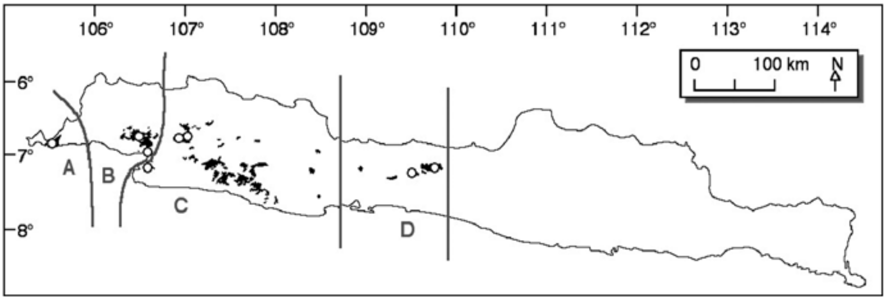

Fig. 6.1 Map of Java showing the forest areas inhabited by gibbons in *black* (gibbon distribution after Kappeler 1984a; Asquith et al. 1995; Nijman 1995; Andayani et al. 1998; V. Nijman pers. comm.). *Circles* indicate the localities where gibbon songs were recorded. *Gray bars* and letters indicate the major gibbon populations identified in this paper: A = Ujung Kulon complex (including localities Kalejetan and Tereleng); B = Gunung Halimun complex (including localities Pelabuhanratu and Gunung Halimun); C = Gunung Pangrango complex (including localities Ciletu, Cibodas, and NW-Gunung Pangrango); D = Central Java (including localities Gunung Lawét and Linggo Asri)

Methods

Study Animals

We analyzed a total of 373 great-calls from 38 different *H. moloch* females. Tape-recordings were carried out by Markus Kappeler in 1976 and 1978, one of us (TG) in September 1998, and Björn Merker in 2000. Tape-recording localities are shown in Fig. 6.1, and sample sizes (number of individuals and great-calls) are listed in Table 6.1. Tape-recordings from eight different localities were available for this study, covering most of the current distribution of the silvery gibbon. We divided our sample into four distinct populations by pooling localities in the same forest system or mountain complex; all populations are divided by major rivers (Table 6.1 and Fig. 6.1). These populations are (A) the Ujung Kulon complex (including localities Kalejetan and Tereleng); (B) the Gunung Halimun complex (including localities Pelabuhanratu and Gunung Halimun); (C) the Gunung Pangrango complex (including localities Ciletu, Cibodas, and NW-Gunung Pangrango); and (D) Central Java (including localities Gunung Lawét and Linggo Asri). All available great-calls were analyzed if the recording quality was good enough for analysis (i.e., depending on the amount of background noise and the distance of the calling animal).

Recording and Analysis Equipment

Field recordings were made with a SONY WM–D6C cassette recorder and a JVC MZ–707 directional microphone by T. Geissmann, with a UHER REPORT 4200 tape recorder and a NIVICO IVC directional microphone by M. Kappeler, and with a SONY TDC-D8 DAT recorder and two SONY electret condenser ECM 150 microphones with plastic parabolic reflectors by B. Merker.

The recordings were digitized with a sample rate of 11 kHz and a sample size of 16 bits. Time versus frequency displays (sonograms) of the sound material were generated using the Canary version 1.2.4 on a Power Macintosh G3 (Charif et al. 1995). The FFT size of the sonograms was 2048 points with an overlap of 75% and a frame length of 1024 points (time resolution = 11.5 msec, frequency resolution = 5.371 Hz).

Acoustic Analysis

The female song bout of *H. moloch* consists mainly of two different acoustic components: (1) great-call phrases, which are uttered at intervals of about two minutes, and (2) single *wa*-notes and phrases of *wa*-notes, which are produced before, after, and between the great-calls. Whereas *wa*-phrases are of variable

Table 6.1 Origin, number of individuals, number of great-calls per locality, and individual and recording information of the sound material analyzed in this study

			Number of great-calls		Number of song-bouts	
Population	Locality* (abbreviation)	*N* (individuals)	Total	Median (range) calls/ individual	Total	Median (range) bouts/individual
A	Kalejetan[1] (*ka*)	9	100	9 (3–26)	11	1(1–2)
	Tereleng[1] (*te*)	3	14	3 (2–9)	3	1
B	Gn. Halimun[5] (*ha*)	6	43	5.5 (3–15)	7	1(1–2)
	Pelabuhanratu[2] (*pe*)	1	10	10	1	2
C	Cibodas[2] (*cb*)	1	12	12	1	1
	Ciletu[3] (*ci*)	2	3	1.5 (1–2)	2	1
	Gn. Pangrango[3] (*pa*)	3	67	30 (5–32)	3	1
D	Gunung Lawét[2] (*la*)	2	3	1.5 (1–2)	1	1
	Linggo Asri, Dieng[4] (*as*)	11	121	6 (2–37)	20	1(1–5)
Total		38	373	6 (1–37)	49	1(1–5)

*Code to sources of tape-recordings: [1]Markus Kappeler (1976); [2]Markus Kappeler (1978); [3]Marshall and Marshall (1976); [4]Thomas Geissmann (1998); [5]Björn Merker (2000).

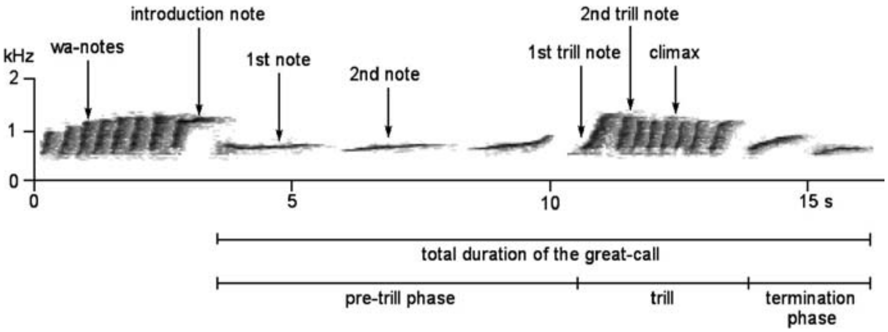

Fig. 6.2 Sonogram of a great-call phrase produced by a female silvery gibbon, illustrating the three main phases (i.e., pretrill phase, trill phase, and termination phase), which are typical features of this species' great-calls, and some of the variables measured

organization even within the same song bout, great-call phrases are highly stereotypic and species-specific (Kappeler 1981; Haimoff 1984; Kappeler 1984b; Dallmann and Geissmann 2001a). Like most previous studies on songs of female gibbons, we analyze the great-call exclusively because it is the longest and most standardized part of the female's song repertoire (Haimoff and Gittins 1985; Haimoff and Tilson 1985). Figure 6.2 shows a sonogram of a typical great-call phrase of a female silvery gibbon. The great-call is usually about 15 s in duration and the fundamental frequency ranges between 0.5 and 1.5 kHz. The great-call can be divided into three main parts: (1) a slow pre-trill phase with long howling notes, (2) an accelerando-decelerando of *wa*-notes that is commonly named a trill, and, finally, (3) a termination phase, during which notes slow down in speed and frequency. In order to quantify acoustic characteristics of the great-call, we defined 39 variables, as defined in Table 6.2.

Table 6.2 Descriptions of the variables analyzed in this study

No.	Variable (Unit)	Description
1	Total great-call duration (s)	Time interval between start of the 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

Table 6.2 (continued)

No.	Variable (Unit)		Description
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
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

Table 6.2 (continued)

No.	Variable (Unit)	Description
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

Statistics

All data for each variable were standardized with a mean of 0 and a standard deviation of 1 in order to allow comparison of the variability among variables and individuals. Because our variables were highly correlated, we conducted a factor analysis, and all subsequent statistics were performed with the principle components derived from this procedure. We discarded all factors with an eigenvalue below one, and hence retained 10 factors, which explained 84.2% of the total variation. On the retained components, the highest-loaded variables were as follows: Factor 1 (Variable 7), Factor 2 (Variable 21), Factor 3 (Variable 32), Factor 4 (Variable 39) Factor 5 (Variable 26), Factor 6 (Variable 11), Factor 7 (Variable 28), Factor 8 (Variable 14), Factor 9 (Variable 36), and Factor 10 (Variable 17). All retained factor loadings were above 0.8.

Differences within and between individuals were analyzed using cluster analysis and multidimensional scaling, described in Sneath and Sokal (1973) and Guttman (1968), respectively. Cluster analysis was carried out using unweighted pair group average linking with squared Euclidean distances.

The aim of multidimensional scaling (MDS) is to build, in a small dimensional space, a pictorial mapping of the distances (or dissimilarities) of a group of objects. To build an optimal representation, the MDS algorithm minimizes a criterion called stress or distortion. The closer the stress is to zero, the better the representation. Each dimension (scale) represents a separate bipolar standard of comparison. The similarity matrix for our MDS analysis was also computed using squared Euclidean distances. The starting configuration for MDS was Guttman-Lingoes and two was chosen as the number of dimensions.

Finally, discriminant function analyses were conducted to compare the quality of different a priori classifications of our populations. This type of analysis automatically determines some optimal combination of variables so that the first function provides the most overall discrimination between groups; the second provides the second most, and so on. The functions are independent; that is, their contributions to the discrimination between groups will not overlap. Computationally, the analysis performs a canonical correlation analysis that will determine the successive functions and canonical roots (the term root refers to the eigenvalues that are associated with the respective canonical function). The models derived from this analysis have been cross-validated.

The three different statistical methods mentioned above were used to first reveal intra- and inter-individual differences (cluster analyses) and, second, to determine the amount of difference within the populations (MDS). Finally, we tested our data set for the proposed existence of two subspecies. Here, we used discriminant analyses because of the necessary a priori assumption of two subspecies, which could not be incorporated using the first two methods.

Statistical analyses were performed on a Windows PC using the STATISTICA (Kernel 5.1) software. All procedures were carried out according to the STATISTICA manual (StatSoft Inc. 1998).

Results

To illustrate the variability of the great calls, Fig. 6.3 shows the representative examples of two great-calls from one individual (a), a second individual from the same population (b), and individuals from all other populations (c–e).

Variability Within and Between Individuals

In Fig. 6.4, a tree plot of a cluster analysis using 53 great-calls from 7 different females from Gunung Halimun (population B) is shown. In this analysis, 47 great-calls (88.7%) fall into individual-specific clusters; only five great-calls (four of female *pe* and one of female *ha2*) fall into other clusters. This shows that similarity among great-calls of the same individual is higher than that among the great-calls of different individuals, suggesting that individual females can be distinguished by their great-calls.

Cluster analysis of great-calls of the other gibbon populations (A, C and D) produced similar results. Individual-specific clusters were found in 97 of 114 great-calls (85.1%) of population A, in 79 of 82 great-calls (96.3%) of population C, and in 106 of 124 great calls (85.5%) of population D. Individual differences in all time and frequency variables are larger than the respective time and frequency resolutions of our sonograms.

The results of the multidimensional scaling for the whole data set are shown in Fig. 6.5. Each dot represents one great-call. Calls by each individual form more or less well-defined clusters that are surrounded in the figure by the minimum polygons. Polygon overlap between individuals varies. In the plot for the population from Gunung Halimun (Fig. 6.5b), for example, only the

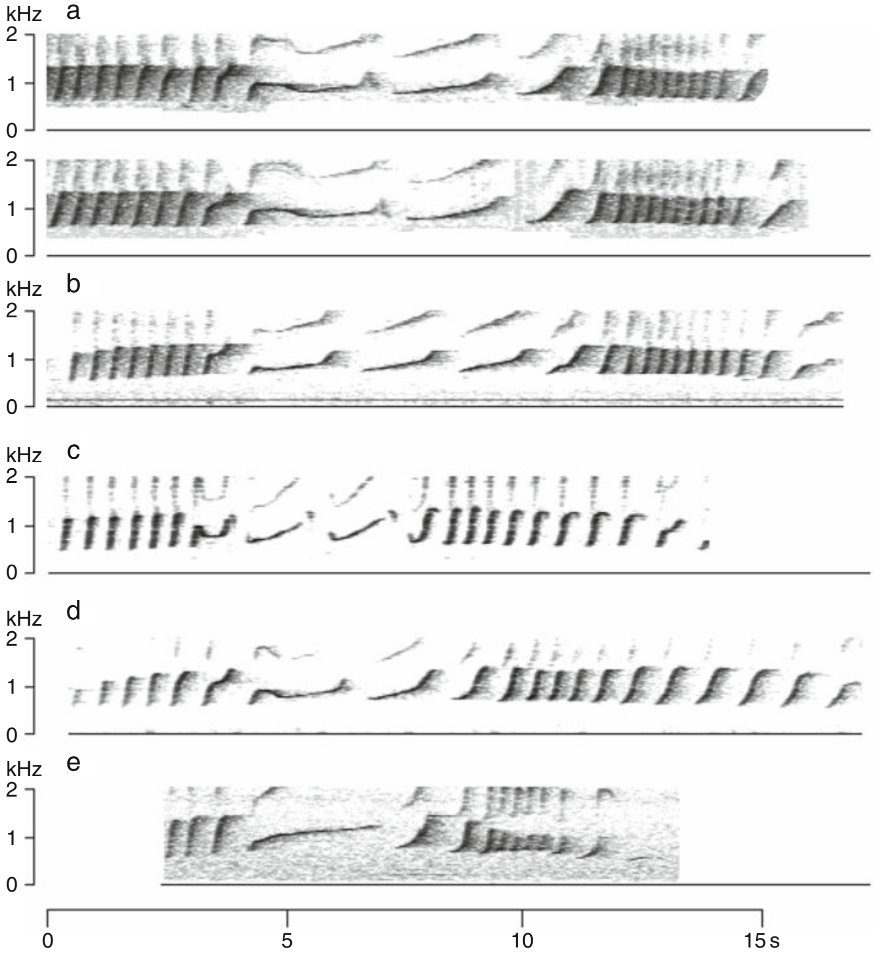

Fig. 6.3 Representative *Hylobates moloch* great-calls: (**a**) two calls of the same individual (*ka2*) from population A, (**b**) call of a different individual (*ka8*) from the same population, and (**c–e**) one call each of a female from populations B (*pe1*), C (*ci1*), and D (*as10*), respectively

polygons of two individuals (*ha1* and *ha6*) show some overlap, which, moreover, includes only one great-call of each individual. In the females from the Gunung Pangrango complex (Fig. 6.5c), overlap is slightly higher, and the females from Kalejetan (Fig. 6.5a) and Linggo Asri (Fig. 6.5d) show even more overlap. In many cases, overlap results from outliers of the respective cluster of dots. This is particularly obvious in Fig. 6.5c, where a single great-call of female *pa2* is solely responsible for the extensive polygon overlap between *pa1* and *pa2*. Similarly, in Fig. 6.5d, the overlap between *as1* and *as2* mostly results from one outlier in the *as2* cluster. We assume that these outliers are

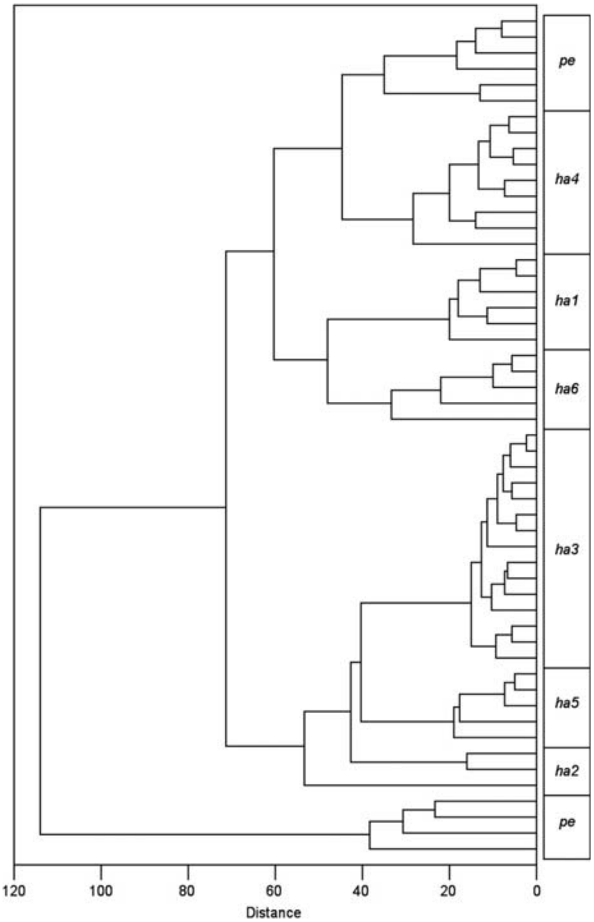

Fig. 6.4 Cluster analysis of seven individuals from the Gunung Halimun population (population B). Each terminal branch represents one of 53 great-calls. Branch length is plotted as squared Euclidian distance

atypical great-calls. Individuals do occasionally produce atypical calls within otherwise typical song bouts. The reasons why they do so are unknown. Our impression is that sometimes, in the middle of a great-call, a gibbon may suddenly become aware of a neighboring call, and while trying to make out what and where the other gibbon is calling, the singer may sometimes draw out one note or one interval of the great-call longer than usual. It is also our impression that great-calls may require a great deal of energy from the singer and that occasionally individuals sound as if they had a throat problem in the middle of a great-call.

As demonstrated by these results, individual females can be fairly well distinguished by the great-call variables measured in the present study.

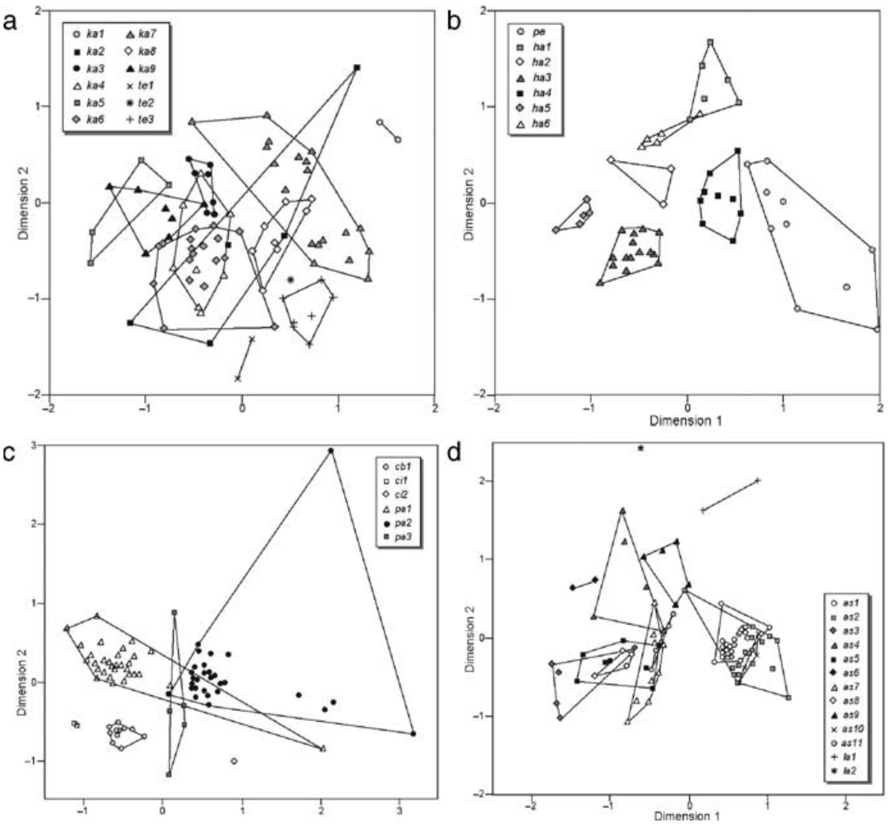

Fig. 6.5 Multidimensional scaling analysis of all 373 great-calls from all populations. Each *dot* represents a single great-call. Different individuals are identified by different symbol shapes. (**a**) Population A (*ka* = Kalejetan, *te* = Tereleng), (**b**) Population B (*ha* = Gunung Halimun, *pe* = Pelabuhanratu), (**c**) Population C (*cb* = Cibodas, *ci* = Ciletu, *pa* = Gunung Pangrango), Population D (*as* = Linggo Asri, *la* = Gunung Lawét)

Variability Between Populations

The results of the discriminant analyses are shown in Table 6.3. Our total sample of 373 great-calls was randomly divided into two subsets of about equal size (with subset *a* consisting of 187 great-calls, and *b* of 186 great-calls). Using subset *a* in a first run of the discriminant analysis, 88.2% of the great-calls were correctly assigned to their respective population (Table 6.3a). In order to validate the calculated model equation, we used the discriminating function to classify the second subset *b*. Here, 83.3% of all great-calls were correctly assigned (Table 6.3b).

Figure 6.6 shows a plot of the two best separating roots computed in the discriminant analysis. In this analysis, Root 1 is most strongly correlated

Table 6.3 Results of discriminant analyses for populations using all individual great-calls. The data were randomly split in two subsets of about equal size: (a) which served to determine the discriminant function (learning sample), and (b) which served to evaluate the derived function (test sample); n = number of great-calls

	Great-calls assigned to					
	A	B	C	D	% correctly assigned great-calls	Total great-calls
Subset (a)						
A	53	1	3	0	93.0	57
B	0	24	3	0	88.9	27
C	7	0	34	0	82.9	41
D	3	3	2	54	87.1	62
Total	**63**	**28**	**42**	**54**	**88.2**	**187**
Subset (b)						
A	53	3	1	0	81.2	57
B	0	24	2	0	80.0	26
C	8	2	31	0	70.7	41
D	3	4	1	54	85.5	62
Total	**64**	**33**	**35**	**54**	**83.3**	**186**

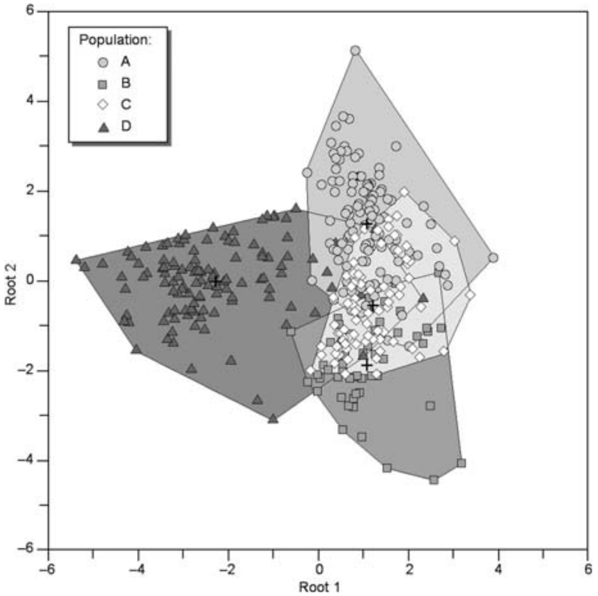

Fig. 6.6 Discriminant analysis of all great-call data. Each dot represents a single great-call. Different populations are identified by different symbol shapes, and population clusters are surrounded by minimum polygons. Heavy crosses identify population centroids. For a definition of "roots" see the Methods section. Populations are: A = Ujung Kulon complex (including localities Kalejetan and Tereleng); B = Gunung Halimun complex (including localities Pelabuhanratu and Gunung Halimun); C = Gunung Pangrango complex (including localities Ciletu, Cibodas, and NW-Gunung Pangrango); D = Central Java (including localities Gunung Lawét and Linggo Asri)

(r= –0.43) with Factor 1 (highest loading: Variable 7), whereas Root 2 is most strongly correlated (r = 0.44) with Factor 7 (highest loading: Variable 28). Each population forms a clearly distinguishable cluster, with the exception of the population from the Gunung Pangrango complex (C), which almost completely overlaps with the other clusters. In West Java, at least, the distances between the clusters do not appear to correspond to the geographical distances between the populations. In the discriminant analysis, the gibbons from Gunung Pangrango (C) take an intermediate position between those of Ujung Kulon (A) and those from the Gunung Halimun complex (B). As shown in Fig. 6.1, this arrangement clearly inverses the actual geographical relationships among the three populations.

To test whether uneven sample sizes for each individual influenced our results, we repeated the discriminant analysis using only mean values for each individual instead of every great-call. The results of this procedure are identical to those described above, and the relationships of the populations in the plot remain as those shown in Fig. 6.6.

We also do not think that the differences we found are due to the recording equipment, because more than one set of recording equipment was used in most populations and none of our analyses group the individuals according to recording equipment. In addition, the two populations (C and D) that were sampled, in part, using the same equipment do not exhibit any particular affinities (Fig. 6.6). Instead, C exhibits the most similarities to A, judging by the number of incorrectly assigned great-calls in the discriminant analyses (Table 6.3).

Possible Taxonomic Boundary

In a discriminant analysis comparing two clusters of gibbon populations corresponding to those proposed by Andayani et al. (2001) (i.e., comparing populations A and B *vs*. C and D), 81.6% of the great-calls of our study animals are correctly assigned to their respective clusters. If the same analysis is repeated comparing two clusters corresponding with biogeographic groupings found in other taxa (Brandon-Jones 1995a, b, 1996; i.e., comparing populations A, B, and C vs. D), we obtain a better separation: in this case, 97.4% of all great-calls are correctly assigned to their respective clusters. Table 6.4 shows the results of this discriminant analysis in more detail.

Discussion

Sody (1949) first described "*Hylobates lar pongoalsoni*" as a gibbon subspecies which occurred in Central Java and which differed from West Javan gibbons in fur coloration. These differences were, however, not confirmed in later studies (Groves 1972; Kappeler 1981), and no subspecies of *H. moloch* have been

Table 6.4 Results of discriminant analyses comparing two different locations of a hypothetical subspecies boundary: (a) boundary located between populations B and C, and (b) boundary located between populations C and D

	Great-calls assigned to			
(a)	A & B	C & D	% correctly assigned great-calls	Total great-calls
A & B	145	22	86.8	167
C & D	27	179	86.9	206
Total	172	201	**86.9**	373
(b)	A & B & C	D		
A & B & C	249	0	100.0	249
D	18	106	85.5	124
Total	267	106	**95.2**	373

recognized in any revisions of gibbon systematics in the past 30 years (e.g., Groves 1972; Marshall and Sugardjito 1986; Geissmann 1995; Groves 2001).

Recent studies comparing mitochondrial DNA sequences of captive silvery gibbons suggested the presence of two genetically distinct lineages: a “western” lineage represented by the gibbons of the Gunung Halimun complex, and a “central” lineage comprising all populations east of the Gunung Halimun complex, including gibbons of the Gunung Pangrango complex and of Central Java (Andayani et al. 1998; Supriatna et al. 1999; Andayani et al. 2001). Apparently based on these reports, several authors appear to recognize two subspecies of *H. moloch* (Hilton-Taylor 2000; Supriatna and Wahyono 2000), although subspecies are not explicitly mentioned in the molecular studies cited above.

Interestingly, the border between the two genetically differentiated lineages was reported to be located between two neighboring mountain complexes, the Gunung Halimun and Gunung Pangrango, which both are situated in West Java (Andayani et al. 2001). This would correspond to the genetic boundary between populations B and C in Fig. 6.1.

A comparison with other Javan mammals suggests, however, that a more likely biogeographical boundary is located between West and Central Java, not in West Java. This boundary appears to be located somewhere between the Gunung Pangrango complex and the Gunung Lawét (i.e., between populations C and D on our map, Fig. 6.1). A similar location of taxonomic boundaries reportedly occurs in other Javanese primates, such as *Trachypithecus auratus* (separating the subspecies *T. a. auratus* and *T. a. mauritius*) and *Presbytis comata* (separating the subspecies *P. c. comata* and *P. c. fredericae*; Brandon-Jones 1995a, b, 1996; Groves 2001). Incidentally, the specimen localities that Sody (1949) mentioned for his two silvery gibbon subspecies suggest exactly such a location of the subspecies boundary.

Molecular and biogeographic data thus provide conflicting evidence on the location of the hypothetical subspecies boundary. Based on vocal evidence, we suggest that if two subspecies exist, the boundary between them is located somewhere between the Pangrango complex and Central Java, as indicated by independent biogeographic evidence, and not between the Pangrango and the Halimun complex, as suggested by Andayani et al. (1998, 2001) and Supriatna et al. (1999).

Our study includes a median of 9.5 individuals per population (range 6–13 individuals), and a median of 98 calls per population (range 53–124 calls, see Table 6.1). This may be one of the largest studies on wild gibbon calls of a single species ever published. Comparable molecular studies on gibbons usually work with much smaller samples of about 1–5 individuals per species (Garza and Woodruff 1992; Hayashi et al. 1995; Hall et al. 1998; Roos and Geissmann 2001), and the largest DNA study on any single gibbon species with the same goal as ours (Andayani et al. 2001) used data from 31 captive Javan gibbons. In comparison, we sampled 38 wild gibbons with exact locality information. Because of the highly stereotyped structure of the gibbon great-calls we studied (Dallmann and Geissmann 2001a, b), these sample sizes should be adequate to accurately represent each individual and population.

It should be stressed that we do not make any statements as to whether subspecies do exist in *Hylobates moloch* or not. Our results offer no conclusive evidence on that question, because we have no comparative data that allow us to decide how large the "vocal distance" should be in order to qualify as evidence for a subspecies difference.

Conclusions

First, we show that individuals can be distinguished by their great-calls. In addition, some, but not all, populations can be distinguished by their great-calls. Vocal distances between populations, however, are not consistent with geographical distances. Our results suggest that if two gibbon subspecies exist on Java, the boundary between them is located somewhere between West and Central Java, and not in West Java, as suggested by molecular evidence.

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