Chapter 4
Vocal Diversity of Kloss's Gibbons (*Hylobates Klossii*) in the Mentawai Islands, Indonesia

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Introduction

Gibbons (family Hylobatidae) are generally described as monogamous, frugivorous, arboreal, and territorial apes and inhabit tropical and subtropical forests of South and Southeast Asia (Marshall and Sugardjito 1986; Leighton 1987; Chivers 2001; Geissmann 2003). All gibbon species 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, 2002b, 2003). Generally, song bouts are produced in the early morning and last approximately 10–30 min. Species-specific song characteristics in gibbons are thought to have a strong genetic component (Brockelman and Schilling 1984; Geissmann 1984; Tenaza 1985; Marshall and Sugardjito 1986; Mather 1992; Geissmann 1993). It has previously been demonstrated that gibbon song characteristics are useful for assessing systematic relationships on the level of the gibbon genus, species and local population, and for reconstructing gibbon phylogeny (Haimoff et al. 1982; Haimoff 1983; Creel and Preuschoft 1984; Haimoff et al. 1984; Marshall et al. 1984; Geissmann 1993, 2002a, b; Konrad and Geissmann 2006; Dallmann and Geissmann this volume).

The Kloss's gibbon (*Hylobates klossii*) is endemic to the Mentawai Islands (Fig. 4.1), which lie 85–135 km off the west coast of central Sumatra in Indonesia (Whitten 1982). The species is sexually monochromatic, with a black pelage and skin color (Geissmann 1995). Kloss's gibbons produce male solo song bouts, which usually occur in the pre-dawn hours, and female solo song bouts, which occur post-dawn (Tenaza 1976; Whitten 1980, 1982, 1984a, b; Haimoff and Tilson 1985). This species is unusual among gibbons because mated pairs do not duet. The lack of duets and the temporal segregation of male and female songs are derived features shared only with Javan

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Fig. 4.1 Map of the Mentawai Islands showing location of study sites. Inset map: location of the Mentawai Islands in Southeast Asia

silvery gibbons (*H. moloch*) (Geissmann 1993, 2002b) and suggest a sister taxon relationship of these two species (Geissmann 2002a, b). This finding was recently supported by molecular data (Takacs et al. 2005; Whittaker et al. 2007).

The Mentawai Islands contain high levels of endemism and have been separated from the mainland for at least 500,000 years (Batchelor 1979). Four nonhuman primates are endemic to the Mentawai Islands: the Kloss's gibbon, the Mentawai macaque (*Macaca pagensis*), the Mentawai langur (*Presbytis potenziani*), and the pig-tailed langur or simakobu (*Simias concolor*). For each primate except the Kloss's gibbon, one subspecies is described as being endemic to the northernmost island of Siberut, and a second subspecies is described as being distributed across the three remaining islands of Sipora, North Pagai, and South Pagai (Chasen and Kloss 1927; Groves 2001; Roos et al. 2003).

The fact that the other three primates all exhibit taxonomic separations at the same boundary suggests that an analogous taxonomic organization could occur in the sympatric Kloss's gibbon. Moreover, many Old World monkeys including macaques and several species of leaf monkeys are known to enter water while foraging and traveling (Kawai 1965; Kawabe and Mano 1972; Kurland 1973; Zeeve 1985; Bennett and Sebastian 1988; Watanabe 1989; Steenbeek 1999; Agoramoorthy et al. 2000; Boonratana 2000; Dudgeon 2000; Pfeyffers 2000; Nikolei 2003). In contrast, wild gibbons have not been reported to enter water. Even shallow moats can prevent zoo gibbons kept on islands from escaping (Delacour 1961; Dathe 1972), and the distribution ranges of different gibbon taxa are often separated by rivers (Parsons 1940; Morris 1943; Marshall and Sugardjito 1986). As a result, the separation between Siberut and the remaining Mentawai islands may present a more serious distribution barrier for gibbons than for macaques and leaf monkeys. Consequently, the gibbon should be the Mentawai primate most likely to have diverged on Siberut and the southern islands.

Originally, the taxonomic distinction between the monkeys of Siberut and those of the three remaining islands was proposed based on differences in fur coloration, specifically darker coloration for Siberut subspecies (Chasen and Kloss 1927; Groves 2001). However, the pelt of the Kloss's gibbon is completely black and, therefore, does not offer any visual cues by which subspecies can be distinguished. Analyses of mitochondrial DNA sequences failed to find evidence for the occurrence of more than one taxon within Kloss's gibbons; however, the small sample size that led to this conclusion means it warrants further investigation (Whittaker 2005a, this volume).

In order to further examine the subspecific taxonomy of Kloss's gibbons, the present study spectrographically and statistically analyzed vocal data from male and female Kloss's gibbons to assess interpopulation diversity. We compared the vocal diversity of wild Kloss's gibbons at four localities (two on Siberut and one each on Sipora and South Pagai) to assess whether vocal differences among populations indicate the occurrence of a distinct subspecies on Siberut, correspond to geographic distance or follow any other recognizable pattern. If the data suggest the existence of more than one taxon, there will be implications for conservation strategies. The Kloss's gibbon is an endangered species with an estimated total population size of 20,000–25,000 individuals (Whittaker 2005b). Currently, only one substantial protected area, Siberut National Park, exists within the range of Kloss's gibbons. Detection of a second taxon on the remaining three islands would indicate a need for the establishment of a second protected area on one of these islands.

Materials and Methods

Field Methods

The gibbon songs included in the present study were recorded by SAK and MSW in four different localities on the Mentawai Islands in 2005. The localities are mapped in Fig. 4.1; coordinates and recording dates are listed in Table 4.1. Field site selection was based on accessibility, the presence of gibbons, and recommendations of previous researchers (Paciulli 2004; Whittaker 2005a). On Siberut, where we sampled more than one population, we selected sites that

Table 4.1 List of field sites where Kloss's gibbons were recorded, with coordinates and recording dates

Locality	Coordinates	Survey and recording date
Simabuggai, Siberut National Park, central Siberut Island	01°22'30.6"S, 098°56'35.2"E	05–14 June 2005
Sikabei, southern Siberut Island	01°37'04.3"S, 099°15'41.5"E	03–14 July 2005
Saureinu, Sipora Island	02°07'15.5"S, 099°38'04.1"E	07–19 August 2005
Malakopa logging concession, South Pagai Island	02°58'00.9"S, 100°17'15.5"E	19–30 July 2005

were >20 km apart to ensure that different populations were sampled. Three to six listening posts were used per study site.

Data Collection

Vocalizations were recorded with a Sony TCM-450DV cassette recorder and a Sennheiser ME66 short directional microphone. The tape recordings were digitized with a sampling rate of 44.1 kHz and a sample size of 16 bits. Sonograms (time versus frequency displays) of the sound material were generated using the Raven version 1.2.1 software (Cornell Laboratory of Ornithology). The sonograms were computed by *Fast-Fourier-Transformation* (FFT). The FFT size of the sonograms was 512 points, using the window function = Hann and a 3dB filter bandwidth of 124 Hz. The time resolution was 256 points with an overlap of 50%, the frequency resolution was 512 points with a frequency grid spacing of 86.1 Hz (Charif et al. 2004).

The variables that were used to measure the great call and the male trill phrase are described in detail in the Appendix.

Kloss's Gibbon Song Structure

The acoustic terminology used in the present study largely follows that proposed by Haimoff (1984). The most relevant terms for the present study are defined below. A *note* is any single continuous sound of any distinct frequency or frequency modulation, which may be produced during either inhalation or exhalation. A *phrase* is a single vocal activity consisting of a larger or looser collection of notes. These parts may be produced together or separately. A *great call* is the most stereotyped and most easily identifiable phrase of the gibbon song, produced by the adult females of all gibbon species. A *song* is "a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time." (Thorpe 1961: p. 15). A *song bout* is all song notes of a gibbon group separated by periods of silence of less than 10 min. A *solo song bout* is a song bout produced by one individual (male or female) alone.

Male Song Structure

A male song bout exhibits a progressive elaboration of call structure from simple notes to more complex phrases. Roughly, the following three stages can be identified: (1) the song bout starts with single "hoo" notes and progresses to short phrases with simple "hoo's"; this stage lasts up to 25 min; (2) the second stage is composed of longer phrases of "hoo" note combinations; and (3) the progression stabilizes with fully developed phrases that exhibit a trill (called trill phrases in the following text). Trill phrases consist of an initial pre-trill, a trill, and a final post-trill part (Fig. 4.2a).

Female Song Structure

The song structure of female Kloss's gibbons consists of an introductory sequence of single-frequency build-up notes, followed by repeated great call phrases. Similar to fully developed male trill phrases, each complete great call phrase consists of an initial pre-trill, a trill, and concluding post-trill phase (Fig. 4.2b). The male trill phrases are much shorter (5–14 s), however, than female great call phrases (22–39 s).

The great call phrase begins with the pre-trill part encompassing a single rising note, followed by single-frequency notes. The trill part consists of rapid notes for a period of approximately 8–12 s. The post-trill part has notes that gradually increase in duration while decreasing in frequency and amplitude. The entire great call usually lasts in the region of 20–30 s. In this study only the first two parts of the great call were analyzed because post-trill notes were often lost from recordings due to inaudibility.

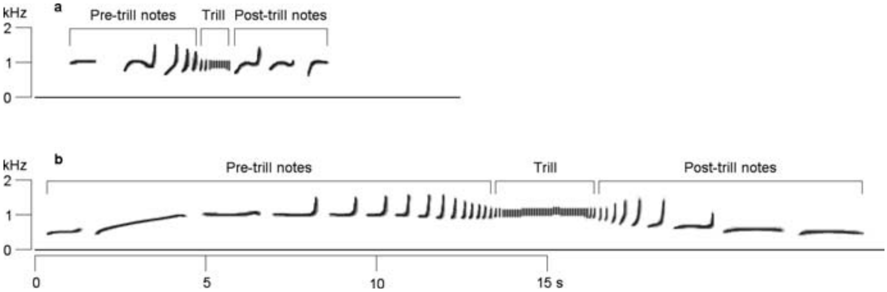

Fig. 4.2 Stylized sonograms of male and female song phrases. (**a**) fully expressed male trill phrase from the stable part of the male solo song. (**b**) female great call phrase

Sample Size of Tape-Recorded Gibbon Songs

We analyzed a total of 137 great call phrases from 24 different females (mean ± SD; 5.7±2.0, range 3–11 great calls per female) and 224 trill phrases from 27 different males (8.3±6.1, range 2–21 phrases per male). All songs are from wild, non-habituated gibbons.

As the actual distribution of the group territories was unknown and the gibbon groups or individuals were generally out of sight while being recorded, we deduced the identity of the tape-recorded individuals from indicators such as position of the singer, simultaneous singing of distinct groups, group composition (e.g., number of singers), or individual vocal characteristics. When in doubt

Table 4.2 The number of song bouts recorded and analyzed at each locality for male and female Kloss's gibbons

	Individual		Song bouts analyzed		Song phrases recorded		Song phrases analyzed	
Location	Female	Male	Female	Male	Female	Male	Female	Male
Central Siberut, Simabuggai	1	1	1	1	7	23	7	20
	2	2	1	1	7	8	7	8
	3	3	1	1	7	8	7	5
	4	4	1	1	5	8	4	8
	5	5	1	1	4	4	4	4
	6	6	1	1	4	6	4	5
	7	7	1	1	5	4	4	4
Southern Siberut, Sikabei	1	1	1	1	6	22	6	21
	2	2	1	1	7	8	6	2
	3	3	1	1	8	2	3	2
	4	4	1	1	5	13	5	9
	5	5	1	1	6	12	6	11
	6	6	1	1	5	5	5	4
	7	7	1	1	9	4	9	4
		8		1		22		19
Sipora, Saureinu	1	1	1	2	9	9	9	6
	2	2	1	1	11	21	11	18
	3	3	1	1	6	19	6	5
	4	4	1	1	6	13	5	13
	5	5	1	1	6	17	6	6
		6		1		9		6
		7		1		8		7
South Pagai, Malakopa	1	1	1	2	10	22	7	21
	2	2	1	1	4	21	3	5
	3	3	1	1	3	10	3	4
	4	4	1	1	7	4	6	4
	5	5	1	1	6	7	4	3
Total	24	27	24	29	153	309	137	224

about whether two recorded songs were produced by the same gibbon or by two distinct gibbons, we excluded the recording of inferior sound quality from the analysis. Table 4.2 lists the number of gibbons recorded at each locality whose recorded songs were found to be suitable for analysis.

Acoustic Analysis

In order to quantify acoustic characteristics of the male and the female phrases, we defined 31 variables with structural parameters consisting of note counts and the frequency or time dimensions (19 for male and 12 for female phrases), which we determined from the sonograms of each phrase. The variables are listed in the Appendix.

Statistical Analysis

All statistical analyses were conducted using the statistical software package SPSS 12.0.1. Data from each female were paired with data from the male that was believed to be of the same group, based on corresponding calling localities. Although there is no guarantee that all pairs were correctly matched, perfect matching is not required to determine the vocal affinities of the four gibbon populations. For three of the 27 study males, songs of the (assumed) female partner could not be recorded in sufficient quality for inclusion in our analyses. Most multivariate statistical analyses cannot be conducted on data sets with a missing value. Therefore, the missing values in the data matrix were replaced by the overall mean for that particular song variable to allow for inclusion of the complete sample (i.e., all 27 assumed gibbon pairs).

Discriminant Function Analysis

We used stepwise discriminant function analysis (DFA) to identify the differences between vocalizations from our four study populations (i.e., central Siberut, southern Siberut, Sipora, and South Pagai). This multivariate method allows the study of group differences with respect to several variables simultaneously. Redundancy among the independent variables is avoided by a tolerance test, which measures the degree of linear association between variables. Variables determined to be redundant are then excluded from the analysis. For the stepwise procedure we determined Wilks' Lambda as the criterion for variable selection. To test the significance of the change in the selection criterion when a variable was entered or removed from the model, we used the probability of F with *p-to-enter* = 0.05 and *p-to-remove* = 0.10. This allowed us to screen out variables that were less efficient discriminators and to identify the combination of song features that best discriminated among the study populations. Based on these selected variables, three linear functions (discriminant functions) were formed – one fewer than the number of groups (i.e., study populations). These functions in turn were used for the classification procedure that assigned each gibbon group to its appropriate population (correct assignment) or to another population (incorrect assignment). We used the percentage of correct assignments as an indicator of how reliably a population could be discriminated, and calculated Cohen's κ to test whether the resulting classification significantly differed from chance (Siegel and Castellan 1998). The model derived from this analysis was cross-validated by the *leaving-one-out method* (Norusis 1994). This method involves leaving out each of the cases in turn, calculating the functions based on the remaining *n–1* cases, and then classifying the left-out case.

Multidimensional Scaling

We used multidimensional scaling (MDS) with ALSCAL and Euclidean distances to visualize (and further analyze) the vocal similarities or dissimilarities (distances) between the recorded gibbon groups and populations. Variables were standardized on a scale of 0–1. MDS plots are better suited to visualize multivariate relationships in two-dimensional plots than discriminant functions, because the resulting plots exhibit a much lower degree of distortion (Sneath and Sokol 1973; Manly 1994). Therefore, we used MDS plots in order to estimate "vocal distances" among gibbon populations.

Results

Figures 4.3 and 4.4 show representative sonograms of male trill phrases and female great call phrases, respectively. Calls of two individuals from each locality are shown in order to exemplify the variability occurring among localities. Two calls from one selected gibbon are also included in each figure in order to depict intra-individual variability.

Discriminant Function Analysis

The discriminant function analysis model used 8 out of 31 submitted variables to create three functions. Seven of them describe the male song (Variables 2, 3, 5, 8, 13, 18, 19), and one describes the female song (Variable 31). This subset of variables was most efficient in distinguishing among the songs of the four gibbon populations. The standardized canonical discriminant function

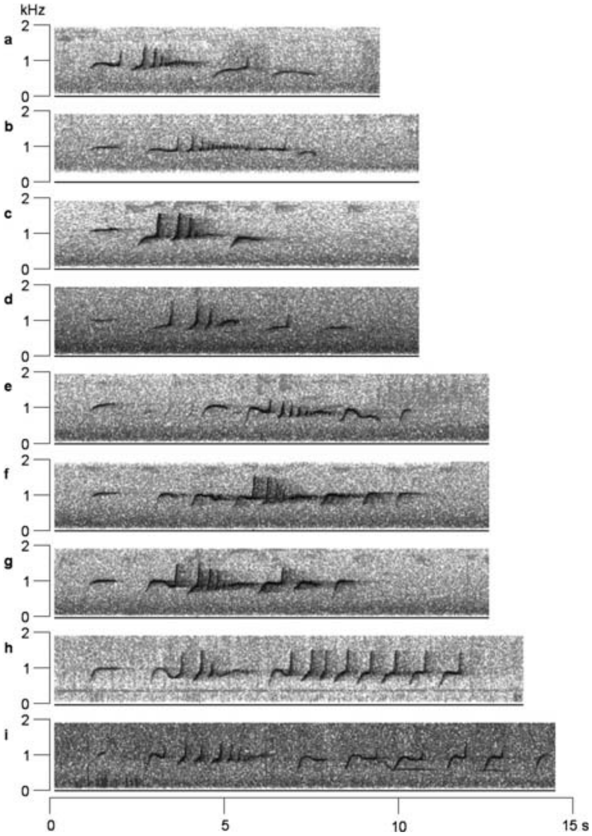

Fig. 4.3 Sonograms of male trill phrases, including two different males from each recording locality: (**a**) and (**b**) central Siberut; (**c**) and (**d**) southern Siberut; (**e–g**) Sipora; and (**h**) and (**i**) South Pagai. Sonograms (**f**) and (**g**) are from the same male in order to show individual variability

coefficients (listed in Table 4.3) of these key variables estimate the relative contribution of a given variable to the three discriminant functions, i.e., the reclassification of gibbon groups into populations. High absolute values represent a large relative contribution.

The discriminant functions represent differing percentages of variance in the populations and, therefore, differing amounts of discriminatory power. The first function normally has the highest discriminatory power and the last function the lowest. This discriminatory strength can be expressed by the percentage of between-group variability attributable to a specific function. Function 1 made the highest contribution to separating the four gibbon populations by explaining 64.5% of the total variability, whereas functions 2 and 3 contributed progressively less (27.6 and 7.8%, respectively).

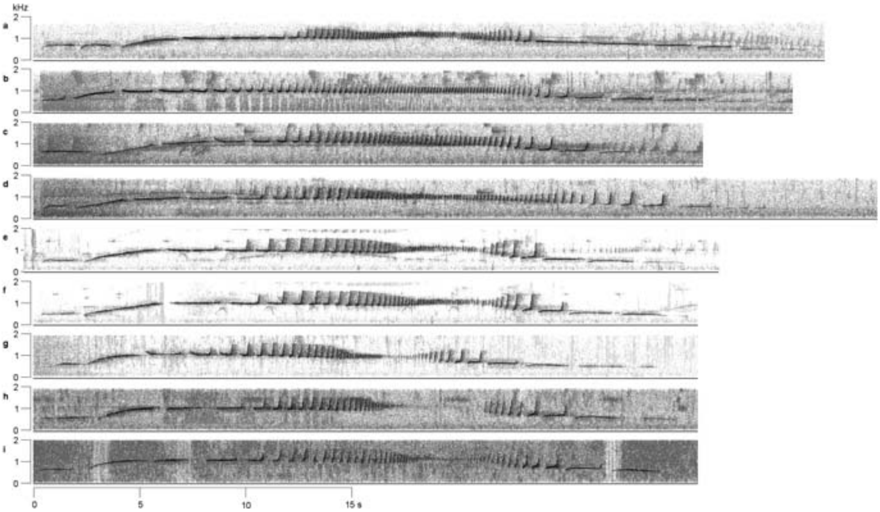

Fig. 4.4 Sonograms of female song phrases, including two different females from each recording locality: (**a**) and (**b**) central Siberut; (**c**) and (**d**) southern Siberut; (**e**–**g**) Sipora; and (**h**) and (**i**) South Pagai. Sonograms (**e**) and (**f**) are from the same female in order to show individual variability

Table 4.3 Standardized canonical discriminant function coefficients

		Function		
Variable number	Song variable	1	2	3
2	Number of male phrase notes	−2.741	0.347	−0.212
3	Minimum frequency of male phrase	−0.927	0.986	0.507
5	Number of male pre-trill notes	1.514	−0.983	−0.500
8	Maximum frequency of male pre-trill	2.589	0.241	−0.297
13	Minimum frequency of male trill	−1.635	1.167	0.271
18	Minimum frequency of male post-trill	2.361	−1.347	−0.643
19	Maximum frequency of male post-trill	0.266	−0.441	1.055
31	Notes/second in female trill	−1.051	0.186	−0.177

Figure 4.5 is a two-dimensional plot of all gibbon groups according to their discriminant scores for the first and the second discriminant functions and illustrates the degree of separation among the overall mean scores for each gibbon population. The discriminant function 1 mainly contributes to separating the Southern Siberut and Sipora populations from the Central Siberut and South Pagai populations (it also discriminates fairly well between the latter two populations), whereas discriminant function 2 elucidates differences between the population from Sipora and all other populations. Clearly, the separation between Siberut and the other islands is less pronounced than the separation between Southern Siberut and Sipora on

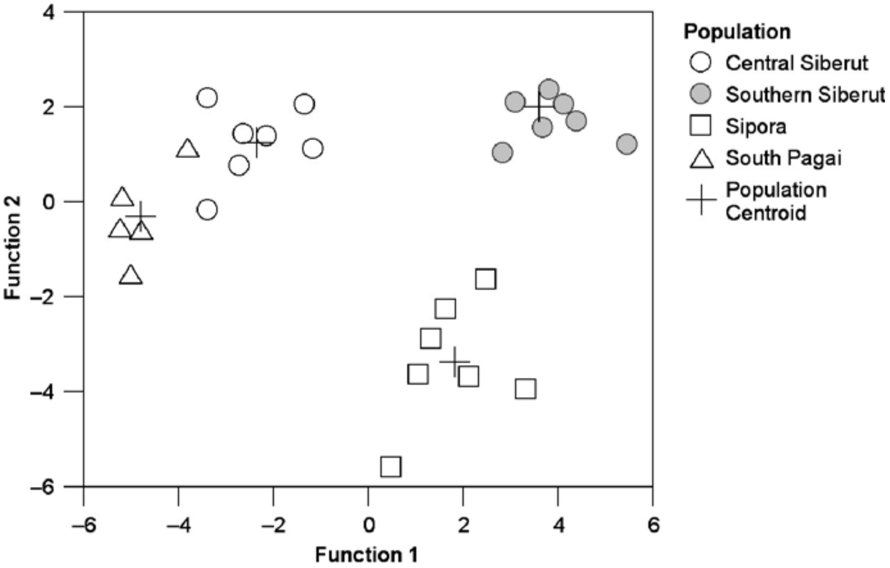

Fig. 4.5 Discriminant scores (*dot symbols*) of all gibbon groups. Different populations are identified with different symbol shapes. *Crosses* indicate population centroids

one hand and Central Siberut and South Pagai on the other. In addition, the two populations from Siberut appear to differ more from each other than the two islands Sipora and South Pagai.

The results of the reclassification procedure are shown in Table 4.4. All gibbon groups (100%) were correctly assigned to their population prior to cross-validation, a result that differed significantly from chance (Cohen's κ = 1.000, $p < 0.001$). The results of our multivariate analysis of vocal characteristics show that local gibbon populations have their own vocal "identities" and can clearly be distinguished from each other.

Classifications were cross-validated using the "leave-one-out" method, which involves taking each single observation in turn (e.g., song bout or individual) and using this to validate the models derived from the rest of the sample. This process greatly improves the accuracy of the classifications, making for a more realistic result. In the cross-validated classification, 85.2% of groups were correctly assigned, which is 14.8% lower than for the original classification.

The accuracy of classification of gibbon groups to populations ranged from 80% for the South Pagai population to 87.5% for the population from southern Siberut. Incorrectly classified groups originally from central Siberut were assigned to South Pagai, and all incorrectly classified groups from other populations were assigned to central Siberut. Despite the lower classification accuracy in the cross-validation, the classification results still differed significantly from chance (Cohen's κ = 0.801, $p < 0.001$).

Table 4.4 Classification results of discriminant analysis using all song material (male and female phrases)[a]

		Predicted groups assigned to population				Total number
	Population	Simabuggai	Sikabei	Saureinu	S. Pagai	of pairs
Original classification	Simabuggai	7	0	0	0	7
	Sikabei	0	8	0	0	8
	Saureinu	0	0	7	0	7
	S. Pagai	0	0	0	5	5
%[b]	Simabuggai	100.0	0.0	0.0	0.0	100.0
	Sikabei	0.0	100.0	0.0	0.0	100.0
	Saureinu	0.0	0.0	100.0	0.0	100.0
	S. Pagai	0.0	0.0	0.0	100.0	100.0
Cross-validated classification	Simabuggai	6	0	0	1	7
	Sikabei	1	7	0	0	8
	Saureinu	1	0	6	0	7
	S. Pagai	1	0	0	4	5
%[c]	Simabuggai	85.7	0.0	0.0	14.3	100.0
	Sikabei	12.5	87.5	0.0	0.0	100.0
	Saureinu	14.3	0.0	85.7	0.0	100.0
	S. Pagai	20.0	0.0	0.0	80.0	100.0

[a] The original classification was obtained when groups were classified by the functions derived from all groups (*n*). In the cross-validation, each group was classified by the functions derived from all groups other than that group (*n*–1).

[b] 100.0% of original grouped cases correctly classified.

[c] 85.2% of cross-validated grouped cases correctly classified.

Multidimensional Scaling

Figure 4.6 shows a two-dimensional representation of the vocal similarities among the recorded gibbon groups resulting from the MDS procedure (Stress = 0.266). Points that are close together represent gibbon groups that exhibit strong vocal similarity, and large distances on the map indicate gibbon groups that exhibit strong vocal dissimilarity. The position of the population centroids and the amount of overlap among the population polygons represent the degree of similarity among the four study populations. The plot demonstrates that distances between the two populations on the same island (Central and Southern Siberut) are equivalent to or exceed distances between the islands (Siberut, Sipora, South Pagai). The two southern islands overlap with each other to a greater degree than they overlap with the two Siberut populations, an observation that is strongly supported by the position of the southern island populations' centroids.

Vocal Versus Geographic Distance

Geographic distance was measured as the minimum distance between the coordinates of the recording sites. The position of each population was

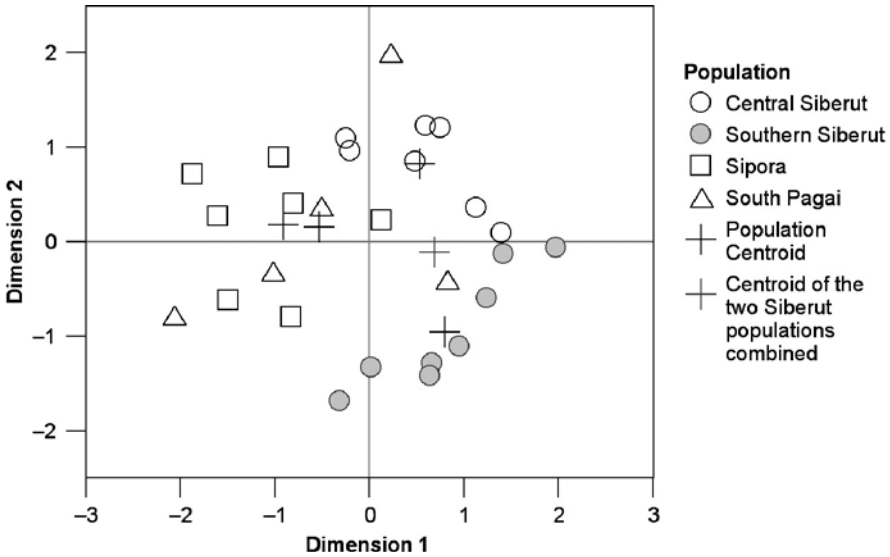

Fig. 4.6 Two-dimensional display representing similarity, as determined by multidimensional scaling (MDS). *Dot symbols* represent individual gibbon groups. Different populations are identified with different symbol shapes. *Crosses* indicate population centroids

represented with the coordinates of one particular recording position. The small distances between the recording positions used when recording gibbon groups in the same population were disregarded. Vocal distance between gibbon populations was measured as the distance between the respective centroids of these populations on the plot of the MDS analysis (Fig. 4.6). No significant correlation was found between geographic and vocal distances (Pearson Correlation: $n = 6, r = -0.402, p = 0.429$) (Fig. 4.7).

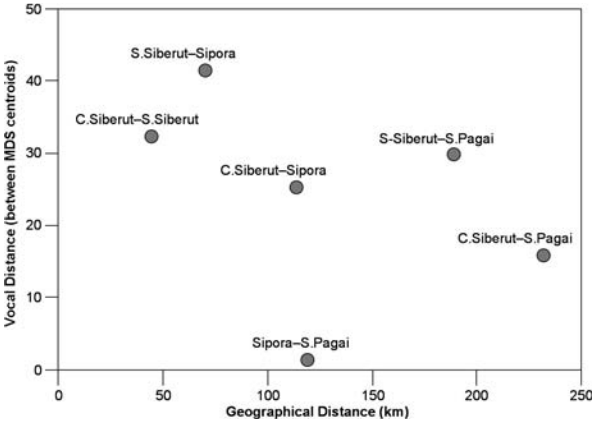

Fig. 4.7 Vocal distance (corresponding to distances between MDS centroids in Fig. 4.6) versus geographic distance (km) between all study populations

Discussion

Both female and male calls of Kloss's gibbons differ among localities and can be correctly assigned to their locality approximately 85% of the time using discriminant analysis. This result is similar to those of studies on Cambodian crested gibbons (genus *Nomascus*) and female Javan silvery gibbons, which were also able to discriminate among localities (Konrad and Geissmann 2006; Dallmann and Geissmann this volume).

In the other primates endemic to the Mentawai Islands (*Macaca pagensis*, *Presbytis potenziani*, and *Simias concolor*), the population of the northernmost island, Siberut, appears to differ from the populations of the other three islands in fur coloration and in DNA sequences, although the latter have been less studied. Based on these differences, distinct subspecies of *Simias concolor* and *Presbytis potenziani* (Groves 2001; Brandon-Jones et al. 2004) and distinct species of *Macaca* (Kitchener and Groves 2002; Roos et al. 2003) are recognized: one taxon for the Siberut population (*Macaca siberu*; *Simias concolor siberu*; *Presbytis potenziani siberu*) and one taxon for populations of the more southern islands (*Macaca pagensis*; *Simias concolor concolor*; *Presbytis potenziani potenziani*) of the Mentawais.

The Kloss's gibbon is also endemic to the Mentawai Islands, but so far, no taxonomic split has been proposed for this species. This is surprising, as water courses and sea channels are thought to represent a more substantial barrier for gibbons than macaques and leaf monkeys.

The results of this study suggest that vocal differences among Kloss's gibbon populations exhibit no apparent relationship to geographic distances. This is not surprising as some of the islands are a further geographic distance from other landmasses than others. However, a larger sample of populations would be required to explore the relationship between geographic and vocal distances fully.

In contrast to expectations, however, vocal differences between the two localities on Siberut are at least as pronounced as those between Siberut and localities on other islands. Affinities among the populations are of comparable degrees and, therefore, recognition of a distinct Siberut subspecies is not warranted. The conclusion drawn from our vocal data is supported by results from a study of the molecular diversity in wild Kloss's gibbons (Whittaker this volume). In contrast, this finding does not reflect the patterns observed in other Mentawai primates. We propose three possible explanations for why the situation in Kloss's gibbons may differ from that observed in the sympatric macaques and leaf monkeys.

(1) Gibbons may have spread across the Mentawai islands at a considerably later date than did other nonhuman primates. During the mid-Pleistocene glaciations, sea levels fluctuated dramatically (Batchelor 1979), repeatedly dropping to 230 m below current levels, exposing the whole Sundaland area as a connected land mass, and then rising again to submerge low-lying areas,

fragmenting the land mass into islands. Whereas the sea channels between the individual Mentawai islands are less than 50 m deep, the Mentawai Islands are separated from Sumatra by deep basins reaching depths of up to 1500 m (Karig et al. 1980; Moore et al. 1980; Whitten et al. 2000).

The Batu Islands to the north of the Mentawai chain provide a link with the Sunda shelf and Sumatra via a periodically exposed land bridge (Batchelor 1979; Dring et al. 1990). Any moderately forested land bridge linking the Mentawais to Sumatra may initially have allowed leaf monkeys and macaques to populate the Mentawai Islands, whereas gibbons would have required a closed-canopy forest for dispersal to the Mentawais. A subsequent rise in sea levels may have resulted in the isolation of the whole island chain from Sumatra and, later, in isolation of Siberut from the remaining islands. This separation may have promoted the evolution of endemic species of these Mentawai primates and the divergence of the southern island and Siberut populations.

Kloss's gibbons may have colonized the Mentawais during a more recent glacial period, and the subsequent isolation of the individual islands by rising sea levels may not have been of sufficient duration to produce taxonomic distinctiveness within the species.

Batchelor (1979) and Milliman and Emory (1968) estimate that the Mentawai Islands were last separated from Sumatra 1.0–0.5 million years ago, whereas the most recent separation among the Mentawai Islands may be as recent as 7000 years (Whittaker 2005a). This very recent divergence date is consistent with the lack of vocal or genetic divergence within the Kloss's gibbon species. However, if these estimates are correct, then the short time frame available for within-Mentawai divergence also raises questions about the validity of taxonomic divisions for the sympatric Mentawai monkeys.

(2) It is also possible that the taxonomic distinctiveness of the three species of Mentawai monkeys on Siberut and the southern islands has been overestimated. The proposed classification for the simakobu subspecific classifications is based on a very small sample size (four individuals from Sipora, three individuals from Siberut), and the main feature purported to establish the distinctiveness of the Siberut subspecies (*Simias concolor siberu*) is its being, "…like *S. concolor* from Sipora island, but darker, especially on the rump" (Chasen and Kloss 1927). The authors acknowledge that the Siberut female specimen cannot be distinguished from the Sipora specimens.

Roos et al. (2003) propose classifying Mentawai macaques as two distinct species: one on Siberut and one on Sipora and the Pagais, as a result of morphological and genetic analyses (Kitchener and Groves 2002; Roos et al. 2003). The genetic analysis utilized mtDNA loci. Use of mtDNA is problematic in phylogeographic analyses involving macaques due to female philopatry (Evans et al. 2003). However, only 5 of the 12 "Siberut" specimens were actually sampled on Siberut. The rest of the sample was collected from the Bukittinggi Zoo and

Padang (presumably from pets), on the Sumatran mainland (Whittaker 2005a). As accurate records of origin are not generally kept for pets, and the dubious conditions in the Bukittinggi Zoo (pers. obs.) raise questions about animal husbandry practices there, the provenance of these animals must be described as questionable. Furthermore, Roos et al. (2003) describe the Siberut macaque *(Macaca siberu)* as being more genetically similar to the Sumatran pig-tailed macaque *(Macaca nemestrina),* which suggests the possibility that the origin of the "Siberut" sample found on mainland Sumatra may not be the Mentawais. Alternatively, genetic mixing between captive macaques may have occurred, thus obscuring their distinctiveness. Morphological evidence, although compelling, must come with a caveat because it is based on a small sample size (Kitchener and Groves 2002). Therefore, ESUs for all Mentawai monkey species need further research to substantiate proposed taxonomic distinctiveness of the Siberut and southern taxa of the Mentawai monkey species.

(3) The estimated generation time for captive gibbons (mean 7.82 years, range 5.18–9.33 years) is almost twice as long as that of macaques (mean 4.57 years, range 3–5.54 years) and Asian colobines (mean 3.97 years, range 3.42–4.58 years) (Harvey et al. 1987; Ross 1992; Kappeler and Pereira 2003). Field studies are rarely of sufficient duration to document even a single generation span, much less produce a meaningful average value for a gibbon taxon. But if we accept the captive data as a first approximation, they suggest that under genetic isolation, macaque and Asian leaf monkey populations should diverge genetically almost twice as fast as gibbon populations.

The study was affected by a number of methodological limitations. For example, we collected a smaller sample of recordings from females than expected, due to a lower-than-expected female calling rate. Whitten (1982) reported that females sing every 3–4 days, whereas during the sampling period, females sang less frequently (pers. obs.). Future research should take this unpredictability in singing behavior into account.

It is also possible that increasing the number of variables measured would reveal more differences or similarities between populations. In particular, future research should have an increased focus on the female song. The use of a larger sample would also be helpful, because it is clear that vocal diversity is high within this species (Keith 2005; Waller 2005). In addition, the exclusion of young adults might reduce the effects of developmental variables (or "practice") on vocal characteristics.

Finally, although previous studies suggest that robust species and subspecies-level taxonomic inferences may be drawn from vocal data (Geissmann 1984, 1993, 1995; Zimmermann et al. 2000; Geissmann 2002a; Merker and Groves 2006), it is unclear to what extent vocal variation at the population level is attributable to the genetic signal.

To summarize, the results of our study on vocal diversity of Kloss's gibbons produced conclusions identical to those of an independent parallel study on molecular diversity of the same species (Whittaker this volume). Although the analysis of DNA produces more characters (base-pairs) than vocalizations for analysis and involves characters that are related to genetic evolution in a more direct manner, vocal data have certain benefits. Vocal data can be collected without approaching or directly observing the calling gibbons, and thus may impose less stress on unhabituated study animals. In addition, vocal data is cheaper to analyze than genetic data. Future studies of gibbon systematics could, therefore, benefit from inclusion of vocal data. This study also demonstrates the validity of using discriminant function analysis as a means for determining the origin of individual Kloss's gibbons based on their vocal characteristics, and suggests that this method has the potential for use in studies of other gibbon species.

Our results suggest that the Kloss's gibbon can be treated as a single Evolutionary Significant Unit (ESU). However, management strategies must also account for high levels of habitat fragmentation and the possibility of incipient divergence on the different islands. Treatment of the species as just one ESU may lead managers to focus on the larger, presumably more viable, Siberut population at the cost of the other island populations.

Without conservation throughout the Mentawai Islands, the Kloss's gibbon will lose genetic variation and subsequently reduce its adaptation potential. This genetic depletion restricts a taxon's ability to cope with future challenges such as climate change. Range shifts to track changing environmental conditions are not generally possible for island species (Mimura et al. 2007), making genetic adaptation the only response available to the Kloss's gibbon. Therefore, we implore the relevant authorities and conservation agencies to strive to maintain the genetic diversity of the Kloss's gibbon.

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Appendix: List of Vocal Variables

Trill Phrase of the Male

1. Duration of entire male phrase (s).
2. Total number of notes in male phrase.
3. Minimum frequency of phrase (Hz).
4. Maximum frequency of phrase (Hz).
5. Number of pre-trill notes.
6. Duration of pre-trill part of male phrase (s).
7. Minimum frequency of pre-trill notes (Hz).
8. Maximum frequency of pre-trill notes (Hz).

9. Frequency modulation (from minimum to maximum) from start to end of second note (Hz).
10. Frequency modulation from start to end of third note (Hz).
11. Number of trill notes.
12. Duration of trill (s).
13. Minimum frequency of trill (Hz).
14. Maximum frequency of trill (Hz).
15. Frequency modulation from start to end of first post-trill note (Hz).
16. Number of post-trill notes.
17. Duration of post-trill part of male phrase (s).
18. Minimum frequency of post-trill notes (Hz).
19. Maximum frequency of post-trill notes (Hz).

Great Call Phrase of the Female

20. Total duration of pre-trill and trill part of female great call (s).
21. Frequency range of pre-trill and trill part of female great call (Hz).
22. Duration of first great call note (s).
23. Frequency modulation from start to end of first great call note (Hz).
24. Duration of second great call note (s).
25. Dominant frequency of second great call note (Hz).
26. Number of pre-trill notes.
27. Duration of pre-trill part of great call (s).
28. Number of pre-trill notes per second.
29. Trill duration (s).
30. Number of trill notes.
31. Number of trill notes per second.

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