Vocal Diversity and Taxonomy of *Nomascus* in Central Vietnam and Southern Laos

by

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Abstract

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Title: Vocal Diversity and Taxonomy of *Nomascus* in Central Vietnam and Southern Laos.

Gibbon song vocalizations have been found to be particularly suitable for studying phylogenetic relationships among taxa, because taxon-specific characteristics of songs are not learned but inherited. Based on calls from captive gibbons, Geissmann et al. (2000) suggested that a previously unrecognized taxon of the genus *Nomascus* (crested gibbons) might exist in Central Vietnam. This is supported by more recent research on the calls of wild crested gibbons suggesting that *Nomascus leucogenys siki* may consist of more than one taxon, a southern and a northern one. This hypothesis should be tested by comparing calls of all potentially distinct populations of *Nomascus leucogenys siki*.

The purpose of the present study was to determine if vocal differences exist between localities of *Nomascus leucogenys siki* occurrence. The study sought to answer the following questions: 1) Are there vocal differences between localities of *Nomascus leucogenys siki* occurrence? 2) What differences are there between the vocalizations of northern *Nomascus leucogenys siki* gibbons and southern *Nomascus leucogenys siki* gibbons?

The songs of seven *Nomascus* populations in Vietnam and Laos were recorded and examined. Sonograms were used to measure 78 variables of gibbon song which were then analyzed using statistical analysis.

Results of both discriminant analysis and multi-dimensional scaling show that the currently named taxonomic entity *Nomascus leucogenys siki* can be split into two distinct geographic populations, northern and southern, based on vocal data. This implies that considerable vocal diversity exists between the northern and southern groups. To date, there has been no published description of the vocalizations of wild *Nomascus leucogenys leucogenys* or northern *Nomascus leucgeonys siki*, and only one study on calls of southern *Nomascus leucgeonys siki*. Therefore, this study presents the first evidence that more than one taxon may be involved in what is currently known as *Nomascus leucogenys siki*. The results are of relevance for gibbon conservation; because discovery of a previously un-described taxon would require a re-evaluation of conservation priorities for Indochinese gibbons.

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1. Introduction

1.1. Gibbon systematics

The focus of this study is essentially taxonomic and has conservation implications. Gibbons are small apes that are grouped in the family Hylobatidae. They are pair bonded, arboreal, and live in East Asian rainforests. Most species are threatened or endangered, generally due to loss of their forest habitat. All gibbon species produce loud and long vocal song bouts and all species but *Hoolock hoolock* have sexually dimorphic vocal repertoires (Haimhoff, 1984a). Territoriality in gibbons is routinely maintained through loud morning song bouts where mates combine their species-specific and often sex-specific vocalizations to produce well patterned duets (Deputte, 1982, Geissmann, 1993, Geissmann & and Orgeldinger, 2000). Species-specific differences in song (structure, the amount of solo singing of either sex, the amount of duetting, and the complexity of vocal coordination) all suggest that the functions of singing differ across gibbon species (Geissmann & Orgeldinger, 2000). It has often been suggested that duetting may serve several functions in gibbons such as territory defense (Geissmann 1984), maintenance of group cohesion (Geissmann & Orgeldinger, 2000) and advertisement of pair bonds (Raemaekers and Raemaekers, 1985). It has also been suggested that the importance of each function may differ between gibbon species (Geissmann, 1984). The song repertoire is notably constant in structure and organization for each species, and according to several authors, is believed to be largely genetically determined (Geissmann, 1984, Leighton, 1986).

Gibbons are highly specialized, but also very homogenous, in their anatomy. Species differ most markedly in pelage coloration. In addition, some species exhibit sexually dichromatic pelage coloration, and undergo striking color changes during their ontogeny. Therefore, a reliable species or subspecies identification of gibbons of unknown provenance is often not possible based on pelage coloration criteria alone. Tape recordings of the gibbon's morning songs are often indispensable for reliable identifications.

It is widely accepted that gibbons can be split into four systematic groups that appear to be of roughly similar phylogenetic age. In the past few years, these four groups have usually been recognized as subgenera (e.g. Geissmann, 1995; Marshall & Sugardjito, 1986; Prouty *et al*., 1983). More recently, it has been reported that the molecular distances among the four gibbon subgenera are in the same range as those between humans (*Homo*) and chimpanzees (*Pan*), or even greater, and that all four gibbon subgenera should be raised to genus rank (Roos & Geissmann, 2001). Results of Roos & Geissmann's study (2001) and subsequent genetic analysis show that the Hylobatidae are subdivided into four well-supported monophyletic clades: *Nomascus*, *Hoolock*, *Symphalangus*, and *Hylobates* (Table 1). Recognition of the four groups as full genera is now widespread (Brandon-Jones *et al*., 2004; Geissmann, 2002; Takacs *et al*., 2005).

Table 1. Classification of the Hylobatidae, showing scientific, English, and common names (after Geissmann, 2002b)

Genus	Group name	Species	Common Name
Hoolock	Hoolocks	*H. hoolock*	*Hoolock*
Nomascus	Crested gibbons, *concolor* group	*N. concolor*	*Black crested gibbon*
		N. sp. cf. *nasutus*	*Eastern black crested gibbon*
		N. gabriellae	*Yellow-cheeked crested gibbon*
		N. siki	*Southern white-cheeked crested gibbon*
		N. leucogenys[a]	*Northern white-cheeked crested gibbon*
Hylobates	Dwarf gibbons, *lar* group	*H. agilis*[b]	*Black handed gibbon*
		H. klossii	*Kloss's gibbon*
		H. lar	*White-handed gibbon*
		H. moloch	*Javan or Silvery gibbon*
		H. muelleri[c]	*Muller's or Grey gibbon*
		H. pileatus	*Pileated gibbon*
Symphal-angus	Siamangs	*S. syndactylus*	*Siamang*

[a] including *N. leucogenys siki*
[b] including *H. agilis albibarbis*
[c] including *H. muelleri abbotti* and *H. muelleri funereus*

As seen in Table 2, *Nomascus* gibbons, with an average body mass of between 7 and 8 kilograms (kg), are of distinctly larger body mass than *Hylobates* (Geissmann, 1993). However, both genera exhibit a much smaller body mass than *Symphalangus*. In general, female gibbons slightly exhibit smaller body mass than males.

Table 2. Gibbon body weights (extracted from Geissmann, 1993).

Genus	Species	Body Mass (kg)	
		Male	Female
Hoolock	*H. hoolock*	*6.87*	*6.88*
Nomascus	*N. concolor*	*7.35*	*7.88*
	N. nasutus	*8.34*	*6.75*
	N. gabriellae	*Data deficient*	*Data deficient*
	N. siki	*7.85*	*7.00*
	N. leucogenys[a]	*7.27*	*7.65*
Hylobates	*H. agilis*[b]	*5.88*	*5.82*
	H. klossii	*5.67*	*5.89*
	H. lar	*5.90*	*5.34*
	H. moloch	*6.58*	*6.25*
	H. muelleri[c]	*5.71*	*5.35*
	H. pileatus	*5.50*	*5.44*
Symphalangus	*S. syndactylus*	*11.88*	*10.71*

[a] including *N. leucogenys siki*
[b] including *H. agilis albibarbis*
[c] including *H. muelleri abbotti* and *H. muelleri funereus*

1.2. The use of gibbon vocalization for systematics

All gibbon species are known to produce elaborate, loud, long, and stereotyped patterns of vocalization often referred to as "songs" (Geissmann, 1993). In this thesis, a song is what fulfills the criteria set forth by Thorpe (1961, p. 15): "What is usually understood by the term song is a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence of pattern in time", or, a song is a succession of phrases with non-random succession probability (Tembroch, 1977, p. 33). Song bouts are separated from each other by an arbitrarily defined interval of at least 5 minutes. In duetting gibbon species, the duet structure of the great call sequence consists of the female interrupting the singing male with her great call phrase, which, in turn, is answered, by a coda phrase of the male.

As pointed out by Geissmann (2000), both the context in which singing occurs in nonhuman primates and the structure of some song contributions show similarities to territorial calls or alarm calls in non-singing species. In contrast to birds, singing behavior is rare in mammals. Among nonhuman primates, singing is known only for members of the following four groups; the genera *Indri*, *Tarsius* (only in members of the Sulawesi species-group), *Callicebus*, and the gibbons (Hylobatidae) (Robinson, 1979, 1981; MacKinnon & MacKinnon, 1980; Haimoff, 1984a; Niemitz *et al*., 1991; Geissmann, 1993, 2000; Thalmann *et al*., 1993; Muller, 1994, 1995; Nietsch & Kopp, 1998). These singing primates comprise about twenty-six species (depending on the currently accepted taxonomy), amounting to about 11% of primate species or 6% of primate genera. Since the four groups of primates that exhibit singing (and duet singing) behavior are not closely related, it is likely that singing (and duet singing) evolved four times independently within the order Primates. In all singing primates, males and females both sing, and in most singing primates, duet singing occurs. It is interesting to note that all primate species that are known to sing are also thought to have a pair bonded social structure. In birds, too, duet songs mainly occur in pair bonded species (Thorpe, 1961). This suggests that the evolution of singing behavior in primates and of duet singing behavior in general is somehow related to the evolution of pair bonds (Geissmann, 1984; Palombit, 1994; Reichard, 1995; Sommer & Reichard, 2000).

Contemporary taxonomies extend the traits used beyond purely anatomical ones that form the basis of traditional classification. It has previously been suggested that gibbon song characteristics are useful for assessing systematic relationships at the genus and the species level and for reconstructing gibbon phylogeny (Creel & Preuschoft, 1984; Geissmann, 1993, 2002a, 2002b; Haimoff, 1983; Haimoff *et al*., 1984a; Marshall *et al*., 1984). Geissmann (2002b), using cladistic methods, compared three different types of data (fur coloration, anatomical/morphological data and vocal data) with respect to their relevance for the reconstruction of gibbon phylogeny. Of the three data sets, vocal data produced the most reliable phylogeny, to judge by various standard measures calculated to assess the "quality" of phylogenetic trees.

A species identity is maintained by selection for compatible reproductive biology at the behavioral, physiological and anatomical level (Patterson, 1985). In determining species and subspecies of gibbons I explicitly use species-specific vocalizations to infer discrete breeding patterns within natural populations. In some cases anatomically indistinguishable populations may be reproductively isolated by their respective vocalizations. Descriptions of gibbon songs aid species and subspecies definition, but for some gibbon taxa, good recordings of song vocalizations are still lacking. Remedying this problem would allow more accurate identification of taxa and would help recognition of wild populations.

1.3. Crested gibbons (genus *Nomascus*)

In terms of singing behavior, crested gibbons (*Nomascus*) exhibit a number of unique characteristics that set them apart from other gibbons. Song bouts of mated pairs of the genus *Nomascus* are highly stereotyped and male-dominated, whereas solo songs appear to be produced by non-mated individuals only. In addition, crested gibbons exhibit the highest degree of sex-specificity in their songs, as there is typically no overlap between the sexes in either note repertoire or phrase repertoire (Goustard, 1984).

The most widely accepted and best-described *Nomascus* species are *N. concolor*, *N. leucogenys* and *N. gabriellae* (Table 1). A suggested species-level differentiation between these three species is supported by the fact that all three forms differ markedly in their songs (Geissmann, 1993; Geissmann *et al*., 2000). Based on vocalization and fur characteristics, Geissmann postulated the recognition of a fourth distinct species, the eastern black crested gibbon, tentatively identified as *N.* sp. cf. *nasutus* (Geissmann 1997; Geissmann *et al*., 2000). Because of nation-wide survey work in Vietnam (Geissmann *et al*., 2000, 2003), the status of crested gibbons (genus *Nomascus*) is particularly well known, at least if compared to the situation in the other countries where these gibbons occur (Cambodia, Laos, and China). The distribution areas of all of the species in the genus *Nomascus* can be observed in Figure 1.

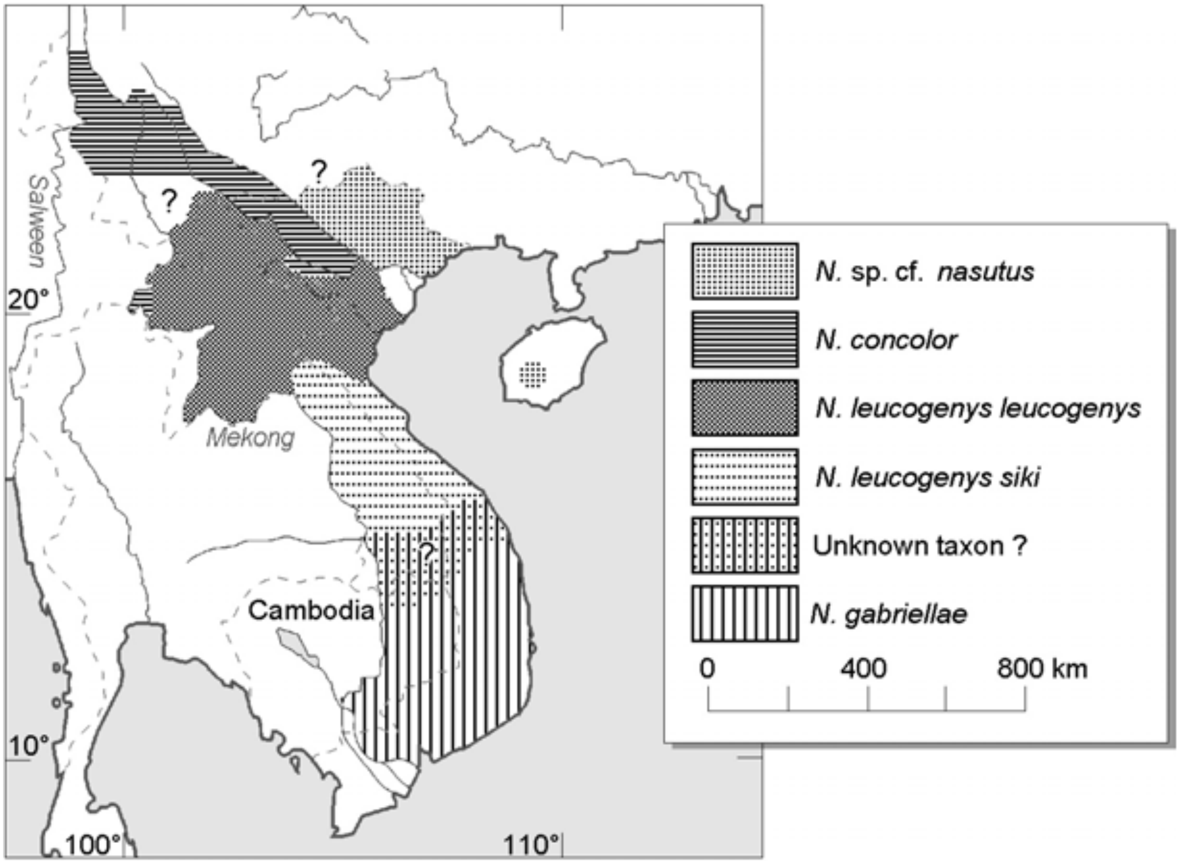

Figure 1: Distribution of the species of the genus *Nomascus* (from Konrad and Geissmann, 2006). Question marks refer to, from north to south, (1.) the unknown survival (and identity) of Chinese gibbons east of the red river in Yunnan Province; (2.) a large apparent gap in the distribution area of gibbons in Yunnan Province and (3.) the unknown identity of gibbons in a large area between the distribution areas of *N. leucogenys* and *N. gabriellae*, respectively. Dashed lines indicate political boundaries.

1.4. White-cheeked crested gibbons (*Nomascus leucogenys*)

Known from Vietnam and Laos, the white-cheeked crested gibbon is recognized as a distinct species, (*Nomascus leucogenys*), with two subspecies – the northern (*Nomascus leucogenys leucogenys*) and the southern (*Nomascus leucogenys siki*) (Geissmann, 2002; Geissmann *et al*., 2000; IUCN, 2004). *Nomascus leucogenys leucogenys* is categorized as "Endangered" on the IUCN red list, with subcategories A1cd + 2cd, indicating that the taxon has seen a population reduction of at least 50% over the last three generations, due to habitat modification and taxon exploitation, and a similar reduction is projected over the next three generations (IUCN, 2004). *Nomascus leucogenys siki* is categorized as "Data Deficient" meaning there is not enough information to place them in a category (IUCN, 2004).

White-cheeked crested gibbons (*N. leucogenys*) are distributed in southern Yunnan Province (China), northern and central Laos, northern Vietnam and central Vietnam (Geissmann *et al.*, 2000). This species is virtually unstudied in the field. The only published field study was conducted by Hu *et al.* (1989, 1990) and was a report on the ecology of *N. leucogenys* in Yunnan Province, southern China. Other studies have been conducted on the call structure of captive *N. leucogenys leucogenys* (for example, Deputte, 1982; Deputte and Leclerc-Cassan, 1981; Goustard 1984; Haimoff, 1984a; Schilling, 1984), but these individuals were of unknown provenance. To date, there has been no published description of the vocalizations of wild *N. l. leucogenys* or northern *N. l. siki*, and only one study on calls of southern *N. l. siki* (Konrad & Geissmann, 2006). The status of the northern white-cheeked crested gibbon (*N. leucogenys leucogenys*) in Vietnam appears to be particularly critical, because the taxon appears to be locally extinct in 74 % of the localities where it was known to have occurred previously (Geissmann *et al*., 2003). The situation of the southern white-cheeked crested gibbon (*N. leucogenys siki*) appears to be less alarming but more difficult to evaluate (Konrad & Geissmann, 2006).

The taxonomic affinities of the southern white-cheeked crested gibbon (*N. l. siki*) have been under debate. There is some difference of opinion as to whether *N. l. siki* is a subspecies of *N. leucogenys* or of *N. gabriellae* (refer to Table 1 and Figure 1). Some authors even recommend giving this form full species rank (Groves, 2001; Zhang, 1997). The chromosomes of *N. l. siki* were reportedly different from those of both *N. leucogenys* and *N. gabriellae* (Couturier & Lernould, 1991). Furthermore, *N. l. siki* appears to occupy an intermediate position between the two species both in the light facial hair pattern of the male as well as in the distribution area (Geissmann *et al*., 2000).

Adult females of *N. l. siki* are, however, indistinguishable in fur coloration from *N. leucogenys leucogenys*, whereas both forms differ from females of *N. gabriellae* (Geissmann, 1995; Geissmann *et al*., 2000). In addition, song patterns of *N. l. siki* more closely resemble those of *N. leucogenys leucogenys* than those of *N. gabriellae* (Geissmann *et al*., 2000). Analyses of mitochondrial DNA suggest that *N. l. siki* is more closely related to *N. leucogenys leucogenys* than to *N. gabriellae* (Garza & Woodruff, 1992, 1994; Zhang, 1997). As a result, Geissmann (1995, 2003) and Geissmann *et al*. (2000) recognized this form as a subspecies of *N. leucogenys* namely, *N. l. siki*. This classification was followed in the present study.

Based on calls from captive gibbons, Geissmann *et al*. (2000) suggested that a previously unrecognized subspecies of the genus *Nomascus* might exist in Central Vietnam. This is supported by more recent research on the calls of wild crested gibbons suggesting that *N. l. siki* (the southern white-cheeked crested gibbons) may consist of more than one taxon, a southern and a northern one (Konrad & Geissmann, 2006). Comparing calls of all potentially distinct populations of *N. l. siki* will test this hypothesis.

A comparison of the wild northern *N. l. siki* song with that of wild southern *N. l. siki* may help to verify their affinities and to test the hypothesis that more than one taxon may be included in what is currently known as *N. l. siki*. The result would be of relevance for gibbon conservation, because discovery of a previously un-described taxon would require a re-evaluation of conservation priorities for Indo-Chinese gibbons. Therefore, the aim of this project was to analyze calls of northern and southern *N. l. siki* and to compare them.

1.5. Aim of this study

The primary focus of this study is to determine if there are vocal differences between localities of *N. l. siki* occurrence. In addition, it will be possible to verify, whether the vocal differences between the subspecies of *N. leucogenys* described by Geissmann *et al*. (2000) based on recordings made of captive gibbons of unknown provenance are representative of a previously unrecognized form.

Fieldwork consisted of visiting Phong Nha Ke Bang NP (National Park) in Vietnam (a locality of northern *N. l. siki* occurrence). Recordings from seven geographic areas were analyzed and multivariate analysis of call characteristics was carried out in order to answer the following questions:

- Are there vocal differences between localities of *N. leucogenys siki* occurrence?
- What differences are there between the vocalizations of northern *N. l. siki* gibbons and southern *N. l. siki* gibbons?

The description from Geissmann *et al*. (2000) of song differences between *N. l. leucogenys, N. l. siki*, and *N. gabriellae* is based on data that also included zoo recordings carried out under optimal condition, unlike many field recordings. One should especially take into consideration that the vocal criteria for *N. l. siki* are based almost exclusively on zoo gibbons, for which there is uncertainty about the exact origin of an individual (or its ancestors) and thus knowing the exact taxonomic status is problematic. Though songs of zoo gibbons regarded as *N. gabriellae* correspond with songs of wild gibbons in the proposed distribution range of the taxon (Konrad & Geissmann, 2006), the same does not appear to be the case for *N. l. siki*. Because Bach Ma National Park (NP) is very close to the type locality of *N. l. siki*, Thua Luu (Delacour, 1951), and because no obvious geographic barrier appears to occur between Bach Ma NP and the type locality, it can be assumed that the gibbons from Bach Ma NP are, in fact, *N. l. siki*. Furthermore, Bach Ma NP (at a latitude of *ca*. 16.12° N) is in the assumed distribution range of *N. l. siki* (i.e., between 15.45° N and *ca.* 20.0° N, according to Groves, 2001). Apparently, the zoo gibbons identified by fur coloration as *N. l. siki* produce a different song than that of gibbons from Bach Ma NP (Geissmann, 2001; Geissmann, pers. comm.).

If Konrad & Geissmann's hypothesis (2006) is correct then there should be different calls between the northern and southern *N. l. siki*. It is conceivable that two distinct populations exist that both exhibit the *Nomascus leucogenys siki* morphotype but that differ in their calls. One would be represented by the Bach Ma NP population, and possibly include all northeast Cambodian study populations from Konrad and Geissmann's study (2006). The other may be located further to the north and be represented by the zoo gibbons that were the basis of the vocal criteria of *N. l. siki* that Geissmann *et al*. (2000) reported.

There are three possible outcomes of this study. First, if *N. l. leucogenys* is distributed to the south more than assumed (i.e., this would mean that the northern gibbons are *N. l. leucogenys*) then the hypothesis is wrong. However, this seems unlikely because in that case the gibbons at Phong Nha Ke Bang National Park would look like *N. l. leucogenys* but they do not, they look like the *N. l. siki* form (Groves, 1993). Second, if the calls do not differ from each other (northern and southern) it means that they are all the same. Lastly, if the calls from the northern groups are different from the southern groups, it would support the hypothesis that there is more than one taxon involved in what is now called *N. l. siki*.

2. Methods

2.1. Recording sites

The tape recordings of gibbon songs included in the present study originated from seven areas in Vietnam and Laos. The location of these sites can be viewed in Figure 2. In this thesis I numbered each population in a north-south direction. This convention is used consistently through out the text in order to refer to populations without confusion.

1) Nakai Nam Theun National Biodiversity Conservation Area (NBCA), Laos. All recordings from Laos were made by Robert Timmins, Peter Davidson, Pham Nhat, and Anthony Stones (1993-1999).

2) Hin Namno National Biodiversity Conservation Area (NBCA), Bua La Pha District, Kham Muam Province, Laos.

3) My recordings from Phong Nha Ke Bang National Park (NP) (2006) Quang Binh Province Vietnam.

4) Barney Long's recordings from Thua Thien Hue Province (2005) were made in cooperation with Management of Strategic Areas for Integrated Conservation (MOSAIC). Recordings originated from seven communes within Thua Thien Hue Province: Hong Ha, A Roang, Hong Van, Thuong Quang, Houng Nguyen, Thi Tran Phu Loc, and Loc Thuy.

5) Thomas Geissmann's recordings from Bach Ma National Park (NP) (2001), Thua Thien Hue Province, Vietnam.

6) Xe-Bang Nouan National Biodiversity Conservation Area (NBCA), Laos and Xe Sap National Biodiversity Conservation Area (NBCA), Laos.

7) Barney Long's recordings from Quang Nam Province (2004) made in cooperation with Management of Strategic Areas for Integrated Conservation (MOSAIC). Recordings originated from five communes within Quang Nam Province: Phuoc Xuan, Ma Cooih, West La Dee, Phuoc My, and Tabhing.

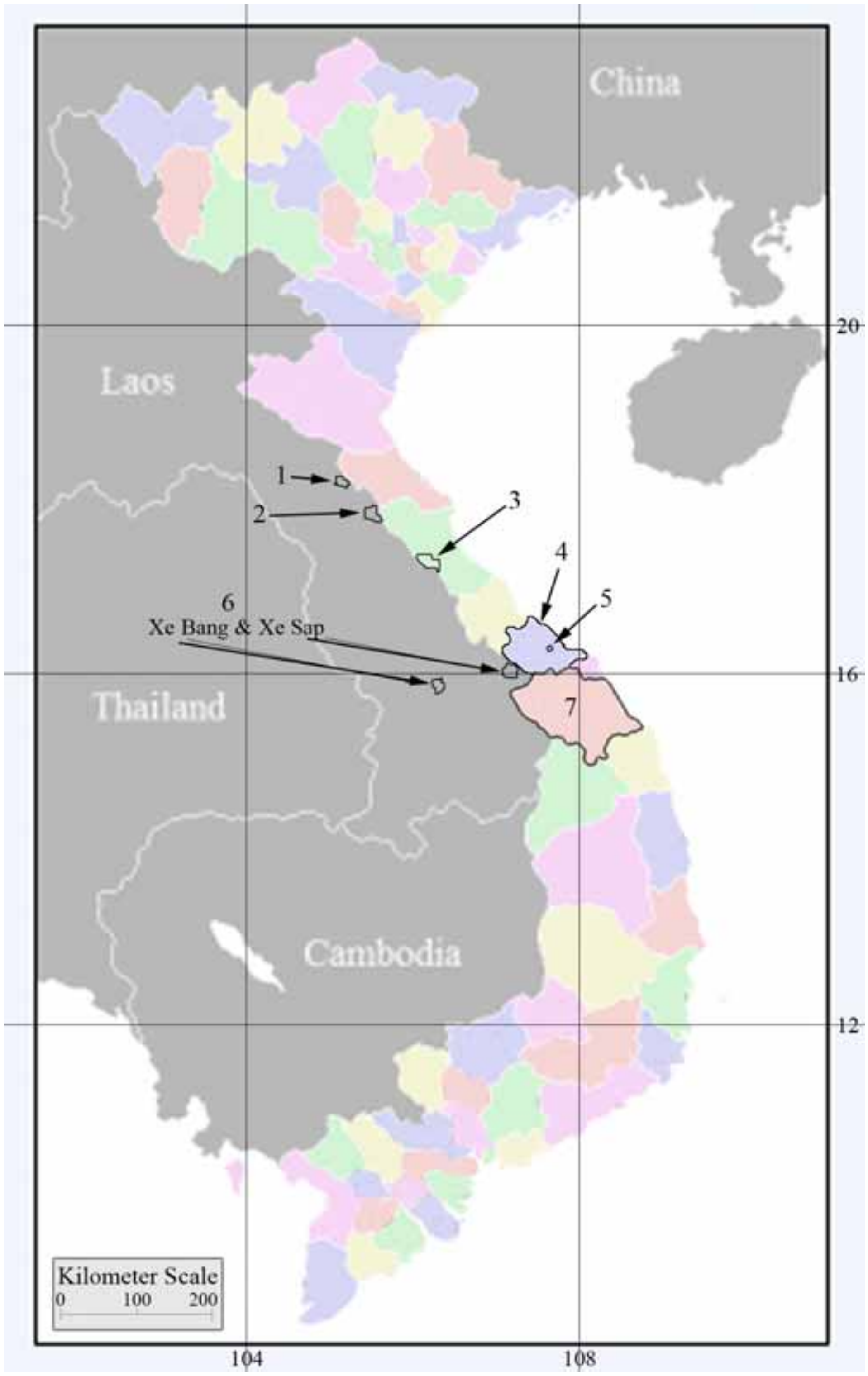

Figure 2: Recordings sites used in this study
1 = Nakai Nam Theun NBCA, Laos, 2 groups
2 = Hin Namno NBCA, Laos, 3 groups
3 = Phong Nha Ke Bang NP, Vietnam, 10 groups

4 = Thua Thien Hue Province, Vietnam, 7 groups
5 = Bach Ma NP, Vietnam, 5 groups
6 = Xe Bang NBCA and Xe Sap NBCA, Laos, 5 groups
7 = Quang Nam Province, Vietnam, 10 groups

2.1.1. Site details

The recordings from Laos were made by several people between the years of 1993 and 1999. The recordings were sent to Thomas Geissmann and up to this point had not been analyzed. I digitized the recordings from cassette tapes.

I visited Phong Nha Ke Bang National Park in July 2006. The park is contained within two districts (Bo Trach and Minh Hoa) in Quang Binh Province. The vast area, extending to the border of the Lao People's Democratic Republic, contains spectacular formations including 65 km of caves and underground rivers. The white-cheeked gibbons at Phong Nha Ke Bang NP had not been studied previously.

Bach Ma National Park is situated in Thua Thien Hue Province in central Vietnam. In April 2001 Thomas Geissmann conducted a gibbon survey in the north-eastern part of the park, in collaboration with "Fauna and Flora International (FFI) (Tallents *et al*., 2001). On this occasion, tape-recordings of the gibbon songs were made.

Quang Nam Province is in central Vietnam and is the southern most location to be used in this study. Thua Thien Hue is a Province on the north central coast of Vietnam, next to the former capital of Hue. Because Bach Ma National Park is located is north of Quang Nam Province and within Thua Thien Hue Province it is assumed that the gibbons in all three localities are closely related.

2.1.2. Carrying out tape-recordings in the field

Because no detailed gibbon surveys had been previously carried out in the area where I conducted my data collection, I generally had no knowledge of the gibbon density and the distribution of individuals, groups and territories. Local people provided a good source of information and were consulted as to whether gibbons had been heard in the area recently. Once at a locality in the field, a camp and listening post were set up. If gibbons were heard, the listening post was moved in the direction of the gibbon group during subsequent mornings, in order to obtain clearer recordings. Once a good set of recordings for a group was collected, I attempted to locate a different group in the same locality. Because gibbons live in pair bonds, a group can be defined when a male and female duet is recorded for one location. Each duet that was heard on a given day was recorded and the direction of the group song was noted using a GPS and compass. This process ensures that the number of gibbon groups heard each day can be differentiated from each other during data analysis. Solitary individuals were identified when song phrases were heard as a solo without a responding counterpart.

A Marantz PMD (tape recorder) and a directional microphone were used for recording. “Good” recordings are those which can be used for sonagraphic analysis. These are recordings that are made at close distance to the singer (effective distance depending on background noise level at a given time), with all gibbon song notes clearly audible and with little background noise on the recording (rivers, wind, rain, cicadas, moving the fingers holding the microphone, etc.). The above information on how to tape-record wild gibbons was referenced from Geissmann (2003).

Song recording is most efficient on nice days when it is sunny (Geissmann, 2003). Gibbons sing everyday throughout the year, although the time gibbons sing varies depending on the season. Because gibbons are shy and difficult to approach in the wild, the recording method using the directional microphone was the most efficient method in the field during this study. Recording gibbon song is also useful for identifying the number of populations in research areas without scaring the gibbons. By recording, individual groups can be studied more easily without many of the difficulties involved in observing primates in tall tropical rain forest. They can be studied without intruding into their habitat, without habituating groups, and without disturbing groups (Geissmann, 2003). Vocal recognition might be a more suitable tool for surveying and studying this critically endangered primate than some traditional methods. Although my study was not long-term, it should be noted that vocal recognition facilitates longitudinal studies which otherwise often require intrusive methods (Geissmann, 2003).

2.1.3. Survey in Phong Nha Ke Bang NP

Phong Nha Ke Bang NP is one of the remaining areas in Vietnam that still supports gibbons (Geissmann *et al*., 2000). During a survey covering about 3 km^2 of the whole park (857.54 km^2) we (my Vietnamese assistants and I) monitored gibbon song activity from listening posts on five hilltops along the road between km 40 and km 52, trying to locate and record as many gibbons as possible. Every day, we arrived on our chosen listening post between 04:00 and 04:30 hrs and stayed there until 11:30 hr. During afternoons, we made survey walks in the forest. During ten consecutive days of monitoring, a total of 31 song bouts were recorded. I heard 3.1±1.0 songs per day (average ± standard deviation; range 2-

5 song bouts). Gibbons often started a few minutes before sunrise (i.e. 05:26 hr local time), and 80% of all songs started between 05:00 and 05:30. No song started earlier than 04:58 hr and no songs were heard that started after 05:53 hr.

Songs of ten groups were effectively tape-recorded. At least three other groups were heard between km 40 and km 52, but they were too far away to be tape-recorded. Therefore my estimate for the area between km 40 and km 52 is that there are at least 13 groups (30+ individuals) living in this area.

2.1.4. Tape recording equipment

I made my recordings with a Marantz PMD 660 Flash Recorder and a Rode NTG 1 Directional Condenser Shotgun Microphone. Thomas Geissmann used a SONY WM-D6C cassette recorder with a JVC MZ-7-7 directional microphone and alternatively, a SONY TC-D5M cassette recorder with a Senheiser ME80 directional microphone. The recording equipment used for the tape-recordings carried out by Barney Long (Quang Nam, Thua Thien Hue) and by Robert Timmins, Peter Davidson, Pham Nhat, and Anthony Stones (central Laos) is not known.

2.2. Acoustic terms and crested gibbon song structure

2.2.1. Acoustic terms

Sonograms (time versus frequency displays) of the sound material were generated using the Raven version 1.2.4 software (Cornell Laboratory of Ornithology) on a Dell Inspiron computer. Gibbon song bouts are long, loud and relatively stereotyped. They are typically produced in the early morning and include sex specific and species-specific characteristics. Investigators of gibbon vocalizations use various acoustic terms and definitions to describe gibbon song characteristics. Haimoff (1984a) presented a set of acoustic terms, which is consistent and reliable among all gibbon taxa. Therefore, the acoustic terminology used in the present study largely follows that proposed by Haimoff (1984a). The most relevant definitions for the present study are listed in Table 3.

Table 3. Acoustic terms and definitions for gibbon song (adapted from Konrad & Geissmann, 2006).

Term	Definition
Note	Any single continuous sound of any distinct frequency or frequency modulation which may be produced during inhalation or exhalation
Element	A basic recognizable vocal unit of a single animal and composed of a single note or a short series of notes
Phrase	A single vocal activity consisting of a larger or looser collection of notes and elements. These parts may be produced together or separately.
Coda	A phrase produced by the male as a response to and at or near the end of a female's great call
Great Call	The most stereotyped and most easily identifiable phrase of the gibbon song and produced by adult females
Great Call Sequence	Combination of the female great call and the corresponding successive coda of the male
Song	After Thorpe (1961, p. 151) 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
Song Bout	Includes the first to last loud note produced with no period of silence of more than 10 minutes between notes
Solo Song Bout	Song bout produced by a single individual (male or female) alone
Duet Song Bout	Song bout in which both sexes produce their loud sounds and exhibit vigorous movements in an interactive manner (i.e. performing a mutually cooperative and coordinated display).

2.2.2. The *Nomascus* song structure

The song structure of crested gibbons (genus *Nomascus*) differs in several respects from that of other gibbons and has been described in several previous studies (e.g; Deputte, 1982; Goustard, 1976; Haimoff, 1984a; Schilling, 1984). In this section some specific terms, which have been used to describe the components and structure of crested gibbon songs are briefly summarized. These definitions are not necessarily applicable to songs of other (non-crested) gibbons.

2.2.2.1. Female song contributions

Adult *Nomascus* females produce great call phrases only. All great calls begin with long notes of slowly increasing frequency (termed *fa*-notes). These notes are also called *oo* notes; the latter term is used in the present study. In the course of a great call, note durations and interval durations become continuously shorter and *oo* notes gradually change to short notes of steeply increasing frequency (Figure 3). These notes are referred to as bark notes (*fb*). After the climax of the acceleration, bark notes tail off into a twitter (*fc*).

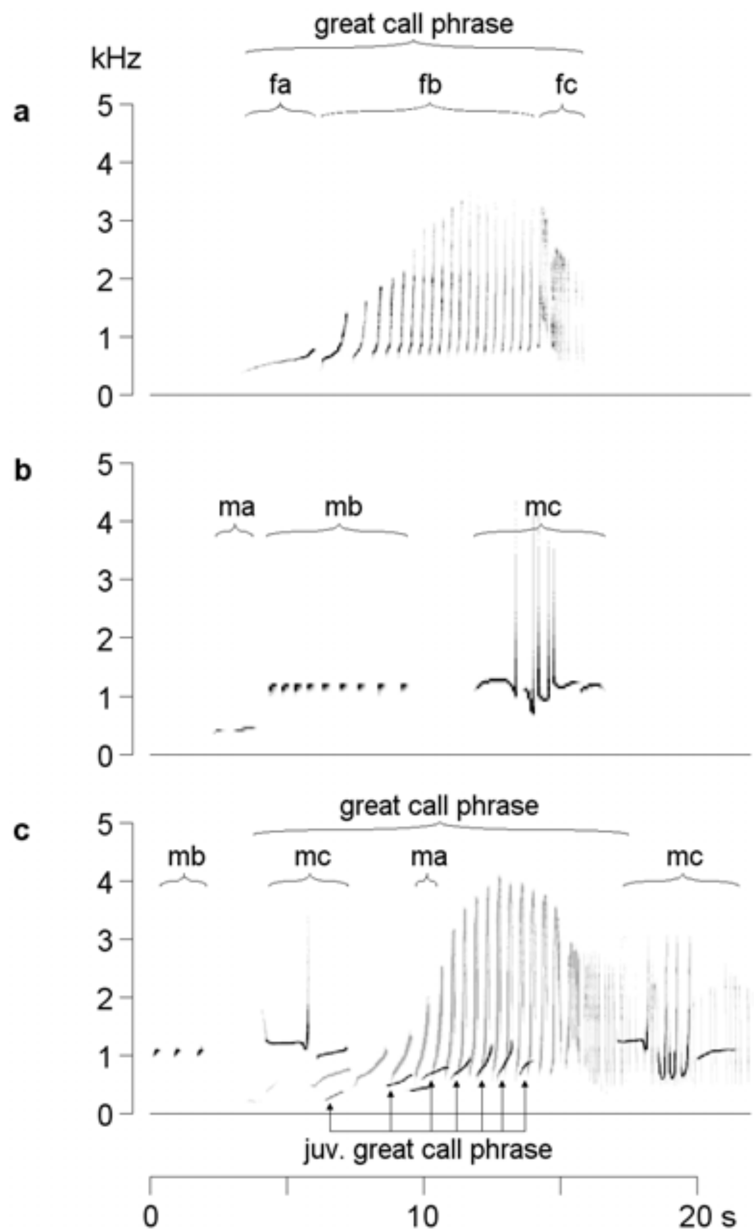

Figure 3. Sample Sonogram (from Geissmann *et al*., 2000, and Konrad and Geissmann, 2006). Sonograms showing sexual dimorphism in song phrases of the Northern white-cheeked crested gibbon: **a**. great call phrase of an adult female. The great call begins with *oo* notes (*fa*), followed by bark notes (*fb*) and ends with twitter notes (*fc*); **b**. phrases of an adult male begins with booms (*ma*), followed by staccato notes (*mb*) and ends with a multi-modulated phrase (*mc*); **c**. trio song of an adult pair and their juvenile son. The female sings a great call into the phrases of her mate, who pauses his song after a boom note (*ma*), and adds a multi-modulated phrase (*mc*) to the end of the female's great call. During her great call, her juvenile son accompanies the female with a short, great call-like phrase. In order to facilitate "reading" of this sonogram, the female contributions are artificially lightened and the juvenile phrase is darkened.

Reading the sonogram and indicating the length of different pieces of individual songs enables scrutiny of vocal differences. For example, the length of *oo* notes (*fa*), barking notes (*fb*), and twitter notes (*fc*) is different depending on the species or subspecies of crested gibbon.

2.2.2.2. Male song contributions

Fully developed song phrases of adult *Nomascus* males typically consist of three different note types (i.e., *ma*, *mb*, *mc*) (Figure 3). The boom note (*ma*) is a very deep note of constant frequency and is produced during inflation of the throat sac. Boom notes are usually produced as single notes, unlike other male notes, which usually occur in a short series (phrases). The staccato notes (*mb*) are short, relatively monotonally repeated sounds. The most conspicuous part of the male song is the multi-modulated phrase (*mc*). This phrase consists of several notes, which exhibit rapid and steep frequency modulations. Adult males typically utter a multi-modulated phrase (also called a coda) at or shortly after the climax of the female great call phrase.

In the course of a complex song bout, the male phrases are gradually built up. At the beginning of the song bout, the male produces long un-modulated notes that are precursors of the multi-modulated phrases. Later in the song bout, the phrases become more and more modulated and boom notes and staccato phrases are added.

In a fully developed duet song bout, the male singer continuously cycles through the three types of phrases (boom phrase, staccato phrase, and multi-modulated phrase, usually in this order). When the female starts a great call phrase, the male interrupts and at the end of the great call, answers with a coda (also called multi-modulated phrase or *mc*). After that, he resumes cycling through the three types of phrases.

2.2.3. Comparison of the song structure of *N. leucogenys leucogenys*, *N. leucogenys siki* and *N. gabriellae*

This section summarizes the differences between song phrases of the taxon being analyzed in this study *N. leucogenys* and *N. gabriellae* for comparative purposes, as reported by Geissmann *et al*. (2000).

Geissmann *et al*. (2000) states that complete great call phrases of adult females usually exhibit 8-18 notes in *N. l. siki* and about 15-30 (up to 39) in *N. l. leucogenys*. However, in *N. gabriellae*, great calls consist of fewer notes (5-13). Each note begins with ascending frequency in these taxa, but starting frequencies generally seem to be higher in *N. gabriellae* than in *N. leucogenys*.

In the song repertoire of adult male *N. gabriellae*, boom notes appear to be absent, in contrast to male songs of other crested gibbon taxa. Males of *N. gabriellae* produce rapid frequency modulations only in the second note of the multi-modulated phrase, whereas males of *N. l. leucogenys* and *N. l. siki* produce such up and down sweeps on the third note as well, although they are more common on the second note (Geissmann *et al*., 2000). Table 4 presents an overview of the differences in song characteristic mentioned above. For this study, a fourth taxa may be identified which likely represents characteristics intermediate between *N. l. leucogenys* and *N. l. siki*.

Table 4. List of suggested differences in song features between three Nomascus species after Geissmann et al., 2000, p.45ff.

	Song Characteristics	*N. l. leucogenys*	*N. l. siki*	*N. gabriellae*
Male Song:	Boom Phrase	Present	Present	Absent
	Stacatto Phrase	Loud, stable	Present	Soft, irregular
	Beginning Note 1	Long section of stable frequency	Long section of stable frequency	Long section of descending frequency
	Duration of Rolls	Not very fast	Not very fast	Extremely fast
	Occurrence of Rolls	On second and third note	Only on second note	Only on second note
Female Song:	Number of Notes	15-30 notes	8-18 notes	5-13 notes
	Start frequency	Low	Low	High
	Frequency overall	Remains constant	Remains constant	Ascending

2.3. Material

2.3.1. Sample size of recorded gibbon songs

In order to avoid redundancy in the data, I had to make sure that all recorded song bouts of the same group (or individual) were combined. This required being able to tell which of the song bouts I recorded in a particular area were produced by the same group and which were not. The following criteria were used to discriminate groups or individuals:

- **Position** from which the recorded group produced its song (territoriality of gibbons)
- **Simultaneous singing** of more than one group or individuals from different positions.
- **Group composition** can be deduced from the number of singers and may vary among different groups.

As the actual distribution of the group territories was unknown and the gibbon groups or individuals were generally out of sight while being recorded, some uncertainty about the actual group identity remains. When in doubt about whether two recordings were produced by the same group or by two distinct groups, I excluded recordings of inferior quality from the analysis. Due to low recording quality and thus low sonogram quality, some additional recordings were excluded from the analysis. Appendix 1 lists the number of gibbon groups whose recorded songs were found to be suitable for analysis and their locality of origin.

The amount of sound material available for analysis varied considerably among groups. Gibbon males only produce fully developed multi-modulated phrases after several minutes of producing simpler, less modulated phrases. I aimed to include only phrases in the analysis that represented the most developed stage of each male gibbon. Female crested gibbons sing only during great calls while males sing during and between each great call. Therefore, song bouts include far fewer female phrases than male phrases.

2.4. Sound analysis software

The tape-recordings were digitized with a sampling rate of 44 kHz and a sample size of 16 bit (the storage size of each recording in terms of memory used). A byte is a unit of measurement of information storage and is used to denote the number of bits that use memory on a computer. Sonagrams (time versus frequency displays) of the sound material were generated using the Raven version 1.2.1 (Cornell Laboratory of Ornithology) on a Dell XPS M1210.

2.5. Measurement procedure

For measuring various dimensions in the sonograms, I determined various characteristic positions on the sonogram line of the multi-modulated male phrases and female great call phrases. At each point I measured the time or duration (in seconds) and frequency using the measurement features implemented in the Raven software. The definition of note types, note parts, anchor points and tangents measured in this study are explained in Appendix 2 and correspond with the stylized sonograms in Appendix 3. Further details on the measuring procedure applied to the male and female phrases are provided below.

2.5.1. Multi-modulated male phrase

Only fully developed phrases were included in the analysis. A male phrase was regarded as fully developed if it consisted of at least two notes of which the second one exhibited at least one rapid frequency modulation consisting of a steep up and down sweep (roll).

Note 1 consists of two parts in the sonogram: a horizontal part and a “trough” part (see stylized sonogram in Appendix 3.1.a and 3.1.b). The maximum frequency of note 1 (reached with the terminal up-sweep) usually cannot be determined with any degree of reliability in field recordings, and is often difficult to determine even in zoo recordings (Geissmann, pers. comm). Therefore, only a local frequency maximum was measured.

Note 2 consists of three parts: An initial part, a roll part, and a terminal part. The initial and terminal parts exhibit moderate frequency modulation, whereas the roll part may include several rolls but includes at least one roll in fully developed phrases (see stylized sonogram in Appendix 3.2).

Note 3 may include one or several rolls as well, but in general, the third male notes are generally simpler in structure and no separate parts were defined for them.

2.5.2. Female great call

Females sing great call phrases or fragments of great call phrases. Only complete great call phrases were analyzed. Aborted phrases were excluded. Complete great call phrases have a stereotyped structure and can easily be recognized (Appendix 3.3). Most aborted great calls comprise less than 5 notes while most complete great calls include at least 5 notes. Great calls consist of three phases: *Oo* phase, Bark phase (accelerando-part), and twitter phase (Figure 3). *Oo* notes are identified by a frequency increase of not more than 1 kHz per second and bark notes by a frequency increase of more than 1 kHz per second. In late bark notes, the frequency increases extremely steeply and the true end point of the note (end frequency) cannot be determined reliably. However, for early bark notes the end point is visible. Therefore, it can be reliably determined if a note exceeds the critical value of 1 kHz per second. In subsequent notes the frequency gradient always increases but never decreases and so these notes can be considered bark notes.

2.6. Song variables

In order to measure acoustic characteristics of the male and female phrase, I defined 79 variables (adapted from Konrad & Geissmann, 2006). Quantitative variables were calculated from the values measured in Raven. Definitions of all variables are listed in Table 5. For each gibbon group the measurements were averaged. Therefore each individual group was characterized by one mean value for every variable defined. Durations were measured in seconds (s) and frequencies were measured in Hertz (Hz), as seen in the table below. Several variables represent relative durations as well as frequency ranges. These variables were calculated from the values of other variables. For example, the relative duration of the horizontal part of the male's first note (variable 8) is calculated by dividing the duration of the horizontal part (variable 7) by the total duration of the first note (variable 4). The required computation is clarified in the description column of Table 5 for each variable that is derived from other variables.

Table 5. Definitions of all variables that were used in this study.

Variable type	**Number**	**Description**
Male		
Overall Variables	1.	Number of notes
	2.	Duration of entire male phrase (s)
	3.	Absence (0) or presence (1) of loud staccato notes in the male song.
Note 1 Variables	4.	Duration of first note (s)
	5.	Maximum duration (s) Duration of single longest first note per individual
	6.	Minimum duration (s) Duration of single shortest first note per individual
	7.	Duration of horizontal part (s)
	8.	Relative duration of horizontal part (%) #7 in % of #4
	9.	Duration of trough part (s)
	10.	Relative duration of trough part (%) #9 in % of #4
	11.	Start frequency (Hz)
	12.	Maximum frequency of horizontal part (Hz)
	13.	Maximum frequency (Hz)
	14.	Minimum frequency (Hz)
	15.	Frequency range (Hz) Max-Min
	16.	Frequency halfway (Hz)
	17.	Frequency range to halfway point (Hz) #16 minus # 14 (frequency halfway- minimum frequency)
	18.	Relative frequency range to halfway point (%) # 17 in % of # 15
	19.	Duration to maximum bend (s) maximum bend in transition from horizontal part to trough part
	20.	Relative duration to maximum bend (%) #19 in % of #4
	21.	Frequency at maximum bend (Hz)
	22.	Duration to peak intensity (s) Duration from the beginning of the note to the point on the sonogram where the intensity of the signal is greatest (represented by the darkest grayscale value)
	23.	Relative duration to peak intensity (%) # 22 in % of #4
	24.	Frequency at peak intensity (Hz) frequency at point of peak intensity
	25.	Frequency range to peak intensity (Hz) Frequency at peak intensity (#24) minus minimum frequency (#14)
	26.	Relative frequency range to peak intensity (%) #25 in % of #15
Note 2 Variables	27.	Duration of second note (s)
	28.	Duration of initial part (s)

	29.	Relative duration of initial part (%) # 28 in % of #27
	30.	Duration of roll part (s)
	31.	Relative duration of roll part (%) # 30 in % of #27
	32.	Number of rolls
	33.	Number of “long” troughs in roll part
	34.	Duration of first roll in roll part (s)
	35.	Duration of terminal part (s)
	36.	Relative duration of terminal part (%) #35 in % of #27
	37.	Start frequency (Hz)
	38.	Maximum frequency (Hz) Maximum frequency outside of a roll or terminal up-sweep (frequency at E, H or Kin Appendix 3.2)
	39.	Minimum frequency (Hz)
	40.	Frequency range (Hz)
	41.	Minimum frequency of initial part (Hz)
	42.	Frequency range of initial part (Hz)
	43.	Frequency at first trough in roll part (Hz)
	44.	Frequency range to first trough in roll part (Hz)
	45.	Frequency at last trough in roll part (Hz) if there is more than one trough
	46.	Frequency range to last trough in roll part (Hz)
	47.	Frequency range to lowest trough in roll part (Hz)
	48.	Minimum frequency of terminal part (Hz)
Note 3 Variables	49.	Duration of third note (s)
	50.	Number of rolls
	51.	Start frequency (Hz)
	52.	Maximum frequency (Hz) outside of a roll or terminal up-sweep
	53.	Minimum frequency (Hz)
	54.	Frequency range (Hz) Max-Min(52-53)
	55.	Inter-notes frequency range (Hz) Frequency range between min frequency of note 2 (39) and start frequency of note 3 (54)
Female		
Overall variables	56.	Duration of entire great call (s)
	57.	Number of notes
	58.	Range of start frequencies (Hz) range from lowest start frequency (usually first note) to highest start frequency (usually last note) in entire great call
	59.	Number of *oo* notes
	60.	Duration of *oo* phase (s)
	61.	Relative duration of *oo* phase (%) # 60 in % of #56

	62.	Number of bark notes
	63.	Duration of bark phase (s)
	64.	Relative duration of bark-phase (%) # 63 in % of # 56
	65.	Duration of inter-phrase interval (s) Interval between first call and coda, measured as duration from start of last note in great call to start of first note in male coda. (negative value if coda starts before end of great call)
Single-note variables	66.	Duration of first *oo* note (s)
	67.	Frequency range of first *oo* note (Hz)
	68.	Duration of second *oo* note (s)
	69.	Frequency range of second *oo* note (Hz)
	70.	Duration of first bark note (s)
	71.	Frequency range of first bark note (Hz)
	72.	Duration of last bark note (s)
Successive notes variables	73.	First inter-note interval (s) the time interval between 2 notes (time span between the end of first note and the beginning of subsequent note)
	74.	Second inter-note interval (s)
	75.	Last inter-note interval (s)
	76.	First start frequency range (Hz) frequency at beginning of 2nd *oo* note minus beginning of first note
	77.	Second start frequency range (Hz) frequency at beginning of *oo* 3rd note minus beginning of second note
	78.	Last start frequency range (Hz) frequency at beginning of last note minus beginning of second to last note
SPSS grouping variable	79.	Identifies gibbon population (not an actual measured variable)

2.7. Clarification of terms

In this thesis, the term *group* refers to the social groups from which recordings were used. The songs of 42 gibbon groups were analyzed in this study (Appendix 1). The term *population* refers to the seven localities from which recordings were obtained (Figure 2). Each gibbon group is part of a population. A *geographic population* refers to the geographic area that each population falls into. Each of the seven populations is placed into either the northern or southern geographic population (detailed explanation of how populations were placed is in the Results section).

2.8. Multivariate analysis

2.8.1. Discriminant analysis

The discriminant analysis is a parametric multivariate method useful for analyzing population differences. Linear functions of the independent variables (i.e., the song variables) are formed to describe the differences between two or more populations.

The linear discriminant functions require that the independent variables have a multivariate normal distribution and that the covariance matrices are equal for all populations. But the function has been shown to be robust against deviations from multivariate normality or homogeneity of covariances (Backhaus, 1994; Lindman, 1974, p. 33; Norusis, 1994; Statsoft, 2004). It has been pointed out, however, that significance tests in discriminant analysis are particularly sensitive to correlations between the means of variables across populations and the variances (or standard deviations). This may occur if one population in a study contains a few extreme outliers, which have a large impact on the mean and also increase the variability (Statsoft, 2004). As a result, such biased means are not reliable for discrimination between populations.

The discriminant analysis also identifies the relative contribution of a variable (or a set of variables) to the separation of the populations (Rencher, 1995). I made use of this quality to estimate which of the 78 variables determined for this study contribute most to discriminating among populations (Table 5). I conducted a stepwise discriminant analysis.

In this procedure a model of discrimination is built up step-by-step (i.e., variables are included one after the other). At each step all variables are reviewed and the one that contributes the most to separating the populations (i.e., maximizes the defined criterion for selection) is included in the model. This process is repeated until either all variables are included or all redundant variables are excluded. Redundancy among the independent variables is expressed by the tolerance. The tolerance is a measure of the degree of linear association between independent variables. It is used to avoid entering a variable that is a linear combination of a variable already in the model (Norusis, 2005).

I employed two types of coefficients to assess the relative contribution of each variable (that was included in the analysis by the stepwise method) to the separation of the populations; the *standardized discriminant function coefficients* and *correlation coefficients* between the values of the function and the values of the variables.

If there are multiple populations to be compared, multiple discriminant functions are derived. In general, if there are *k* populations, *k*-1 discriminant functions can be computed (Norusis, 2005). The first function provides the most overall discrimination between populations (highest ratio of between-population variability to within-population variability), the second function provides the second highest discrimination, and so on. The functions are all uncorrelated with each other and each function makes its own unique contribution to the discrimination between populations. Computationally, the analysis performs a *canonical correlation analysis* that will determine the successive functions and values.

On the basis of the discriminant functions, cases (i.e., the recorded gibbon groups) are classified into one of the populations (i.e., the seven gibbon populations from which recordings were obtained). Because the actual population membership of each case is known, it can be compared to the predicted population membership derived from the discriminant functions. The percentage of cases classified correctly can be taken as an indicator of the effectiveness of the discriminant function.

The models derived from this analysis were cross-validated by the *leaving-one-out method*. This method involved 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 (Norusis, 2005; Deichsel & Trampisch, 1985). In summary, discriminant analysis is two methods combined, a stepwise analysis which selects variables for discriminating between groups, followed by the discriminant analysis of those variables.

2.8.2. Multi-dimensional Scaling

In addition to discriminant analysis, I also used multidimensional scaling (MDS) which deals non-parametrically with the data. MDS is a valuable method for this study because it operates on data completely differently than discriminant analysis. MDS is designed to analyze distance-like data called dissimilarity data that indicate the degree of difference (or similarity) of two things (Norusis, 2005). MDS analyzes dissimilarity data in a way that displays the structure of the distance-like data as a geometrical picture. An MDS algorithm starts with a matrix of item-item similarities, and then assigns a location of each item in a low-dimensional space, suitable for graphing or 3D visualization.

Multidimensional scaling (MDS) can be considered an alternative to factor analysis. In general, the goal of the analysis is to detect meaningful underlying dimensions that allow the researcher to explain observed similarities or dissimilarities (distances) between the investigated objects (Kruskal & Wish, 1977). In factor analysis, the similarities between objects (e.g., variables) are expressed in the correlation matrix. With MDS one may analyze any kind of similarity or dissimilarity matrix, in addition to correlation matrices. MDS is not so much an exact procedure but rather a way to "rearrange" objects in an efficient manner, so as to arrive at a configuration that best approximates the observed distances (Young & Hamer, 1994). It moves objects around in the space defined by the requested number of dimensions, and checks how well the distances between objects can be reproduced by the new configuration. In more technical terms, it uses a function minimization algorithm that evaluates different configurations with the goal of maximizing the goodness-of-fit or minimizing "lack of fit" (Deleeuw, 1977). The most common measure that is used to evaluate how well (or poorly) a particular configuration reproduces the observed distance matrix is the stress measure. The degree of correspondence between the distances among points implied by an MDS map and the matrix input by the user is measured (inversely) by a stress function (Kruskal & Wish, 1977). The stress measure attempts to reproduce the general rank-ordering of distances between the objects in the analysis. Thus, the smaller the stress value, the better is the fit of the reproduced distance matrix to the observed distance matrix (Norusis, 2005).

On the basis of the multi-dimensional scaling analysis the populations are placed on a map (Euclidean Distance Model). Because origin of each group is known it can be compared to the map which identifies them (Figure 2).

Statistical analyses were performed on a Dell XPS M1210 using the SPSS software (version 14.0). All procedures were carried out according to the SPSS (SPSS Professional Statistics) manual (Norusis, 2005). One single data file can be used for both the discriminant and the MDS analysis. In SPSS, it is not necessary to copy the data in transposed form from one file to the other. In order to use the discriminant data file for an MDS analysis in SPSS, all that needs to be changed during the MDS analysis is: in the dialog box “Create Measure from Data”, check the button “between cases”, not the default button “between variables”.

3. Results

3.1. Vocal differences between northern and southern *N. l. siki*

The sonograms in Appendix 4 represent excerpts of duet song bouts from different gibbon populations. Only sonograms of good quality and with fully developed phrases are shown. For each population, one gibbon group was chosen to represent what the sonograms of their duets look like in that area. The instantly recognizable differences between the northern and southern geographic populations in these representative sonograms are discussed below.

3.1.1. Male song

The examination of variables was the foundation for determining overall differences between note characteristics of the populations of *N. l. siki*. Several note characteristics appeared to be characteristically different between populations. The populations in the north (1) Nakai Nam Theun NBCA, Laos, (2) Hin Namno NBCA, Laos, and (3) Phong Nha Ke Bang NP, Vietnam exhibited three (rarely 4) notes in the multi-modulated phrase. Note 1 exhibited a long horizontal part with an abrubt drop in frequency, note 2 had between one and three rolls, and note 3 usually had a roll as well. In the southern populations (4) Thua Thien Hue Province, Vietnam, (5) Bach Ma NP, Vietnam, (6) Xe Sap NBCA & Xe Bang

NBCA, Laos and (7) Quang Nam Province, Vietnam there were generally 3-5 notes in the multi-modulated phrase. Note 1 appeared to have a short horizontal part, there was almost never a roll in any notes except note 2, and there was usually just one roll in note 2. The males of the southern and northern populations appear to differ in the presence of staccato notes as well (Table 4). Staccato notes in the southern populations are not audible on any of the recordings. However, staccato notes are clearly audible in all but one of the recordings from the northern populations.

In order to test these observations I compared the mean, median and standard deviation for the corresponding variable in each population (list of variables in Table 5). I averaged all of the measurements for each group in a population in order to make a comparison between populations. I had no basis for identifying a value as typical of one either northern or southern. Therefore I looked at the range of the values for a particular variable and considered any value within these ranges as representative of *N. l. siki*. Some values clearly differentiate between the northern and southern populations (Table 6).

In the above table, some of the variables do not show differentiation between geographical populations. The number of notes (variable 1) is not significantly different between the northern and southern geographical populations. The northern range is between 3.19 and 4 notes while the southern range is between 3.33 and 3.8. Thus, the southern populations fall within the range of the northern. The duration of the horizontal part (variable 7) does not show differentiation between geographic populations either. The northern range is between .96 and 1 second, while the southern range is between .5 and .99 seconds. Thus, the northern populations fall closely within the range of the southern. The durations of note 2 (variable 27) and note 3 (variable 49) do not differentiate between geographic populations (the range of the northern populations falls within the range of the southern).

Table 6. Result of the examination of male song differences between northern and southern *N. l. siki*.

Variable[a]	Calc-ulat-ion	Geographic population and population[b]						
		North 1) N=2	North 2) N=3	North 3) N=10	South 4) N=7	South 5) N=5	South 6) N=5	South 7) N=10
1) number of notes	Mean	4	3.2	3.19	3.8	3.34	3.33	3.8
	Med-ian	4	3	3	4	3.23	3	3.8
	SD	0	0.5	0.625	1.1	1.14	1	1.7
3) staccato notes absent = 0 present = 1	Mean	0.5	1	1	0	0	0	0
	Med-ian	0.5	1	1	0	0	0	0
7) duration horizontal part note 1	Mean	0.96	1.0	0.98	0.96	0.5	0.9	0.99
	Med-ian	0.96	1.01	0.97	0.98	0.46	1.2	0.98
	SD	0.47	0.24	0.366	0.28	0.8	0.3	0.29
27) duration note 2	Mean	1.24	1.24	1.47	1.36	1.5	1.3	1.34
	Med-ian	1.24	1.3	1.5	1.36	1.5	1.27	1.3
	SD	0.03	0.26	0.7	0.34	0.39	0.183	0.52
32) number of rolls note 2	Mean	2	1.5	1.95	1.4	2.2	1.7	1.4
	Med-ian	2	1.5	2	1.2	2.3	1.6	1.25
	SD	0	1	0.7	1.2	0.71	0.6	1.2
49) duration note 3	Mean	1.15	1.7	1.33	1.1	1.2	1.7	1.1
	Med-ian	1.15	1.42	1.29	1.2	1.2	1.3	1.2
	SD	0.03	0.92	1	0.22	0.15	0.1	0.47
50) number of rolls note 3	Mean	1	0.58	0.47	0.06	0.03	0.05	0.04
	Med-ian	1	0.5	0.49	0	0	0.06	0
	SD	0	0.25	1	0.2	0.14	0.6	0.2

[a] Refer to variable list in Table 5.
[b] Refers to the grouping variable which identifies gibbon populations
1 = Nakai Nam Theun NBCA, Laos, 2 groups
2 = Hin Namno NBCA, Laos, 3 groups
3 = Phong Nha Ke Bang NP, Vietnam, 10 groups
4 = Thua Thien Hue Province, Vietnam, 7 groups
5 = Bach Ma NP, Vietnam, 5 groups
6 = Xe Bang NBCA and Xe Sap NBCA, Laos, 5 groups
7 = Quang Nam Province, Vietnam, 10 groups

Two variables clearly distinguish between the northern and southern geographical populations. The presence or absence of staccato notes (variable 3) shows that in the northern geographical populations staccato notes are almost always present. In the southern groups, staccato notes were never heard. Only one social group from the northern geographic population lacked staccato notes. It is likely that the absence of staccato notes in this group was due to poor recording quality and not an actual lack of staccato notes. The number of rolls on note 3 (variable 50) also clearly differentiates the geographic populations. The southern geographic population exhibits a range of .03-.06 rolls in the third note. While the northern geographic population shows a much higher occurrence of rolls ranging from 0.47- 1 roll on note 3. Another important point is that the southern populations median for variable 50 is zero in three out of four populations whereas in the northern populations the median is 0.49 and higher.

3.1.2. Female song

Great calls appeared to consist of considerably fewer notes in the southern populations than in the northern ones (Table 7). However, the length of the great call appeared considerably longer in the southern populations. This indicates that there are longer spaces between notes in the great call of the southern populations.

Table 7. Result of the examination of female song differences between northern and southern *N. l. siki*.

Variable[a]	Calcu-lation	Geographic Population and Population[b]						
		North 1) N=2	North 2) N=3	North 3) N=10	South 4) N=7	South 5) N=5	South 6) N=5	South 7) N=10
60) length of Great Call	Mean Med-ian SD	10.48 10.5 0.53	9.75 9.98 2.5	9.47 9.65 3.47	11.5 12 2.2	11.9 11 3.5	10.4 10.4 1.1	11.46 11.7 3.7
61) number of notes	Mean Med-ian SD	15.5 15.5 1	12.8 13 2.5	13.5 13.36 5.5	10.7 10.5 1.3	10.7 11 2.2	10 11 1.5	10.7 10.8 2

[a] Refer to variable list in Table 5
[b] Refers to the grouping variable which identifies gibbon populations
1 = Nakai Nam Theun NBCA, Laos, 2 groups
2 = Hin Namno NBCA, Laos, 3 groups
3 = Phong Nha Ke Bang NP, Vietnam, 10 groups
4 = Thua Thien Hue Province, Vietnam, 7 groups
5 = Bach Ma NP, Vietnam, 5 groups
6 = Xe Bang NBCA and Xe Sap NBCA, Laos, 5 groups
7 = Quang Nam Province, Vietnam, 10 groups

The two variables clearly distinguish between the northern and southern geographic populations. The length of the great call (variable 60) exhibits a range difference of more than a second between the two geographic populations. The northern populations' range between 9.47 and 10.48 seconds is significantly shorter than the southern populations' range of 10.4 seconds to 11.9 seconds. The number of notes (variable 61) in the northern populations ranges from 12.8 to 15.5 notes while the southern populations have a range of 10.0 to 10.7 notes. The values of the mean, median, and standard deviation for this variable do not overlap between geographic populations in any case.

3.2. Multivariate analysis

3.2.1. Discriminant analysis

I ordered and coded all populations in a north-south direction in this text, in the SPSS data files and the output plots as follows:

1 = Nakai Nam Theun NBCA, Laos, 2 groups

2 = Hin Namno NBCA, Laos, 3 groups

3 = Phong Nha Ke Bang NP, Vietnam, 10 groups

4 = Thua Thien Hue Province, Vietnam, 7 groups

5 = Bach Ma NP, Vietnam, 5 groups

6 = Xe Bang NBCA and Xe Sap NBCA, Laos, 5 groups

7 = Quang Nam Province, Vietnam, 10 groups

The discriminant analysis, using the above seven predefined populations effectively separates between southern and northern *N. l. siki*. The samples overlap largely with the other populations of their geographic population. Function 1, which separates northern and southern *N. l. siki* has wide scale, ranging from about -8 to +8. The separation between the taxa on Function 1 is, therefore, quite large. Function 2, on the other hand, ranges from about -3 to +2.

3.2.2. Selected elements of the SPSS output for the Disciriminant Analysis

3.2.2.1 Stepwise Statistics

I conducted a stepwise discriminant analysis. In this procedure a model of discrimination is built up step-by-step (i.e., variables are included one after the other). At each step all variables are reviewed and the one that contributes the most to separating the populations (i.e., maximizes the defined criterion for selection) is included in the model. This process is repeated until either all variables are included or all redundant variables are excluded. Table 8 presents the variables included in the analysis. The tolerance is a measure of the degree of linear association between independent variables. It is used to avoid entering a variable that is a linear combination of a variable already in the model (Norusis, 2005).

Table 8. Variables in the Analysis

Step	Variable	Tolerance	F to Remove	Wilks' Lambda
1	Var 3	1.000	103.056	
2	Var 3	0.970	26.001	0.128
	Var 58	0.970	7.541	0.054
3	Var 3	0.952	17.880	0.057
	Var 58	0.660	9.133	0.036
	Var 64	0.680	3.948	0.023
4	Var 3	0.939	15.201	0.028
	Var 58	0.501	13.370	0.025
	Var 64	0.542	6.089	0.015
	Var 66	0.731	4.592	0.013

3.2.2.2 Summary of Canonical Discriminant Functions

Computationally, the analysis performs a *canonical correlation analysis* that will determine the successive functions and *eigenvalues* (Table 9). For each canonical function, the eigenvalue is the ratio of the between-groups to within-groups sums of squares and this is an estimate of the quality of a discriminant function or a combination of functions. If there are multiple populations to be compared, multiple discriminant functions are derived.

In general, if there are *k* populations, *k*-1 discriminant functions can be computed. The first function provides the most overall discrimination between populations (highest ratio of between-population variability to within-population variability), the second function provides the second highest discrimination, and so on (Table 10). The functions are all uncorrelated with each other and each function makes its own unique contribution to the discrimination between populations (Table 11).

Table 9. Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	47.823[a]	97.3	97.3	0.990
2	0.693[a]	1.4	98.7	0.640
2	0.553[a]	1.1	99.8	0.597
4	0.084[a]	0.2	100.0	0.278

[a] First 3 canonical discriminant functions were used in the analysis.

Table 10. Wilks' Lambda

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 4	0.007	175.195	24	0.000
2 through 4	0.351	37.164	15	0.001
3 through 4	0.594	18.472	8	0.018
4	0.923	2.848	3	0.416

Table 11. Standardized Canonical Discriminant Function Coefficients

Variable	Function			
	1	2	3	4
Var 3	–0.801	0.618	–0.031	0.201
Var 58	1.108	0.676	–0.221	0.513
Var 64	0.782	0.501	0.859	0.494
Var 66	0.600	0.760	0.204	–0.625

For each population the location of the point that represents the means for all variables is determined in the multivariate space defined by the variables in the model. These points are called group centroids (Table 12). They are the un-standardized canonical discriminant functions evaluated at group means.

Table 12. Functions at Group Centroids

Variable 79[a]	**Function**		
	1	2	3
1	–5.954	–2.913	–1.097
2	–7.834	1.411	–0.554
3	–9.080	0.082	0.263
4	4.568	–0.060	0.415
5	4.223	–0.177	0.586
6	5.469	0.462	–1.518
7	4.577	–0.023	0.298

[a] Refers to the grouping variable which identifies gibbon populations
1 = Nakai Nam Theun NBCA, Laos, 2 groups
2 = Hin Namno NBCA, Laos, 3 groups
3 = Phong Nha Ke Bang NP, Vietnam, 10 groups
4 = Thua Thien Hue Province, Vietnam, 7 groups
5 = Bach Ma NP, Vietnam, 5 groups
6 = Xe Bang NBCA and Xe Sap NBCA, Laos, 5 groups
7 = Quang Nam Province, Vietnam, 10 groups

Each variable in each discriminant (canonical) function can be interpreted as the larger the standardized coefficient, the greater the contribution of the respective variable to the discrimination between groups. However, these coefficients do not tell us between which of the groups the respective functions discriminate. We can identify the nature of the discrimination for each discriminant (canonical) function by looking at the means for the functions across groups. We can visualize how the two functions discriminate between groups by plotting the individual scores for the two discriminant functions (Figure 4).

VAR00079 in Figure 4 refers to the grouping variable which identifies gibbon populations but is not an actual measured variable. Figure 4 demonstrates that the geographic populations are distinct.

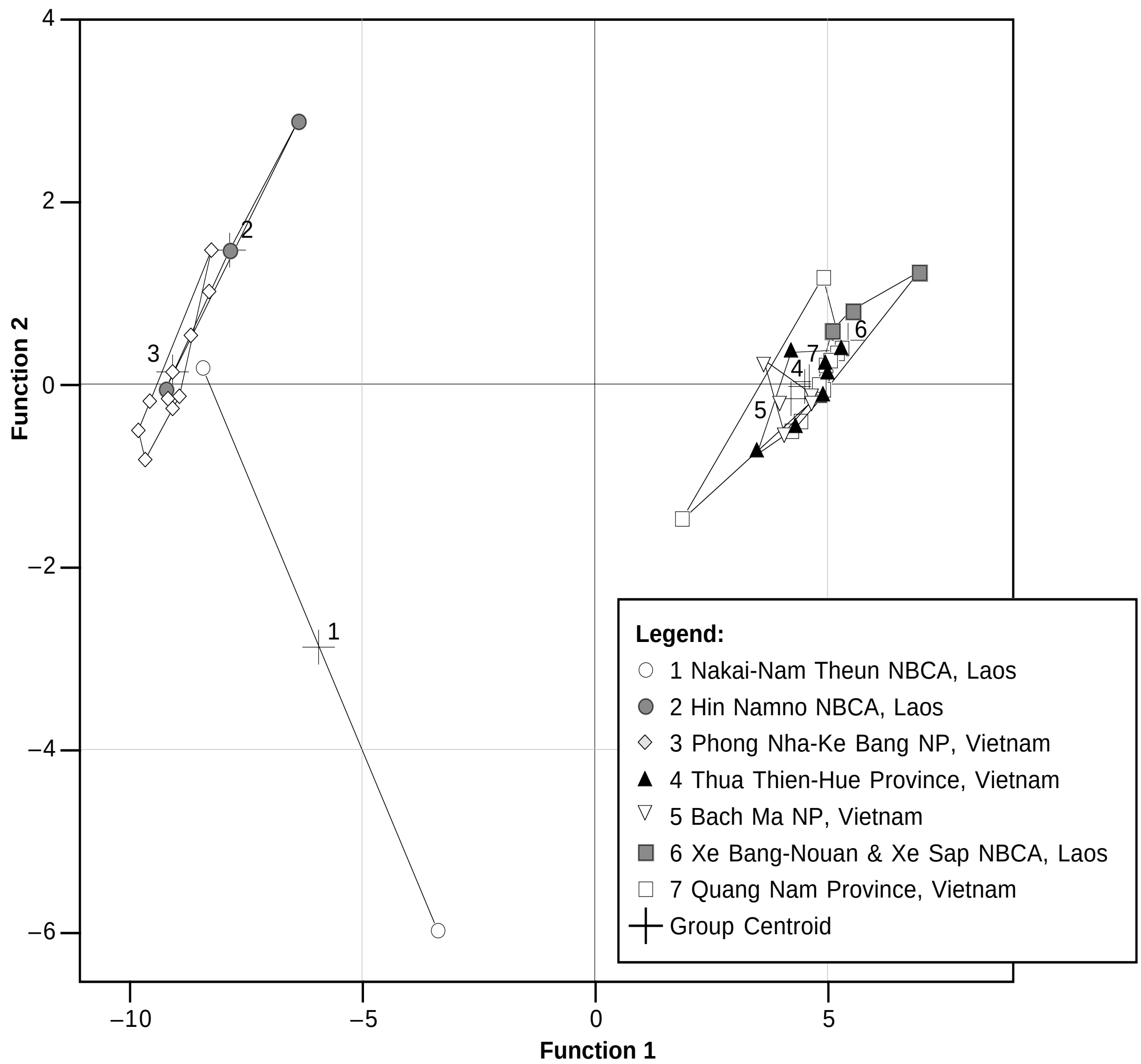

Figure 4. Two dimensional display of the Canonical Discriminant Functions

3.2.2.3 Classification Results

A major purpose to which discriminant analysis is applied is the issue of predictive classification of cases. Classification is used once a model has been finalized and the discriminant functions have been derived to show how well we can predict to which group a particular case belongs. Once the classification scores have been computed for a case, it is easy to decide how to classify the case: in general the case is classified as belonging to the group for which it has the highest classification score. A common result that one looks at in order to determine how well the current classification functions predict group membership of cases is the classification matrix. The classification matrix shows the number of cases that were correctly classified (on the diagonal of the matrix) and those that were misclassified (Norusis, 2005).

The classification table is used to assess the performance of discriminant analysis. In the table the rows are the observed categories of the dependent and the columns are the predicted categories of the dependents (McLachlan, 2004). When prediction is perfect, all cases will lie on the diagonal. The percentage of cases on the diagonal is the percentage of correct classifications. This percentage is called the hit ratio.

The hit ratio must be compared not to zero but to the percent that would have been correctly classified by chance alone (Huberty, 1984). For two-group discriminant analysis with a 50-50 split in the dependent variable, the expected percent is 50%. For unequally split 2-way groups of different sizes, the expected percent is computed in the "Prior Probabilities for Groups" table in SPSS, by multiplying the prior probabilities times the group size, summing for all groups, and dividing the sum by the number of groups (N)

(Norusis, 2005). If group sizes are known a priori, the best strategy by chance is to pick the largest group for all cases, so the expected percent is then the largest group size divided by the number of groups (N) (Huberty, 1994).

Leave-one-out classification is available as a form of cross-validation of the classification table. Under this option, each case is classified using a discriminant function based on all cases except the given case. This is thought to give a better estimate of what classificiation results would be in the population (McLachlan, 2004). If each case is classified into the group for which it has the highest predicted probability, the observed and predicted groups can be compared (Norusis, 2005). It is possible for the model to be correct and informative but for the classification to be poor. When there are groups of unequal sizes, cases will be more likely to be classified to the larger groups regardless of how well the model fits (Norusis, 2005).

As can be seen in Table 13, 54.8% of original grouped cases are correctly classified and 45.2% of cross-validated grouped cases are correctly classified. This indicates a better than chance accuracy in the classification predictions of the discriminant analysis. The expected percent that would be correctly classified by chance alone is the largest population size divided by the number of groups, in this case 10 (groups) divided by 42 (total groups) which equals .238 or 23.8 %. These results are better than chance because in the classification results more than half of the original grouped cases are correctly classified. Populations 1-3 are “northern *N. l. siki*” populations, and 4-7 are “southern *N. l. siki*” populations. Grey cells indicate incorrectly predicted group membership which occurs only among groups of the “northern *N. l. siki*” populations and among groups of the “southern *N. l. siki*” populations, but not between the two forms of *N. l. siki*.

The classification results show that the discriminant analysis assigns each population to the correct geographic population (north or south) 100% of the time.

Table 13. Classification Results of the discriminant analysis.

		Var. 79[a]	Predicted Group Membership							Total
			1	2	3	4	5	6	7	
Original	Count	1	**1**	0	1	0	0	0	0	2
		2	0	**1**	2	0	0	0	0	3
		3	0	1	**9**	0	0	0	0	10
		4	0	0	0	**0**	0	0	7	7
		5	0	0	0	0	**1**	0	4	5
		6	0	0	0	0	0	**4**	1	5
		7	0	0	0	0	1	1	**8**	10
	%	1	**50.0**	0.0	50.0	0.0	0.0	0.0	0.0	100.0
		2	0.0	**33.3**	66.7	0.0	0.0	0.0	0.0	100.0
		3	0.0	10.0	**90.0**	0.0	0.0	0.0	0.0	100.0
		4	0.0	0.0	0.0	**0.0**	0.0	0.0	100.0	100.0
		5	0.0	0.0	0.0	0.0	**20.0**	0.0	80.0	100.0
		6	0.0	0.0	0.0	0.0	0.0	**80.0**	20.0	100.0
		7	0.0	0.0	0.0	0.0	10.0	10.0	**80.0**	100.0
Cross-validated[b]	Count	1	**2**	0	0	0	0	0	0	2
		2	0	**1**	2	0	0	0	0	3
		3	0	1	**9**	0	0	0	0	10
		4	0	0	0	**0**	1	0	6	7
		5	0	0	0	0	**0**	0	5	5
		6	0	0	0	0	0	**4**	1	5
		7	0	0	0	1	2	1	**6**	10
	%	1	**100.0**	0.0	0.0	0.0	0.0	0.0	0.0	100.0
		2	0.0	**33.3**	66.7	0.0	0.0	0.0	0.0	100.0
		3	0.0	10.0	**90.0**	0.0	0.0	0.0	0.0	100.0
		4	0.0	0.0	0.0	**0.0**	14.3	0.0	85.7	100.0
		5	0.0	0.0	0.0	0.0	**0.0**	0.0	100.0	100.0
		6	0.0	0.0	0.0	0.0	0.0	**80.0**	20.0	100.0
		7	0.0	0.0	0.0	10.0	20.0	10.0	**60.0**	100.0

[a] Refers to the grouping variable which identifies gibbon populations

1 = Nakai Nam Theun NBCA, Laos, 2 groups

2 = Hin Namno NBCA, Laos, 3 groups

3 = Phong Nha Ke Bang NP, Vietnam, 10 groups

4 = Thua Thien Hue Province, Vietnam, 7 groups

5 = Bach Ma NP, Vietnam, 5 groups

6 = Xe Bang NBCA and Xe Sap NBCA, Laos, 5 groups

7 = Quang Nam Province, Vietnam, 10 groups

[b] Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case.

3.2.2.4. Discussion of Discriminating variables

The discriminant analysis selected four variables to include in the analysis. These variables were chosen in this order 3, 58, 64, and 66 (refer to Table 5 and Table 8). Only the first of these is a male variable, the others all describe the female call. The discriminant analysis selected these variables because they contribute the most to separating the populations. The other variables were excluded because they are either redundant with the selected variables or they do not contribute to separating groups. The first variable selected to discriminate between groups was variable 3 (presence or absence of staccato notes). Because this variable is so good at separating between groups, the analysis selects it as the best variable to separate any groups and proceeds from there. This changes not only the number of variables that are selected for the rest of the analysis, but also which variables are selected as next-best ones for further differentiating among the populations. The second variable selected to discriminate between variables was variable 58 (range of start frequencies in the female's great call). Variable 64 (relative duration of bark phase in the female's great call) was selected as the third discriminating variable between the geographic populations. Variable 66 (duration of the first *oo* note in the female's great call) was selected last.

3.2.3. Multi-dimensional scaling

The result of the multi-dimensional scaling analysis (MDS) closely mirrors that of the discriminant analysis. Dimension 1 separates the two geographic populations by 100%, (i.e., there is no overlap between northern and southern). MDS clearly separates between northern and southern *N. l. siki*, but not between any other populations. MDS creates a proximity measure for the variables. The proximities are then represented in a geometrical space, e.g. in a Euclidean space. Figure 5 is essentially a scatter-plot of the objects in different two-dimensional planes. The interpretation of dimensions represents the final step of the analysis. The actual orientations of the axes from the MDS analysis are arbitrary, and can be rotated in any direction. The unambiguous results of the MDS analysis can be see in Figure 5 which identifies the populations within the geographic populations that they belong.

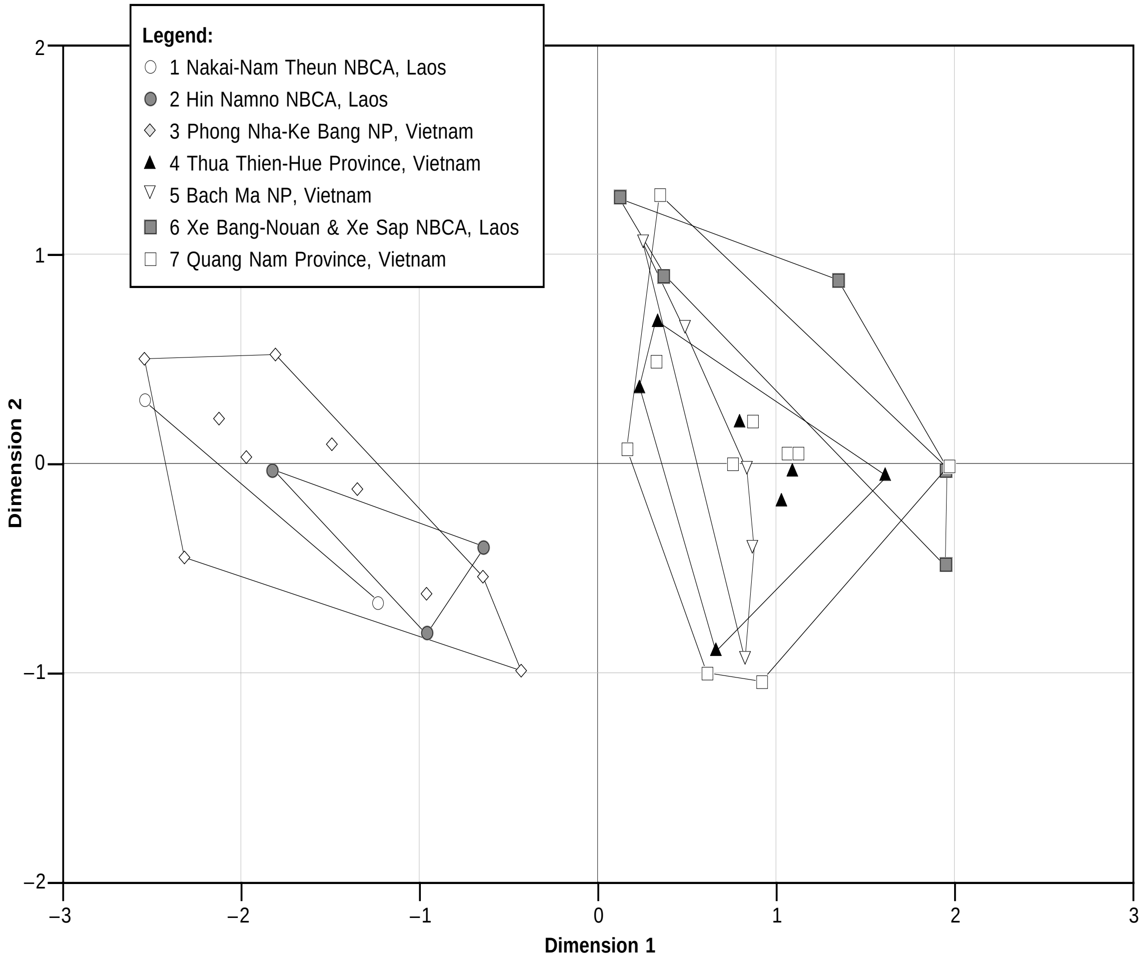

Figure 5. Two dimensional display of the results of multi-dimensional scaling.

4. Discussion

The questions formulated at the outset of this study can be answered as follows:

1) Are there vocal differences between localities of *N. leucogenys siki* occurrence?

Yes. The MDS and discriminant analysis clearly separates between northern and southern *N. l. siki*, but not between any other populations. This is maintained by the fact that within each geographical population each group cannot be differentiated from each other based on vocal data (refer to classification results Table 13). The classification results show that the discriminant analysis assigns each population to the correct geographic population (north or south) 100% of the time. This indicates that the populations within each geographic population have a similar song. The currently named taxonomic entity *N. leucogenys siki* can be split into two distinct geographic populations based on vocal data. (1) Northern (Phong Nha Ke Bang NP, Vietnam; Hin Namno NBCA, Laos; and Nakai Nam Thuen NBCA, Laos) and (2) Southern (Bach Ma NP, Vietnam; Quang Nam Province, Vietnam; Quang Tri Province, Vietnam; and Xe Bang & Xe Sap NBCA, Laos). Figure 6 indicates "northern" and "southern" for the geographic populations.

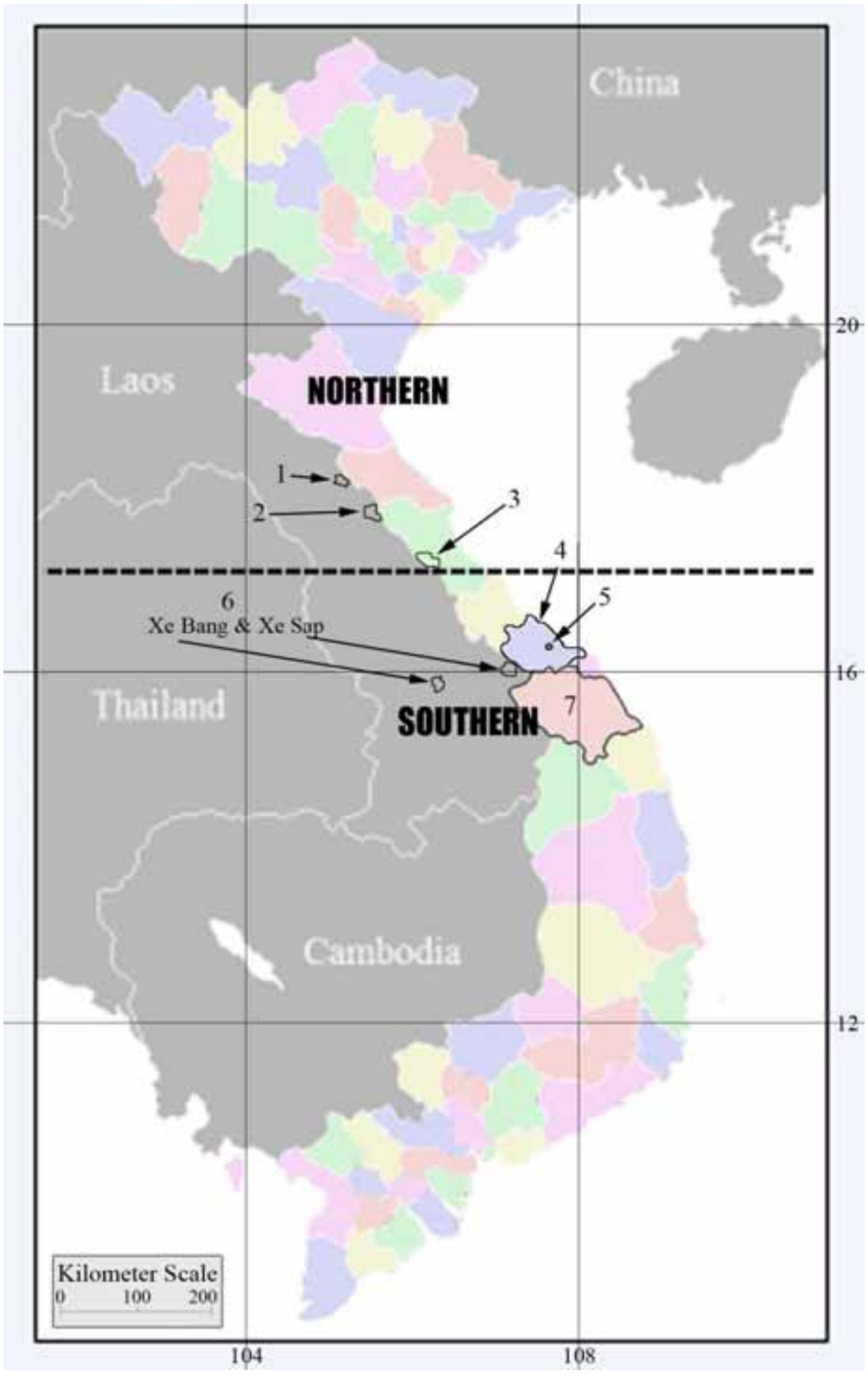

Figure 6: Map showing the possible boundary between northern and southern *N. l. siki*
1 = Nakai Nam Theun NBCA, Laos, 2 groups
2 = Hin Namno NBCA, Laos, 3 groups
3 = Phong Nha Ke Bang NP, Vietnam, 10 groups
4 = Thua Thien Hue Province, Vietnam, 7 groups
5 = Bach Ma NP, Vietnam, 5 groups
6 = Xe Bang NBCA and Xe Sap NBCA, Laos, 5 groups

7 = Quang Nam Province, Vietnam, 10 groups

2) What differences can be presented between the vocalizations of northern *N. l. siki* (Phong Nha Ke Bang NP, Vietnam; Hin Namno NBCA, Laos, Nakai Nam Thuen NBCA, Laos) gibbons and southern *N. l. siki* gibbons (Bach Ma NP, Vietnam; Quang Nam Province, Vietnam; Thua Thien Hue Province, Vietnam; Xe Bang & Xe Sap NBCA, Laos)?

There are many vocal differences between the northern and southern groups of *N. l. siki*. The most significant differences are summarized below. The discriminant analysis selected four variables to include in the analysis. The discriminant analysis selected these variables because they contribute the most to separating the populations. The other variables were excluded because they are either redundant with the selected variables or they do not contribute to separating populations. The first variable selected to discriminate between populations was variable 3 (presence of absence of staccato notes). In the northern geographic populations staccato notes were heard in almost every recording. One sample from Nakai-Nam Theun is shown as an outlier. This is because no staccato notes are audible in this sample (in contrast to all other samples from the northern geographic population). This outlier is probably an artifact of the poor quality and the shortness of the corresponding sound-recording and not due to an actual lack of staccato notes. Staccato notes were not heard on any recordings from the southern geographic population.

The second variable selected by the discriminant analysis was variable 58 (range of start frequencies of the female great call phrase). This variable was measured by calculating the range in Hertz from the lowest start frequency (usually the first note) to the highest start frequency (usually last note) in the great call. The southern geographic population exhibited a greater range of start frequencies (average range 549.5 kH) than the northern geographic population (average range 216.7 kH). Variable 64 (relative duration of bark phase in the female's great call) was selected as the third discriminating variable between the geographic populations. This variable is measured by calculating the percent of the duration of the bark phrase within the duration of the entire great call. The southern geographic population had a longer bark phrase in proportion to the entire great call (average relative duration was 62% of the great call) compared to the northern geographic population (average relative duration was 58% of the great call). Variable 66 (duration of the first *oo* note in the female's great call) was selected last. The first *oo* note of the southern geographic population (average 1.9 seconds) was longer than the first *oo* note of the northern geographic population (average 1.33 seconds).

In addition to the variables chosen by the statistical analysis, I observed several other variables that appear to be consistently different between groups. These variables were likely not chosen by the discriminant analysis because they were either redundant or not as useful for discriminating between groups as other variables. One other variable from the male's multi-modulated phrase clearly distinguish between the northern and southern geographic populations. The number of rolls on note 3 (variable 50) clearly differentiates the geographic populations. The southern geographic population exhibits few rolls on the third note compared to the northern geographic population (Table 6).

There are two variables that clearly distinguish between the northern and southern geographic populations in the female's great call phrase. The length of the great call (variable 60) exhibits a range difference of more than a second between the two geographic populations (Table 7). The length of the great call is consistently shorter in the northern geographic population compared to the southern. The number of notes in the great call phrase (variable 61) is another distinguishing variable. The northern geographic population exhibits a higher number of notes while the southern geographic population exhibits less notes. Because the northern geographic population exhibits more notes overall (variable 61) within a shorter great call (variable 60), this indicates that there must be longer spaces between notes in the great call of the northern geographic population.

4.1. Statistical analysis

Multivariate analyses have been applied in a number of primatological studies to compare vocal characteristics between individuals, groups and populations (Arcady, 1996; Chapman & Weary, 1980; Dallmann & Geissmann, 2001; Maeda & Masataka, 1987). In the present study, this procedure proved suitable for discrimination between gibbon geographic populations of gibbons. In general, discriminant analysis is a very useful tool (1) for detecting the variables that allow the researcher to discriminate between different (naturally occurring) groups, and (2) for classifying cases into different groups with a better than chance accuracy (Norusis, 2005). A further merit of multivariate analysis is that the actual measurements can be used (i.e. coding into discrete character states is not necessary). On the basis of the discriminate model it was possible to verify the differences between vocalizations in geographic populations.

4.2. Summary

All crested gibbons (*Nomascus*) occurring in central Vietnam are currently regarded as *Nomascus leucogenys siki* (Geissmann, 1995; Geissmann *et al*., 2000, Konrad & Geissmann, 2006). Based on a comparison of gibbon songs, it has previously been reported that gibbons in a large area in central and Laos and Vietnam are neither typical *N. l. siki* nor *N. l. leucogenys*. Both fur coloration and vocal data from this area suggest either a large hybrid zone with one subspecies gradually replacing the other, or the existence of a previously unrecognized taxon, or a combination of the two (Konrad & Geissmann, 2006).

Descriptions of gibbon songs aid species and subspecies definition but for these gibbon taxa, good recordings of song vocalizations were lacking. My research remedied this problem allowing more accurate identification of these gibbons and aiding in recognition of wild populations. The primary focus of this study was to determine if vocal differences exist between populations of *N. l. siki*. Therefore, I examined the vocal diversity of four *Nomascus* populations in Vietnam and three in Laos in order to assess their taxonomic relationships.

The results of the present study clearly show that the subspecies currently known as *N. l. siki* can be split into two distinct geographic populations based on vocal data. Results of the discriminant analysis show that it is possible to categorize each of the seven study populations into two geographic populations (1) Northern and (2) Southern. The result of the multi-dimensional scaling analysis also supports my interpretation that northern and southern *N. l. siki* are clearly distinct. This indicates that considerable vocal diversity exists between the gibbons of the northern and southern regions.

I cannot exclude that an intergrade zone may exist, but if it does exist, it can be narrowed down to a relatively small area (Figure 6) Additional tape-recordings from Phou Xang He NBCA and Dong Phou Vieng NBCA in Laos, from southern Quang Binh Province and Quang Tri Province in Vietnam would help to refine results further.

This study has provided one piece of evidence for separating what is currently known as *N. l. siki* into two taxonomic entities. The analysis of morphological and genetic variability of Vietnamese and Laotion gibbons provide avenue for further pursuit. Very little is known about the gibbons in the genus *Nomascus* regarding their ecology and behavior, and even the taxonomy and geographic ranges of taxa is disputed. Therefore, there is much left to learn about these animals.

4.3. Future research

In future studies, this research should be extended to include the neighbouring areas of Laos and Vietnam. It is essential to collect more data from various areas not only in the proposed contact zone but also in areas where known taxa are assumed to occur in non-hybrid (i.e., type localities of taxa) form. One such study will be completed in 2007. I will record Vietnamese gibbons in several sites farther north than any of the sites used in this study (Appendix 5). This study should further elucidate the taxonomy of the crested gibbons in southern Indochina. Such data could be relevant for assessing the actual degree of mixture (if any) between species and subspecies and in identifying possible taxonomic boundaries.

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Appendices

Appendix 1. A list of the number of phrases that were analyzed for each gibbon group

Population	Locality	Group No.	Song Bouts	M phrases	F phrases
Phong Nha Ke Bang NP	N 17.28° 45.5’ E 106.19° 55.9’ Heading 119°	1	2	2	2
	N 17.28° 45.5’ E 106.19° 55.9’ Heading 29°	2	4	4	4
	N 17.28° 55.5’ E 106.19° 60.9’ Heading 320°	3	2	2	1
	N 17.28° 55.5’ E 106.19° 60.9’ Heading 60°	4	2	2	2
	N 17.28° 31.1 E 106.20° 04.5’ Heading 128°	5	10	10	3
	N 17.28° 31.1’ E 106.20° 04.5’ Heading 239°	6	8	6	8
	N 17.28° 13.5’ E 106.23° 03.4’ Heading 123°	7	5	5	3
	N 17.28° 19.7’ E 106.22° 56.2’ Heading 235°	8	10	10	9
	N 17.28° 18.1’ E 106.22° 54.4’ Heading 222°	9	10	10	4
	N 17.28° 13.5’ E 106.22° 55.1’ Heading 99°	10	8	8	8
Quang Nam	Phuoc Xuan	1	2	2	2
	Ma Cooih	1	3	3	3
	Ma Cooih	2	4	4	4

	Ma Cooih	3	4	4	4
	Ma Cooih	4	3	3	3
	West La Dee	1	6	6	6
	Phuoc My	1	2	2	2
	Tabhing	1	4	4	4
	Tabhing	2	4	4	4
	Tabhing	3	7	7	7
Bach Ma NP		1	7	7	7
		2	7	7	7
		3	7	7	7
		4	7	7	7
		5	3	3	3
Laos	Nakai Nam Theun	1	3	3	3
		2	4	4	4
	Hin Namno	1	4	4	4
		2	4	4	4
		3	2	2	2
	Xe Bang & Xe Sap	1	3	3	3
		2	2	2	2
		3	4	4	4
		4	2	2	2
		5	2	3	2
Thua Thien Hue	Hong Ha	1	5	5	5
	A Roang	1	5	5	5
	Hong Van	1	4	4	4
	Thuong Quang	1	2	2	2
	Houng Nguyen	1	5	5	5
	Thi Tran Phu Loc	1	5	5	5
	Loc Thuy	1	6	6	5

Appendix 2. Definition of note types, note parts, anchor points and tangents

Appendix 2.1. The first note of the male's multi-modulated phrase

Note 1	Unit[a]	Description
Horizontal Part		The first of the two distinctive parts of the note, characterized by a relatively constant frequency level (the sonogram line runs almost horizontally).
Trough Part		The second part in the note characterized by a marked frequency decrease to the note frequency minimum and a subsequent rapid and steep increase (the sonogram line forms a trough).
Anchor Points and Tangents		
A	s & Hz	Beginning of note
B	s & Hz	Half duration of note
C	s & Hz	End of Horizontal part
D	s & Hz	Maximum bend in transition from horizontal part to trough part
E	s & Hz	Frequency minmum
e	s	End of note
Peak Intensity		Refers to the position on the sonogram line where the intensity of the signal is greatest (represented by the darkest grayscale value)

[a]Unit of measurement in seconds (s) or Hertz (Hz).

Appendix 2.2. The second note of the male's multi-modulated phrase

Note 2	Unit[a]	Definition
Initial Part		The first of the three distinctive parts of the note, characterized by a marked frequency decrease to a local note frequency minimum
Roll Part		The second part in the note, characterized by including at least one roll. In the case of several rolls a short trough occurs between two successive rolls.
Terminal Part		The third part of the note, characterized by a relatively constant frequency and a more of less marked frequency increase at the end of the note
"Long" trough between rolls		A trough between two subsequent rolls is considered as "long" if a short part of constant frequency can be recognized. Thus, the local frequency minimum consists of a plateau of low frequency.
Anchor Points and Tangents		
E	s & Hz	Beginning of Note
F	s & Hz	Frequency minimum of initial part
G	s & Hz	Boundary between initial part and roll part
H	s & Hz	Frequency minimum between two successive rolls
Hi	s & Hz	If the roll part consists of more than two rolls, there is at least one additional local frequency minimum
J	s & Hz	Boundary between roll part and terminal part, defined as end of steep frequency increase
K	s & Hz	Frequency minimum of terminal part
k	S & Hz	End of note

[a]Unit of measurement in seconds (s) or Hertz (Hz).

Appendix 2.3. The female's great call phrase

Great Call	Unit[a]	Definition
Oo Note		Frequency increase from beginning to end of note is no more than 1 kHz per second
Bark Note		Frequency increase from beginning to end of note is more than 1 kHz per second
Oo Phase		A phase including all oo notes of the great call (Notes 1-3 in Appendix 3.3)
Bark Phase		A phase including all bark notes of the great call (Notes 4-7 in Appendix 3.3)
Anchor points and Tangents		
P	s & Hz	Beginning of note (first oo note)
Q	s & Hz	End of note
R	s & Hz	Beginning of note (second oo note)
S	s & Hz	End of note
T	s & Hz	Beginning of note (last oo note)
U	s & Hz	End of note
V	s & Hz	Beginning of note (first bark note)
W	s & Hz	End of note
X	s & Hz	Beginning of note (second bark note)
x	s	End of note
Y	s & Hz	Beginning of note (third bark note)
y	s	End of note
Z	s & Hz	Beginning of note (last bark note)
z	s	End of note

[a]Unit of measurement in seconds (s) or Hertz (Hz).

Appendix 3. Stylized sonograms

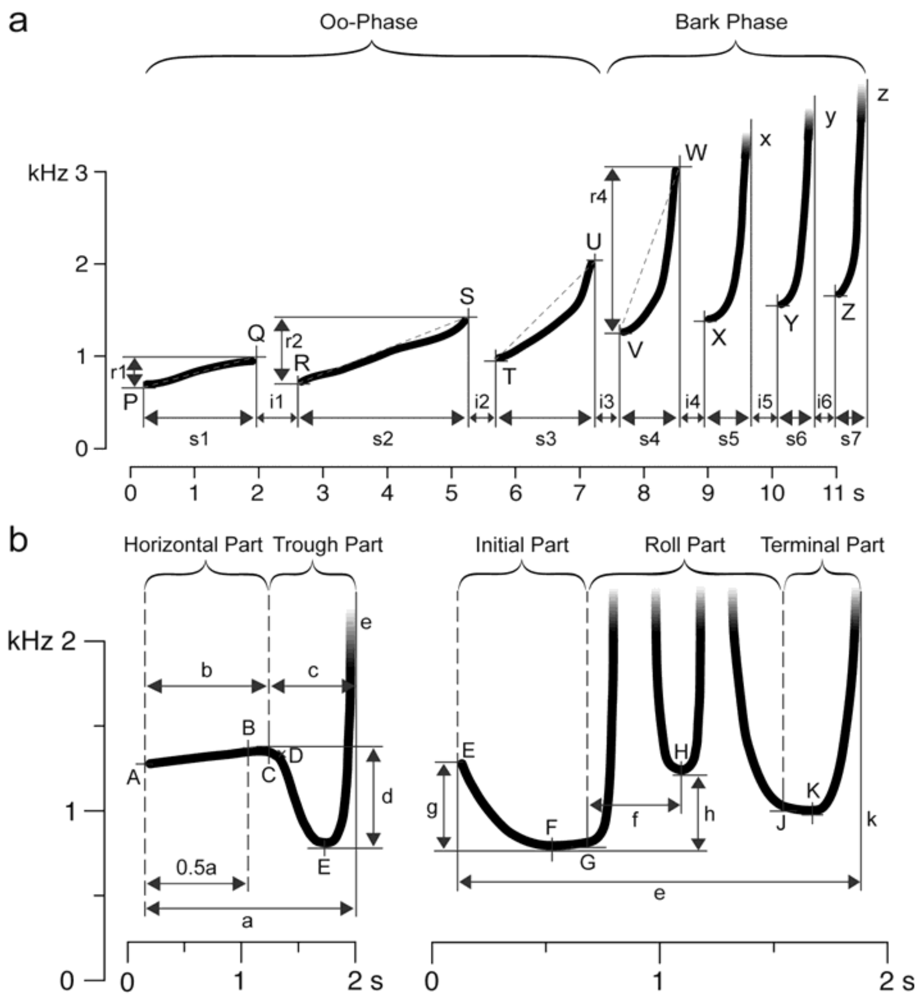
Appendix 3.1. The first note of the male's multi-modulated phrase

Comon sonographic shape of first notes in male phrases (only fundamental frequencies shown)

N. l. leucogenys and northern *N. l. siki*

N. gabriellae and southern *N. l. siki*

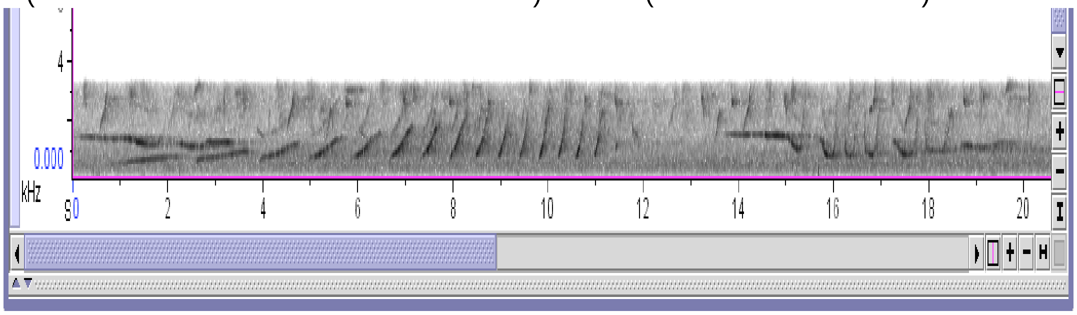
Appendix 3.2. Stylized sonograms showing measurement points



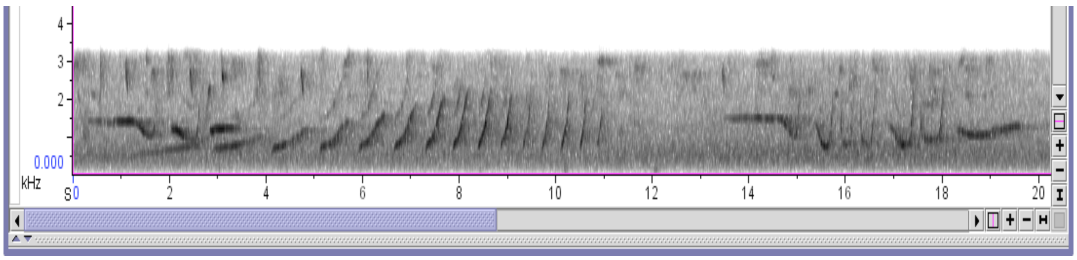
Stylized sonograms (from Konrad & Geissmann, 2006) of (a) the female great call phrase. Durations and ranges are measured on this note corresponding with Appendix 2.3. Great calls of female crested gibbons have a stereotyped structure and can easily be recognized. (b) the first note and the second note of the male's multi-modulated phrase, showing the split in different parts, all measurement points and tangents, durations and ranges measured on these notes. Durations and ranges are measured on this note corresponding with Appendices 2.1 and 2.2. The initial and terminal parts of the second note exhibit moderate frequency modulation, whereas the roll part may include several rolls but includes at least one roll in fully developed phrases. Only fundamental frequencies are shown.

Appendix 4. Excerpts of duet song bouts from each gibbon population

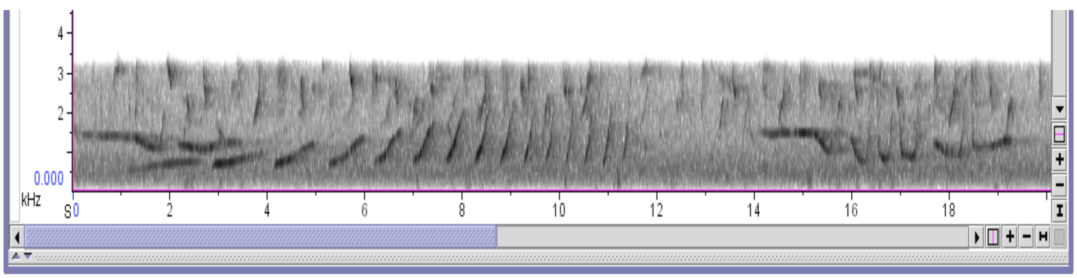
Great call phrase of the female (---) Multi-modulated phrase of the male (-----------------------------)



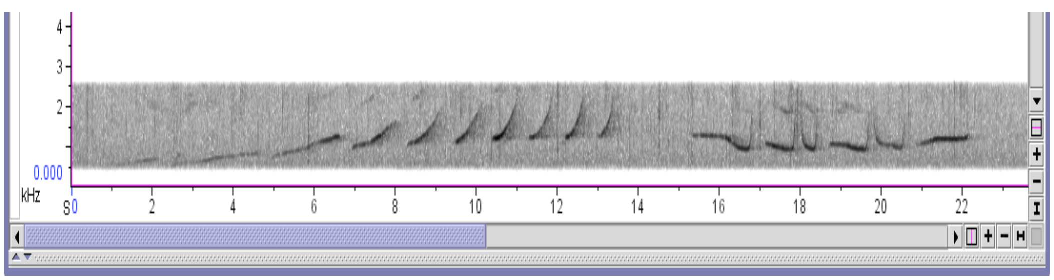
Group 1 from Nakai Nam Thuen NBCA, Laos



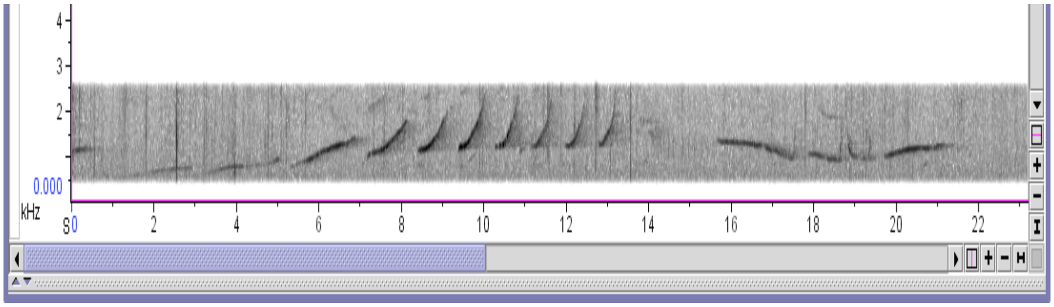
Group 2 from Hin Namno NBCA, Laos



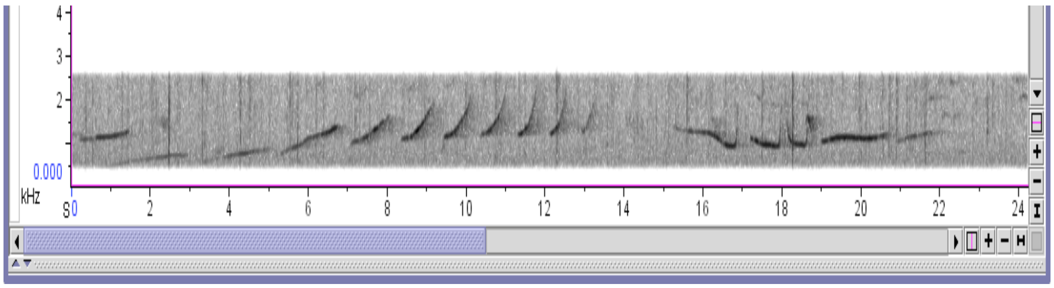
Group 10 from Phong Nha Ke Bang NP, Quang Binh Province, Vietnam



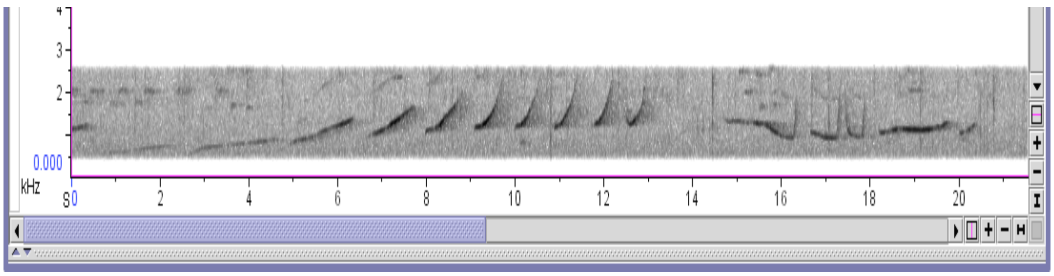
Group 1 from Hong Ha commune, Quang Tri Province, Vietnam.



Group 5 from Bach Ma NP, Thua Thien Hue Province, Vietnam



Group 2 from Xe Bang NBCA, Laos.



Group 3 from Tabhing commune, Quang Nam Province, Vietnam

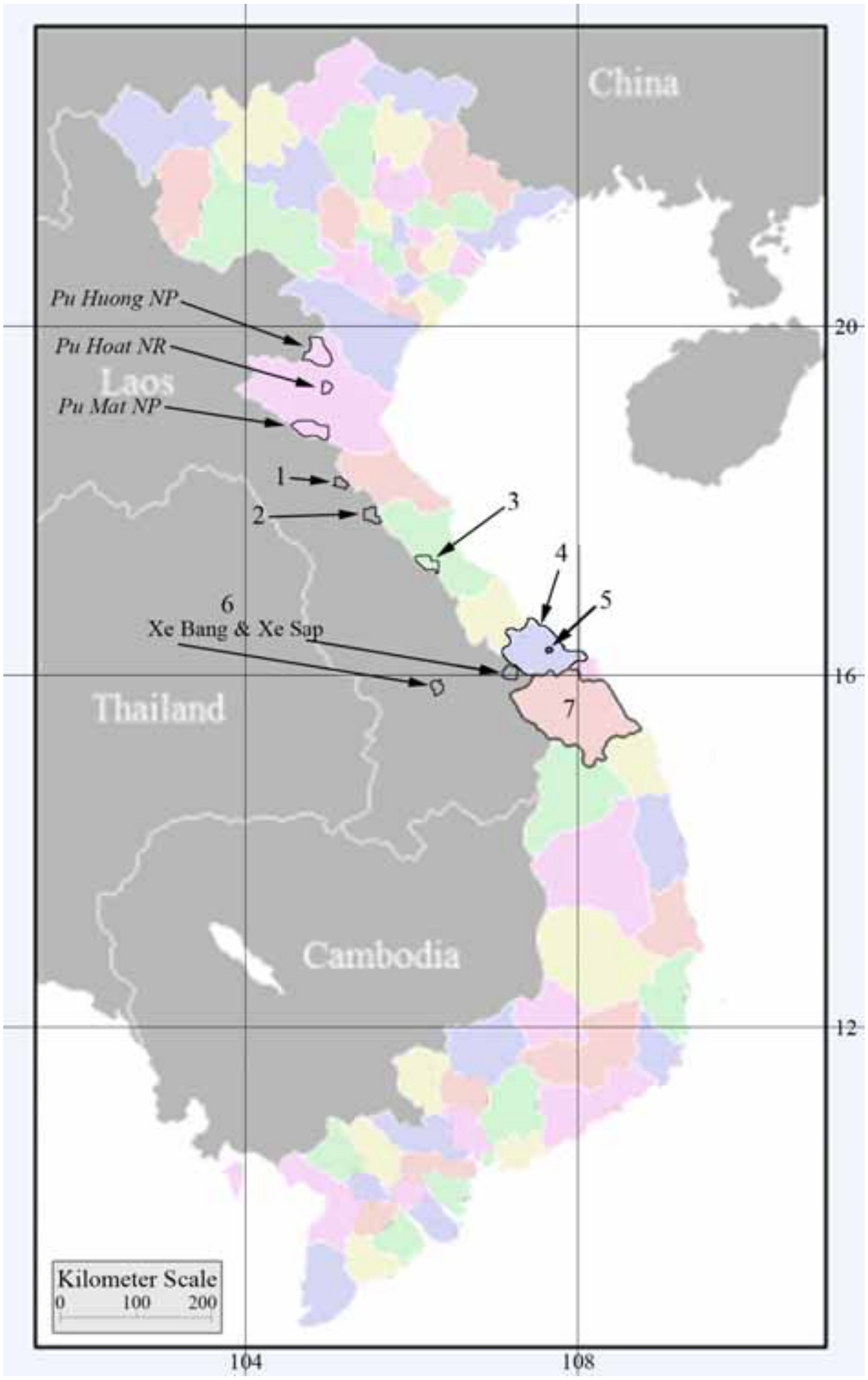
Appendix 5. Sites of future research in Vietnam

Information on the present occurrence of N. l. leucogenys has been gathered from previous contacts in Vietnam and at present, localities to be included in a future study have been selected. Site choices were also based on reports of gibbon distribution by Mr. Nguyen Manh Ha of Vietnam National University's CRES (2005).

N. l. leucogenys: Pu Huong National Park (NP), Nghe An Province, at least 7 groups (Nguyen Manh Ha, 2005)

N. l. leucogenys: Pu Hoat Nature Reserve (NR), Nghe An Province, at least 5 groups and 1 individual (Nguyen Manh Ha, 2005)

N. l. siki: Pu Mat National Park (NP), Nghe An Province, number of groups is unknown, several confirmed sites (Geissmann et al., 2000)



1 = Nakai Nam Theun NBCA, Laos, 2 groups
2 = Hin Namno NBCA, Laos, 3 groups
3 = Phong Nha Ke Bang NP, Vietnam, 10 groups
4 = Thua Thien Hue Province, Vietnam, 7 groups
5 = Bach Ma NP, Vietnam, 5 groups
6 = Xe Bang NBCA and Xe Sap NBCA, Laos, 5 groups
7 = Quang Nam Province, Vietnam, 10 groups