Vocal Diversity and Taxonomy of the Crested Gibbons (Genus *Nomascus*) in Cambodia

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1. Introduction

1.1 Gibbon systematics

The gibbons or small apes (family Hylobatidae) are a relatively small and uniform group of primates distributed throughout the tropical rain forests of South-east Asia (Chivers, 1977; Geissmann, 1995a; Marshall & Sugardjito, 1986). They live in monogamous, territorial family groups, which typically consist of an adult pair and 1-3 immature offspring (Brockelman & Srikosamatara, 1984; Chivers, 1977, 1989; Leighton, 1987).

The systematic relationships among gibbons appear to be difficult to resolve. So far, several revisions of gibbon systematics have been published (e.g. Geissmann, 1995a; Groves, 1972, 2001; Marshall & Sugardjito, 1986; Pocock, 1927) and various scenarios have been proposed to describe the radiation of this group (e.g. Chivers, 1977; Geissmann, 2002b; Groves, 1972, 1993; Haimoff et al., 1982). The phylogenetic relationships among the gibbon taxa are still under debate and various different views exist (e.g. Chivers, 1977; Creel & Preuschoft, 1984; Garza & Woodruff, 1992; Geissmann, 2002b; Groves, 1972; Haimoff et al., 1982; Roos & Geissmann, 2001). Most authors agree that the gibbons can be divided into four systematic groups, which have been recognized as subgenera (i.e. *Bunopithecus, Hylobates*, *Nomascus,* and *Symphalangus*) for several years (Marshall & Sugardjito, 1986, Prouty et al, 1983a). Each of these four groups is, among other characteristics, identified by a distinctive karyotype (Prouty et al., 1983a, b), song structure (Geissmann, 2002b), and DNA sequences (Garza & Woodruff, 1992; Hall et al., 1998; Hayashi et al., 1995; Roos & Geissmann, 2001; Zhang, 1997).

The participants of a Workshop on Primate Taxonomy held in Orlando (Florida, USA) in February 2000 proposed to elevate the four gibbon subgenera to genus rank. This view was affirmed by a comparative analysis of DNA sequences by Roos & Geissmann (2001). They found that “the molecular distances among the four gibbon subgenera are in the same range as those between *Homo* and *Pan*, or even higher” and proposed, as a consequence of these findings, “to raise all four gibbon subgenera to genus rank”. I follow this recommendation in the present study and, therefore, refer to the four major gibbon divisions as genera (Table 1.1).

Table 1.1. Gibbon classification used in the present study, showing the four main divisions of the family Hylobatidae (from Geissmann, 2002b).

Genus	Diploid number of chromosomes	Other division names	Species
Bunopithecus	38	Hoolocks	*B. hoolock*
Nomascus	52	*Concolor* group, crested gibbons	*N. concolor* *N.* sp. cf. *nasutus* *N. gabriellae* *N. leucogenys*
Hylobathes	44	*Lar* group	*H. agilis* *H. klossii* *H. lar* *H. moloch* *H. muelleri* *H. pileatus*
Symphalangus	50	Siamangs	*S. syndactylus*

1.2 The use of gibbon vocalization for gibbon systematics

All gibbon species are known to produce elaborate, loud, long and stereotyped patterns of vocalization often referred to as “songs” (Geissmann, 1993, 1995a, 2002a; Haimoff, 1984a; Marshall & Marshall, 1976). Preferentially, song bouts are uttered in the early morning and last for about 10–30 minutes. In most gibbon species, mated individuals combine their respective songs in the form of well-coordinated duets.

The stereotyped, highly species-specific structure of gibbon songs, and the fact that it appears in typical form in gibbons taken from their parents at an early age, first led authors to suggest that these characteristics are inherited rather than learned (Boutan, 1913; Carpenter, 1940; Marler, 1963).

In more recent years, this view has been supported by studies of the vocal patterns of hybrid gibbons, either bred in captivity or naturally occurring in the wild in areas with interspecies hybridization (Brockelman & Schilling, 1984; Geissmann, 1984, 1993; Marshall & Sugardjito, 1986; Mather, 1992; Tenaza, 1985). These studies revealed that hybrids of the *lar* group exhibit a hybrid-specific song repertoire and a song structure, which differs from the songs of both parental species. Hybrid songs are intermediate between the parental types in several aspects, suggesting that species-specific song characteristics in gibbons are largely genetically determined.

It has previously been demonstrated that gibbon song characteristics are useful for assessing systematic relationships on the genus and the species level and for reconstructing gibbon phylogeny (Creel & Preuschoft, 1984; Geissmann, 1993, 2002a; Haimoff, 1983; Haimoff et al., 1982, 1984; Marshall et al., 1984). Furthermore, Geissmann (2002b), using cladistic methods, compared three different types of data (i.e. 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. The author concluded that vocal data appeared to be better suited for reconstructing gibbon phylogeny than the other two data sets.

1.3 Crested gibbons (genus *Nomascus*)

Crested gibbons are characterized by various morphological and anatomical features. For instance, crested gibbons are intermediate in body weight between the large siamang (*Symphalangus*) and the small gibbons of the genus *Hylobates* (Geissmann, 1993). They exhibit a marked sexual dimorphism in fur coloration with adult males being mainly black and adult females being mainly buffy-colored with a black longitudinal streak on the crown. The name "crested gibbons" refers to the erect and elongated crown hair of adult males (Geissmann, 1995a). For more anatomical and morphological characteristics of the genus *Nomascus* and morphological distinguishing features for the species identification within this genus see Geissmann (1994, 1995a), Geissmann et al. (2000), Groves (1972, 2001) and Schilling (1984a).

In terms of singing behavior, crested gibbons exhibit a number of unique characteristics that set them apart from the other gibbons. Geissmann et al. (2000, p.39) describe them as follows:

> "Song bouts of mated pairs of the genus *Nomascus* typically are duet song bouts (as in *Bunopithecus* and *Symphalangus*). In contrast, mated pairs in all species of the genus *Hylobates* are known to produce male solo song bouts *and* duet song bouts (or male solo song bouts and female solo song bouts) (Geissmann, 1993, 2002a). In crested gibbons, solo songs appear to be produced by non-mated individuals only, and are heard more frequently from males than from females (Geissmann, unpublished data)."

According to Geissmann (2002a, p.65), the genus *Nomascus* exhibits the highest degree of sex-specificity in its songs, as "there is no overlap between the sexes in note repertoire and no overlap in the phrase repertoire. Female song contributions consist of great-calls only which consist of female-specific notes, whereas males produce short phrases only, and these consist of male-specific notes."

Traditionally, the crested gibbons have been regarded as a single species, *Hylobates concolor* (e.g. Groves, 1972; Marshall & Sugardjito, 1986), but more recent studies suggest that this group should be split into several distinct species (Geissmann, 1997; Geissmann et al., 2000).

The most widely accepted and best-described *Nomascus* species are *N. concolor*, *N. leucogenys* and *N. gabriellae* (eastern black crested gibbon, white-cheeked crested gibbon, and yellow-cheeked crested gibbon, respectively). They were first recognized as separate species mainly due to anatomical differences (Dao Van Tien, 1983; Groves, 1993; Groves & Wang, 1990; Ma & Wang, 1986). 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 western black crested gibbon, tentatively identified as *N.* sp. cf. *nasutus* (Geissmann 1997; Geissmann et al., 2000).

The taxonomic affinities of a further form, the southern white-cheeked crested gibbon (*N. l. siki*), have been under debate. There is some difference of opinion as to whether *siki* is a subspecies of *H. leucogenys* or of *H. gabriellae*. Some authors even recommend giving *siki* full species rank (Groves, 2001; Zhang, 1997). The chromosomes of this taxon were reported to differ from those of both (Couturier & Lernould, 1991), and *siki* appears to occupy an intermediate position between the two species both in the light facial hair pattern of the male (Schilling, 1984a) as well as in the distribution area (Geissmann et al., 2000).

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

Crested gibbons occur in tropical evergreen and less seasonal parts of semi-evergreen rain forests of Indochina (i.e. southern China, Vietnam, Laos and Cambodia). The southern white-cheeked crested gibbon (*N. l. siki*) and the yellow-cheeked crested gibbon (*N. gabriellae*) are restricted to the southern parts of this distribution range (Figure 1.1). *Nomascus l. siki* occurs in central Vietnam and Laos, whereas *N. gabriellae* is distributed in eastern Cambodia, southern Vietnam, and possibly southernmost Laos (Geissmann et al., 2000).

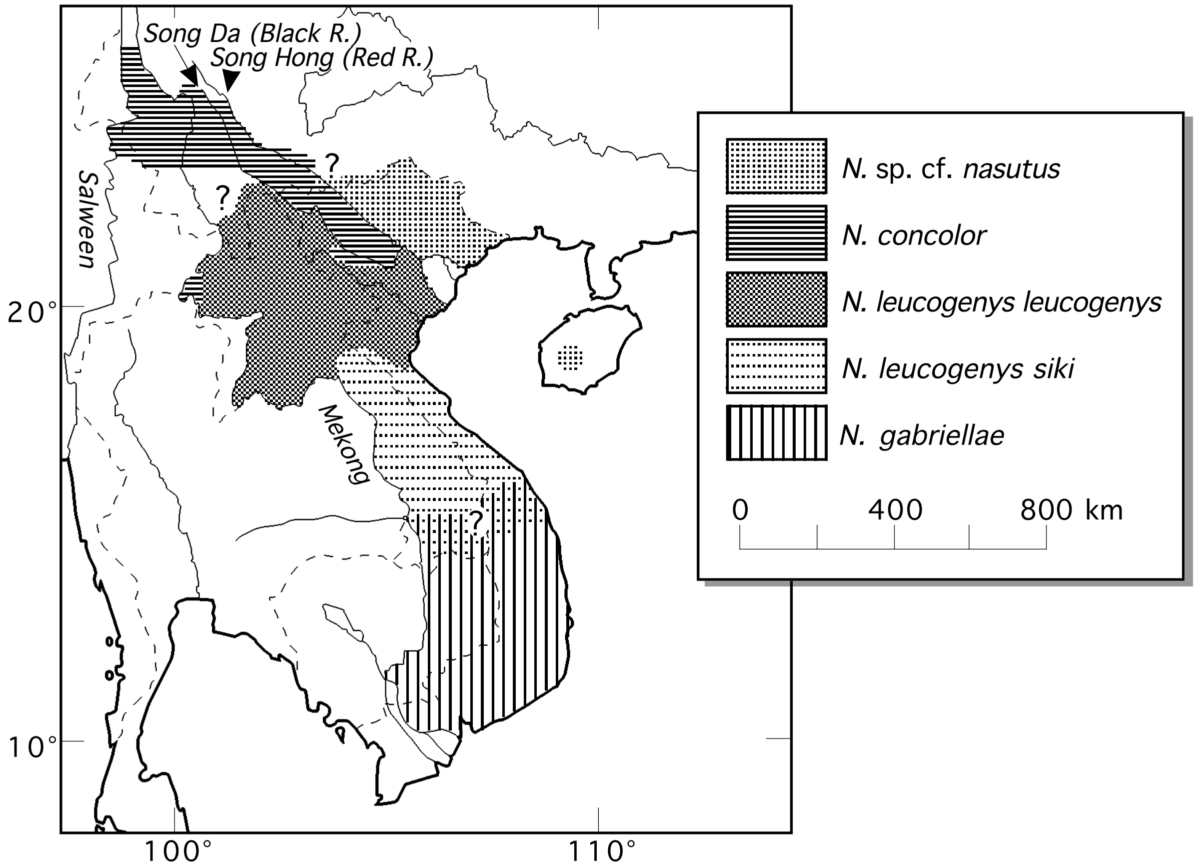

Figure 1.1. Distribution of the species of the genus *Nomascus* (from Geissmann et al., 2000). Question marks refer to, from north to south, (1.) the unknown survival (and identity) of Chinese gibbons east of the red river in Yunnan province; (2.) a large apparent gap in the distribution area of gibbons 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.

The distribution ranges of different gibbon taxa are often separated by rivers and straits, and sympatry occurs only rarely (e.g. Marshall & Sugardjito, 1986). The only extensive sympatry occurs between the siamang and gibbons of the *lar* group. Furthermore, three smaller areas of sympatry among members of the *lar* group (with some hybridization) are known (e.g. Brockelman & Gittins 1984; Geissmann, 1991; Gittins, 1978; Marshall & Sugardjito, 1986; Mather, 1992).

Contact zones between species of the *concolor* group may exist as well but have not been studied. Dao Van Tien (1983) and Ma & Wang (1986) reported small areas of sympatry between *N. concolor* and *N. leucogenys* in northern Vietnam and southern Yunnan, China, respectively, but these reports remain unconfirmed (Geissmann et al., 2000).

Another contact zone may occur between *N. l. siki* and *N. gabriellae* (Figure 1.1). Delacour (1951) and Groves (1972) regarded museum specimens from Saravane and Savannaket (southern Laos) as intergrades between *N. gabriellae* and *N. l. siki*.

Geissmann et al. (2000) re-examined the museum specimens from Savannaket and found no conclusive evidence for intergradation, with specimens more resembling *N. l. siki*. Gibbon songs from the Bolovens Plateau (southern Laos, south of Saravane and Savannaket) sounded more like *siki*, but museum specimens from the same localities clearly look like *gabriellae* (Geissmann et al., 2000). Gibbon songs from Xe Piane (southernmost Laos), however, appear to be intermediates between *gabriellae* and *siki* (Geissmann, 1995a).

A similar pattern was found in Bach Ma National Park (central Vietnam): Gibbon songs from this area clearly differ from *N. gabriellae* (Tallents et al., 2001). At least one museum specimen from the vicinity of Bach Ma (Thua Luu, south of Hue) looks like *N. l. siki* and actually is the holotype of *Hylobates concolor siki*, whereas another specimen from the same locality clearly is of the *N. gabriellae* phenotype (Geissmann, 1995a; Geissmann et al., 2000).

Consequently, Geissmann (1995a) suggested that "a contact zone of unknown extent, possibly with some hybridization, may occur between the respective distribution areas of *H. gabriellae* and *H. leucogenys siki* in southern Vietnam and Laos, but not much data from that zone is available". It is difficult to draw any conclusion from this preliminary and very conflicting data. Geissmann et al. (2000, p.49) argued that

> "the easiest interpretation of these preliminary data on the 'gibbons between *N. l. siki* and *N. gabriellae*' probably is to postulate a broad intergrade zone in which one species gradually replaces the other. The possibility should not be ruled out, however, that previously unrecognized taxa may occur in this large area. This second interpretation would be supported if it could be demonstrated that (1) songs of several individuals in a particular area follow the same pattern, and that (2) songs do not exhibit a clinal change from the typical *N. gabriellae* to the typical *N. l. siki* pattern as one moves from the *N gabriellae* area in the south to the *N. l. siki* area in the North, but that the cline is interrupted over larger areas in which song patterns remain stable."

The postulated large contact zone between the respective distribution ranges of *N. l. siki* and *N. gabriellae* was reported to be situated in southern Vietnam and Laos (Geissmann et al., 2000). But north-eastern Cambodia may belong to the contact zone as well. This possibility was first indicated when two gibbon song fragments were tape-recorded by Tim Redford in Virachey National Park in northern-eastern Cambodia. These recordings appeared to differ from the typical song pattern of *N. gabriellae* and resembled the song of *N. l. siki* (Geissmann, pers. comm.). Unfortunately, the small sample size and the low sound quality of the recordings did not permit any reliable conclusions do be drawn.

North-eastern Cambodia, southern Vietnam and southern Laos are part of the same ecoregion, the Greater Annamites (Baltzer et al., 2001). The Annamites are a chain of mountains lying east of the Mekong River. Together with the surrounding lowlands, the mountains make up the *Greater Annamites Ecoregion*. The northern part of the mountain chain is running between Laos and Vietnam. The southern part lies in southern Vietnam with the western slopes extending to east Cambodia. The Greater Annamites are characterized by rich tropical evergreen forests, which harbor a distinctive biodiversity. In two areas, this habitat reaches into Cambodia: (1) The Cambodia/Laos/Vietnam Tri-border Forests (TBF) are located in the very north-east of Cambodia; (2) the Southern Annamite Western Slopes (SAWS) are located further to the south. Both areas (TBF and SAWS) are separated from each other by extensive areas of open dry forests and grasslands, and several major rivers running east to west.

The only taxon of crested gibbons occurring in Cambodia is currently thought to be *N. gabriellae*, distributed in the eastern part of the country (east of Mekong River). Consequently, all Cambodian gibbon populations east of Mekong River are assigned to this species, although no museum specimens from this area exist and no studies on the morphological, genetic or vocal characteristics of the Cambodian crested gibbons have ever been conducted so far.

If all crested gibbon populations in Cambodia really belonged to *N. gabriellae*, they should all be expected to exhibit the species-specific song characteristics typical of *N. gabriellae*, none of the patterns specific to *N. l. siki*, and they should be a vocally homogenous group, comparable to other gibbon populations of one taxon (e.g. Dallmann & Geissmann, 2001, submitted).

1.4 Aims of my study

It is the aim of this study to examine the vocal diversity among different local populations of crested gibbons in Cambodia. I will try to answer the following questions:

(1) Do all crested gibbons in Cambodia exhibit the same song pattern?

(2) To which degree do their song patterns correspond to, or deviate from, the previously described patterns of *N. gabriellae* and *N. l. siki*?

(3) If the crested gibbon populations in Cambodia exhibit deviations from the previously described patterns of *gabriellae* and *siki*, does this result in a high intra-population variability in some or all local populations, or do local populations exhibit a stable, population-specific song patterns?

(4) What are the relationships among the local populations, as indicated by their song patterns?

(5) Does the geographical distribution of song patterns suggest the presence of (a) genetical boundary or (b) a cline among the crested gibbons in Cambodia?

I will assess the degree of inter-population and intra-population variability in song patterns. Furthermore, I will examine, whether changes in vocal characteristics follow a recognizable geographical pattern. This will be relevant for evaluating the taxonomic relationships among *Nomascus* populations. For instance, a gradual change from the typical *N. gabriellae* song pattern in the south to the typical *N. l. siki* song pattern in the north would indicate the occurrence of a large hybridization belt with one species gradually replacing the other. On the other hand, if song characteristics were stable over large areas and changed relatively abruptly from one group of localities to another, this would imply the existence of a genetic boundary between two gibbon taxa.

A possible shift from one song pattern to another may be influenced by geographical barrier (e.g. large rivers, open habitat or forests which do not support gibbons etc.). Evidence for genetic isolation between any two of my sample sites could help to locate a possible subspecies or species boundary. Such a finding could be relevant for population management and conservation strategies in Cambodia.

Finally, I will compare my findings from Cambodia with the available gibbon data from southern Laos and Vietnam in order to assess the systematic relationships of populations currently referred to *N. l. siki* and *N. gabriellae*.

2. Material and Methods

2.1 Field work methods

2.1.1 Time schedule for the field study

For data acquisition, I spent 116 days in Cambodia. Table 2.1 shows how this amount of time was split into different activities. I spent the largest part of my time in Cambodia in the forest tape-recording gibbon vocalizations. An almost equal amount of time was spent for traveling. Traveling was very time-consuming due to the remoteness of most recording sites and the poor infrastructure in these regions. The time I stayed in Phnom Penh (capital) and Banlung (provincial capital of Rattanakiri) was used for organizing the field trips. Minor fractions of the time were devoted to interviews with local people prior to some field trips and to a brief field survey to the western part of the country where another gibbon species (*Hylobates pileatus*) occurs.

Table 2.1. Amount of time dedicated to different activities during my stay in Cambodia.

Activity	Amount of time	
	in days	in %
Data acquisition (forest)	34	29
Traveling	32	28
Phnom Penh (capital)	23	20
Banlung (provincial capital)	11	9
Interviews	8	7
Hylobates Survey	8	7
Total	116	100

2.1.2 Recording sites

The tape-recordings of gibbon songs included in the present study originated from three different areas in Cambodia and two separate areas in Vietnam (Table 2.2, Figure 2.1). These areas are shortly described in the following section. A further area (Lomphat) was surveyed during this field trip as well, although no gibbon recordings were obtained.

Samling Logging Concession

The Samling Logging Concession is contained within three provinces in eastern Cambodia (i.e. Mondulkiri, Kratie, and Kampong Cham). It is bordered by Phnom Prich Wildlife Sanctuary to the north and Snoul Wildlife Sanctuary and the Cambodian-Vietnamese border to the south. This area is a mosaic of many different habitat types and appears to support a very rich wildlife (e.g. Clements, 2003; Desai & Vuthy, 1996; Timmins & Ou Rattanak, 2001; Walston et al., 2001). The rain forests in the Samling Logging Concession have been exploited by logging to various extents. In recent years, conservation efforts started in this area in order to limit hunting of key species and to prevent illegal logging. It is one of the priority areas for the “Wildlife Conservation Society” (WCS) in Cambodia.

In 2002, Benjamin Rawson, PhD student at the Australian National University Canberra, Australia, started the first study on the ecology and behavior of wild yellow-cheeked crested gibbons in the Samling Logging Concession.

Table 2.2. List of field sites where tape-recordings were carried out, with coordinates, information on estimated gibbon density, recoding dates and identity of recordists [1]

Locality	Province, region	Pooled	Coordinates	Gibbon density [2]	Survey and recording Date	Conductor of survey and / or recordist [3]
Trung Khanh District	Cao Bang, NE Vietnam	Cao Bang	106 31’ E 22 54’ N	Intermediate	May & Aug. 2002	TG, TDH & LQT
Bach Ma NP	Thua Thien Hue, C Vietnam	Bach Ma	107 51’ E 16 13’ N	Intermediate	April 2001	TG
Taveng District	Rattanakiri, NE Cambodia	Virachey	107 18’ E 14 11’ N	High	March 2003	RK
Veunsai District	Rattanakiri, NE Cambodia	Virachey	107 00’ E 14 12’ N	High	March 2003	RK
Mas Village	Rattanakiri, NE Cambodia	Poey	107 08’ E 13 57’ N	Low	April 2003	RK
Khamaeng Village	Rattanakiri, NE Cambodia	Poey	107 00’ E 13 57’ N	Low	April 2003	RK
Lomphat District	Mondulkiri, E Cambodia	Lomphat	106 41’ E 13 10’ N	Absent (or low?)	May 2003	RK
Samling LC Coupe 2A	Mondulkiri, E Cambodia	Samling	unknown	unknown	April 2000 & March 2002	FG & PD
Samling LC Coupe 3	Mondulkiri, E Cambodia	Samling	106 56’ E 12 09’ N	High	April 2002	TG
Samling LC Coupe 5	Mondulkiri, E Cambodia	Samling	106 55’ E 12 15’ N	Low	Jan. 2003	RK

[1] Abbreviations: C = central; E = east; LC = logging concession; NE = north-east; NP = national park,

[2] This is just a rough and personal estimate based on the number of gibbons heard and tape-recorded in a particular area.

[3] Abbreviations: PD = Pete Davidson; FG Frédéric Goes; TG = Thomas Geissmann; TDH = Trinh Dinh Hoang; RK = Roger Konrad, present study; LQT= La Quang Trung.

Lomphat Wildlife Sanctuary

Lomphat Wildlife Sanctuary stretches from the south of Rattanakiri Province (south of Srepok River) to the very north of Mondulkiri Province. The park area consists mainly of very dry, open woodland (e.g. Desai & Vuthy, 1996; Long & Swan, 2000; Long et al., 2000; Timmins & Ou Rattanak, 2001). In some parts, the open habitat is mixed with relatively small patches of wetter grassland and evergreen forest. The block of evergreen rainforest that I visited is located in the south-west of the park area. It had been subjected to selective logging. Although lined out as an officially protected area, very limited means are available for conservation law enforcement. During my stay in the area, I never heard any gibbon songs. Because it was impossible to systematically survey the whole area during this short study, some gibbons may still occur there. In any case, their density would probably be very low. The inquiries I made prior to my trip to the Lomphat Wildlife Sanctuary about the presence of gibbons produced very inconsistent information and varied among the different sources.

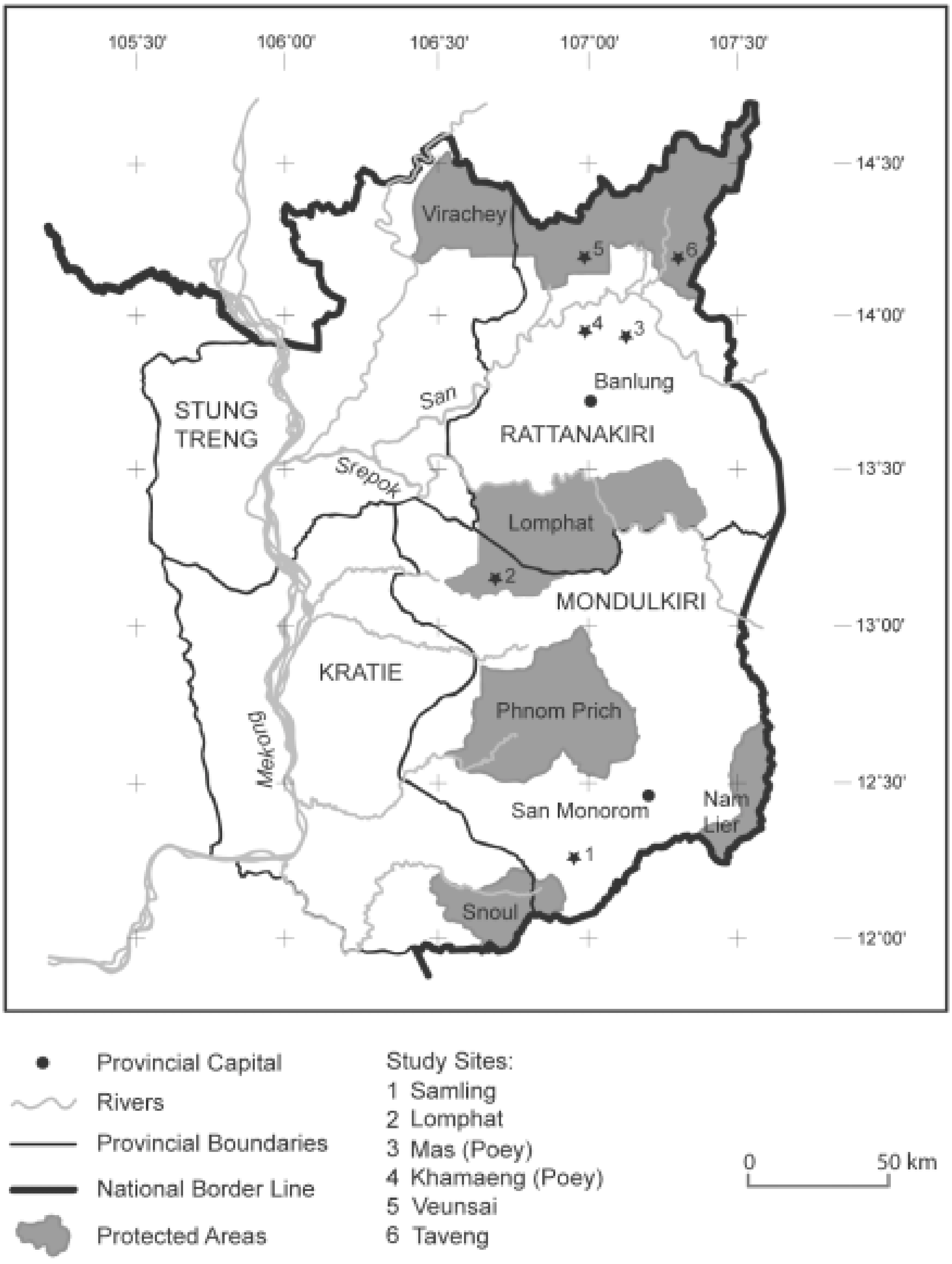

Figure 2.1. Map showing the study sites in east Cambodia. Adapted from *Land cover representation, WWF-Cambodia*.

Central Rattanakiri Province (Poey Commune)

In the central part of Rattanakiri Province (between San River in the north and Srepok River in the south), the evergreen forest is very fragmented and the remaining patches are often restricted to the slopes and crests of hill chains. In most areas with remains of potential gibbon habitat, interviews with local people revealed that gibbons had not been sighted or heard for several years, although they were reported as present in the past. Only in one area called Poey Commune (Ou Chum District), people reported that gibbons still occurred in the area, and I conducted several tips to its remaining forest patches. On some of these trips gibbons were found, although in very low density.

Virachey National Park

Virachey National Park is the largest national park in South-east Asia. It is located in the north-eastern corner of Cambodia, bordering on Laos in the north and Vietnam in the east. Most of the park area is mountainous and still covered with large, continuous and relatively undisturbed blocks of dense forest. The park is professionally managed, and efforts are taken to minimize illegal hunting and logging activities in Virachey (Seng, 2001).

I conducted two trips to the Virachey National Park, one to the central part (Veunsai District) and one to the eastern part (Taveng District). In both areas, gibbons occurred in a relatively high density.

Tape-recordings of gibbon songs from these two parts of Virachey National Park are analyzed separately and assigned to two different gibbon populations. Such a distinction may be artificial and questionable, because the two recording sites are only separated by a relatively short distance (about 32 km) and no obvious geographical barriers (e.g. wide rivers or habitat unsuitable for gibbons) appear to separate the two localities. In the present study, I kept the two samples separated in order to determine whether song structure differs among local populations, which are in relatively close geographical proximity. The geographical distance between Poey Commune and either of the recording localities in Virachey is relatively short as well (30 - 35 km, Table 3.8) and the gibbons in Poey Commune are treated as a separate population even so. This distinction is plausible with respect to the large river (San River) separating Virachey (north of the river) from Poey (south of the river). This river is a potential geographical barrier for gibbons and may inhibit gibbon dispersal.

Bach Ma National Park

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 carried out.

Cao Bang Province

This province lies in the very north-east of Vietnam. In the north-eastern part of the province (Trung Khanh District), FFI biologists discovered the probably last remnant mainland population of the eastern black crested gibbon (*N.* sp. cf. *nasutus*) in January 2002 (La Quang Trung et al., 2002). In August 2002 Thomas Geissmann and FFI staff conducted a population survey and tape-recorded the morning songs of this highly endangered species (Geissmann et al., 2002, 2003). The forest area inhabited by the gibbons is very small and the few remaining individuals are highly threatened by illegal logging and hunting.

2.1.3 Carrying out tape-recordings in the field

Because no detailed gibbon surveys had been previously carried out in the areas where I conducted my data collection, I generally had no knowledge of the gibbon density and the distribution of individuals, groups and territories (with the exception of Ben Rawson's focus groups in the Samling Logging Concession in southern Mondulkiri Province). In each study site, I defined listening posts from which I listened for gibbon songs, noted the distance (estimated by the loudness of the vocalization) and the direction of the vocalizing gibbons and made tape-recordings if the animals were within reasonable distance. Preferred listening posts were elevated (on a hill side or on the top of a hill), because it is possible to scan a wider area, hear gibbon vocalizations more easily and determine the direction and the distance of the singing gibbons more accurately from there. As a rule, better tape-recordings can be achieved from elevated positions.

Camp sites were usually not in the immediate vicinity to listening posts, since the criteria of a good camp site (e.g. availability of water, even ground, not too dense undergrowth, etc.) do not necessarily match with the described requirements of a listening post.

Crested gibbons utter their songs in the early morning hours. They usually start singing shortly after dawn (Geissmann, pers. comm., my own observations). Later in the morning, songs become increasingly rare. For the present study, the vast majority of the tape-recordings were carried out in the time interval between 05:00 and 07:00 in the morning. Some songs were recorded later in the morning, the latest around 10:00.

Generally, I tried to make sure to be within a distance suitable for carrying out tape-recordings before the gibbons started calling (i.e. before dawn). To achieve this, I followed either of the following two basic strategies:

(1) I spent the night in the camp (usually on the bottom of a valley near a water course), got up some time before dawn, left the camp and climbed to the listening post that had been located on the previous day. The walk to the listening post had to occur as silently and inconspicuously as possible. This method bore the risk of inadvertently disturbing gibbons in the vicinity, in which case the gibbons might either not sing or move to another part of their territory before calling. On the other hand, this strategy brought the amenity of spending the night in the camp.

(2) I left the camp site in the evening (shortly before or around dusk), walked to the listening post and spent the night there. On the following morning, I was already in the appropriate place for carrying out tape-recordings. This reduced the risk of disturbing the gibbons while climbing to the listening post, but spending the night there was less comfortable than in a camp.

Which of these two strategies was followed depended on the immediate circumstances (e.g. terrain, distance between camp and listening post, number of team members, etc.) and was decided for each site separately.

When a gibbon group called from too far away to make a decent tape-recording, I left the listening post and tried to approach the singing group if the terrain was not too difficult to pass or the group was not too far away.

In general, I avoided approaching singing gibbons so closely to see them in order to minimize the risk of being heard or seen by them. Such a disturbance could have caused them to abort their song bout. Because sighting was not required for carrying out tape-recordings, I made only very few direct observations of gibbons in the forest.

Good tape-recordings can usually be carried out within a distance of 100 – 200 meters to the singing gibbons. Of course, the recording quality also depends to a large extent on the level of sounds from sources other than the gibbons (e.g. cicadas, birds, water courses, rain, wind, etc.). It is also influenced by the topography of the recording site, the position of the vocalizing gibbons, and the recording equipment. Under favorable circumstances, usable tape-recordings can be carried out over distances of several hundred meters.

2.1.4 Tape-recording equipment

I made my field recordings with a SONY TCD-D8 DAT recorder and a SONY Electret Condenser Microphone ECM-MS957 (one-point stereo, unidirectional). Thomas Geissmann used a SONY WM-D6C cassette recorder with a JVC MZ-707 directional microphone and, alternatively, a SONY TC-D5M cassette recorder with a Sennheiser ME80 (+K3U) directional microphone. La Quang Trung und Trinh Dinh Hoang used a Marantz PMD-222 cassette recorder with a Sennheiser ME 66 (+K6) directional microphone. The recording equipment used for the tape-recordings carried out in Samling LC Coupe 2A is not known.

2.2 Acoustic terms and crested gibbon song structure

2.2.1 Acoustic terms

Investigators of gibbon vocalizations used various acoustic terms and definitions to describe gibbon song characteristics. Haimoff (1984a) presented a set of acoustic terms, which was consistent among all gibbon taxa. 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 2.3.

Table 2.3. Acoustic terms and definitions for gibbon song vocalizations

Term	Definition
Note	Any single continuous sound of any distinct frequency or frequency modulation, which may be produced during either 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/or 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, the female’s great call
Great call	The most stereotyped and most easily identifiable phrase of the gibbon song and produced by the adult females of all gibbon species
Great call sequence	Combination of the female great call and the corresponding successive coda of the male
Song	After Thorpe (1961, p.15): 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, 1984b; Schilling, 1984b). 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 gibbons.

Female song contributions

Adult *Nomascus* females produce great call phrases only (or fragments of great call phrases) (Figure 2.2). All great calls begin with long notes of slowly increasing frequency (termed *fa*-notes). These notes are also called *oo* notes; this name 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 (*fb*). These notes are referred to as bark notes. After the climax of the acceleration, bark notes tail off into a twitter (*fc*). In the eastern black crested gibbon (*N.* sp. cf. *nasutus*) *fb* and *fc* notes are missing and vibrato-like notes are produced over almost the entire course of the great call phrase (Geissmann, 1997; Geissmann et al., 2000).

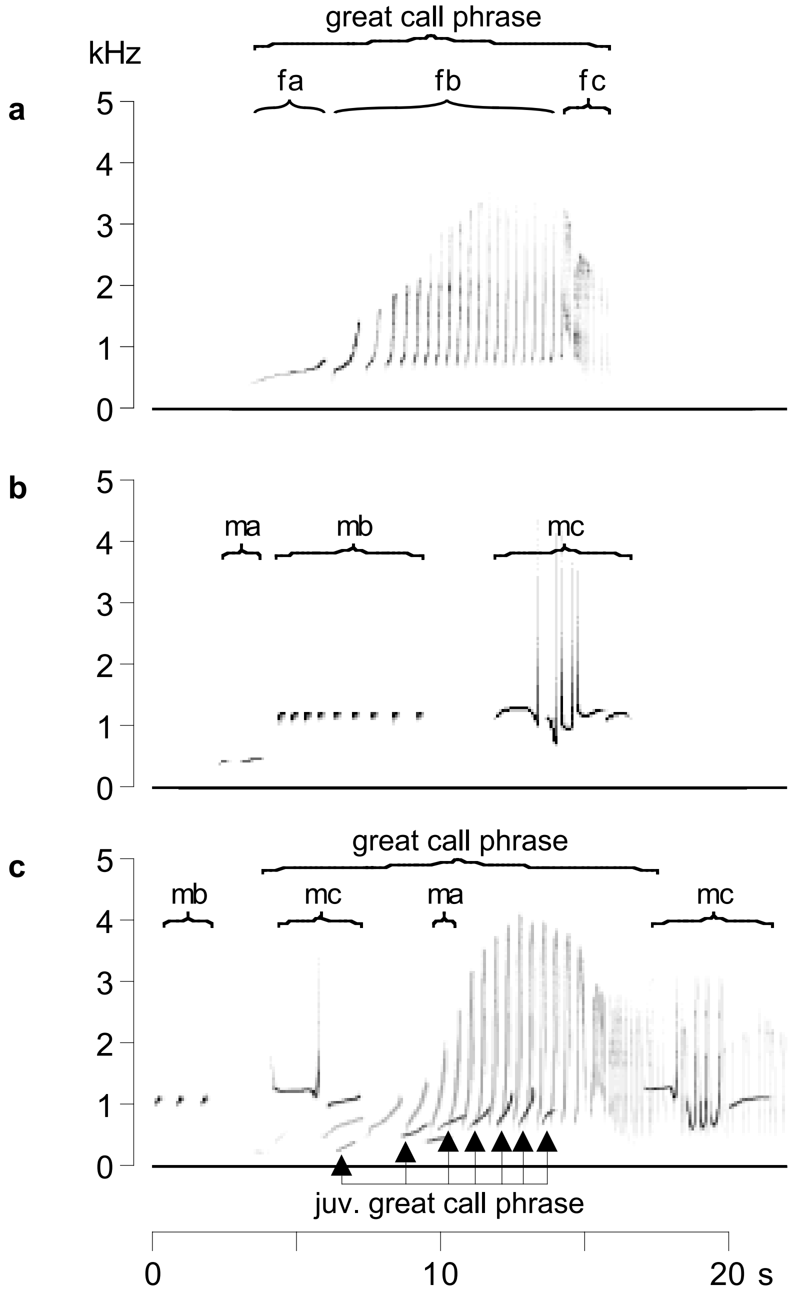

Figure 2.2. Sonagrams (fundamental frequencies only) showing sexual dimorphism in typical song phrases of northern white-cheeked crested gibbons (*Nomascus leucogenys leucogenys*): a. great call phrases of an adult female (Eberswalde Zoo, Germany, 11 July 1988). The great call begins with *oo* notes (*fa*), followed by bark notes (*fb*), and ends with twitter notes (*fc*); b. phrases of an adult male (Ménagerie du Jardin des Plantes, Paris, 17 May 1988). This sequence 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 (Hannover Zoo, Germany, April 1999, juvenile born on 23 Dec. 1995). 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, the female is accompanied with a short, great call-like phrase by her juvenile son. In order to facilitate "reading" of this sonagram, the female contributions were artificially lightened and the juvenile phrase were darkened (from Geissmann et al., 2000, p.42).

Male song contributions

Fully developed song phrases of adult *Nomascus* males typically consist of three different note types (i.e. *ma*, *mb*, *mc*) (Figure 2.2). The boom note 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 short series (phrases). The *aa* notes are short, relatively monotonally repeated sounds, which are therefore also referred to as staccato notes. 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 (coda) at or shortly after the climax of the female great call phrase.

In the course of a complete song bout, the male phrases are gradually built up. At the beginning of the song bout, the male produces long hardly 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 his song and, at the end of the great call, answers the great call with a coda. After that, he resumes cycling through the three types of phrases.

The sonagrams in Appendix 1 show examples of the course of a typical duet song bout in *N. gabriellae*. A song excerpt of an early stage from the song bout is presented in Appendix 1.1, and an excerpt from later in the song bout, when all phrases are fully developed, is shown in Appendix 1.2.

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

This section summarizes the differences between the song phrases of *N. leucogenys* and *N. gabriellae*, as reported by Geissmann et al. (2000). These observations provided a preliminary basis for selecting characteristics (i.e. variables) for comparing the songs of the gibbon populations analyzed in the present study.

Geissmann et al. (2000) state 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*. In *N. gabriellae*, however, 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. The staccato notes of *N. gabriellae* also appear to differ from those typically found in other crested gibbons. In *N. gabriellae*, they are very soft and often occur at irregular intervals, whereas they are loud and produced in more rhythmic intervals in other crested gibbons (thus the name “staccato”). 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). These repeated down-and-up sweeps in frequency are extremely fast and resemble a trill in *N. gabriellae*, whereas they are much slower in the male songs of other crested gibbons. Table 2.4 presents an overview of the differences in song characteristics mentioned above.

Table 2.4. List of suggested differences in song features (labeled A to H) between three *Nomascus* species after Geissmann et al., 2000, p. 45ff.

Label	Song characteristics	*N. l. leucogenys*	*N. l. siki*	*N. gabriellae*
	Male song:			
A	Boom phrase	Present	Present	Absent
B	Staccato phrase	Rel. loud, stable frequency, rhythmic intervals	Rel. loud, stable in frequency, with rhythmic intervals	Soft, varying frequency, irregular intervals
	Multi-modulated phrase:			
C	Begin of first note	Long section of rel. stable frequency	Long section of rel. stable frequency	Long section of descending frequency
D	Duration of rolls	Not very fast	Not very fast	Extremely fast, resembling a trill
E	Occurrence of rolls	On second and third note	Only on second note (for some individuals)	Only on second note
	Female song:			
	Great call phrase:			
F	Number of notes	15-30 notes (up to 39)	8-18 notes	5-13 notes
G	Start frequency of notes	Low	Low	High
H	Start frequency of notes	Remains constant	Remains constant	Ascending

2.3 Material: the tape-recordings

2.3.1 Sample size of tape-recorded gibbon songs

The study included a total of 40 song bouts (36 duet and 6 male solo songs) from different gibbon groups either referred to *N. l. siki* or *N. gabriellae*. All songs are from wild, non-habituated gibbons. Of these song, bouts I analyzed 151 female phrases (great calls) from 33 different female gibbons (average: 4.6 phrases/individual) and 235 male phrases (92 of them codas) from 39 different male gibbons (average: 6.0 phrases/individual).

Most of the tape-recordings were carried out during my four-months stay in Cambodia (19 January 2003 – 14 Mai 2003). Additional tape-recordings were made by Thomas Geissmann in April 2002 in Cambodia and in April 2001 and August 2002 in Vietnam.

2.3.2 Selection and classification of tape-recordings

In order to avoid redundancy in the raw data (and thus artifacts in the resulting affinities among samples), I had to make sure that all tape-recorded song bouts of the same group (or individual) were combined. This required that I was able to tell which of the song bouts I tape-recorded in a particular area were produced by the same group and which were not. The following indicators were useful for identification of, and discrimination between, recorded groups or individuals:

Position from which the recorded group or individual produced its song (territoriality of gibbons).

Simultaneous singing of more than one group or individual from different positions.

Group composition can be deduced from the number of singers and may vary among different groups.

Individuals can sometimes be recognized by individual-specific song characteristics.

As the actual distribution of the group territories was unknown and the gibbon groups or individuals were generally out of sight while being tape-recorded, some uncertainty about the actual group identity remained. When in doubt about whether two tape-recordings were produced by the same group or by two distinct groups, I excluded the recording of inferior sound quality from the analysis.

Due to low recording quality and thus low sonagram quality, some additional tape-recordings or parts of them were excluded from the analysis. Table 2.5 lists the number of gibbon groups that were recorded at each locality and the number of gibbon groups whose recorded songs were found to be suitable for analysis. The majority of song bouts included in the analysis are duets, but a few male solo song bouts were also included.

Table 2.5. Localities where tape-recordings were carried out, with names of pooled samples, supposed gibbon taxa occurring at each locality, number and type of analyzed song bouts.

Locality	Pooled samples [1]	Assumed taxon (provisional) [2]	Number of groups		Type of analyzed song bouts	
			Re-corded	Ana-lyzed	Duet	Male solo
Trung Khanh District	Cao Bang	*N.* sp. cf. *nasutus nasutus* [3]	5	3	3	0
Bach Ma NP	Bach Ma	*N. leucogenys siki*	8	5	4	1
Taveng District	Virachey	*N. gabriellae*	14	11	10	1
Veunsai District	Virachey	*N. gabriellae*	19	13	9	4
Mas Village	Poey	*N. gabriellae*	3	3	3	0
Khamaeng Village	Poey	*N. gabriellae*	2	1	1	0
Lomphat District	Lomphat	*N. gabriellae*	0	0	0	0
Samling LC Coupe 2A	Samling	*N. gabriellae*	2	2	2	0
Samling LC Coupe 3	Samling	*N. gabriellae*	12	4	4	0
Samling LC Coupe 5	Samling	*N. gabriellae*	1	1	1	0
Total			66	43	37	6

[1] For further analysis (cladistic and multivariate), data from Mas and Khamaeng were pooled to one sample referred to as Poey.

[2] Gibbons from Bach Ma are assumed to be *N. l. siki* because of the close proximity to the type locality of that taxon. All gibbons south of Bach Ma are provisionally identified as *N. gabriellae* because their phenotype resembles this taxon, as far as known.

[3] *N.* sp. cf. *nasutus nasutus* represents the outgroup in the cladistic analysis (see below).

2.3.3 Selecting procedure of phrases included in analysis

The amount of sound material available for analysis varied considerably among groups and individuals. It ranged from only one male and one female phrase of one gibbon group to two virtually complete song bouts, each lasting for several minutes, of another group.

Due to time constraints, no more than 7 complete and fully developed phrases per individual were analyzed.

As mentioned above, gibbon males gradually build up the complexity of their phrases in the course of a complete song bout. They only produce fully developed multi-modulated phrases after several minutes of producing simpler, less modulated phrases. A similar but reverse effect appears to occur at the end of some complete song bouts (Geissmann, pers. comm.; my own observations). In the last few phrases of the song bout, the complexity of male phrases was observed to decrease (possibly as a result of reduced song motivation). If more than 7 phrases from a single male were suitable for analysis, I excluded the earliest and the last phrases of the song bout. I aimed to include only phrases in the analysis that represented the most developed stage of each male gibbon.

Crested gibbon song bouts include much fewer female phrases than male phrases (great calls). Only few groups of my samples did include more than 7 female phrases (groups 35, 49, 71, 74). In these cases I always used sonagram quality as the selection criterion and chose the 7 female phrases that produced the clearest sonagrams and therefore guaranteed the most accurate measurements for analysis.

For some gibbon groups or individuals, less than 7 phrases were suitable for analysis. Table 2.6 presents a list of the number of phrases that were analyzed of each gibbon group or individual.

Table 2.6. Number of male and/or female phrases per group included in the analysis, and composition of male phrases and great call sequences. 1)

		A	B	C	D	E	F	G	H	I	J	K	L
Locality	Group	Male	Number of single notes available						Female	Coda			
		Number of phrases 2)	Note 1	Note 2	Note 3	Note 4	Note 5	Not a coda	Number of great calls 3)	Coda absent	Not fully developed	Fully developed	Following coda used
Cao Bang	337	4	4	4	4	4	0	0	4			4	4
Cao Bang	339	4	4	4	4	4	0	0	4			4	4
Cao Bang	341	5	5	5	5	4	0	0	5			5	5
Bach Ma	70	7	7	7	7	6	2	6	6		2	4	1
Bach Ma	71	7	7	7	7	1	0	2	7			7	4
Bach Ma	72	7	7	7	7	1	0	1	6			6	6
Bach Ma	74	7	7	7	7	0	0	4	7			7	3
Bach Ma	76	3	3	3	3	1	0	3	solo				
Veunsai	3	3	3	3	3	1	0	0	4		1	3	3
Veunsai	4	7	7	7	7	4	0	4	4			4	3
Veunsai	5	6	6	6	6	6	6	2	low				
Veunsai	7	7	7	7	7	3	0	5	3			3	2
Veunsai	8	6	6	6	6	6	4	2	7		3	4	4
Veunsai	9	7	7	7	7	7	5	7	solo				
Veunsai	10	3	3	3	3	3	3	3	solo				
Veunsai	11	7	7	7	7	6	6	7	solo				
Veunsai	12	7	7	7	7	7	4	5	7			7	2
Veunsai	14	6	6	6	6	6	0	6	solo				
Veunsai	15	6	6	6	6	3	0	4	6	1	3	2	2
Veunsai	16	1	1	1	1	1	0	0	1			1	1
Veunsai	18	7	7	7	7	2	0	1	7			7	6
Taveng	19	7	7	7	7	7	5	5	3			3	2
Taveng	20	4	4	4	4	3	1	3	2			2	1
Taveng	21	5	5	5	5	5	4	3	2			2	2
Taveng	23	7	7	7	7	7	2	6	3			3	1
Taveng	25	4	4	4	4	4	1	3	1			1	1
Taveng	26	7	7	7	7	7	1	4	4			4	3
Taveng	27	6	6	6	6	5	5	4	2			2	2
Taveng	29	7	7	7	7	6	0	7	solo				
Taveng	30	low							1			1	0
Taveng	31	5	5	5	5	2	0	3	2			2	2
Taveng	32	6	6	6	6	6	0	2	4			4	4
Khamaeng	34	7	7	7	7	6	1	6	4			4	1
Mas	35	7	7	7	7	7	4	4	7			7	3
Mas	36	7	7	7	7	3	0	5	5		1	4	2
Mas	37	7	7	7	7	5	0	5	6			6	2
Samling	38	7	7	7	7	5	0	3	6			6	3
Samling	40	7	7	7	7	3	0	3	7			7	4
Samling	41	7	7	7	7	4	0	3	6		2	4	4
Samling	42	4	4	4	4	2	0	3	2		1	1	1
Samling	47	6	6	6	6	6	0	1	5			5	3
Samling	48	7	7	7	7	6	0	4	7		1	6	3
Samling	49	7	7	7	7	5	2	5	7			7	2
Total 4)		235						143	151				

1) Column abbreviations: A: The number of male phrases in the analysis. B-F: Number of single notes that compose a male phrase in the analysis. Variability in phrase composition within and between individuals can be seen. G: Number of male phrases in the analysis that were not part of a great call sequence (i.e. not following a great call, not a coda). If a male phrase included in the analysis actually was a coda, its preceding great call was almost always included in the analysis as well. H: Number of female phrases (great calls) in the analysis. I-K: Describe the male's vocal response (Coda) to the great calls included in the analysis. These codas were not necessarily included in the analysis. The number of codas included in the analysis is Column A minus Column G (I: Coda completely absent. J: Coda is not fully developed. K: Fully developed coda). L: The number of fully developed codas included in the analysis that follow a great call included in the analysis.

2) low: The quality of the sonagramed phrases of the male was too low to be included in the analysis, therefore, only female vocal data were available of this song bout.

3) solo: These are male solo song bouts, therefore, only male vocal data were available of these song bouts.

4) Total excludes gibbon groups from Cao Bang (outgroup).

2.4 Sound analysis equipment

The tape-recordings were digitized with a sampling rate of 22 kHz and a sample size of 16 bit. Sonagrams (time versus frequency displays) of the sound material were generated using the Canary version 1.2.4 software (Cornell Laboratory of Ornithology) on a Power Macintosh G4. The sonagrams were computed by *Fast-Fourier-Transformation* (FFT). Table 2.7 shows the parameter settings applied when generating the sonagrams (Charif et al., 1995).

Table 2.7. List of parameters and applied settings for the sonagrams in Canary 1.2.4 (Spectrogram Options).

Parameter	Setting
Analysis Resolution:	
Filter Bandwidth	87.42 Hz
Frame Length	1024 Points
Grid Resolution:	
Time	256 Points
Overlap	75%
Frequency	10.77 Hz
FFT Size	2048 Points
Window Function	Hamming
Clipping Level	- 80 dB
Display Style	Smooth
Amplitude	Logarithmic

2.5 Measurement procedure

For measuring various dimensions on the sonagrams, I determined various characteristic points on the sonagram line of the multi-modulated male phrases and female great call phrases. These points are referred to as *anchor points* (Appendix 2). At each anchor point, I measured the time and/or the frequency using the measurement features implemented in the Canary software. Appendix 2 presents descriptions of the general terms employed in this study for defining the song variables. Further comments on the measuring procedure applied to the male and the 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 sonagram: a horizontal part and a “trough” part (Appendices 3 and 4). 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 (anchor point C).

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.

Note 3 may include one or several rolls as well, but in general, subsequent 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 as such, if a longer excerpt of a song bout is available for analysis. Most aborted great calls comprise less than 5 notes (not including twitter), most complete great calls comprise at least 5 notes.

Great call phrases consist of three phases: *Oo* phase, bark phase (accelerando-part), and twitter phase (Appendices 3 and 4).

As described in Appendix 3.3, *oo* notes are identified by a frequency increase of no more than 1 kHz per second and bark notes by a frequency increase of more than 1 kHz per second. But in late bark notes, the frequency increases extremely steeply and the true end point of the note (and thus the end frequency) cannot be determined reliably. As a result, late bark notes cannot actually be identified as barks with the "1 kHz per second" rule. However, for early bark notes the end point is visible and one can reliably determine, 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 correctly be considered as bark notes.

2.6 Song variables

In order to quantify acoustic characteristics of the male and the female phrase, I defined 90 variables, including qualitative and quantitative variables. The quantitative variables were calculated from the values measured at the anchor points. The values for qualitative variables (e.g. present/absent) were directly visually determined from the sonagram. Definitions of all variables are listed in Appendix 5.

2.7 Comparing multiple independent samples

In order to get a first estimate on the question, if the different gibbon populations under examination actually differ in song features and if at least some of the defined song variables express such differences, I conducted a *Kruskal-Wallis one-way analysis of variance by ranks*. This non-parametric test is useful for deciding whether *k* independent samples are from genuinely different populations or if the observed differences among the samples are in the range, which is expected among random samples from the same population (Siegel & Castellan, 1988). Significance implies that at least one pair of groups has different medians, but is does not specify between which groups such differences exist.

2.8 Sub-sets of variables

The total number of variables measured is very large and complicated to handle in one piece. Especially in cladistic analyses computational constraints limit the number of characters that can be included.

However, it is clear that not all 90 variables are equally informative for discriminating between the populations and revealing phylogenetic differences. Song features (and thus the variables that measure these features) may exhibit different levels of variability or some variables may be correlated or redundant. In order to reduce the number of variables to a manageable amount and at the same time, to select the most informative variables, I formed two sub-sets of variables. For each sub-set a different selection procedure was applied.

2.8.1 Variables selection by Kruskal-Wallis: the *KW* set

The *Kruskal-Wallis one-way analysis of variance by ranks* was used to build the first sub-set of variables. This non-parametric test is useful for deciding whether *k* independent samples are from genuinely different populations or if the observed differences among the samples are in the range, which is expected among random samples from the same population (Siegel & Castellan, 1988). Significance implies that at least one pair of groups has different medians, but is does not specify between which groups such differences exist.

Significance in the Kruskal-Wallis test was the selection criterion for this sub-set of variables. I tested all variables and included the ones, which revealed significant differences ($p \leq 0.05$) between the samples (gibbon populations) in the sub-set, subsequently called the *KS* set. The set includes a total of 40 variables, 35 that show significance in the Kruskal-Wallis test and 5 outgroup variables (Table 2.8). The outgroup variables are dichotomous and clearly differentiate between the gibbon groups representing the outgroup (eastern black crested gibbons from Cao Bang) and the rest of the sample (white-cheeked and yellow-cheeked crested gibbons). They depict fundamental differences between the song patterns of the outgroup taxon and the ingroup taxa. All specimens of the outgroup taxon exhibit one character state and all specimens of the ingroup taxa homogeneously show the other character state. The outgroup variables are thus non-informative for the ingroup taxa. They were added to the set to support the outgroup comparison, since a lot of the variable included in the first place either are not applicable to the outgroup taxon due to differences in song structure or don't set the outgroup taxon clearly apart and thus provide only little information for polarization.

Table 2.8. The variables included in the *KW* set.

	Variables included in the set (No.)	n
Male song:		
Note 1	01, 06*, 14, 20	4
Note 2	27, 28*, 29, 30, 33, 36, 37, 39-42, 44-46, 49	15
Note 3	55	1
Note 4	60-61	3
Female song:		
Great Call	64-66, 67*, 68, 69, 71, 72, 74*, 75, 76*, 78, 80, 83, 87, 89, 90	17
Total number of variables included in the set:		40

* Outgroup variables. For description see text.

2.8.2 Variables selection by multivariate analysis: the *DA* set

For this sub-set of variables a discriminant analysis was performed. This multivariate method is described below. I included all variables in the analysis and conducted a stepwise variable selection with *Wilks' lambda* as selection method and the F value as entry/removal criterion (F-to-enter=1.0 and F-to-remove=0.9). The variables selected by the discriminant analysis formed the sub-set subsequently termed the *DA* set. The set includes a total of 26 variables, 21 variables selected by the stepwise discriminant analysis and 5 outgroup variables (Table 2.9). The outgroup variables were added for the same reasons as described in the preceding paragraph.

Table 2.9. The variables included in the *DA* set.

	Variables included in the set (No.)	n
Male song:		
Note 1	06*, 12, 18, 19, 20, 26	6
Note 2	28*, 29, 33, 35, 41, 43, 45, 47	8
Note 3	55	1
Note 4	58, 59, 60, 61	4
Female song:		
Great Call	67*, 68, 74*, 76*, 79, 86, 89	7
Total number of variables included in the set:		26

* Outgroup variables. For description see text.

2.9 Previously suggested vocal differences between *N. leucogenys* and *N. gabriellae*

Several differences in song characteristics between *N. l. leucogenys*, *N. l. siki,* and *N. gabriellae* have been pointed out (e.g. Geissmann et al., 2000) (Table 2.3). These suggested differences rely on tendencies and have not been quantified so far. In order to find out, whether, and to which degree, my samples corresponded to these characteristics, I determined their presence/absence or quantifed them as follows (A to H refer to the labels assigned to the song differences as in Table 2.4):

A: Qualitative examination of sonagrams
B: Qualitative examination of sonagrams
C: Relative duration horizontal part (no. 8), Frequency halfway (no. 16), rel. frequency range to halfway point (no. 18), rel. duration to maximum bend (no. 20), frequency at maximum bend (no. 21)
D: Relative duration roll part (no. 32), number of rolls (no. 33), number of “long” troughs in roll part (no. 34), duration of first roll in roll part (no. 35)
E: Number of rolls on note 3 (no. 51)
F: Number of notes in great call (no. 65)
G: Start frequency of first note of great call, start frequency of last note of great call, mean of all start frequencies of great call notes
H: Range of start frequencies of great call notes (no. 66), first start frequency range (no. 88), last start frequency range (no. 90)

For each of the quantitative variables (C-H), I determined the mean, standard deviation, median, and interquartile range in each of the study populations. Then I examined whether any of my samples consistently (i.e. in all or most of the variables) corresponded to one of the taxa (i.e. *N. l. siki* or *N. gabriellae*).

2.10 Cladistic analysis

2.10.1 Introduction

Cladistics is a method of classification that groups taxa hierarchically into discrete sets and subsets and conventionally represents these relationships as a cladogram (Kitching et al., 1998).

I carried out cladistic analyses to investigate phylogenetic (or sister-group) relationships among the different gibbon populations in east Cambodia and central Vietnam. In cladistics, sister-groups are hypothesized through the analysis of characters (Kitching et al., 1998). In the present study I employed vocal characters measured on gibbon songs (i.e. the song variables described above).

2.10.2 OTU's (operational taxonomic units)

In a classificatory study one first has to decide on what should be the taxonomic rank of the basic units. The term OTU's refers to the lowest rank taxa employed in a given study (Sneath & Sokal, 1973). From study to study, they can differ in rank, but the species is the most common unit in classificatory studies.

For the present study OTU's represent mated gibbon pairs (strictly speaking, two individual gibbons combining their respective vocalizations in a duet song) or gibbon groups. In favor of a more fluent readability, I subsequently use the term *groups* when OTU's are meant.

2.10.3 Data coding

For each gibbon group or individual the measurements taken on different phrases (multi-modulated phrase or great call) were averaged. As a result, each group or individual was characterized by one mean value for every variable defined. Because cladistic methods require that observations are translated into discrete characters (character states), these means were coded across the groups for each variable. Appendix 6 shows the character states and the limits of each character state for all variables and Appendix 7 represents the complete coded data matrix. The dichotomous variables were naturally discrete-valued (e.g. variable no. 6, *presence of trough part*). But most variables included continuous data, which had to be grouped before coding (e.g. variable no. 3, *duration first note*). In order to get an idea of the distribution and the variability of the values for a certain variable, I plotted the values in box plots, with a separate plot for the values from different gibbon populations. I compared the plots of the same variable with respect to aggregations of values and the position of such aggregations. Then I arbitrarily defined bands with minimal overlap between the scatters of different populations as the limits between discrete states. So I determined ranges and all values that fell into the same range were coded as the same character state.

I used the program MacClade version 4.0 to set up a data matrix and enter the coded data (Maddison & Maddison, 1992). The following character types were specified:

Unordered-ordered: Most variables or characters were defined as *ordered*. In ordered (multistate) characters the transformation between two non-adjacent states would oblige the character to proceed progressively through every adjacent state.

For freely reversible binary characters, it makes no difference whether they are defined as *ordered* or *unordered* (Swofford, 1990). Some characters included the state *Not Applicable* (NA) for certain gibbon groups (e.g. variable no. 9, *duration trough part*). Such characters were specified as *unordered*. In unordered characters, any state is capable of transforming directly to any other state, with equal cost (Swofford, 1990). In the complete data matrix (Appendix 7), the following characters were defined as *unordered*: 09, 10, 19 - 21, 29, 30, 42, 43, 59, 68 - 73, 82 - 84.

Weighted-unweighted: The characters were defined to have an *equal weight*. Hereby, all variables had the same value in the analysis independent to their number of character states (Swofford, 1990).

Polarized-unpolarized: All characters were determined as *unpolarized*. This means that no ancestral state was specified.

Directed-undirected: All characters were determined as *undirected*, assuming that the transformation between two states costs in both directions.

If poor sonagram quality made it impossible to reliably measure a certain variable, the character was recorded as *missing* for the particular gibbon group or individual. The same applied for all great call variables in male solo song bouts.

2.10.4 Calculation of phylogenetic trees

For the cladistic analysis, I used the PAUP software version 4.0b10 on a Macintosh G4. Character types were applied as mentioned above.

Included groups

I included only gibbon song bouts that consisted of vocalizations of both sexes (duets). Solo song bouts (as found in groups 5, 9, 10,11, 14, 29, and 76) and duet songs for which the contributions of either sex had been recorded with considerably poorer quality (as in group 30), were deleted from the group list. This resulted in a markedly reduced amount of missing values in the data matrix. But, of course, it also led to a reduced number of groups in the data matrix, subsequently referred to as the *reduced group list*.

Included characters

Due to computational constraints not all characters could be included in the cladistic analysis. As described above, I determined two sub-sets of characters (KW set and DA set). I performed two separate cladistic analyses, one with each sub-set of characters.

Outgroup

The three groups of the eastern black crested gibbon (*N.* sp. cf. *nasutus*) recorded in Cao Bang Province in northeast Vietnam were defined as *outgroup*. In cladistics, the outgroup is used for comparative purposes, usually with respect to character polarity determination (Kitching et al., 1998).

With each sub-set of characters two types of maximum-parsimony analyses were performed: A *heuristic search* yielded the shortest tree and the *bootstrap* method was used to examine the robustness of internal nodes.

Heuristic search

For the reconstruction of the most parsimonious cladograms I conducted a heuristic search. This method uses an approximate algorithm and thus does not guarantee to find the most parsimonious solution. But for large data sets it is favorable to an exact algorithm (exhaustive or branch-and-bound) since it greatly reduces computational time. I applied the general search options, which include two search components: (1) stepwise addition of taxa to a developing tree until all have been connected, and (2) rearrangement of these trees via *branch-swapping* techniques (Swofford, 1990).

A cladistic analysis of one data set often generates numerous conflicting most parsimonious cladograms (*fundamental cladograms*) (Kitching et al., 1998). Then consensus methods can be used to reduce the number of fundamental cladograms to one tree showing their common components. They thus summarize agreement and disagreement, or congruence and incongruence, between two or more cladograms.

Results of the heuristic search were summarized in a *strict consensus tree* and a *50% majority-rule consensus tree*.

A strict consensus tree is derived by combining only those components that appear in all members of a set of fundamental cladograms and thus is the most conservative consensus tree. This can lead to a tree with very little resolution.

The 50% majority-rule consensus tree is specified to retain those components that occur in more than 50% of the fundamental cladograms. It is less conservative than the strict consensus tree, but may be preferable when many trees are being compared.

Bootstrap analysis

The bootstrap method provides an estimate of the relative support of each relationship in the resultant topologies of the clusters in the most parsimonious trees. In this approach the characters are sampled randomly with replacement to produce a pseudoreplicate data set of the same size as the original (Kitching et al., 1998). On the basis of this pseudoreplicate data set, most parsimonious cladograms are constructed by the means of a heuristic search. This process is repeated a large number of times. Then, the percentage of bootstrap replications that support a particular grouping (*bootstrap values*) is derived. These values provide approximate estimates for the amount of support afforded to groups by the data.

The results were summarized in a *50% majority-rule consensus tree.*

2.10.5 Indices of tree "quality"

In order to assess the "quality" of the resulting cladograms I stated the following standard measures: tree length, ensemble consistency index (CI), ensemble retention index (RI), and the rescaled consistency index (RC). The term *tree length* refers to the minimum number of character changes (appearance or disappearance of characters) required on a cladogram to account for the data (Kitching et al., 1998). It is minimized when searching for the optimal (most parsimonious) cladogram, but can also provide an estimate of the amount of discordance with a particular cladogram (*homoplasy*). A large number of extra steps required for a character to fit a cladogram, will result in a larger tree length. The *ensemble consistency index* (CI) is a measure of the amount of homoplasy in a data set relative to a given cladogram and is defined as the ratio M/S. M is the sum of the minimum numbers of changes all characters can show on any cladogram. S is the sum of minimum numbers of changes all characters exhibit on a particular cladogram (Kitching et al., 1998). CI ranges from 0 –1 with 1 expressing complete consistency of the data set with the cladogram under examination (thus no homoplasy). It has been noted that the consistency index bears several problems as a measure of homoplasy (e.g. with respect to uninformative characters, decreasing CI values with increasing number of taxa, missing data). The *ensemble retention index* (RI) circumvents these problems. It measures the amount of similarity among all characters that can be interpreted as *synapomorphy*. It is calculated as the ratio (G-S)/(G-M). G is the sum of the greatest numbers of changes all characters can perform on any cladogram. As for CI, RI ranges from 0 –1 with 1 expressing that all similarity found in the cladogram under question is interpretable as synapomorphy (Kitching et al., 1998).

The *rescaled consistency index* (RC) is the product of the consistency index and the retention index of a character. Thus, characters with no similarity interpreted as synapomorphy (ri=0) will be disregarded, irrespective of their level of homoplasy (Kitching et al., 1998).

2.11 Multivariate analysis

The discriminant analysis is a parametric multivariate method useful for analyzing group differences. Linear functions of the independent variables (i.e. the song variables) are formed to describe or elucidate the differences between two or more groups (i.e. the gibbon populations from which tape-recordings were taken).

The linear discriminant functions require that the independent variables have a multivariate normal distribution and that the covariance matrices are equal for all groups. 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 groups and the variances (or standard deviations). This may occur if one group in the study contains a few extreme outliers, which have a large impact on the means and also increase the variability (Statsoft, 2004). As a result, such biased means are not reliable for discrimination between groups.

The discriminant analysis also identifies the relative contribution of a variable (or a set of variables) to the separation of the groups (Rencher, 1995). I made use of this quality to investigate which of the 90 variables determined for this study contribute most to discriminating among groups. The term *group* here refers to the 5 gibbon populations including Samling Logging Concession, Poey (Mas and Khamaeng), Veunsai, Taveng and Bach Ma (Table 2.4).

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), and at each step, all variables are reviewed and the one that contributes most to separating the groups (i.e. maximizes the defined criterion for selection) is included in the model. This process is repeated until either all variables are included or only variables remain excluded, which either wouldn’t significantly improve the discrimination between groups or are completely redundant. Redundancy or colinearity among the independent variables is expressed by the *tolerance*. The tolerance is a measure of the degree of linear association between independent variables and was used to avoid entering a variable, which is a linear combination of a variable already in the model (Norusis, 1994). The applied tolerance level was 0.001.

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 groups: the *standardized discriminant function coefficients* and *correlation coefficients* of correlations between the values of the function and the values of the variables.

If there are multiple groups to be compared, multiple discriminant functions are derived. In general, if there are *k* groups, *k*-1 discriminant functions can be computed. The first function provides the most overall discrimination between groups (highest ratio of between-groups variability to within-groups 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 groups. Computationally, the analysis performs a *canonical correlation analysis* that will determine the successive functions and *eigenvalues*. For each canonical function, the eigenvalue is the ratio of the between-groups to within-groups sums of squares and thus is an estimate of the quality of a discriminant function or a combination of functions.

On the basis of the discriminant functions, cases (i.e. the recorded gibbon groups) are classified into one of the groups (i.e. the five gibbon populations from which recordings were obtained). Because the actual group membership of each case is known, it can be compared to the predicted group 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 involves leaving out each of the cases in turn, calculating the functions based on the remaining *n*-1 cases, and then classifying the left-out case (Norusis, 1994; Deichsel & Trampisch, 1985).

Statistical analyses were performed on a Macintosh G3 using the SPSS software (version 11.0 for Mac OS X) (SPSS, 2003). All procedures were carried out according to the SPSS (SPSS Professional Statistics 6.1) manual (Norusis, 1994).

3. Results

3.1 Vocal differences between *N. l. siki* and *N. gabriellae*

The sonagrams in Appendix 8 represent excerpts of duet song bouts from different gibbon groups and different populations. Only sonagrams of good quality and with fully developed phrases are shown. They are not necessarily representative for the population from which they originate.

3.1.1 Male song

For all recorded gibbon songs boom phrases are neither hearable nor visible on the sonagram (Table 3.1). Since boom phrases are not very loud and do not carry very far, the absence of this type of phrase can be interpreted in two ways: Either booms simply do not appear on the recordings due to the long recording distances and the degree of background noises in field recordings or they are actually not part of the vocal repertoire of the gibbon populations included in the analysis. However, boom phrases cannot even be found on the best field recordings, whereas staccato phrases, for instance, are depicted very clearly on these recordings.

Staccato phrases appear on some sonagrams (e.g. groups 08, 15, and 38), but are absent on most sonagrams. Since staccato notes are very short and, as the booms, do not carry very far, their rare appearance on the sonagrams is probably caused by the difficult recording conditions in the field. It is unlikely that staccato phrases are completely absent since they are found in all crested gibbons, although in slightly different form in *N. gabriellae* (Geissmann et al., 2000). All staccato notes recognizable on the sonagrams were soft and occurred at irregular intervals and slightly varying frequencies. This is the type that Geissmann et al. (2000) described as typical for *N. gabriellae*. It has to be pointed out, that in the present study all staccato phrases were found in populations from Cambodia. No staccato phrases were found on the Bach Ma sonagrams. Therefore, the form of staccato phrases in this population could not be determined.

If the first note of the multi-modulated phrase begins with a long section of descending frequency, one would expect that (1) the horizontal part of this note (variable no. 08) is relatively short, (2) the point of maximum bend of the sonagram line (variable no. 20) occurs early in the note, and (3) in the halfway point the frequency is considerably lower compared to the frequency of the horizontal part (variable no. 18). For variables 08 and 18 these expectations are confirmed for the gibbon population from Samling, but not for the other Cambodian populations. Interestingly, results for Bach Ma are similar to those from Samling for variables 08 and 18. This is not the case for variable 20, where Bach Ma differs from all Cambodian populations.

The roll part of note 2 (variable no. 32) is relatively short in Veunsai, Poey and Samling. This may imply that single rolls are fastest in these populations, especially in Samling. In this population the short roll part includes the largest number of rolls (variable no. 33). This is not true for Poey and Veunsai, where fewer rolls occur.

Rolls do not occur regularly in note 3 (variable no. 51) in either of the 5 gibbon populations. They are found in one out of four phrases in Samling and Taveng, whereas they occur only very rarely in Poey, Veunsai and Bach Ma.

Table 3.1. Results of the qualitative examination of suggested song differences between *N. l. siki* and *N. gabriellae*. Labels refer to the type of difference and are consistent with those given in table 2.5. Variables are selected to measure these specific characteristics. For each variable four descriptive statistics are given. Results for single gibbon groups or individuals are pooled within populations. Populations are assigned to a taxon according to the known distribution ranges of these taxa.

a) Male song			Taxon and population:				
Label	Variable	Statistics [1]	*N. l. siki*	*N. gabriellae*			
			Bach Ma	Taveng	Veunsai	Poey	Samling
			n = 5	n = 10	n = 13	n = 4	n = 7
A	Booms		Present	Absent	Absent	Absent	Absent
B	Staccato		Stable [2]	Varying [3]	Varying	Varying	Varying
C	No. 08	Mean	32.8	48.2	44.7	43.8	29.1
		SD	14.9	14.2	9.9	10.2	21.8
		Median	30.3	49.3	44.6	46.9	29.3
		IQ	22.2	14.9	16.4	18.3	44.5
	No. 18	Mean	75.6	92.3	90.6	91.1	81.5
		SD	17.4	9.7	9.0	11.5	15.4
		Median	68.6	95.5	91.2	95.2	83.6
		IQ	32.6	13.5	18.0	20.3	26.6
	No. 20	Mean	69.7	57.6	54.2	52.2	53.4
		SD	4.5	7.6	8.5	10.2	8.8
		Median	69.6	58.7	56.8	55.8	52.0
		IQ	8.1	10.8	16.5	18.0	13.8
D	No. 32	Mean	51.8	46.5	36.6	40.2	37.1
		SD	11.6	9.3	9.3	11.6	8.3
		Median	54.0	50.3	41.8	37.8	39.3
		IQ	18.8	17.3	14.7	20.9	16.4
	No. 33	Mean	2.2	2.1	1.6	1.6	2.8
		SD	0.3	0.5	0.4	0.8	0.9
		Median	2.3	2.0	1.6	1.3	3.3
		IQ	0.6	0.7	0.7	1.4	1.8
E	No. 51	Mean	0.03	0.25	0.08	0.04	0.23
		SD	0.06	0.25	0.14	0.07	0.20
		Median	0.00	0.24	0.00	0.00	0.25
		IQ	0.07	0.52	0.14	0.11	0.43

[1] Abbreviations: SD = standard deviation, IQ = interquartile range

[2] "Stable" means that staccato notes are relatively loud, stable in frequency and uttered at rhythmic intervals.

[3] "Varying" means that staccato notes are soft, varying in frequency and uttered irregular intervals.

Table 3.1. (continued).

b) Female song			Taxon and population:				
Label	Variable	Statistics	*N. l. siki*	*N. gabriellae*			
			Bach Ma	Taveng	Veunsai	Poey	Samling
			n = 4	n = 10	n = 8	n = 4	n = 7
F	No. 65	Mean	10.7	12.5	10.5	9.9	7.3
		SD	1.1	3.2	2.3	1.5	0.6
		Median	11.1	12.5	10.3	9.8	7.5
		IQ	1.8	4.4	4.1	2.8	1.2
G	Mean Start Freq.	Mean	1030	1085	1033	1119	1267
		SD	20	89.5	93	58	108
		Median	1027	1060	1048	1118	1254
		IQ	37	131	168	113	178
	Start Freq. Note 1	Mean	656	586	572	636	621
		SD	44	102	150	89	86
		Median	650	590	536	614	619
		IQ	83	190	275	165	143
	Start Freq. Note 7	Mean	1097	1171	1129	1232	1619
		SD	21	111	77	103	117
		Median	1093	1181	1120	1212	1605
		IQ	40	121	157	194	146
H	No. 66	Mean	586	756	727	671	1121
		SD	36	95	198	98	166
		Median	595	773	679	653	1154
		IQ	66	174	338	184	378
	No. 88	Mean	87	143	103	231	155
		SD	27	89	85	119	127
		Median	93	133	122	217	120
		IQ	51	119	125	217	240
	No. 90	Mean	38	68	81	53	171
		SD	31	49	34	33	92
		Median	46	52	71	46	134
		IQ	58	68	50	61	94

3.1.2 Female song

Great calls consist of considerably fewer notes in Samling than in all other gibbon populations included in the analysis (variable no. 65). Samling falls exactly into the *N. gabriellae* range proposed by Geissmann et al. (2000). However, the other populations cannot be unequivocally assigned to one of the taxa based on this feature solely. The mean start frequency of great call notes is highest in Samling and lowest in Bach Ma. Veunsai is similar to Bach Ma (although exhibiting much more variability), Poey and Taveng are intermediate. As the comparison of early and late great call notes reveals (start frequency of note 1 and note 7), the notes later in the great call seem to account for the observed differences between the mean start frequencies. It appears that in Samling notes start at increasing frequencies in the course of a great call. This is consistent with the results from examining the ranges of start frequencies. The range of all start frequencies is high in Samling, in contrast to all other populations where this range is homogeneously lower (variable no. 66). Again, increasing start frequency in late great call notes seems to occur in Samling and, in this respect, sets this population apart from others (variables no. 88 and 90).

3.1.3 Overview

Apart from the number of great call notes, all song differences between *N. l siki* and *N. gabriellae* suggested by Geissmann et al. (2000) were strictly qualitative. Therefore, I had no reference for identifying a resulting value as typical for one of the two taxa. So I just looked at the range of the resulting values for a particular variable and defined the extremes as representative for the two taxa. Results of populations were then arbitrarily classified as being in the same range as one of the extremes or as intermediate between the extremes.

For all song differences the gibbon population from Samling came closest to the assumed *N. gabriellae* condition. For the population from Bach Ma the results of most variables suggested affinities to *N. l. siki*, although not as consistently as for the Samling population. Variables 08 and 18 (begin of note 1 of multi-modulated phrase) contradict with this assignment and the number of great call notes falls in the overlap between the two typical ranges. For the populations from Poey, Veunsai, and Taveng the results are very inconsistent. The values of about half the variables examined are in the range assigned to *N. l. siki* (variables 08 and 18, variables 32 and 33, variable 51 [although not for Taveng], and variable 66). Only the type of staccato notes and the relatively early occurrence of the maximum bend in note 1 (variable 20) suggest affinities to *N. gabriellae.* For two great call characteristics the values are intermediate between the two extremes.

Geissmann et al.'s (2000) description of song differences between *N. l. leucogenys*, *N. l. siki* and *N. gabriellae* was based on vocalizations recorded in the field and in zoos. One should take into consideration that *N. l. siki* was represented almost exclusively by zoo animals (Geissmann, pers. comm.). These animals were officially referred to *N. l. siki*. However, for zoo animals some uncertainty about the exact origin of an animal (or its ancestors) and thus the exact taxonomic status remains. Implications of this fact with regard to my results will be discussed in chapter 4.

3.2 Cladistic analysis

The first heuristic search was performed on the basis of the *reduced group list* and the *KW* set of characters (40 characters included, 31 of the type *ordered*, 9 of the type *unordered*, all had equal weight and were parsimony-informative). 31 best trees (equally maximally parsimonious cladograms) were found and two resulting consensus trees (50% majority-rule consensus of 31 trees and bootstrap 50% majority-rule consensus tree) were derived (Figure 3.1). The strict consensus tree showed a similar arrangement of the gibbon groups as the 50% majority-rule consensus tree, but with considerably less resolution.

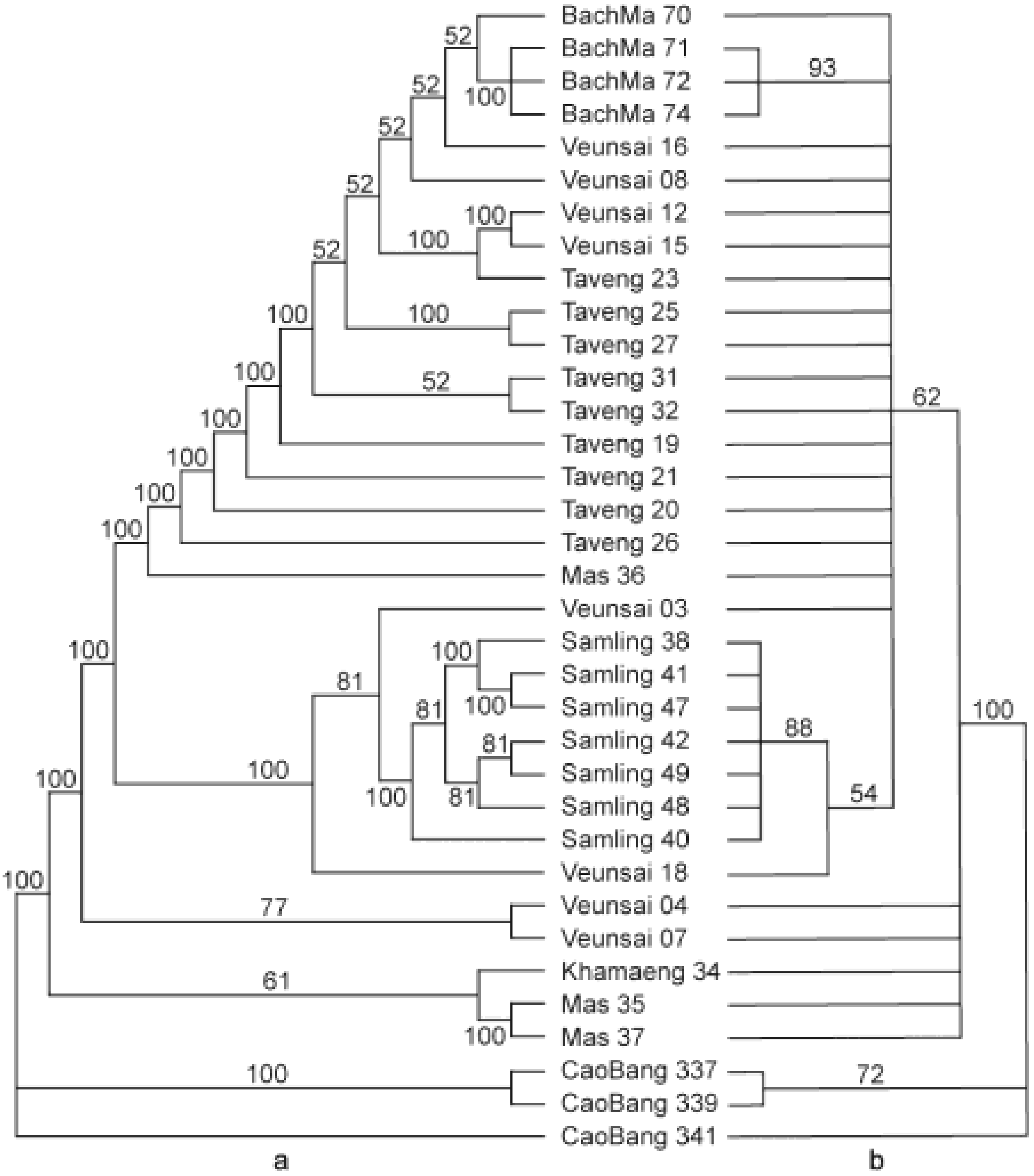

Figure 3.1. Maximum parsimony cladograms of the *reduced group list* and the *KW* character set. (a) 50% majority-rule consensus tree of 31 best trees obtained in a heuristic search (Tree Length 204, CI 0.328, RI 0.719, RC 0.236). Values represent the percentage of fundamental cladograms, which support the accompanying clade. (b) 50% majority-rule consensus tree of bootstrap analysis with bootstrap values (as percentages) obtained in 1000 replicates. Only bootstraps values larger than 50 are shown.

The 50% majority-rule consensus tree shows that all fundamental cladograms support a monophyletic grouping of three groups from Bach Ma, whereas a cluster containing all four groups from Bach Ma is found in only 52% of the fundamental cladograms (Figure 3.1a).

The groups from Virachey National Park (Veunsai and Taveng) and from Poey Commune (Khamaeng and Mas) are only little resolved in the cladogram. However, a large cluster including all groups from Bach Ma and Taveng and half of the groups from Veunsai is supported by all fundamental cladograms. All groups from Samling are homogeneously grouped in a monophyletic cluster.

The bootstrap 50% majority-rule consensus tree contains very little resolution (Figure 3.1b). Only two groupings with relatively strong support from the fundamental cladograms can be found.

Three groups from Bach Ma are combined monophyletically with a bootstrap value of 93. The fourth group of the same population is not included in the clade.

A cluster containing all groups from Samling is found in 88% of the most parsimonious cladograms resulting from the pseudoreplicates.

As expected, a monophyletic grouping of the entire ingroup sample excluding the three outgroups (groups from Cao Bang) is most strongly supported (bootstrap value 100).

The second heuristic search was performed on the basis of the *reduced group list* and the *DA* character set (26 characters included, 20 of the type *ordered*, 6 of the type *unordered*, all had equal weight and were parsimony-informative). 805 best trees were found and again, two types of maximum-parsimony trees were generated (Figure 3.2). As before, the strict consensus tree was very similar to the 50% majority-rule consensus tree and is not presented.

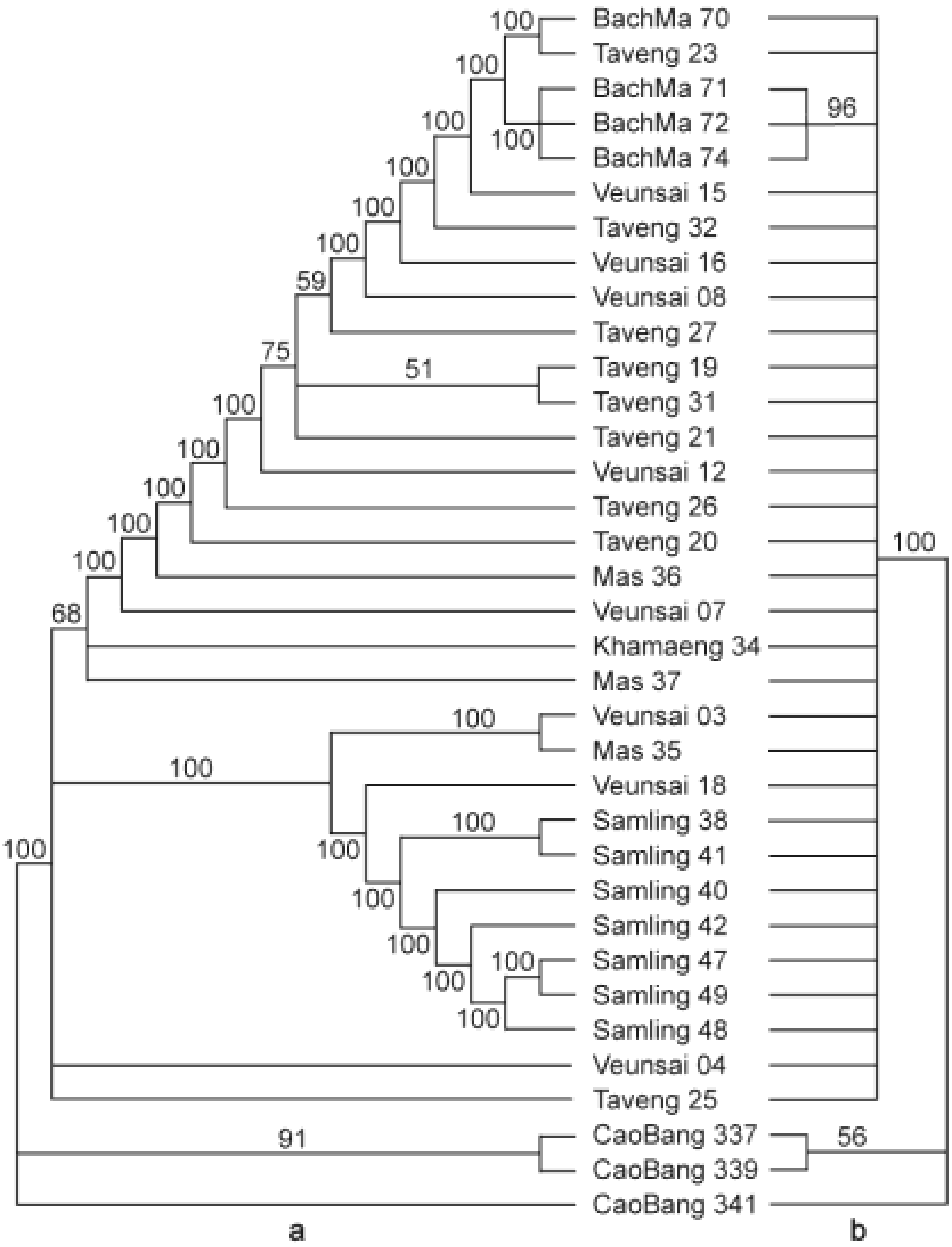

Figure 3.2. Maximum parsimony cladograms of the *reduced group list* and the *DA* character set. (a) 50% majority-rule consensus tree of 805 best trees obtained in a heuristic search (Tree Length 129, CI 0.295, RI 0.647, RC 0.191). Values represent the percentage of fundamental cladograms, which support the accompanying clade. (b) 50% majority-rule consensus tree of bootstrap analysis with bootstrap values (as percentages) obtained in 114 replicates. Only bootstraps values larger than 50 are shown.

Again, three groups from Bach Ma form a monophyletic clade (Figure 3.2a). But in contrast to the first analysis, the fourth group from Bach Ma (group 70) is combined with a group from Taveng (group 23) constituting a sister group to the Bach Ma clade. As in the first

PAUP analysis, a monophyletic cluster containing all groups from Samling is supported by all fundamental cladograms.

Apart from the described clusters, the cladogram contains very little resolution. Gibbon groups from Poey (Mas and Khamaeng), Veunsai, and Taveng are disarranged and no homogeneous clade can be recognized.

As in the first cladistic analysis, the bootstrap 50% majority-rule consensus tree resulting from the second analysis shows a cluster containing three (of totally four) groups from Bach Ma with a bootstrap value of 96 (Figure 3.2 b).

For the rest of the ingroup sample the cladogram is not resolved.

3.3 Multivariate analysis

For the discriminant analysis I always used the stepwise method. This means that (1) a variable was only included if it fulfilled the entry criterion and (2) only remained in the model as long as it did not meet the removal criterion. The significance of the change in the selection criterion when a variable is entered or removed from the model can be based on an F statistic (Norusis, 1994). Either the actual value of F or its significance level can be used as the criterion for variable entry and removal.

For all analyses I used the significance level (probability of F) and applied the default settings (p-to-enter=0.05 and p-to-remove=0.10). As a consequence, a variable was only entered if its significance level remained lower than 0.05.

In SPSS several criteria for variable selection are available: Wilks' lambda, Unexplained variance, Mahalanobis distance, Smallest F ratio, and Rao's V. Because these selection criteria optimize different estimates of separation, they reveal different results. I performed a separate analysis with the same data for each of them. The results were then compared with regard to the variables included in the analysis, attributes of the discrimination functions and the classification of gibbon groups to populations.

3.3.1 Variables included in the analysis

Table 3.2 presents the variables included in the analysis for each of the five selection criteria. For each variable the standardized discriminant function coefficient (FC) and the correlation coefficient (CC) for the first and the second discriminant function are listed. These values are estimates of the relative contribution of a variable to the separation of groups, i.e. gibbon populations. "Relative" means that a single variable's contribution can only be assessed in combination with other variables included in the model. It is not possible to assess the importance of an individual variable.

For both coefficients (FC and CC) high absolute values represent a large relative contribution of a certain variable. The actual signs of the FC are arbitrary (Norusis, 1994).

When interpreting the correlation between the values of the function and the values of the variables (CC's), one should be aware that correlations between variables affect the magnitude and signs of the CC. If one variable exhibits a high CC and another variable is strongly correlated with this variable, both will show high CC's, but the individual coefficients are not meaningful (Norusis, 1994).

Table 3.2. Variables selected by five types of discriminant analyses. Stepwise selection was used in each case. The criteria used for selection are listed in the first column. For each variable the discriminant function coefficient and the correlation coefficient for the first two functions are given. [1)]

Wilks' Lambda														
Variable	45	89	18	60	79	43	47	26	59	61	33			
DF1 FC	1.63	1.22	-1.55	1.72	0.86	-1.86	1.36	1.17	0.57	0.24	0.44			
DF1 CC	0.27	0.17	-0.07	0.09	-0.01	-0.03	0.03	-0.03	-0.04	0.11	0.09			
DF2 FC	0.70	-0.08	0.97	-4.18	1.97	1.59	-0.71	-1.21	-0.31	1.71	1.26			
DF2 CC	0.04	0.07	-0.04	-0.19	0.12	0.01	0.00	-0.03	0.10	-0.04	0.03			
Unexplained Variance														
Variable	44	87	18	40	82	89	35	04	51	39				
DF1 FC	2.87	1.53	-2.25	-2.29	1.57	1.31	-0.89	1.08	1.01	0.56				
DF1 CC	0.22	-0.06	-0.08	0.01	0.03	0.15	-0.07	-0.02	0.02	-0.01				
DF2 FC	-0.01	-1.03	0.62	-1.40	-0.91	0.91	1.70	-0.99	0.59	1.46				
DF2 CC	0.00	-0.16	0.15	-0.13	-0.02	0.33	0.08	-0.13	0.14	-0.08				
Mahalanobis-Distance														
Variable	62	64	75	16	60	87	89	41	83	52	54	90	80	51
DF1 FC	17.22	1.81	2.89	-10.02	-12.02	0.60	1.40	7.11	4.89	7.91	5.53	2.01	-3.49	-1.20
DF1 CC	0.04	-0.03	0.03	-0.01	0.02	-0.02	0.05	0.05	0.03	-0.01	0.02	0.03	0.04	0.01
DF2 FC	-1.48	0.45	0.20	1.15	-1.07	0.54	0.95	0.75	0.03	-0.96	0.20	0.21	-0.19	0.53
DF2 CC	-0.27	0.13	0.20	-0.11	-0.27	0.08	0.16	0.02	-0.07	-0.04	-0.10	0.08	-0.09	0.15
Smallest F Ratio														
Variable	62	89	87	52	16	45	13	82	12	58	02			
DF1 FC	2.04	0.87	-0.45	0.95	-4.45	1.66	0.45	0.41	2.53	-0.99	1.15			
DF1 CC	0.12	0.16	-0.09	-0.04	0.00	0.26	0.04	0.04	0.05	-0.05	0.00			
DF2 FC	-2.87	1.28	2.33	-1.77	0.72	1.19	6.96	1.46	-5.97	1.30	-0.39			
DF2 CC	-0.14	0.06	0.13	-0.03	-0.13	0.05	-0.06	0.00	-0.10	0.06	0.02			
Rao's V (V=0)														
Variable	45	89	09	88	33	52	44	26	55	41				
DF1 FC	-2.03	2.86	2.81	-1.22	-0.09	-1.04	5.32	-0.23	-3.89	2.22				
DF1 CC	0.17	0.12	0.03	0.01	0.05	-0.03	0.15	-0.02	0.03	0.08				
DF2 FC	1.45	-1.13	1.46	-0.43	1.77	2.06	-0.93	1.29	2.75	-1.24				
DF2 CC	0.12	-0.13	0.12	0.06	0.07	0.05	0.21	0.01	0.19	0.02				

[1)] Variables are identified by their variable numbers and are listed in the same order as included in the analysis. Abbreviations: DF1 = discriminant function 1, DF2 = discriminant function 2, FC = standardized discriminant function coefficient, CC = correlation coefficient.

Of the totally 90 song variables defined in this study, 36 were selected by at least one of the 5 types of discriminant analyses that were performed (Table 3.3). One variable was included by all of them, three variables were included thrice, 9 variables twice, and 23 variables once.

Table 3.3. Variables that were selected by at least one of the 5 types of discriminant analyses. For each variable, the X indicates the type of discriminant analysis that selected the variable.

Variable No.	Selection criterion				
	Wilks' Lambda	Unexplained Variance	Mahalanobis Distance	Smallest F Ratio	Rao's V
02				X	
04		X			
09					X
12				X	
13				X	
16			X	X	
18	X	X			
26	X				X
33	X				X
35		X			
39		X			
40		X			
41			X		X
43	X				
44		X			X
45	X			X	X
47	X				
51		X	X		
52			X	X	X
54			X		
55					X
58				X	
59	X				
60	X		X		
61	X				
62			X	X	
64			X		
75			X		
79	X				
80			X		
82		X		X	
83			X		
87		X	X	X	
88					X
89	X	X	X	X	X
90			X		

3.3.2 Effectiveness of discriminant functions

Table 3.4 shows a number of estimates of the effectiveness in population separation of the discriminant functions. In addition to the percentage of groups correctly classified and the eigenvalue, which both are described above, the percentage of the total between-groups variability is presented. This value expresses the amount of variability attributable to a specific function and can be used to compare the merits of each function. Finally, the mean function scores of each gibbon population for the significant discriminant functions are given. They show between which populations the respective functions seem to discriminate.

Table 3.4. Parameters to assess the discrimination quality of discrimination functions. Analyses with five different selection criteria were performed. Only functions with significant ($p \leq 0.05$) contribution to discrimination between populations are listed. [1)]

Selection criterion	Correctly classified [%]	Significant functions	Eigenvalue	Var.	Mean function score for each population				
					1	2	3	4	5
Wilks' Lambda									
% of groups correctly classified:	82.5%	DF 1	59.50	69.9%	11.97	0.27	-2.87	-3.50	-3.42
		DF 2	18.84	22.1%	0.61	-7.13	-1.89	3.50	0.73
% of cross-validated groups corr. classif.:	90.0%	DF 3	6.08	7.1%	-0.45	0.87	-3.10	0.26	2.42
Unexplained Variance									
% of groups correctly classified:	80.0%	DF 1	65.33	85.2%	11.82	-6.40	-3.72	-1.94	0.19
		DF 2	6.82	8.9%	0.85	0.90	0.90	0.48	-3.62
% of cross-validated groups corr. classif.:	87.5%	DF 3	3.94	5.1%	-0.93	-2.74	-0.48	1.38	1.44
Mahalanobis-Distance									
% of groups correctly classified:	77.5%	DF 1	379.33	95.4%	26.63	-8.78	-11.47	-6.47	9.68
		DF 2	9.28	2.3%	0.19	-4.48	-0.39	2.24	-2.48
% of cross-validated groups corr. classif.:	95.0%	DF 3	7.85	2.0%	-2.15	0.96	-0.82	1.44	4.51
Smallest F Ratio									
% of groups correctly classified:	75.0%	DF 1	63.92	73.6%	12.29	0.00	-1.89	-3.78	-1.86
		DF 2	18.34	21.1%	0.63	-6.08	-0.17	1.67	4.73
% of cross-validated groups corr. classif.:	80.0%	DF 3	4.29	4.9%	-0.58	1.29	-0.70	-0.85	4.70
Rao's V									
% of groups correctly classified:	75.0%	DF 1	147.18	91.9%	18.96	-7.47	-3.31	-3.70	-7.28
% of cross-validated groups corr. classif.:	75.0%	DF 2	11.55	7.2%	0.47	3.22	-2.31	-1.55	2.70

[1)] Abbreviations: DF = discriminant function, Var. = between-groups variability as percentage.

3.3.3 Classification results

The percentage of groups correctly classified to populations ranges from 75% (with *Rao's V* or *smallest F ratio* as selection criterion) to 82.5% (with *Wilks' lambda* as selection criterion). For the discriminant analysis with the lowest (*Rao's V*, if cross-validation is considered as well) and the one with the highest classification accuracy (*Wilks' lambda*), the results are shown in more detail (Tables 3.5 and 3.6, respectively).

Table 3.5. Classification results of discriminant analysis with *Rao's V* as selection criterion. All song material (duet and solo phrases) was used. The original classification was obtained when groups were classified by the functions derived from all groups in the analysis (*n*). In the cross-validation, each group was classified by the functions derived from all groups other than that group (*n*-1).

Population Nr.		Groups assigned to population					% of groups correctly classified	Total number of groups
		1	*2*	*3*	*4*	*5*		
Original classification								
1	Samling	7	0	0	0	0	100.0	7
2	Poey	0	2	1	1	0	50.0	4
3	Veunsai	0	1	10	2	0	76.9	13
4	Taveng	1	0	3	7	0	63.6	11
5	Bach Ma	0	0	0	1	4	80.0	5
	Total	8	3	14	11	4	75.0	40
Cross-validated classification								
1	Samling	7	0	0	0	0	100.0	7
2	Poey	0	3	0	0	1	75.0	4
3	Veunsai	0	0	8	5	0	61.5	13
4	Taveng	1	0	3	7	0	63.6	11
5	Bach Ma	0	0	0	0	5	100.0	5
	Total	8	3	11	12	6	75.0	40

Table 3.6. Classification results of discriminant analysis with *Wilks' lambda* as selection criterion. All song material (duet and solo phrases) was used. The original classification was obtained when groups were classified by the functions derived from all groups (n). In the cross-validation, each group was classified by the functions derived from all groups other than that group (n-1).

Population Nr.		Groups assigned to population					% of groups correctly classified	Total number of groups
		1	*2*	*3*	*4*	*5*		
Original classification								
1	Samling	7	0	0	0	0	100.0	7
2	Poey	0	2	2	0	0	50.0	4
3	Veunsai	0	1	9	3	0	69.2	13
4	Taveng	0	0	0	11	0	100.0	11
5	Bach Ma	0	0	1	0	4	80.0	5
	Total	7	3	12	14	4	82.5	40
Cross-validated classification								
1	Samling	7	0	0	0	0	100.0	7
2	Poey	0	4	0	0	0	100.0	4
3	Veunsai	1	0	12	0	0	92.3	13
4	Taveng	1	0	1	9	0	81.8	11
5	Bach Ma	0	0	0	1	4	80.0	5
	Total	9	4	13	10	4	90.0	40

Figures 3.3 and 3.4 are two-dimensional plots of all gibbon groups according to their discriminant score on the first and the second discriminant function. The results of the analysis with *Rao's V* as selection criterion are shown in Figure 3.3 and with *Wilks' lambda* in Figure 3.4. These plots visually represent the degree of spatial separation among the overall mean scores (centroids) of each gibbon group on the first two discriminant functions.

On both plots the values for the groups from Samling scatter only little around their population centroid and the latter lies apart from those of all other populations. The values for the populations from Poey, Veunsai, and Taveng are spread more widely around their respective population centroid. In addition, the centroids of these populations are closer to each other than any of them to Samling. With *Rao's V* as selection criterion (Figure 3.3) the values of Veunsai and Taveng almost completely overlap (except for a few outliers) and their overlying centroids differ markedly not only from that of Samling, but also from those of Poey and Bach Ma.

With *Wilks' lambda* as selection criterion (Figure 3.4) the values of Veunsai and Taveng do not overlap as strongly as in the previous plot. Thus, discrimination between these two populations is better. This time, the values of Bach Ma are placed at an intermediate position between Veunsai and Taveng, whereas Poey is separated again. The values for the population from Bach Ma are grouped quite closely around their population centroid and exhibit more spatial proximity to the Veunsai-Taveng-cluster than any other population.

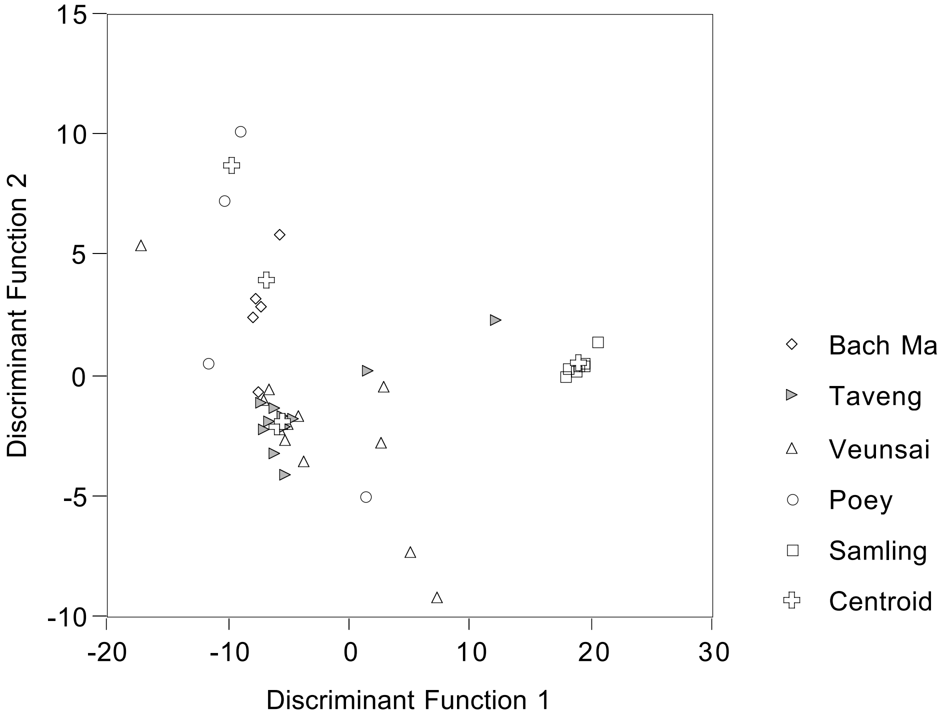

Figure 3.3 Discriminant scores (dot symbols) of all gibbon groups resulting from analysis with *Rao's V* as selection criterion. Different populations are identified with different symbol shapes. Crosses indicate population centroids.

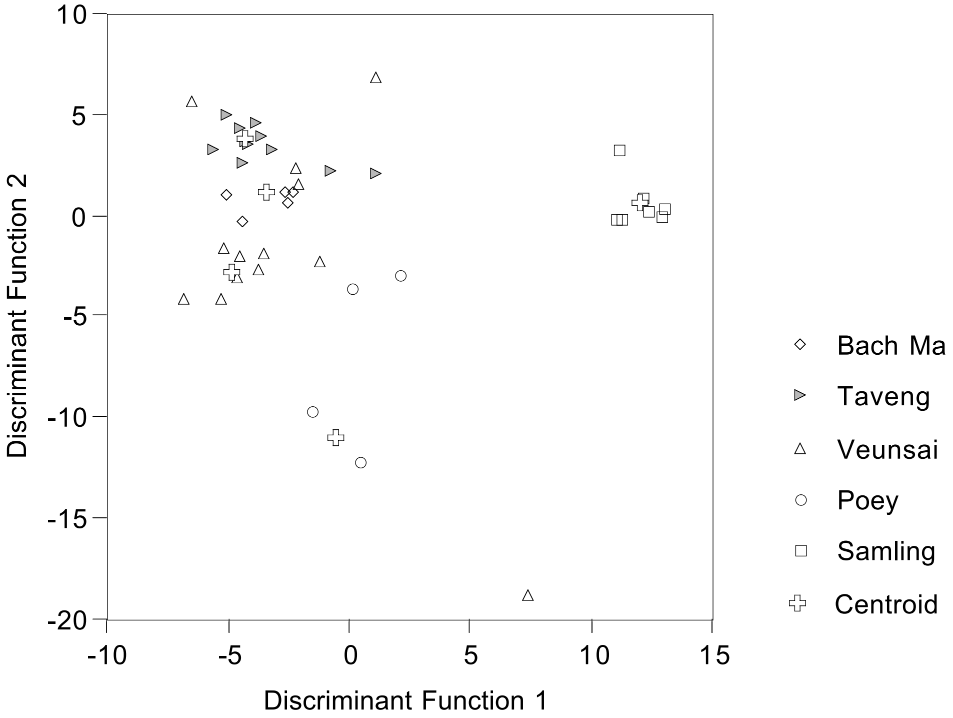

Figure 3.4 Discriminant scores (dot symbols) of all gibbon groups resulting from analysis with *Wilks' lambda* as selection criterion. Different populations are identified with different symbol shapes. Crosses indicate population centroids.

In both plots, the centroid of Poey appears to be placed inappropriately, i.e. considering only two of the four points. This is owing to the fact that only groups with a complete data set are used for calculating the centroid. For the discriminant analysis, i.e. the computation of the discriminant functions, groups with missing values for any of the variables are excluded in the first place. The population membership of the groups with missing values is then predicted on the basis of the derived model. Thus, the groups with missing values usually appear as outliers on the plot and are more likely to be classified incorrectly.

Another common trait of the plots presented in Figure 3.3 and 3.4 (as for the other three types of discriminant analysis) is the fact that the discriminant function 1 contributes mainly to the marked discrimination between Samling and the rest of the sample, whereas discriminant function 2 elucidates differences between the populations from Poey, Veunsai, Taveng, and Bach Ma.

The classification results (Tables 3.5 and 3.6) correspond to those obtained with the plotted discriminant scores in clearly separating the Samling population from all other samples. None of the Samling groups was classified incorrectly. The closer proximity of the populations from Poey, Veunsai, and Taveng previously observed in Figures 3.3 and 3.4 is also reflected in the classification results. The percentage of groups correctly classified is considerably lower in both analyses for the populations from Poey and Veunsai, and for the population from Taveng in the case of *Rao's V* as selection criterion. The percentage of groups correctly classified for the population from Bach Ma is intermediate in both analyses.

Of the totally 17 groups from Poey, Veunsai, Taveng or Bach Ma that were misclassified in either of the two analyses shown, 16 were wrongly assigned to either of the populations from Poey, Veunsai or Taveng.

As pointed out above, some gibbon groups contain missing values in their data list (e.g. owing to the fact that values for great call variables were not applicable in male solo song bouts). Groups with an incomplete data set appear to be particularly susceptible to misclassification: Of the totally 44 cases when a group was misclassified (in either of the 5 types of discriminant analysis) 38 contained missing values. The reverse, that all groups with missing values are automatically classified incorrectly, appears not to be true.

3.3.4 Intra-population variability in song characteristics

As can be seen in Figures 3.3 and 3.4, the discriminant scores of some gibbon groups scatter more widely around their population centroid than others. For each gibbon group, I determined the distance between its discriminant scores and its population centroid. The standard errors of these intra-population vocal distances are listed in Table 3.7. The results for the discriminant analyses with *Rao's V* or *Wilks' lambda* as selection criterion are shown. In both analyses, the standard errors of the gibbon populations from Samling and Bach Ma are considerably smaller than the values for the north-east Cambodian populations (Poey, Veunsai, and Taveng).

These results may indicate that song variability is more pronounced in the north-east Cambodian populations compared to the southernmost and northernmost study populations (Samling and Bach Ma, respectively).

Table 3.7. Standard errors of intra-population vocal distances in every study population. Intra-population vocal distances are measured as minimal distance between the discriminant scores of a study group (OTU) and its population centroid. Standard errors of vocal distances derived from discriminant analyses with *Rao's V* and *Wilks' lambda* as selection criterion are listed separately.

Selection criterion	Standard error				
	Samling n = 7	Poey n = 4	Veunsai n = 13	Taveng n = 11	Bach Ma n = 5
Rao's V	0.22	3.79	1.53	1.65	0.64
Wilks' lambda	0.29	1.84	1.57	0.51	0.21

3.3.5 Comparison of vocal and geographical distance between populations

Geographical distance was measured as the minimum distance between the recording sites whose position is given in Table 2.2. The position of each population was represented with the coordinates of one particular recording position. The small distances between the various recording positions when recording gibbon groups of the same population were neglected. The recording positions in Khamaeng village and Mas village (Poey Commune) were averaged owing to the relative proximity of these two places and the low number of gibbon groups tape-recorded in either of them.

Vocal distance between two gibbon populations was measured as the distance between the respective centroids of these populations on the scatter plots of the discriminant scores (Figure 3.3 and 3.4). The vocal distances were derived separately for the discriminant analyses with *Rao's V* and *Wilks' lambda* as selection criterion.

It was then examined, whether the geographical distance corresponded to the vocal distance between populations. The distance matrices are presented in Table 3.8.

Table 3.8. Distance matrices showing geographical (a) and vocal (b and c) pairwise distances for all gibbon populations. Geographical distances are measured as minimal distances between the coordinates of representative recording positions for each study area. Vocal distances are measured as minimal distances between the population centroids of discriminant scores. Results of discriminant analysis with *Rao's V* as selection criterion are listed in (b), with *Wilks' lambda* in (c).

a) Geographical distance				
	Poey	Veunsai	Taveng	Bach Ma
Samling	188 km	215 km	217 km	440 km
Poey		30 km	35 km	254 km
Veunsai			32 km	229 km
Taveng				223 km

b) Vocal distance, using Rao's V as selection criterion				
	Poey	Veunsai	Taveng	Bach Ma
Samling	29.8	24.5	25.1	26.1
Poey		11.4	11.5	5.5
Veunsai			0.7	6.0
Taveng				6.2

c) Vocal distance, using Wilks' lambda as selection criterion				
	Poey	Veunsai	Taveng	Bach Ma
Samling	17.1	17.1	16.6	15.4
Poey		9.2	15.3	12.4
Veunsai			6.6	4.2
Taveng				2.9

No significant correlation was found between geographical and vocal distances, regardless of whether *Rao's V* or *Wilks' lambda* was used as selection criterion for the latter (Pearson correlation, $r = 0.443$, $p = 0.207$, and $r = 0.204$, $p = 0.584$, respectively). Yet, a non-significant correlation does not exclude that geographical distance has an influence on vocal distances.

In order to determine the vocal distances between populations that were independent from geographical distances, I determined the vocal residuals in a least squares regression between vocal distances (dependent variable) and geographical distances (independent variable). This procedure was carried out with both types of vocal distances (i.e. either derived from *Wilks' lambda* or from *Rao's V*). The residuals calculated from both regressions were similar and highly correlated with each other (Figure 3.5, $r = 0.824$, $p = 0.0034$). Large positive residuals indicate vocal distances that are larger than expected for their geographical distance, whereas large negative residuals indicate populations that are vocally more similar than expected based on their geographical distance. The residuals are uninfluenced by the independent variable (geographical distance), any correlation between the geographical and the vocal distance that may exist, but did not come out significantly due to the small sample size, has no impact on the residuals.

As can be seen in the distance matrix (Table 3.8), the largest vocal distances occur between Samling and the other populations. The vocal distance between Samling and Bach Ma is in the same range as the distances between Samling and either of the populations from north-east Cambodia (Poey, Veunsai, Taveng), although the geographical distance is approximately twice as large. Smaller vocal distances are found (1) among the three populations from northeast Cambodia and (2) between either of them and Bach Ma. The first finding is in congruence with the geographical distances but the second is inconsistent since Bach Ma is geographically very distant.

The regression analyses (Figure 3.5) support these qualitative observations. Relatively large positive residuals are found in dyads including the Samling population on one hand and the north-east Cambodian populations on the other. In contrast, the dyads including the Bach Ma population and the north-east Cambodian populations exhibit the largest negative residuals.

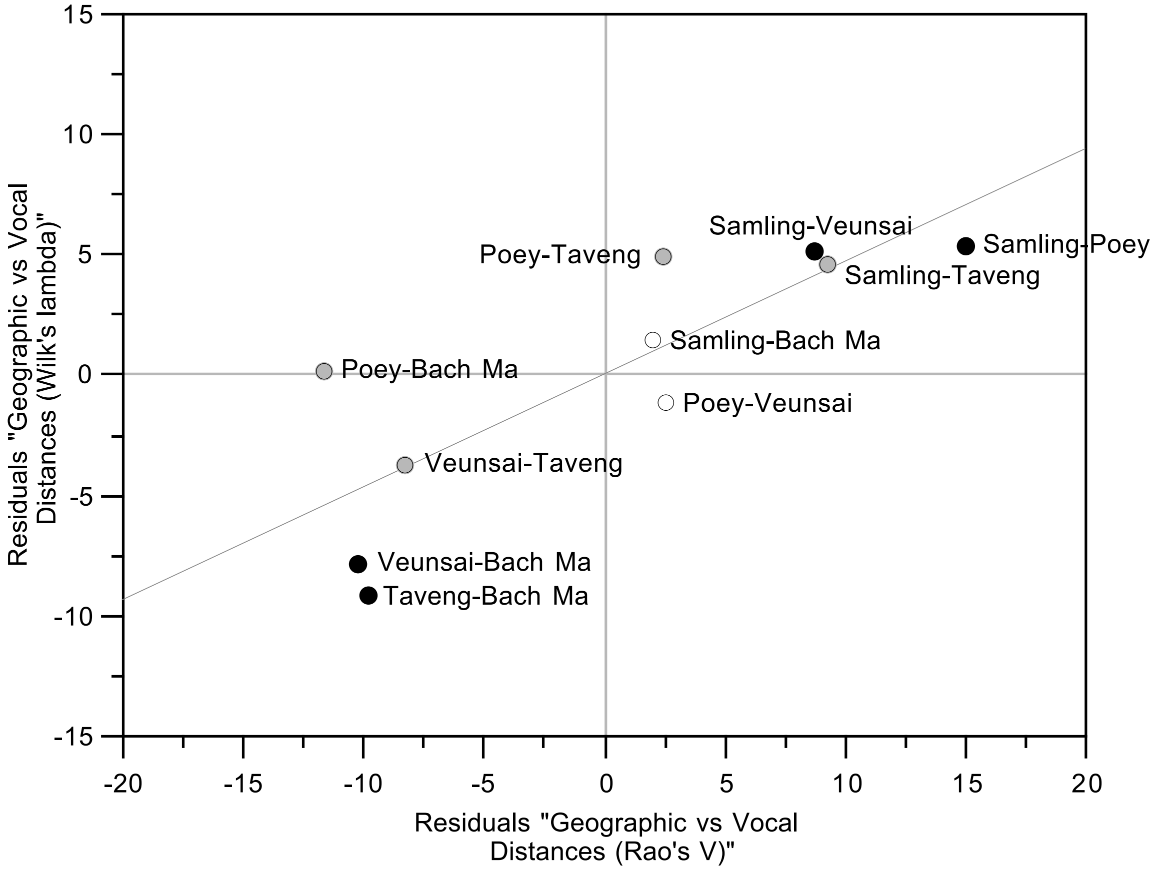

Figure 3.5. Residuals from two regression analyses of geographical *vs.* vocal distance among all study populations plotted against each other (in one case, vocal distance is based on *Wilks' lambda*, in the other on *Rao's V*, as listed in Table 3.8). The least squares regression is also shown in the graph ($y = 3.52 * 10^{-15} + 0.469 * x$). The two types of residuals are significantly correlated with each other ($r = 0.824$, $p = 0.0034$). Filled circles indicate the population dyads with the lowest and with the highest residuals (black circles = dyads that qualify for this criterion in both types of residuals, grey circles = dyads that qualify for this criterion in only one type of residuals).

4. Discussion

4.1 Vocal diversity

4.1.1 Phylogenetic and multivariate analyses of vocal diversity

All crested gibbons (genus *Nomascus*) occurring in Cambodia (i.e. east of Mekong River) are currently regarded as *N. gabriellae* (Figure 1.1). However, a large area between the respective distribution ranges of *N. leucogenys siki* and *N. gabriellae* in central Vietnam, southern Laos and possibly north-eastern Cambodia was recently discovered, where calls appear to differ from the typical calls of either taxon (Geissmann, 1995a; Geissmann et al., 2000). Both fur colouration and vocal data from this area suggest either a large hybridization zone with one species gradually replacing the other, or the existence of a previously unrecognized taxon, or a combination of the two. Since this discovery, the taxonomy of the crested gibbons from the southern half of their distribution area is under debate.

In the present study, I examined the vocal diversity of four *Nomascus* populations in Cambodia (Samling Logging Concession, Poey Commune, and two localities in Virachey National Park) and one locality in central Vietnam (Bach Ma) in order to assess their taxonomic relationships and in order to examine whether their vocal patterns corresponded to those previously described of *N. l. siki* and *N. gabriellae*.

Results of the discriminant analysis show that it is possible to distinguish the five study populations based on vocal data. Depending on the selection criterion applied, the overall classification accuracy (i.e. percentage of correctly classified group members) ranged from 75% to 82.5%. This implies that considerable vocal diversity exists among at least some of the gibbon populations included in the analysis.

The extent of vocal differences among the study populations is not the same for all pairs of populations compared, and the examined populations appear to differ in variability and the expression of population-specific song characteristics. Summarizing the results of both the phylogenetic and the discriminant analyses, it becomes apparent, that the study populations can best be arranged into the following three groups, ordered by decreasing distinctiveness: (1) Samling (south-east Cambodia), (2) Bach Ma (central Vietnam), and (3) Veunsai, Taveng and Poey (north-east Cambodia). These three groups will be individually discussed below.

4.1.2 Samling

The gibbon population from Samling differs most clearly from all other populations in the analysis. The discriminant analysis consistently and completely separates the Samling population from all other samples, suggesting a taxonomic split between the Samling population and the remaining populations of this study. In the phylogenetic analysis, all gibbon groups from Samling are combined in a monophyletic clade.

To summarize, vocal characteristics support a homogeneous entity of the Samling gibbon population, which differs from all other Cambodian populations.

4.1.3 Bach Ma

Although Bach Ma is, in geographical terms, situated about as far away from the north-east of Cambodia as Samling, the songs from Bach Ma appear to be less distinctive than those of Samling. The discriminant analysis provides ambiguous results for the vocal data from Bach Ma: On one hand, the classification accuracy is relatively high, with only one group misclassified (a male solo song bout). On the other hand the centroid of the discriminant scores of Bach Ma is close to the centroids of Veunsai and Taveng in some analyses (e.g. when using *Wilks' lambda* as selection criterion). It is possible that the relatively low number of gibbon groups (5) representing this population may have reduced the power of the discriminant analyses for Bach Ma. The results of the phylogenetic analysis are similarly ambiguous: Some, but not all groups of the population tend to form a monophyletic clade which exhibits affinities to gibbon groups from Veunsai and, even more so, Taveng.

Bach Ma appears to be a distinct gibbon population with some affinity to the populations in north-east Cambodia.

4.1.4 North-east Cambodia (Veunsai, Taveng and Poey)

Discrimination power between the populations of Veunsai and Taveng is weak. Their respective ranges of discriminant scores overlap and the classification accuracy is reduced. Most of the misclassified groups are members of these two populations (and, to a lesser degree, of the Poey population). In 4 of the 5 discriminant analyses performed, the percentage of correctly classified groups is lower for Veunsai than for Taveng. This may have been caused by the higher fraction of groups with missing data (e.g. male solo song bouts) in the Veunsai sample. In the cladograms of the phylogenetic analyses, the groups from Veunsai and Taveng are virtually unresolved.

The admittedly arbitrary decision to treat the gibbon groups from two localities in the Virachey National Park as two distinct populations in this study (i.e. Veunsai and Taveng), is reflected by the results of this study. Of all study populations, Veunsai and Taveng exhibit the closest proximity in vocal characteristics. Discrimination between these two localities is weak and in the phylogenetic analysis, the two populations are the least resolved. In the remaining discussion, the gibbon groups from Veunsai and Taveng will be regarded as one unit and termed the Virachey population. This pooling makes also sense because both recording sites are located in the same large forest. I am not aware of any physical barriers that could prevent genetic exchange between the gibbon groups occurring at the two recording sites.

The status of the Poey population (localities Mas and Khamaeng) is difficult to evaluate because of the small sample size (4 gibbon groups). In the discriminant analysis, the centroid of the Poey population is clearly separated from all other study populations, but this result might be influenced by the sample size and the relatively high proportion of groups with missing values (50%). In the phylogenetic analysis, the population remained unresolved. For a more reliable evaluation of the affinities of the Poey gibbon population, it would be essential to tape-record song material of additional gibbon groups. This might be difficult to achieve, however, because only few gibbon groups appear to remain in this area due to the immense reduction and degradation of the gibbon habitat occurring in this area.

Vocal separation among the populations from Poey, Veunsai and Taveng appears to be poorly expressed. Therefore, it appears plausible to consider them as one taxonomic group, which clearly differs from the Samling population but shows some affinities to the Bach Ma population. It should be noted, however, that the variability in song characteristics appears to be larger in this cluster from north-eastern Cambodia than in either the Samling or the Bach Ma population (Table 3.7). This finding will be discussed below (section 4.4.3).

4.2 Taxon-specific vocal characteristics

Geissmann et al. (2000) described a series of song characteristics suitable for differentiation between various crested gibbon taxa, including *N. l. leucogenys, N. l. siki,* and *N. gabriellae*. According to the commonly assumed distribution ranges of these taxa, *N. l. siki* and *N. gabriellae* should each be represented in my study with at least one population (Bach Ma and Samling, respectively). In a qualitative analysis, I examined my sound material in order to see whether any of my populations consistently matched the previously described vocal characteristics of one of the crested gibbon taxa (Geissmann et al., 2000). Then, I tested whether this assignment of populations to taxa based on vocal characteristics corresponded with their assumed distribution ranges.

All song characteristics that could be examined in all populations (C to H in Table 3.1) exhibited considerable variability. In each feature, at least one population differed markedly from all others. The qualitative assignment of populations to taxa based on the previously reported taxon-specific song characteristics only partially corresponds to the assumed taxonomic status of the populations under analysis.

A classification of the populations from Samling and Bach Ma as *N. gabriellae* and *N. l. siki*, respectively, was largely confirmed. Only for Bach Ma, one characteristic (type of staccato notes) could not be examined and another (begin of the first note of the multi-modulated phrase) revealed conflicting results. The populations from Poey, Veunsai and Taveng, on the other hand, could not be assigned unequivocally to either one of the two taxa under consideration. In this qualitative analysis, different characteristics either produced conflicting taxon identifications, or in some characteristics, the gibbons revealed character states that were intermediate between those reported for the two taxa.

In summary, the qualitative comparison of the study populations' vocal characteristics with the taxon-specific song characteristics described by Geissmann et al. (2000) suggested a taxonomic identification of two of the populations, Samling and Bach Ma, as *N. gabriellae* and *N. l. siki*, respectively. A convincing identification of the samples from north-eastern Cambodia was not possible with this method.

The results of the phylogenetic and the multivariate analyses are consistent with these findings. In these analyses, the populations from Samling and Bach Ma appear as the two most distinct groups among the study populations. The distinctiveness is more pronounced in Samling than in Bach Ma, and the latter exhibits some proximity to the large, variable and poorly resolved cluster containing the gibbon populations from Poey, Veunsai and Taveng.

However, certain limitations of the qualitative analysis described in this section should be taken into consideration: In this procedure, I assumed that populations were taxonomically homogeneous and, therefore pooled all groups of the same population. The population samples consisted of unequal numbers of gibbon groups, and some populations were represented with particularly few groups. The taxonomic assignment was strictly dichotomous and used qualitative characteristics (except for the number of great call notes). Because no quantitative data of the song differences between *N. l. siki* and *N. gabriellae* is available as a reference, it cannot be assessed whether the observed differences among the population means just represent the variability within one taxon or whether they are actually due to distinct, taxon-specific character states. Furthermore, it might be relevant that in Geissmann et al.'s (2000) study, *N. l. siki* was represented by zoo animals only (Geissmann, pers. comm.). Although songs of zoo gibbons regarded as *N. gabriellae* correspond with songs of wild gibbons found in the proposed distribution range of this taxon, the same may not be the case in *N. l. siki* (Geissmann, pers. comm.). This should be examined in a future study comparing song characteristics of *N. l. siki* individuals kept in zoos and individuals living in their natural habitat.

4.3 Vocal distance *vs.* geographical distance

So far, most studies on geographic variation and inter-population variability in primate vocal behavior compared only two samples (e.g. Arcady, 1996; Fischer et al., 1998; Hafen, 1998; Maeda & Masataka, 1987; Mitani et al., 1992, 1999). This makes it difficult to draw any conclusions on the actual relevance of the observed vocal differences. From a comparison of more than two populations, one can derive more meaningful results. In such a study, more pairwise distances between populations are involved and multiple comparisons are possible.

The present study compares vocal samples from five different localities with various geographical distances among the localities. This allowed for ten pairwise comparisons. For each "pair", the relative amount of vocal differences can be determined (for instance with a multivariate analysis). The degree of vocal differences can be used as an indicator for the degree of genetic divergence between the populations. It can be examined to what extent vocal differences among local populations correspond to the geographical distances. Furthermore, vocal differences can provide useful evidence for determining the position of possible taxonomical and biogeographical boundaries between populations. This has been done in studies on birds, tree frogs and primates (Baker, 1974, 1975; Dallmann & Geissmann, 2001a; Ralin, 1977).

In the present study, a comparison of vocal and geographical distances among populations was used in order to further evaluate the taxonomic status of the gibbon study populations (especially the populations in northeast Cambodia). If vocal differences among local populations correspond to geographical distances, one can assume that they probably just reflect random genetic drift. A deviation from such a simple relationship, however, could suggest genetic isolation among populations.

Vocal distances among gibbon populations were measured as the distances among the respective population centroids of the discriminant scores (Figures 3.3 and 3.4).

The correlation between vocal and geographical pairwise distances was not significant. Instead, the comparison of vocal and geographical pairwise distances revealed that the vocal distance between Samling and Bach Ma is in the same range as the vocal distances between Samling and any other study population, whereas the geographical distance between Samling and Bach Ma is approximately twice as large as that between Samling and other study populations. In other words, using the north-eastern Cambodian populations (Poey, Veunsai and Taveng) as a starting point, the geographical distances to Samling in the south and Bach Ma in the north are approximately the same (about 200 km), but the vocal distances to Samling are about four to five times larger than those to Bach Ma (Table 3.8). The same result is obtained, if residuals of vocal distances (dependent variable) versus geographical distance (independent variable) are calculated. These residuals should, per definition, represent the vocal differences among populations after any influence of the geographical distance has been removed. The residuals (Figure 3.5) suggest high relative vocal differences between north-eastern Cambodian populations and Samling, low relative vocal differences between the north-eastern populations and Bach Ma. This finding suggests that an isolation mechanism is operational between the three populations in the north-east of Cambodia on one hand and Samling on the other, whereas such an effect is absent or weaker between north-eastern Vietnam and Samling.

4.4 Implications for gibbon taxa and hybridization

4.4.1 Samling

Based on the qualitative analysis of vocal features, the Samling gibbon population appears to represent the "typical" *N. gabriellae*. *Nomascus gabriellae* is the southernmost species of the crested gibbons (genus *Nomascus*), and the Samling population is the southernmost gibbon population of this study (and probably one of the most southern populations in Cambodia). In addition, Samling is also the geographically most remote of the Cambodian study populations. The Samling Logging Concession is also located well in the southernmost third of the entire proposed distribution range of *N. gabriellae* (e.g. Geissmann et al., 2000). As a result, the vocal identification of this population as *N. gabriellae* is fully consistent with the taxon’s reported distribution range.

This conclusion remains to be verified by comparing the songs from Samling with those of other gibbon populations within the proposed distribution range of *N. gabriellae*, preferably from the southern part like Nam Cat Tien Reserve in southern Vietnam, where gibbons have been reported to occur (Adler, 1991; Geissmann, 1995b; Geissmann et al., 2000; Robson, 1990; Robson et al., 1991). Comparative studies using non-vocal data could also be used to verify the identification of the Samling gibbons. This would, however, not be an easy task. Because no museum specimens from Samling are known to exist, such comparative work would probably have to focus on DNA sequences extracted from feces samples collected from wild gibbons.

4.4.2 Bach Ma

All results of the present study suggest that the gibbon population in Bach Ma clearly differs from that in Samling in its song characteristics. The discriminant analysis separates the two populations very accurately. Both samples show relatively little variability. The results of the phylogenetic analysis suggest a split into two distinct clades.

The gibbon population from Bach Ma probably represents *N. l. siki*. This view is supported by the qualitative comparison of its vocal characteristics with those previously described for various taxa of crested gibbons by Geissmann et al. (2000). Furthermore, Bach Ma (with latitude of about 16 12’N) is not only located in the postulated distribution range of *N. l. siki* (between 15 45’N and about 20 N, according to Groves, 2001), but also very close to the type locality of *N. l. siki* (Geissmann, pers. comm.).

4.4.3 North-east Cambodia

For the gibbon populations in Samling and Bach Ma, the results of my analysis of vocal characteristics confirmed the taxonomic status that was assumed based on the geographic location of these populations. For the gibbon populations from north-eastern Cambodia, i.e. from Poey Commune and Virachey National Park (Veunsai and Taveng), a taxonomic assignment is much more complicated.

As described above (section 4.1.4), there is little evidence for a geographic barrier between the gibbon groups from Veunsai and Taveng. They are therefore regarded as belonging to the same population.

Results for the population from Poey are difficult to interpret due to the small sample size and high fraction of groups with missing values. This may lead to biased results if the few groups in the analysis are not representative for the entire population. If the obtained population centroid for the discriminant scores is representative for the population in Poey, then this population can easily be separated from all other populations in the sample. In the phylogenetic analysis, the groups from Poey are as unresolved as the groups from Virachey National Park. In the qualitative comparison with taxon-specific vocal characteristics, the results for Poey resemble those for Virachey. The vocal distance is closer between Poey and Bach Ma, and larger between Poey and Samling, than what could be expected from the corresponding geographical distances. In this respect, Poey also resembles the samples from Virachey.

The results summarized above suggest that there is probably no reproductive isolation among the study populations from north-east Cambodia. This appears to be trivial if one considers the short geographical distances between the localities. Genetic proximity between these gibbon groups is not self-evident, however, if one takes into account that river the San River separates Virachey National Park from Poey Commune. This major river has its source in the Annamite Mountains near the Cambodian-Vietnamese border and is between 60 and 100 m wide on Cambodian territory (my personal estimate). Since watercourses often represent boundaries between the distribution ranges of gibbon taxa (e.g. Marshall & Sugardjito, 1986), the San River could well represent geographical barrier and therefore a reproductive barrier between the Virachey population and the Poey population. Based on the currently available data, however, this appears not to be the case.

Combined, the gibbon groups in north-east Cambodia form a large, heterogeneous cluster that is clearly distinct from Samling and, to a lesser extent, from Bach Ma. This cluster appears to about intermediate between Samling and Bach Ma both in geographical position as well as vocal characteristics. These affinities are suggested by the results of the qualitative and the discriminant analyses. The results of the phylogenetic analysis are not conclusive enough to explicitly suggest the same interpretation, but they are at least compatible with it.

The study populations from north-east Cambodia differ in vocal characteristics from either *N. gabriellae* in Samling and, to a lesser extent, *N. l. siki* in Bach Ma. What taxon, then, are they?

The following three explanations are possible: Gibbons from north-east Cambodia may either refer to *N. l. siki* (A), they may be hybrids between *N. gabriellae* and *N. l. siki* (B), or they may represent a previously unrecognized new taxon (C).

If interpretation A was correct, the song pattern of north-east Cambodian gibbon populations should closely correspond to that of *N. l. siki* (represented in this study by the Bach Ma sample). This correspondence is far from perfect, however, but the two groups resemble each other more closely than each of them resembles the Samling population.

If interpretations A or C were correct, one would expect the north-east Cambodian gibbon populations to be vocally as homogeneous as the other study populations. This does not appear to be the case however, with populations from north-east Cambodia being more variable and gibbon groups scattered all over the cladograms instead of forming monophyletic clusters.

If interpretation B was correct, we should expect the north-east Cambodian gibbon songs to exhibit a higher inter-group variability than songs of the other study populations, because variability should be higher in a hybrid populations than in pure ones. This does appear to be the case. As a result, interpretation B is more likely to be true. The scattering of the north-east Cambodian gibbon groups in the phylogenetic trees and the increased vocal variability within this sample could be the result of hybridization in this area.

A high degree of vocal variability may also be observed in an area with two vocally distinct taxa occurring sympatrically. In this case, the groups of such a mixed population should fall into two separate and taxon-specific vocal clusters. This, however, does not appear to be the case in the study populations from north-east Cambodia.

4.4.4 Possible taxon boundary

The finding that the study populations in north-east Cambodia appear to be genetically more isolated from the south-east Cambodian Samling population (*N. gabriellae*) than from the Vietnamese Bach Ma population (*N. l. siki*) suggests that *N. gabriellae* is not the only taxon of crested gibbons occurring in Cambodia. It is unclear though, whether the hypothetical second taxon in Cambodia occurs in a pure or in a hybridized population. In either case, some form of a more or less efficient taxon boundary should exist in east Cambodia somewhere between the north-eastern corner of Cambodia and Samling in the south-east. Examination of maps and observations in the field revealed two geographical features, which represent more or less efficient barriers for gibbon distribution. (1) The Srepok is a large river, which runs east-west about 50 km south of Poey Commune. It would separate the north-eastern corner of Cambodia from the rest of east Cambodia. (2) Another potential geographical barrier is the eastern part of the central Indochina dry forests (Baltzer et al., 2001). These forests are dominated by dry, open woodlands with interspersed fragments of wetter grasslands and evergreen forest (Legris & Blasco, 1972). Most of this habitat is not suitable for gibbons. To the east, the lowland is encompassed in a semi-circle by the Annamites mountain chain with its rich evergreen forests. As described above (chapter 1), the foothills of the Annamites extend into Cambodia in two areas: (1) in the very north-east, the area of Virachey National Park and Poey Commune, and (2) further south in east Cambodia, where the Samling Logging Concession is situated. It is possible that the gibbon populations in these two areas are genetically isolated from each other by the large area of relatively open habitat typical of the central Indochina dry forest. It is possible, however, that this large area of dry forest was crossed by bridges of wet evergreen forest in the past, thus linking the extended gibbon forests in the north and south. Similarly, dry dipterocarp forest has been proposed to act as a barrier to gibbon dispersal in north-east Thailand (Srikosamatara & Doungkhae, 1982).

To assess the degree of genetic isolation occurring between the gibbons in north-east Cambodia and those in the south-east (e.g. in Samling), it would be essential to have vocal samples from the large area in-between. In order to collect such a sample, I visited the area with evergreen forest in Lomphat Wildlife Sanctuary, which is located about halfway between the localities of the north-eastern and south-eastern gibbon samples analyzed in this study. Unfortunately, I did not hear any gibbons during my stay in Lomphat. It is unknown whether this wildlife sanctuary still supports gibbons. If it does, it may be difficult to find them in the predominantly open area because the interspersed patches of evergreen forest, while being naturally fragmentary in the first place, have been subjected to deforestation and degradation.

Because it was not possible during this study to collect samples in the large area between Virachey National Park and Samling Logging Concession, it cannot be determined how and where the distinctive vocal patterns of the north-eastern and south-eastern gibbon populations replace each other. Is there a more or less sharp boundary between the southern and the northern song pattern or do these patterns just represent the end points of a more or less extensive cline? The former situation should occur, if the respective populations were separated by an efficient barrier to gibbon dispersal, the latter should occur in the absence or weak expression of such a barrier.

4.4.5 The larger picture

Based on a comparison of gibbon songs, it has previously been reported that gibbons in a large area in southern Laos and central Vietnam are neither typical *N. gabriellae* nor typical *N. l. siki* (Geissmann, 1995a; Geissmann et al., 2000). The authors suggested that this finding either represent evidence for a previously undescribed gibbon taxon, or for a large intergrade area between *siki* and *gabriellae*, or a combination of the two. These earlier findings (Geissmann, 1995a; Geissmann et al., 2000) are virtually identical to those of the present study. Apparently, the large area with the unidentified gibbons is even larger than assumed and extends well into north-eastern Cambodian territory.

Gibbon songs from the Xe Piane Biodiversity Conservation Area, situated adjacent to the Laotian-Cambodian border, have been reported to be intermediate between those of *N. gabriellae* and *N. l. siki* (Geissmann, 1995a; Geissmann et al., 2000). This would suggest that Xe Piane and Virachey are not only geographically very close, but also similar with respect to their gibbon vocalizations. Further to the north in Laos (Bolovens Plateau) and Vietnam (Bach Ma), gibbon vocalizations appear to become similar to what has been described as the typical *N. l. siki* song type. Again, it should be pointed out that the description of this song type (Geissmann, 1995a; Geissmann et al., 2000) was based on zoo animals of unknown provenance. Their song may not necessarily be identical to that of the gibbons in Bach Ma, which are thought to represent *N. l. siki* in the present study.

For some areas in the large area with the unidentified gibbons, evidence from museum specimens and vocalizations seem to contradict each other (Geissmann et al., 2000). If the localities for the very few museum specimens from this area are correct (which, however, may not always be the case), this would either mean that (1) morphological and vocal phenotypes do not necessarily agree, or (2) more than one taxon occurs in this area (sympatry), or (3) that one taxon replaced the other relatively recently.

The results of the present study on the vocal diversity of Cambodian crested gibbons do not reliably resolve the identity of the gibbon populations in north-east Cambodia, but provide a first element to a puzzle. In future studies, this research should be extended to include the neighboring areas of Laos and Vietnam. To further elucidate the taxonomy of the crested gibbons in southern Indochina, it would be 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 pure form. Such data could be relevant for assessing the actual degree of mixture (if any) between *N. gabriellae* and *N. l. siki*, estimating the geographical extent of the area, and identifying possible taxonomic boundaries.

4.5 Limitations of significance

4.5.1 Cladistic analysis

The cladistic analysis of gibbon song characteristics resulted in little resolved cladograms with a large amount of discordance among the fundamental cladograms. Only one homogeneous grouping, a monophyletic clade including all gibbon groups from Samling, is strongly supported. The disarrangement of the other groups included in the phylogenetic study is surprising, considering that a correct assignment of the same groups to their respective population was in most cases possible with multivariate analysis. The low resolution of the cladograms may have been caused by the character state differences between OTU's being either (1) too small or (2) too variable to provide sufficient information for untangling phylogenetic relationships.

(1) Cladistic analysis examines changes between discrete character states. This requires transformation of variables into arbitrarily defined character states. If the original variables are continuous data (as is the case in most of the vocal data of this study), and if the differences between individuals or groups are small, a lot of subtle information will get lost when characters are coded into discrete character states. The multivariate analysis does not share this handicap.

(2) If characters, on average, differ among groups but are very variable, it can be difficult to find the phylogenetic relationships. Highly variable characters overlap in their ranges among non-related groups. As a result, many individuals may be coded “incorrectly” and false groupings are derived. This problem could be reduced by using average values of populations as OTU's instead of individuals, as in the present study.

4.5.2 Multivariate analysis

Multivariate analyses have been applied in a number of primatological studies comparing vocal characteristics between individuals, groups or populations (Arcady, 1996; Arcady et al., 1998; Chapman & Weary, 1980; Dallmann & Geissmann, submitted; Maeda & Masataka, 1987; Mitani et al., 1992; Mitani et al., 1999). In the present study, this procedure proved to be suitable for vocal discrimination between gibbon groups. On the basis of the derived discrimination model it would be possible to estimate vocal affinities of gibbon vocalizations whose origin is not known. A further merit of multivariate analysis is the fact that the original measurements can be used, i.e. coding into discrete character states is not necessary. On the other hand, discrimination between groups is based on the presence or absence of similarities only. Although similarity often correlates with phylogenetic relatedness, this is not always the case (Geissmann, 2003). Similarities do not necessarily indicate phylogenetic relationships, but can also be based on retained primitive (symplesiomorphic) characteristics or result from convergent evolution. For phylogenetic purposes, this is a drawback of multivariate analysis as compared to cladistic analysis.

4.6 Conclusions

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

(1) Not all crested gibbons in Cambodia exhibit the same song pattern.

(2) Song patterns of the southern population (Samling) correspond to the previously described pattern of *N. gabriellae*. Gibbon songs from north-eastern Cambodia, however, differ from both the previously described patterns of *N. gabriellae* and *N. l. siki* (as represented by the study population from Bach Ma, central Vietnam).

(3) Gibbon songs from north-eastern Cambodia exhibit a higher intra-population variability than songs from the other study populations.

(4) Gibbons from north-eastern Cambodia appear to be both vocally and geographically intermediate between the population from south Cambodia and the one from Bach Ma, but exhibit closer affinities to the Bach Ma sample, in contrast to the geographical distances.

(5) The vocal difference between crested gibbons in south-east and north-east Cambodia is larger than expected from the geographical distance. This suggests that some reproduction barrier exists between these two populations. Whether the north-eastern population is a new, previously unrecognized taxon or part of a large intergrade zone between *N. gabriellae* and *N. l. siki* cannot be answered conclusively based on the results of this study.

5. Summary

In gibbons (family Hylobatidae), species-specific call patterns are largely inherited. Vocal characteristics have been found particularly useful for assessing systematic relationships among hylobatids and to reconstruct their phylogeny. The taxonomy of the crested gibbons (genus *Nomascus*) is currently under debate. For instance, Geissmann et al. (2000) discovered a large area between the respective distribution ranges of *N. leucogenys siki* and *N. gabriellae* in central Vietnam, southern Laos and possibly north-eastern Cambodia, where calls appear to differ from the typical calls of either species. Both fur colouration and vocal data from this area suggest either a large hybridization zone with one species gradually replacing the other, or the existence of a previously unrecognized taxon. *Nomascus gabriellae* is usually thought to be the only *Nomascus* species occurring in Cambodia. I studied the vocal diversity among different wild *Nomascus* populations in Cambodia in order to assess their taxonomic relationships and to examine whether their vocal patterns corresponded to those previously described of *N. l. siki* and *N. gabriellae*.

Going from south to north, I tape-recorded crested gibbon songs in southern Mondulkiri Province, in central Rattanakiri Province and in two different districts of the Virachey National Park in northern Rattanakiri. Additional tape-recordings provided by Dr. Thomas Geissmann included samples from southern Mondulkiri Province, a sample of typical *N. leucogenys siki* songs tape-recorded near the type-locality of that taxon in the Bach Ma National Park in central Vietnam, and a sample of *N.* sp. cf. *nasutus* from Cao Bang Province, NE-Vietnam that was used as an outgroup in the cladistic analysis.

The tape-recordings were digitized and sonagraphically analyzed. A total of 40 song bouts (36 duet songs and 6 male solo) from different gibbon groups were included in this study. I analyzed 151 female phrases (great calls) of 33 different female gibbons (average: 4.6 phrases/individual) and 235 male phrases (92 of them codas) of 39 different male gibbons (average: 6.0 phrases/individual). On the sonagrams, I determined a total of 90 variables including time and frequency measurements and qualitative parameters. Various discriminant analyses were performed in order to select the variables that were most effective for discrimination between gibbon populations and to assess the vocal differences among them.

A phylogenetic (cladistic) analysis using the selected variables produced some support for a monophyletic grouping of all gibbon groups from southern Mondulkiri. The discriminant analyses revealed little vocal variability in this sample and marked separation of these songs from those of all other localities. In many respects, the vocal pattern of this population exhibited similarities to the pattern typical of *N. gabriellae*. The samples of the other gibbon populations either remained unresolved in the phylogenetic analysis or were not arranged in monophyletic clades. The vocalizations from Bach Ma, the northernmost sample, were identified as relatively homogeneous and distinct in the discriminant analyses, but not as pronounced as the sample from southern Mondulkiri. Most vocal characteristics were compatible with a taxonomic assignment of this population to *N. l. siki*. The gibbon populations in north-east Cambodia (Rattanakiri Province) were the vocally most variable but, on average, differed least among each other. Their vocal pattern differed both from *N. l. siki* and *N. gabriellae,* but exhibited more similarity to the *siki* pattern. They may be regarded as a large, heterogeneous cluster that appears to be vocally more distinct from the southernmost population (southern Mondulkiri) than from the northernmost population (Bach Ma), although geographical distances to either of them are almost identical.

The results of this study suggest that considerable vocal diversity occurs both among and within different local populations of crested gibbons in Cambodia. Only the southernmost Cambodian population exhibits marked vocal similarity to the pattern described for *N. gabriellae*. The north-east Cambodian populations, on the other hand, appear to be intermediate between the southern population and the more northern sample from Bach Ma (central Vietnam) or possibly closer to the latter. The intermediate position of the populations from north-east Cambodia, together with their apparently elevated vocal variability, may result from hybridization between *N. gabriellae* and *N. l. siki* in this area. Alternatively, the gibbons in northeastern Cambodia may represent a distinct taxon, in which case a taxon boundary should exist between the southernmost and all other Cambodian samples. Because no data is available from a large geographical area between these two groups of samples, it cannot be assessed whether the observed vocal differences between them represent just the end points of a cline or if they result from an isolation factor causing genetic divergence.

5.1 Zusammenfassung

Die artspezifischen Gesänge der Gibbons (Familie Hylobatidae) sind weitgehend vererbt und eignen sich deshalb besonders gut, um die verwandtschaftlichen Beziehungen zwischen den Gibbons aufzuklären und ihre Stammesgeschichte zu rekonstruieren. Die Systematik der Schopfgibbons (Gattung *Nomascus*) ist zur Zeit jedoch noch unklar. So fanden Geissmann et al. (2000) zwischen den Verbreitungsgebieten von *N. leucogenys siki* und *N. gabriellae* ein Gebiet, in dem sich die Gesänge vom typischen Gesangsmuster beider Arten unterscheiden. Diese Region erstreckt sich über das zentrale Vietnam, das südliche Laos und vermutlich den Nordosten Kambodschas. Die bisher vorhandenen Daten über Fellfärbung und Gesang der Tiere in diesem Gebiet lassen vermuten, dass sich dort die beiden Arten entweder genetisch durchmischen (Hybridisation) und eine Art somit schrittweise in die andere übergeht, oder aber dass dort ein bisher unbekanntes Taxon existiert. Bis anhin wurde allgemein angenommen, dass *Nomascus gabriellae* die einzige Schopfgibbonart Kambodschas ist. In dieser Studie wird die Gesangsdiversität verschiedener wild lebender Schopfgibbon-Populationen in Kambodscha untersucht, um ihre verwandtschaftlichen Beziehungen zu studieren und um zu prüfen, inwiefern ihr Gesang mit den als typisch für *N. l. siki* oder *N. gabriellae* beschriebenen Gesängen übereinstimmt.

Von Süden nach Norden wurden in folgenden Regionen Ostkambodschas Gesangsaufnahmen von Gibbons gemacht: im Süden der Provinz Mondulkiri, im zentralen Teil der Provinz Rattanakiri und in zwei verschiedenen Teilen des Virachey Nationalparks im Norden der Provinz Rattanakiri. Dr. Thomas Geissmann stellte zusätzliche Tonaufnahmen zur Verfügung, welche einerseits im Süden der Provinz Mondulkiri, andererseits im Bach Ma Nationalpark in Zentralvietnam nahe der Typuslokalität von *N. leucogenys siki*, sowie in der Provinz Cao Bang im Nordosten Vietnams (Aufnahmen von *N.* sp. cf. *nasutus*) gemacht wurden.

Die Tonaufnahmen wurden am Computer digitalisiert und sonagraphisch dargestellt. Die Stichprobe umfasste Gesänge von 40 verschiedenen Gibbongruppen (36 Duette und 6 Männchen-Soli). Davon analysierte ich 151 Strophen (*great calls*) von 33 verschiedenen Weibchen und 235 Strophen (davon 92 Codas) von 39 verschiedenen Männchen. Dies ergab im Durchschnitt 4.6 Strophen pro Weibchen und 6.0 Strophen pro Männchen. Anhand der Sonagramme definierte ich 90 Variablen, die Zeit- und Frequenzmesswerte sowie einige qualitative Parameter enthielten. Anhand von Diskriminanzanalysen eruierte ich diejenigen Variablen, die am meisten zur Unterscheidung der Gibbonpopulationen beitrugen, und beurteilte das Ausmass der Gesangsunterschiede zwischen den Populationen.

Die phylogenetische Analyse deutet auf eine monophyletische Gruppe hin, die alle Gibbons aus dem Süden der Provinz Mondulkiri (Südost-Kambodscha) umfasst. Mittels Diskriminanzanalyse konnte diese Population sehr gut von den anderen unterschieden werden, und sie wies auch eine relativ geringe Gesangsvariabilität auf. Die meisten Gesangseigenschaften dieser Population scheinen typisch für *N. gabriellae* zu sein. Die übrigen Gibbonpopulationen wurden in den Kladogrammen entweder gar nicht oder zumindest nicht in monophyletischen Gruppen zusammengefasst. Die Gesänge der Gibbongruppen von Bach Ma (Zentralvietnam) zeigten relativ wenig Variablilität und liessen sich mittels Diskriminanzanalyse ebenfalls von den anderen Gruppen unterscheiden, wenn auch nicht so deutlich wie die Stichprobe aus Mondulkiri. Die meisten gesanglichen Eigenschaften der Gibbons von Bach Ma glichen denjenigen, die für *N. l. siki* beschrieben wurden. Die Gibbonpopulationen aus Nordostkambodscha (Provinz Rattanakiri) wiesen die grösste Gesangsvariabilität auf und unterschieden sich nur sehr unvollständig voneinander. Sie liessen sich aufgrund ihrer Gesangseigenschaften weder *N. l. siki* noch *N. gabriellae* eindeutig zuordnen, scheinen aber *N. l. siki* näher zu stehen. Fasst man die Gibbonpopulationen aus Nordostkambodscha zusammen, scheinen sie sich insgesamt von der südlichsten Stichprobe gesanglich mehr zu unterscheiden als von der nördlichsten, obwohl die geographische Distanz zu beiden in etwa dieselbe ist.

Die Resultate dieser Studie zeigen, dass sowohl zwischen als auch innerhalb verschiedener Schopfgibbon-Populationen in Kambodscha eine beträchtliche Gesangsdiversität besteht. Von den kambodschanischen Populationen wies lediglich diejenige aus dem Süden deutliche Ähnlichkeiten mit den für *N. gabriellae* beschriebenen Gesangseigenschaften auf. Die Gibbons aus Nordostkambodscha scheinen gesanglich intermediär zwischen der Population aus Südostkambodscha und der Population aus Zentralvietnam zu liegen oder derjenigen aus Zentralvietnam ähnlicher zu sein. Die gesanglich intermediäre Position der Gibbons in Nordostkambodscha fällt mit der Tatsache zusammen, dass ihre Gesangsvariabilität besonders hoch zu sein scheint. Dies könnte das Resultat von Hybridisation zwischen *N. gabriellae* und *N. l. siki* sein. Andererseits wäre es aber auch möglich, dass die nordostkambodschanischen Gibbons ein eigenes Taxon darstellen und dass zwischen der Gibbonpopulation im Südenosten und den Populationen im Nordosten Kambodschas eine Taxongrenze besteht. Weil keine Aufnahmen aus dem Gebiet zwischen diesen beiden Stichprobengruppen vorliegen, lässt sich nicht beurteilen, ob die gefundenen Gesangsunterschiede lediglich Stadien in einem graduellen Übergang darstellen oder das Resultat genetischer Isolation sind.

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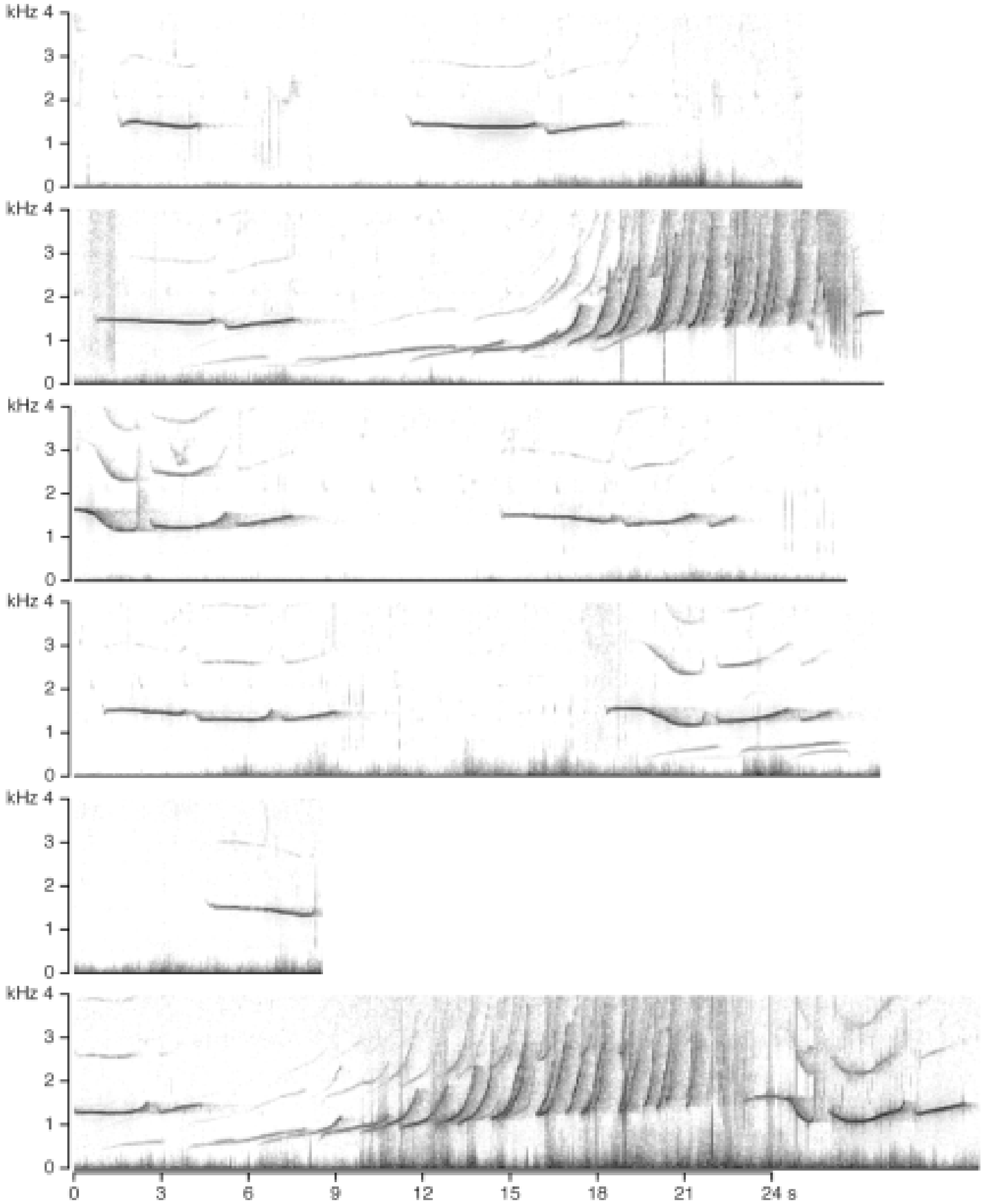
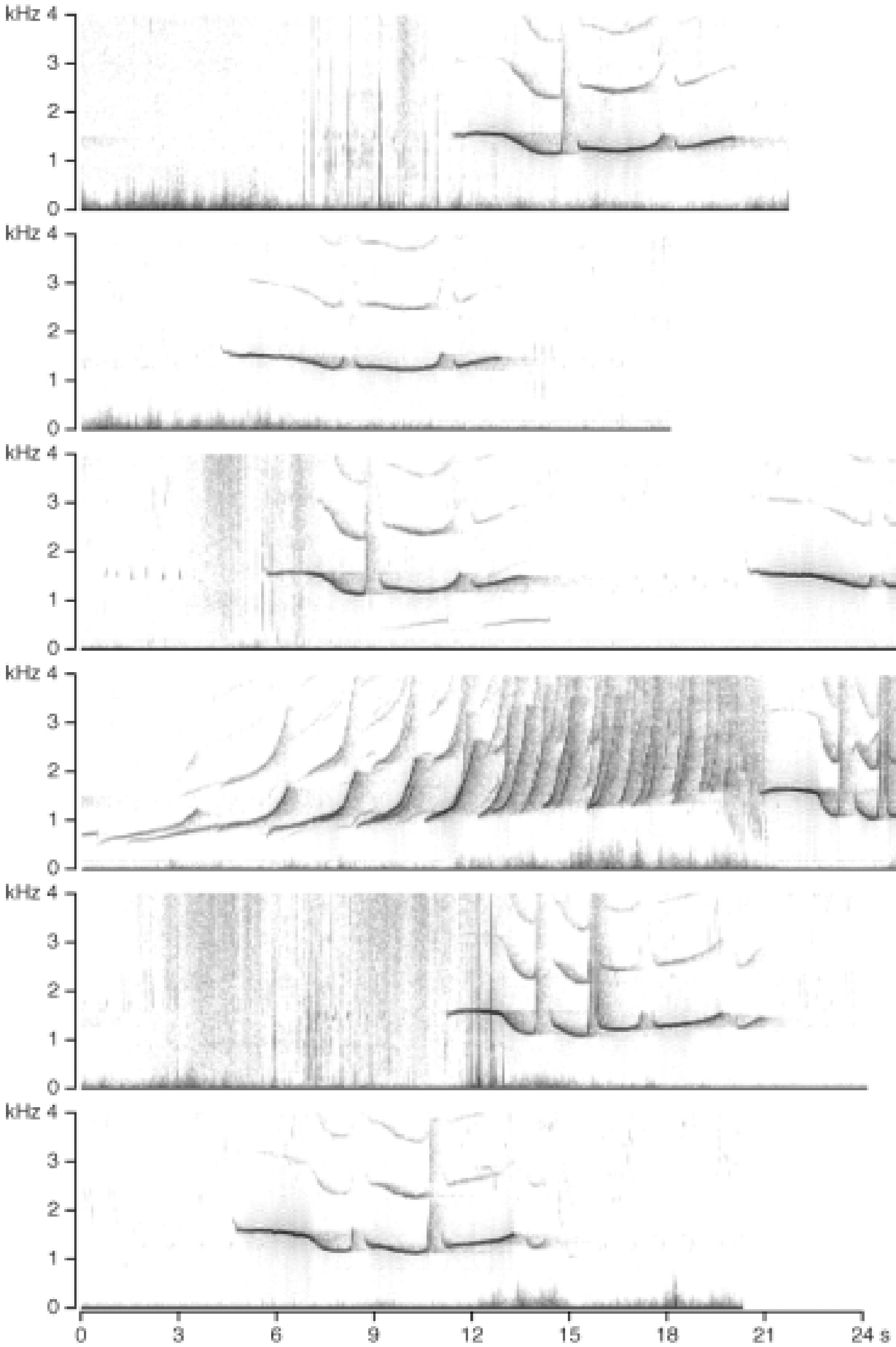
8. Appendices

Appendix 1. Sonagraphic excerpts of a typical song bout

Continuous sonagrams of a particularly short duet song bout of gibbon group 15 from Veunsai District in Virachey National Park. The sonagrams summarize the course of a typical duet song bout in crested gibbons showing the gradual build-up of male phrase complexity during the early part of the song bout (lines 1-11). Shown here is a complete duet song bout, except the first few male phrases (consisting of single notes), which were missed in the tape-recording.

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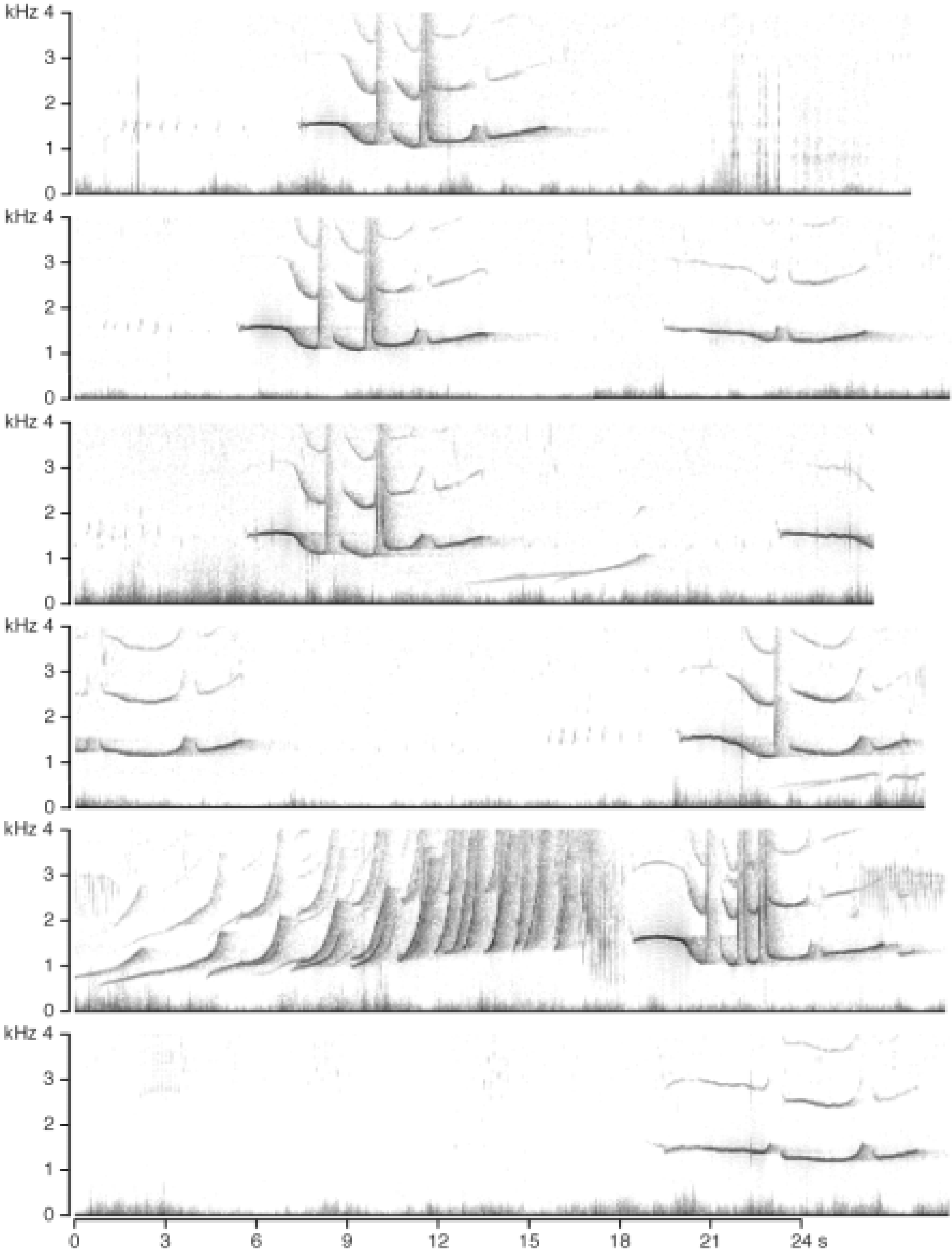
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9
12
15
18
21
24 s

Appendix 2. Acoustic terms used for variable definitions

Terms	Definition
Roll	A rapid sequence consisting of a steep frequency up- and down-sweep
Twitter	Repeated rapid changes between two frequencies (tones). A twitter does not carry very far. It is therefore only rarely visible on the sonagram.
Terminal up-sweep	A steep rapid frequency increase at the end of a note. On the sonagram identified by a nearly vertical line. Generally, the frequency at the end point of the note cannot be determined reliably, since the sonagram line gradually pales with increasing frequency. As a result, only measurements of the time domain can be taken.
Duration	Refers to the duration of a note. Measured in seconds, as the time span between the beginning and the end of a note.
Interval	Refers to the time interval between two subsequent notes. Measured in seconds, as the time span between the end of one note and the beginning of the subsequent note.
Range	Refers to the frequency range between two different frequencies. Measured in Hz, calculated as the frequency of the higher point minus the frequency of the lower point.
Anchor point	Characteristic position on the sonagram line where I measured the time an/or the frequency. See also Appendices 3 and 4.

Appendix 3. Definition of note types, note parts, anchor points and tangents

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

Note 1	Unit	Definition
Note composition:		
Horizontal Part		The first of the two distinctive parts of the note, characterized by a relatively constant frequency level, i.e. no steep frequency increase or decrease. Thus, the sonagram 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. Thus, the sonagram line forms a trough.
Anchor points & tangents:		
A	s & Hz	Beginning of note
B	s & Hz	Half duration of note
C	s & Hz	End of horizontal part, defined as point of divergence of the sonagram line and the tangent applied to it from above; synonymic with frequency maximum outside of the terminal up-sweep.
D	s & Hz	Maximum bend in transition from horizontal part to trough part
E	s & Hz	Frequency minimum
e	s	End of note, defined as position of vertical tangent applied from the right to the sonagram line
Peak intensity		Refers to the position on the sonagram line where the intensity of the signal (in dB) is greatest (represented by the darkest grayscale value).
At the point of peak intensity the following two measurements were taken:		
Peak frequency	Hz	The frequency at which the highest amplitude in a selection occurs.
Peak time	s	The time at which the highest amplitude in the selection occurs.

Appendix 3.2 The second note of the male's multi-modulated phrase

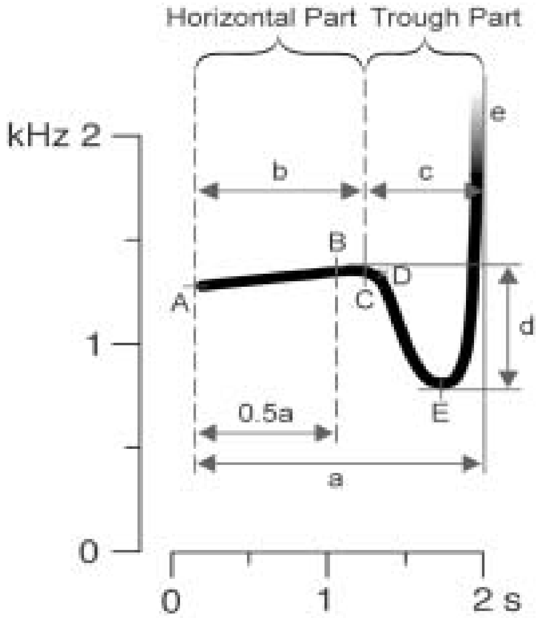
Note 2	Unit	Definition
Note composition:		
Initial part		The first of the three distinctive parts of the note, characterized by a marked frequency decrease to a local note frequency minimum.
Roll part		The second part in the note, characterized by including several rolls but at least one roll. In the 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 or 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 rather consists of a "plateau" of low frequency than of just one point of minimum frequency.
Anchor points & 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, defined as beginning of steep frequency increase
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 decrease
K	s & Hz	Frequency minimum of terminal part
k	s	End of note, defined as position of vertical tangent applied from the right to the sonagram line

Appendix 3.3 The female's great call phrase

Great Call	Unit	Definition
Note types:		
Oo note		Frequency increase from beginning to end of note no more than 1 kHz per second
Bark note		Frequency increase from beginning to end of note more than 1 kHz per second
Twitter note		A note in which the twitter part amounts to at least 50% of the duration of the entire note.
Intermediate notes		Intermediate notes between barks and twitters may occur, beginning as a bark and ending in a twitter. As long as the steep frequency increase is not markedly reduced as compared to the previous note, it they are regarded as bark notes.
Phrase composition:		
Oo phase		A phase including all *oo* notes of the great call. (Notes 1-3 in Appendix 4.3)
Bark phase (Accelerando-part)		A phase including all bark notes of the great call. (Notes 4-7 in Appendix 4.3)
Twitter phase		A phase including all twitter notes of the great call.
Anchor points & 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, defined as position of vertical tangent applied from the right to the sonagram line
Y	s & Hz	Beginning of note (third bark note)
y	s	End of note, defined as position of vertical tangent applied from the right to the sonagram line
Z	s & Hz	Beginning of note (last bark note)
z	s	End of note, defined as position of vertical tangent applied from the right to the sonagram line

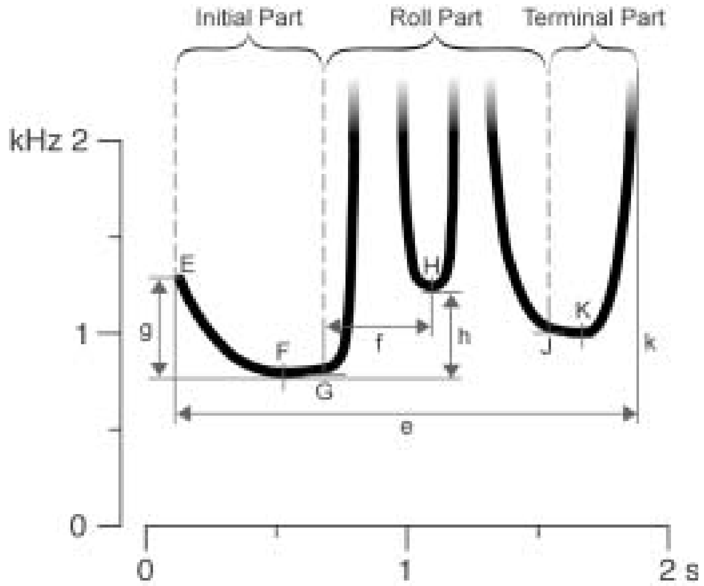
Appendix 4. Determination of variables on sonagrams

Appendix 4.1 The first note of the male’s multi-modulated phrase



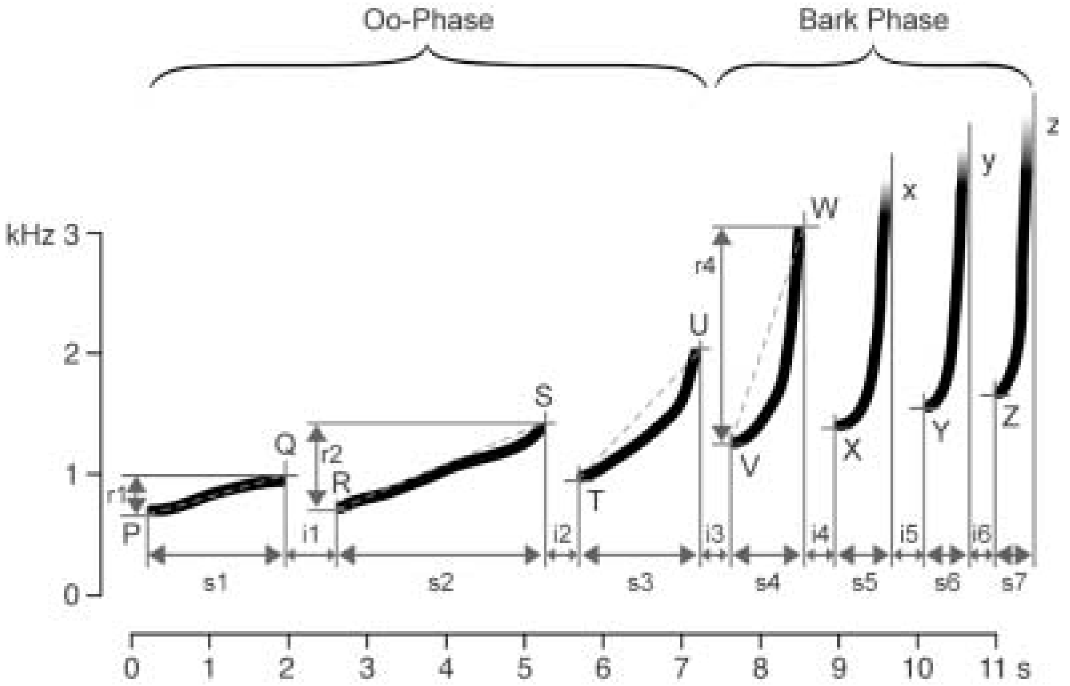
Stylized sonagram (only fundamental frequencies shown) of the first note of the multi-modulated phrase, showing the split in two parts, all anchor points and tangents, durations, and ranges measured on this note.

Appendix 4.2 The second note of the male’s multi-modulated phrase



Stylized sonagram (only fundamental frequencies shown) of the second note of the multi-modulated phrase showing the split in three parts, all anchor points and tangents, durations, and ranges measured on this note.

Appendix 4.3 The female's great call phrase



Stylized sonagram (only fundamental frequencies shown) of the great call showing the split in two phases, all anchor points and tangents, durations, intervals, and ranges measured on this phrase.

Appendix 4.4 The basic types of bark notes

Five basic note shapes (A-E) that were recognized among the bark notes of the female's great call.

Appendix 5. Definitions of variables

Abbreviation: Rel.=Relative.

Appendix 5.1 Variables of the male's multi-modulated phrase

No.	Variable (Unit)	Description
Overall Variables		
1	Number of notes	Number of notes in entire male phrase
2	Duration of entire male phrase (s)	Duration from beginning of first note (A) to end of last note in phrase
Note 1		
3	Duration first note (s)	a
4	Maximum duration (s)	Duration of single longest first note
5	Minimum duration (s)	Duration of single shortest first note
6	Presence of trough part	Trough part is either present or absent
7	Duration horizontal part (s)	b
8	Rel. duration horizontal part (%)	No. 7 in % of No. 3
9	Duration trough part (s)	c
10	Rel. duration trough part (%)	No. 9 in % of No. 3
11	Start frequency (Hz)	Frequency at A
12	Maximum frequency horizontal part (Hz)	Frequency at C
13	Maximum frequency (Hz)	Frequency at A or C
14	Minimum frequency (Hz)	Frequency at E
15	Frequency range (Hz)	No. 13 minus No. 14 (=d, if frequency at C higher than at A)
16	Frequency halfway (Hz)	Frequency at B
17	Frequency range to halfway point (Hz)	No. 16 minus No. 14
18	Rel. frequency range to halfway point (%)	No. 17 in % of No. 15
19	Duration to maximum bend (s)	Duration to D
20	Rel. duration to maximum bend (%)	No. 19 in % of No. 3
21	Frequency at maximum bend (Hz)	Frequency at D
22	Duration to peak intensity (s)	Duration from beginning of note to peak intensity
23	Rel. duration to peak intensity (%)	No. 22 in % of No. 3
24	Frequency at peak intensity (Hz)	Frequency at point of peak intensity
25	Frequency range to peak intensity (Hz)	No. 24 minus No.14
26	Rel. frequency range to peak intensity (%)	No. 25 in % of No. 15

Appendix 5.1 (continued).

No.	Variable (Unit)	Description
Note 2		
27	Duration of second note (s)	e
28	Presence of initial part	Initial part is either present or absent
29	Duration initial part (s)	Appendix 4.2
30	Rel. duration initial part (%)	No. 29 in % of No. 27
31	Duration roll part (s)	Appendix 4.2
32	Rel. duration roll part (%)	No. 31 in % of No. 27
33	Number of rolls	e.g. 2 Appendix 4.2
34	Number of "long" troughs in roll part	
35	Duration of first roll in roll part (s)	f
36	Duration terminal part (s)	Appendix 4.2
37	Rel. duration terminal part (%)	No. 36 in % of No. 27
38	Start frequency (Hz)	Frequency at E
39	Maximum frequency (Hz)	Maximum frequency outside of a roll or terminal up-sweep, i.e. frequency either at E, H or K
40	Minimum frequency (Hz)	Minimum frequency anywhere in note
41	Frequency range (Hz)	No. 39 minus No. 40
42	Minimum frequency initial part (Hz)	Frequency at F
43	Frequency range initial part (Hz)	g
44	Frequency first trough roll part (Hz)	Frequency at first trough in roll part, e.g. point H in Appendix 4.2
45	Frequency range first trough roll part (Hz)	h
46	Frequency last trough roll part (Hz)	Frequency at last trough in roll phase (Hi), if there is more than one trough
47	Frequency range last trough roll part (Hz)	hi
48	Frequency range lowest trough roll part (Hz)	hmin
49	Minimum frequency terminal part (Hz)	Frequency at K

Appendix 5.1 (continued).

8	Variable (Unit)	Description
Note 3		
50	Duration of third note (s)	
51	Number of rolls	
52	Presence of terminal up-sweep	Terminal up-sweep is either present or absent.
53	Start frequency (Hz)	
54	Maximum frequency (Hz)	Maximum frequency outside of a roll or terminal up-sweep
55	Minimum frequency (Hz)	Minimum frequency anywhere in note
56	Frequency range (Hz)	No. 54 minus No.55
57	Inter-notes frequency range (Hz)	Frequency range between minimum frequency of note 2 (No. 40) and start frequency of note 3 (No. 53)
Note 4		
58	Duration of fourth note (s)	
59	Terminal up-sweep	Terminal up-sweep is either present or absent.
60	Start frequency (Hz)	
61	Maximum frequency (Hz)	Maximum frequency outside of a roll or terminal up-sweep
62	Minimum frequency (Hz)	Minimum frequency anywhere in note
63	Frequency range (Hz)	No. 61 minus No. 62

Appendix 5.2 Variables of the female’s great call phrase

No.	Variable (Unit)	Description
Overall Variables		
64	Duration of entire great call (s)	Duration from beginning of first note (P) to end of last note in phrase (z)
65	Number of notes	Number of notes in entire great call
66	Range of start frequencies (Hz)	Range from lowest start frequency (usually first note) to highest start frequency (usually last note) in entire great call
67	Maximum frequency great call (Hz)	Indicates, if maximum frequency exceeds 2500 Hz or not
68	Number of *oo* notes	
69	Duration of *oo* phase (s)	Appendix 4.3
70	Rel. duration of *oo* phase (%)	No. 69 in % of No. 64
71	Number of bark notes	
72	Duration of bark phase (s)	Appendix 4.3
73	Rel. duration of bark-phase (%)	No. 72 in % of No. 64
74	Rel. duration twitter part (%)	Duration of twitter part in % of total note duration
75	Inter-phrase interval (s)	Interval between great call and coda, measured as duration from start of last note in great call (Z) to start of first note in coda (A). Negative value, if coda starts before end of great call
76	Male staccato notes during great call	The male either utters staccato notes at regular intervals simultaneously to the great call of the female, or does not.
Single note variables		
77	Duration first *oo* note (s)	s1
78	Frequency range first oo-note (Hz)	r1
79	Duration second *oo* note (s)	s2
80	Frequency range second *oo* note (Hz)	r2
81	Shape last *oo* note	The last *oo* note is qualitatively assigned to one of the 5 basic shape types (Appendix 4.4)
82	Duration first bark note (s)	s4
83	Frequency range first bark note (Hz)	r4
84	Duration last bark note (s)	s7
Successive notes variables		
85	First inter-note interval (s)	i1
86	Second inter-note interval (s)	i2
87	Last inter-note interval (s)	i6
88	First start frequency range (Hz)	Frequency at R minus Frequency at P
89	Second start frequency range (Hz)	Frequency at T minus Frequency at R
90	Last start frequency range (Hz)	Frequency at Z minus Frequency at Y

Appendix 6. Character state coding and threshold values

Abbreviations: Rel.=Relative, Freq.=Frequency, NA=Not Applicable.

Appendix 6.1 Variables of the male's multi-modulated phrase

No.	Variable (Unit)	Character states and threshold values			
Overall Variables					
1	Number of notes	0: < 3.2	1: 3.2-4.19	2: ≥ 4.2	
2	Duration of entire male phrase (s)	0: < 4.0	1: 4.0-5.49	2: ≥ 5.5	
Note 1					
3	Duration first note (s)	0: < 1.0	1: 1.0-1.59	2: ≥ 1.6	
4	Maximum duration (s)	0: < 1.8	1: ≥ 1.8		
5	Minimum duration (s)	0: < 1.2	1: ≥ 1.2		
6	Presence of trough part	0: <abs.	1: ≥ present		
7	Duration horizontal part (s)	0: < 0.5	1: ≥ 0.5		
8	Rel. duration horizontal part (%)	0: < 35	1: 35-64.99	2: ≥ 65	
9	Duration trough part (s)	0: < 0.8	1: ≥ 0.8	2: NA	
10	Rel. duration trough part (%)	0: < 65	1: ≥ 65	2: NA	
11	Start frequency (Hz)	0: < 1400	1: ≥ 1400		
12	Maximum freq. horizontal part (Hz)	0: < 1440	1: ≥ 1440		
13	Maximum frequency (Hz)	0: < 1450	1: ≥ 1450		
14	Minimum frequency (Hz)	0: < 900	1: 900-1099	2: 1100-1299	3: ≥ 1300
15	Frequency range (Hz)	0: < 550	1: ≥ 550		
16	Frequency halfway (Hz)	0: < 1450	1: ≥ 1450		
17	Freq. range to halfway point (Hz)	0: < 450	1: ≥ 450	2: ≥	
18	Rel. freq. range to halfway point (%)	0: < 70	1: ≥ 70	2: ≥	
19	Duration to maximum bend (s)	0: < 0.8	1: 0.8-0.99	2: 1.0	3: NA
20	Rel. duration to maximum bend (%)	0: < 67	1: ≥ 67	2: NA	
21	Frequency at maximum bend (Hz)	0: < 1300	1: ≥ 1300	2: NA	
22	Duration to peak intensity (s)	0: < 0.8	1: ≥ 0.8		
23	Rel. duration to peak intensity (%)	0: < 55	1: 55-64.99	2: ≥ 65	
24	Frequency at peak intensity (Hz)	0: < 1300	1: 1300-1549	2: ≥ 1550	
25	Freq. range to peak intensity (Hz)	0: < 300	1: ≥ 300		
26	Rel. freq. range to peak intensity (%)	0: < 60	1: ≥ 60		

Appendix 6.1 (continued).

No.	Variable (Unit)	Character states and threshold values			
Note 2					
27	Duration of second note (s)	0: < 1.0	1: 1.0-1.89	2: ≥ 1.9	
28	Presence of initial part with trough	0: absent	1: present		
29	Duration initial part (s)	0: < 0.4	1: ≥ 0.4	2: NA	
30	Rel. duration initial part (%)	0: < 25	1: 25-34.9	2: ≥ 35	3: NA
31	Duration roll part (s)	0: < 0.65	1: ≥ 0.65		
32	Rel. duration roll part (%)	0: < 45	1: 45-79.9	2: ≥80	
33	Number of rolls	0: < 3.1	1: ≥ 3.1		
34	Number of “long” troughs in roll part	0: < 0.2	1: ≥ 0.2		
35	Duration of first roll in roll part (s)	0: < 0.26	1: ≥ 0.26		
36	Duration terminal part (s)	0: < 0.1	1: 0.1-0.59	2: ≥ 0.6	
37	Rel. duration terminal part (%)	0: < 33	1: ≥ 33		
38	Start frequency (Hz)	0: < 1200	1: ≥ 1200		
39	Maximum frequency (Hz)	0: < 1050	1: 1050-1299	2: ≥ 1300	
40	Minimum frequency (Hz)	0: < 1000	1: 1000-1199	2: ≥ 1200	
41	Frequency range (Hz)	0: < 300	1: ≥ 300		
42	Minimum frequency initial part (Hz)	0: < 940	1: ≥ 940	2: NA	
43	Frequency range initial part (Hz)	0: < 200	1: 200-299	2: ≥300	3: NA
44	Frequency first trough roll part (Hz)	0: < 1200	1: 1200-1399	2: ≥ 1400	
45	Freq. range first trough roll part (Hz)	0: < 400	1: ≥ 400		
46	Frequency last trough roll part (Hz)	0: < 1000	1: 1000-1099	2: ≥ 1100	
47	Freq. range last trough roll part (Hz)	0: < 30	1: ≥ 30		
48	Freq. range lowest trough roll part (Hz)	0: < 30	1: ≥ 30		
49	Minimum frequency terminal part (Hz)	0: < 1000	1: 1000-1199	2: ≥ 1200	

Appendix 6.1 (continued).

No.	Variable (Unit)	Character states and threshold values		
Note 3				
50	Duration of third note (s)	0: < 1.0	1: 1.0-1.29	2: ≥ 1.3
51	Number of rolls	0: < 0.2	1: 0.2-0.99	2: ≥ 1.0
52	Presence of terminal up-sweep	0: < 0.2	1: 0.2-0.89	2: ≥ 0.9
53	Start frequency (Hz)	0: < 1100	1: ≥ 1100	
54	Maximum frequency (Hz)	0: < 1300	1: ≥ 1300	
55	Minimum frequency (Hz)	0: < 1060	1: ≥ 1060	
56	Frequency range (Hz)	0: < 220	1: ≥ 220	
57	Inter-notes frequency range (Hz)	0: < 200	1: ≥ 200	2: neg. value
Note 4				
58	Duration of fourth note (s)	0: < 0.4	1: 0.4-0.99	2: ≥ 1.0
59	Terminal up-sweep	0: = 0	1: > 0	2: NA
60	Start frequency (Hz)	0: < 1170	1: ≥ 1170	
61	Maximum frequency (Hz)	0: < 1350	1: 1350-1449	2: ≥ 1450
62	Minimum frequency (Hz)	0: < 1100	1: 1100-1169	2: ≥ 1170
63	Frequency range (Hz)	0: < 220	1: 220-699	2: ≥ 700

Appendix 6.2 Variables of the female's great call phrase

No.	Variable (Unit)	Character states and threshold values		
Overall Variables				
64	Duration of entire great call (s)	0: < 9.5	1: 9.5-12.89	2: ≥ 12.9
65	Number of notes	0: < 8.0	1: ≥ 8.0	
66	Range of start frequencies (Hz)	0: < 620	1: 620-909	2: ≥ 910
67	Maximum frequency great call (Hz)	0: < 2500	1: ≥ 2500	
68	Number of *oo* notes	0: < 3.0	1: ≥ 3.0	2: NA
69	Duration of *oo* phase (s)	0: < 6.5	1: ≥ 6.5	2: NA
70	Rel. duration of *oo* phase (%)	0: < 50	1: ≥ 50	2: NA
71	Number of bark notes	0: < 6.0	1: ≥ 6.0	2: NA
72	Duration of bark phase (s)	0: < 4.0	1: ≥ 4.0	2: NA
73	Rel. duration of bark-phase (%)	0: < 45	1: ≥ 45	2: NA
74	Rel. duration twitter part (%)	0: < 50	1: ≥ 50	
75	Inter-phrase interval (s)	0: = 0	1: 0.001-2.699	2: ≥ 2.7
76	Male staccatos during great call	0: absent	1: present	
Single note variables				
77	Duration first *oo* note (s)	0: < 2.0	1: ≥ 2.0	
78	Freq. range first oo-note (Hz)	0: < 130	1: 130-349	2: ≥ 350
79	Duration second *oo* note (s)	0: < 1.3	1: 1.3-1.79	2: ≥ 1.8
80	Freq. range second *oo* note (Hz)	0: < 700	1: ≥ 700	
81	Shape last *oo* note	0: A or AB	1: B or BD	2: D
82	Duration first bark note (s)	0: < 0.75	1: ≥ 0.75	2: NA
83	Freq. range first bark note (Hz)	0: < 1100	1: ≥ 1100	2: NA
84	Duration last bark note (s)	0: < 0.26	1: ≥ 0.26	2: NA
Successive notes variables				
85	First inter-note interval (s)	0: < 0.6	1: ≥ 0.6	
86	Second inter-note interval (s)	0: < 0.35	1: ≥ 0.35	
87	Last inter-note interval (s)	0: < 0.4	1: ≥ 0.4	
88	First start frequency range (Hz)	0: < 120	1: 120-399	2: ≥ 400
89	Second start freq. range (Hz)	0: < 150	1: 150-249	2: ≥ 250
90	Last start frequency range (Hz)	0: < 100	1: ≥ 100	

Appendix 7. Data matrix for the cladistic analysis

Locality	OTU	Variable No.																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Veunsai	03	2	2	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Veunsai	04	1	1	1	0	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0
Veunsai	05	2	2	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Veunsai	07	1	1	1	1	0	1	1	1	0	0	1	1	1	1	0	1	0	1	1	0
Veunsai	08	2	2	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0
Veunsai	09	2	2	2	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0
Veunsai	10	2	2	1	0	0	1	1	1	0	0	1	0	1	0	1	0	1	1	0	0
Veunsai	11	2	2	2	1	1	1	1	1	1	0	1	0	0	0	1	0	0	1	1	0
Veunsai	12	2	2	2	1	1	1	1	1	1	0	0	1	0	0	1	0	1	1	2	0
Veunsai	14	1	2	2	1	1	1	1	1	1	0	0	0	0	1	0	0	0	1	1	0
Veunsai	15	1	2	2	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	2	0
Veunsai	16	1	2	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Veunsai	18	1	2	2	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	2	0
Taveng	19	2	2	1	0	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0
Taveng	20	2	2	1	0	0	1	1	1	0	0	1	1	1	1	0	0	0	1	0	0
Taveng	21	2	2	1	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0	0
Taveng	23	2	2	2	1	1	1	1	1	0	0	1	0	1	0	1	0	1	1	2	1
Taveng	25	2	2	2	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	1	0
Taveng	26	1	2	1	1	0	1	1	1	1	0	1	1	1	1	0	0	0	1	0	0
Taveng	27	2	2	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0
Taveng	29	1	2	2	1	1	1	0	0	1	1	1	1	1	1	0	0	0	1	2	0
Taveng	30	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Taveng	31	1	2	1	0	1	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0
Taveng	32	1	2	1	0	0	1	1	1	0	0	1	0	0	1	0	0	1	1	0	0
Khamaeng	34	1	2	1	1	1	1	1	1	0	0	0	1	1	2	0	1	0	1	1	0
Mas	35	2	2	2	1	1	1	1	1	1	0	1	1	1	2	0	1	0	1	2	0
Mas	36	1	2	1	0	1	1	0	0	1	1	1	0	0	1	0	0	0	1	0	0
Mas	37	1	1	1	1	0	1	1	1	0	0	1	1	1	2	0	1	0	1	1	0
Samling	38	1	2	2	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	0
Samling	40	1	2	2	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	2	0
Samling	41	1	2	2	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	2	0
Samling	42	1	2	1	0	0	1	0	0	1	1	1	0	0	1	0	0	0	1	0	0
Samling	47	1	2	1	0	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0
Samling	48	1	2	1	0	0	1	0	0	1	1	1	1	0	1	0	0	0	1	0	0
Samling	49	1	2	1	0	0	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0
Bach Ma	70	1	2	2	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	2	1
Bach Ma	71	0	1	1	0	1	1	0	0	1	1	1	1	1	1	1	0	1	0	2	1
Bach Ma	72	0	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	2	1
Bach Ma	74	0	1	1	0	1	1	0	0	1	1	1	1	1	1	1	0	1	0	2	1
Bach Ma	76	1	1	1	0	1	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0
Cao Bang	337	1	0	0	0	0	0	1	2	2	2	1	1	1	3	0	1	0	1	3	2
Cao Bang	339	1	0	0	0	0	0	1	2	2	2	0	1	1	3	0	1	0	1	3	2
Cao Bang	341	1	0	0	0	0	0	1	2	2	2	1	1	1	3	0	1	0	1	3	2

Appendix 7. (continued)

Locality	OTU	Variable No.																			
		21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Veunsai	03	0	0	0	0	1	1	1	1	1	2	0	0	0	0	1	2	1	0	0	0
Veunsai	04	1	1	2	1	1	1	1	1	0	1	0	0	0	0	1	1	0	1	1	1
Veunsai	05	0	0	0	0	1	1	1	1	1	2	0	1	0	0	1	1	0	0	0	0
Veunsai	07	1	1	2	1	0	0	1	1	1	1	0	0	0	0	1	1	0	1	1	1
Veunsai	08	0	0	0	0	1	1	1	1	1	2	0	0	0	0	1	1	0	0	0	0
Veunsai	09	0	1	1	0	0	0	2	1	1	2	1	0	0	0	1	1	0	0	0	0
Veunsai	10	0	0	1	0	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0
Veunsai	11	0	1	1	0	1	0	1	1	1	2	0	0	0	0	1	1	0	0	0	0
Veunsai	12	1	1	0	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	0	0
Veunsai	14	0	1	2	0	0	0	2	1	1	2	0	0	0	0	1	2	1	0	1	0
Veunsai	15	1	1	0	1	1	1	2	1	1	1	1	0	0	1	1	2	1	1	0	0
Veunsai	16	0	0	1	0	1	1	1	1	1	2	0	0	0	0	1	1	0	1	0	0
Veunsai	18	0	1	2	0	0	0	2	1	0	0	1	0	0	1	1	2	1	1	0	0
Taveng	19	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	0	0	1	0
Taveng	20	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	1	0
Taveng	21	0	1	2	0	0	0	1	1	0	0	1	1	0	1	1	1	0	1	1	0
Taveng	23	0	1	1	0	1	1	1	1	1	1	1	1	0	0	1	1	0	0	0	0
Taveng	25	1	1	1	1	1	1	1	1	1	2	0	0	0	1	1	1	1	0	0	0
Taveng	26	0	1	1	0	0	0	1	1	1	2	0	0	0	0	1	1	0	0	1	0
Taveng	27	0	0	0	0	1	1	1	1	1	1	0	1	0	0	1	1	0	0	0	0
Taveng	29	0	1	2	0	0	0	2	1	0	0	1	1	0	1	1	2	0	1	1	0
Taveng	30	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Taveng	31	0	1	1	0	0	1	1	1	0	0	1	1	0	1	1	1	0	0	0	0
Taveng	32	1	0	1	1	1	1	1	1	0	0	1	1	0	1	1	1	0	0	0	0
Khamaeng	34	1	1	0	1	0	1	1	1	1	2	0	0	0	0	1	1	1	0	1	1
Mas	35	1	1	0	1	1	1	1	1	1	2	0	0	0	0	1	1	0	1	1	1
Mas	36	0	1	2	0	0	0	1	1	1	2	1	0	0	0	1	1	0	0	1	0
Mas	37	1	1	1	1	1	1	1	1	0	1	1	1	0	1	0	1	0	1	1	1
Samling	38	1	0	0	1	1	1	2	1	1	1	1	0	1	0	0	1	0	1	0	0
Samling	40	0	1	2	0	0	0	1	1	1	1	0	0	0	0	1	2	1	1	0	0
Samling	41	0	1	2	0	1	0	2	1	1	0	1	0	1	0	0	2	1	1	0	0
Samling	42	0	0	0	0	0	0	2	1	1	1	0	0	0	1	1	2	1	0	0	1
Samling	47	1	0	0	1	1	1	2	1	1	0	1	0	1	1	0	2	1	0	0	0
Samling	48	0	0	0	0	0	0	2	1	1	1	1	0	0	0	0	2	1	0	0	0
Samling	49	0	0	1	0	0	0	2	1	1	0	1	1	1	1	0	2	1	0	1	0
Bach Ma	70	0	1	1	0	1	1	1	1	1	2	0	0	0	0	1	1	0	0	0	0
Bach Ma	71	1	1	2	1	1	0	1	1	0	0	1	1	0	0	1	1	0	1	0	0
Bach Ma	72	0	1	2	0	1	0	1	1	0	0	1	1	0	0	1	1	0	1	0	0
Bach Ma	74	0	1	2	0	1	0	1	1	0	1	1	1	0	0	1	1	0	1	0	0
Bach Ma	76	0	1	2	0	0	0	1	1	0	0	1	1	0	0	1	1	0	1	0	0
Cao Bang	337	2	0	1	2	0	1	0	0	2	3	0	2	0	0	1	0	0	1	2	2
Cao Bang	339	2	0	1	2	0	1	0	0	2	3	0	2	0	0	1	0	0	1	2	2
Cao Bang	341	2	0	2	2	0	1	0	0	2	3	0	2	0	0	1	0	0	1	2	2

Appendix 7. (continued)

Locality	OTU	Variable No.																			
		41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Veunsai	03	0	0	0	?	?	?	?	?	0	2	0	0	1	1	1	1	1	1	0	1
Veunsai	04	0	1	1	0	0	2	1	1	1	2	1	0	1	1	1	1	0	1	0	0
Veunsai	05	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0
Veunsai	07	0	1	1	0	0	2	1	1	1	1	0	1	1	0	1	0	0	1	0	0
Veunsai	08	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	0	0
Veunsai	09	0	0	0	0	0	0	1	1	0	2	0	1	0	0	0	0	0	2	1	0
Veunsai	10	1	0	2	1	1	2	1	1	0	1	0	0	0	0	0	1	1	2	0	0
Veunsai	11	0	0	0	?	?	?	?	?	0	1	0	0	0	0	0	1	0	2	0	0
Veunsai	12	0	0	1	0	0	0	1	1	0	2	1	0	0	0	0	1	1	2	0	0
Veunsai	14	0	1	0	?	?	?	?	?	1	2	0	0	0	0	0	0	0	1	0	0
Veunsai	15	1	0	2	0	0	0	1	1	0	2	0	0	1	0	0	1	1	1	0	1
Veunsai	16	1	0	2	0	0	0	1	1	0	2	0	0	1	0	1	0	1	1	0	0
Veunsai	18	1	0	2	0	0	1	1	1	1	2	0	0	1	1	1	1	1	2	0	1
Taveng	19	0	0	1	0	0	0	0	1	1	2	0	0	0	0	0	1	0	2	1	0
Taveng	20	0	0	1	0	0	2	1	1	1	1	0	1	0	1	0	1	0	1	0	0
Taveng	21	0	1	1	0	0	1	1	1	1	2	1	1	1	1	0	1	1	2	1	1
Taveng	23	0	0	1	0	0	0	1	1	0	1	1	1	0	0	0	1	1	1	1	0
Taveng	25	0	0	1	0	0	0	1	1	0	2	0	1	0	1	0	1	1	1	0	0
Taveng	26	0	0	1	0	0	1	1	1	1	1	0	0	0	1	0	1	0	2	0	0
Taveng	27	0	0	1	0	0	0	1	1	0	1	1	1	0	0	0	1	0	2	1	0
Taveng	29	1	0	2	1	0	1	1	1	1	2	0	0	1	0	0	1	0	1	0	0
Taveng	30	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Taveng	31	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	2	0	0
Taveng	32	1	0	2	0	0	0	1	1	0	2	1	0	1	1	0	1	1	2	0	0
Khamaeng	34	0	1	0	?	?	?	?	?	1	2	0	0	1	1	1	1	0	2	0	0
Mas	35	0	1	0	1	0	2	1	1	1	1	0	1	1	1	1	0	0	2	0	1
Mas	36	0	1	1	?	?	?	?	?	1	2	0	0	1	0	1	0	0	1	0	0
Mas	37	0	1	1	1	0	2	0	1	1	1	0	0	1	1	1	0	0	1	0	1
Samling	38	1	0	2	2	1	1	1	1	0	2	0	0	1	1	1	1	1	1	0	1
Samling	40	1	0	1	2	1	2	1	1	0	1	1	0	1	1	1	1	1	1	0	1
Samling	41	1	0	1	2	1	2	1	1	0	1	0	0	1	1	1	1	1	1	0	1
Samling	42	1	1	0	2	1	0	0	0	1	2	1	0	1	1	1	1	0	1	0	0
Samling	47	1	1	0	2	1	1	1	1	0	2	1	0	1	0	0	0	0	1	0	1
Samling	48	1	1	0	2	1	1	1	1	0	2	1	0	1	1	1	0	0	1	0	0
Samling	49	1	1	0	1	0	0	0	0	1	2	0	0	0	1	0	1	0	2	0	0
Bach Ma	70	1	0	1	0	0	0	1	1	0	0	0	1	0	0	0	1	0	2	1	0
Bach Ma	71	1	0	2	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0
Bach Ma	72	1	0	2	0	0	0	0	0	0	0	0	0	1	1	1	1	1	2	0	0
Bach Ma	74	1	0	2	0	0	0	0	0	0	0	0	0	1	1	1	1	1	?	?	?
Bach Ma	76	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	2	0	0
Cao Bang	337	0	2	3	2	0	2	0	0	2	0	2	2	1	1	1	1	2	0	2	0
Cao Bang	339	0	2	3	2	0	2	0	0	2	0	2	2	1	1	1	0	2	0	2	0
Cao Bang	341	0	2	3	2	0	2	0	0	2	0	2	2	1	1	1	0	2	0	2	0

Appendix 7. (continued)

Locality	OTU	Variable No.																			
		61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Veunsai	03	2	2	0	0	1	1	1	0	0	0	1	1	1	0	1	0	0	1	1	0
Veunsai	04	1	1	1	1	1	0	1	0	0	1	1	1	1	0	1	0	1	1	2	1
Veunsai	05	0	0	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Veunsai	07	1	1	0	1	1	0	1	0	0	0	1	1	1	0	1	0	0	1	1	1
Veunsai	08	0	0	0	0	1	1	1	0	0	0	1	1	1	0	1	0	0	1	1	0
Veunsai	09	0	0	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Veunsai	10	0	0	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Veunsai	11	0	0	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Veunsai	12	0	0	0	2	1	2	1	1	0	0	1	1	1	0	1	0	0	1	1	0
Veunsai	14	0	0	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Veunsai	15	0	0	0	2	1	2	1	1	1	1	1	1	0	0	1	0	1	1	2	0
Veunsai	16	0	0	0	1	1	0	1	1	1	1	1	1	0	0	1	0	1	1	2	0
Veunsai	18	1	1	1	1	1	1	1	0	0	0	1	1	1	0	2	0	1	2	1	0
Taveng	19	0	0	1	2	1	1	1	1	1	1	1	1	0	0	2	0	0	1	2	0
Taveng	20	1	0	1	2	1	1	1	1	0	0	1	1	1	0	2	0	0	2	0	0
Taveng	21	0	1	0	2	1	1	1	1	1	1	1	1	1	0	2	0	1	1	2	0
Taveng	23	0	0	1	2	1	1	1	1	1	1	1	1	0	0	1	0	1	1	2	0
Taveng	25	2	0	1	2	1	1	1	0	1	1	1	1	1	0	2	0	1	2	2	1
Taveng	26	2	0	1	2	1	1	1	1	1	0	1	1	1	0	2	0	1	2	1	0
Taveng	27	0	0	0	2	1	1	1	1	1	0	1	1	1	0	2	0	1	2	2	1
Taveng	29	0	0	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Taveng	30	?	?	?	2	1	0	1	1	1	1	1	1	0	0	1	?	0	1	2	0
Taveng	31	0	0	0	2	1	1	1	1	1	1	1	1	0	0	2	0	1	2	2	0
Taveng	32	0	0	1	2	1	1	1	1	1	1	0	0	0	0	2	0	0	1	2	0
Khamaeng	34	1	1	1	1	1	0	1	0	1	1	0	1	0	0	1	0	1	2	1	1
Mas	35	2	2	1	1	1	1	1	0	0	0	1	1	1	0	2	0	1	2	0	1
Mas	36	1	1	0	2	1	1	1	1	1	1	0	0	0	0	2	0	1	2	2	0
Mas	37	1	2	0	1	1	0	1	0	0	0	1	1	1	0	1	0	1	2	0	1
Samling	38	2	2	1	0	0	2	1	0	0	1	0	0	0	0	2	0	1	2	1	1
Samling	40	2	2	1	1	1	2	1	1	1	1	0	0	0	0	2	0	1	2	2	1
Samling	41	2	2	1	0	0	2	1	0	0	0	0	0	1	0	2	0	1	2	1	1
Samling	42	2	1	1	0	0	2	1	0	0	1	0	0	0	0	2	0	0	1	2	1
Samling	47	1	2	1	0	0	2	1	0	0	1	0	0	0	0	2	0	0	2	2	1
Samling	48	2	1	1	1	0	2	1	0	1	1	0	0	0	0	2	0	1	2	2	1
Samling	49	1	0	1	0	0	2	1	0	0	1	0	0	0	0	2	0	0	1	1	1
Bach Ma	70	1	0	1	1	1	0	1	0	0	0	1	1	1	0	1	0	1	1	1	1
Bach Ma	71	1	1	0	2	1	0	1	1	1	1	1	1	0	0	1	0	0	1	2	0
Bach Ma	72	2	1	1	2	1	0	1	1	1	1	1	1	0	0	1	0	0	1	2	0
Bach Ma	74	?	?	?	2	1	0	1	1	1	1	1	1	0	0	1	0	0	1	2	0
Bach Ma	76	1	1	0	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Cao Bang	337	2	0	2	0	1	?	0	2	2	2	2	2	2	1	0	1	0	0	0	0
Cao Bang	339	2	0	2	0	1	?	0	2	2	2	2	2	2	1	0	1	0	0	0	0
Cao Bang	341	2	0	2	1	1	?	0	2	2	2	2	2	2	1	0	1	0	0	1	0

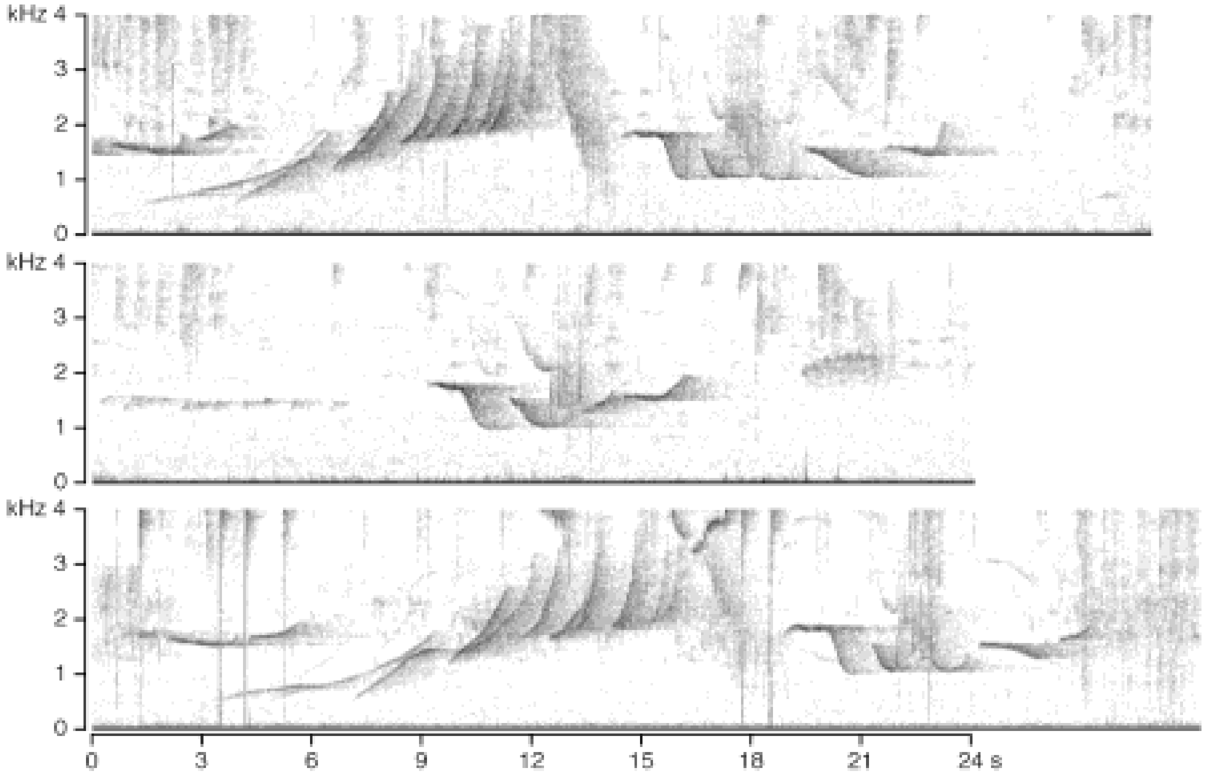
Appendix 7. (continued)

Locality	OTU	Variable No.									
		81	82	83	84	85	86	87	88	89	90
Veunsai	03	2	0	1	1	0	0	0	1	1	0
Veunsai	04	1	1	1	0	1	0	0	0	1	0
Veunsai	05	?	?	?	?	?	?	?	?	?	?
Veunsai	07	1	1	0	0	0	1	1	1	1	0
Veunsai	08	2	0	0	0	0	0	1	1	1	0
Veunsai	09	?	?	?	?	?	?	?	?	?	?
Veunsai	10	?	?	?	?	?	?	?	?	?	?
Veunsai	11	?	?	?	?	?	?	?	?	?	?
Veunsai	12	1	0	0	0	0	1	0	0	1	1
Veunsai	14	?	?	?	?	?	?	?	?	?	?
Veunsai	15	1	1	1	0	1	1	0	0	0	1
Veunsai	16	1	0	0	0	0	0	1	0	1	0
Veunsai	18	1	0	0	0	0	1	0	1	2	0
Taveng	19	1	1	0	0	1	1	1	0	1	0
Taveng	20	1	0	0	0	1	1	1	1	0	0
Taveng	21	1	0	0	0	1	1	1	0	1	0
Taveng	23	1	0	0	0	0	1	0	0	0	0
Taveng	25	1	1	1	0	0	0	1	1	1	1
Taveng	26	1	1	0	0	0	1	1	1	1	0
Taveng	27	1	1	1	0	1	0	0	0	1	0
Taveng	29	?	?	?	?	?	?	?	?	?	?
Taveng	30	1	0	0	1	1	0	1	0	1	0
Taveng	31	1	0	0	0	0	1	1	1	1	1
Taveng	32	1	0	0	0	1	1	1	1	0	0
Khamaeng	34	0	1	1	1	1	1	0	1	1	0
Mas	35	2	1	1	0	0	0	0	1	0	0
Mas	36	1	0	0	1	1	1	1	1	2	0
Mas	37	0	1	0	1	0	1	0	1	0	0
Samling	38	1	1	1	1	1	0	0	1	2	0
Samling	40	1	1	1	0	0	1	0	1	2	1
Samling	41	0	1	1	1	0	0	0	1	2	1
Samling	42	1	1	1	0	1	0	0	0	2	1
Samling	47	1	1	1	0	1	1	0	0	2	1
Samling	48	1	1	1	0	1	0	0	0	2	1
Samling	49	2	1	1	0	1	0	0	0	2	1
Bach Ma	70	1	1	0	1	0	1	1	0	0	0
Bach Ma	71	2	1	1	1	1	1	1	0	0	0
Bach Ma	72	1	1	0	1	1	1	1	0	0	0
Bach Ma	74	2	1	0	0	0	1	1	0	0	0
Bach Ma	76	?	?	?	?	?	?	?	?	?	?
Cao Bang	337	?	2	2	2	0	0	?	2	0	?
Cao Bang	339	?	2	2	2	0	0	?	2	?	?
Cao Bang	341	?	2	2	2	0	0	?	1	1	?

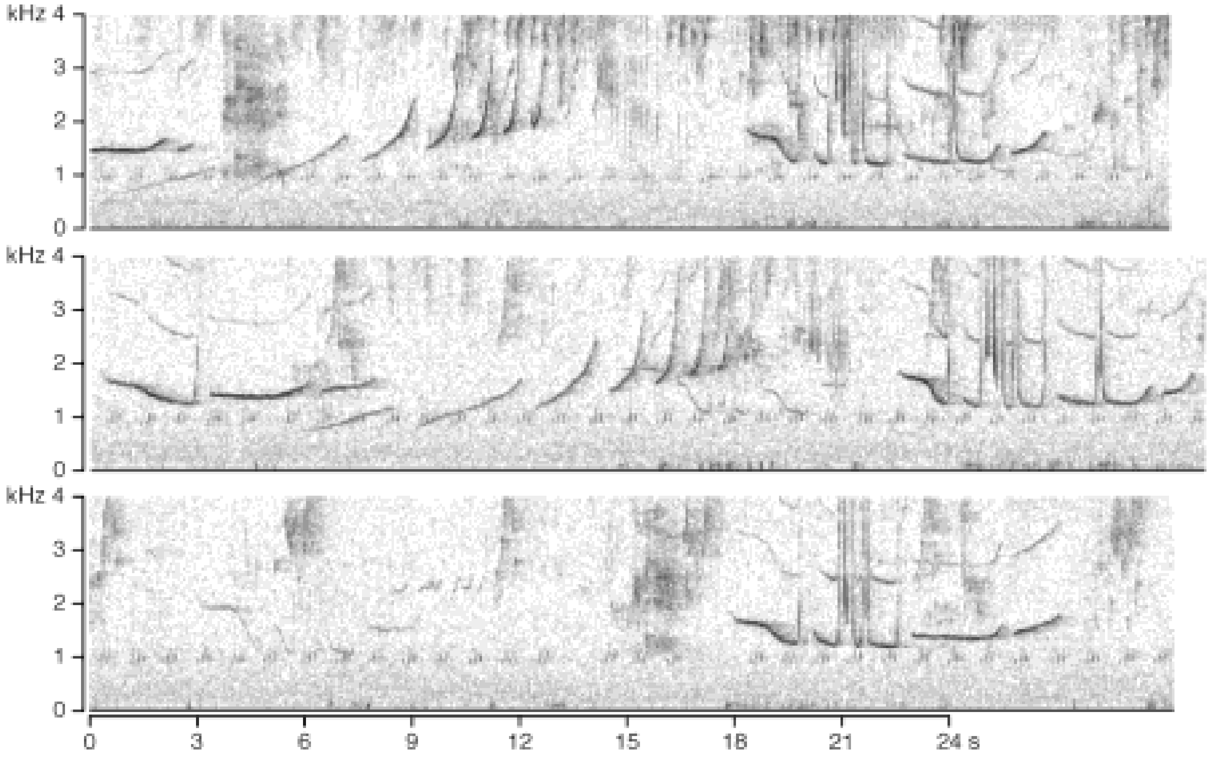
Appendix 8. Sonagraphic excerpts of different duet song bouts

The sonagrams represent excerpts of song bouts from different gibbon groups and different populations. All sonagrams presented here originate from duet songs and exhibit at least one fully developed male and female phrase (except in group 09).

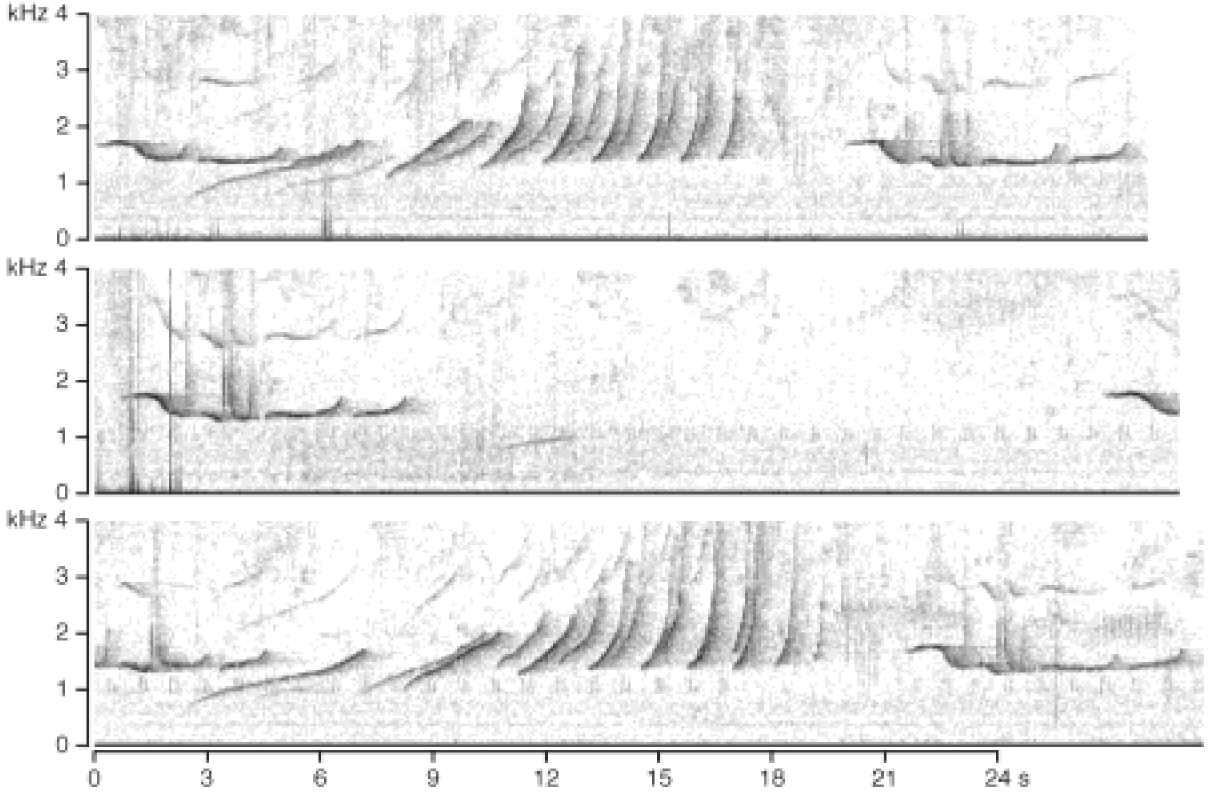
Group 38 from the Samling Logging Concession in southern Mondulkiri Province, Cambodia.



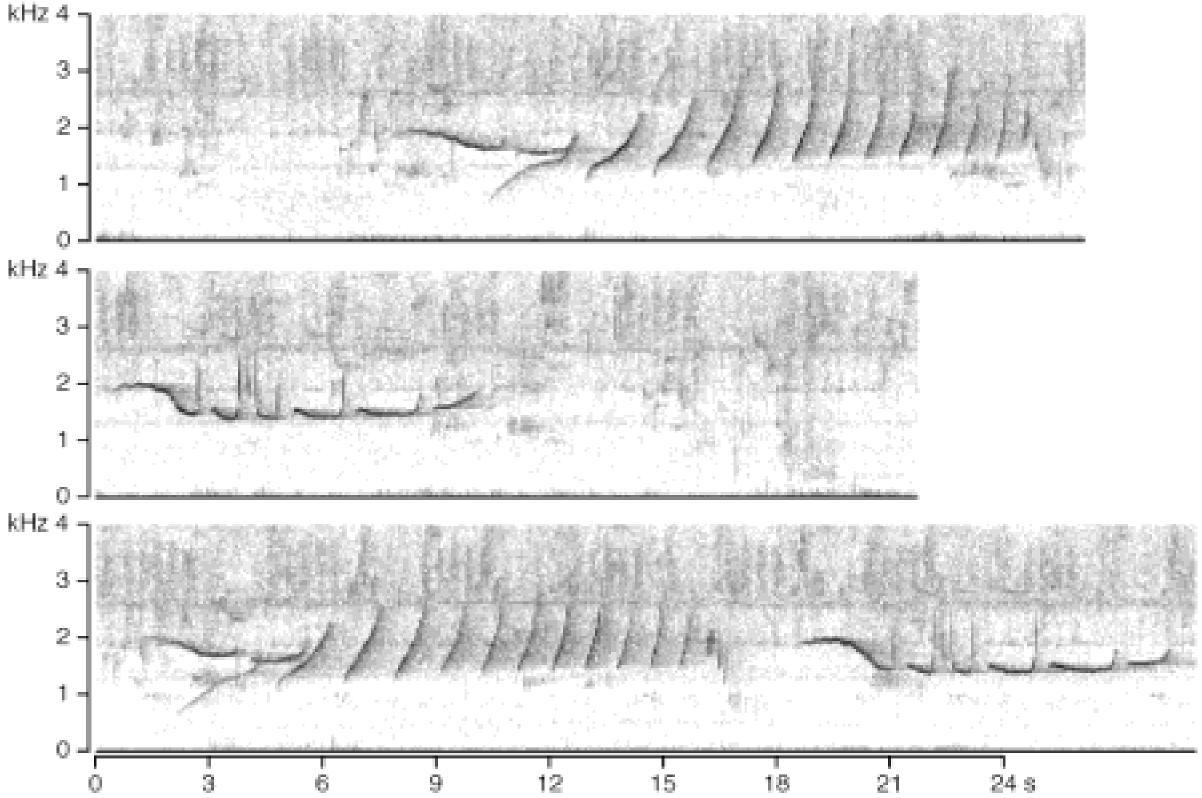
Group 48 from the Samling Logging Concession in southern Mondulkiri Province, Cambodia.



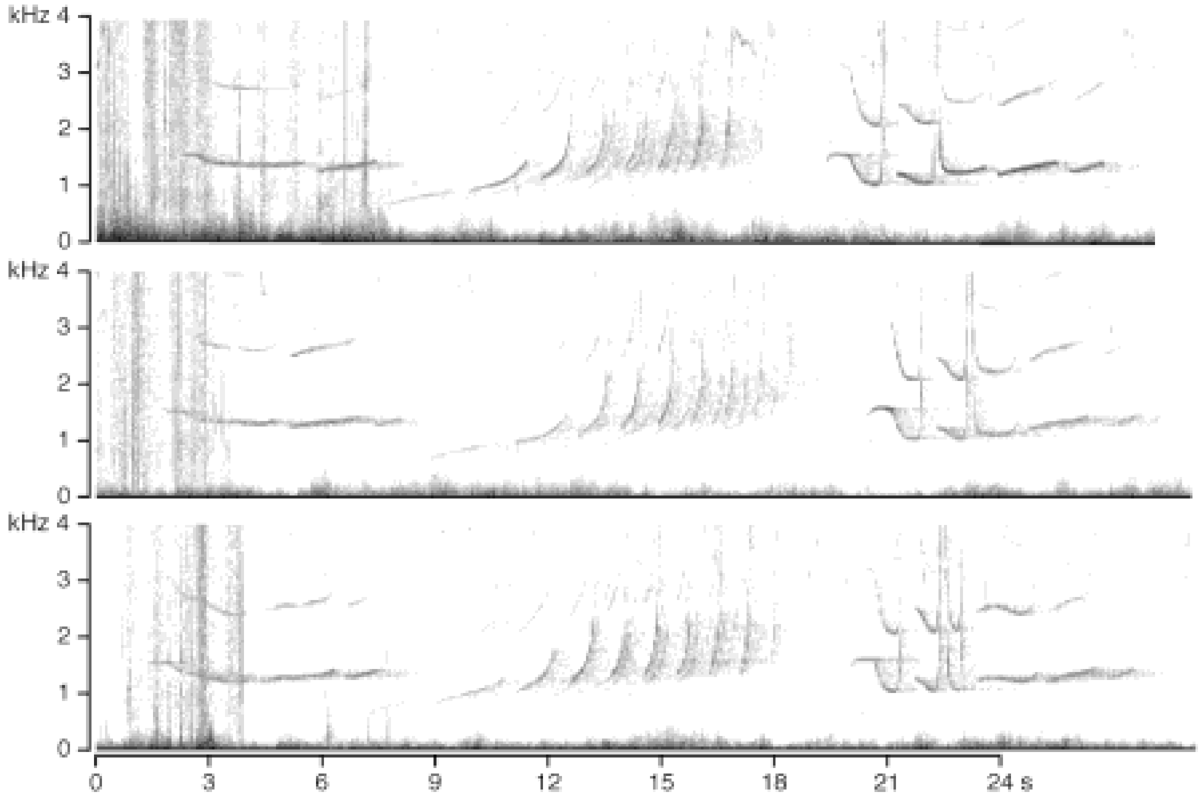
Group 34 from Poey Commune in central Rattanakiri Province, Cambodia.



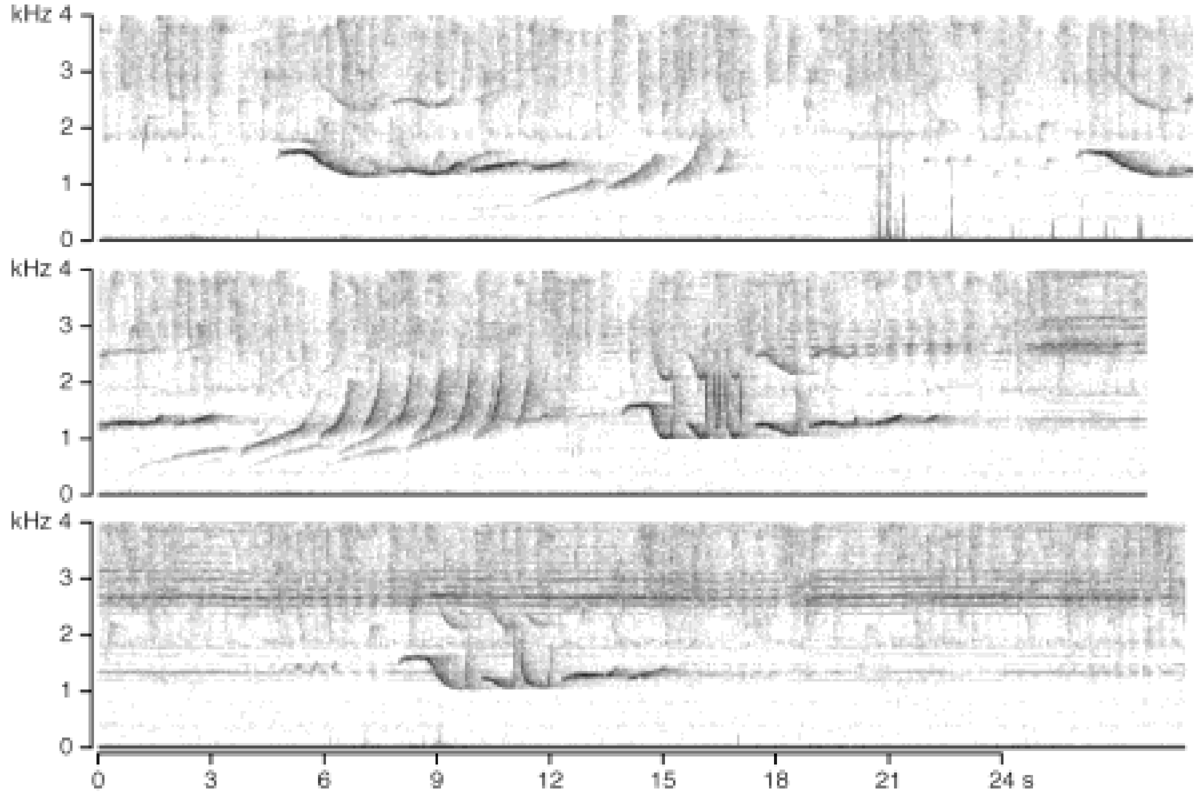
Group 35 from Poey Commune in central Rattanakiri Province, Cambodia.



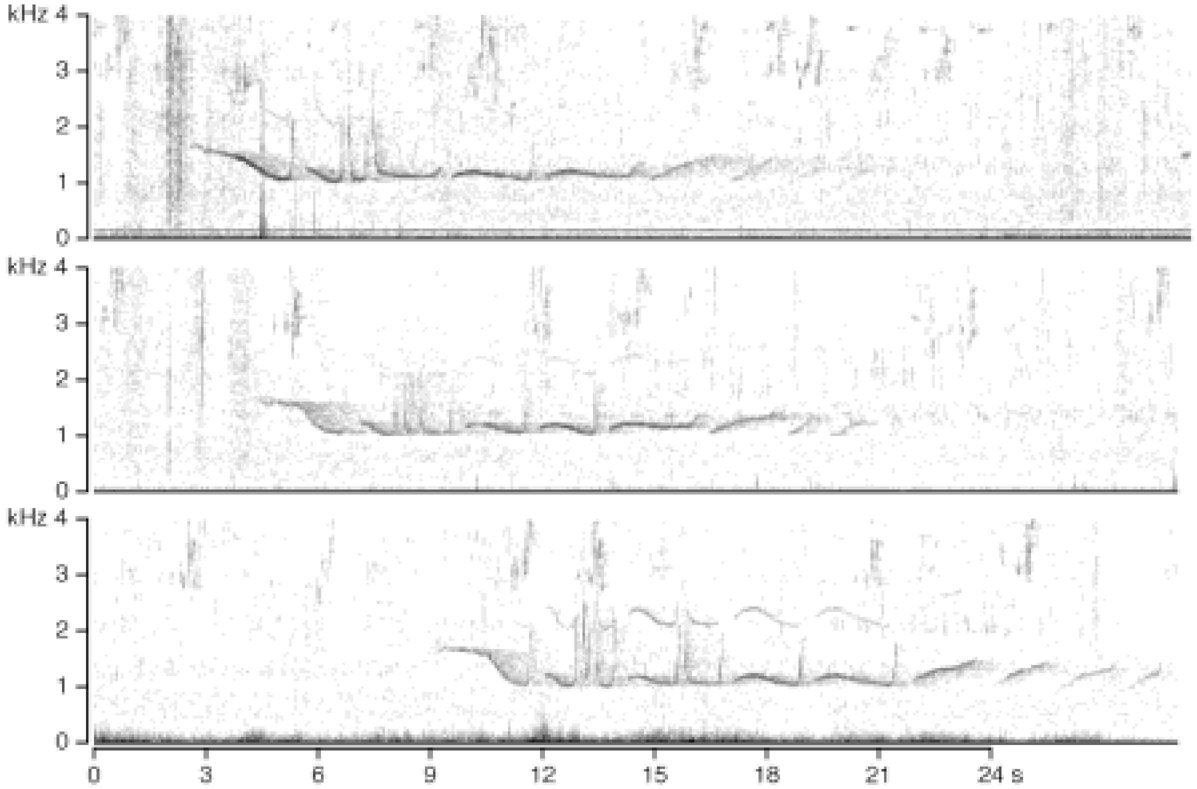
Group 03 from the central part of Virachey National Park (Veunsai District) in northern Rattanakiri Province, Cambodia.



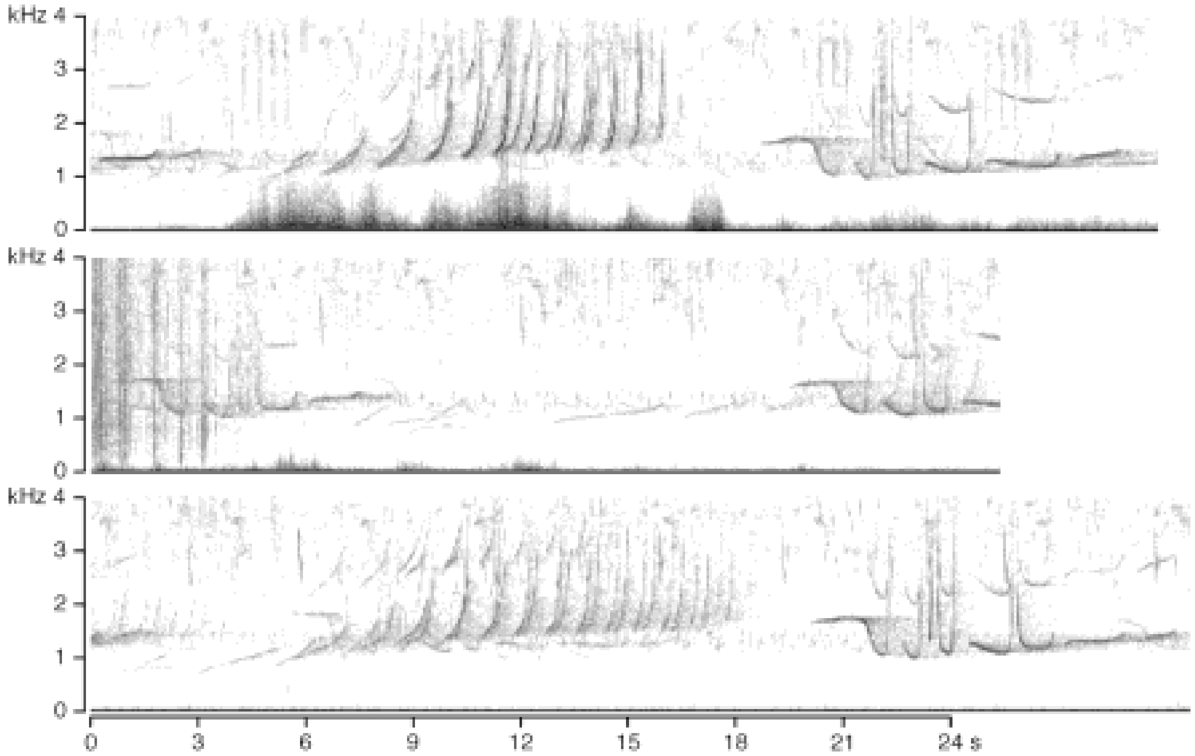
Group 08 from the central part of Virachey National Park (Veunsai District) in northern Rattanakiri Province, Cambodia.



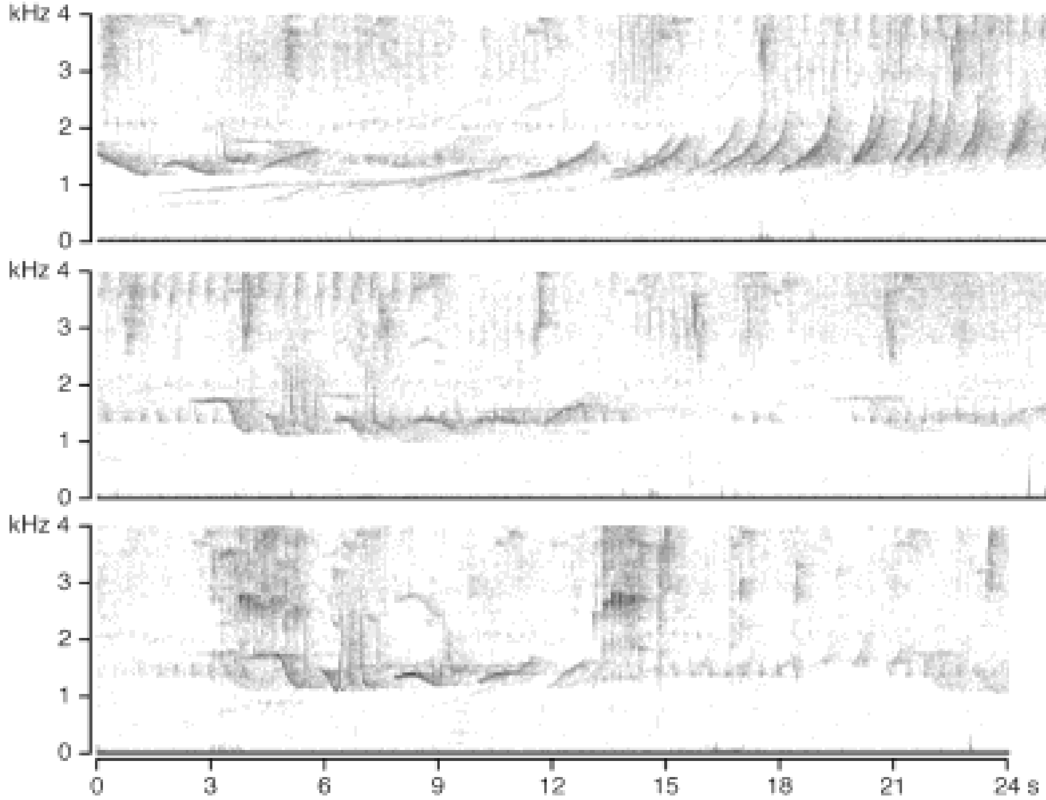
Group 09 (solo male) from the central part of Virachey National Park (Veunsai District) in northern Rattanakiri Province, Cambodia.



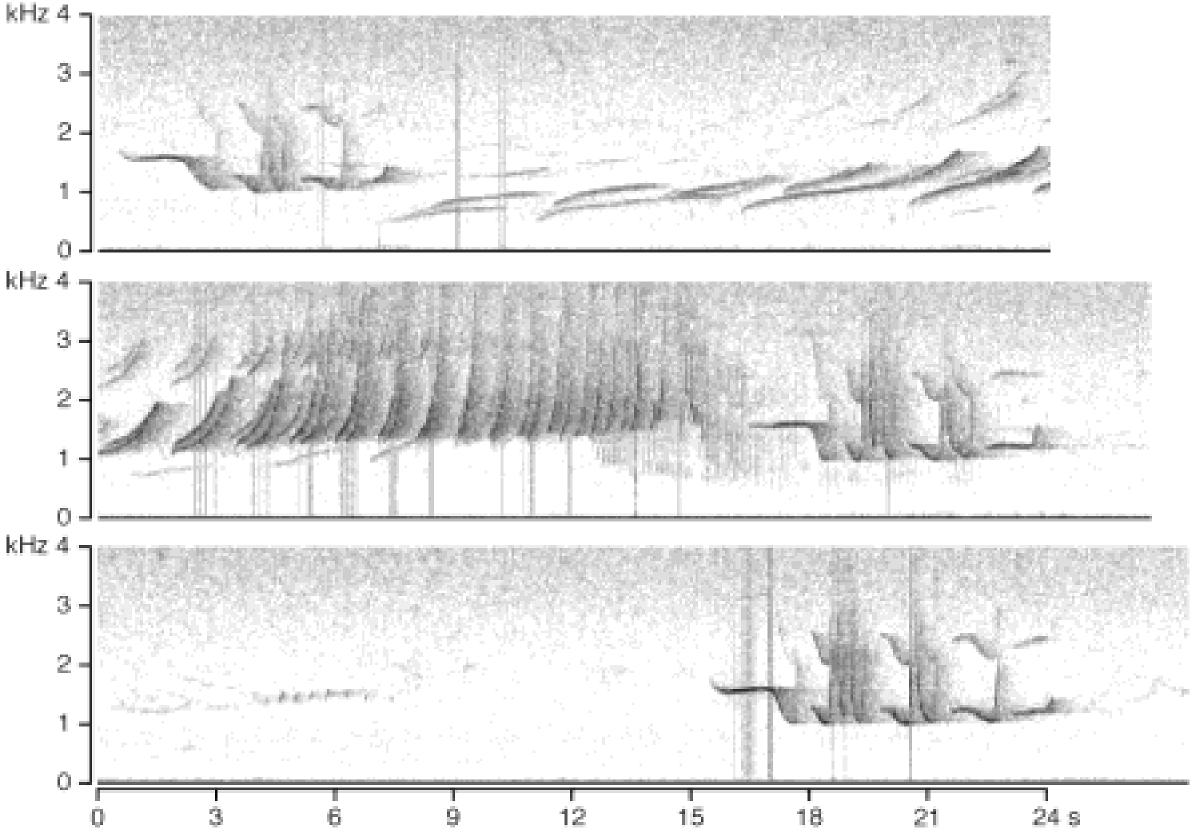
Group 12 from the central part of Virachey National Park (Veunsai District) in northern Rattanakiri Province, Cambodia.



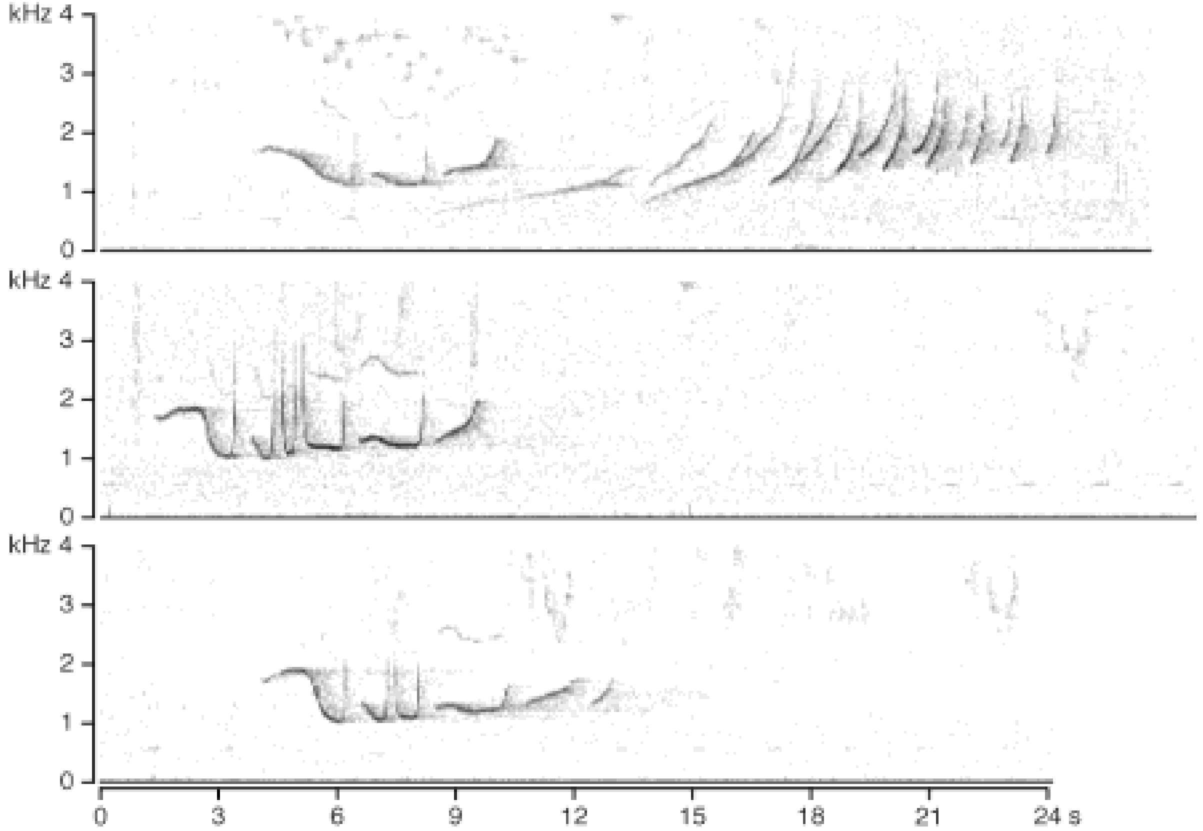
Group 19 from the eastern part of Virachey National Park (Taveng District) in northern Rattanakiri Province, Cambodia.



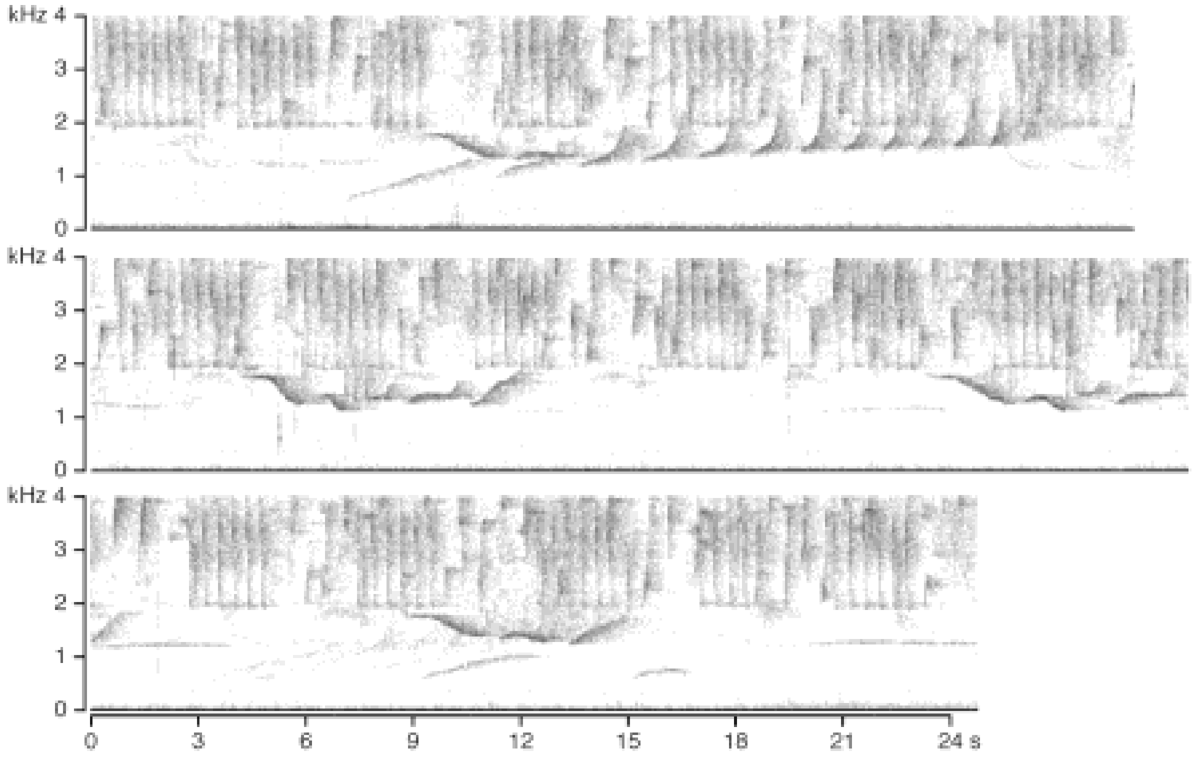
Group 23 from the eastern part of Virachey National Park (Taveng District) in northern Rattanakiri Province, Cambodia.



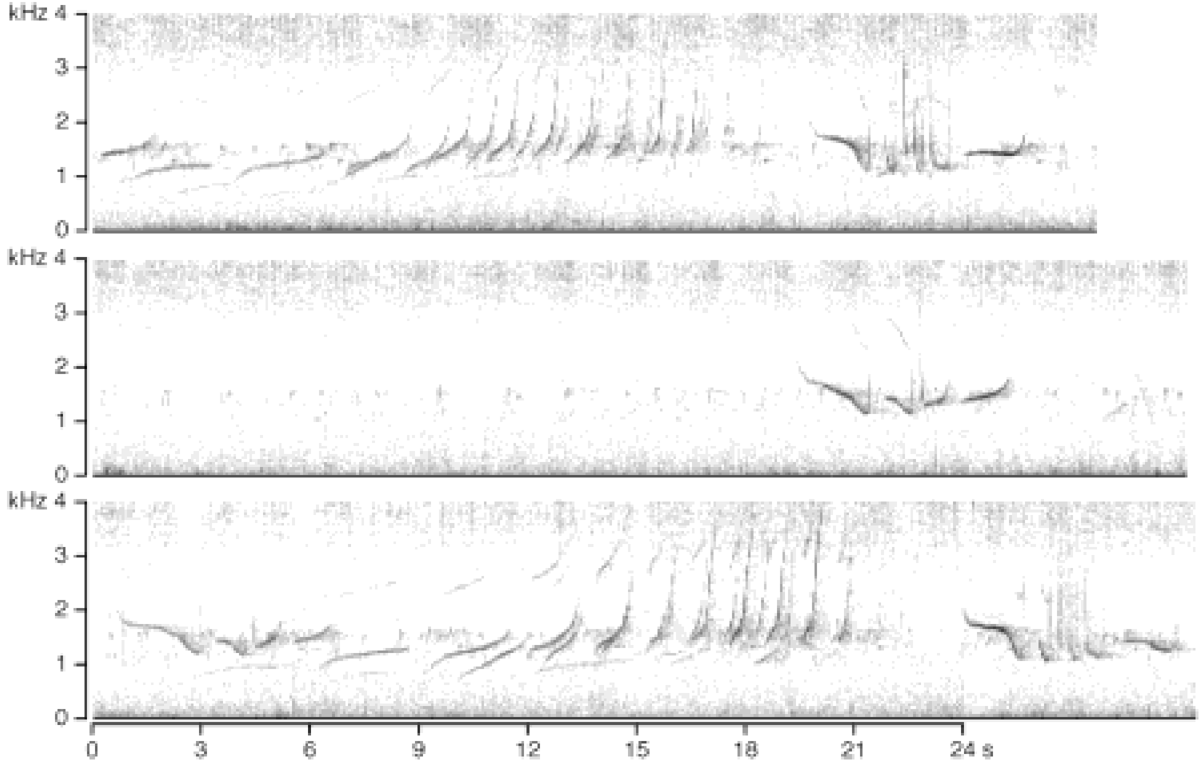
Group 25 from the eastern part of Virachey National Park (Taveng District) in northern Rattanakiri Province, Cambodia.



Group 26 from the eastern part of Virachey National Park (Taveng District) in northern Rattanakiri Province, Cambodia.



Group 71 from the Bach Ma National Park in Thua Thien Hue Province, central Vietnam.



Group 74 from the Bach Ma National Park in Thua Thien Hue Province, central Vietnam.