

**Intra- and Inter-Group Communication in the Southern-Bornean
Gibbon (*Hylobates albibarbis*) in the National Laboratory for
Peat-Swamp Forest, Sabangau Catchment, Indonesia.**



Adult female *H. albibarbis*. Photo ©Andrew Walmsley

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Stap (2006) once said; “It has always been birdsong that has most enthralled and mystified us. Frogs croak, crickets chirp, wolves howl, and lions roar, but birds sing.”

Stap had obviously never met a gibbon.

Statement of originality

Except for those parts in which it is explicitly stated to the contrary, this project is my own work. It has not been submitted for any degree at this or any other academic or professional institution.



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Abstract

In this study, the degradation rate of the duet song of wild, southern-Bornean gibbons (*Hylobates albibarbis*) and its potential implications for intra- and inter-group communication was investigated. This was achieved by recording two gibbon groups (Group C and Karate) at two different distances. The recordings were taken from under the singing group and at a distance of 350 meters (the first distance at which a loss of entire notes was present in the spectrograms) simultaneously. A total of 40 duet songs were recorded for each group at the two distances, meaning that a total of 160 duet songs were included in the analysis. The duet songs were analysed for 46 acoustic and temporal variables. The variables selected were: no. of notes, duration, minimum frequency, maximum frequency, dominant frequency, and maximum amplitude for each of the 6 phrases in the duet sequence as well as for the duet sequence (or song) as a whole. No. of total male notes, no. of total female notes, no. of complete male phrases and no. of complete female phrases in the duet song were also included.

Principal component analysis was performed to summarise this set of variables into a total of four principal components (PCs). A one-way multivariate analysis of variance (MANOVA) followed by post-hoc Tukey's test was then performed. There was a significant difference for PC1 ($p < 0.01$), PC3 ($p < 0.01$), and PC4 ($p < 0.01$), but not for PC2 ($p > 0.05$), between the duet sequences recorded under Group C and those recorded at 350 m away. These results reflect the significant loss of amplitude across all parts of the song, as seen in the spectrograms, eventually leading to the degradation of entire notes, particularly in the female organisational phrase, the female terminal phrase and the male organisational phrase. There was a significant difference for PC1 ($p < 0.01$) but not for PC2 ($p > 0.05$), PC3 ($p > 0.05$), or PC4 ($p > 0.05$), between the duet sequences recorded under Karate and those recorded at 350 m away. The duet song of Karate seems to degrade in much the same way as the duet song of Group C. However, only one of the phrases, the female terminal phrase, appears to suffer a significant loss of notes.

GPS data showed that the gibbons were mostly singing from within core areas of their home range which means that around 70-75% of songs sung by both focal groups were structurally compromised by the time they reached an adjacent group's home range. Therefore, it appears that the gibbon duet song most likely have a purely defensive function. However, for the outermost singing points, the duet song may have an offensive function. Alternatively, it may be the case that certain parts of the song are purely intended for inter-group communication and certain parts are purely intended for intra-group communication.

Acknowledgements

I never intended this project to be an incredible team effort but an incredible team effort is what it was and, as such, I must give thanks to many people.

Firstly, I would like to say thank you to everybody who assisted with data collection for this project. Sam Tesoriero and my assistant, Azis Kelasi, in particular, were outstanding throughout. Adul and Jono, who are potentially the greatest gibbon following duo in the history of mankind, were also fantastic.

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LIST OF ABBREVIATIONS

Hz	- Hertz
kHz	- Kilohertz
dB	- Decibels
MB	- Megabytes
GB	- Gigabytes
MOP	- Male Organisational Phrase
FOP	- Female Organisational Phrase
FIP	- Female Introductory Phrase
FCP	- Female Climactic Phrase
FTP	- Female Terminal Phrase
MTP	- Male Terminal Phrase
K	- Karate
C	- Group C
NLPSF	- Natural Laboratory of Peat-Swamp Forest
OuTrop	- Orangutan Tropical Peatlands Project
CIMTROP	- Center for International Cooperation in Sustainable Management of Tropical Peatlands

CHAPTER I: INTRODUCTION

1.1 Study Species

Generally speaking, gibbons are small, territorial, monogamous, arboreal apes with groups being formed by a mated pair and their offspring (Chivers, 1977; Tenaza, 1975). Although their historical range, was much larger and extended further north (Chatterjee, 2009; Grueter et al., 2009), all living gibbon taxa inhabit the forests of South and South-East Asia (see Figure 1.1) Currently there are 16 species (with 12 subspecies) of gibbon recognised by the IUCN Red List of Threatened Species (2013) and as many as 18 species (with 7 subspecies) recognised in the literature (Thinh et al., 2010), making them the most diverse group of apes.

Phylogenetic relationships within and between the family Hylobatidae has been a subject of much debate since a first real attempt at classifying them was made by Elliot (1913) (as cited in Mootnick & Groves, 2005). Elliot divided the hylobatids into 2 distinct genera; *Hylobates* (smaller gibbons) and *Symphalangus* (siamangs). Groves (1968) (as cited in Mootnick & Groves, 2005) proposed a single genus with 3 subgenera; *Hylobates*, *Nomascus*, and *Symphalangus*. This was supported in large part by karyological and chromosomal characteristics (Groves, 1972; de Boer & Van Oostrum-Van der Horst, 1975). A fourth subgenus called *Bunopithecus* was recognised by Prouty et al. (1983a; 1983b). This too was based on karyological characteristics. The taxonomic nomenclature of dividing the family Hylobatidae into four subgenera became the accepted classification for nearly two decades until all four gibbon subgenera were elevated to genus rank (Roos & Geissmann, 2001; Brandon-Jones et al., 2004). Then, Mootnick & Groves (2005) proposed changing the name of the genus *Bunopithecus* to *Hoolock*, arguing that the history of the name was spurious.

These studies and proposed changes have presented us with the current, widely accepted, classification of the hylobatids, i.e. that the family Hylobatidae is divided into four genera; *Hylobates*, *Hoolock*, *Nomascus*, and *Symphalangus*.

Other methods, including examining morphology (Leslie, 2010), biogeographic distribution (Chatterjee, 2009), and species-specific vocalisations (or songs) (Marshall & Marshall, 1976; Geissmann, 2002a; 2002b), have been employed alongside genetics when investigating the relationships among the hylobatids. More often than not, vocal analysis and morphological studies supports cytogenetic classifications. However, there remains some debate about the

relationships found within and between the four hylobatid genera, and the number of species and subspecies in each, across all of these methods.

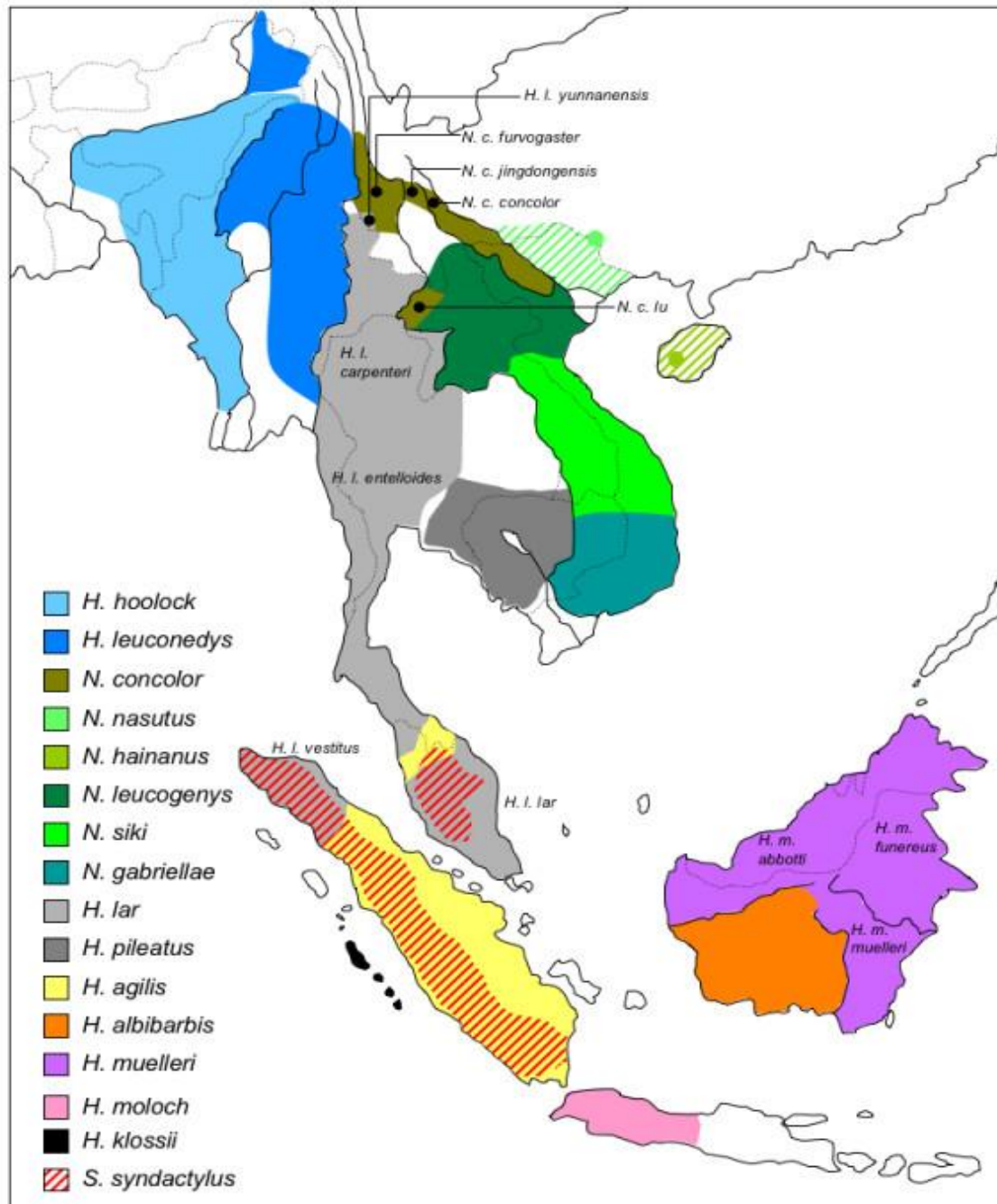


Figure 1.1: Approximate geographical distribution of species and subspecies of gibbons in South and South-East Asia. Historical distribution of *N. hainanus* and *N. nasutus* is hatched.

Image from Thinh et al. (2010)

The gibbon species that this study is concerned with is *Hylobates albibarbis*. Until recently, *H. albibarbis* was considered a subspecies of *Hylobates agilis* but has now been elevated to species level (Groves, 2001; Geissmann 2007). This species inhabits the area bordered to the west by the Kapuas River (West Kalimantan), to the east by the Barito River (Central Kalimantan), to the north by the Busang River (Central Kalimantan) and to the south and east by the Schwaner Mountains (Cheyne, 2010) (see Figure 1.2). There are several forested areas that house large populations of *H. albibarbis* but the largest contiguous population of this species is found in the Sabangau National Park with an estimated 30,000+ individuals (Cheyne et al., 2007).

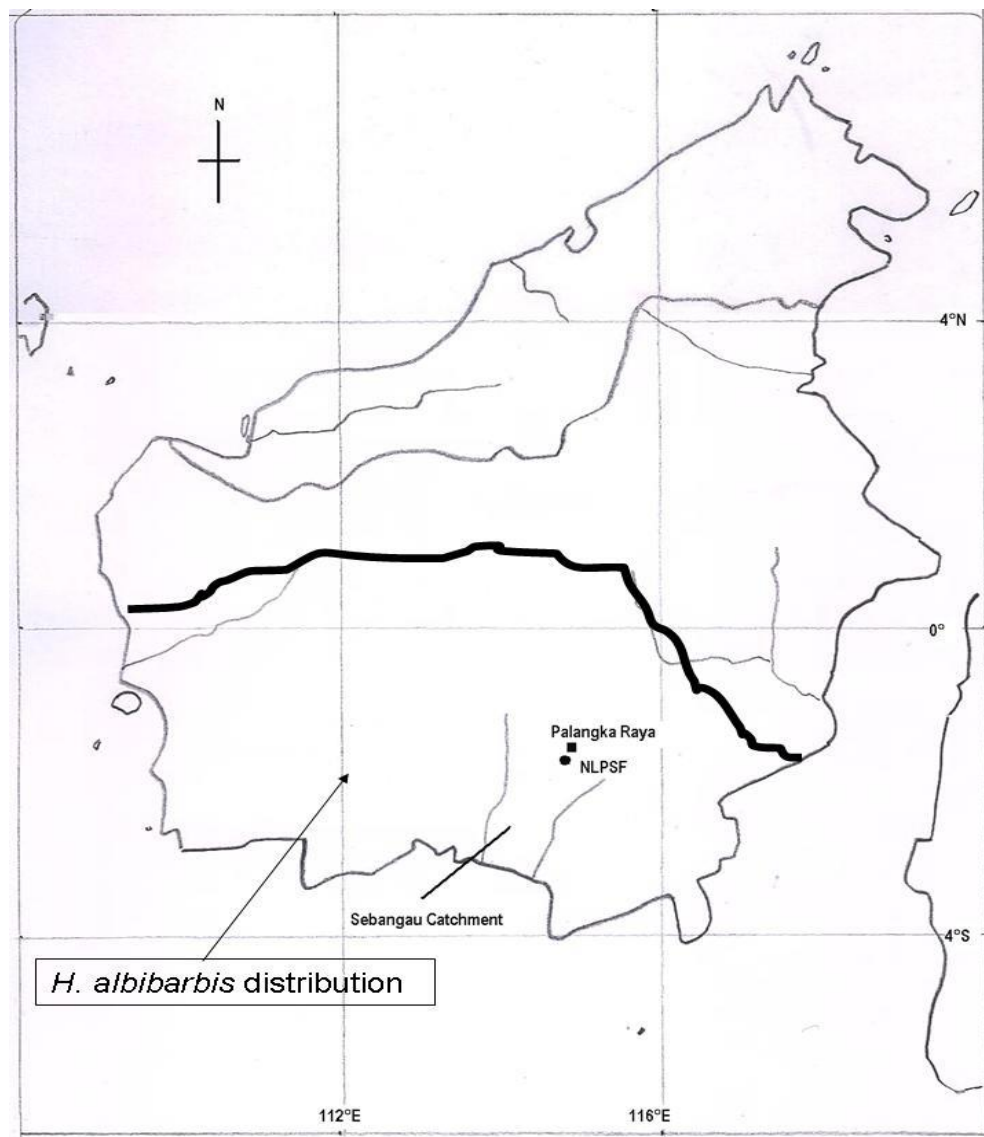


Figure 1.2: Distribution of *H. albibarbis*. Image from Cheyne (2010).

H. albibarbis size is consistent with other small gibbon species with males weighing 6.1-6.9 kg and females weighing 5.5-6.4 kg (Susan Cheyne, pers. comm.). Generally speaking, *H. albibarbis* pelage is characterised by black hands and feet with brown arms and legs, with many individuals having white eyebrows and/or cheeks. The main body colour is usually dark brown with a dark chest and head cap. The pelage of new born infants is a very pale brown and they have no hair on the face, palms of the hands, and soles of the feet (which are all black (pers. obs.)). There is little, if any, sexual dimorphism found in adult gibbons (females can sometimes be larger than males and vice versa), leading to the theory that neither sex is dominant (Gittins and Raemaeker, 1980). Gibbons are predominantly frugivorous but commonly supplement their diet with flower buds, leaf shoots, and invertebrates (Gittins and Raemaekers, 1980; Cheyne, 2008b; 2008c).

H. albibarbis seem to be quite an adaptable species with relatively large populations being found across primary forest, disturbed secondary forest, and in lowland and montane forest including peat-swamp forest (Cheyne et al., 2007)

Gibbons generally live in small familial groups. These groups include a mated adult male and female pair (7+ years old), possibly one or two sub-adults (4-6 year old), a juvenile (2-4 years old) and an infant (0-2 years old), although some species are known to live in groups with several females (e.g. black-crested gibbon (*Nomascus concolor jingdongensis*); Fan et al., 2006). *H. albibarbis* can live in groups of up to five individuals, or arguably six when including a 'lingering' or frequently returning sub-adult as has been observed in one of the study groups (Karate). Average group size is 4.45 individuals with group size ranging from 3-5 individuals (Cheyne et al., 2007, Cheyne, 2010). Presumably, group size is limited, at least in part, by *H. albibarbis* gestation periods and inter-birth intervals. The gestation period in *H. albibarbis* ranges from 7-9 months, which is leaning towards the higher end of gibbon gestation periods (Cheyne, 2010; Geissmann, 1991). Gibbons have relatively large inter-birth intervals when compared with other mammals and many other primates, with a range across all gibbon species from twenty-two months to one hundred and twenty months between births (Chivers & Raemaekers, 1980; Reichard & Barelli, 2008). *H. albibarbis* falls at the lower end of this range where the inter-birth interval is 2.4 years (Cheyne, 2010).

Females reach sexual maturity at about 7-8 years old and have an oestrus cycle that lasts 6.3 days (Cheyne & Chivers, 2006). While several gibbon species have been known to engage in extra-pair copulations (Palombit, 1994a; 1994b; Sommer & Reichard, 2000; Bartlett, 2001), they are,

for the most part, socially monogamous (Cheyne & Chivers, 2006; Gittins & Raemaekers, 1980). Monogamy seems to be the predominant social system in this species. Recently, however, a potential extra-pair copulation was witnessed but it remains unconfirmed as to whether it was an adult female in the group who was involved in the copulation or whether it was the recently dispersed sub-adult female who had rejoined the group for several days. Gibbons do not appear to have reproductive suppression and sub-adults are ejected from the natal familial group by the same-sex parent (Chivers, 1972). This ejection or dispersal usually occurs at the age of 7 years old, presumably so the mature sub-adults can leave to find a mate and establish their own territories. However, the behaviour of recently dispersed sub-adults is extremely understudied, and the mechanisms that lead to the establishment of a new mated pair and a new territory are poorly understood.

1.2 Gibbon Song

Researchers working on an array of gibbon taxa have attempted to untangle the function of gibbon solo songs and duets. Theories on the function of gibbon songs include mate attraction (Raemaekers et al., 1984; Mitani, 1988), mate defence (van Schaik & Dunbar, 1990; Cowlshaw, 1992), territorial defence (Mitani, 1985a; Raemaekers & Raemaekers, 1984; Cowlshaw, 1992; Fan et al., 2006; 2009), pairbond formation and maintenance (Evans & Poole, 1984; Haimoff, 1984; Geissmann, 1986; 1999; Cowlshaw, 1992; Geissmann & Orgeldinger, 2000; Fan et al., 2009), and pairbond advertisement (Haimoff, 1984; Maples et al., 1989; Cowlshaw, 1992). Some of these proposed functions have roles within the family group (intra-group communication) and some of them have roles between family groups (inter-group communication). We know that each male and female has a distinct individual voice though they obviously follow the sex- and species-specific song pattern (Raemaekers & Raemaekers, 1984), and there is at least some evidence to support each of the aforementioned song functions. However, all of these theories are based on playback experiments and/or on recordings made directly under the groups (or as close as possible) and based on analysing the songs from the point of view of the singers, not another group hearing the gibbons at distance, i.e. the receivers.

The playback experiments of Haimoff and Mitani (among others) in the 1980s have gone some way in formulating these hypotheses. Indeed, playback experiments are a useful way of gaining insight into behavioural events that are otherwise uncommon and difficult to document in nature. However, these experiments can be unreliable in that the acoustical structure of the songs can be compromised in the playbacks (Mitani, 1985b). The quality of recording equipment and sound analysis software has increased since these studies were conducted so one would expect a more accurate study to be possible now.

If one is to formulate hypotheses on both intra- and inter-group communication in gibbons, analysing the songs from the perspective of both the singer and the receiver seems essential and yet previous research in this area has failed to incorporate these elements effectively. The method of making recordings from two points simultaneously and thus analysing the songs from both the point of view of the singers and another group hearing the singers seems to be the most logical next step in this line of research.

Similar studies on signal propagation and degradation have been conducted on other taxa (insects: Cocroft et al., 2006; marmots: Daniel & Blumstein, 1998; and birds: Brenowitz, 1982), but never on primates. There have been a few studies focused on gibbon vocal behaviour in the NLPSF (Cheyne, 2008a; Wanelik, 2012) but none concerning variability in intra- and inter-group communication.

As with any type of sound, the sounds produced by gibbons when they sing are subject to acoustic variables (reverberations, echoes, etc.) and governed by the laws of acoustical physics. Wiley & Richards (1980), and Richards & Wiley (1978) conducted experiments to show how complicated sound transmission in heterogenous environments can be and what measures animals take to become effective vocal communicators in such environments (i.e. the ‘acoustic adaptation hypotheses’; Morton, 1975). This study aims to recognise these acoustic variables and investigate if gibbons sing across a broad enough frequency range for certain elements of the song to degrade differently to others over distance.

Before a complete acoustic analysis can be performed, a structured terminology of the visual representation (i.e. what appears on the spectrogram) of the gibbon duet must be established. The terminology for the basic temporal structures of the gibbon song follows, loosely, Haimoff (1984) (see Table 1.2 below) with several personal changes aimed at making the phrase-level classification more efficient for acoustic analyses.

A spectrogram of the distinct duet song that *H. albibarbis* sings is displayed below (see Figure 1.3). Table 1.1 accompanies Figure 1.3 for a more concise overview of the structure of the duet song for both the male and female parts. The terminology used therein mostly follows previous studies but slight changes have been made to more accurately describe the entire song.

Table 1.1: Table summarising the terminology used to describe the duet song of *H. albibarbis* for both the male and female parts. Accompanies Figure 1.3.

FEMALE GREAT CALL		
Phrase	Note	Spectrogram No.
Female Organisational Phrase (FOP)	1st Introductory Wa-Note	1
	2nd Introductory Wa-Note	2
	3rd Introductory Wa-Note	3
	4th Introductory Wa-Note	4
Female Introductory Phrase (FIP)	1st Introductory Note	5
	2nd Introductory Note	6
Female Climactic Phrase (FCP)	1st Climactic Note	7
	2nd Climactic Note	8
Female Terminal Phrase (FTP)	1st Terminal Note	9
	2nd Terminal Note	10
	3rd Terminal Note	11
	4th Terminal Note	12
	5th Terminal Note	13
	6th Terminal Note	14
	7th Terminal Note	15
	8th Terminal Note	16
	9th Terminal Note	17
MALE CODA		
Male Organisational Phrase (MOP)	1st Organisational Coda Note	1
	2nd Organisational Coda Note	2
	3rd Organisational Coda Note	3
	4th Organisational Coda Note	4
	1st Introductory Wa-Note	5
	2nd Introductory Wa-Note	6
	3rd Introductory Wa-Note	7
Male Terminal Phrase (MTP)	1st Terminal Coda Note	8
	2nd Terminal Coda Note	9
	3rd Terminal Coda Note	10
	4th Terminal Coda Note	11

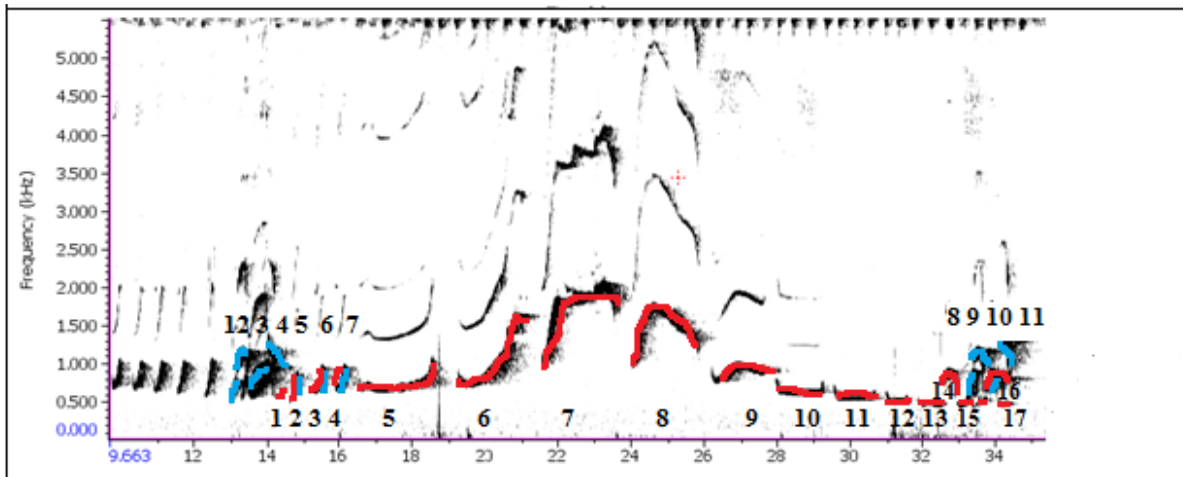


Figure 1.3: Spectrogram of a *H. albibarbis* duet sequence, where the red notes illustrate the female section and the blue illustrate the male section

Like most other gibbon species, with the notable exception of the Kloss's gibbon (*Hylobates klossii*) and the Javan gibbon (*Hylobates moloch*) which are not known to duet, the duet song *H. albibarbis* consists of a female great call and male coda. Singing bouts are initiated by the male with a series of wa-notes and wa-oo notes with the occasional quaver-type note. The female then joins in with a series of slightly lower frequency wa-notes of her own. This is the introductory sequence and it occurs once in the singing bout. When the female wa-notes and male wa-notes are sufficiently synchronised (almost overlapping or completely overlapping), the female great call begins and the male stops singing. Towards the end of the female terminal notes, the male rejoins with a terminal coda, always taking the form of a four-note sequence (wa-aa-oo-aa).

Every duet sequence thereafter is initiated by the males' organisational coda which generally takes the same form of a terminal coda or the form of a 'half terminal coda' in that it contains the first two notes of the terminal coda (wa-aa). The organisational coda is followed immediately by a series of male organisational wa-notes. If the female does not join in with sufficiently synchronised organisational wa notes of her own, the full duet sequence does not take place. In a sense, the male organisational coda 'invites' the female to sing with the male. If the female fails to synchronise with the male wa -otes following the male organisational coda, the male will repeat the organisational coda until the female synchronises and a full duet sequence is sung.

The female great call consists of several introductory notes (together forming the introductory phrase), followed by a few climactic notes (together forming the climactic phrase), followed by a series of terminal notes (together forming the terminal phrase). The male coda usually occurs twice for every one great call, once at the beginning of the introductory phrase of the great call and once towards the end of the terminal phrase of the great call. In that way, it almost ‘sandwiches’ the great call, marking its beginning and end. The male coda can thus be divided into two phrases, more or less consisting of the same number of notes; the introductory coda phrase and the terminal coda phrase. To avoid confusion between duet songs bouts and single duet songs, the terms ‘duet sequence’ and/or ‘duet song’, will be used to describe a single great call sequence complete with male coda. The number of notes per sequence in both the male and female phases of a duet sequence are quite variable and, as such, will be discussed in further detail in the discussion chapter of this dissertation paper.

Table 1.2: Acoustic terms and definitions as described by Haimoff (1984)

Term	Definition
Figure	A very short group of notes that are produced together and one or more of them are hardly ever produced independently.
Phrase	A larger group of notes where different parts of it can be produced independently of the others, for example the male coda that is produced only by the agile, lar, concolor and pileated species.
Coda	A structured series of sex- and species-specific notes sung at or near the end of the female’s great call.
Great Call	Produced by females as the least variable and most easily identifiable part because it is sex- and species-specific.
Song	Defined by Thorpe (1961) as “all notes pure in tone and musical in nature, produced without external stimulus” in relation to birds.
Song Bout	Includes the first and last note without a period of silence of more than ten minutes between notes.
Note	Any single continuous sound which can be produced either by expiration or inhalation and can be of any distinct frequency or frequency modulation.
Duet	Song bout in which both sexes produce their loud song in an interactive manner.

1.3 Research Aims, Objectives, and Hypotheses

1.3.1 Research Aim and Objectives

1. To provide insight into the degradation rates of gibbon songs in a densely vegetated environment, and the implications this may have with regards to current theories on gibbon song functions.
2. To assist conservation efforts for this endangered gibbon species by providing further knowledge on their vocal and territorial behaviour.
3. To provide insight into how *H. albibarbis* use their home range, and the tree species within, with regards to their vocal behavior.
4. To highlight the importance of peat-swamp forest as a refuge for endangered species.
5. To provide a basis for similar studies in gibbons and other highly vocal primate species.

1.3.2 Hypotheses

1. Certain acoustic elements of the duet song will degrade faster than others
2. The entirety of the gibbon song is not heard by all neighbouring gibbon groups and this should have implications on intra- and inter-group communication
3. The degradation rate of the gibbon duet will change with group composition
4. The gibbons are singing from strategic positions within their home range.
5. The gibbons are singing from preferred singing tree species and specific heights in the canopy

CHAPTER II: METHODS

2.1 Study Site

The study site is located in the NLPSF (Natural Laboratory of Peat Swamp Forest). The NLPSF covers an area of 500 km² within the 9,200 km² Sabangau River catchment. The catchment itself makes up a major part of the 22,000 km² of tropical peat-swamp forest found in the south of the Indonesian province of Central Kalimantan. Central Kalimantan is one of four provinces located in the Indonesian portion of the island of Borneo (more commonly known as Kalimantan). Indonesia (along with its surrounding islands and the Malay Peninsula) belongs to a biogeographic region known as Sundaland. Sundaland is named so because it encompasses the Sunda shelf, i.e. the section of the Asian continental shelf that was exposed during the last ice age.

The Sabangau forest catchment is enclosed by the Katingan River to the west and the Kahayan River to the east. Within the catchment, 6,000 km² of forest can be found in the area bordered by the Sabangau River to the east and Katingan River in the west and this is where the NLPSF is located (see Figure 2.1). Apart from the villages that are present along the banks of both rivers, most of the area is forested.

Although the first research concerning primates (Bornean orangutans: *Pongo pygmaeus wurmbii*) was conducted as early as 1995, it was not until 1997, when the Setia Alam Jaya timber concession ended, that the then Governor of Central Kalimantan designated the NLPSF as an area of scientific research, to be managed by CIMTROP (the Centre for International Cooperation in Management of Tropical Peatland) and the University of Palangka Raya. The findings of this study and later studies confirmed the largest known contiguous population of wild orang-utans was present in the area with a population size estimated at between 5671 (\pm 955) and 8951 (\pm 1509) individuals (Morrogh-Bernard et al., 2003). The area was given National Park status in 2004.

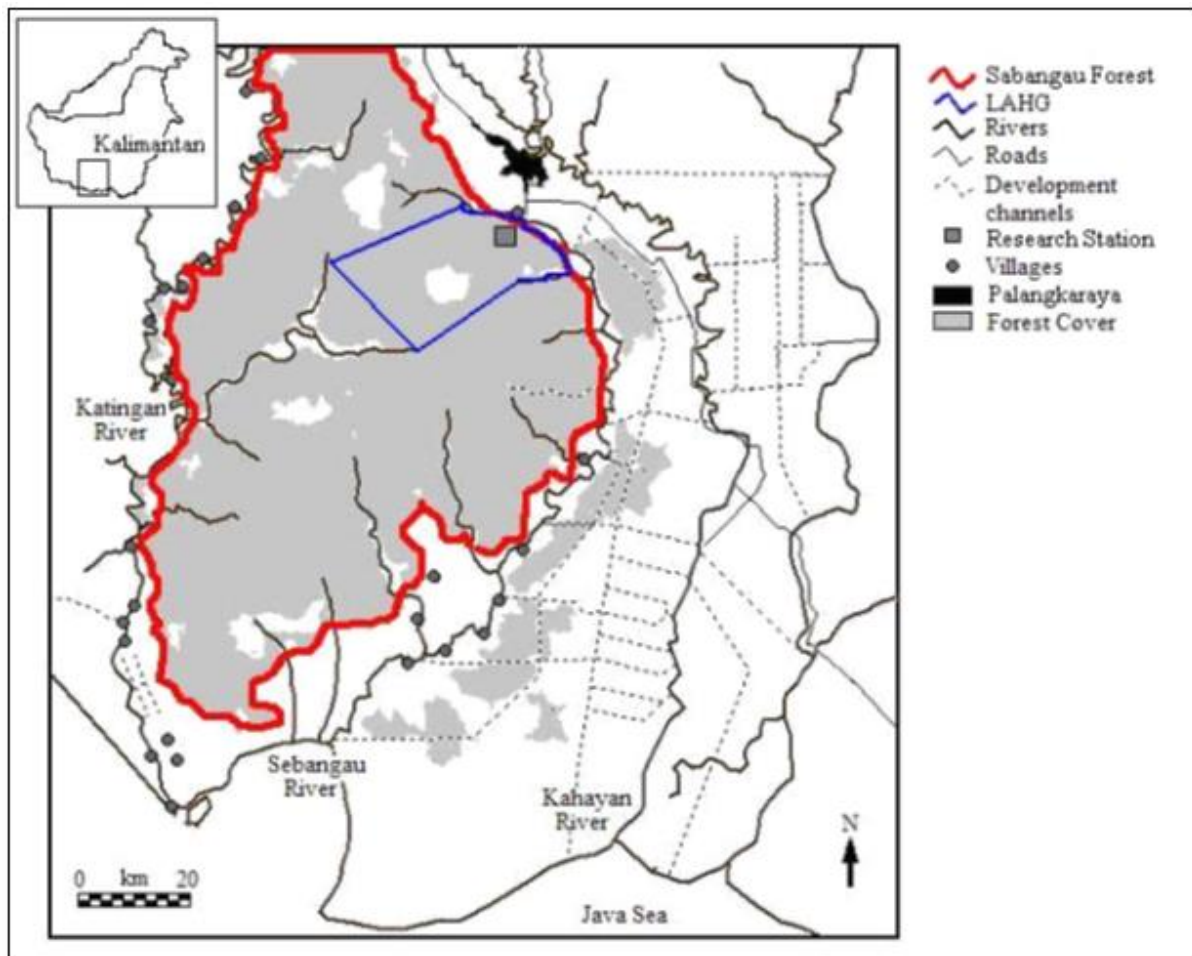


Figure 2.1: Map showing the location of the Sabangau peat-swamp forest within Kalimantan.
Image from Morrogh-Bernard (2009)

The base camp, named Setia Alam, is located 20 km south-west of the provincial capital of Palangka Raya, at coordinates 2° 19'S and 114° 00'E. It is positioned on the forest edge that borders the Sabangau river (see Figure 2.1), and is accessed by using the old railway (constructed during the logging concession) that leads in from the river. The grid system in which all of the research is conducted consists of transects, cut roughly every 250 m, west from base camp along Transect 0, that run in a southerly direction for 3 km, and transects, cut roughly every 200-300 m south from base camp along Railway transect, that run in a westerly direction for 3 km. Thus, the grid system covers a total 9 km². Railway transect is constructed along the old logging railway route. The route actually extends much further into the forest, as far as 13 km, and through the three largest forest habitat sub-types, the mixed-swamp forest, the low-pole forest, and the tall-interior forest. The peat-swamp forest in Sabangau has been categorised

into five distinct habitat sub-types (see Figure 2.2), based on their respective structures and vegetation composition (Shepherd et al., 1997; Page et al. 1999). The entirety of the 9 km² grid system lies within the mixed-swamp habitat-subtype.

This forest sub-type stands upon peat up to 6 m deep. It is heavily flooded during the wet season and remains flooded for much of the dry season with the surface peat (acrotelm) only becoming completely dry towards the end dry season. The forest here is tall and stratified, with the upper canopy being as high as 35 m, and is the most extensive of all five habitat sub-types. Most of the illegal logging in the forest was concentrated here due to its accessibility and the presence of commercially-valuable trees, such as ramin (*Gonystylus bancanus*) and mentibu (*Dactylocladus stenostachys*) (Morrogh-Bernard et al., 2003).

The Sabangau Forest is classified as peat-swamp forest. The peat on which the forest grows is formed from the accumulation of partially decayed woody plant debris (called peat) in waterlogged (areas of high-rainfall and poor drainage) and high-temperature conditions. This peat accumulates over long time periods until it is above the groundwater level which eventually creates dome-shaped or "ombrogenous" raised bog that is fed only by rainwater with the peat dome acting as a reservoir holding water by capillary forces (Andriesse, 1988).

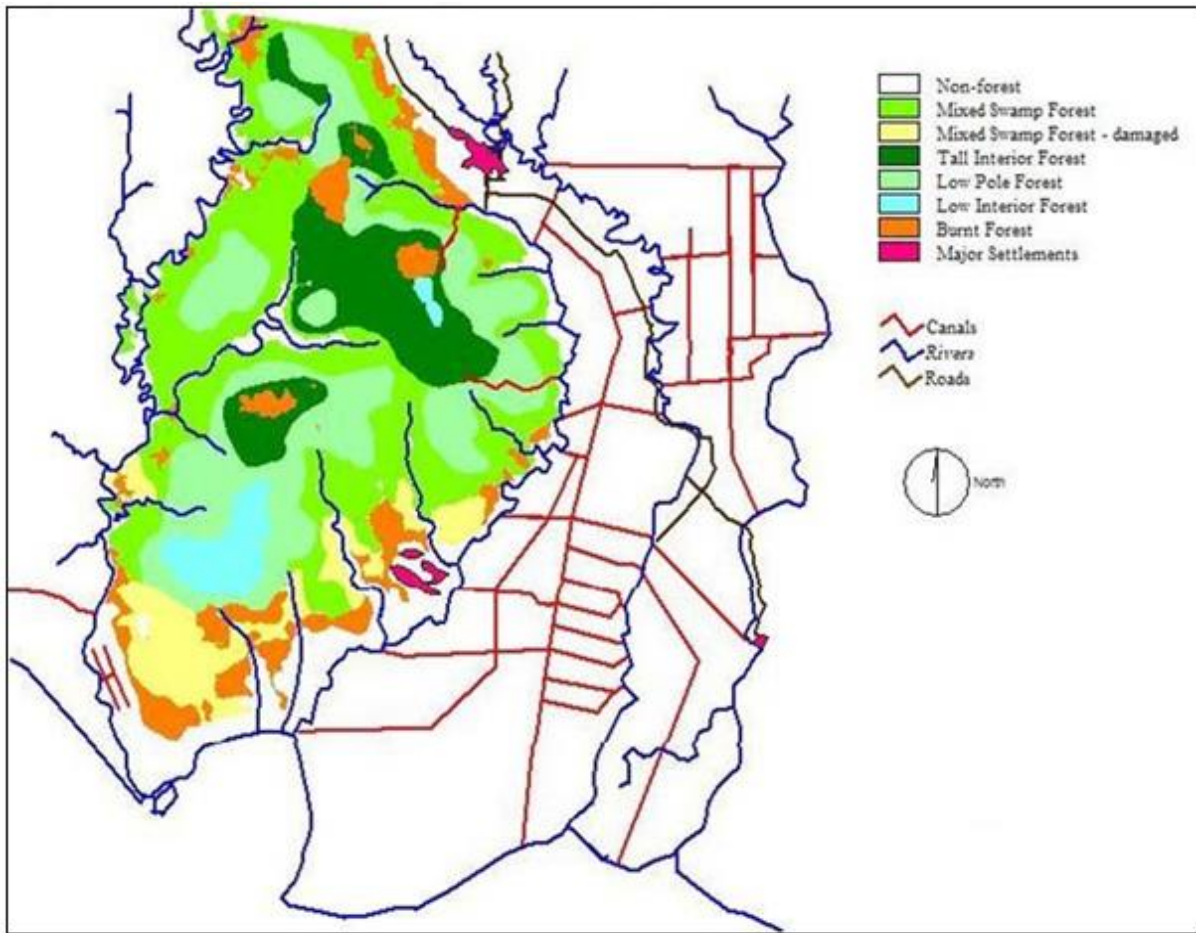


Figure 2.2: Map displaying distribution of habitat sub-types and nearby settlements within the Sabangau forest. Image from Morrogh-Bernard (2009)

2.2 Study Groups

Due to time and manpower restrictions, recordings for this project were exclusively limited to the two most habituated gibbon groups at the field site; Group C and Karate. Group demographics are shown below (Table 2.1 and Figure 2.3).

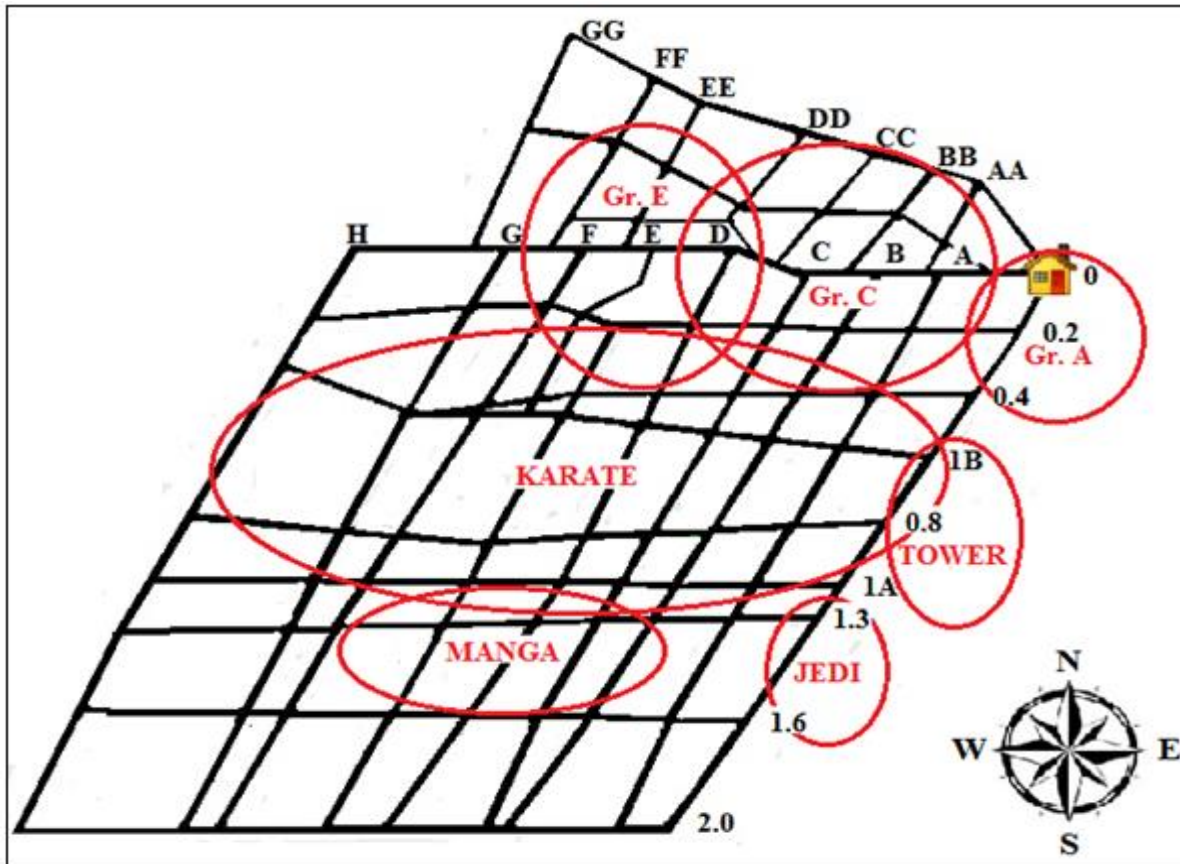


Figure 2.3: Map showing known (Group C and Karate) and estimated (all other featured groups) home ranges in the grid system in the NLPSF

Table 2.1: Table showing group demographics for Group C and Karate as of 2013

GROUP NAME	INDIVIDUAL NAME	SEX	AGE CLASS	PARTICIPATION IN DUET
Group C	Captain	Male	Adult Male	Singing
	Coklat	Female	Adult Female	Singing
	Ceeka	Female	Sub-Adult Female	Singing
	Chilli	Unknown	Juvenile	Not Singing
Karate	Bruce Lee	Male	Adult Male	Singing
	Chun Lee	Female	Adult Female	Singing
	Jet Lee	Female	Sub-Adult Female	Singing
	Brandon Lee	Male	Juvenile	Singing

2.3 Recording of Gibbon Song

A ZOOM H2 Handy Recorder and a ZOOM H2n handheld recorder were used to record the gibbon duets. Both of the recorders were fitted with a Hama RMZ-10 Zoom-Universal directional external microphone each.

The two external microphones used were identical and only had two directional and sensitivity settings, i.e. HIGH: supercardioid directionality (with a sensitivity of -56 dB, and LOW: cardioid directionality (with a sensitivity of -78 dB). As the lower sensitivity was deemed too low after several trials, the HIGH setting was used throughout recording proper. However, as the digital recorders were not identical models, several trials had to be run to standardise them.

Both recorders were set to a sampling rate of 44.1 KHz and a bit depth of 24-bit, with the recordings being stored as uncompressed WAVE (.WAV) files. The mechanism for altering gain settings for each recorder was not as straightforward. The newer ZOOM H2n model had a simple and more traditional 0-10 ‘gain dial’, whereas the older ZOOM H2 model had a more complicated LOW-MEDIUM-HIGH ‘gain switch’, which was also accompanied by a sensitive 0-127 ‘Rec Level’ option. The gain was eventually standardised (ZOOM H2 was set to HIGH gain with a ‘Rec Level’ of 112, and the ZOOM H2n gain dial was set to 9) by altering the gain settings on each recording, using many recordings of music, human speech, and gibbon song

at different distances, until the relative amplitude between the two recordings was no more than 1 dB (0.8 dB).

Once the equipment was standardised, a threshold distance, at which the gibbon duet was acoustically compromised to the extent that the entire duet could not be effectively communicated beyond that distance, was investigated. The distance was established by recording the duet of both groups every 50 meters (m) away from the focal singing group, starting at 0 m and ending at 600 m, and acoustically analysing each recording with Raven Pro 1.4 software.

The threshold distance was determined to be 350 m. From that point onwards, all duets were recorded at both 0-10 m (under the gibbon group) and 350 m simultaneously, with the digital recorders and microphones being switched daily to further eliminate differences in equipment as a variable. The distance of 350 m was maintained through the use of two GPS units, one for the individual recording at the 350 m position and one for the individual recording at the 0-10 m position (who was always positioned centrally between the adult male and adult female of the group to avoid sex bias within the duet recording). The individual recording at the 0-10 m position followed the gibbons until such time as the gibbons had completed their duet. On days where the gibbons did not duet, they were followed until 1000 hours, as singing after this time is extremely rare. The individual recording at the 0-10 m position also sent an SMS to the phone of the individual recording at the 350 m position every 20 minutes with an updated GPS coordinate which allowed that individual to reposition themselves accordingly and thus continuously maintain a distance of 350 m from the gibbons.

All recordings were taken above the level of severe ground attenuation, i.e. 1 m above the ground. Due to the variable (and most often short) duration of the duet, recordings were only possible when the gibbons were followed from their sleeping tree. This allowed accurate instantaneous recordings, regardless of when, or for how long, the gibbons duetted.

2.4 Acoustic Analysis of Gibbon Song

2.4.1 General Settings

Spectrograms of the recorded vocalisations were generated using sound analysis software (Raven Pro 1.4). A view range of approximately 5000 Hz and a window length of approximately 25 s were used. Both brightness and contrast were set to 80 and the spectrogram window size (FFT size) was set to 4096 for every recording that was analysed.

2.4.2 Acoustic Variables

In order to contrast the duet song of the two groups at two different distances in this study, a total of 46 acoustic and temporal variables at the phrase- and song-level were selected (see Appendix V for a full list of variables). Note-level investigation would have led to roughly 256 variables being included in the statistical analyses. Given that the sample size was not nearly large enough for this level of analysis and given that phrase- and song-level analysis was deemed sufficient to accurately portray the degradation of the of the duet sequence, only phrase- and song-level acoustic and temporal variables were included. These variables were chosen by inspecting the spectrograms for interesting and obvious differences related to degradation and by building upon the methods of similar previous studies (Sorjonen, 1976; Mitani 1987, 1988; Wanelik, 2012). The variables selected were: no. of notes, duration, minimum frequency, maximum frequency, dominant frequency, and maximum amplitude for each of the 6 phrases in the duet sequence as well as for the duet sequence (or song) as a whole. No. of total male notes, no. of total female notes, no. of complete male phrases and no. of complete female phrases in the duet sequence were also included. Figure 2.4 shows how the variables were measured from the spectrogram.

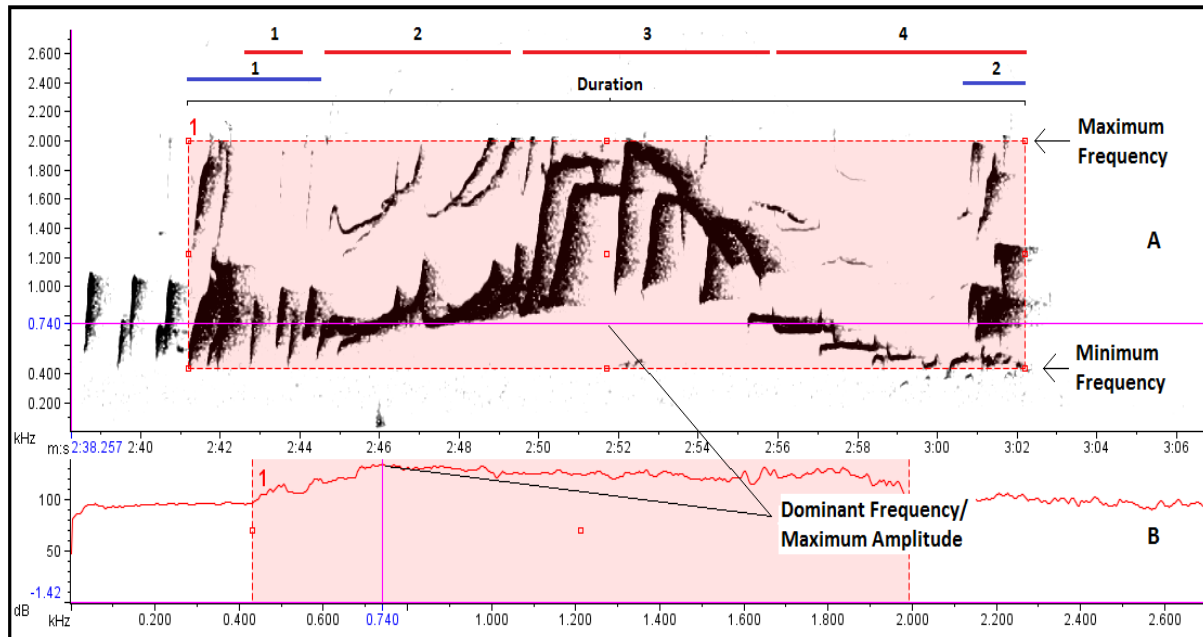


Figure 2.4: Labelled spectrogram showing how some of the acoustic variables were measured. The red lines denote the four female phrases while the blue lines denote the two male phrases. A is a spectrogram and B is a power spectrum

Spectrograms display sound in three dimensions and, as such, they have three axes: 1) the x-axis displays time, 2) the y-axis displays frequency, and 3) the z-axis displays amplitude, also called energy (measured in decibels (dB)). As such, it is difficult to include all measurements in a single figure. Maximum amplitude and dominant frequency (the frequency at which the most ‘energy’ is focused at a particular moment in time), for example, were measured from the z-axis. This was done by creating a power spectrum in Raven Pro 1.4 for the desired section of the spectrogram which gives a reading of changes in amplitude at a given frequency over time. As such, measurements were taken both manually (i.e. by eye from the spectrogram) and by using Raven Pro 1.4 features such as the power spectrum feature.

2.5 Other data collected on singing behaviour

The height of singers during the duet, the distance between the mated pair during the duet, and which individuals participated in the duet singing bout were all noted for each singing bout that was recorded. The height of the singers and distance between the mated pair were both measured by eye at 5 meter intervals, i.e. 1-5 m, 6-10 m, 11-15 m, 16-20 m, 21-25 m, and 26-30 m.

2.6 Factors Affecting Presence or Absence of the Gibbon Duet

External factors (number of adjacent groups singing, morning rainfall (mm), afternoon rainfall (mm), total daily rainfall (mm), minimum temperature (°C), maximum temperature (°C), cloud cover (given as a percentage of total sky coverage), and wind level (where 0-25% represented no wind to light breeze, 26-50% represented light wind, 51-75% represented strong winds, and 76-100% represented gale force winds)) that could potentially affect whether or not the gibbons would duet on any given day were recorded and subsequently investigated for each group separately.

2.7 Sleeping and Singing Tree Choice in *H. albibarbis*

GPS and observational data on both sleeping and singing trees, e.g. height, species, number of trees used per singing bout, and position within their home range, were collected for each day that singing was recorded.

2.8 Statistical Analysis

All statistical analyses were performed using IBM SPSS Statistics v21.

2.8.1 Acoustic Analysis

Given the complicated nature of an analysis including 46 variables and the relatively small sample size, a data reduction procedure was deemed not only necessary but more efficient in describing the results. As all of the assumptions were met to perform principal component analysis (PCA), this was the data reduction procedure that was chosen (see McGarigal et al. (2000) for the full list of PCA assumptions). PCA reduces the dimensionality of a data set while

still retaining a large amount of the variation (Jolliffe, 2005). This is achieved by transforming the original variables into a new smaller set of uncorrelated variables or principal components (PC's). 40 duet sequences were taken for each group and each of the 40 duet sequences were recorded at both a distance of 0-10 m (i.e. under the singers) and 350 m simultaneously. This meant that the sample size for the PCA was 160.

A one-way multivariate analysis of variance (MANOVA) was then performed with the independent variable being a four group (or level) variable named group/distance (Group C 0 m; Group C 350 m; Karate 0 m; Karate 350 m) and the dependent variables being the PC's derived from PCA. To determine which dependent variables contributed most to the statistically significant MANOVA, a post-hoc Tukey's test was also used. This produced post-hoc tests for the statistically significant follow-up univariate ANOVAs for each dependent variable, and not the MANOVA itself. Previous studies on vocal sound/signal propagation in other taxa have used similar statistical analyses to good effect (Cocroft et al., 2006; Daniel & Blumstein, 1998).

2.8.2 Factors Affecting Presence or Absence of the Gibbon Duet

The effect of external factors on the presence or absence of the gibbon duet were investigated using a one-way MANOVA, where the presence/absence of duetting was the independent variable and the number of adjacent groups singing, morning rainfall (mm), afternoon rainfall (mm), total daily rainfall (mm), minimum temperature (°C), maximum temperature (°C), cloud cover (%), and wind levels (%) were the dependent variables. A separate MANOVA was performed for each group. Only days where all the dependent variables were accounted for were included in the analysis.

CHAPTER III: RESULTS

3.1 Initial Trial Recordings of the Duet Song of *H. albibarbis*

The spectrograms displayed below (Figure 3.2.1 – 3.2.9) illustrate how the *H. albibarbis* duet song degrades at 50 meter intervals in a mixed-swamp forest from 0 m to 400 m. The first elements of the duet to degrade are the harmonics, which are no longer present in the spectrograms after 250 meters. However, it is not until 350 meters that the fundamental begins to degrade to a point where entire notes are lost.

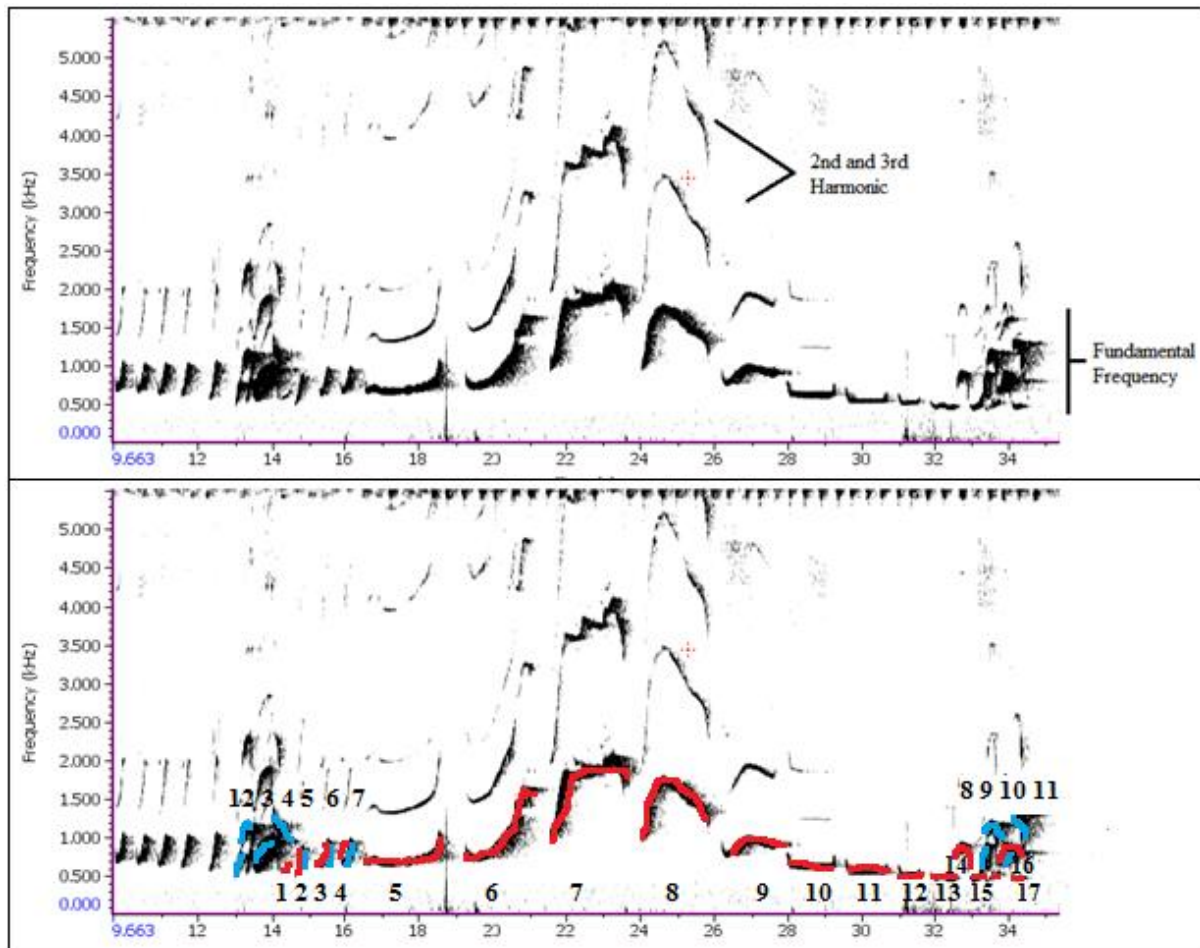


Figure 3.1: Spectrogram of a *H. albibarbis* duet song showing the fundamental frequency and the 2nd and 3rd harmonics. Red notes illustrate the female section and blue notes illustrate the male section.

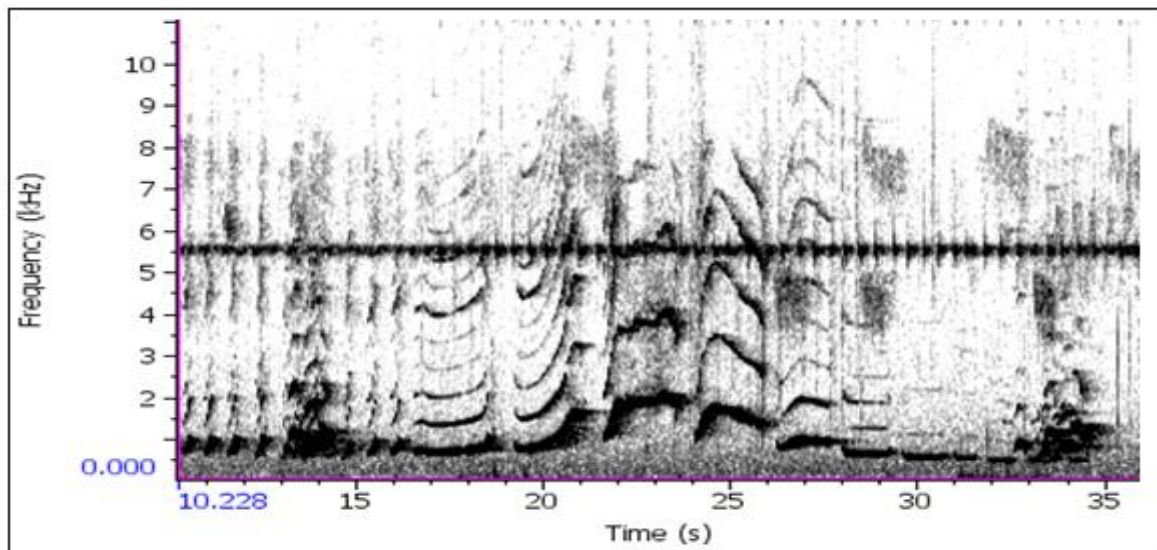


Figure 3.2.1: Spectrogram of a gibbon duet song recorded from 0 m. All elements of the song are still present at a high amplitude, including ~ 10-12 harmonics.

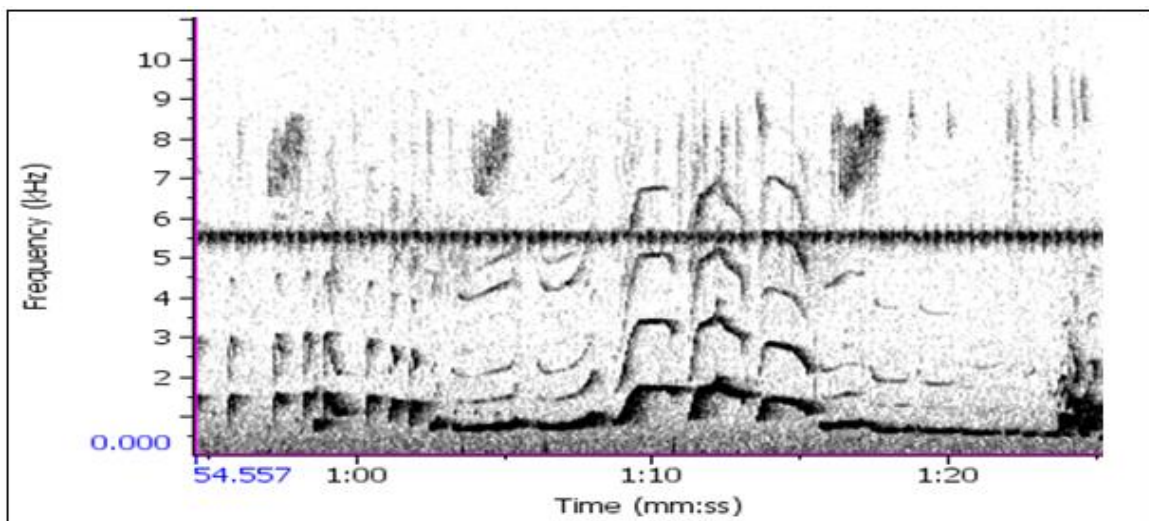


Figure 3.2.2: Spectrogram of a gibbon duet song recorded from 50 m. All elements of the song are still present at a high amplitude but there is a decrease in the number of harmonics.

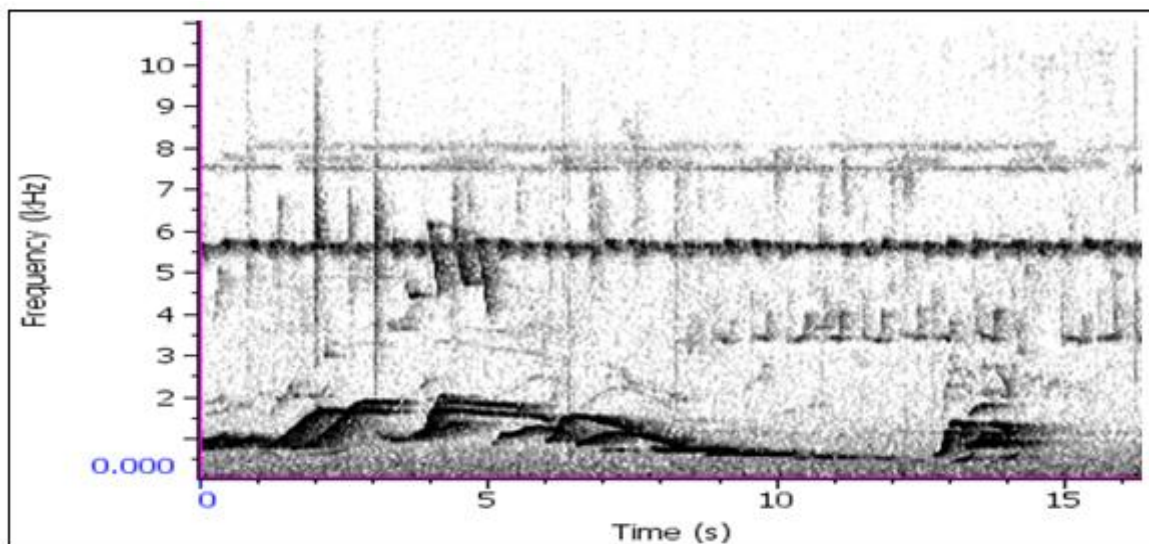


Figure 3.2.3: Spectrogram of a gibbon duet song recorded from 100 m. All elements of the song are still present at a high amplitude. There is a heavy decrease in the number of harmonics

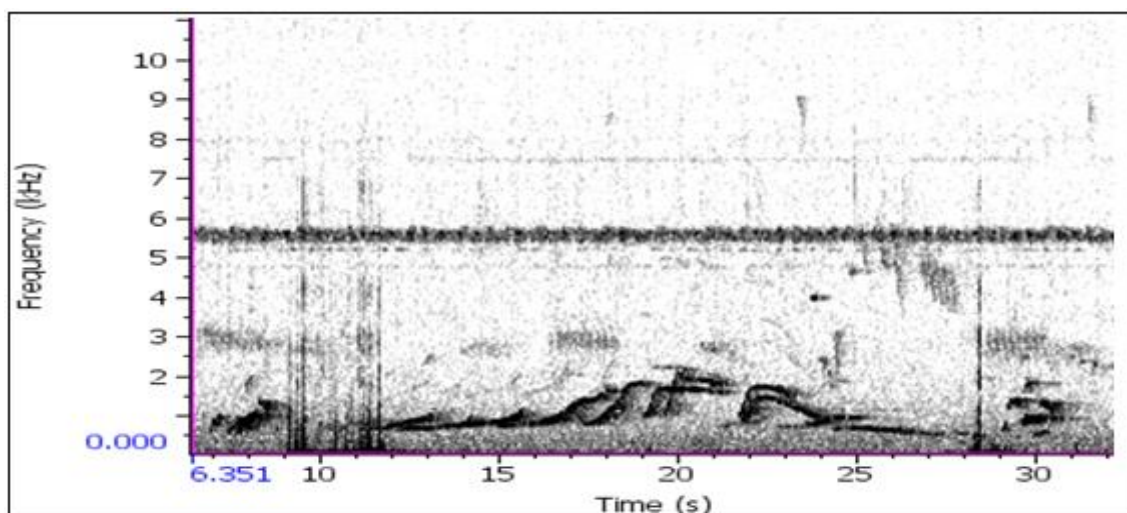


Figure 3.2.4: Spectrogram of a gibbon duet song recorded from 150 m. All elements of the song are still present at a relatively high amplitude. Only the 2nd and 3rd harmonics are still present but at a very low amplitude.

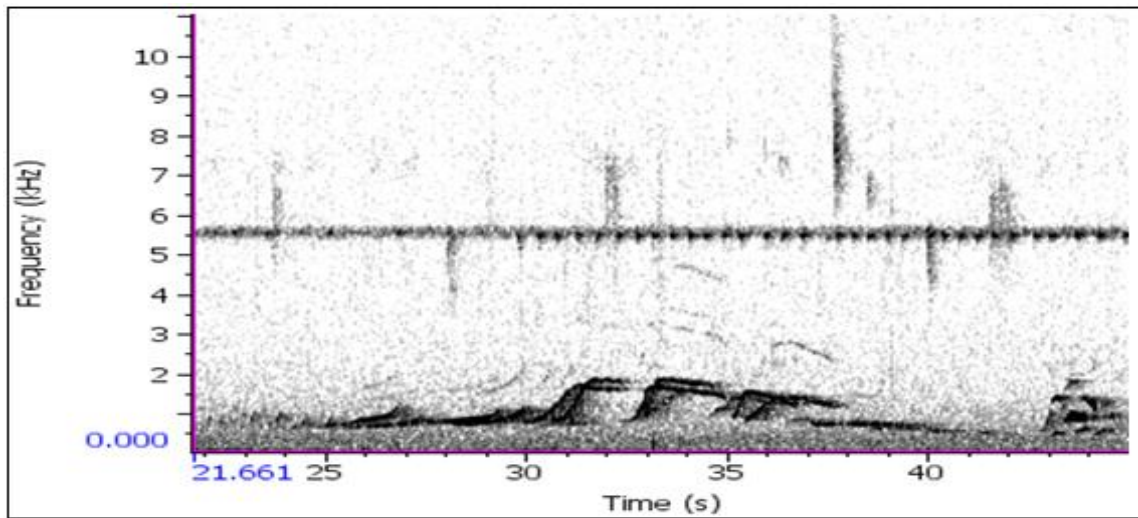


Figure 3.2.5: Spectrogram of a gibbon duet song recorded from 200 m. All elements of the song are still present at a relatively high amplitude. The 2nd and 3rd harmonics are barely audible.

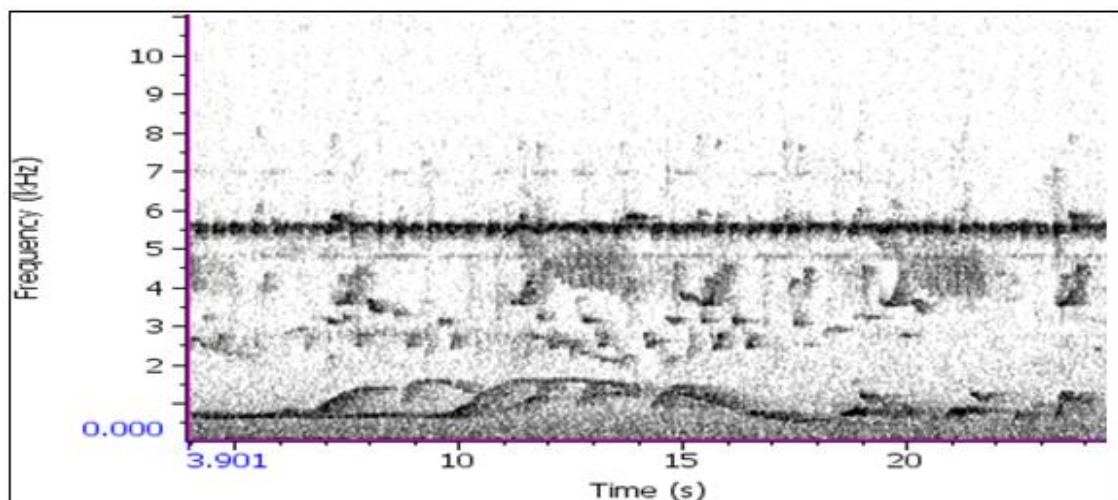


Figure 3.2.6: Spectrogram of a gibbon duet song recorded from 250 m. All elements of the song are still present at a relatively high amplitude but the highest and lowest frequency notes are beginning to noticeably degrade. Harmonic are no longer present.

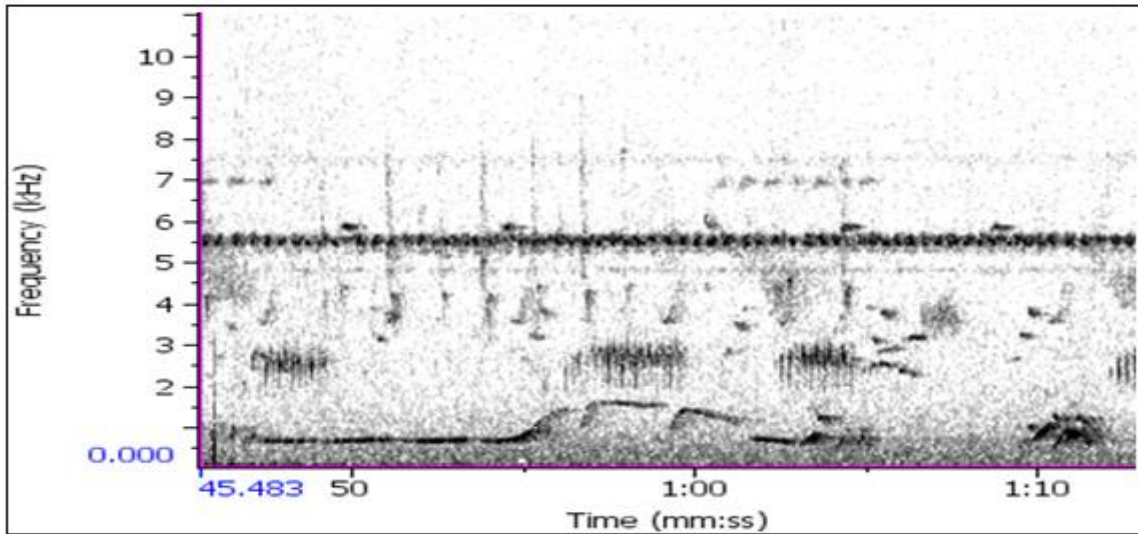


Figure 3.2.7: Spectrogram of a gibbon duet song recorded from 300 m. All elements of the song are still present but the highest and lowest frequency notes are almost completely degraded.

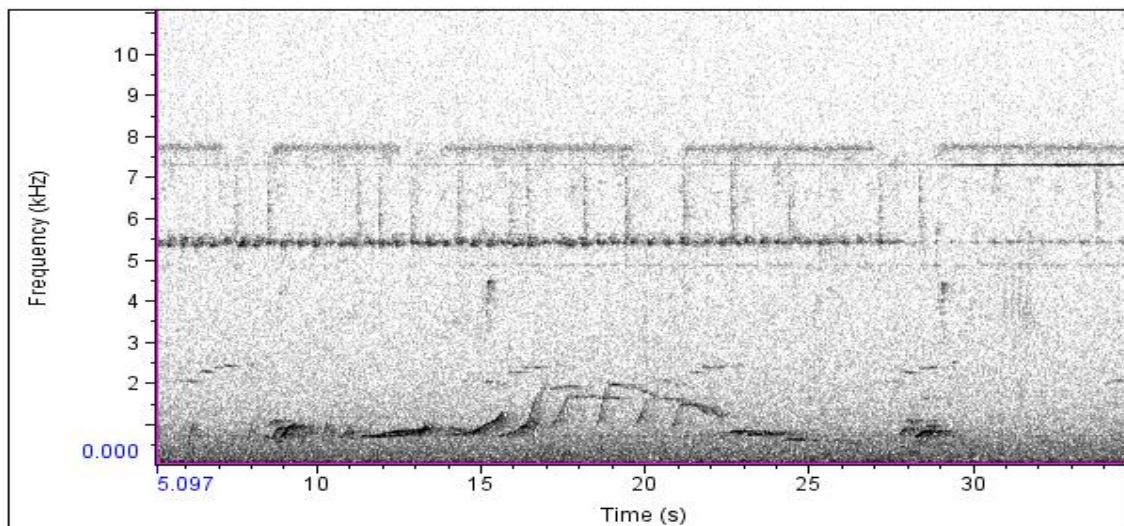


Figure 3.2.8: Spectrogram of a gibbon duet song recorded from 350 m. Several of the MOP, FOP, and FTP notes have become completely degraded.

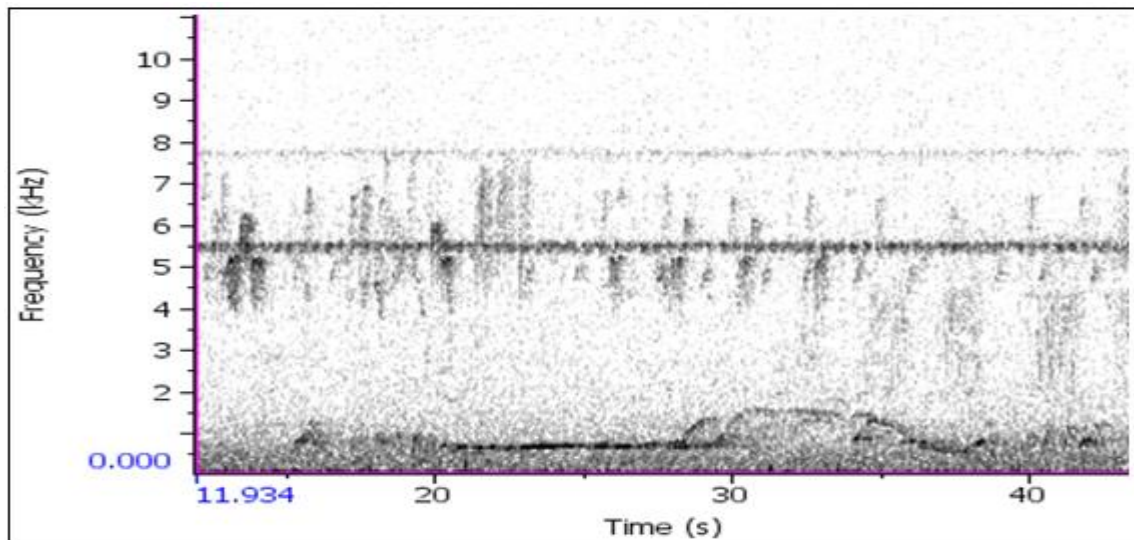


Figure 3.2.9: Spectrogram of a gibbon duet sequence recorded from 400 m. All parts of the song have become notably degraded. Several of the MOP, FOP, FTP, and MTP notes have become completely degraded.

3.2 PCA and MANOVA Analysis

4 PC's were chosen because they had an eigenvalue of >1.5 and they explained 71.66% of the variance in the dataset (see Figure 3.3).

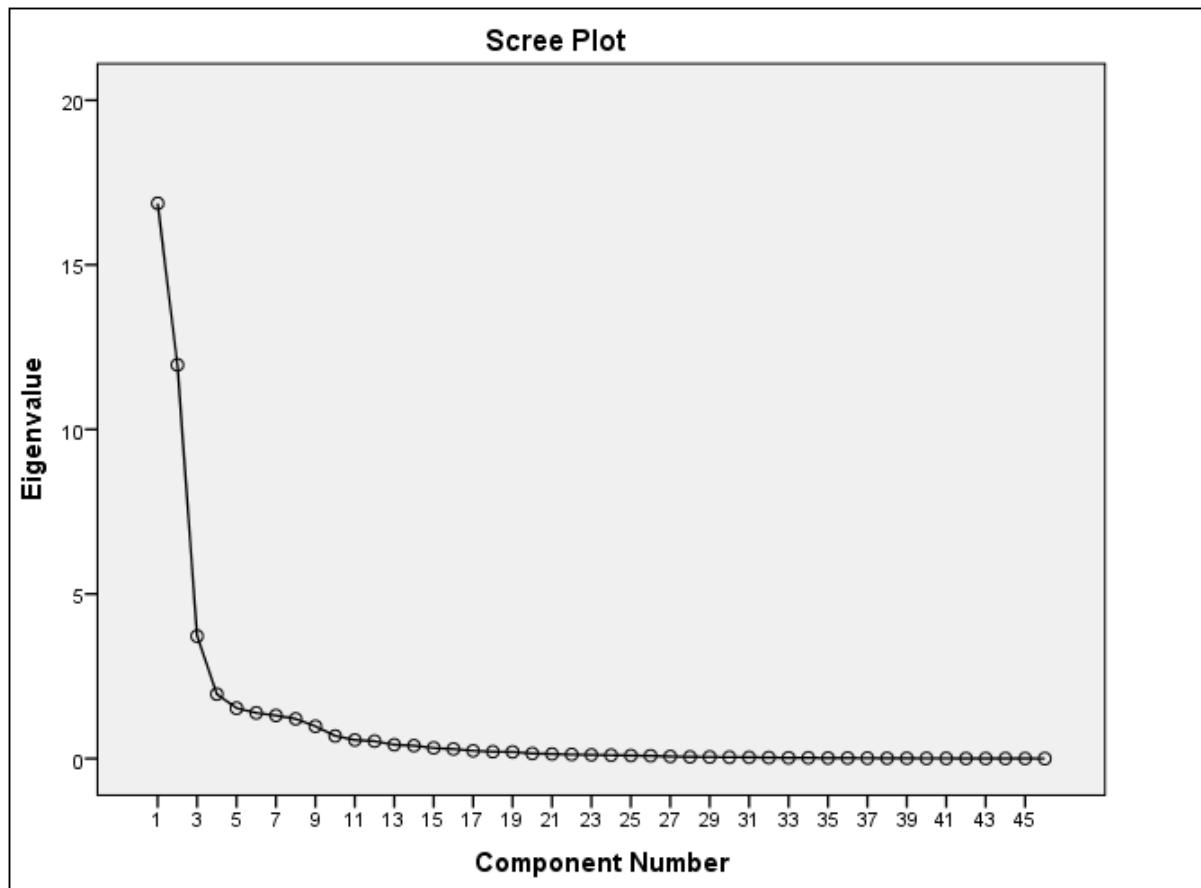


Figure 3.3: Scree plot showing total variance explained by each component (i.e. its eigenvalue) against its respective component

The variables that PC1 most loaded on (i.e. the variables that had a coefficient of > 0.6 with PC1) were: maximum amplitude (for all six phrases and the duet song as a whole), no. of complete female phrases, minimum frequency (for the FTP and for the song as a whole), no. of notes (for the FTP, total female notes, and total song notes), dominant frequency (of the FCP, the MTP, and the song as a whole), and FTP duration.

The variables that PC2 most loaded on were: no. of notes (for the FIP and the FCP), maximum frequency (of the FCP, the FIP, the MTP, and the song as a whole), minimum frequency (of

the MTP, the FIP, and the FCP), dominant frequency (of the MTP), and duration (of the FIP, the FCP, and the MTP).

The variables that PC3 most loaded on were: FOP; minimum frequency, maximum frequency, and dominant frequency. The variables that PC4 most loaded on were: no. of notes (for the MOP and for the male song as a whole) and MOP duration.

The difference between the duet sequences at group- and distance-level was statistically significant on the combined dependent variable ($F_{12,405} = 411.705$, $p < 0.001$, Wilks' $\Lambda = .001$, partial $\eta^2 = .897$). Follow-up univariate ANOVAs showed that PC1 ($F_{3,156} = 1351.834$, $p < 0.001$; partial $\eta^2 = 0.963$), PC2 ($F_{3,156} = 591.198$, $p < 0.001$; partial $\eta^2 = 0.919$), PC3 ($F_{3,156} = 4.689$, $p < 0.05$; partial $\eta^2 = 0.083$), and PC4 ($F_{3,156} = 5.274$, $p < 0.05$; partial $\eta^2 = 0.092$) were all statistically significantly different between the duet sequences of the two groups for both distances. Tukey post-hoc tests showed that of 24 comparison made, 15 were statistically significantly different ($p < 0.05$) (see Table 3.1 for summary).

Table 3.1: A comparison between the duet song of two gibbon groups at two different distances using a MANOVA, univariate ANOVA's, and post-hoc Tukey's test. C = Group C and K = Karate

Group-Distance	Dependent Variable	Significance Level
C 0m/C 350m	PC1	***
	PC2	ns
	PC3	***
	PC4	***
C 0m/K 0m	PC1	***
	PC2	***
	PC3	ns
	PC4	***
C 0m/K 350m	PC1	***
	PC2	***
	PC3	ns
	PC4	**
K 0m/K 350m	PC1	***
	PC2	ns
	PC3	ns
	PC4	ns
K 0m/C 350m	PC1	***
	PC2	***
	PC3	ns
	PC4	ns
K 350m/C 350m	PC1	***
	PC2	***
	PC3	**
	PC4	ns
ns - not significant, ***p < 0.01, **p < 0.05		

3.3 Other data collected on singing behaviour

The mean duration of Karate's male solo song is 32.66 ± 12.39 minutes ($n = 21$), with a duration ranging from 11 to 60 minutes. The mean duration of Karate's duet song bout is 11.08 ± 4.8 minutes ($n = 25$), with the duration ranging from 6 to 23 minutes. The mean duration of Group C's male solo song is 37.66 ± 13.97 minutes ($n = 6$), with a duration ranging from 19 to 61 minutes. The mean duration of Group C's duet song bout is 11.76 ± 5.18 minutes ($n = 21$), with duration ranging from 7 to 24 minutes.

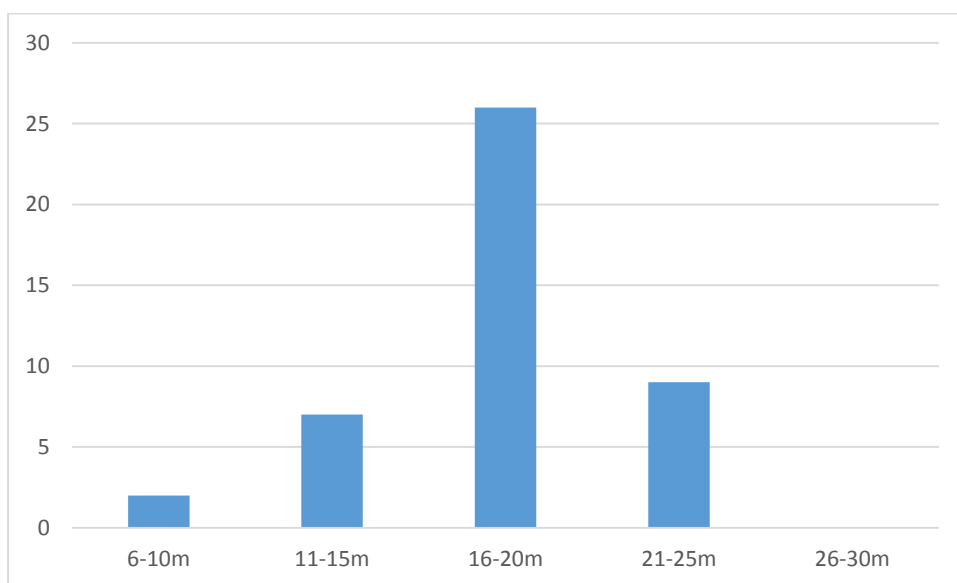


Figure 3.4: Bar chart showing the heights in the canopy used by *H. albibarbis* during singing bouts. Frequency is plotted on the y-axis.

The most commonly utilised height in the canopy during the duet song bout is 16-20 m ($n = 26$) (see Figure 3.4). The most commonly recorded distance between the adult male and adult female during the duet song bout was 6-10 m ($n = 16$) (see Figure 3.5).

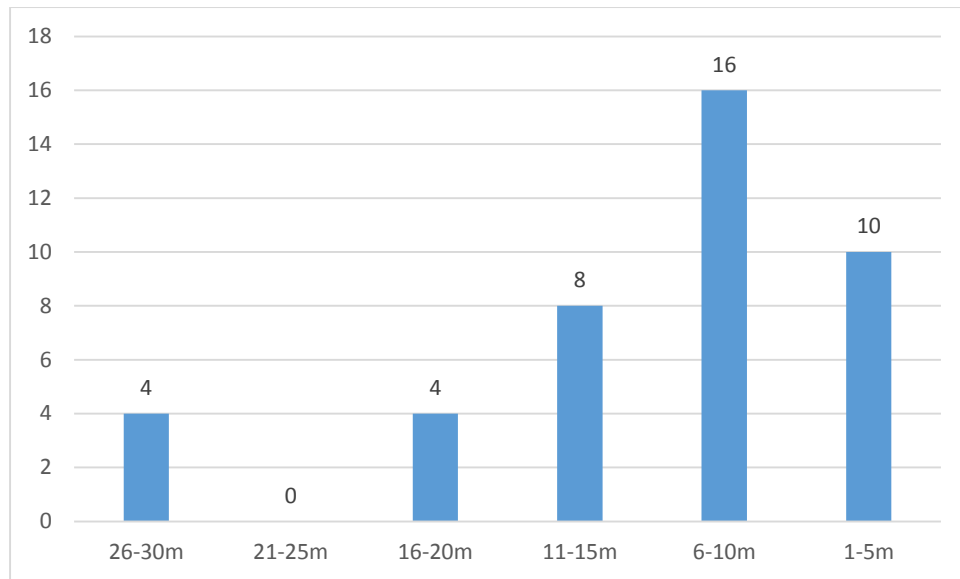


Figure 3.5: Bar chart displaying the distribution of recorded distances between the adult male and adult female of the mated pair during singing bouts for both gibbon groups combined. Frequency is plotted on the y-axis.

Karate sung an average of 7.72 ± 3.58 great calls per singing bout, with the number of great calls per singing bout ranging from 2 to 17 ($n = 39$). Group C sung a slightly higher average of 8.84 ± 4.88 great calls per singing bout with a wider range of 2 to 24 great calls per bout.

3.4 Factors Affecting Presence or Absence of the Gibbon Duet

Of the 33 days included in the analysis, Karate only sang on 10 of those days while Group C sang on 12. The difference between singing and non-singing days was not statistically significant on the combined dependent variable for either group (Karate: $F_{8,24} = 1.929$, $p > 0.05$, Wilks' $\Lambda = .609$, partial $\eta^2 = .391$; Group C: $F_{8,24} = 0.719$, $p > 0.05$, Wilks' $\Lambda = .807$, partial $\eta^2 = .193$).

There was a higher mean number of adjacent groups singing on singing days (K: 4.8 ± 1.55 ; C: 4.66 ± 1.37) than on non-singing days (K: 3.87 ± 1.55 ; C: 3.86 ± 1.65) for both focal groups but the difference was not statistically significant (K: $F_{1,31} = 2.062$, $p > 0.05$, partial $\eta^2 = .062$; C: $F_{1,31} = 1.929$, $p > 0.05$, partial $\eta^2 = .391$).

Morning rainfall (mm) was higher on non-singing days (K: 3.19 ± 8.21 ; C: 3.72 ± 8.55) than on singing days (K: 0.82 ± 2.07 ; C: 0.28 ± 0.98) but the result was not statistically significant (K: $F_{1,31} = 0.797$, $p > 0.05$, partial $\eta^2 = .25$; C: $F_{1,31} = 1.902$, $p > 0.05$, partial $\eta^2 = .058$).

Afternoon rainfall (mm) was higher on singing days (K: 10.0 ± 21.11 ; C: 6.17 ± 19.43) than on non-singing days (K: 0.42 ± 1.48 ; C: 1.69 ± 4.42). The difference was significant for Karate but not for Group C (K: $F_{1,31} = 4.881$, $p < 0.05$, partial $\eta^2 = .136$; C: $F_{1,31} = 1.045$, $p > 0.05$, partial $\eta^2 = .033$).

Total rainfall (mm) was higher on singing days (K: 10.72 ± 21.33 ; C: 6.45 ± 19.36) for both groups than on non-singing days (K: 3.61 ± 8.32 ; C: 5.37 ± 9.6) but the difference was not statistically significant (K: $F_{1,31} = 1.94$, $p > 0.05$, partial $\eta^2 = .059$; C: $F_{1,31} = 0.047$, $p > 0.05$, partial $\eta^2 = .002$).

Minimum temperature ($^{\circ}\text{C}$) was almost exactly the same for both singing (K: 21.7 ± 0.67 ; C: 21.83 ± 0.83) and non-singing days (K: 21.83 ± 0.94 ; C: 21.76 ± 0.90) for both groups and, as such the difference was not statistically significant (K: $F_{1,31} = 0.147$, $p > 0.05$, partial $\eta^2 = .005$; C: $F_{1,31} = 0.051$, $p > 0.05$, partial $\eta^2 = .002$).

Maximum temperature ($^{\circ}\text{C}$) was almost exactly the same for both singing (K: 28.1 ± 2.77 ; C: 29.25 ± 1.48) and non-singing days (K: 28.95 ± 2.5 ; C: 28.38 ± 3.0) for both groups and, as such the difference was not statistically significant (K: $F_{1,31} = 0.770$, $p > 0.05$, partial $\eta^2 = .024$; C: $F_{1,31} = 0.871$, $p > 0.05$, partial $\eta^2 = .027$).

Cloud cover (%) was higher on non-singing days (K: 65.09 ± 35.37 ; C: 69.0 ± 33.44) than on singing days (K: 47.7 ± 40.91 ; C: 43.75 ± 39.84) for both groups but the difference was not statistically significant (K: $F_{1,31} = 1.534$, $p > 0.05$, partial $\eta^2 = .047$; C: $F_{1,31} = 3.789$, $p > 0.05$, partial $\eta^2 = .109$).

Wind levels (%) were very low across all days included in the analysis. The wind was slightly stronger on non-singing days (K: 3.48 ± 4.63 ; C: 3.33 ± 4.83) than on singing days (K: 1 ± 2.11 ; C: 1.67 ± 2.46) for both groups but, again the difference was not statistically significant (K: $F_{1,31} = 2.593$, $p > 0.05$, partial $\eta^2 = .077$; C: $F_{1,31} = 1.233$, $p > 0.05$, partial $\eta^2 = .038$).

3.5 Sleeping and Singing Tree Choice in *H. albibarbis*

Results of sleeping tree choice and singing tree choice are displayed in the charts below (Figure 3.6 – 3.12). *Shorea spp.* (n = 8), *Gonystylus bancanus* (n = 6), and *Litsea rufofusca* (n = 6) are the most commonly used sleeping tree species used by *H. albibarbis* in this study, with the most commonly used sleeping tree height being 21-25 meters (n = 11). A total 29 species were used for the gibbons during singing bouts over 37 days.

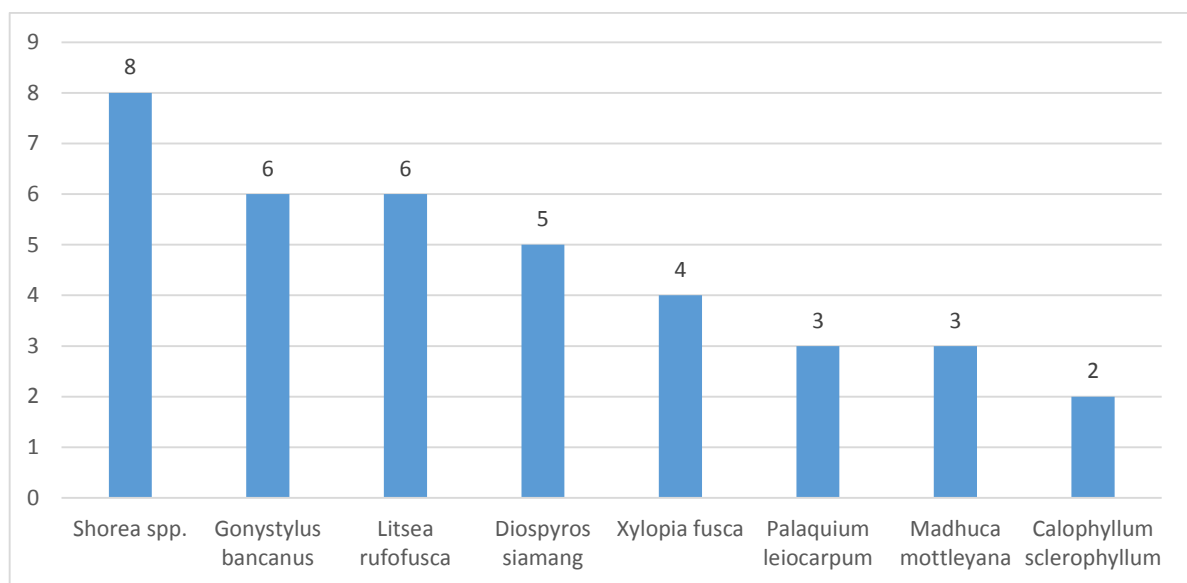


Figure 3.6: Bar chart showing the most commonly used sleeping trees for Karate and Group C combined.

Shorea spp. (n = 25), *Camposperma coriaceum* (n = 19), and *Neoscortechinia kingii* (n = 14) are the most commonly used singing tree species used by *H. albibarbis* in this study, with the most commonly used singing tree height being 16-20 meters (n = 80). The mean number of trees used per duet song bout is 3.94 ± 2.08 . See Appendix III A, III B, III C, and IV for a full list of sleeping and singing tree species.

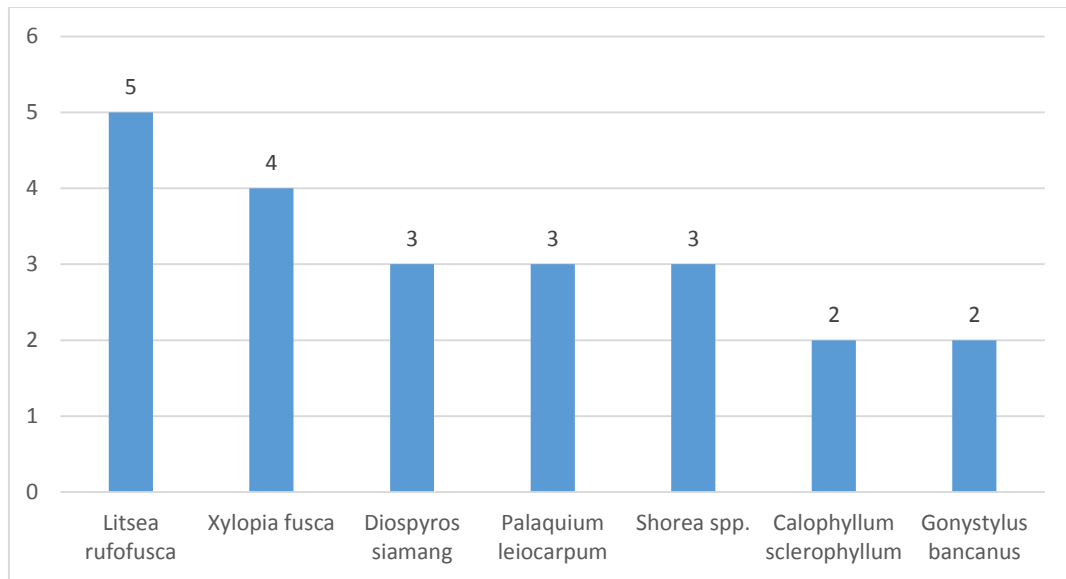


Figure 3.7: Bar chart showing the most commonly used sleeping trees for Karate only.
Frequency is plotted on the y-axis.

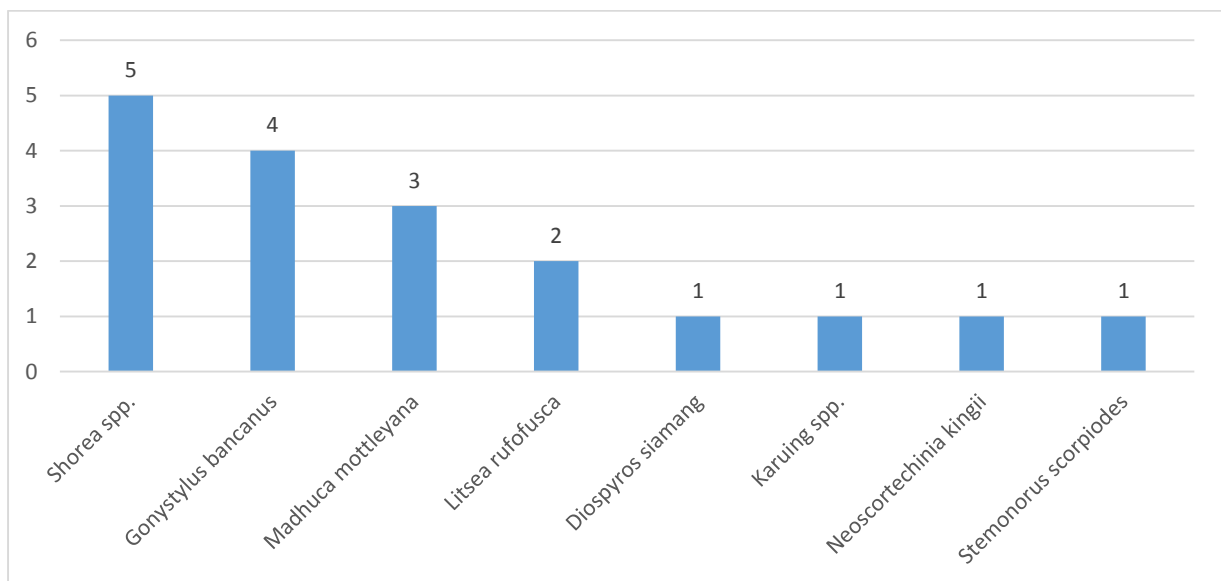


Figure 3.8: Bar chart showing the most commonly used sleeping trees for Group C only.
Frequency is plotted on the y-axis.

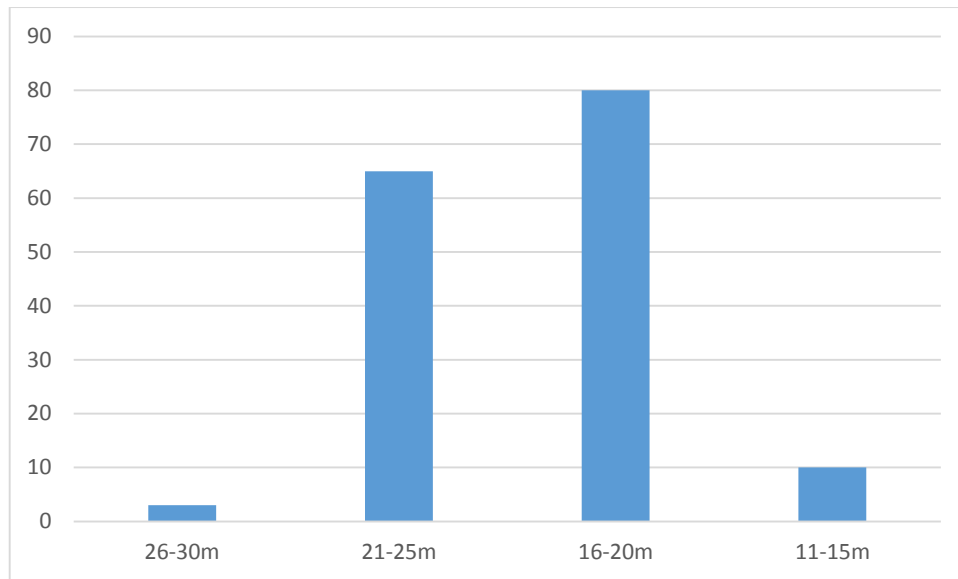


Figure 3.9: Bar chart showing the distribution of the recorded singing tree heights for both gibbon groups combined. Frequency is plotted on the y-axis.

Karate sung from a mean number of 4.04 ± 1.85 ‘singing trees’ per singing bout, using anywhere from 2 to 9 trees in a single bout ($n = 21$). Group C sung from a mean number of 4.06 ± 3.03 singing trees per singing bout, using anywhere from 2 to 13 trees ($n = 17$).

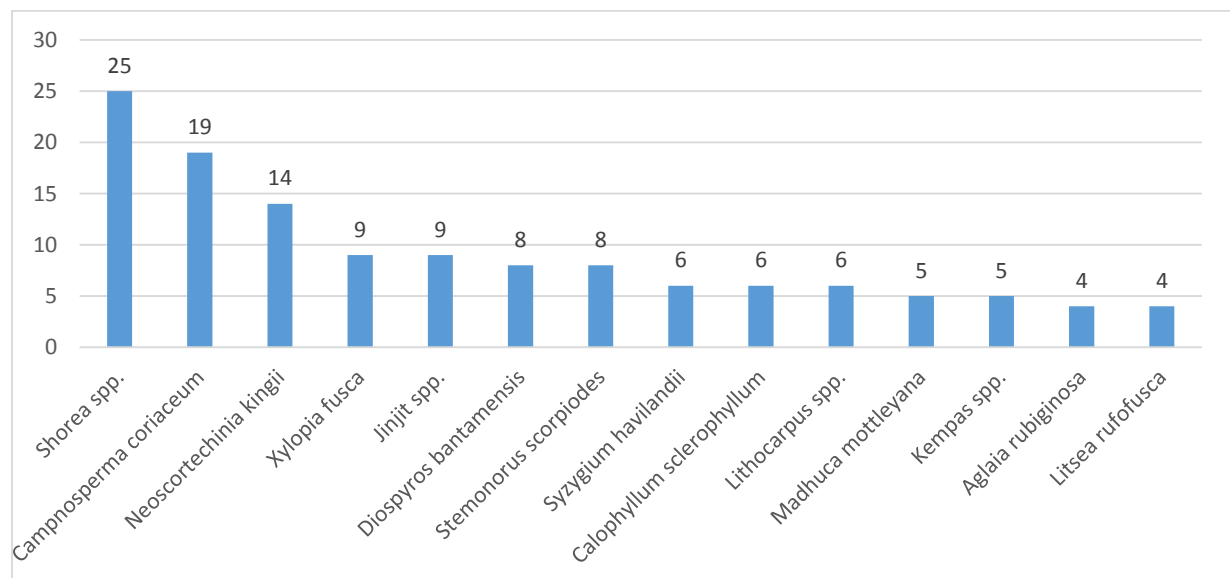


Figure 3.10: Bar chart showing the most commonly used singing trees for Karate and Group C combined. Frequency is plotted on the y-axis.

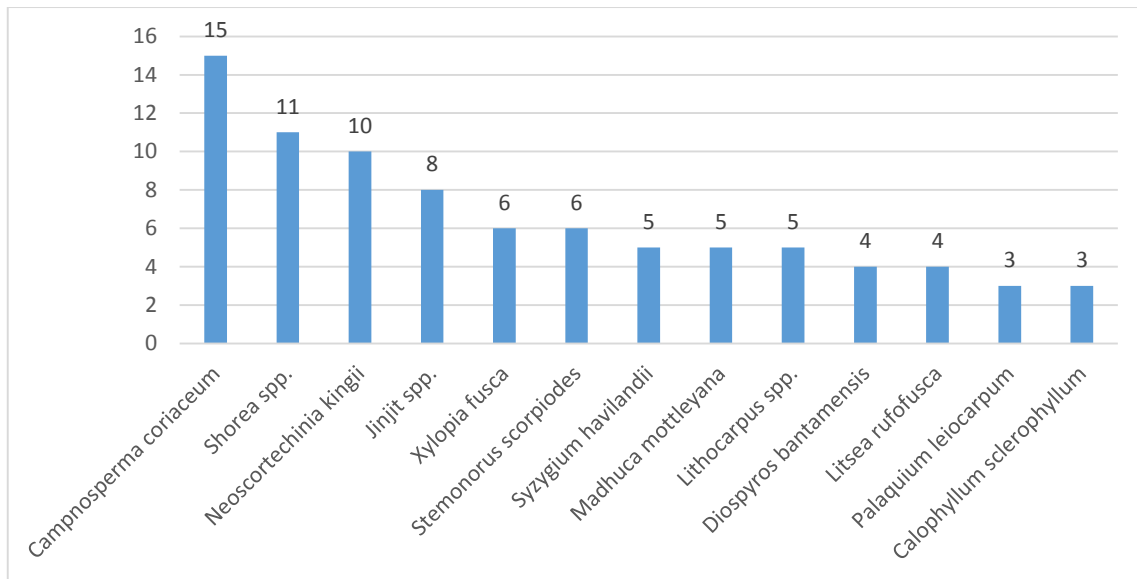


Figure 3.11: Bar chart showing the most commonly used singing trees for Karate only.
Frequency is plotted on the y-axis.

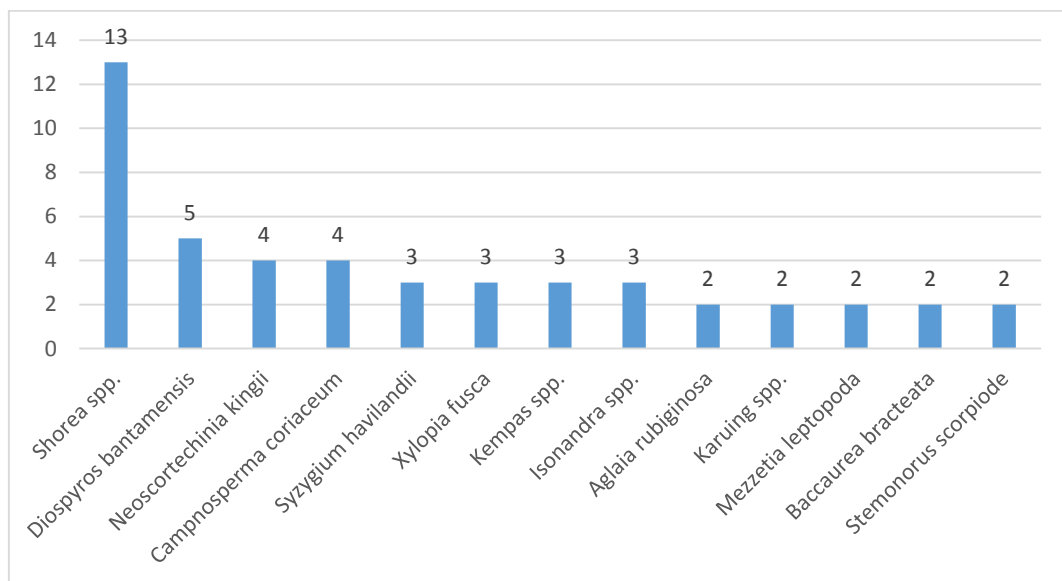


Figure 3.12: Bar chart showing the most commonly used singing trees for Group C only.
Frequency is plotted on the y-axis.

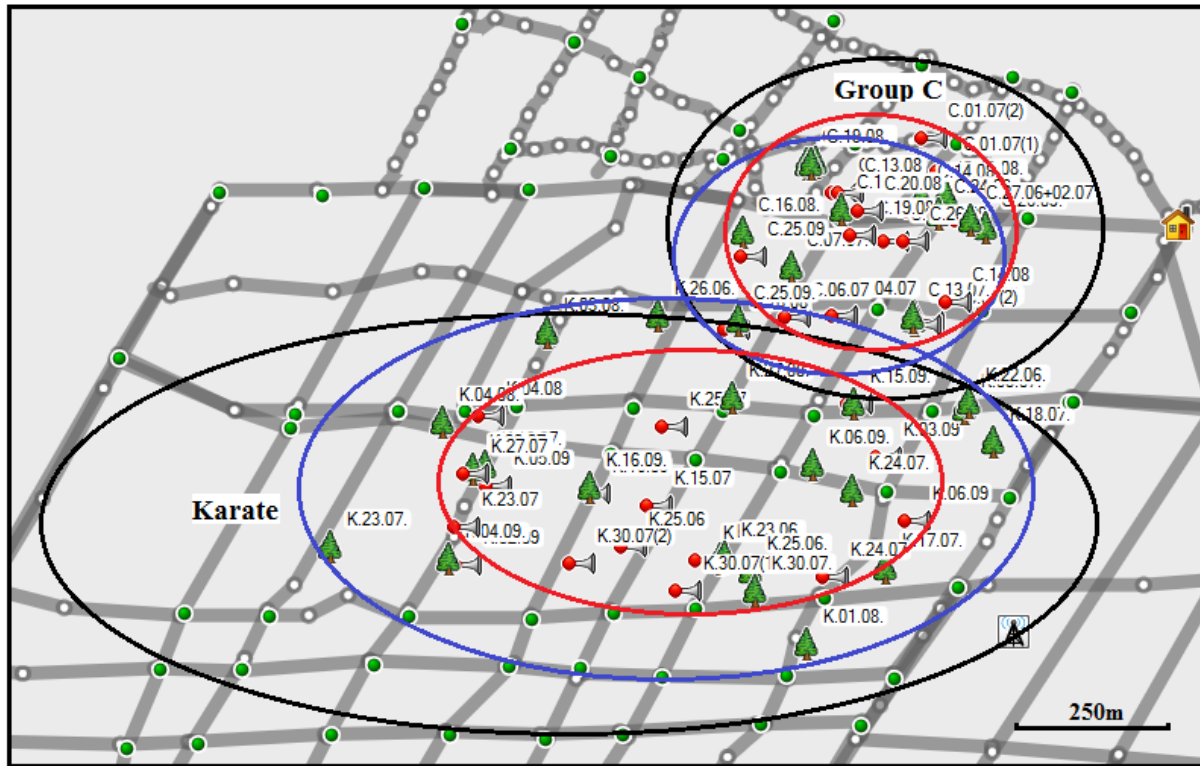


Figure 3.13: Map of singing tree and sleeping tree GPS points within the NLPSF grid system. Black lines mark the boundaries of Karate and Group C's home ranges. Red lines highlight the core areas in which the singing trees are focused. Blue lines highlight the core areas in which the sleeping trees are focused.

Only 5 of 16 (31.25%) of Karate's singing points and 4 of 15 (26.66%) of Group C's singing points were close enough to the edge of their respective home ranges for adjacent groups to potentially hear the duet song in its entirety (see Figure 3.14).

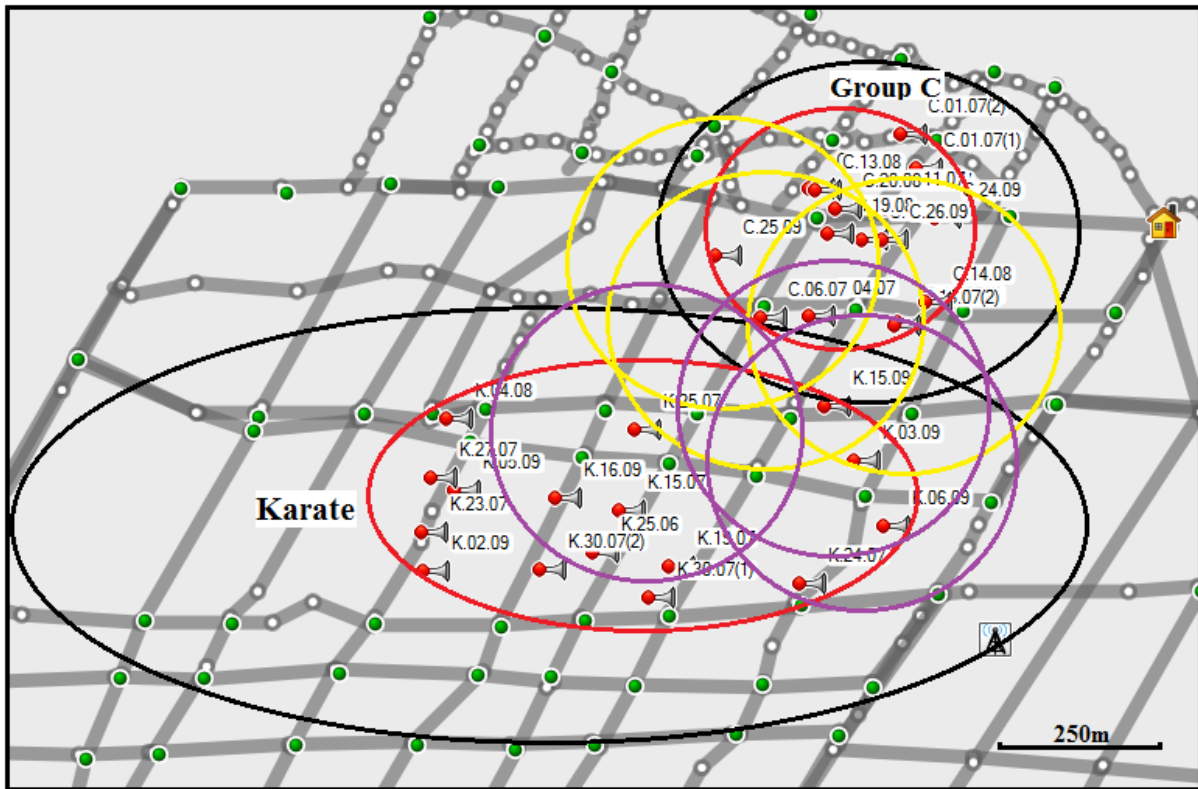


Figure 3.14: Map of singing tree GPS points within the NLPSF grid system. Black lines mark the boundaries of Karate's and Group C's home ranges. Red lines highlight the core areas in which the singing trees are focused. Purple circles show the broadcast range of Karate's duet song before loss of notes (radius: ~ 350 meters) around some of the outermost singing tree GPS points while the yellow circles denote the same for Group C.

CHAPTER IV: DISCUSSION

4.1 Inter- and Intra-Group Communication in *H. albibarbis*

4.1.1 Degradation of the Duet Song and Home Range Use

The question that this study is concerned with is not whether or not the duet will degrade over distance. The fact that sound will degrade over distance is a well-known physical phenomenon. The real questions of interest here are: the degree to which it degrades, whether certain elements of the duet are degrading earlier than others, and how does this relate to where the gibbons are singing from within their home ranges, i.e. what are adjacent groups hearing by the time the duet has travelled from singer to receiver and is what the function of the singing at both an intra- and inter-group level?

There was a significant difference for PC1, PC3, and PC4, but not for PC2, between the duet sequences recorded under Group C and those recorded at 350 m away. These results reflect the expected results from preliminary trials and spectrogram analyses, i.e. they reflect the significant loss of amplitude across all parts of the song, eventually leading to the degradation of entire notes, particularly in the FOP, the FTP and the MOP. The minimum frequency of the FOP and the FTP is higher at 350 m (FOP: 516.64 ± 36.27 Hz; FTP: 459.76 ± 40.29 Hz) than at 0 m (FOP: 507.8 ± 157.04 Hz; FTP: 413.46 ± 17.96 Hz) suggesting very low frequencies degrade earlier than others. The dominant frequency of the FOP, the FCP, and the MTP also appear to change significantly over distance with the most notable shift seen in the female climactic phrase. The dominant frequency of the FCP shifts from 1840.8 ± 69.54 Hz at 0 m to 876.45 ± 81.0 Hz at 350 m, suggesting that the highest frequencies are also highly susceptible to degradation.

There was a significant difference for PC1 but not for PC2, PC3, or PC4, between the duet sequences recorded under Karate and those recorded at 350 m away. These results also reflect the expected results from preliminary trials and spectrogram analyses. Karate's song appears to degrade in much the same way as Group C's in that there is significant loss of amplitude across all parts of the song, eventually leading to the degradation of entire notes. However, only one of the phrases, the FTP, appears to suffer a significant loss of notes (0 m: 6.0 ± 0.91 notes; 350 m: 3.65 ± 0.48 notes). The same narrowing of the frequency range of the song that

can be seen in Group C is present in Karate's song, with the lowest and highest frequencies becoming degraded and/or lost first.

There was a significant difference for PC1, PC2, and PC4, but not for PC3, between the duet sequences of Group C and those of Karate. There were several notable differences between the duet songs of Karate and Group C. Not all of these were explained by the PCA because the variables included in the analysis were more directed towards recognising degradation rather than inter-group differences but are nonetheless worthy of note. These include no. of FIP notes (K: 3.0 ± 0.0 ; C: 2.0 ± 0.0), no. of FCP notes (K: 4.0 ± 0.0 ; C: 3.0 ± 0.32), song dominant frequency (K: 1533.9 ± 41.65 Hz; C: 843.65 ± 69.51 Hz), and song maximum amplitude (K: 145.28 ± 1.27 dB; C: 135.07 ± 3.62 dB). The former two variables highlight very noticeable differences between the songs of the two groups and aided greatly in distinguishing between the two groups on occasions when both sung from the same general direction. The latter two differences imply a 'louder' and potentially further propagating duet song is sung by Karate. The 'louder' duet song sung by Karate may be as a result of a fourth singer (Brandon Lee) that Group C lacks or an older sub-adult in Karate that is 'hitting more notes' than the sub-adult in Group C. This contrast in degradation may have an influence on the home range size in these groups. Karate's louder duet may be allowing them to maintain control over their abnormally large home range. However, without more detailed data on fruit availability across several home ranges and data on the physical condition of the gibbons, it is difficult to imply whether this could actually be the case.

Given that both groups appear to singing from core areas of their respective home ranges for ~70-75% of the time, the duet song, in its entirety, is rarely heard beyond the boundaries of a group's home range. This is likely to be even truer for Karate because of their extensive home range size. This could mean that the gibbon groups may have to sing from strategic positions on certain days in order to effectively defend their territories, assuming that the song has a territorial function.

The average home range size in Sabangau is 50 ha (range 39-264 ha). However, this is based on only 8 groups, 6 of which are infrequently followed. Indeed, the two largest home ranges recorded are those of the two groups most frequently followed (Group C and Karate). This may be coincidence but it is more likely that the home ranges are larger than previously thought and can only be truly gauged with an increased number of follows for each group. Karate, however,

do seem to be an extreme example with a home range of ~264 ha, 195 ha larger than the next largest recorded home range (Group C; 69 ha), and there is evidence to suggest that they are still expanding this (pers. obs.). This may be due to a greater level of physical health or strength within this group, it may reflect a peak in a cycle aided by their current maximised group size (5-6 individuals), or may simply be that there is low fruit abundance in this area of the forest. However, further investigation is required before attempting to make any strong judgement on this. Whatever the reason, the scale of their home range is very impressive. Despite the large home range sizes in this species, there is a high level of group cohesion (with all members being together for ~85% of the day; Cheyne, 2010).

Based upon previous detailed maps generated using GPS data, territorial overlap within this species is ~15%. This is very low when compared to the only other territorial overlap data recorded for another gibbon species; 64% in *H. lar* inhabiting Khao Yai National Park in Thailand (Reichard and Sommer, 1997). This may be due to the much lower density of gibbons in Sabangau (2.6 gibbons/km² (Cheyne et al., 2007b; Hamard, 2008), compared to 5 gibbons/km² in Khao Yai (Brockelman et al., 1998)). This lower density, in turn, may reflect the low productivity environment found in Sabangau (Morrogh-Bernard et al., 2003; Page et al., 1999).

The larger territories and lower densities found here may also be contributing to the relatively low rate of inter-group encounters and thus inter-group aggression. Adult gibbons are generally highly tolerant of their partners with aggressive interactions between the mated pair being a rare event (Gittins and Raemaekers, 1980). Cheyne (2010) found that inter-group encounters only occurred on 4.55% of follows. This study suggests more than twice that number with inter-group encounters occurring on 10% of follows (5 out of 50 days). However this is based on a much smaller data set.

The implications of the findings regarding degradation of entire notes in the duet song at around 350 meters, combined with the data on how the gibbons are using their home ranges, can only be speculated about but there are several hypotheses that can be drawn from them:

- 1 - The gibbon duet song is firmly maintaining a defensive function as previously suggested by many previous studies (e.g. Mitani, 1985a; Raemaekers & Raemaekers, 1984; Cowlishaw, 1992). If the entire song can only be heard from within that groups home range then it may only be important for the entire song to be heard by 'invading' adjacent group, i.e. when a receiver ('invading' adjacent group member) hears the song of another group in its entirety,

they know that they are occupying and/or approaching an actively defended territory. Upon receiving this message, they can choose to continue forward or retreat. The degraded song, that preliminary tests show can be heard up to ~900 meters away, may simply serve as a positional indicator beyond 350 meters.

2 - The gibbon duet song has both a defensive and offensive function. When the song is sung from the core area of a group's home range, it serves a defensive function. This is usually the case. However, on the occasions when it sung from close to a home range boundary, thus penetrating one or more of the adjacent group's home ranges, it may signal intent to expand and/or invite a confrontation.

3 - Considering that organisational phrases seem to become degraded first, e.g. the MOP, the FOP, and the FTP (which may cue the MTP), there may be certain parts of the song that are purely intended for inter-group communication and certain parts that are purely intended for intra-group communication. The faster degrading organisational phrases may only be important for intra-group communication, with the adult male and adult female cueing each other up to accurately launch a solid duet sequence, allowing for the slower degrading parts to reach their intended target more efficiently each time. These slower degrading elements, e.g. the first few notes of the MOP and the FTP, the FIP, the FCP, and the MTP may be the only important elements for inter-group communication.

4.1.2 Communication in a Complex Heterogenous Environment

Much bioacoustics research finds its foundations in the Sender-Propagation-Receiver (SPR) model (Pijanowski et al., 2011). The SPR model describes the three proposed primary elements of information propagation: (1) the sender's morphological characteristics and the intent of its propagated signal, (2) the effect of the physical environment on that signal, and (3) how that signal is perceived and interpreted by its recipient (or receiver). The way in which an acoustic signal propagates is heavily dependent on the medium through which it propagates (e.g. air, water, etc.) and the nature of the physical environment present throughout that medium (e.g. trees in a forest that bend, reflect, and absorb sound waves). The ability of the receiver to hear and interpret an acoustic signal is just as important as the production and propagation that signal. This mostly relies on the auditory anatomy of the receiver and the cognitive ability of the receiver to decode that signal (Forrest, 1994). As such, vocalisations should also have an important role to play in species recognition. The species recognition hypothesis (part of the

‘recognition concept of species’; Patterson, 1985) proposes that variation in the structure of animal vocalisations among species have evolved to aid in differentiating between closely related species and ultimately reduce hybridization.

There are two complementary hypotheses to the SPR model: (1) the acoustic adaptation hypothesis (AAH) and (2) the morphological adaptation hypothesis (MAH). Testing the MAH is beyond the scope of this study. The AAH states; the sources of selection acting on animal vocalisations are derived from the acoustic properties of their habitats. Because certain sounds do not propagate as efficiently as others in a particular habitat, “selection should favour the use of sounds that give the greatest broadcast area for a given source sound pressure level” (Morton 1975). The hypothesis relies on the existence of “sound windows”, i.e. frequency channels in which signals are propagated most effectively (Morton, 1975; Waser & Brown, 1984). These “sound windows” change with habitat structure, height from the ground, and atmospheric composition. Animals that rely on vocalisations for long distance communication should then be adapted to a particular “window” depending on what type of habitat they communicate in and what particular part of that habitat they occupy.

Forest habitats present animals with a difficult, complex, heterogenous environment (that absorbs and reflects sound) in which to communicate (Wiley & Richards, 1978; Waser & Brown, 1986). Several studies concerning the acoustics of forest habitats have revealed what acoustic properties a sound (e.g. animal vocalisation) should have in order to maximise its propagation through said habitat. Marten & Marler (1977) found that height above ground level was the greatest source of excess attenuation of sound in forest habitats. This was suggested to be because of ground attenuation (due to the interaction of sound with the ground surface and the air turbulence and temperature gradients at the air-ground interface) and the differences in canopy structure/composition at different heights in the forest. *H. albibarbis* appear to have a strong preference for singing at higher positions in the canopy, particularly at the 16-20 m height category (n = 26). This may mean that the 16-20 m canopy height is the most efficient height to sing from for the transmission of gibbon song. However, it could also be a compromise between being high enough to reduce the risk of predation during a singing bout while not being so high as to have their physical display compromised by the weaker vegetation structure in the highest parts of the canopy.

Reverberation is most severe outside of the 2-7 kHz and in heterogenous environments. It is accompanied with prominent echoes below 2 kHz (Richards & Wiley, 1980, Wiley & Richards, 1982). However, these reverberations can become advantageous with the use of narrow frequency ranges as narrow frequency bandwidth notes are increased in volume and length by reverberations in densely vegetated habitats. Vocal signals above the level of severe ground attenuation in forests should be of a low frequency (< 3 kHz), have a narrow frequency range, and be pure tones (i.e. tones with a sinusoidal waveform like whistles) for effective long distance signal transmission (LDST) in a forest (Morton, 1975; Marten & Marler, 1977). The duet song *H. albibarbis* seems to be well adapted for LDST with the duet song being sung within a narrow frequency range (~ 400 -2000 Hz) with low frequency pure tone notes at a height well above the level of excess ground attenuation.

4.2 Factors Affecting Presence or Absence of the Gibbon Duet

Of the 33 days included in the analysis, Karate only sung on 10 of those days while Group C sang on 12. The difference between singing and non-singing days was not statistically significant for either group on any variable with the exception of afternoon rainfall which was shown to be significantly higher on singing days than non-singing days for Karate. It is difficult to speculate about what effect afternoon rainfall could have on morning singing bouts. It could be coincidence or could mean that the gibbons may be able to anticipate wet conditions due to variations in air pressure and/or humidity levels. Subsequently, they may sing in anticipation of prolonged wet conditions that are unsuitable for singing.

Minimum and maximum temperature show almost no variation between singing and non-singing days and, as such, probably do not require much further investigation. The remaining variables, i.e. number of adjacent groups singing, morning rainfall, total rainfall, cloud cover, wind levels, did show variations between singing and non-singing days but the difference was not significant. Empirical evidence did suggest that there was a significant difference between singing and non-singing days for these variables but, because only days when all of the measurements were taken were included in this analysis, the sample size was quite small ($n = 33$). Based on empirical evidence and the results of previous studies at the site that did show that there was a significant difference for some of these variables (e.g. Cheyne, 2008a), these

variables do merit further investigation with a larger sample size and over a longer period of time.

4.3 Sleeping and Singing Tree Choice in *H. albibarbis*

The results of this study suggest that *H. albibarbis* do favour certain tree species for sleeping and singing with many being used for both. *Shorea spp.*, *Gonystylus bancanus*, *Litsea rufofusca*, and *Diospyros siamang* are the most commonly used sleeping tree species used by *H. albibarbis* in this study, with the most commonly used sleeping tree height being 21-25 meters. The gibbons had a number of preferred sleeping trees that they returned to on fairly regular basis (pers. obs.). *Shorea spp.*, *Campnosperma coriaceum*, *Neoscortechinia kingii*, *Xylopius fusca*, and *Diospyros bantamensis* are the most common singing tree species used by *H. albibarbis* in this study, with the most commonly used singing tree height being 16-20 meters.

The high number of singing trees used per bout (3.94 ± 2.08) reflects the active physical display that accompanies a singing bout. This display may have a role in the pairbonding of the mated pair. Other groups are not close enough to see this display so it is very unlikely that it has a role in inter-group communication. The distance between the mated pair during a singing bout was predominantly in the 6-10 m range but this varies greatly from day to day and even during a bout but the gibbons were always within at least 30 m of each other. Again, this reflects the active nature of the physical display and highlights the potential role of the song in maintaining the pairbond.

Several species were commonly used as both singing and sleeping trees, most notably *Shorea spp.* and *Xylopius fusca*. Cheyne et al. (2013) suggest that gibbon sleeping trees are most likely selected due their stability and availability of predator access routes. The same could be assumed for singing trees. A singing bout would certainly make their location known to any predators in the area and the increased noise levels could make it more difficult to notice an approaching predator. Stability is a concern during sleep as a gibbon can sometimes have to endure very wet and windy conditions during the night. Given that *H. albibarbis* partake in a very active physical display during singing bouts, stability could also be a concern when considering singing trees. This could explain why some of these larger tree species are used for

both sleeping and singing. Several of the most common sleeping and singing trees are also important feeding trees e.g. *Diospyros bantamensis*, *Stemonoros scorpiodes*, *Camptosperma coriaceum*, and *Isonandra spp.*.

The male solo song, which has not been intensively investigated in this study, likely has a very important role in the nature of the duet song. Empirical evidence suggests that the male solo song is sung before the duet song and is sung at relatively large distances away from the rest of the group (~ 50-100 meters). These songs also appears to be sung more frequently, and for longer, than the duet song. Male solo songs usually take place in or near the sleeping area, many of which are quite close to the edge of the gibbon's home ranges (see Figure 3.13). In addition, they appear to encourage other males from neighbouring groups to sing very frequently. Therefore, it may well be the case that the purpose of the male solo song is to gather information on the position, status, and/or intent of neighbouring groups. Based on what the male has learned during his solo bout and/or the solo bouts of other males, the male may assess the threat to his family group or partner and subsequently decide whether or not to initiate a duet singing bout. However, this is purely speculation and, as such, requires further investigation.

4.4 Shortfalls of Primate Bioacoustics and Recommendations for Future Research

4.4.1 Background to Bioacoustics

Bioacoustics is the study of how animals use sound(s) to communicate (Stap, 2006). When implemented properly, bioacoustics is a perfect marriage of the fields of biology and acoustics. A skilled bioacoustician should have a deep understanding of both biology and acoustical physics.

The earliest known instance of animal vocalisations being recorded dates back to 1889 when Ludwig Koch recorded a captive Indian Shama (*Copsychus malabarius*) using an Edison wax cylinder (Popper & Dooling, 2002). However, the first researcher to actually delve into the field of bioacoustics, i.e. the first researcher to record animal sound for the purpose of an experiment, was Richard Garner in 1890 (Garner, 1892). Garner used Edison's "speaking machine" to record capuchin and rhesus monkey vocalisations. Garner used these recordings to conduct playback experiments with conspecifics housed in Washington Zoo and New York Zoo to investigate primate communication and cognition. However, as a consistent framework for ethology, within which to work, had not yet been developed, Garner's work was largely ignored and mostly forgotten.

Bioacoustics research in the twentieth century was championed by Peter Marler, who made the first great strides in both primate and avian bioacoustics, publishing influential works such as "Characteristics of some Animal Calls" (Marler, 1955) and "Vocalizations of Wild Chimpanzees" (Marler, 1968) amongst others. However, it was not until Struhsaker's (1967) work on the vocal behaviour of vervet monkeys (*Chlorocebus pygerythrus*), and his findings concerning complex referential signalling, that a certain sense of excitement surrounded the field of primate bioacoustics, forcing other scientists (e.g. Seyfarth et al., 1980a; 1980b) to recognise its potential in furthering the field of cognitive research and primatology in general.

Bioacoustics has flourished in recent decades, mainly a result of two key inventions from the middle of the twentieth century: the tape recorder and the audiospectrograph or sonograph (Stap, 2006). Unlike other disciplines in primatology such as ethology, which have greatly benefitted in terms of efficiency with advances in technology, bioacoustics is intricately linked

with technological advancement. This statement is true to the extent that it is only in the past two decades that bioacoustics, with the introduction of digitilised recording and advanced sound analysis software, has become a truly modern and accurate science in itself.

The speed at which techniques in bioacoustics have advanced has left many previous studies outdated and led to much confusion in the literature about the most scientifically sound methods to use when recording animal sounds. What's more, the vast majority of studies do not document why they used the techniques they did which has led to it becoming a rather stagnant discipline within primatology, a discipline in which the same technical mistakes are made time after time. It would also appear that these mistakes are going largely unnoticed because those who review these papers are most likely biologists and do not have the technical ability or knowledge of acoustical physics to fully recognise these mistakes. There is only a single paper that has gone some way to resolve this issue, i.e. Fischer et al. (2013). In an attempt to be part of the solution rather than part of the problem, an in depth discussion on appropriate techniques and equipment used in the field of primate bioacoustics will follow.

4.4.2 Initial Planning

The first question one should ask themselves before conducting a real-time study of primate vocalisations is: are the study animals sufficiently habituated to allow for such recordings? More often than not, high quality recordings rely heavily on your proximity to the animal. If the animals are not sufficiently habituated, close proximity recordings are almost an impossibility. The next important consideration is whether or not there are enough habituated study subjects in your study area and whether you have enough time in the field to make at least the minimum required recordings to answer your research question in a statistically sound fashion. See Fischer et al. (2013) for further information on commonly used statistical tests in primate bioacoustics.

4.4.3 Equipment

4.4.3.1 Digital Recorder

When purchasing a digital audio recorder, there are five key specifications to consider, sample rate and bit depth, recording format, gain settings, storage device, and input (i.e. what external devices can be connected to the device, e.g. microphones which will be discussed in the next section). Some high quality, yet affordable handheld digital audio recorders include: the Sony PCM-M10 pro-grade audio recorder, the Zoom H4n, the Olympus LS-100 Linear PCM digital recorder, and the Tascam DR07 MkII Digital Audio Recorder.

Sampling Rate, Bit Depth, and Recording File Format

Digital acoustic recorders process sound waves detected by microphones, converting analogue signal to digital signal and storing information about the timing and intensity (or amplitude) of the sounds (Smith, 2003). The sound is then reconstructed as the frequency distribution of signal intensity over time. Amplitude is given in decibels (dB), although digital audio recorders store amplitude in decibels full scale (dBFS) with the peak value set at 0.

Most modern digital recorders facilitate recording at several different sampling rates and bit depths. Sampling rate is the rate at which samples of an analogue signal are taken when being converted into digital signal. As a general rule, the more sampling points per unit time, the more accurate the representation of the analogue signal, the higher the temporal resolution, and, arguably, the better the quality of the recording.

However, it is not as simple as to say; the higher the sampling rate, the higher the quality of the recording. The sampling rate must be carefully tailored to the sound that is being recorded. The sampling rate chosen is largely governed by the Nyquist theorem. Adhering to the Nyquist theorem means that the sampling rate chosen should be at least twice the frequency of the highest frequency in the sound (the Nyquist frequency) (Pijanowski, 2011). If the recording contains sound above the Nyquist frequency, it can lead to “aliasing.” Aliasing manifests itself as a wave pattern where two waves travel in different directions, resulting in an inaccurate

representation of the sound being recorded at certain frequencies (Scholte et al., 2005). However, if one uses a sampling rate that is higher than is required, there will be a trade-off between sampling frequency and frequency resolution in the spectral analysis. A frequently given example is that of the commercial compact disc (CD) which uses a sampling frequency of 44.1 kHz. This sampling rate is tailored to the spectrum of human hearing (20 Hz to 20 kHz).

The commercial CD also provides a good example for appropriate use of the file format in which recordings should be made. Modern CDs are generally recorded in Windows Media Audio (WMA) format. WMA is a compressed file format which delivers relatively high quality (at least when compared to the likes of MP3 format). The file is compressed by removing audio data that cannot be heard by the human ear. This makes perfect sense as CDs are tailored for human listeners. The vocalisations of wild animals are presumably tailored for conspecifics. The auditory spectrum of wild animals can vary greatly from species to species and can be extremely different to that of a human. As a result of this, it would be inaccurate to record vocalisations in a file format tailored specifically for the human ear. All recordings of animals should be taken in Pulse-Code Modulation (PCM) format (which is stored as a .WAV file in most digital storage systems). PCM files are completely uncompressed which gives a more accurate representation of audio spectrum within which an animal calls. Much of the audio spectrum captured in PCM recordings may not be audible to the human ear but a spectrogram generated from a PCM file provides a true representation of the sound in question.

Another important consideration when recording animal vocalisations is bit depth. Bit depth refers to the amount of bits (binary digits; a basic unit of digital information) you have to capture audio. Let's say that I have recorded a sound at a sampling rate of 44.1 kHz and a bit depth of 16-bit. A sampling rate of 44.1 kHz means that the audio being recorded is sampled 44,100 times per second. Try to envisage each of the 44,100 samples as a point in the audio frozen in time. At each point in time, the audio has been captured at a certain bit depth. This 'depth' can be thought of as a series of levels. A bit depth of 16-bit allows you to capture a single point in time on 65,536 levels. With every bit of greater resolution, the number of levels doubles. If we record in 24-bit resolution, we will have 16,777,216 levels. Essentially, bit depth corresponds to the resolution (and arguably, quality) of each sample (see Figure 4.1). Variations in bit depth can influence the signal-to-noise ratio (SNR) and dynamic range within an audio recording. Generally speaking, recordings made at a quality of 16-bit are of a high enough quality for almost all acoustic analyses but if storage space is not an issue, 24-bit is recommended.

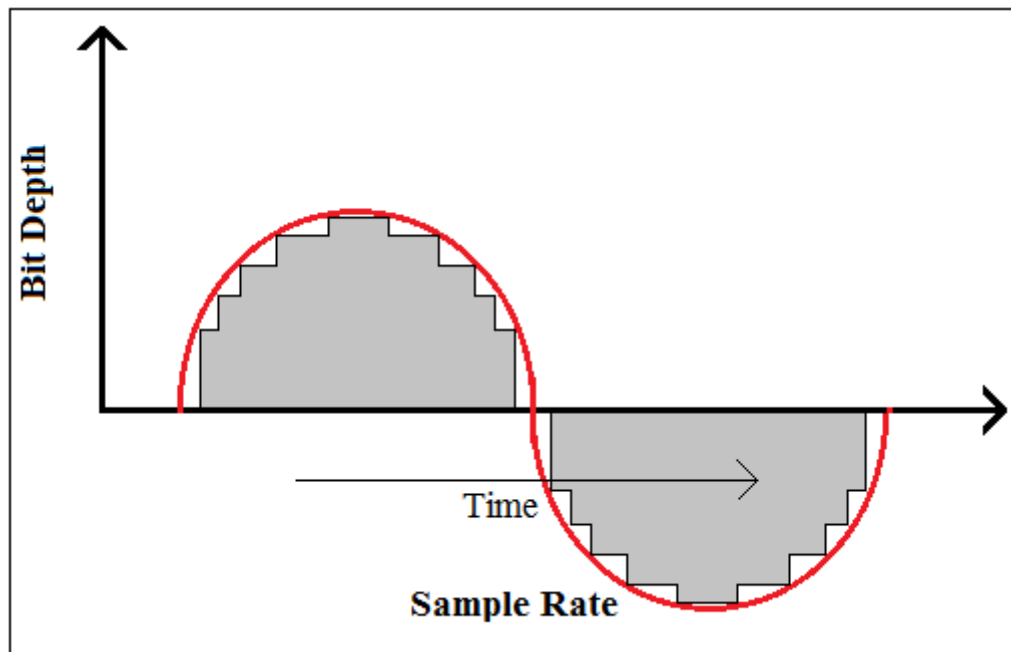


Figure 4.1: Diagram showing relationship between bit depth and sampling rate over time.

In summary, the minimum requirements for high quality recordings in the field is a digital recorder that can record with a sampling rate of 44.1 kHz, a bit depth of 16-bit, and in PCM file format. Sampling rate should be altered depending on the species, and in cases concerning animals communicating in the infra- (less than 20 Hz) and/or ultra- (greater than 20 kHz) sound acoustic spectrum, should be altered quite dramatically.

Gain

Gain is a measure of the ability of an amplifier to increase the amplitude of a signal from the input to the output, by increasing the energy of the signal that is being converted from some power supply (Zoom™ technical staff, pers. comm.). On a digital recorder, gain is usually adjustable via a dial or switch (commonly on a 0-10 scale). By adjusting the level of gain on a digital recorder, you adjust the amount of sound being ‘picked up’, i.e. increasing the gain increases the volume of the audio being recorded. The gain level that is selected is subjective and depends on factors like the volume of the sound at its source and the distance from which you record it. Thus, gain settings are most likely only chosen in the very early stages of trialling

the recording equipment whilst in the field and not prior to arrival at a field site. Modern digital recorders will generally display a level meter showing the input level from both the left (L) and right (R) stereo track on the LCD display screen. This level meter is on a scale of -48 dB (most quiet) to 0 dB (most loud). Optimal recordings should level out at about -6 dB at their loudest points. Under no circumstances should the gain settings be set high enough for the sound level meter to hit 0 dB (termed 'overloading') as this results in heavy distortion within an audio file.

Storage Device

The most commonly used and convenient storage device used in modern digital audio recorders is the SD (Secure Digital) card. SD cards are small removable storage devices which most modern portable electronic devices use to store data. The best type of SD card to use for field recordings are Speed Class 10 SDHC (Secure Digital High-Capacity) cards. Class 10's transfer data at the high rate of 10 MB/second. This allows for many short recordings to be made in quick succession without large loading periods between recordings which can result in data loss. The amount of storage required obviously depends on what research questions are being addressed and the frequency and duration with which an animal vocalises in a day. Assuming that recordings are being uploaded from the SD card to a main storage device each day, 32 GB of storage should be more than enough for any study.

4.4.3.2 Microphone

Whilst almost all modern digital audio recorders come fitted with an internal microphone, the use of an external microphone is strongly recommended and should be standard practice in bioacoustics. The type of microphone used for a bioacoustics study is entirely dependent of the research question and the type of vocalisations being recorded. Modern microphones are incredibly complicated pieces of equipment and there are many technical specifications that make a microphone work like it does. However, for the majority who do not understand this technical jargon, there are four key specifications to look out for when purchasing a microphone: directionality, frequency response, sensitivity, and impedance.

Directionality

A summary of the different directionalities available are shown in Figure 4.2. The recommended directionality for recording animal vocalisations in a rainforest environment is supercardioid or shotgun. Supercardioid and shotgun microphones intensely focus on the sound source at which they are pointed and minimise the audio input from other sound sources in the surrounding area, a very useful feature in a noisy rainforest filled with chorusing birds and chirping, clicking insects.

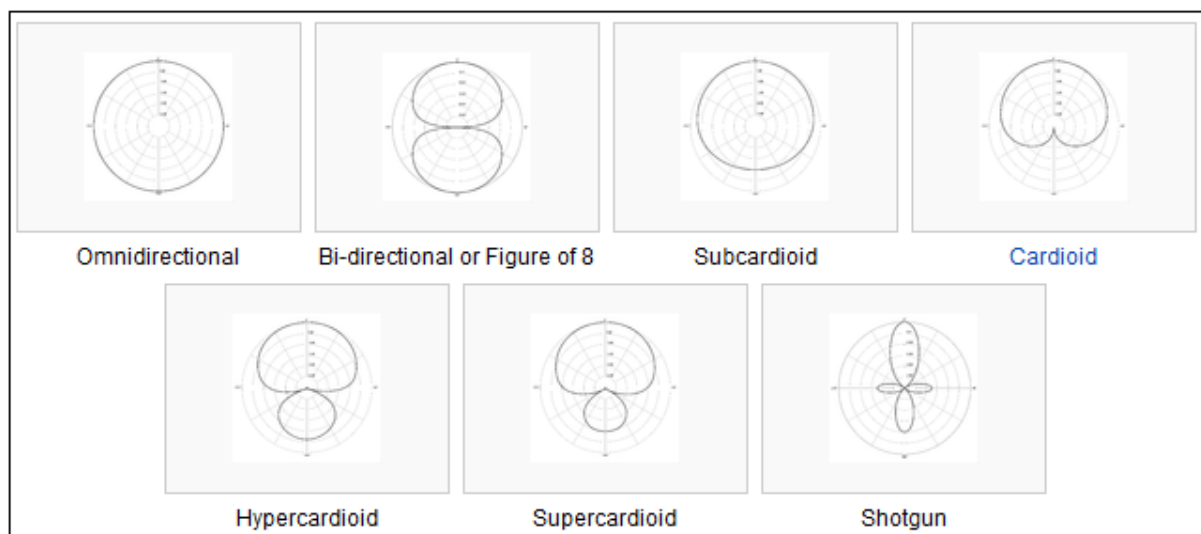


Figure 4.2: Illustration of various microphone directionalities. Image adapted from image by Galak47 sourced @ <http://commons.wikimedia.org>

Frequency response

Frequency response is the way in which an audio device responds to different frequencies of sound (Shelswell, 1995). A perfect microphone would have a perfectly flat frequency response right across the audio spectrum. In the history of audio, this has never been achieved, but high quality modern microphones are extremely close. The vast majority of modern microphones are designed with a low-frequency ‘roll off’, meaning they are less sensitive to frequencies below about 50Hz, reducing low-frequency vibrations and interference e.g. hand movements, breathing, and other such low-frequency output signals. Some microphones are often designed to accentuate specific parts of the audio spectrum in order to create a flattering sound (Utz, 2003). The benefits of a more flat frequency response are obvious: the flatter the frequency response, the more accurate the representation of a sound being recorded.

Most microphone manufacturers (e.g. Sennheiser, Rode, etc.) will feature a frequency response chart with a frequency response curve (see Figure 4.3 for an example) for a given microphone model in the specifications section of their website. Any model that has a heavily irregular frequency curve or does not have a frequency response curve featured in its specification details is not worth buying. The frequency response curve should also display the frequency range of the microphone, although this should also be given as a separate specification.

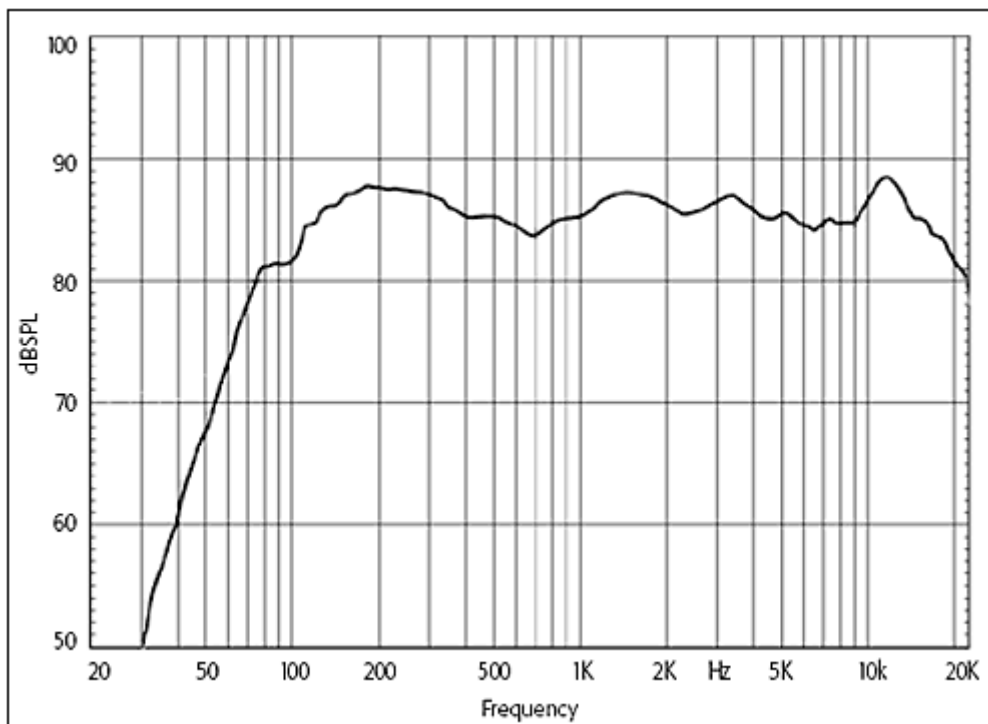


Figure 4.3: Frequency response chart showing a typical frequency response curve with frequency plotted on the x-axis, and level in dB plotted on the y-axis. Image sourced @ www.qcsaudio.com

Sensitivity

Sensitivity is measure the microphone's ability to convert acoustic input to electric voltage, i.e. sensitivity controls what voltage a microphone will produce at a certain sound pressure level (Utz, 2003). A high sensitivity microphone will give a high voltage output and, thus, does not need as much amplification (gain) as a lower sensitivity microphone. High sensitivity

microphones are prone to overloading the input when recording louder sound (or simply from being close to a sound source), producing clipping and distortion. However, a higher sensitivity may be desirable in far-field applications, such as recording vocalisations from a specified distance or recording animals from which you must keep your distance, as sound can become heavily attenuated as the distance from the microphone to the sound source increases. The level of an acoustic signal is decreased by 6 dB (one-half) for each time the distance from the sound source is doubled (Lewis, 2012). On the other hand, a microphone with low sensitivity generally requires you to increase the gain on the digital recorder when recording quiet sounds which can often add unwanted noise to the mix.

The sensitivity of a microphone is generally measured with a 1 kHz sine wave at a 94 dB sound pressure level (SPL). Using that input stimulus as a standard, the magnitude of the analogue or digital output signal from the microphone is a measure of its sensitivity. Sensitivity of a digital microphone depends on a single design parameter: maximum acoustic input. Sensitivity is essentially the difference between this maximum acoustic signal and the 94 dB SPL reference. For example, if a digital microphone's maximum SPL is 120 dB (a very common SPL in modern digital mics, then its sensitivity will be -26 dBFS (94 dB - 120 dB).

In this way, when looking at the specifications of a digital microphone, sensitivity should always be given as a minus value. A figure of -70 dBV to -50 dBV would suggest a low sensitivity mic, a figure of -50 dBV to -35 dBV would suggest a medium sensitivity mic, and a figure of -35 dBV to -15 dBV would suggest a high sensitivity mic. Most modern digital microphones have both a high and low sensitivity setting.

Other important parameters to consider, which are related to sensitivity (and sometimes better indicators of microphone quality than sensitivity itself) are signal-to-noise ratio (SNR; the difference between the 94 dB SPL reference and the noise level), the microphone's dynamic range (the difference between the largest (maximum SPL) and smallest (noise floor) signals that it can accurately reproduce), total harmonic distortion, and power supply rejection (Lewis, 2012). The relationship between all of these parameters is displayed in Figure 4.4.

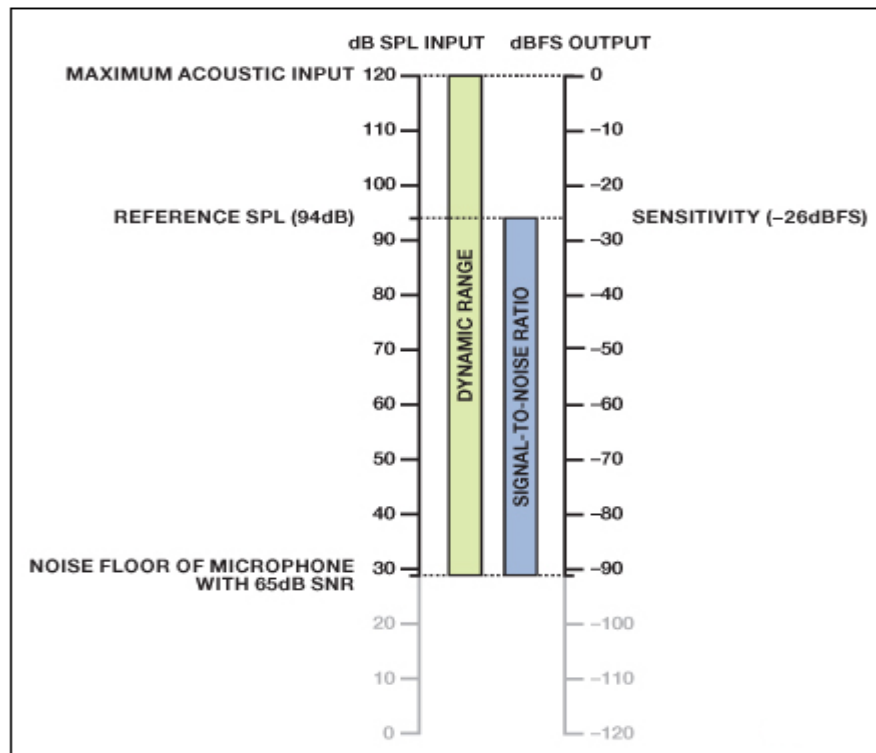


Figure 4.4: Diagram showing a -26 dBFS sensitivity, 65 dB SNR microphone. Image from Lewis (2012)

Thus, a high sensitivity microphone is not necessarily better than a low sensitivity microphone. Sensitivity is less an indicator of quality and more an indicator of how the microphone will behave given a certain sound and/or sound source. The key is to get a microphone with a good balance between, sensitivity, noise level, clipping point, and distortion. This will determine whether a microphone is suited to a particular application and as always, the research question and type of call that is being recorded are the key factors in determining the most suitable mic for the job.

Impedance

Impedance is a measures of the amount of ‘opposition’ a microphone has to an audio signal. It is the combined effect of capacitance, inductance, and resistance on a signal (Utz, 2003). The letter Z is a commonly used shorthand for the word impedance, e.g. High-Z or Low-Z. Impedance is measured in ohms which is represented with the Greek symbol Omega (Ω). Generally speaking, a low impedance mic is less than 600Ω , a medium impedance mic is 600Ω

- $10,000\Omega$, and a high impedance mic is greater than $10,000\Omega$. A low impedance mic is better than a high impedance mic. High impedance microphones regularly suffer a loss of high frequencies the longer the signal has to travel, i.e. the longer the sound recorder to mic cable is (Barnard & Rao, 2004). While impedance is not usually considered a key microphone specification, it can be strong indicator of a microphone's overall quality and, thus, should not be so readily overlooked.

4.5 Potential Shortfalls of this Study

Although the equipment in this study has been standardised to the highest level possible with the resources at hand, the fact still remains that the digital recorders are different models and, as such, they will vary slightly. A study like this should never be conducted without completely standardised equipment. Also, it is almost impossible to account for vegetation density and the vocalisations of other animals in the forest between different recordings on different days, i.e. almost every recording is taken from a different position and at a different time on each day of data collection. As a result, the calculation of an absolute rate of degradation for the gibbon duet song in this forest, is not practical on this scale.

The microphone used in this study was a very low sensitivity microphone. Because of this, the gain levels on the digital recorders had to be set very high in order to obtain an accurate representation of the gibbon song. This led to higher levels of interference on the recordings than would have been preferred and sometime made spectrographic analysis quite difficult.

The 350 m distance from which the gibbon song was recorded was established by extensive trialling and the confidence levels of using this distance are high. However, to ensure that this was in fact the correct distance to record from, at least one more recording point would have been preferred e.g. the last distance at which the song could be heard in its entirety (~ 300 m). This was impossible to include in this study due the equipment and manpower restrictions.

The technique used in this study for coordinating and maintaining the distance between the researcher recording under the gibbons and the researcher recording from a distance of 350 m was the regular sending of GPS points via SMS. As phone signal was very poor in this forest (and entirely absent at many other research sites around the world), SMS communication was an extremely inconvenient and often ineffective method of communication. However, it was the only remaining option after it was discovered that the radios housed on-site had a range of less than 200 meters.

4.6 Potential Implications for Primate Conservation

The focal species in this study is listed as Endangered on the *IUCN Red List of Threatened Species* (2008) on the basis of major, unceasing threats to its habitat and its removal from the forest for the pet trade, despite its classification in the CITES Appendix I (Geissmann, 2007). Peat-swamp forests are of paramount importance in the conservation of this species, being home to the largest population of *H. albibarbis* in the world (Cheyne et al., 2007). The more we can learn about how this species utilises its peat-swamp forest habitat, the more effective conservation management plans can be made to protect them.

This species of gibbons lives sympatrically with ~ 6 other primate species including the largest known wild population of the critically endangered orangutan (*Pongo*). It has been suggested that gibbons may be one of the most effective seed dispersers in Asian forests (McConkey & Chivers, 2007). The loss of this gibbon species would mostly likely have a detrimental effect on the forest ecosystem and thus, a detrimental effect on the other primate species also. Any effort to conserve this gibbon species habitat is also indirectly helping to conserve the other native primate species.

As there is evidence to suggest that gibbon singing behaviour has functions in territorial defence, mate defence, strengthening the pairbond, as a ranging mechanism, reproductive behaviour, social behaviour, distinguishing between individuals, and distinguishing between species, studies like this one could potentially have huge implications in both how they are housed in captivity and in assessing what effects deforestation may have on their ranging behaviour and reproductive success. Gibbons housed in captive settings are known to vocalise far more frequently than those living in the wild (Dr. Susan M. Cheyne, pers. comm.). The findings of this study suggest that it is predominantly ‘invading’ adjacent groups that hear the duet song in its entirety. Captive gibbons housed in close proximity to other groups hear the entire song of neighbouring groups on a far more regular basis. This may be stimulating them to sing (in defence) more frequently and potentially lead to additional and unnecessary stress.

The tree species identified as common sleeping and singing trees in this study will aid in identifying important tree species for ensuring natural behavior in this species and potentially aid in future habitat management plans concerning this species.

CHAPTER V: CONCLUSIONS

5.1 Specific Conclusions

The findings of this study suggest that inter- and intra-group communication may be much more complex than previously thought. It can be said with some confidence that 350 m is the distance at which the duet song of *H.albibarbis* begins to become structurally compromised. This finding, combined with the apparent preference of the two focal groups in this study for singing from core areas within their respective home ranges, means that several compelling hypotheses can be presented but no concrete conclusions can be drawn:

1 - The gibbon duet song may have a purely defensive function as previously suggested by many studies. The broadcast range of the entire song does not often reach beyond the edge of a group's home range which may mean that is only important for the entire song to be heard by 'invading' adjacent groups. The 'invaders' may then know that they are occupying and/or approaching an actively defended territory and act accordingly.

2 - The gibbon duet song has both a defensive and offensive function. On the occasions when it sung from close to a home range boundary, thus penetrating one or more of the adjacent group's home ranges, it may signal intent to expand their territory and/or invite a confrontation.

3 - Certain parts of the song are purely intended for inter-group communication and certain parts are purely intended for intra-group communication. The faster degrading organisational phrases may only be important for intra-group communication, assisting the mated pair to coordinate the further reaching parts of the song. These slower degrading elements, may be the only important elements for inter-group communication.

The duet song of this species of gibbon is highly adapted to long distance sound transmission in a dense forest and is a wonderful example in support of Morton's (1975) acoustic adaptation hypothesis.

The data collected during this study suggests that weather conditions and the number of neighbouring groups singing do not have a significant effect on the likelihood of either of the

focal groups to sing. However, this was based on an extremely small sample size in which there was not much variation in weather conditions.

H. albibarbis appear to show a strong preference for certain species of trees in which to sleep and from which to sing, with species like *Shorea spp.*, *Xylopia fusca*, and *Campnosperma coriaceum* being particularly important. This may aid in targeting key tree species to conserve in future habitat management plans that may concern this species.

5.2 Recommendations for Future Research

Future studies concerning vocalisation degradation should incorporate more groups and/or individuals, especially when dealing with territorial animals. The use of just two groups in this study only allowed assumptions to be made on a single territorial boundary where several exist for each group.

This study may pave the way for future playback experiments at different distances which would allow researchers to see the effect of a vocalisation at different stages of degradation on a neighbouring gibbon group, thus drawing stronger conclusions from the results. However, one should remember that the effects of playback experiments on wild animals are not fully understood and, as such, experiments of this kind should be conducted with caution.

Much bioacoustics research finds its foundations in the Sender-Propagation-Receiver (SPR) model (Pijanowski et al., 2011). The vast majority of these studies focus on making assumptions about the effect of these vocalisations on receivers without actually fully realising how the receiver perceives a song, i.e. how much is the receiver actually hearing? As such, more research is needed on the degradation rates of vocalisations in different habitats.

Future research on inter-conspecific communication would also benefit from incorporating more detailed analyses of how the animals use their habitat spatially to vocalise, considering where the animals are with respect to conspecifics and how they are utilising a particular height in the canopy. Again, this should be investigated from both the senders and receivers perspective.

Most previous research has treated the gibbon duet song and male solo song as separate entities. An intensive investigation of the male solo song and its potential relationship to the duet song could shed further light on why and how the duet song is sung.

There is a need for a radical modernisation of primate bioacoustics techniques. When considering a field like avian bioacoustics, it's easy to see that primate bioacoustics is more than a few steps behind. An improved knowledge of basic acoustical physics and a familiarity with bioacoustics equipment is essential if primate bioacoustics is to move forward into the modern age. This study, while it is by no means perfect, aims to help to start that trend.

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APPENDIX I: SINGING BEHAVIOUR DATA SHEET

[illegible]

APPENDIX II: SLEEPING AND SINGING TREE DATA SHEET

[illegible]

APPENDIX III A: LIST OF ALL SINGING TREE SPECIES IDENTIFIED DURING THE STUDY

RANK	LOCAL NAME	BOTANICAL NAME	TIMES USED
1	Meranti	<i>Shorea spp.</i>	25
2	Terontang	<i>Camptosperma coriaceum</i>	19
3	Pupu Palanduk	<i>Neoscortechinia kingii</i>	14
4	Jankang Kuning	<i>Xylopia fusca</i>	9
4	Jinjit	<i>Unknown</i>	9
6	Malam Malam	<i>Diospyros bantamensis</i>	8
6	Tabaras Akar Tinggi	<i>Stemonorus scorpiodes</i>	8
8	Jambu Jambu	<i>Syzygium havilandii</i>	6
8	Kapur Naga	<i>Calophyllum sclerophyllum</i>	6
8	Pampaning	<i>Lithocarpus spp.</i>	6
11	Katiau	<i>Madhuca mottleyana</i>	5
11	Kempas	<i>Unknown</i>	5
13	Kajalaki	<i>Aglaia rubiginosa</i>	4
13	Tampang	<i>Litsea rufofusca</i>	4
15	Bintan	<i>Licania splendens</i>	3
15	Hangkang	<i>Palaquium leiocarpum</i>	3
15	Karuing	<i>Unknown</i>	3
15	Nyato Babi	<i>Isonandra spp.</i>	3
19	Geronggang	<i>Cratoxylon spp.</i>	2
19	Madang Marakuning	<i>Dactylocladus stenostachys</i>	2
19	Mandarahan Daun Besar	<i>Unknown</i>	2
19	Pisang Pisang Besar	<i>Mezzetia leptopoda</i>	2
19	Rambutan	<i>Baccaurea bracteata</i>	2
24	Lalas	<i>Eugenia spicata</i>	1
24	Lilin Lilin	<i>Parartocarpus venenosus</i>	1
24	Kenari	<i>Blumeodendron elateriospermum</i>	1
24	Mankinang	<i>Elaeocarpus mastersii</i>	1
24	Papong	<i>Sandoricum beccanarium</i>	1
24	Tumih	<i>Combretocarpus rotundatus</i>	1

**APPENDIX III B: LIST OF ALL IDENTIFIED SINGING TREE SPECIES USED BY
KARATE DURING THE STUDY**

RANK	LOCAL NAME	BOTANICAL NAME	TIMES USED
1	Terontang	<i>Camptosperma coriaceum</i>	15
2	Meranti	<i>Shorea spp.</i>	11
3	Pupu Palanduk	<i>Neoscortechinia kingii</i>	10
4	Jinjit	<i>Unknown</i>	8
5	Jankang Kuning	<i>Xylophia fusca</i>	6
5	Tabaras Akar Tinggi	<i>Stemonorus scorpiodes</i>	6
7	Jambu Jambu	<i>Syzygium havilandii</i>	5
7	Katiau	<i>Madhuca mottleyana</i>	5
7	Pampaning	<i>Lithocarpus spp.</i>	5
10	Malam Malam	<i>Diospyros bantamensis</i>	4
10	Tampang	<i>Litsea rufofusca</i>	4
12	Hangkang	<i>Palaquium leiocarpum</i>	3
12	Kapur Naga	<i>Calophyllum sclerophyllum</i>	3
14	Bintan	<i>Licania splendens</i>	2
14	Geronggang	<i>Cratoxylon spp.</i>	2
14	Kajalaki	<i>Aglaia rubiginosa</i>	2
14	Kempas	<i>Unknown</i>	2
14	Madang Marakuning	<i>Dactylocladus stenostachys</i>	2
19	Karuing	<i>Unknown</i>	1
19	Lilin Lilin	<i>Parartocarpus venenosus</i>	1
19	Mandarahan Daun Besar	<i>Unknown</i>	1
19	Mankinang	<i>Elaeocarpus mastersii</i>	1
19	Papong	<i>Sandoricum beccanarium</i>	1

**APPENDIX III C: LIST OF ALL IDENTIFIED SINGING TREE SPECIES USED BY
GROUP C DURING THE STUDY**

RANK	LOCAL NAME	BOTANICAL NAME	TIMES USED
1	Meranti	<i>Shorea spp.</i>	13
2	Malam Malam	<i>Diospyros bantamensis</i>	5
3	Pupu Palanduk	<i>Neoscortechinia kingii</i>	4
3	Terontang	<i>Camptosperma coriaceum</i>	4
5	Jambu Jambu	<i>Syzygium havilandii</i>	3
5	Jankang Kuning	<i>Xylopia fusca</i>	3
5	Kempas	<i>Unknown</i>	3
5	Nyato Babi	<i>Isonandra spp.</i>	3
9	Kajalaki	<i>Aglaia rubiginosa</i>	2
9	Karuing	<i>Unknown</i>	2
9	Pisang Pisang Besar	<i>Mezzetia leptopoda</i>	2
9	Rambutan	<i>Baccaurea bracteata</i>	2
9	Tabaras Akar Tinggi	<i>Stemonorus scorpiodes</i>	2
14	Bintan	<i>Licania splendens</i>	1
14	Jinjit	<i>Unknown</i>	1
14	Kapur Naga	<i>Calophyllum sclerophyllum</i>	1
14	Kenari	<i>Blumeodendron elateriospermum</i>	1
14	Lalas	<i>Eugenia spicata</i>	1
14	Mandarahan Daun Besar	<i>Unknown</i>	1
14	Pampaning	<i>Lithocarpus spp.</i>	1
14	Tumih	<i>Combretocarpus rotundatus</i>	1

APPENDIX IV: LIST OF ALL SLEEPING TREE SPECIES IDENTIFIED DURING THE STUDY

TOTAL			
RANK	LOCAL NAME	BOTANICAL NAME	TIMES USED
1	Meranti	<i>Shorea spp.</i>	8
2	Ramin	<i>Gonystylus bancanus</i>	6
2	Tampang	<i>Litsea rufofusca</i>	6
4	Ehang	<i>Diospyros siamang</i>	5
5	Jankang Kuning	<i>Xylopius fusca</i>	4
6	Hangkang	<i>Palaquium leiocarpum</i>	3
6	Katiau	<i>Madhuca mottleyana</i>	3
7	Kapur Naga	<i>Calophyllum sclerophyllum</i>	2
8	Karuing	<i>Unknown</i>	1
8	Pisang Pisang Besar	<i>Mezzetia leptopoda</i>	1
8	Pupu Palanduk	<i>Neoscortechinia kingii</i>	1
8	Tabaras Akar Tinggi	<i>Stemonorus scorpiodes</i>	1
8	Terontang	<i>Camnosperma coriaceum</i>	1
KARATE			
RANK	LOCAL NAME	BOTANICAL NAME	TIMES USED
1	Tampang	<i>Litsea rufofusca</i>	5
2	Jankang Kuning	<i>Xylopius fusca</i>	4
3	Ehang	<i>Diospyros siamang</i>	3
3	Hangkang	<i>Palaquium leiocarpum</i>	3
3	Meranti	<i>Shorea spp.</i>	3
6	Kapur Naga	<i>Calophyllum sclerophyllum</i>	2
6	Ramin	<i>Gonystylus bancanus</i>	2
GROUP C			
RANK	LOCAL NAME	BOTANICAL NAME	TIMES USED
1	Meranti	<i>Shorea spp.</i>	5
2	Ramin	<i>Gonystylus bancanus</i>	4
3	Katiau	<i>Madhuca mottleyana</i>	3
4	Tampang	<i>Litsea rufofusca</i>	2
5	Ehang	<i>Diospyros siamang</i>	1
5	Karuing	<i>Unknown</i>	1
5	Pupu Palanduk	<i>Neoscortechinia kingii</i>	1
5	Tabaras Akar Tinggi	<i>Stemonorus scorpiodes</i>	1

APPENDIX V: FULL LIST OF ACOUSTIC AND TEMPORAL VARIABLES

No.	Variable	No.	Variable
1	Total No. of Song Notes	24	FIP Duration
2	Total No. of Female Notes	25	FIP Minimum Frequency
3	Total No. of Male Notes	26	FIP Maximum Frequency
4	Total No. of Complete Female Phrases	27	FIP Dominant Frequency
5	Total No. of Complete Male Phrases	28	FIP Maximum Amplitude
6	Song Duration	29	No. of FCP Notes
7	Song Minimum Frequency	30	FCP Duration
8	Song Maximum Frequency	31	FCP Minimum Frequency
9	Song Dominant Frequency	32	FCP Maximum Frequency
10	Song Maximum Amplitude	33	FCP Dominant Frequency
11	No. of MOP Notes	34	FCP Maximum Amplitude
12	MOP Duration	35	No. of FTP Notes
13	MOP Minimum Frequency	36	FTP Duration
14	MOP Maximum Frequency	37	FTP Minimum Frequency
15	MOP Dominant Frequency	38	FTP Maximum Frequency
16	MOP Maximum Amplitude	39	FTP Dominant Frequency
17	No. of FOP Notes	40	FTP Maximum Amplitude
18	FOP Duration	41	No. of MTP Notes
19	FOP Minimum Frequency	42	MTP Duration
20	FOP Maximum Frequency	43	MTP Minimum Frequency
21	FOP Dominant Frequency	44	MTP Maximum Frequency
22	FOP Maximum Amplitude	45	MTP Dominant Frequency
23	No. of FIP Notes	46	MTP Maximum Amplitude

MOP = Male Organisational Phrase	FCP = Female Climactic Phrase
FOP = Female Organisational Phrase	FTP = Female Terminal Phrase
FIP = Female Introductory Phrase	MTP = Male Terminal Phrase