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Vocal Diversity of The Kloss's gibbon, *Hylobates klossii,* in The Mentawai Islands, Indonesia.

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Research Award: Raven Sound Analysis software

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ABSTRACT

This is the first study to examine the vocal diversity of the male Kloss's gibbon (*Hylobates klossii*) endemic to the Mentawai Islands, Indonesia. The Kloss's gibbon is unusual because it is the only species that does not produce duets, with the exception of the silvery gibbon (*H. moloch*). Three other species of monkey are endemic to the islands and each has been classified into two subspecies; one on Siberut and the second spread over the three southern islands. This is based on morphological and some genetic differences, with the Siberut subspecies exhibiting a darker colouration. The Kloss's gibbon is completely black and exhibits no variation in pelt, so no subspeciation has previously been demonstrated. However, studies on the silvery and crested gibbons (*Nomascus sp.*) have shown that subspecies can be determined through examining vocal variation. Therefore Kloss's males were tape-recorded in four different locations; Simabuggai and Sikabae on Siberut island, Sipora and South Pagai islands. A total of 244 trill phrases from 27 individuals were examined using sonographic analysis (Raven 2.1) and non-parametric statistical tests (SPSS). The degree of variability was examined at the following levels; intra-individual, intra-population, intra-island and inter-population. Results from a Kruskal-Wallis one way ANOVA and post-hoc test indicated that the two populations within Siberut are significantly different to one another and that they are both significantly different to the Southern island populations, Sipora and South Pagai, which are very similar to one another. It was an unexpected result to find that Siberut contains two subspecies and this is most likely due to the prevention of dispersal by the numerous rivers, mountains and forest fragmentation. This division into three distinct units is supported by results from the discriminant function analysis; individuals can be classified back into their correct populations with an accuracy of 92.6%. Therefore, on the basis of male vocalisations it is concluded that the Kloss's gibbon is composed of three subspecies.

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Cover photo of Kloss's gibbon by M. Waller, August 2005, Siberut.

1. INTRODUCTION

This introductory chapter is composed of background information essential to the research aims outlined below; first a brief introduction to the currently accepted form of gibbon taxonomy, distribution, behaviour and morphology are explained and then key points in primate and gibbon vocalisation research are described, followed by information specific to Kloss's gibbon vocalisations. Next a brief description of the Mentawai islands, their geological history, climatic changes and local subspecies are given.

1.1 Research aims & objectives

The central aim is to determine the degree of vocal diversity in the male Kloss's gibbon (*Hylobates klossii*) and therefore whether subspecies exist, because it has been shown in the other species of endemic monkeys that they are composed of two subspecies (Groves, 2001; Roos et al. 2003; IUCN, 2003). Few studies have looked at the vocal diversity of gibbons (Haimoff & Gittins, 1985; Haimoff & Tilson, 1985) and the Kloss's gibbon is the least known of the gibbon species, which makes this a unique and interesting topic. In addition, the determination of whether subspecies occur has vital consequences for local threat evaluation and conservation management strategies.

The objective is to find out 1, whether there are significant differences in male vocalisations between localities; 2, whether vocal differences between islands are larger than differences between localities of the same island; 3, whether these differences can be used to predict provenience of singing gibbons and the percentage of correct identification; and 4, whether differences exist that allow discrimination by trained observers without using statistics.

To establish the degree of vocal variation the following levels will be examined; intra-individual, intra-population, intra-island and inter-population, using sound analysis and statistical tests. If inter-population vocal variability is greater than intra-island variability, it will support the idea that subspeciation has occurred.

1.2 Gibbon taxonomy & distribution

Gibbons are small apes found only in the tropical forests of south and southeast Asia. The family Hylobatidae consists of twelve species, see figure 1.1. Research shows that differences in molecular distance between them supports a split into four main monophyletic genera, based on a similar range to that between *Pan* and *Homo* (chimpanzees and humans) (Geissmann, 2002b; Roos & Geissmann, 2001; Brandon-Jones et al. 2004; Whittaker, 2005).

Note that the Kloss's gibbon and Javan silvery gibbon are sister taxa (Geissmann, 2002c). Previously the Kloss's was placed between *Symphalangus* and *Hylobates* because it is completely black like the siamang, but smaller like other hylobatids (Chivers, 1977; Geissmann, 2003b).

Fig. 1.1 A phylogenetic tree of gibbon species; from a combination of trees based on vocal and molecular data. (Geissmann, 2002b; Roos & Geissmann, 2001)

Evidence from the mitochondrial DNA D-loop supports the idea that the Kloss's gibbon is closest overall to the agile gibbon and the silvery gibbon (Whittaker, 2005), both of which are the closest species geographically (Fig. 1.2).

Species can be identified by differences in pelt colouration, vocalisation and location. Other morphological differences include cranial shape, number of chromosomes and body size (Geissmann, 2002b). Most species are allopatric but the siamang, agile and lar gibbons are exceptions with areas of sympatric living, as shown in figure 1.2.

Fig. 1.2 A map showing the distribution of the gibbon genera *Hylobates* (Chivers & Gittins, 1978; Geissmann, 1991). Numbers 1 – 3 are areas of sympatry and hybridisation.

1.3 Gibbon behaviour & morphology

1.3.1 Gibbons

Gibbons are characterised by a ‘socially monogamous’ lifestyle, where a family group consists of an adult male and female and up to four offspring (Chivers, 1984). Gibbons are mainly frugivorous, but will also consume varying amounts of insects, buds, leaves and eggs (Rowe, 1996; Whitten 1982a, 1984a). Gibbons play an important role in rainforest regeneration because their consumption of fruits and movement around territories results in the wide dispersal of seeds (McConkey et al. 2000).

They are diurnal and arboreal and their form of locomotion is brachiation, this is rapid swinging underneath the branches of trees, and running along the top of branches. Gibbons have small bodies, extremely long arms and no tail (Chivers, 1977). Most species exhibit sexual dichromatic pelage but little difference in size. Changes in pelt colouration can be shown during ontogeny such as in the agile gibbon. Females usually have their first birth at about nine years old, gestation takes seven months and generally there is only one offspring per litter, which can be every three years (Gittins, 1978).

1.3.2 Kloss's gibbon

The Kloss's gibbon (Miller, 1903) is stated as vulnerable, VU A1c + 2c, B1 + 2ac, (IUCN, 2003) on the redlist, and is under Hylobatidae species in appendix 1 on CITES (2003).

The Kloss's gibbon is completely black and has no facial markings in either sex, unlike other gibbon species. It has several features that are considered to be 'primitive', these are webbing between the second and third toes (Chivers, 1977), smaller cranial measurements and capacity, reduced hair density (Whitten, 1984a), longer limbs, more vertebrae and comparatively long thumbs and great toes (Schultz, 1933; Whittaker, 2005).

Kloss's gibbons are unusual because they sleep in groups, it has been found that they show a 91% preference for sleeping in trees without lianas and this is probably because of an increased risk from nocturnal predators, such as snakes and humans (Tenaza & Tilson, 1985; Tilson & Tenaza, 1982) and also due to the potential increase in biting ants (Whittaker, 2005). Usually gibbons exhibit a monogamous social system (Brockelman et al. 1998; Bernstein & Schusterman, 1964) but larger groups have been recorded for the

Kloss's, ranging from 4-15 individuals and an average of 10 in North Pagai (Whittaker, 2005).

1.4 Vocalisation research

1.4.1 Primates

Singing is a rare quality in mammals and only four genera of primates exhibit this (Geissmann, 2000b), these are the indri (*Indri*), titi monkey (*Callicebus*), gibbon (*Hylobates*) and tarsier (*Tarsius*) (Nietsch & Kopp, 1998). In addition, the vocalisations of orang-utans (*Pongo pygmaeus*), gorillas (*Gorilla spp.*) and chimpanzees (*Pan trogloydytes*) reflect similarities to gibbons in factors such as volume, acceleration of note rhythm and locomotor displays (Geissmann, 2000b). Variation in the pant-hoots (long distance call) produced by male chimpanzees (*P. t. schwienfurthii*) was examined using principle components analysis (PCA) by Notman and Rendall (2005). They found that the variation in pant-hoots related to specific conditions such as abundant food sources or social contexts such as travelling in small groups before meeting with the rest of the community. Research also showed that there is geographic variation in the quality of pant-hoots (Mitani et al., 1999), particularly in note length and rate. Discriminant function analysis showed that it was possible to assign individuals to their correct population based on vocal characteristics.

1.4.2 Gibbons

All gibbon species are characterised by producing loud and long bouts of song in the morning, these are species and sex-specific songs (Konrad & Geissmann, 2004), and they are also repetitive and stereotyped (Brockelman, 1984). The accepted definition of a song is "a series of notes, generally of more than one type, uttered in succession and so relates as to form a recognisable sequence or pattern in time" as described by Thorpe (1961) in relation to birds. However, the term song can be applied to gibbons too when they produce loud, long and complex vocalisations (Haimoff, 1984). Acoustic analysis and playback experiments have shown that variation in male songs exists between species and that they are able to discriminate individuals, as neighbours or strangers, by their vocalisations (Mitani, 1987). However, the same vocalisation can mean different things depending on who is hearing it, for example in birds the male robin can discourage other males entering the territory whilst simultaneously attract females (Gittins, 1978) and it is likely that gibbons do this too.

All species produce a duet, consisting of mated male-female pairs (Cowlishaw, 1992) who "combine their sex-specific repertoire in a relatively rigid, precisely timed and complex vocal interaction" (Geissmann, 2000a), with the exception of the Javan silvery (*H. moloch*) and Kloss's gibbon (Gittins, 1984; Geissmann, 1993). Although duet splitting is demonstrated in the silvery and Kloss's gibbon, males of the first sing far less frequently than the latter (Geissmann & Nijman, 1999) and the female silvery gibbons are believed to compensate for this (Kappeler, 1984). The function of duets is to maintain pair-bonds (Geissmann, 2000b; Geissmann & Orgeldinger, 2000); however the lack of duetting in Kloss's and Javan silvery gibbons does not denote a lack of pair-bonding, just that the function of singing differs between species (Geissmann & Orgeldinger, 2000; Geissmann, In press). Male gibbons are known for using singing as a form of territorial advertisement, mate attraction, and defence (Ahsan, 2001; Haimoff & Tilson, 1985; Tenaza, 1975; Whitten, 1982a, 1984b) of areas typically between 20-40 hectares (Geissmann, 1993). Whereas female songs indicate that the male has already formed a pair-bond (Whitten, 1982a).

Immature gibbons also join in with the singing, especially the females and their ability to match the adult female develops with age. Young males are thought to be discouraged from joining in because it indicates they are developing to an age where it is possible for them to set up territories and attract mates of their own, which obviously conflicts with the adult male's own territory (Gittins, 1978).

1.4.3 Kloss's gibbon

Kloss gibbons are particularly interesting because unlike other gibbon species they do not duet and it is proposed that this is a derived trait (Geissmann, 2002a). There are different types of vocalisations produced by the Kloss's gibbon which relate directly to the environment and changing stimuli. These include 'hoo' and 'howl' which indicate the detection of other primates, a ‘whup’ is found during a females song bout, a ‘whistle’ can occur before male songs and within the female song, a ‘whoo’ precedes the female song, ‘sirening’ and ‘alarm trill’ indicate the presence of humans, ‘quivering squeals’ and ‘whistle-howls’ are produced by males and females respectively during male fighting (Tenaza & Tilson, 1977). Finally, there are the male and female songs. Production of any one type of vocalisation is independent of any other vocalisation (Whitten, 1982a).

Females sing every 3-4 days post-dawn and it includes an energetic visual display (Whitten, 1982a, c) where they move rapidly around the trees. They produce a short introductory phrase with simple single-pitched hoots (0.7 kHz) and complex hoots (oo-wa) and no trills. Then the great call, see figure 1.3, has an acceleration-type climax (0.6-1.0 kHz), similar to muelleri (*H. muelleri)*, with fast bubbling notes (1.0-1.2 kHz). The last phase is the interlude with slower falling notes (1.0-0.4 kHz) at the end. Kloss’s great calls are longer than in other species. It has been shown that the duration and number of notes in the different phases of great calls are quite variable and can indicate individuals (Haimoff & Tilson, 1985) and in the wild this aids identification of neighbours (Haimoff & Gittins, 1985). The duration of female song bouts is about 20 minutes (Cowlishaw, 1992).

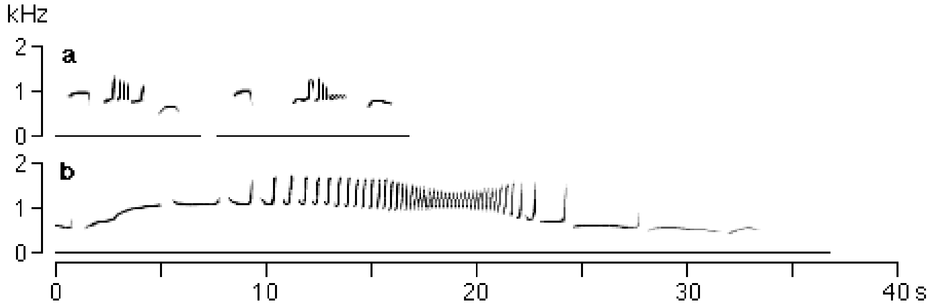

Fig. 1.3 Sonograms of a) male kloss’s short phrases (Twycross, 02/10/1988) and b) female Kloss’s great call (South Pagai, 27/11/1987, Tilson) (Taken from Geissmann, 2005).

Males sing pre-dawn on average every 2 days (Whitten, 1984b) and in a study by Whitten (1982a) the modal time class for singing was 05.00-05.15 when 20% of the songs began. They produce songs in three parts; short phrases with simple hoots at the start of a song

(± 0.7 kHz), more complex hoots (ow-oo), and finally short trilling phrases (0.6-1.0 kHz) with 3-4 terminal notes, as shown in figures 1.3 and 1.4 .

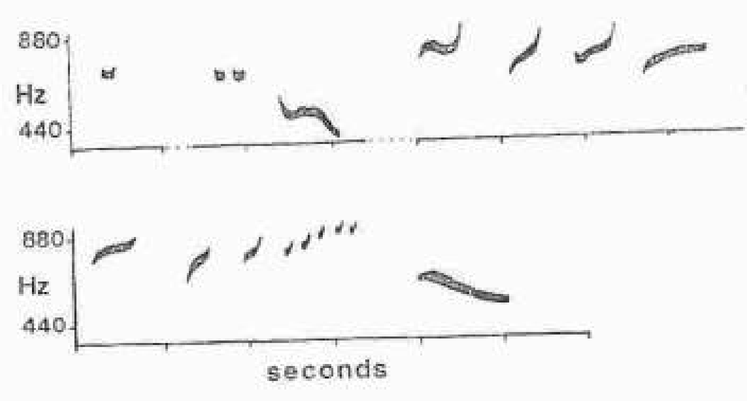

Fig. 1.4 Sonograms of the progressive stages in the male kloss's song (Whitten, 1982a).

No codas (Table 2.1) are performed at the end of a female's great call (Geissmann, 1993, 2002a 2005; Haimoff, 1984; Tenaza & Hamilton, 1971; Whitten, 1982a). Whitten (1982a) found that the median length of a male's song was 44 minutes with a range of 3-108 minutes. The interval between the stages of the song becomes shorter as it increases in complexity (Whitten, 1984b).

Male Kloss's gibbons often sing at the same time as those in neighbouring territories, this countersinging is a form of competition (Whitten, T., 1982a). If there is rain during the night or temperatures reach below a threshold of 21.5 ^{0}C singing is often inhibited (Ahsan, 2001). It is has also been shown that males are recognisable by their songs alone because there are obvious variations in the species-typical song (Tenaza, 1976).

1.5 West Sumatra

The Mentawai Islands are positioned 85-135km off the west coast of Sumatra (Fuentes, 1996/1997; Whitten, 1982a) and consist of Siberut, the largest and most northern, Sipora, North Pagai and South Pagai (Chasen & Kloss, 1927). They lie between 0^{0}55' to 3^{0}20' South and 98^{0}31' to 100^{0}40 East, see figure 2.1. The major forest types present are primary dipterocarp, primary mixed forest, secondary regenerating logged dipterocarp forest, and other types present include mangrove, freshwater and sago swamps, and west coast beach vegetation (Whittaker, 2005).

1.6 Geological history & climate changes

Approximately two hundred million years ago the Mentawai Islands were formed due to the collision of the Indian plate into the Asian (Eurasion) plate. Therefore, causing an upward shift and the formation of a chain of volcanic mountains along Sumatra, and also causing submergence which created the deep sea trenches, about 1000 fathoms (Chasen & Kloss, 1927), to the west of Sumatra. Further west this caused a smaller uplift thus creating a chain of islands, including the Mentawai (Whitten, T., 1982b) see figure 1.5.

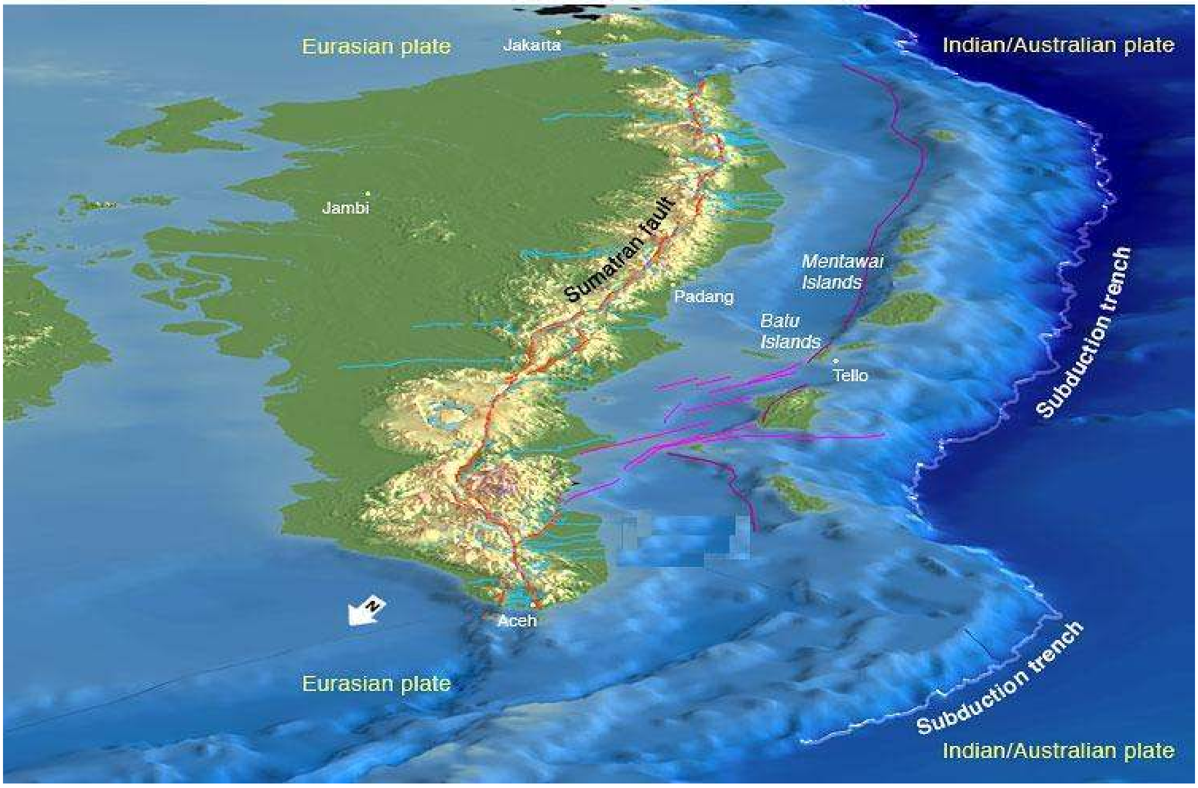

Figure 1.5 Map showing fault lines (purple) and the subduction zones around the Sunda shelf area (Anon., 2005)

Changes in climate and cycles of glaciation and deglaciation during the Pleistocene are responsible for significant changes in sea levels, which affect the degree of separation between land masses (Chivers, 1977; Voris, 2000), especially in the Sunda Shelf region. The consequences of climate change were apparent through habitat loss and fragmentation (Cowlishaw & Dunbar, 2000). These cycles of genetic isolation can explain the high number of phenotypically distinct gibbon populations and possibly genotypically distinct (Fleagle, 1999). The Mentawai have been separated from mainland Sumatra by the deep sea trenches for approximately 500,000 years (Whittaker et al. 2004), whereas Sumatra and the rest of Southeast Asia were joined till about 10, 000 years ago. Thus, the biodiversity of the Mentawai is quite distinct from the mainland and has a high degree of endemicity (Whitten, T., 1982b).

1.7 Identifying subspecies of the Mentawai primates

The taxon level subspecies is a lower division of species and the members of one subspecies differ morphologically and/or genetically from members of other subspecies belonging to the same species (Wikipedia, 2005; O'Brien & Mayr, 1991). Members of a subspecies share a unique geographic range or habitat, allopatric, but they are still reproductively compatible with other subspecies (Avise & Ball, 1991), and share a unique natural history relative to other subspecies of the species. It is important to acknowledge subspecies levels because of their potential to possess unique characteristics and therefore, their contribution to biological diversity and influence on conservation management units (Stanford, 2001).

It is possible that subspeciation has taken place in the Kloss's gibbon because the three other species of endemic primates, Mentawai macaque (*Macaca pagensis & M. siberu*), Mentawai langur (*Presbytis potenziani & P. siberu*) and the pig-tailed langur (*Simias concolor concolor & S. c. siberu*) (Groves, 2001; Roos et al. 2003; Whittaker, 2005) exhibit 2 subspecies; one on Siberut and a second on the three southern islands. These subspecies are easy to identify due to differences in pelt colouration (Groves, 2001) for example the Siberut forms are darker than on the southern islands. Additional differences between the southern islands of Sipora and the Pagais have been suggested for the

Mentawai langur (Brandon-Jones, 1993). However, no such variation in morphology is present in the Kloss's, so vocal diversity is the key non-invasive determinant.

Previous studies have shown that gibbon vocalisations are ideal for analysing phylogenetic relationships among taxa, because specific characteristics of songs are inherited, not learnt (Brockelmann & Schilling, 1984; Cheyne & Brule, 2004; Geissmann, 1984, 1993, 2002b, 2005; Marshall & Sugardjito, 1986; Tenaza, 1985). It has been shown that individuals can produce their species-specific songs even when reared in isolation (Geissmann, 1984; Tenaza, 1985). In addition, evidence from hybridisation in zoos and the wild support this; for example the hybrids of *Hylobates pileatus* and *H. lar* showed elements of both parents species specific song, even though it was only exposed to the song of one species relevant to it is own gender. Therefore the intermediate version must be a result of inheritance rather than learning (Brockelman & Schilling, 1984; Geissmann, 1984; Tenaza, 1985; Short, 2004). Vocalisations can also be used to analyse inter-individual and inter-population variability (Dallmann & Geissmann, 2001a, b; Haimoff & Gittins, 1985; Haimoff & Tilson, 1985).

It is important to note that whilst some aspects of a vocalisation are the same amongst all individuals of a population, species or sex, that there are also aspects which are highly variable. It is therefore important to determine which factors are constant within the population but vary between populations, and also at the species or sex level, for efficient identification. Determining specific subspecies vocal characteristics can aid accurate identification and therefore greatly influence conservation programmes.

Gibbons, unlike macaques and langurs, are known to show avoidance of all water bodies, such as streams (Marshall & Sugardjito, 1986; Morris, 1943; Parsons, 1940, 1941), and they rarely come to the ground (Whittaker, 2005). It is geographical barriers such as these which have the potential to prevent dispersal and thus allow allopatric subspeciation to take place. Differences can also evolve by random historical mechanisms such as genetic drift, bottlenecks, hybridisation, environmental effects and social adaptation (Dallmann & Geissmann, 2001b).

1.8 Report structure

This report is split into five chapters, each with a summary at the start and subdivisions that proceed logically through the topics. The first chapter describes the aims and all relevant background information to the research. Chapter 2 is the methods; this is composed of details about the field sites, data collection, sonographic analysis and statistical analysis at different levels. The different levels are intra-individual, intra-population, inter-island and inter-population. The results, chapter 3, first of all contains a qualitative description of the male Kloss's trill phrase vocalisation, then the statistics are split into sections corresponding to the levels that variation was examined in. The discussion, chapter 4, follows the same order of levels used in the results section and additional evidence of subspeciation is presented in order to answer the objectives described in chapter 1. Finally the fifth chapter contains the central conclusions and ideas for extended research.

2. METHODS

This chapter explains the methods used to obtain and analyse vocalisation data, exploiting sonographic and statistical software, from the male Kloss's gibbon. A comprehensive review of features such as the pilot study, complimentary research, acoustic terms and definitions, field site locations, materials and recording techniques are also included.

2.1 Pilot study

The only captive Kloss's gibbon outside of Southeast Asia is a single adult male held at Twycross Zoo, England. Observations over four mornings in January 2005 provided a familiarity with the species; such as forms of locomotion, morphology and ethology. Recordings of several different gibbon species, including the Kloss's, were taken, thus allowing researchers to gain experience of using different combinations of equipment. Potential sources of error were recognised, for example excess background noise can be minimised by holding the microphone very still and through using wind shields. The procedure for recording was also established, such as the use of verbalising important notes onto the tape between song bouts and the use of standardised phrases by both researchers to avoid confusion.

2.2 Complimentary research

Recordings of female Kloss's gibbons were collected from each of the field sites in the Mentawai using the same methods, to be analysed by Miss Sally Keith as a complimentary project. Therefore both researchers collected data on both sexes using identical equipment and adhering to the same protocol before exchanging recordings later for analysis. The focus of the female vocalisations is the great call and a slightly different set of variables were used to assess the degree of variability. It is important that both sexes were researched because it has been found that females exhibit more variation in their songs and individuality than males (Dallmann & Geissmann, 2001b) but male Kloss's gibbons sing more regularly so it is easier to get a larger sample size.

2.3 Acoustic terms & definitions

The following table presents the currently accepted terms and definitions that are relevant to vocalisation research, and that are used in this paper.

Table 2.1. 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.

2.4 Location of field sites

The selection of field sites was based on accessibility, presence of rainforest and gibbons and whether they had been visited by previous researchers. Additionally a minimum of 20km between sites within an island was maintained to ensure that different populations were sampled and overlap avoided.

1. Taman Nasional Siberut, Simabuggai consisted of primary dipterocarp forest. Its topography is mountainous and the GPS (Global Positioning system) positions for the three listening posts used to collect data from are

LP1)	S 01^0 22'30.6"	E 098^0 56'35.2"	Elevation 69m
LP2)	S 01^0 23'13.3"	E 098^0 57'05.6"	Elevation 146m
LP3)	S 01^0 22'25.7"	E 098^0 56'54.2"	Elevation 135m

2. South Siberut, Sikabae was comprised of a mixture of mangrove and dipterocarp forest. The majority was primary forest with patches of secondary forest on hilly terrain. The GPS positions for the three listening posts were

LP1) S 01^0 37’04.3” E 099^0 15’09.4” Elevation 39m
LP3) S 01^0 37’20.0” E 099^0 15’41.5” Elevation 26m
LP4) S 01^0 26’44.8” E 099^0 15’00.1” Elevation 120m

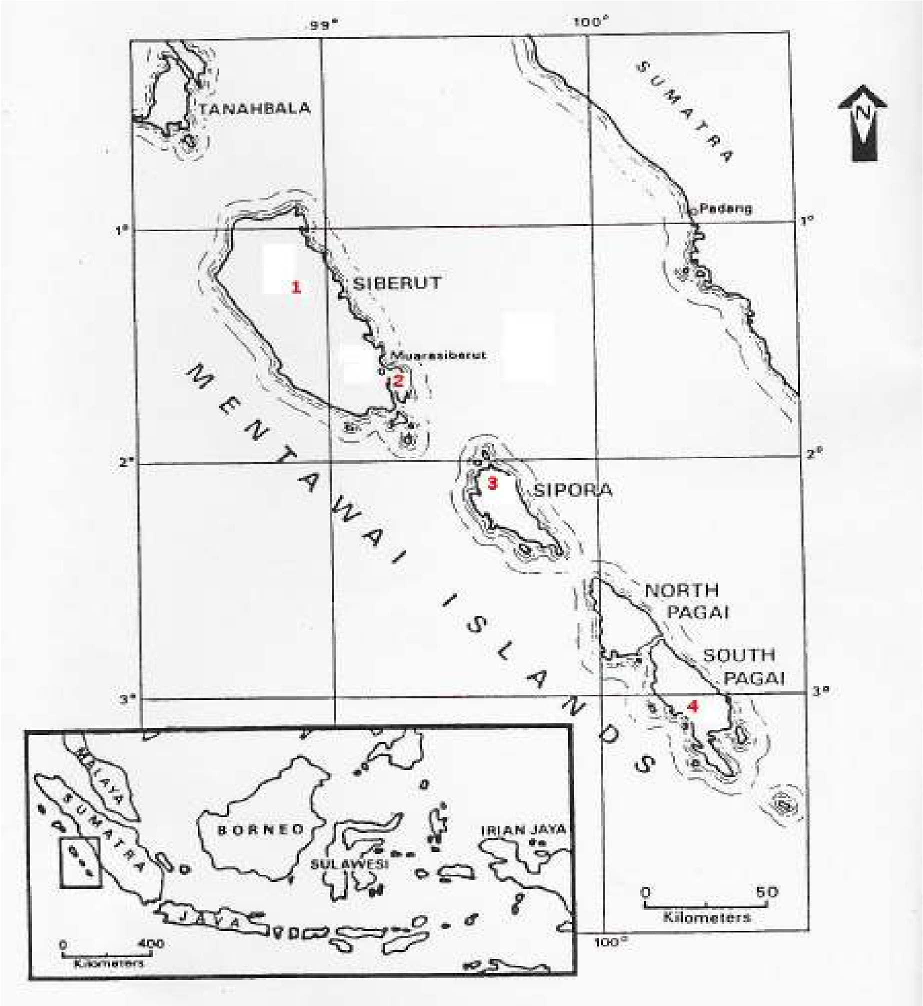

Fig. 2.1 Map of the Mentawai Islands, Indonesia showing the location of field sites, numbers 1 to 4 and the 183 meter isobath - - - - - (Taken from Fuentes, 1996).

3. North Sipora, Saureinu consisted of primary, dipterocarp forest in extremely mountainous topography. The GPS positions for the three listening posts were

LP1) S 02^0 07’15.5” E 099^0 38’04.1” Elevation 97m
LP3) S 02^0 07’52.0” E 099^0 37’33.7” Elevation 140m
LP4) S 02^0 07’49.2” E 099^0 37’01.7” Elevation 145m

4. South Pagai, Malakopa contained mostly secondary, regenerating logged dipterocarp forest at a high elevation with hilly topography. The four listening posts used for data collection were LP1) S 02^0 58’00.9” E 100^0 17’15.5” Elevation 215m
LP2) S 02^0 58’06.1” E 100^0 18’12.6” Elevation 221m
LP4) S 02^0 57’26.7” E 100^0 18’35.6” Elevation 194m
LP5) S 02^0 57’54.3” E 100^0 18’38.8” Elevation 231m

2.5 Data collection

2.5.1 Data collection method

All recordings were taken between May and September 2005 by M. Waller and S. Keith. At each field site a point census technique was used to determine listening points, however it was modified because listening posts could not be chosen randomly for the following reasons. Some areas of the site were inaccessible because the terrain consists of steep hills and mountains, dense vegetation, uncrossable rivers, mangrove forests and peat swamps. Vocalisations were easiest to hear from the top of hills because Kloss’s gibbons show a preference for using tall trees at the top of hills for singing from because there are fewer obstructions. In addition, background noise from insects is minimised, this is called the ‘sound window’ (Whitten, 1981). Vocalisations travel a long distance; approximately 1km, so a minimum of 2km from other listening points should be ensured to avoid recording the same individual twice (Geissmann, 2005). Listening points were reached before the male starts singing (~4.00am) every morning and remained until about 10.00am because females sing post dawn (~7.00am onwards). Researchers aimed to record seven individual males and females at each field site to provide an adequate sample for statistical analysis and at least two recordings from an individual to determine the degree of intra-individual variability (Geissmann, T., pers. comm.). Recordings of all stages in the male’s song were taken, as shown in figure 1.4, and of the great call by females.

Before vocalisations began the time, date, direction of sound (by compass bearing), and researchers name and reference code were recorded onto the tape, as recommended by Lehner (1996). In addition, notes of the weather (rainfall and temperature), GPS (Global Positioning System) location, time vocalisation starts and ends, duration, and other information were recorded into waterproof notebooks. Triangulation methods would have been employed, as described by Buckley (2004), if GPS systems had failed.

2.5.2 Alterations to data collection method

It was not possible to obtain recordings from seven different males at each field site due to excess rain inhibiting the chance of gibbons vocalising and by creating too much noise for good quality recordings to be taken. Inaccessibility of the terrain prevented researchers from maintaining a minimum distance of 2km between listening posts. However, by thorough cross-checking of recordings any potential pseudo-replication was eliminated if individual identity was uncertain. It was clear from personal observations that song recordings of high quality were within 400m of the listening post and did not disperse efficiently beyond 600m.

2.6 Materials

An ME66 Sennheiser shot gun microphone and K6 power module was used with a Sony VOR cassette recorder TCM–450DV, as used in similar research on the Kloss's gibbon (Whittaker et al. 2004). The microphone was chosen for its high quality, durability, low noise figure, relative immunity to high humidity and directionality which allow the researcher to focus on vocalisations from a single direction (Geissmann, 2003a). To minimise background noise, such as wind, rain and insects (Bearder, 2004; Geissmann, 2003a; Lehner, 1996) a rubber foam windscreen was placed over the directional microphone. The recorder was chosen because it has a frequency range of 250 – 6300 Hz, ability to take good quality recordings (Lehner, 1996), built in speaker for playback (Geissmann, 2003a) and compact size which is favourable in field conditions. TDK 60 minute tapes were used because they are 'more time accurate' than longer tapes and have a low signal to noise ratio (Geissmann, 2003a). The use of headphones whilst recording allowed researchers to accurately aim the microphone towards the target gibbon. The Garmin eTrex Global Positioning System (GPS) was chosen because it is particularly durable, accurate and has memory adequate for this research.

2.7 Sonographic analysis

Only the last stage of a males song are analysed, this consists of the pre-trill, trill and post-trill notes as defined in the sonogram below. All parts are analysed to maximise the chance of finding differences between populations. Sonographic analysis is achieved using 'Raven 1.2.1' on the variables described in table 2.2.

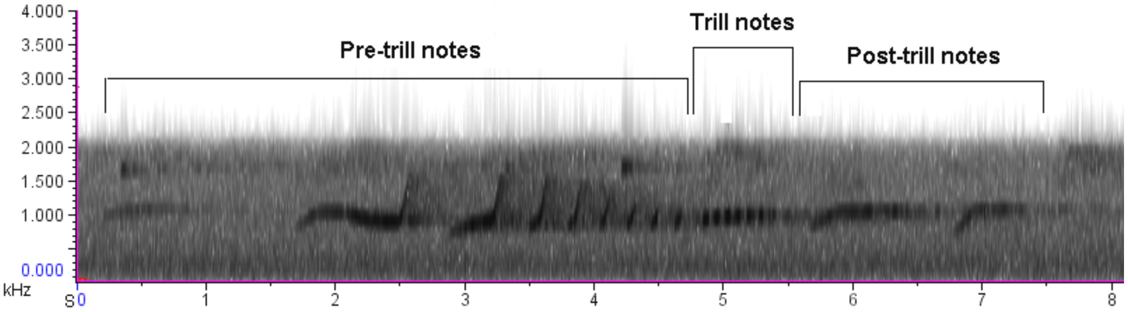

Fig. 2.2 Sonogram showing the three parts of a male trill phrase. (Kloss's sampled from Sipora, June 2005).

The sound material was digitised with a sample rate of 44100Hz and a sample size of 16 bit. Sonograms were constructed with a time versus frequency display. This software was chosen for its ability to edit sounds efficiently without needing specialist training. It is an updated version of the canary software used in similar research by Konrad and Geissmann (2006).

Table 2.2 Variables to measure male Kloss's gibbon trill phases (Haimoff & Tilson, 1985)

Variable	**Description**
1. Duration of phrase	Time in seconds from the start to the end of the phrase
2. Total number of notes in phrase	Count of the number of notes in whole phrase
3. Minimum frequency of phrase	Frequency measured in Hertz
4. Maximum frequency of phrase	Frequency measured in Hertz
5. Number of notes pre trill	Count of the number of notes pre trill
6. Duration of pre trill notes	Time in seconds for duration of pre trill notes
7. Minimum frequency of pre trill notes	Frequency measured in Hertz
8. Maximum frequency of pre trill notes	Frequency measured in Hertz
9. Frequency modulation of second note	The change in frequency of this note from start to end, measured in Hertz.
10. Frequency modulation of third note	The change in frequency of this note from start to end, measured in Hertz.
11. Number of notes within trill	Count of the number of notes within trill
12. Duration of trill	Time in seconds for trill duration
13. Minimum frequency of trill	Frequency measured in Hertz
14. Maximum frequency of trill	Frequency measured in Hertz
15. Frequency modulation of first post trill note	The change in frequency of this note from start to end, measured in Hertz
16. Number of post trill notes	Count of the number of notes post trill
17. Duration of post trill notes	Time in seconds for post trill notes
18. Minimum frequency of post trill notes	Frequency of post trill notes measured in Hertz
19. Maximum frequency of post trill notes	Frequency of post trill notes measured in Hertz

2.8 Sample size

A total of 224 song bouts were analysed from 27 different males. Song bouts were considered unsuitable for reliable measurements if recording quality was low, due to noise or absence of notes, for example if no post trill notes were performed. The measurements of song bouts taken from each individual were converted to mean values for comparison, but variables which were counts, for example the number of notes per phrase was converted to median values because it is clearly impossible to have 2.3 notes in a phrase.

Table 2.3 Song bouts analysed for each male at all locations.

Location	Individual	Recorded bouts	Analysed bouts
Simabuggai, Siberut	1	23	20
	2	8	8
	3	8	5
	4	8	8
	5	4	4
	6	6	5
	7	4	4
Sikabae, Siberut	1	22	21
	2	8	2
	3	2	2
	4	13	9
	5	12	11
	6	5	4
	7	4	4
	8	22	19
Saurineau, Sipora	1	9	6
	2	21	18
	3	19	5
	4	13	13
	5	17	6
	6	9	6
	7	8	7
Malakopa, South Pagai	1	22	21
	2	21	5
	3	10	4
	4	4	4
	5	7	3
TOTAL	**27**	**309**	**224**

2.9 Statistical analysis

All tests used were non-parametric due to the non-random method of data collection, small and unequal sample size. All tests were conducted using the statistical software package SPSS 12.1. The variation of vocalisations was examined at the intra-individual, intra- and inter-population and intra-island levels.

2.9.1 Intra-individual vocal variation

To look at how each variable varies within an individual, simple descriptive statistics were used; the standard deviation is divided by the mean and multiplied by 100 so the coefficient of variation is expressed as a percentage. This method is more reliable than measures such as 'variance' because it allows the separate variables to be compared despite their varying scales of measurement (Fowler et al. 1998). Those with low coefficient values are considered as stable, whereas high values indicate a higher level of variation.

2.9.2 Intra-population vocal variation

The coefficient of variation will be calculated using all the individuals within a population to determine how much variation is shown in each variable of the trill phrase, as detailed above.

2.9.3 Intra-island vocal variation

The Mann-Witney U test (Kranzler & Moursund, 1999) was used to determine whether two populations within an island are significantly different to each other. The tests were done between Simabuggai and Sikabae; both sites on Siberut island, and also on Sipora and South Pagai; the southern islands. Therefore, the null hypothesis is: 'there is no difference in the vocalisation variables between the two populations'.

2.9.4 Inter-population vocal variation

To determine whether significant differences in male vocalisations exist between the four populations sampled, a Kruskal-Wallis one way analysis of variance (ANOVA) was conducted (Fowler et al. 1998). A significance level of 5% was used, as used by Haimoff & Tilson (1985) in a similar study on Kloss's gibbons. The null hypothesis is: 'there is no difference in vocalisation variables between the four populations of male Kloss's gibbons sampled'.

A post-hoc test will be used to show which pairs of populations differ from one another, if significant differences are found in the Kruskal-Wallis test. This will be a pair wise Mann-Witney U test with the Bonferroni adjustment (Scholfield, 2005)

.

2.9.5 Discriminant function analysis

This test determines the likelihood of the variables to be used as a model for placing unknown individuals into their correct populations, other than by chance alone, based on the characteristics of their vocalisation. DFA identifies differences in the vocalisations amongst the four populations. A multivariate, stepwise approach using Wilks' lambda method will be used, as by Konrad & Geissmann (2006) in a similar study on Cambodian gibbons. A tolerance test will be performed to measure the degree of linear association between variables and therefore avoid redundancy amongst independent variables. The probability of F will be used, therefore *p entry = 0.05* and *p to remove = 0.10*, thus screening out variables that are inefficient discriminators and identifying those which are good discriminators.

The selected variables, functions, are used in the classification procedure that assigns individual gibbons to their correct or incorrect populations. The percentage of correct classifications can then be used to indicate the discriminability of populations, and by calculating Cohen's **k** (Siegel & Castellan, 1988) it is possible to determine whether the classification differs significantly from chance. The model is then cross-validated using the *leaving-one-out method*, this is where each of the cases are left out in turn, therefore the functions are calculated on the rest of the cases and the one left out is classified.

3. RESULTS

The results chapter is divided into logical sections, first a description of the qualitative characteristics of male Kloss's gibbon songs is provided with some key findings about the circumstances within which they sing. An examination of variation in the trill phase at the following levels; intra-individual, intra-population, intra-island and finally inter-population will be presented, plus results from the discriminant function analysis.

3.1 Qualitative description of the male Kloss's trill phrase

As detailed in chapter 1, the song of male Kloss's gibbons starts with the repetition of a single long, descending note that is repeated for approximately half an hour, then it gradually builds up to a three note phrase, then a five note phrase and finally the trill phrase which often alternates with an identical phrase without the trill section. The gaps between these stages become shorter as the singing progresses. Researchers described the initial notes as haunting, particularly in reference to the Siberut populations.

As expected, the trill phrase consisted of the three parts; the number of pre trill notes vary but they increase in speed to build up to the trill, which is a rapid succession of notes alternating slightly in frequency and then ending in a few post trill notes that are longer and slower. However, there appears to be a difference between Siberut and the two southern islands; the post trill of Siberut males consists of notes which sound like they are descending, whereas the Southern islands are more varied, sometimes ending with ascending notes or notes with a greater frequency modulation such as awoo-oo that is sung with an ascending and descending part, as shown in figure 3.1 c.

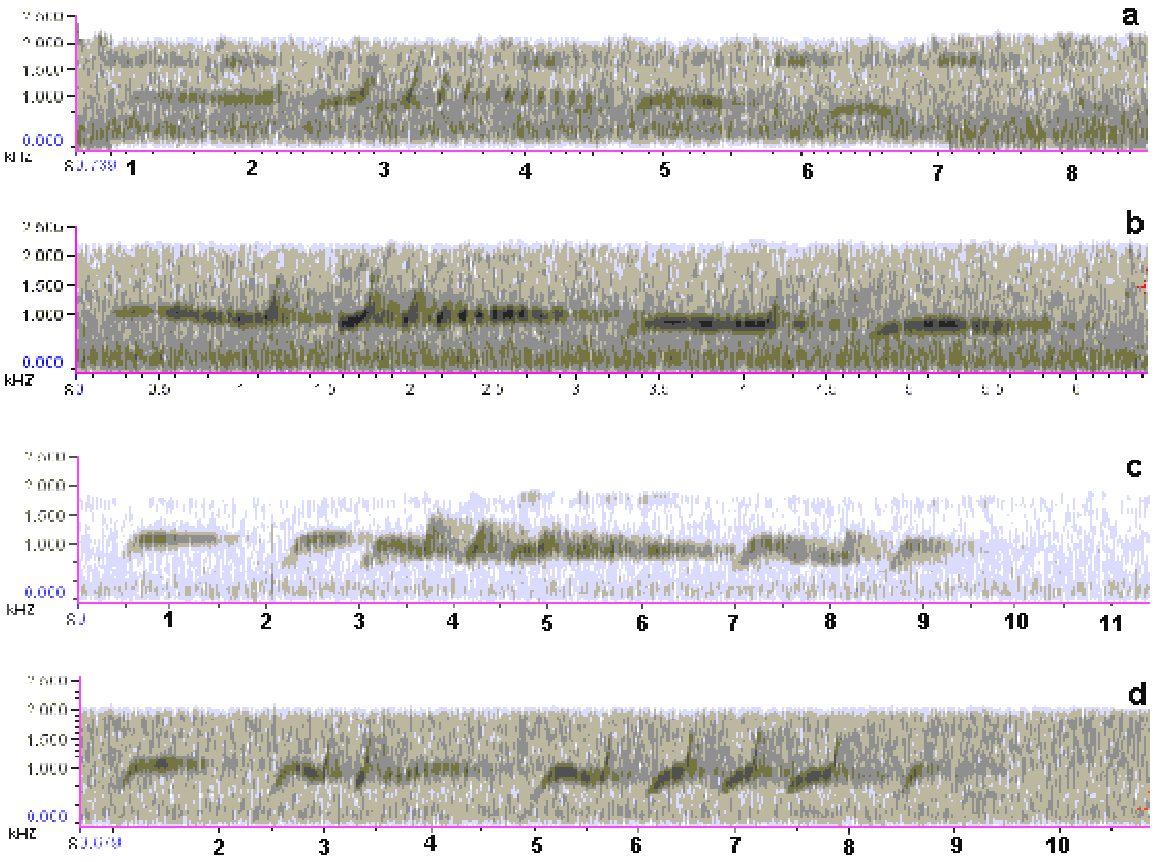

Fig. 3.1 Sonograms of the male trill phase from a) Simabuggai, Siberut; b) Sikabae, Siberut; c) Sipora; d) South Pagai.

Kloss's gibbons were observed singing at a variety of times during the daily cycle; the peak time for males was between 05.00 and 07.00, which reinforces past research, as described in the introduction. However, it is important to note that male Kloss's gibbons are also likely to sing at other times, such as between 09.00 and 11.00 after their first feeding session, especially if there has been heavy rain earlier in the morning. The most unusual finding was a bout of singing from 23.30 to 01.08 am, which is when gibbons typically sleep (Whitten, 1982c). The cause of this is unknown but it is possible that the session of female great calls that morning stimulated the males to sing.

It is also important to note that Kloss's gibbons do sing in light rain and just after heavy rain, despite findings from previous research. Although it is the norm for males to sing before the females, on one occasion males were heard singing before and just after the females great call bout.

3.2 Intra-individual vocal variation

This will be examined through calculating the coefficient of variation for all the phrases that were measured for each individual. The coefficient allows all the variables to be directly compared because it accounts for the different means of each variable.

The table shows the five most constant variables, therefore low in variation represented by low coefficient values, for each individual in bold. The variables minimum and maximum frequency of trill, notes per pre trill, duration of pre trill and maximum frequency of whole phrase are constant in most of the individuals. Generally the coefficient of variation is low, < 35%, amongst all the individuals, with only a few exhibiting variables with values over 50%. The highly varied variables are the frequency modulation of the third pre trill note and duration of the post trill and number of notes in the post trill.

However, it is important to note that although all the variables of some individuals may appear constant this is not necessarily accurate because the coefficient of variation may have been based on a small sample of phrases, as exhibited in individuals Sikabae 1 and 2.

Table 3.1. Table showing the coefficient of variation for all the variables of each individual male gibbon sampled. The five most constant variables for each individual are highlighted in bold.

Variable No → Individual ↓	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Simabuggai 1	23.57	11.01	**5.24**	**8.85**	**8.48**	10.14	19.09	16.90	19.19	30.18	16.11	14.44	12.55	**9.39**
Simabuggai 2	45.11	9.63	6.21	**3.34**	6.81	**3.34**	43.71	33.96	16.88	31.18	13.28	8.52	**4.54**	**1.14**
Simabuggai 3	27.52	6.98	**2.99**	**2.69**	5.17	**2.69**	34.46	4.08	19.86	22.31	5.13	10.31	4.11	**3.22**
Simabuggai 4	47.74	10.84	6.48	**2.17**	**3.40**	**2.17**	4.99	13.88	16.33	28.28	9.07	11.19	**3.74**	**0.55**
Simabuggai 5	20.76	21.13	**4.86**	8.72	**4.56**	8.72	13.59	16.15	17.43	14.97	39.37	16.69	**8.30**	**5.22**
Simabuggai 6	18.59	10.48	10.17	**3.88**	7.46	**3.21**	12.99	10.83	15.12	42.02	10.09	6.15	**3.23**	**3.28**
Simabuggai 7	**3.76**	4.03	13.42	7.82	4.81	7.82	13.30	22.48	8.60	7.40	16.11	18.62	**3.57**	**2.36**
Sikabae 1	22.31	8.29	8.57	**7.39**	**6.91**	**7.34**	13.25	25.59	19.35	38.69	15.71	12.50	**5.78**	**3.00**
Sikabae 2	25.78	8.91	7.14	5.55	**5.83**	**5.55**	11.52	36.67	**0.00**	39.24	16.33	7.15	**3.97**	**3.22**
Sikabae 3	16.20	**7.44**	8.88	**2.19**	7.51	**1.91**	**7.20**	9.28	10.56	25.17	15.95	10.51	**4.38**	11.33
Sikabae 4	25.89	4.56	16.33	**0.89**	8.66	**0.89**	**0.87**	8.26	**0.00**	14.59	15.71	30.51	4.20	**2.60**
Sikabae 5	6.16	8.32	**0.41**	2.98	**1.46**	2.98	**2.56**	6.18	12.86	17.85	15.71	10.07	**0.00**	3.40
Sikabae 6	16.38	**0.00**	4.70	6.71	**1.81**	6.71	9.95	17.71	12.83	11.20	7.41	11.00	**0.99**	**2.29**
Sikabae 7	30.11	7.04	10.41	**5.81**	**5.88**	**5.81**	12.18	13.62	17.35	45.34	12.90	15.88	**2.25**	**2.21**
Sikabae 8	20.29	6.63	11.47	**1.71**	**4.54**	**1.56**	12.61	6.60	13.64	31.75	13.26	17.41	**3.75**	**2.69**
Sipora 1	18.63	10.41	9.41	**4.06**	11.56	**4.01**	26.57	14.85	19.56	23.25	10.30	15.19	**6.98**	**2.76**
Sipora 2	15.87	7.45	10.63	**5.00**	**2.46**	**5.93**	32.62	12.48	36.45	31.21	15.80	19.45	**3.55**	**3.13**
Sipora 3	26.51	12.61	9.81	**4.24**	11.26	**3.73**	17.33	19.40	11.47	30.94	14.85	22.45	**4.39**	**4.87**
Sipora 4	20.27	**7.30**	14.67	**4.17**	24.81	13.97	29.56	33.93	47.71	39.27	13.43	25.53	**6.51**	**2.29**
Sipora 5	30.96	**12.26**	**8.95**	12.93	**5.51**	12.86	38.85	22.08	22.27	40.95	16.97	23.45	**6.41**	**1.37**
Sipora 6	13.41	15.54	9.98	**1.79**	11.09	**1.79**	30.74	19.24	15.94	30.81	17.11	11.96	**8.43**	**5.95**
Sipora 7	14.75	9.30	24.08	**3.41**	17.35	**3.41**	29.88	11.26	31.02	32.19	10.10	**6.73**	6.99	**1.96**
South Pagai 1	27.33	11.36	12.22	**2.36**	13.98	**2.58**	31.09	**10.14**	20.90	45.98	15.07	13.31	**5.46**	13.71
South Pagai 2	36.42	16.81	14.79	**8.24**	12.52	**8.24**	27.57	19.48	31.88	43.13	17.68	**3.91**	**1.79**	**4.13**
South Pagai 3	8.01	12.41	8.42	**3.74**	10.90	9.33	37.41	**3.30**	35.29	47.18	23.56	10.18	**4.09**	**3.25**
South Pagai 4	31.91	11.98	15.92	**4.63**	**5.39**	**5.62**	29.52	19.85	16.33	58.30	13.21	12.71	**3.70**	**5.31**
South Pagai 5	11.51	**0.00**	**1.46**	5.38	7.77	13.10	7.20		0.00	56.02	12.37	16.02	**4.66**	**1.43**

Table 3.1 cont. Table showing coefficient of variation for the variables of each individual male gibbon sampled. The five most constant variables for each individual are highlighted in bold.

Variable No→ Individual↓	**15**	**16**	**17**	**18**	**19**
Simabuggai 1	44.85	72.04	**4.91**	18.66	37.37
Simabuggai 2	18.86	11.62	**3.40**	11.32	28.87
Simabuggai 3	55.92	62.61	**3.86**	6.67	20.58
Simabuggai 4	54.71	89.45	4.39	32.24	41.21
Simabuggai 5	46.48	44.49	**4.80**	21.36	40.03
Simabuggai 6	46.29	20.01	10.30	**2.47**	16.01
Simabuggai 7	34.23	23.56	10.27	**2.09**	21.69
Sikabae 1	41.92	37.73	7.45	19.76	38.01
Sikabae 2	28.57	28.40	6.15	8.19	21.78
Sikabae 3	32.27	31.57	9.68	18.76	31.65
Sikabae 4	47.14	63.85	13.21	4.23	8.31
Sikabae 5	**0.00**	4.72	7.07	14.38	5.55
Sikabae 6	28.57	33.45	**3.26**	20.15	46.78
Sikabae 7	35.90	36.69	10.34	12.89	22.00
Sikabae 8	42.43	38.65	8.07	23.17	45.72
Sipora 1	20.82	19.63	9.60	**7.76**	12.31
Sipora 2	33.47	44.44	18.00	15.11	34.46
Sipora 3	46.49	42.13	10.41	**8.44**	9.09
Sipora 4	45.53	55.74	16.74	18.53	23.99
Sipora 5	41.95	47.81	16.56	12.60	31.48
Sipora 6	45.25	33.23	20.99	**9.04**	18.17
Sipora 7	43.24	29.71	19.73	**6.73**	21.56
South Pagai 1	17.54	23.44	13.46	**6.01**	15.70
South Pagai 2	42.38	59.75	18.68	10.22	24.85
South Pagai 3	36.89	34.32	16.50	**3.88**	11.55
South Pagai 4	40.82	36.25	18.11	9.53	12.44
South Pagai 5	24.74	33.40	**3.99**	7.71	30.56

3.3 Intra-population vocal variation

To determine the degree of variation within a population the coefficient of variation can be calculated using the average figures from each of the males in that population. The most constant variables within each population are the shortest bars in figure 3.2.

The lowest coefficient values that occur in several of the populations are maximum frequency of the whole phrase, the number of notes and duration of the pre trill, minimum frequency of the trill and maximum frequency of the trill. All of these variables were the most constant at the intra-individual level too. The variables which exhibit high variation in more than one population are the maximum frequency of the pre trill, frequency modulation of the third pre trill notes and the number of notes and duration of the post trill. The last two of these were also the most diverse at the intra-individual level.

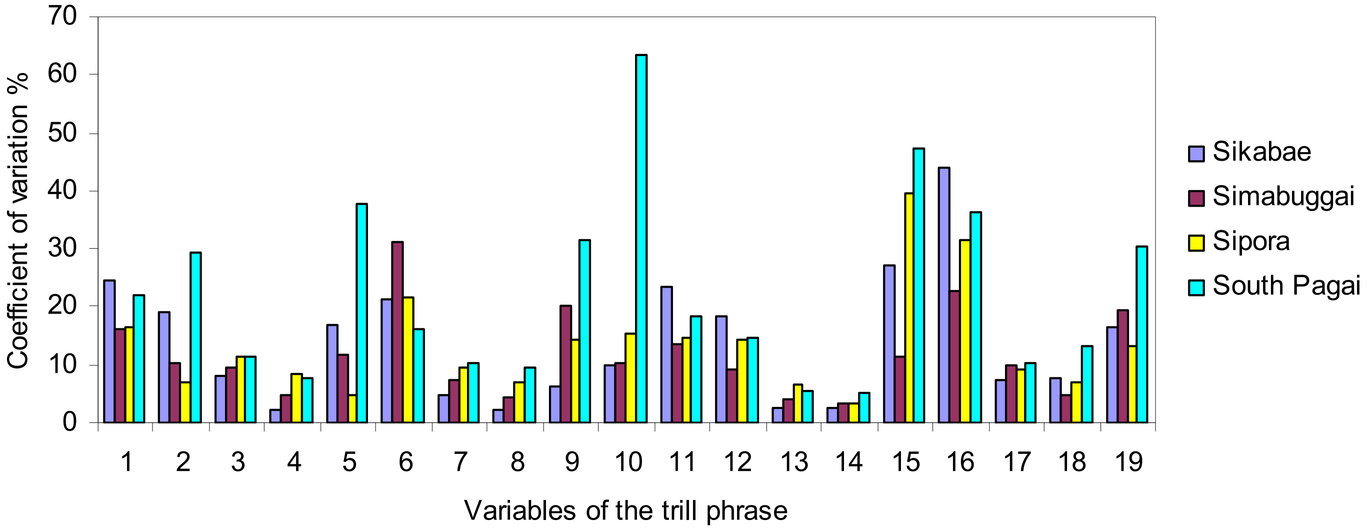

Fig. 3.2 Bar chart showing the coefficient of variation within each population for every variable of the male Kloss's trill phrase.

3.4 Intra-island vocal variation

A Mann-Witney U test was conducted to look at the degree of variation between the two populations on the same island, Siberut, and then between the two southern island populations. The results show that for eight of the vocal variables measured there is a significant difference ($p<0.05$) between the Simabuggai and Sikabae population, see table

3.2, and one highly significant difference ($p<0.001$). Therefore, the null hypothesis is rejected and it can be concluded that these two populations are not the same vocally.

It was not expected that these two populations would be so distinctive from one another, but some of the variables shown to be constant at the previous levels are shown here to be different between the Siberut population, for example maximum frequency of the phase and notes per pre trill. Thus they are effective discriminating variables. In addition variables that were shown to be highly variable at the previous levels are also effective discriminators, such as the maximum frequency of the pre trill and frequency modulation of the third pre trill note, because their ranges of variation are significantly different.

Table 3.2 Table showing significant results, from a Mann-Witney U test, between Simabuggai and Sikabae populations.

Test variable	**U value**	**Asymp Sig (2 tailed)**	**Exact Sig**
Notes per phrase	8.5	0.023	0.021
Maximum frequency of phrase	2.0	0.003	0.010
Frequency modulation of third pre trill note	8.0	0.021	0.021
Notes per pre trill	9.0	0.019	0.029
Maximum frequency of pre trill	0.0	0.001	0.000
Notes per trill	9.5	0.027	0.029
Duration of trill	8.0	0.021	0.021
Maximum frequency of post trill notes	5.0	0.008	0.006
Frequency modulation of first note after trill	6.0	0.011	0.009

Table 3.3 Table showing variables with a significant difference, from a Mann-Witney U test, between Sipora and South Pagai populations.

Test variable	**U value**	**Asymp Sig (2 tailed)**	**Exact Sig**
Duration of the pre-trill	2.0	0.012	0.010

Only one variable was found to be significantly different between Sipora and South Pagai, table 3.3, therefore there are less defining factors between them than there are between the Siberut populations.

3.5 Inter-population vocal variation

The degree of vocal variation amongst all four populations was examined using the Kruskal-Wallis test and the results (table 3.4) from this show that there is a significant difference (p<0.05) between them for nine variables, a highly significant difference (p<0.001) between them for six variables and no difference (p>0.05) for the duration of the post trill or for the minimum frequency of the post trill. Thus, the null hypothesis is rejected; the vocalisation variables are different between the four populations.

Table 3.4 Table showing variables which are significantly different between all populations sampled, using a Kruskal-Wallis test at 3 degrees of freedom.

Test Variable	H Stat	P value
Duration of phrase	11.651	0.009
Total number of notes in phrase	9.804	0.020
Minimum frequency of phrase	8.644	0.034
Maximum frequency of phrase	8.654	0.034
Number of notes pre trill	10.95	0.012
Duration of pre trill notes	10.470	0.015
Minimum frequency of pre trill notes	15.691	0.001
Maximum frequency of pre trill notes	13.220	0.004
Frequency modulation of second note	11.905	0.008
Frequency modulation of third note	7.959	0.047
Number of notes within trill	8.346	0.039
Duration of trill	7.898	0.048
Minimum frequency of trill	16.153	0.001
Maximum frequency of trill	7.887	0.048
Frequency modulation of first post trill note	10.580	0.014
Number of post trill notes	8.857	0.031
Duration of post trill notes	7.019	0.071
Minimum frequency of post trill notes	6.947	0.074
Maximum frequency of post trill notes	14.293	0.003

The variable minimum frequency of the trill was identified at the intra-individual and intra-population level as being low in variation, yet this test reveals it to also be different between the populations. These qualities make it an effective tool for identifying the origin of an individual by vocalisations alone. The maximum frequency of the pre trill is a variable that showed high coefficient values but it is also shown to be significantly different between the four populations and is therefore a good discriminator too.

Results from a post hoc test, see table 3.5, show which pairs of populations differ for the variables found to be significant different in the previous test. Note that no significant differences were found between Sipora and South Pagai for any of the variables measured; it is clearly harder to discriminate between these two populations using vocal characteristics, supporting results from the initial Mann-Witney U test.

These results agree with those from the intra-island level; again the maximum frequency of the whole phrase and the pre trill are different between Sikabae and Simabuggai. As expected the majority of significant differences are between Sikabae and the southern islands, Sipora and South Pagai, or Simabuggai and the southern islands.

Table 3.5. Showing the results of a post hoc analysis with a pair wise Mann-Witney U test using the Bonferroni correction (p x number of comparisons, therefore p x 6).

Site	Site	Variable	U Stat	p Value
Sikabae	Simabuggai	Max. freq. of phrase	2.0	0.018
		Max. freq. of pre trill	0.0	0.006
Sikabae	Sipora	Duration of phrase	5.0	0.048
		No. notes per phrase	4.0	0.030
		Min. freq. of trill	0.0	0.006
		Freq. modulation of 2nd note pre trill	2.0	0.018
		No. notes per pre trill	3.0	0.080
		Duration of pre trill	2.0	0.018
		Min. freq. of pre trill	1.0	0.012
Sikabae	South Pagai	Freq. modulation of 2nd note pre trill	2.0	0.048
		Min. freq. of pre trill	1.0	0.030
		Min. freq. of trill	2.0	0.048
Simabuggai	Sipora	Duration of phrase	3.5	0.042
		Max. freq. of post trill	0.0	0.012
		Freq. modulation of 1st note post trill	2.0	0.024
Simabuggai	South Pagai	Max. freq. of post trill	0.0	0.024

3.6 Discriminant Function Analysis

Out of the 19 variables for male Kloss's trill phases subjected to the DFA analysis, five were included in the discriminant model by the stepwise method. These variables (table 3.6) were the most efficient at distinguishing between the songs sampled from the four populations. The standardised canonical discriminant function coefficients for these variables are shown in table 3.7. They estimate the relative contribution of a variable to the three discriminant functions, therefore the reclassification of individual gibbons to the correct population (Konrad & Geissmann, 2006). Low absolute values indicate a small relative contribution.

Table 3.6 Table showing the variables used for the DFA at each step

Variable	Step
Minimum frequency of the trill	1
Maximum frequency of the post trill	2
Maximum frequency of the pre trill	3
Number of notes per phase	4
Duration of the post trill notes	5

Table 3.7 Table showing the standardised canonical discriminant function coefficients for each discriminant function.

	Function		
Variables	**1**	**2**	**3**
No. notes per phase	-1.119	-0.719	-0.219
Max. freq. pre trill	0.912	-0.031	-0.883
Min. freq. trill	0.924	0.136	0.785
Duration of post trill	1.001	0.042	0.882
Max. Freq. post trill	-0.772	1.058	0.042

The DFA created three discriminant functions (one less than the number of populations, grouping variable) and they vary in their ability for group separation. The first function contains the highest discriminatory power and the last the lowest power. This power to discriminate can be shown by the percent of 'between groups variability' attributable to a particular function. The first function makes the highest contribution to separating the four gibbon populations, by explaining 78.7% of the variability, whereas function 2 contributed just 15.5% and function 3 only 5.9%.

The discriminance scores of every individual gibbon are shown in figure 3.3, based on the first and second discriminant function. The chart illustrates the degree of separation between the mean scores of each population. The Sikabae and Simabuggai populations are clearly defined as populations using both functions, but to separate them from the Sipora and South Pagai populations the first function contributes most. It is less easy to differentiate between Sipora and South Pagai, but the second discriminant function is more useful here.

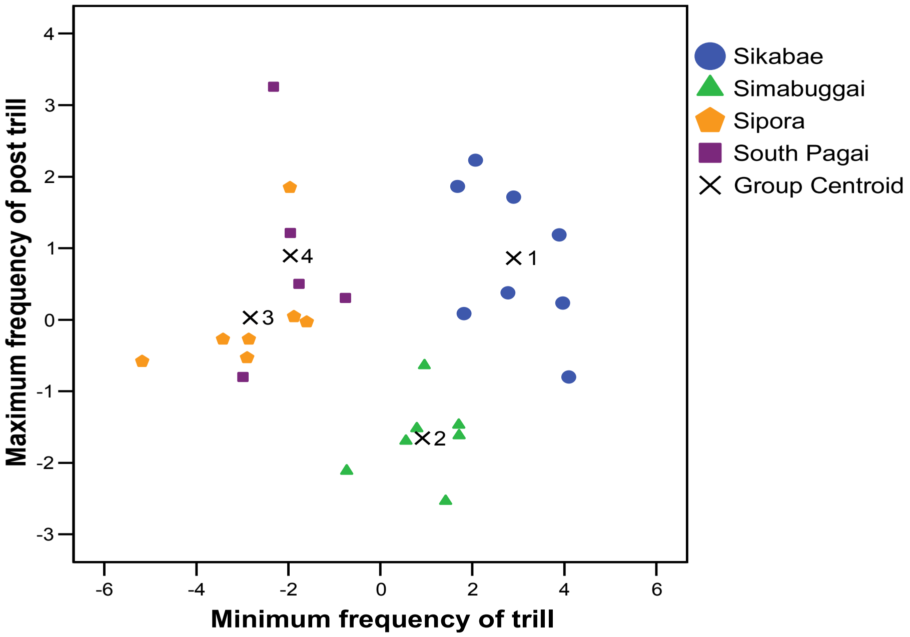

Fig. 3.3 Chart showing the discriminant scores for all individual male Kloss's gibbons with their population identity shown by the relevant symbol shapes.

The overall percentage of original gibbon groups correctly classified to their population is 92.6% (table 3.8). For both populations in Siberut, Sikabae and Simabuggai, and for South Pagai 100% of the cases were correctly assigned. For Sipora 71.4% of cases were classified correctly. Cohen's **k** demonstrates that the classification achieved is significantly different from chance (**k** = 0.901, $p < 0.000$). These results demonstrate that each population has its own set of distinguishing vocal characteristics in the trill phase that differ to one another. Only 2 cases, 28.6%, were classified wrongly, these were individuals from Sipora being placed into the South Pagai population, thus demonstrating that these two populations are more similar to each other than found within the Siberut populations.

The accuracy of the cross-validation (table 3.8) produces an overall percentage of 77.8%, which is 14.8% lower than the original classification. Cohen's **k** again shows how the assigned results differ from chance (**k** = 0.703, $p < 0.000$), despite a decrease in accuracy. 100% of cases were still correctly assigned for Sikabae, however the values for classifying the other populations decreased. Simabuggai was 85.7% correct, Sipora 57.1% and South Pagai 60% correct, suggesting that Sipora is the least distinct and Sikabae the most distinct.

Table 3.8 Classification results of discriminant analysis. The original classification was obtained when groups were classified by the functions derived from all groups (n). The cross-validation was achieved by classifying each group by the function derived from all groups other than that group (n-1). Site 1, Sikabae; 2, Simabuggai; 3, Sipora and 4, South Pagai.

			Predicted Group membership				
		Site	**1.00**	**2.00**	**3.00**	**4.00**	**Total**
Original	**Count**	**1.00**	8	0	0	0	8
		2.00	0	7	0	0	7
		3.00	0	0	5	2	7
		4.00	0	0	0	5	5
	%	**1.00**	100.0	.0	.0	.0	100.0
		2.00	.0	100.0	.0	.0	100.0
		3.00	.0	.0	71.4	28.6	100.0
		4.00	.0	.0	.0	100.0	100.0
Cross- validated	**Count**	**1.00**	8	0	0	0	8
		2.00	0	6	0	1	7
		3.00	0	0	4	3	7
		4.00	0	0	2	3	5
	%	**1.00**	100.0	.0	.0	.0	100.0
		2.00	.0	85.7	.0	14.3	100.0
		3.00	.0	.0	57.1	42.9	100.0
		4.00	.0	.0	40.0	60.0	100.0

4. DISCUSSION

This chapter discusses the results of the previous chapter and places them into the context of the background information in chapter 1, starting at the level of variation within individuals, within populations, within islands and then between populations and discriminant function analysis. The features described in the qualitative section of the results highlight the importance of being prepared to sample vocalisations at different points in the daily cycle, not just peak times, and even after periods of heavy rain because the Kloss's gibbon clearly does vocalise at unexpected times.

4.1 Intra-individual vocal variation

The descriptive statistics illustrate that the degree of variation is relatively low (< 35%) within individuals for many of the variables measured in the trill phrase, yet there are several variables which are consistently low (< 10%) in variation amongst most individuals, these are detailed in the results section 4.2. The amount of vocal variation within individuals reflects which aspects are under strict selection pressure; if variables are constant, therefore low in variation, they are likely to be the factors that convey particular information pertaining to species and sex specific qualities, that do not need to change. Variables that exhibit low variation (< 35%) are more likely to convey information regarding current circumstances, such as mate status, health, unique individual identification and a degree of individuality. Unstable variables (> 35%) are likely to be less efficient for use in individual identification unless their range does not overlap with that of conspecifics.

The difference in the amount of variation shown between the variables of the trill phrase reinforces the idea that they are under varying degrees of selection pressure. It is therefore logical to propose that some parts of the song are under stricter genetic control than others.

Only eight individuals have variables with coefficient of variation values that are over 50%, and they are equally distributed between the four populations. For six males high variation is expressed in the post trill variables. Other studies (Dallmann & Geissmann, 2001a, b; Mather, 1992) found that in female agile, silvery, and muelleri (*H. agilis, H. moloch & H. muelleri*) gibbons the most variable part of the great call are the terminal notes, analogous to the post trill notes of a male. It was proposed that this is because the terminal notes are under the least amount of selective pressure. It is possible that this relates to the Kloss's gibbon too, although support from female vocalisation analysis would be more comparable and therefore reliable.

One problem with this research is that although the terminal and post trill notes may appear to be the most variable this could simply be an erroneous feature resulting from data that is not representing the whole truth. It was noted in the field that the notes that were most likely to be missed during recording are the terminal notes because they are quieter and usually of a lower frequency. Despite being heard by ear they were not necessarily picked up by recording equipment and thereby post trill notes were often misrepresented in the analysis. Another issue with the study comparing female vocalisations (Dallmann & Geissmann, 2001b) of different species, is that the data is from a very small sample size that is unequal; 4 Kloss's, 8 agile and 8 moloch, which are analysed using a Kruskal-Wallis one way ANOVA with the post hoc Nemenyi test that are particularly susceptible to small sample sizes and therefore less reliable.

Initial observations of table 3.1 does not appear to show any pattern of intra-individual variation between the populations, but without using a statistical test it is impossible to be sure whether they are definitely the same or different. In a study on female silvery gibbons (Dallmann & Geissmann, 2001a) it was shown that there are significantly different amounts of intra-individual variation between the populations. They proposed that this is a consequence of varying population densities; if the population is small then there is more opportunity for individuality to be expressed because there are fewer individuals to identify, so the songs do not need to be as stable. However, the study does not have any relevant population density figures and it has not been shown that silvery gibbons are able to identify other individuals by their vocalisations; therefore this explanation is merely speculation.

In summary, it is clear that some parts of the trill phrase are more variable than others and that this reflects the degree of selection pressure and their function. This emphasises the importance of focusing on all parts of the phrase, because it is not known which section is species, subspecies, sex or individually specific without examining their degree of intra-individual variation first.

4.2 Intra-population vocal variation

The variation of vocal features within populations is quite low, reflecting the pattern found at the within individual level. Three variables that were the most constant at the previous level are also constant at this level and the post trill variables are again the most unstable. The bar chart reveals that the South Pagai population is the most varied for twelve variables, this could be due to the smaller sample size for this population, or perhaps it is just more varied.

Clearly vocal characteristics vary between individuals of a population; one purpose of this is to inform other gibbons about their personal qualities. For example it has been shown that male Kloss's sing about seven times more often than females. This allows neighbouring males to assess their competition because the lowest pitch they achieve relates to their body size and consequently can aid decisions regarding engagement in conflict (Whitten, 1984b). Therefore vocal qualities relate directly to 'fitness' and males which are larger are likely to have more success in defending their territory and mates, thus resulting in higher reproductive success compared to smaller males.

It is important that males are able to differentiate between other individuals, by vocalisations (Tenaza, 1976), because it allows them to make appropriate responses to neighbours and strangers, and it may also be used as a mechanism to avoid inbreeding by recognising specific factors in family vocalisations when choosing mates (Dallmann & Geissmann, 2001).

Variables that were shown to be constant at the intra-individual level and the intra-population level are important, because if they can be shown to differ between the populations, then accurate identification is possible.

4.3 Intra-island vocal variation

The results (table 3.2) from the Mann-Witney U test support a rejection of the null hypothesis, there is a significant difference between the vocalisations of Simabuggai and Sikabae. It is expected that gene flow between populations within an island is greater than between populations on different islands. However, results reveal that the Siberut populations are easier to differentiate from one another, than the two southern islands, where only one variable was found to be significantly different. This suggests that the two Siberut populations have either undergone or are undergoing allopatric subspeciation. It is obvious that the further the distance between populations the lower the degree of gene flow between them simply because individuals are more likely to breed with close neighbours than distant individuals, but this alone does not explain the significant vocal differences. Therefore, some additional factors must be at work, such as dispersal prevention, potential barriers include the numerous rivers and mountain ranges that characterise Siberut. Additionally, factors such as discontinuous tracts of forest isolating populations and pressure from hunting may limit dispersal. However, it is not possible to determine which of these is responsible because no detailed maps for the region can be accessed and none accurately display relevant geographic features throughout their history. These findings were replicated in post-hoc tests from the inter-population level, where two variables were again shown to be significantly different.

Two variables, maximum phrase frequency and notes per pre trill, which were illustrated to be constant at the previous levels, are significantly different between the two Siberut populations, which makes them efficient discriminators of individual origin. Thus highlighting the importance of looking at the degree of vocal variation at all levels.

Only one significant vocal difference was found between the Sipora and South Pagai populations, this indicates that there is still a degree of gene flow between the populations or that there has been until quite recently. The reasons behind this are discussed fully in the next section.

Overall the results illustrate that there is a clear difference between the vocalisations of the two Siberut populations, and limited differences between the Southern islands. The next step is to compare differences between all four populations.

4.4 Inter-population vocal variation

The results from the Kruskal-Wallis test for many of the variables are significant at the 0.05 level (table 3.4) therefore the null hypothesis of no difference in vocalisations between the four populations is rejected. As expected there are major differences between Siberut and the two southern island populations, this is caused by a lack of dispersal from the most northern island to the southern islands. The straits of water between the Mentawai islands are difficult to cross due to the strong currents, caused by the Indian Ocean, thus making dispersal by rafting virtually impossible (Dring, 1990; Whittaker, 2005). Even people travelling between the Mentawai Islands return to mainland Sumatra first, before going travelling back out to another island.

In a similar study it is proposed that the importance of vocal differences between populations of female silvery gibbons (*H. moloch*) actually indicate subspecies. It was found that variables in the first part of the great call were the most ideal for individual identification (Dallmann & Geissmann, 2001b). Therefore it is possible to suggest that the differences found between Siberut and the other islands are also indicative of a subspecies division.

It is odd that the two southern populations are less different to one another than the two Siberut populations. It suggests that there is a degree of gene flow between the southern islands despite the large distance and barriers separating them, or that there has been until very recently. Sea levels between the islands are approx 10-25m deep but 7000 years ago sea levels were even lower between the four islands and they formed a single continuous landmass, therefore it is possible that gene flow was maintained till then. However, this does not explain why differences within Siberut should be greater than differences between the southern islands. It is not a viable proposal that dispersal between these two islands has been maintained by human intervention and the pet trade, because it is notoriously difficult to release gibbons successfully back into the wild (Cheyne & Brule, 2004). Alternatively, it could just be due to the small sample size or that they differ in characteristics not measured in this analysis.

Limitations of the Kruskal-Wallis test are that the different levels cannot be compared, for example within and between individuals, within and between populations. This would be desirable because it would allow researchers to identify whether vocal variation is lower within populations than between populations, thus demonstrating that they are different subspecies. One method that has been designed by Dallmann & Geissmann (2001) to do this is the Mean Pairwise Difference (MPD) of scaled variables. It was found that inter-individual variability is significantly higher than intra-individual variability, and that intra-population variability is lower than inter-population variability in the female silvery gibbon (*H. moloch*). This test could be applied to the Kloss's vocalisations in the future to support findings from this analysis.

Results from the Kruskal-Wallis and post hoc analysis show that there are three distinct units; the Sikabae population, Simabuggai population and a Southern population covering Sipora and South Pagai islands and each of them have a unique set of vocal characteristics defining them from the other units. These groups must have arisen by allopatric speciation; this is where populations can not interbreed with others due to an inability or opportunity to disperse. In time the populations diverge genetically through random genetic events and in relation to selection pressures and these differences are reflected in their phenotypic traits such as vocalisations.

4.5 Discriminant function analysis

The discriminant function analysis demonstrates that it is possible to differentiate between the four populations of Kloss's gibbons sampled using the trill phrases of their vocalisations at a highly accurate level of 92.6% (percentage of individuals correctly classified to their populations). This suggests that there is a high degree of vocal diversity amongst the sampled populations of male Kloss's gibbons. Therefore, the populations must differ in their expression of population-specific vocal characteristics.

The 7.4% which were wrongly assigned were all from the Sipora population and placed into the South Pagai population, this could be due to the small sample size of South Pagai which may be less representative of their variation and therefore more difficult to distinguish between the two. This pattern is not however unexpected; it was anticipated that the populations of Sipora and South Pagai would be more similar to each other, yet easily differentiated from Siberut populations because this follows the pattern of other endemic primate subspecies distributions. In contrast to expectations, the Simabuggai and Sipora populations are more easily distinguished than expected, supporting results from the Kruskal-Wallis and post-hoc test. Overall the results from the all the analysis support a split of the Kloss's gibbon into three distinct units; two in Siberut and one on Sipora and South Pagai. It is unfortunate that no populations could be sampled in North Pagai, but it is highly likely, due to its close proximity to South Pagai and Sipora that the vocal characteristics are more similar to these populations than to Siberut's populations.

Variation in vocalisations has also been successfully used to distinguish populations in the gibbon genus *Nomascus*. It was found, through using discrimination analysis, that there was a significant difference between populations in South and North Cambodia, thereby resulting in a newly suggested taxonomic grouping with *N. Gabrielle* in the south and *N. l. siki* in the North. In this example it is likely that dispersal between these different populations is prevented by geographical barriers, such as the mountain range, thus resulting in allopatric subspeciation (Konrad & Geissmann, 2006).

Discriminant analysis has also been used on vocalisations on the Thomas langur (*Presbytis thomasi*) where researchers showed that 95.6% of individuals could be placed into their correct populations (Wich et al. 2003). This evidence adds support to findings from the male Kloss's gibbon that vocal variation can be a valid discriminator of population differences and subspecies distributions and confirms that the DFA is a valid choice of statistical test.

4.6 Other evidence of Kloss's subspeciation

Despite the lack of fur colour variation in the Kloss's gibbon, other morphological evidence supports the DFA results of a subspecies classification. Usually in gibbons the hair on the outer side of the forearm flows towards the wrist except in siamangs where it flows towards the elbow. Interestingly the hair of Kloss's gibbons in Sipora flows to the elbow but in Siberut it flows towards the wrist, this may be indicative of the subspecies differences too (Chasen & Kloss, 1927; Groves, 2001).

Although vocal data supports a division of the Kloss's into subspecies, it is uncertain whether these phenotypic differences are supported by differences in their genotype. Research (Whittaker et al. 2004; Whittaker, 2005) on the D-loop of mitochondrial DNA, suggested that there are no subspecies divisions between the islands and that these populations have not been separated long enough for lineage sorting to occur. However, a small sample size was used and no comparative study was done on the other three primate species to determine whether subspecies differences are shown in that area of mtDNA. A study on a fragment from the mitochondrial cytochrome *b* gene of Mentawai macaques supported the morphological evidence and separates it into two subspecies because variation within the populations was low whilst variation between populations was high (Roos et al, 2003). So perhaps there is genetic evidence yet to be analysed in a region which highlights significant differences and subspecies divisions for the Kloss's.

An alternative idea is that variation is not reflected in the genotypes of Kloss's gibbons yet because of the short time span allowed for genetic divergence. The average generation time for macaque species is 54 months (Harvey et al 1987) whereas the average generation time for hylobatids is 110 months. So, for every 1000 years of separation this equals 222 generations for macaques and just 110 for gibbons and the islands have been separated for approximately 7000 years (Whittaker, 2005). Therefore, although these endemic primate species share the same biogeographical history, it is possible that different degrees of lineage sorting have occurred and this is why no significant differences in genetic material have been detected.

The differences that have been shown between the populations would not be suitable for discriminating individual identity on the basis of just listening to the vocalisations; this is because the most efficient functions are frequency based. However, individual identification can be achieved by comparing vocalisations to the data already presented. Although this is a lengthier process it is still a potentially important tool in conservation, especially since there are no comparable morphological traits available that represent the three different subspecies populations of the Kloss's gibbon (Geissmann, 1995).

Based on their vocal diversity it is clear that there are three distinct units of the Kloss's gibbon, two within Siberut and the third on Sipora and South Pagai, this is demonstrated by results from the post hoc test of Kruskal-Wallis and the discriminant function analysis. Evidence from vocalisations of male Kloss's gibbons therefore supports their division into three distinct subspecies. Although, speculative, the most likely cause of this variation are dispersal barriers leading to allopatric speciation.

5. CONCLUSION

5.1 Conclusion

In respect to the initial objectives formed in the introduction, 1, there are significant differences in the trill phrase of the male's vocalisation between Siberut and the southern populations. 2 vocal differences within Siberut are equal to differences between Siberut and the southern islands, and there are few differences between the southern islands. 3, these vocal differences can be used to predict provenience of singing Kloss's gibbons at an accuracy of 92.6% using discriminant function analysis. 4, the vocal differences that exist would not allow discrimination by trained observers without using sound and statistical analysis because the best discriminators are frequency based measurements.

5.2 Further research

It is possible that other vocal differences exist between the populations that could be exploited to allow discrimination simply by listening, only the last phrase of the males vocalisations were analysed and there are potentially more differences in the initial phrases.

It is clear that male Kloss's gibbons exhibit some individuality in their vocalisations, but it is not known whether they remain stable over time. Neither is it known if male Kloss's gibbons are able to differentiate between conspsecifics and strangers. Therefore, the vocalisations that have already been collected could be used in playback experiments to investigate both of these features and determine which constant variables are the sex and species specific characteristics.

Alternatively, there is potential for vocalisations studies on the other Mentawai primates with the aim of determining levels of diversity and therefore continuing the investigation into the subspecies debate. Finally, a study of captive Kloss's gibbons has the potential to discover their subspecies origin, possibly looking at hybridisation and its effects on vocal characteristics and to provide a comparison to their wild counterparts.

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Appendix 1 – Table showing the average measurements for each variable for every male Kloss's sampled

		whole phase				pre trill					
Site	**Individual**	**duration**	**no notes**	**min freq**	**max freq**	**2nd freq mod**	**3rd freq mod**	**no notes**	**duration**	**min freq**	**max freq**
Sikabae	**m2**	5.25	11.3	603.75	1645.39	911.06	802.71	3.6	2.82	686.95	1647.15
	m4	5.69	10.8	595.08	1633.63	911.23	759.83	4.0	2.58	685.30	1633.63
	m3	5.91	11.6	540.79	1700.27	1023.81	950.48	3.8	3.31	630.31	1695.41
	bert	7.68	15.5	551.25	1685.60	889.95	950.95	5.0	3.64	734.60	1685.60
	boris	9.89	17.0	676.55	1732.65	885.50	1005.45	5.5	4.19	727.10	1732.65
	bob	5.61	13.0	548.98	1659.05	973.00	823.58	4.5	2.30	675.45	1659.05
	basco	6.16	11.0	548.78	1662.50	864.56	850.06	3.7	3.83	699.96	1662.50
	beck	5.39	10.7	618.66	1622.47	858.83	849.82	3.7	2.73	710.18	1618.62
Simabuggai	**s2**	7.33	15.2	505.06	1635.49	943.00	856.06	4.6	3.28	608.62	1618.05
	gerald	8.15	16.1	538.51	1597.56	586.19	718.94	5.3	5.57	647.25	1597.56
	jim	8.07	18.5	641.95	1407.55	537.18	677.38	6.5	4.69	719.60	1407.55
	a6	7.81	15.8	476.00	1532.95	874.80	848.55	5.0	3.20	616.95	1532.95
	jon	7.19	16.6	560.70	1507.24	892.56	706.56	4.8	3.02	614.44	1507.24
	tod	5.56	14.4	570.30	1567.93	818.28	700.93	5.0	2.72	716.80	1556.11
	sid	5.44	13.6	563.56	1544.66	843.52	692.16	5.2	2.60	686.14	1544.66
Sipora	**male4**	11.03	16.7	481.19	1529.52	696.77	837.84	6.2	6.60	499.13	1521.77
	male9	11.49	17.4	458.74	1733.41	557.68	810.02	5.9	6.21	566.74	1568.91
	male8	7.59	15.8	617.30	1499.33	693.85	732.00	5.5	3.85	647.35	1502.87
	male7	10.47	18.8	525.87	1503.30	698.08	726.25	6.2	3.99	599.43	1503.30
	male5	8.48	17.0	472.36	1503.38	806.70	813.44	6.2	4.53	538.34	1503.38
	male2	8.15	18.5	513.82	1729.53	871.72	1108.10	5.7	4.48	547.82	1728.32
	male6	8.53	15.8	454.80	1370.86	649.92	790.95	5.8	5.04	503.69	1366.14
South Pagai	**male9**	6.64	9.0	594.70	1390.07	333.30	0.00	2.0	2.68	619.67	1274.30
	male8	6.21	14.3	541.55	1479.50	630.00	590.90	5.0	3.31	661.63	1468.90
	male5	8.34	15.3	524.70	1438.95	696.45	694.60	4.3	3.45	565.95	1396.55
	male2	9.06	21.2	513.28	1506.14	810.98	752.50	6.8	3.83	572.24	1506.16
	male1	10.58	18.3	429.73	1694.28	878.34	1085.30	4.8	4.18	502.28	1650.94

Appendix 1 Cont. – Table showing the average measurements for each variable for every male Kloss's sampled

		trill				**post trill**				
Site	**Individual**	**no notes**	**duration**	**min freq**	**max freq**	**notes**	**duration**	**min freq**	**max freq**	**1st note**
Sikabae	**m2**	6.0	0.80	783.54	1187.25	1.6	1.60	625.08	1341.40	696.27
	m4	5.0	0.70	787.10	1165.65	1.8	2.37	640.90	1218.10	586.93
	m3	6.2	0.83	760.07	1207.29	1.6	1.78	532.92	1341.55	751.47
	bert	9.0	1.18	757.10	1221.85	1.5	2.90	562.20	1251.85	637.15
	boris	9.0	1.03	749.60	1244.35	3.0	4.70	599.70	1318.20	764.60
	bob	6.8	0.84	783.48	1147.00	1.8	2.49	564.23	1086.25	495.50
	basco	5.8	0.80	796.75	1205.35	1.5	1.49	554.39	1136.28	538.22
	beck	5.3	0.75	799.60	1172.72	1.7	1.84	646.33	1280.97	528.11
Simabuggai	**s2**	8.8	1.17	708.16	1237.31	1.9	2.81	508.85	1104.01	518.88
	gerald	9.0	1.19	742.88	1136.21	1.9	2.51	553.25	1018.93	427.24
	jim	9.8	1.07	790.65	1179.90	2.3	2.30	649.35	1089.25	357.75
	a6	9.0	1.10	714.40	1114.83	1.8	3.51	470.83	1099.95	520.20
	jon	10.0	1.08	770.34	1163.38	1.8	3.17	564.68	1179.26	602.60
	tod	7.4	0.93	767.70	1190.69	2.0	2.03	562.21	1063.55	394.91
	sid	6.8	0.95	762.84	1161.18	1.6	1.89	555.84	1037.62	390.90
Sipora	**male4**	8.0	1.28	663.91	1077.28	2.3	3.11	509.29	1261.18	668.68
	male9	8.3	1.17	726.23	1177.76	3.3	3.99	522.60	1499.53	824.30
	male8	7.8	1.02	725.87	1161.68	2.5	2.77	614.37	1273.75	552.83
	male7	6.8	1.04	626.82	1139.60	5.8	5.55	467.18	1357.97	681.30
	male5	7.0	0.90	679.34	1104.02	3.8	3.05	506.92	1280.58	580.84
	male2	10.3	1.04	689.58	1170.42	2.5	2.63	564.50	1357.58	670.27
	male6	7.5	0.84	615.38	1132.08	2.3	2.62	496.07	1219.32	631.78
South Pagai	**male9**	4.7	1.25	669.63	1049.40	2.3	2.78	574.70	1214.37	486.43
	male8	7.3	0.85	758.00	1168.75	2.0	2.02	524.73	1242.95	527.40
	male5	7.3	0.95	722.13	1116.28	3.5	3.54	548.88	1295.15	644.65
	male2	8.0	1.00	739.72	1206.18	4.6	4.26	476.76	1357.00	755.36
	male1	7.2	1.08	674.08	1132.82	6.3	5.41	443.59	1659.36	1004.27