VOCAL DIVERSITY OF FEMALE KLOSS'S GIBBONS (*Hylobates klossii*) IN THE MENTAWAI ISLANDS, INDONESIA

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DEDICATION

I dedicate my dissertation to my Grandma who sadly passed away while I was still in Indonesia, but who's belief in me has never faltered and who had the most knowledge about gibbons I have ever seen in an 89 year old!

ABSTRACT

The vocal diversity of female Kloss's gibbons was assessed by spectrographically analysing the sex-specific, stereotypic great call phrase of the female. Songs were recorded during a period from June – August 2005 in the Mentawai Islands 85-135km off the coast of West Sumatra, Indonesia. Four locations on three different islands in the chain were used: Simabuggai (Siberut), Sikabei (Siberut), Saureinu (Sipora) and South Pagai (South Pagai). Songs were recorded from three to six listening posts per location using a modified point census technique. A total of 24 females and 137 great calls were of sufficient quality to be spectrographically analysed from the four populations.

Spectrographic analysis was achieved using 'Raven 1.2' software and data was obtained for 12 variables: (1) Pre-trill + trill duration, (2) Frequency band exploited during pre-trill and trill, (3) Duration of 1st note, (4) Frequency modulation of 1st note, (5) Duration of 2nd note, (6) Frequency of 2nd note, (7) Number of pre-trill notes, (8) Pre-trill duration, (9) Notes/second in pre-trill, (10) Trill duration, (11) Number of trill notes, (12) Notes/second in trill. No variables were included from the post-trill element of the great call phrase because of insufficient recording quality. Statistical tests determined significance of diversity in the following categories: Intra-individual, inter-individual, inter-population, intra-island, inter-island, and Siberut group and Sipora & South Pagai group. Coefficient of variation, Mann Whitney U and Kruskal Wallis non-parametric analysis of variance tests demonstrated significant diversity of individual, population and island categories. Discriminant function analysis assigned great calls to individuals correctly in a range of 47.8-81.1% of cases in the 4 populations, assigned individuals to populations correctly in 58.3% of cases, and assigned individuals to their correct islands in 70.8% of cases. Discriminant function analysis for classification of individuals to either a Siberut group or Sipora & South Pagai group, assigned individuals correctly in 62.5% of cases when all variables were included, and in 79.2% of cases when the variable ‘ Number of notes in trill’ was removed.

Results suggest individuals are distinguishable from each other and therefore there is potential for individual recognition among conspecifics. Three hypotheses are proposed to explain inter-individual diversity: (1) Trilling as a handicap, (2) Neighbour-stranger discrimination, (3) Relaxed selection. Inter-individual diversity differs between populations and this is suggested to be because of local differences in forest structure and characteristics. Inter-population differences are hypothesised to be due to rivers acting as facilitators to speciation. Intra-island (Siberut) diversity is lower than inter-island diversity as expected. Inter-island diversity is significant but implies an invalid clinal relationship throughout the island chain. The level of diversity between the Siberut group and the Sipora & South Pagai group indicates the Kloss’s gibbon should remain with no Evolutionarily Significant Units (ESUs) despite a trend suggesting a process of divergence, and advocate a reassessment of the current classifications of the three endemic Mentawai monkey species.

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1. INTRODUCTION

1.1. BACKGROUND

1.1.1. HYLOBATIDS

Hylobatids, commonly called gibbons, are monogamous, frugivorous, arboreal and territorial apes (Brockelman, 1984; Chivers, 1977). Known as the 'Lesser Apes', the amount of scientific and media interest attracted is very small in relation to the 'Great Apes'. Gibbon conservation, taxonomy and general behavioural ecology has thus been overshadowed by their more easily accessible counterparts. Gibbon species include the most threatened primates in the world, with the Hainan black crested gibbon being placed in the top 25 endangered primates in the world (Mittermeier *et al.*, 2005). All gibbon species are listed under Appendix 1 of the Convention on International Trade in Endangered Species (CITES, 2005) and all are near threatened, vulnerable, endangered or critically endangered on the World Conservation Union (IUCN) Redlist (IUCN, 2005).

1.1.2. THE KLOSS'S GIBBON *(Hylobates klossii)*

The Kloss's gibbon (*Hylobates klossii*) is endemic to the Mentawai Islands of Indonesia and is sexually monomorphic, black in colour and the smallest of all gibbon species (Geissmann, 1993). IUCN (2005) class the species as Vulnerable, primarily due to hunting and habitat destruction caused by humans (Tenaza & Tilson, 1985). However, the data the IUCN classification is based on is out-dated and recent data recommends the species be elevated to 'Endangered' status (Whittaker, 2005).

Kloss's gibbons typically have a home range of 5-8 hectares (Tenaza, 1975) and use set arboreal routes to travel around their range, utilising the upper canopy for singing and sleeping, and the middle canopy for feeding and travelling (Whitten, 1982b). Sleeping trees are 35-55m tall, 0.5-1.5m wide and liana-free, and are usually situated towards the centre of the gibbon territory (Tenaza & Tilson, 1985). In contrast, langurs (*Presbytis potenziani*) use sleeping trees on the periphery of a gibbon's territory, implying interspecific competition (Tilson & Tenaza, 1982). In comparison to other *Hylobates* species, Kloss's gibbons eat a high percentage of insects and low percentage of leaves within their diet (Whitten, 1982b). The reason for this is unknown but may be linked to chemical defences within leaves in the Mentawai Islands. Kloss's gibbons also spend more time resting than other gibbon species, and this may be linked to neutralising chemical defences in the small amount of foliage they do consume.

The Kloss's gibbon song is unusual for hylobatids because the male and female do not duet – the male sings pre-dawn and the female sings post-dawn (Haimoff & Tilson, 1985). The only other hylobatid to not duet is the Javan gibbon (*Hylobates moloch*). It is postulated the function of the male song of the Kloss's gibbon is to attract mates and that it conforms to 'Zahavi's Handicap Principle' because males spend a greater time singing than females and the song exposes the male gibbon to dangers and therefore indicates fitness (Whitten, 1984b; Geissmann *et al.*, in press). Duet-splitting is the term for the process by which solo songs have emerged in both Kloss's gibbons and their sister taxon, Javan gibbons, and is thought to be a derived characteristic (Geissmann, 2002).

Morphological features can also be labelled primitive or derived. The absence of a face ring or brow band in Kloss's gibbons was originally thought to be a primitive feature because it is a simple monochromatic form, but it has recently also been labelled a derived feature after captive studies with Siamangs (*Symphalangus syndactylus*), which are also black (Geissmann, 2003).

In light of this evidence, Kloss's gibbons are not the most primitive gibbon species as once thought, but are a more recently diverged species. However, trilling, exhibited within the song of Kloss's gibbons, is a primitive characteristic (Dallman & Geissmann, 2001b). This characteristic may have remained unchanged simply because there has been no selection pressure for it to change. The duet-splitting of Kloss's gibbons and Javan gibbons is thought to be due to relaxed selection because these species do not live alongside other gibbon species (sympatry) and therefore there is a reduced need to prevent interspecies breeding (Geissmann, 2002)

Research of Kloss's gibbons and understanding of the species is limited. Published papers specifically researching Kloss's gibbon song number only three (Haimoff & Wilson, 1985; Whitten, 1984; Whitten, 1981) and all focus on the island of Siberut, and until this work and a recent PhD project (Whittaker, 2005), the Kloss's gibbon had not been studied since the 1980s.

1.1.3. SONG STRUCTURE

The terminology used to describe gibbon song in this work follows that used in previous studies of gibbon song for consistency (Short, 2005; Konrad & Geissmann, 2004, unpub.; Dallmann & Geissmann, 2001a,b; Haimoff & Gittins 1985; Haimoff & Tilson, 1985). The song structure of the Kloss's gibbon consists of single frequency build-up notes, followed by repeated great call phrases. Each great call phrase consists of three elements: the pre-trill, the trill and the post-trill (Fig. 1.1).

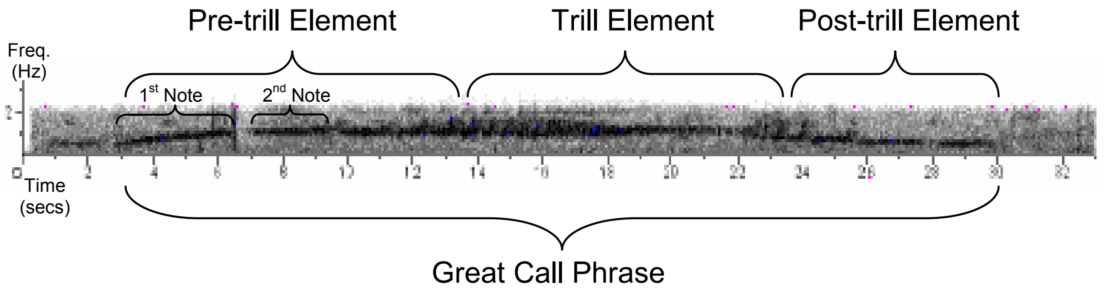


Fig. 1.1. Great call phrase of female Kloss's gibbon (*Hylobates klossii*)

The phrase begins with a single rising note, followed by single frequency notes in the pre-trill element. The trill element consists of rapid notes for a period of around eight to twelve seconds and involves in the region of 65 notes. The trill can also be referred to as an amplitude modulated structure. The post-trill element has notes which gradually lengthen and decrease in frequency and amplitude. The entire great call usually lasts in the region of 25-30 seconds.

1.1.4. GIBBON PHYLOGENY

Phylogeny is the practice whereby the genetic relationships between species are determined, ultimately producing an evolutionary tree. Gibbon phylogeny is debatable and various methods have been employed to attempt its resolution. Vocal data are more reliable in phylogeny construction of Hylobatids than molecular or morphological data (Geissmann, 2002). The use of vocal data is supported by hybrid studies and rehabilitation studies, which indicate it is a genetically transmitted characteristic (Cheyne & Brule, 2002; Geissmann, 1984; Tenaza, 1984). Thus vocal data provides information about population and species differences on a genetic level, and this is exemplified because gibbon species can be distinguished by species-specific vocalisations (Geissmann, 1993; Mitani, 1987).

The function of gibbon song is proposed to be the advertisement and defence of territory/mates and pair bond reinforcement (Ahsan, 2001; Cowlishaw, 1992; Brockelman, 1984; Gittins, 1984; Marshall & Marshall, 1976) therefore a species-specific song is desirable. Geissmann (1993) initiated the exploitation of these species-specific songs for taxonomic determination of a given population of gibbons. The use of vocalisation as a diagnostic tool for taxonomy has been pioneered with relation to gibbons by Geissmann (1993) and the Gibbon Research Laboratory.

Individual song variability within gibbon species has been researched (Geissmann *et al.*, in press; Dallmann & Geissmann, 2001a, 2001b; Haimoff & Gittins, 1985; Haimoff & Tilson, 1985), however, there is as yet no published study utilising gibbon song as a diagnostic tool for identification of Evolutionarily Significant Units (ESUs). ESUs are used to define management units within a species and operate at the genetic level (Frankham *et al.*, 2004), but can be adapted to gibbon vocalisations because of the genetic basis. ESUs are defined as unique groups within a species due to the genetic composition of that group. ESUs are often used in conservation to guide management strategies because they allow unique groups of animals or plants to be identified and managed in light of this knowledge of uniqueness (Alpers *et al.*, 2004; Holder *et al.,* 2004; Daugherty, 1990). Gibbon song has recently been used to investigate species boundaries in crested gibbons (Konrad & Geissmann, in press).

Galagos have been successfully split into species with call variability as a key characteristic (Ambrose & Bearder, 1998; Bearder *et al.*, 1996; Bearder, 1995; Courtenay & Bearder, 1989).

Chromosome number can be used as a defining feature of a genus or species. Gibbons have recently been divided into four genera, elevated from subgenera, to reflect the chromosome number inherent within certain groups (Roos & Geissmann, 2001). These genera are as follows: *Hylobatidae, Bunopithecus, Nomascus* and *Symphalangus* (Table 1.1).

Table 1.1. Gibbon Systematics with Recently Split Genera (Geissmann, 2005)

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

Subspecies exist for some species of hylobatid, however, the determination of the subspecies is often not straightforward. For example, *H. agilis agilis* and *H. a. unko* are only differentiated by a variation in the ratio of pale and dark pelage colour morphs (Brandon-Jones *et al.*, 2004), which is clearly unreliable. Andayani *et al.*

(2001) named the Javan gibbon as two subspecies by the use of molecular data but the samples of individuals were small and the nature of molecular data means only small parts of the genome are examined, although, it is likely the Javan gibbon exhibits two subspecies due to the habitat fragmentation on Java. Whittaker *et al.* (2004) used molecular data to look at Kloss's gibbon population differences and found no significant difference between populations, however, the same limitations as just discussed apply to this study.

Vocal data allow a much more holistic and less invasive method of examining the relationship of gibbon populations, whilst remaining genetic in origin. Therefore, investigation of Kloss's gibbon vocal diversity yields information about the phylogeography of the species i.e. the relationship between genetics and geography.

1.1.5. THE MENTAWAI ISLAND MONKEYS

An indication that differences are present in the endemic primates on the different islands in the chain comes from studies on the other three Mentawai Island primates, the Mentawai monkeys. The Mentawai Island macaque was recently split into two species following genetic analysis of populations on different Mentawai islands (Roos *et al.*, 2003). The snub-nosed pig-tailed langur (*Simias concolor*) exists throughout the Mentawai Islands and has been classified as two subspecies, *Simias concolor concolor* and *Simias concolor siberu* (Chasen & Kloss, 1927), one of which occurs on Sipora and the Pagais, and one which occurs on Siberut. The species is in the top 25 endangered primates in the world (Mittermeier *et al.*, 2005). The Mentawai langur (*Presbytis potenziani*) has also been classified as two subspecies, *Presbytis potenziani potenziani* and *Presbytis potenziani siberu*, (Chasen & Kloss, 1927) with the same pattern of geographic occurrence as the Mentawai langur.

1.1.6. THE MENTAWAI ISLANDS AND THEIR BIOGEOGRAPHY

The Mentawai Islands are an island chain 85-135km off the coast of West Sumatra, Indonesia in the Indian Ocean (Whitten, 1982) (Fig. 1.2). The chain consists of four islands: Siberut, Sipora, North Pagai and South Pagai. The islands and have vegetation consisting primarily of tropical and subtropical moist broadleaf forest of the Dipterocarpaceae family (WWF, 2005), and a mountainous terrain. In order to understand the population relationships of a species, the general biogeography of an area must be discussed because of the effects of isolation. The Mentawai Islands exist as part of the Sunda Shelf, an area with highly unique geological features. The tectonics of the region led to a number of islands forming along the West coast of Sumatra, including the Mentawais. Sundaland is currently a focus of biodiversity interest at Conservation International (CI) (CI Padang, pers. comm.) and has been deemed a biodiversity hotspot (Myers *et al.*, 2000).

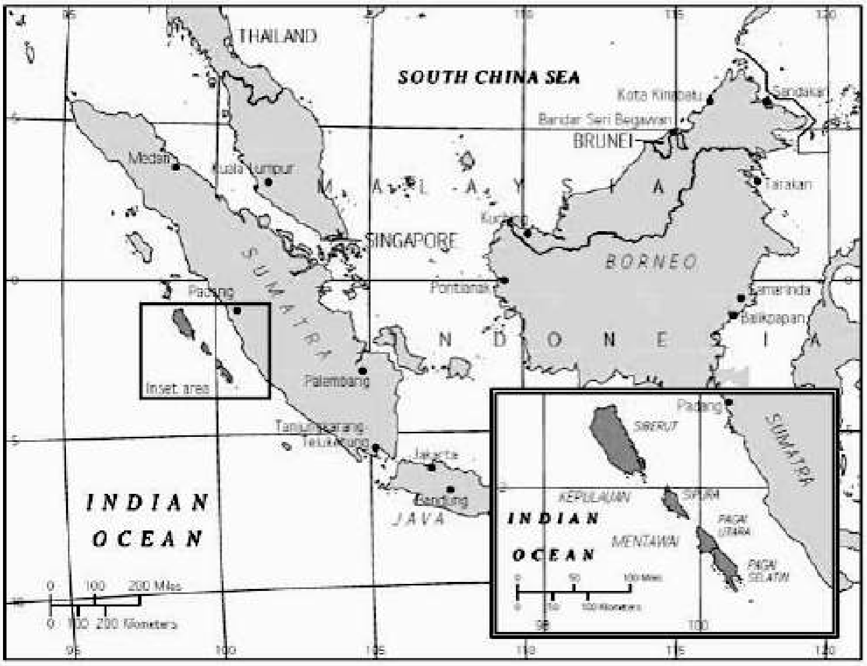


Fig. 1.2. The Mentawai Islands and Indonesia (Falk, 2000)

Due to a subduction zone between two tectonic plates, a 1000m deep trench exists between the Mentawai Islands and Sumatra (Moore *et al.*, 1980). This has served to isolate them from the rest of the Sunda Shelf even during substantial drops in sea level (Baroux *et al.*, 1998). The isolation has been complete for at least 500,000 years because it has been this long since sea levels were 200m below present levels (BPL), and although the 1000m trench was still submerged, land surrounding the trench is at a depth of 200m and land bridges may have formed in these exposed areas, connecting the Mentawais indirectly to the Sunda Shelf (Batchelor, 1979). Prolonged isolation has meant that a large proportion of the islands flora and fauna is endemic (39% mammal species: WWF, 2001). The map illustrates sea levels at 120m BPL and the Mentawai Islands remain separate from the rest of the Sunda shelf (Fig. 1.3).

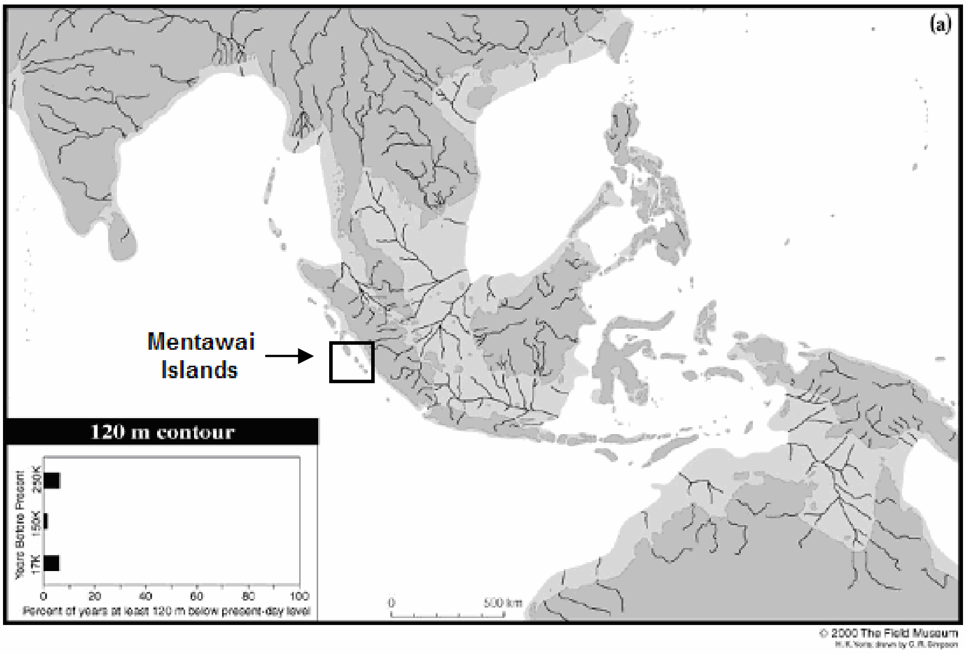


Fig. 1.3. Exposed Land Mass with Sea Levels 120m BPL
(Adapted from Voris, 2000)

The Mentawais are thought to have remained forested during the last glacial maximum (LGM) and subsequently contain mainly forest-dependent species

(Meijaard, 2003). The land connecting the islands to Sumatra at periods of low sea level may have contained more open habitat (for example, savanna), therefore providing a barrier to dispersal even during connection events, and serving to further increase the isolation of the Mentawai Islands.

The islands used for field sites in this study are Siberut, Sipora and South Pagai. Siberut is the northernmost of the four Mentawai Islands and is 4,030 km^2 with an estimated population of 25,000 people and 68,000 non-human primates in 1995 (Fuentes, 1996/1997). It is likely the non-human primate figure has decreased with a corresponding increase in humans.

Sipora contains the provincial capital of the Mentawai Islands and thus has a relatively large population, despite it being the smallest of the four islands, with a total area of 845km^2 (Fuentes, 1996/1997). South Pagai Island is the southernmost island and is 900km^2. The island was only colonised by humans in the last 300 years (Fuentes, 1996/1997) along with North Pagai, however, it is these two most recent observers of human activity that have witnessed the greatest amount of human related destruction, with primary forest on North Pagai no longer existent due to logging (PT Minas, pers. comm.). It is for this reason no research was conducted on North Pagai.

1.2. REPORT OBJECTIVES

1.2.1. AIMS AND HYPOTHESES

The study aims to assess the diversity of vocalisations produced by the Kloss's gibbon (*Hylobates klossii*), the ape endemic to the Mentawai Islands, Indonesia. The study will determine whether there is significant vocal diversity of female Kloss's gibbons within the island chain at the individual, population, island and a Siberut and Sipora & South Pagai group's level. Previous studies have assessed geographic variation in vocalisations in primates (Gamba & Giacoma, 2001; Mitani *et al.*, 1999, 1992; Fischer *et al.*, 1998; Ambrose & Bearder, 1998; Arcadi, 1996). The aim will be achieved by recording the gibbons' songs using a modified point census technique and analysing the great calls of the song using spectrographic methods. The overall hypothesis for this study is that the vocal diversity of female Kloss's gibbons will not be significant. This is broken down into six smaller hypotheses:

(1) There is no significant intra-individual diversity in female Kloss's gibbons.

(2) There is no significant inter-individual diversity in female Kloss's gibbons. and therefore, is no potential for individual recognition by conspecifics.

(3) There is no significant inter-population diversity in female Kloss's gibbons.

(4) There is no significant intra-island diversity in female Kloss's gibbons on Siberut island.

(5) There is no significant inter-island diversity in female Kloss's gibbons and therefore no divergence has occurred between the islands.

(6) There is no significant diversity between a Siberut group and a Sipora & South Pagai group and therefore, the Kloss's gibbon species is not significantly diverse enough to consist of Evolutionary Significant Units (ESUs).

1.2.2. REPORT STRUCTURE

The methodology describes how fieldwork was undertaken and data obtained. Spectrographic methods and statistical methods are explained and justified. The results section details the diversity within each of the following groups: Intra-individual, inter-individual, inter-population, intra-island, inter-island, and Siberut group and Sipora & South Pagai group. Non-parametric tests and discriminant function analysis is used where appropriate.

The discussion offers explanations of the results in the same format as the results section by discussing each group separately. Environmental fluctuations, age, and individual recognition are discussed in relation to individuals. Population differences focus on local habitat and how these differ, in addition to attempting to explain unexpected results by a tentative hypothesis. Island diversity focuses on the quality of results in this section. The Siberut, and Sipora & South Pagai section discusses the possibility of ESUs within the Kloss's gibbon species, and the impact this has on existing classifications of the Mentawai monkeys. A critique of this work highlights limitations of the project, and possibilities for future research are suggested, before a succinct summary section.

2. METHODOLOGY

2.1. PILOT STUDY

Prior to the project, four days was spent at Twycross Zoo, Leicester, UK. Twycross Zoo is the only institution outside of South-East Asia to hold a Kloss's gibbon in its collection and the individual is a lone adult male. The researcher observed the gibbon for four mornings between the 16th and 19th of January 2005 and made *ad libitum* recordings of its behaviour. Any vocalisations were recorded in the way detailed in the main project methods and using the same equipment. Equipment use was also practised on other gibbon species within Twycross Zoo. The aim of this pilot study was to provide a familiarity with the study species and the recording equipment and to identify any possible problems before departing for Indonesia.

The pilot study was successful and on completion the researcher was familiar with the equipment needed to record gibbon vocalisation, and of the protocols required (Section 2.4.1). The Kloss's gibbon sang once but the song was not a full song, likely due to his age and that he was housed alone. The timing of the singing was later than anticipated by wild studies at 11:25am and I would suggest that this is because at this time, gibbons in the surrounding enclosures ceased singing. This therefore supports the fact that Kloss's gibbons sing alone. However, the gibbon may have sung before the zoo was opened, at the time expected for a male of the species, and the song recorded could be an example of the post-dawn song (Haimoff & Tilson, 1985).

2.2 STUDY SUBJECTS

The study subjects were the populations at the sites detailed in the following section. The populations were wild-living Kloss's gibbons (*Hylobates klossii*) on the islands of Siberut, Sipora and South Pagai. Demographic information for the study subjects and populations is unavailable; however, the sample is assumed to be representative due to the methods employed to obtain recordings. A total of 24 females were recorded to a sufficient quality allowing analysis in the following breakdown: Simabuggai 7, Sikabei 7, South Pagai 5, and Saureinu 5. A total of 137 great calls were of sufficient quality to be analysed (average 5.7 per female).

2.3 STUDY SITES

Songs were recorded from four sites as detailed below. Sites were chosen on the basis of recommendation from previous researchers or were *ad lib.* The four sites covered a wide range of the Mentawai Island chain (Fig. 2.1). There were three to six listening posts per study site (Fig. 2.2). GPS waypoints can be found in Appendix 1 for each study site and its listening posts.

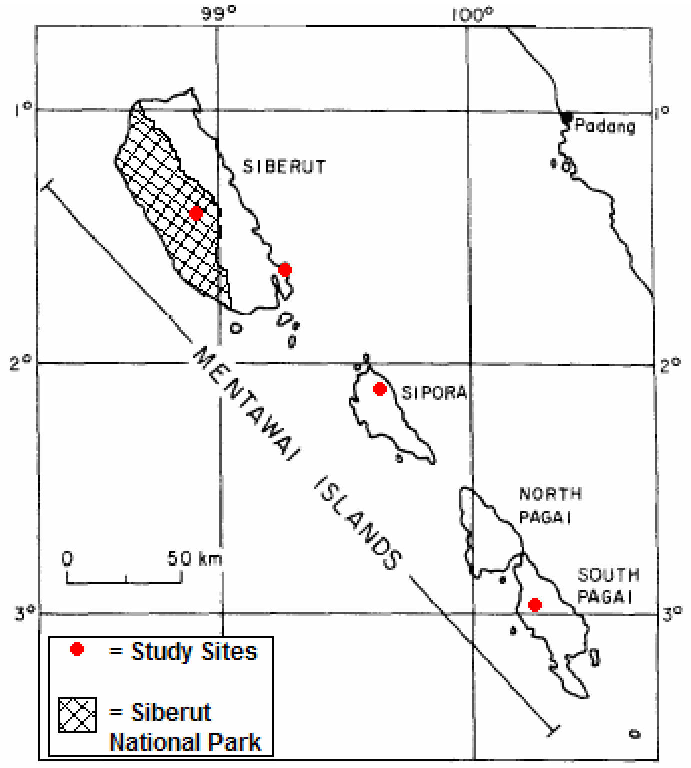


Fig. 2.1. Approximate Locations of Study Sites used for this Project (Adapted from Whitten 1982c)

CENTRAL SIBERUT – SIMABUGGAI

Site one was located within the traditional use zone of Siberut National Park (TNS). The area is primary dipterocarp forest with some secondary forest. Siberut National Park is a protected area located on the Western side of Siberut and covers an area of 192,660 hectares (Whittaker, unpub.).

SOUTH SIBERUT – SIKABEI

Site two was on the coast in South Siberut. Mangrove forest bordered the coast and gave way to primary dipterocarp forest further inland. No listening posts were located in the mangrove forest because gibbons do not inhabit this forest type. Some secondary forest was recovering from a small amount of logging activity by the local people.

SOUTH PAGAI

Site three was on South Pagai and was within a logging concession owned by PT Minas Logging Corporation. Base camp was located at 37km on the central logging road that ran vertically down the island, and listening posts were at 34km and 32km. The majority of forest was secondary or converted to agricultural land, with only small strips of primary forest. Despite the nature of such an area, it was used as a location in previous Kloss's gibbon research (Paciulli, 2004; Whittaker, 2004) and therefore is known to have a population of the species.

SIPORA – SAUREINU

Site four was on the island of Sipora, 6km from the village of Saureinu. The area contained primary forest and recovering secondary forest which had been logged twenty years previously (Whittaker, 2005). However, logging had recently begun in the area and a large logging road was present (pers. obs.).

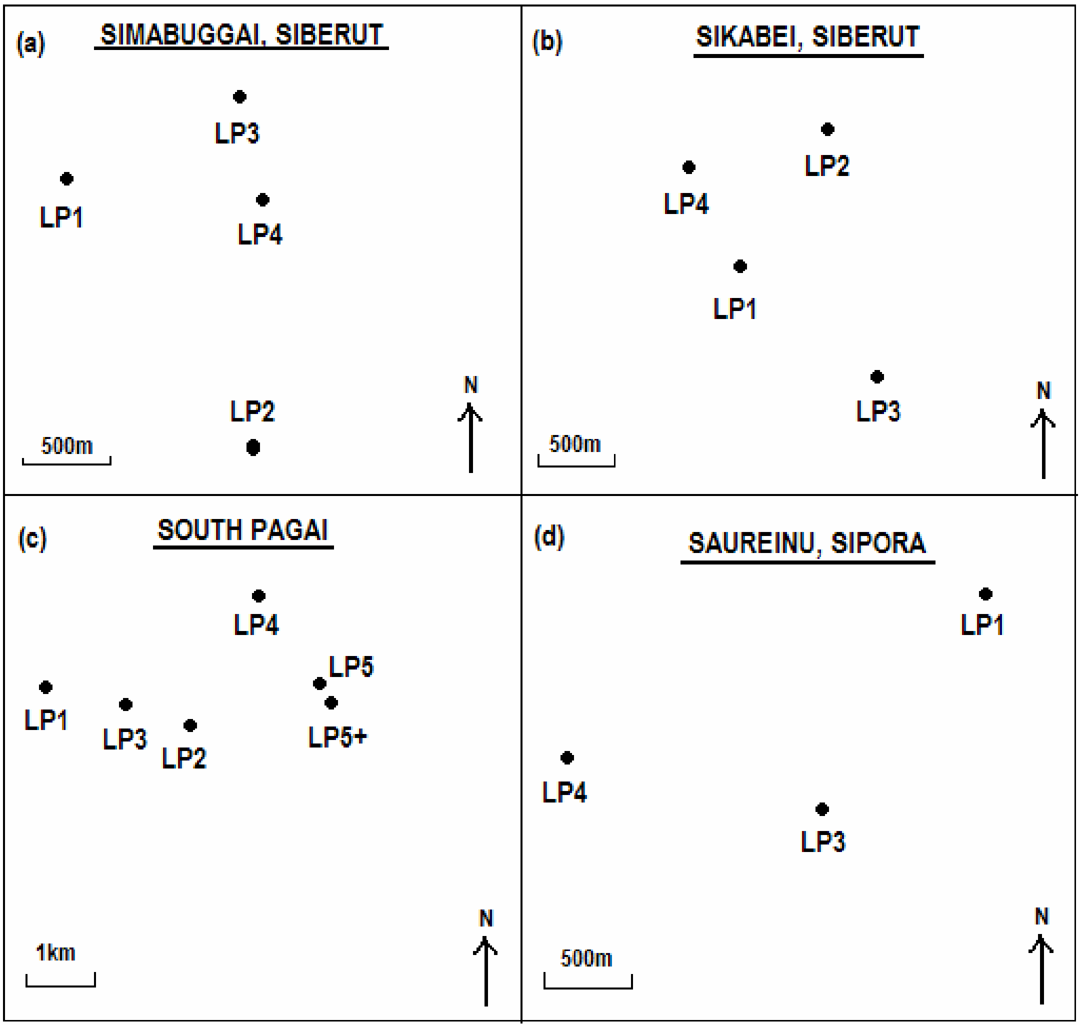


Fig. 2.2. Approximate Sketch Maps of Relative Positions of Listening Posts.

2.4 METHODS

2.4.1 FIELD METHOD

Ten to twelve days were spent recording at each of the four sites because the female Kloss's gibbon sings every three to four days on average (Whitten, 1981). In addition to recording female vocalisations, male Kloss's gibbon vocalisations were recorded for a complementary study.

In each location the researcher applied a modified point census technique to obtain recordings of Kloss's gibbon song. The modification was necessary due to three criteria that must be met. First, the terrain consists of steep ridges, large rivers and impenetrable forest so the point cannot be random due to inaccessibility to many areas. Second, gibbon calls can be heard and recorded well from high ridges with little obstructions which are within a 'sound window' and therefore these points were desirable for listening posts (Whitten, 1981). Thirdly, the distance between each point was necessarily at least 800m because although gibbon song carries over 800-1000m (Whittaker, pers. comm.), the song is only recordable to sufficient quality at an estimated distance of 400m maximum. Therefore this minimised the possibility of recording the same gibbon twice without realising. Any calls that were recorded with the possibility of duplicates resulting from recording from two different listening post at the same time, did not use the recordings from one of the listening posts. The necessity of meeting these criteria therefore means the technique was not random and was modified to accommodate such requirements.

Where possible, existing trails used by the local people were exploited to reach listening posts. This was to allow maximum time for recording, as oppose to trail-making, and to minimise destructive practices on the forest. Listening points were recorded by a global positioning system (GPS) to enable a complete record and to allow navigation. A minimum of five individual females per location was recorded to gain a suitable sample size for statistical analysis.

The researcher reached the point/listening post at 03:30 each morning because male Kloss's gibbons sing pre-dawn (~5:00) and female Kloss's gibbons begin to sing at sunrise (~06:30) (Whittaker, pers. comm.). At the start of gibbon calls the researcher vocally recorded the date, start time, end time, location and researcher on the tape. In addition, the researcher recorded the same information by hand in a notebook, plus direction, estimated distance, GPS waypoint and individual (if known), with room for supplementary information. Individuals could be identified because the same positions were used for singing from at each occasion and thus direction and distance would determine which individual was being recorded (pers. obs.).

2.4.2 ANALYSIS

SPECTROGRAPHIC ANALYSIS

The recordings were placed onto the spectrographic analysis software 'Raven 1.2' software and a set of predetermined variables was measured/counted (Table 2.1). Great call samples were digitised from tape-recordings with a 16 bit sampling size and 44.1 kHz sampling rate. The variables focus on the female great call because it is a highly stereotyped phrase within female gibbon song. It is unique to each species and therefore, population differences are most easily observable within the great call. Each great call phrase has three elements: pre-trill, trill and post-trill (Fig. 1.1). Only pre-trill and trill elements were analysed because post-trill elements were not of sufficient quality. Post-trill sections tend to reduce dramatically in amplitude and therefore are difficult to record (pers. obs.). Dallman and Geissmann (2001b) point out that if the post-trill element becomes inaudible at a short distance, then it is likely it is not used by individuals of the species to communicate with conspecifics. In light of this information, removing the post-trill elements from the analysis should not have a great effect on diversity. The female Kloss's gibbon sang no other phrase apart from single notes as build-up to the great call, great call fragments and the great call itself. Great call fragments result from a female aborting the phrase and these fragments are therefore not included in the analysis.

Table 2.1. Variables Used in Spectrographic and Statistical Analysis (adapted from Haimoff & Tilson, 1985)

Variable	Explanation	Unit of Measurement
1. Pre-trill + Trill Duration	Measured from the beginning of the great call to the end of the trill element of the great call	Seconds
2. Frequency band exploited during pre-trill +trill	Frequency range within which the pre-trill and trill elements of the great call are produced	Hertz
3. Duration of 1st note	Duration of the 1st note in the great call	Seconds
4. Frequency modulation of 1st note	Total rise in frequency during the 1st note of the great call	Hertz
5. Duration of 2nd note	Duration of the 2nd note in the great call	Seconds
6. Frequency of 2nd note	The frequency of this normally monotonal note	Hertz
7. Number of pre-trill notes	The total number of notes produced prior to the rapid trill notes	Count
8. Pre-trill duration	Measured from the beginning of the great call to the beginning of the trill element	Seconds
9. Notes/second in pre-trill	The total number of notes produced prior to the rapid trill notes, divided by the pre-trill duration	Count/Second
10. Trill duration	Measured from the end of the pre-trill element to the end of the trill element	Seconds
11. Number of trill notes	The total number of rapid notes produced during the trill element	Count
12. Notes/second in trill	The total number of notes produced during the trill element, divided by the trill duration	Count/Second

STATISTICAL ANALYSIS

All statistical tests were performed using ‘Statistical Package for the Social Sciences’ (SPSS) version 12.0 software. All tests performed are two-tailed.

INTRA-INDIVIDUAL ANALYSIS

Intra-individual diversity was analysed using the coefficient of variation (CV), and then each variable was judged to be consistent within females subjectively because of an unawareness of any objective tests available (CV=standard deviation/mean). CV was necessary because standard deviation alone did not give sufficient information due to some variables using a different measurement and/or the variables have very different values. For example, frequency is a much higher value than trill duration, and therefore comparing the standard deviations of these two variables is of no use.

KRUSKAL-WALLIS AND MANN WHITNEY U

Kruskal-Wallis one-way analysis of variance comparing medians was the test used to determine if a significant level of variance existed between individuals within the same population (intra-population), the diversity between the populations (inter-population), and the diversity between islands (inter-island). The test was used because both of the groups contained multiple independent samples data which required non-parametric analysis due to small sample size. Intra-population variation was tested using all the great calls which had been analysed spectrographically. Mann Whitney U analysis of variance comparing medians was used to determine if a significant level of variance existed between the two populations within Siberut (intra-island). The test was used here because there were two samples of unrelated data that required non-parametric testing due to small sample sizes.

Inter-population, intra-island and inter-island variance was tested using the means of great calls for all individuals, to prevent the data being skewed by some individuals being overrepresented or underrepresented in the data due to sample size differences of great calls. Significance for both Kruskal-Wallis and Mann Whitney U tests was determined at an alpha level of 5%, meaning there is only a 5% probability the results are caused by chance.

DISCRIMINANT FUNCTION ANALYSIS

I performed stepwise discriminant function analysis to determine whether individuals, populations and islands could be classified on the basis of statistically determined functions (Konrad & Geissmann, in press). The functions signify combinations of variables that between them represent as much of the data as possible, and is a way of streamlining multivariate data. Variables were selected using Wilks' λ which determines the variation between samples (i.e. populations or islands). A function selected by the discriminant function analysis will be a particular variable or combination of variables that represents other variables in addition to itself due to linear correlations. Variables were accepted or rejected from the model by a probability of F (accepted=0.5, rejected=0.10) which was used to show the alteration caused to the model when a variable was entered or removed. Prior probabilities to each group were adjusted based on the sample size in each group using the 'compute from group size' function on SPSS.

Classification tables showed whether individuals had a correct or incorrect predicted assignment to their population using the discriminatory functions and were cross validated using the leave-one-out method, which gives a more conservative estimate of correct predicted assignment. Cross validated classifications are the classifications referred to throughout this work unless otherwise stated. A Cohen's κ test was then performed to see whether inter-rater reliability was significant. Inter-rater reliability is the extent to which the predicted assignments (predicted by the discriminant function analysis) agree with the actual assignments, accounting for how chance alone would assign individuals. The probability of individuals being assigned by chance is provided by the prior probabilities calculated by SPSS. A higher κ value is indicative of greater inter-rater reliability. Canonical discriminant function graphs are used to visually illustrate function relationships between groups. The graphs use 'centroids' to show the centre point in the functions for a group as a whole, and great calls or individuals within that group are clustered around the relevant centroid.

Discriminant function analysis for individuals was conducted separately for each population. The reason for this is because, for individual recognition to be possible, individuals only need to be different from other individuals within their population.

The addition of a discriminant function analysis that attempts to classify Siberut individuals in one group and Sipora & South Pagai into another group is included in the results section and needs explanation of its inclusion because the reason is not obvious. The discriminant function analysis is attempting to answer the final hypothesis in the aim (Section 1.2.1.), and to determine if the Kloss's gibbon species consists of ESUs, one on Siberut and one on the other islands. If a division in the species exists, it is likely it will be in this pattern because of the subspecies and species divisions of the Mentawai monkeys.

2.4.3 EQUIPMENT

The study used a Sony TCM-450DV cassette-corder and a Sennheiser ME66 Short Gun Microphone to record the Kloss's gibbon vocalisations. This equipment has been used in similar experiments in the past (Whittaker, 2005; Paciulli, 2004; Whittaker *et al.*, 2004) with *H. klossii*. GPS points were taken using a Garmin eTrex Venture GPS system.

3. RESULTS

Full data can be found in Appendix II (Coefficients of Variation), Appendix III (All data from spectrograms) and Appendix IV (Means of all variables for each individual and population).

3.1. INTRA-INDIVIDUAL DIVERSITY

Coefficients of Variation (CV) were determined for each variable within each individual. The value of CV ranged from 0% to 56.3%. The highest value (56.3%) was within a female that had unusually high CV values for all variables. Means of CVs for all variables were calculated to determine the diversity within individuals across the whole sample (Fig. 3.1).

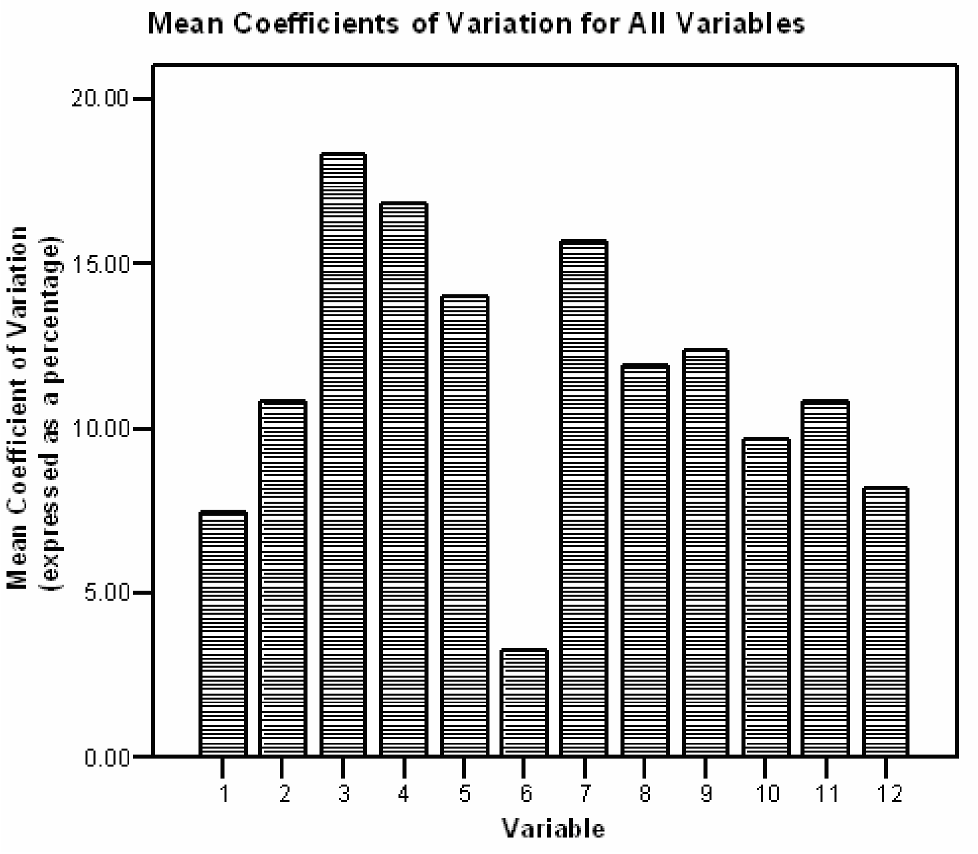


Fig. 3.1. Mean Coefficients of Variation Across the Sample for all Variables

Variable 6 (‘Frequency of 2nd note’) was the most consistent variable with a mean CV of 3.28%. ‘Duration of pre-trill + trill’ and all variables concerned with the trill element had a mean that indicated consistency. Although the other variables are less consistent, all have a mean CV of 18.3% or less, illustrating intra-individual diversity is fairly low.

3.1.1. INDIVIDUAL DISCRIMINANT FUNCTION ANALYSIS

Discriminant function analysis conducted with females and their great calls has shown great variation between the populations in both intra- and inter-individual diversity. Each population was analysed separately for reasons explained in the methods (Section 2.4.2.). Functions chosen in discriminant function analysis for each population vary.

Table 3.1. Discriminant Function Analysis for Individuals in all Populations

Population	% Correct Assignments (Original Classification)	% Correct Assignments (Cross-Validated Classification)	Cohen’s κ Value	Significance of Cohen’s κ
Simabuggai	75.7	56.8	0.485	p<0.001
Sikabei	97.5	62.5	0.554	P<0.001
S.Pagai	56.5	47.8	0.313	P<0.005
Saureinu	97.3	81.1	0.757	P<0.001

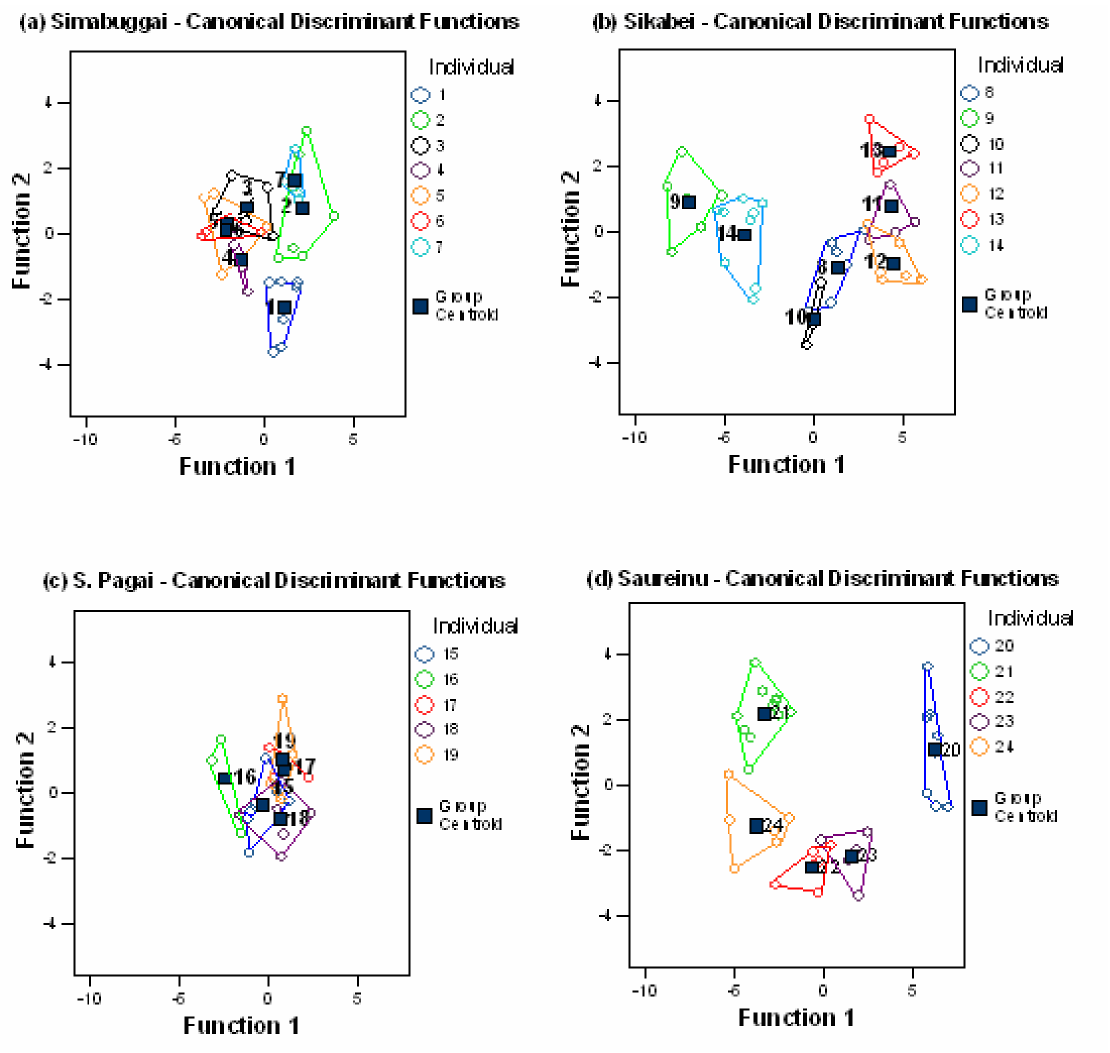
The results show how well a great call can be assigned to the female who emitted it (Table 3.1). Clearly, Saureinu has females which are either very consistent within their own great calls and/or very diverse individuals because cross validated classification shows a correct assignment rate of 81.1%, which is high. South Pagai has the lowest correct assignment rate in both original and cross-validated classifications with 56.5% and 47.8% respectively. Sikabei shows high original correct assignment (97.5%) but this is reduced to just 62.5% on cross-validation.

Simabuggai is similar to Sikabei in that both populations show an intermediate level of correct classification compared to the other two populations.

Cohen's κ shows the inter-rater reliability, with a higher value indicating a higher reliability. The two Siberut populations have intermediate but significant values (Simabuggai: $p<0.001$, $\kappa = 0.485$; Sikabei: $p<0.001$, $\kappa = 0.554$) showing great calls can be classified correctly using the discriminant function analysis significantly more than would be expected by chance. South Pagai has a much lower value ($p<0.005$, $\kappa = 0.313$) meaning great calls could not be classified very well to the correct individuals but still significantly more than would be expected by chance. Saureinu has a rate of correct assignment that suggests great calls will be assigned to the correct female very consistently ($p<0.001$, $\kappa = 0.757$).

The canonical discriminant functions graphs (fig. 3.2) allow further information to be gained from the discriminant function analysis. Simabuggai individuals (fig. 3.2.(a)) are close together (inter-individual) and great calls of each individual are relatively spread out from the individual centroids (intra-individual). The discriminant function analysis classification is thus resulting from a combination of well spread great calls and close together individuals. Sikabei individuals (fig. 3.2.(b)) are markedly further apart than the Simabuggai individuals and have a similar degree of spread of great calls around each individual centroid. Sikabei is therefore achieving a slightly higher percent of correct assignments because although great call differences within individuals are similar, there is greater inter-individual diversity.

South Pagai (fig. 3.2.(c)) females are extremely similar in their characteristics for F_1 (‘Frequency band exploited during pre-trill + trill’) and F_2 (‘Number of trill notes’), resulting in the bunching effect visible on the graph. Great call variation is similar to the two Siberut populations already described. The low inter-individual diversity accounts for such a low rate of classification and is very different to the two Siberut populations. Saureinu individuals (fig. 3.2.(d)) show a similar pattern to the Sikabei individuals and have well separated individuals with a great call spread around the individual centroids that is similar to the other populations.


(a) Simabuggai - Canonical Discriminant Functions

(b) Sikabei - Canonical Discriminant Functions

(c) S. Pagai - Canonical Discriminant Functions

(d) Saureinu - Canonical Discriminant Functions

Fig. 3.2. Canonical Discriminant Function Graphs for each Population.

3.2. INTRA-POPULATION DIVERSITY

I will describe each population separately within this section, noting the most significant variables in each population (Table 3.2). Results in this section are backed up by canonical discriminant functions graphs (Fig. 3.2).

SIMABUGGAI

The most significantly diverse variables within the Simabuggai population are 'Trill duration' ($p<0.001$, $k=25.508$, d.f.=6), 'Number of trill notes' ($p=0.001$, $k=23.620$, d.f.=6) and 'Notes/second in trill' ($p<0.001$, $k=24.354$, d.f.=6). These three variables all relate to the trill element of the great call and therefore the trill is the most variable element of the great call within this population. Four other variables are also significant at $p<0.05$. The population shows a moderate to high level of intra-population diversity.

SIKABEI

Eleven variables have significance values of $p<0.05$. Therefore this population is highly diverse in virtually all aspects of the great call.

SOUTH PAGAI

'Pre-trill + trill duration' ($p=0.012$, $k=12.944$, d.f.=4), 'Trill duration' ($p=0.035$, $k=10.358$, d.f.=4) and 'Number of trill notes' ($p=0.047$, $k=9.621$, d.f.=4) all show significant variation within the South Pagai population. Intra-population diversity is low in this population relative to the other populations studied.

SAUREINU

All twelve variables are significant to p<0.05 (d.f.=4) demonstrating a very high diversity in this population and the highest of all the populations studied. The four most significant variables (p<0.001, d.f.=4) are all linked to the pre-trill element of the great call. This differs from the pattern seen in the other populations which have tended to have the most significantly diverse variables being those linked with the trill element of the great call.

Table 3.2. Significance Results from Kruskal-Wallis Tests for Intra-Population and Inter-Population Diversity.

VARIABLES	INTRA-POPULATION				INTER-POPULATION
	Sim.	Sik.	S.Pag.	Sau.	
1. Pre-trill + Trill Duration	0.022	0.001	0.012	0.005	0.198
2. Frequency band exploited during pre-trill + trill	0.450	0.001	0.094	0.014	0.059
3. Duration of 1st note	0.054	0.035	0.085	0.001	0.091
4. Frequency modulation of 1st note	0.022	0.002	0.254	0.001	0.035
5. Duration of 2nd note	0.224	0.001	0.393	0.001	0.078
6. Frequency of 2nd note	0.024	0.001	0.712	0.001	0.105
7. Number of pre-trill notes	0.195	0.001	0.265	0.002	0.114
8. Pre-trill duration	0.718	0.001	0.089	0.002	0.182
9. Notes/second pre-trill	0.013	0.071	0.403	0.001	0.117
10. Trill duration	0.001	0.001	0.035	0.018	0.111
11. Number of trill notes	0.001	0.001	0.047	0.002	0.030
12. Notes/second trill	0.001	0.001	0.697	0.007	0.206

a. Sim.=Simabuggai, Sik.=Sikabei, S.Pag=South Pagai, Sau.=Saureinu.
b. Values in red are significant

3.3. INTER-POPULATION DIVERSITY

3.3.1. KRUSKAL-WALLIS ANALYSIS OF VARIANCE

Inter-population diversity is lower than intra-population diversity (Table 3.2). The significant variables within the inter-population diversity are ‘Frequency modulation of 1st note’ (p=0.035, k=8.599, d.f.=3) and ‘Number of trill notes’ (p=0.030, k=8.952, d.f.=3). These variables appear unrelated. Significance of variation between populations does not vary markedly between the variables suggesting most variables play a similar role in the overall variation.

3.3.2. POPULATION DISCRIMINANT FUNCTION ANALYSIS

Discriminant function analysis performed on the populations resulted in three functions (F_1, F_2, F_3) defined from the original twelve variables. The major variables associated with each function in this analysis are F_1= 'Duration of first note', F_2= 'Frequency modulation of 1st note', F_3='Notes/second in pre-trill'. Each of these functions represents a proportion of all the variance within the data (Table 3.3). The Eigenvalue (information captured) of a function represents the spread of group means, with the largest value indicating the function that has the biggest spread of group means. The percent of total variation represented by each function is shown in the '% of variance' column, with a 'cumulative %' column showing the percent of all functions so far added together. From this, it can be seen that these three functions together have captured 100% of the information available from all twelve variables.

Table 3.3. Summary of Canonical Discriminant Functions from SPSS

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	2.719(a)	81.7	81.7	.855
2	.380(a)	11.4	93.1	.525
3	.229(a)	6.9	100.0	.432

The Wilks' λ value for each function demonstrates the amount a function differs between populations. F_1 ($p<0.001$, $\lambda=0.158$) differs significantly between populations, F_3 ($p=0.45$, $\lambda=0.813$) is more similar between populations but still significant, and F_2 ($p=0.036$, $\lambda=0.589$) lies somewhere in-between.

Prior probabilities of an individual belonging to a group (i.e. population) differ depending on the actual number of individuals within that group. The classification table (Table 3.4) places the individuals in the correct group in 79.2% of cases which is much higher than the prior probabilities for all populations (range of 0.208-0.292). After cross-validation this is reduced to 58.3% of cases being classified correctly, which is still much higher than the prior probability.

The highest rate of correct classification after cross-validation is within the South Pagai population with 80% correct assignment. This means 80% of the individuals from South Pagai were correctly assigned to being from this population by discriminant function analysis. This fits with the Kruksal-Wallis analysis of variance intra-population because the test showed it to be the least variable population, and therefore it would be expected that it would be more easily classified.

Simabuggai has the second highest rate of correct assignment in the cross validated table (however, it has the highest in the non-cross validated table) with 71.4% correct classification. Saureinu and Sikabei have the lowest rates of correct classification with 20% and 57.1% respectively. This also corresponds with Kruskal-Wallis tests of intra-population diversity because these were the two most diverse populations and thus it would be expected, more difficult to classify because common ground is harder to identify between individuals. Cohen's κ test statistic shows inter-rater reliability is significant ($\kappa = 0.437$, $p<0.001$) within the cross validated classifications.

Table 3.4. Discriminant Function Analysis for Populations

	Population	**Predicted Group Membership**				**Total**	**% of individuals correctly classified**
		Simabuggai	**Sikabei**	**S.Pagai**	**Saureinu**		
Original classification							
Count	Simabuggai	6	1	0	0	7	
	Sikabei	0	5	0	2	7	
	S.Pagai	0	1	4	0	5	
	Saureinu	0	1	0	4	5	
	Total	6	7	5	6	24	
%	Simabuggai	85.7	14.3	0.0	0.0	100.0	85.7
	Sikabei	0.0	71.4	0.0	28.6	100.0	71.4
	S.Pagai	0.0	20.0	80.0	0.0	100.0	80.0
	Saureinu	0.0	20.0	0.0	80.0	100.0	80.0
	Total						79.2
Cross-validated classification [a]							
	Simabuggai	5	1	0	1	7	
	Sikabei	0	4	1	2	7	
	S.Pagai	0	1	4	0	5	
	Saureinu	1	3	0	1	5	
	Total	5	7	6	6	24	
%	Simabuggai	71.4	14.3	0.0	14.3	100.0	71.4
	Sikabei	0.0	57.1	14.3	28.6	100.0	57.1
	S.Pagai	0.0	20.0	80.0	0.0	100.0	80.0
	Saureinu	20.0	60.0	0.0	20.0	100.0	20.0
	Total						58.3

Simabuggai appears to be the most ‘separate’ of all the populations in the canonical discriminant functions graph, thus calling into question whether the original classification is more accurate than the cross validated classification for this population, because it intrinsically looks like the most easily identifiable population (Fig. 3.3).

Sikabei, in this diagram, is the most central population and the population centroid is approximately equally set between South Pagai and Saureinu. Despite appearing very different from the other Siberut population, Sikabei is only markedly different in F_1, the difference in F_2 between the two Siberut populations is minor. Therefore, the difference is one of frequency and not duration.

Considering the amount of intra-population diversity identified by the previously mentioned Kruskal-Wallis test (Section 3.4.1), the Sikabei individuals look relatively close together on the diagram compared to the other three populations. Simabuggai and Saureinu have especially 'stretched' populations. The canonical discriminant functions diagram does only use the first two functions and therefore 6.9% of the variance (as accounted for by F_3) is not included here.

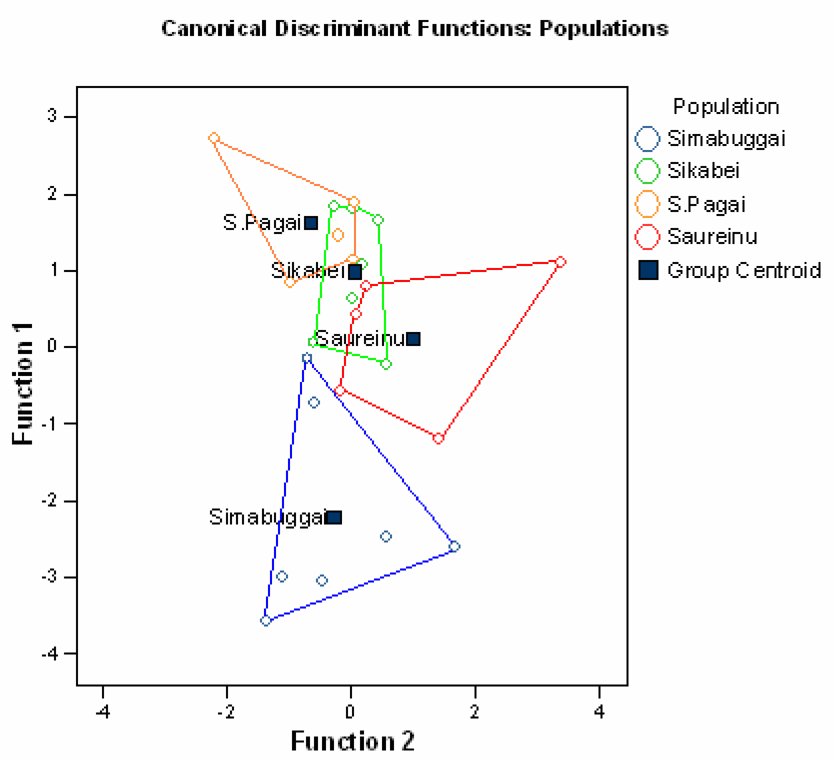


Fig. 3.3. Canonical Discriminant Functions diagram using F_1 and F_2.

3.4. INTRA-ISLAND DIVERSITY

Mann Whitney U was used to test for variation between medians in intra-island analysis (Table 3.5). Diversity between the two populations within the island of Siberut is significant in only one variable: 'Frequency modulation of 1st note' ($p=0.017$, $U=6$, d.f.=1).

Table 3.5. Significance Results from Mann Whitney U Test for Intra-Island Diversity and Kruskal Wallis Test for Inter-Island Diversity

VARIABLES	INTRA-ISLAND (SIBERUT)	INTER-ISLAND
1. Pre-trill + Trill Duration	0.209	0.720
2. Frequency band exploited during pre-trill + trill	0.710	0.031
3. Duration of 1st note	1.000	0.041
4. Frequency modulation of 1st note	0.017	0.939
5. Duration of 2nd note	0.456	0.050
6. Frequency of 2nd note	0.209	0.259
7. Number of pre-trill notes	0.165	0.307
8. Pre-trill duration	0.259	0.222
9. Notes/second in pre-trill	0.165	0.120
10. Trill duration	0.259	0.139
11. Number of trill notes	0.097	0.079
12. Notes/second in trill	0.165	0.406

a. Values in red are significant

3.5. INTER-ISLAND DIVERSITY

3.5.1. KRUSKAL-WALLIS ANALYSIS OF VARIANCE

Kruskal-Wallis analysis of variance confirms diversity between islands (i.e. Siberut, Sipora and South Pagai) and is higher than intra-island diversity for Siberut (Table 3.5). Three variables are significant: 'Frequency band exploited during pre-trill + trill' (p=0.031, *k* =6.931, d.f.=2). 'Duration of 1st note' (p=0.041, *k* = 6.411, d.f.=2) and 'Duration of 2nd note' (p=0.05, *k* = 5.991, d.f.=2).

3.5.2. ISLAND DISCRIMINANT FUNCTION ANALYSIS

An inter-island discriminant function analysis combined the two populations from Siberut and then discriminated amongst the three islands: Siberut (Simabuggai + Sikabei), Sipora (Saureinu), and South Pagai. The analysis used two functions comprising of the 'Duration of 1st note' (F_1) and 'Notes/second in pre-trill' (F_2) which combined, account for 100% of variance. Eigenvalues show the two functions have an intermediate spread of means between islands. The Wilks' λ values (F_1: $p=0.005$, $\lambda=0.480$; F_2: $p=0.016$, $\lambda=0.752$) for both functions suggests they have significant variance between the islands.

The discriminant function analysis classification table (Table 3.6) for the islands shows a 75% correct classification of cases for the original classification, dropping to 70.8% correct classification of cases in the cross-validated classification. The inter-rater reliability of this classification is significantly acceptable ($p=0.003$, $\kappa = 0.411$). Siberut individuals are assigned correctly in 92.9% of cases, Sipora individuals to 40% of cases and South Pagai individuals to 40% of cases after cross validation. Sipora and South Pagai both show equal difficulty in classification of individuals. Sipora and South Pagai individuals are incorrectly assigned to Siberut in 60% of cases. The only incorrectly assigned Siberut individual was assigned to South Pagai.

Table 3.6. Discriminant Function Analysis Classification Results for Islands

	Island	**Predicted Group Membership**			**Total**	**% of individuals correctly classified**
		Siberut	**Sipora**	**South Pagai**		
Original classification						
Count	Siberut	13	0	1	14	
	Sipora	3	2	0	5	
	South Pagai	2	0	3	5	
	Total	18	2	4	24	
%	Siberut	92.9	0.0	7.1	100.0	92.9
	Sipora	60.0	40.0	0.0	100.0	40.0
	South Pagai	40.0	0.0	60.0	100.0	60.0
	Total					75.0
Cross-validated classification [a]						
Count	Siberut	13	0	1	14	
	Sipora	3	2	0	5	
	South Pagai	3	0	2	5	
	Total	19	2	3	24	
%	Siberut	92.9	0.0	7.1	100.0	92.9
	Sipora	60.0	40.0	0.0	100.0	40.0
	South Pagai	60.0	0.0	40.0	100.0	40.0
	Total					70.8

The canonical discriminant functions graph demonstrates a clear relationship between the islands (Fig. 3.4). The graph shows what can be interpreted as a slight clinal relationship, although the islands overlap. Siberut is above the other islands in the graph, Sipora is in between, and South Pagai is below the other islands. The variance within each island is high with a large spread of values around each island centroid.

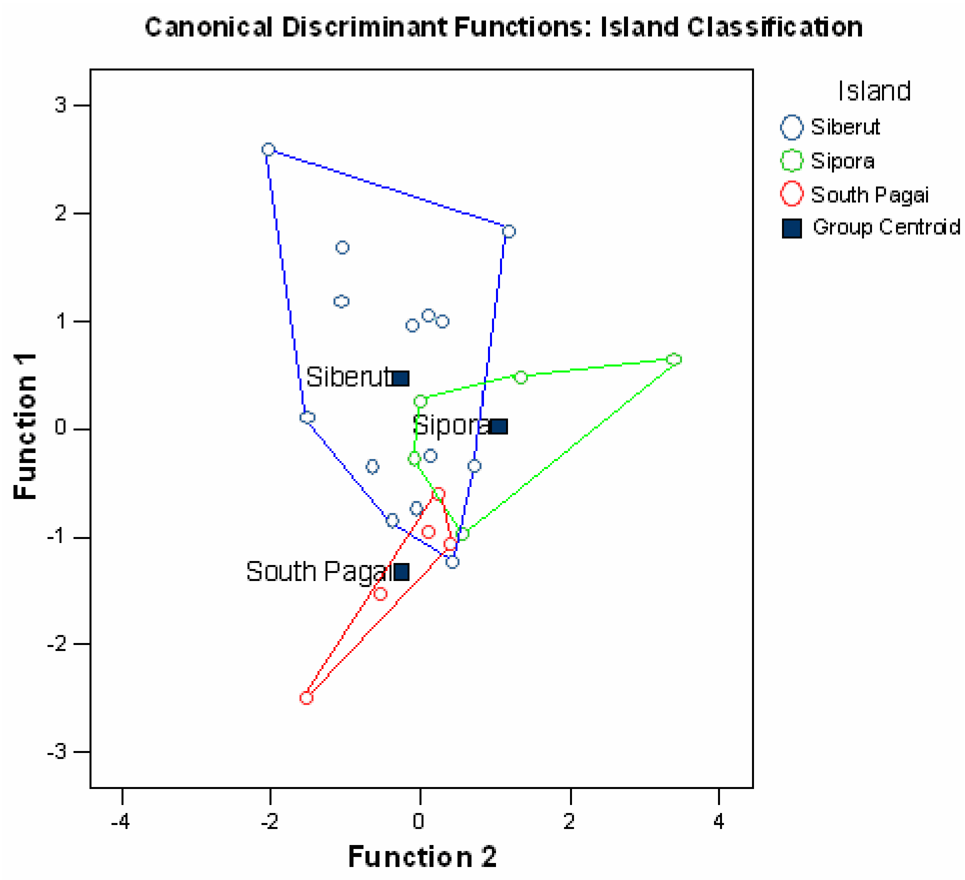


Fig. 3.4. Canonical Discriminant Functions diagram including F_1 and F_2.

Siberut individuals differ a lot in both F_1 and F_2. Sipora individuals differ mildly in their F_1 value and are much more variable in the value of F_2. South Pagai individuals show the opposite pattern, with the biggest differences in F_1.

3.6. SIBERUT, AND SIPORA & SOUTH PAGAI DISCRIMINANT FUNCTION ANALYSIS

The discriminant function analysis attempted to classify Siberut individuals into one group, and Sipora & South Pagai into another group. The reason behind this discriminant function analysis is explained in the methods section (Section 2.4.2.). The discriminant function analysis produced a model with only one function (F_1) and is referred to as discriminant function analysis (1). The function uses the variable 'Number of trill notes' which represents 100% variance via linear correlations with other variables. The Wilks' λ value ($p=0.042$, $\lambda=0.825$) suggests the function has significant variance between the islands. The Eigenvalue is 0.212, thus the spread of the means is less than for each function in the inter-population discriminant function analysis.

The classification table (Table 3.7) shows 66.7% of cases were classified correctly in the original classification, and this percent was reduced to 62.5% after cross validation. Prior probabilities for group classification range are 0.583 for Siberut and 0.417 for Sipora & South Pagai, and therefore the results must be treated with caution because they are very close to the prior probability values.

Table 3.7. Discriminant Function Analysis (1) Classification Results for the Siberut Group and Sipora & South Pagai Group

	Group	Predicted Group Membership		Total	% of individuals correctly classified
		Siberut	**Sipora & S.Pagai**		
Original classification					
Count	Siberut	10	4	14	
	Sipora & S.Pagai	4	6	10	
	Total	14	10	24	
%	Siberut	71.4	28.6	100.0	71.4
	Sipora & S.Pagai	40.0	60.0	100.0	60.0
	Total				66.7
Cross-validated classification [a]					
Count	Siberut	9	5	14	
	Sipora & S.Pagai	4	6	10	
	Total	13	11	24	
%	Siberut	64,3	35.7	100.0	64.3
	Sipora & S.Pagai	40.0	60.0	100.0	60.0
	Total				62.5

Correct assignment of Siberut individuals was 64.3% after cross validation whereas correct assignment for Sipora & S.Pagai individuals was 60% after cross validation. Therefore, Siberut individuals are more likely to be correctly classified than Sipora & South Pagai individuals. Cohen's κ test statistic shows inter-rater reliability is not significant ($p<0.239$, $\kappa = 0.239$) within the cross validated classifications.

The clustered bar chart (Fig. 3.5) shows mean 'Number of trill notes' in each population. The populations are clustered into Siberut, and Sipora & South Pagai. Although there is an obvious difference between the two clusters, note that Sikabei and South Pagai have the same mean 'Number of trill notes'. Therefore, Sikabei and South Pagai are closer to each other in this variable than to the other population of their own clusters. It would therefore seem that the discriminant function analysis for inter-island diversity is unreliable because this is the major component of the function the model uses.

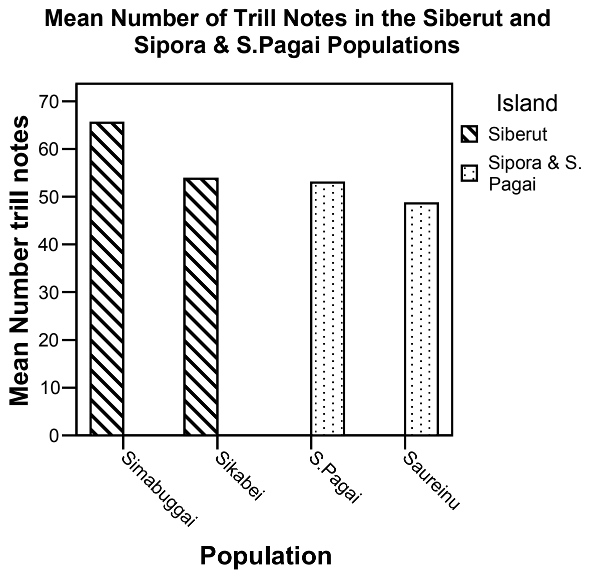
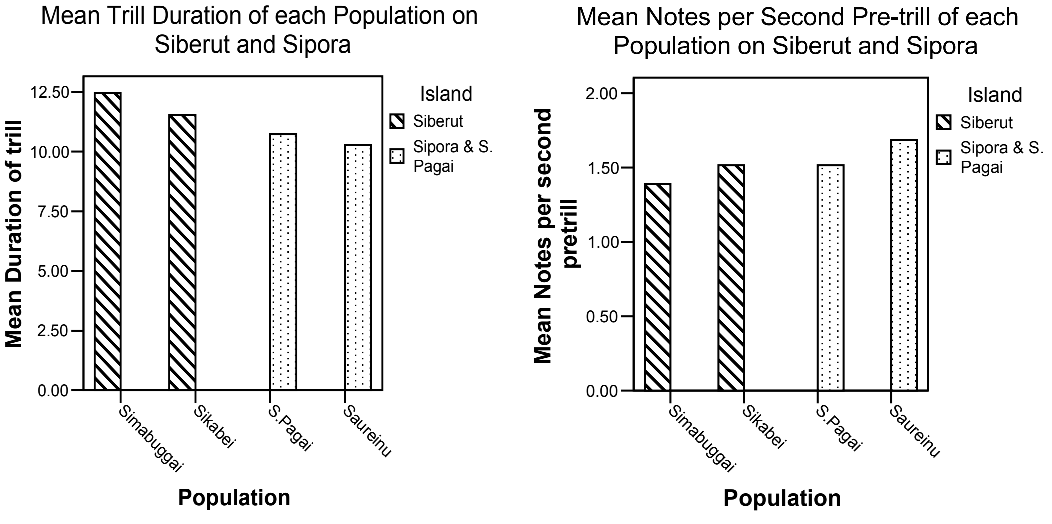

Mean Number of Trill Notes in the Siberut and Sipora & S.Pagai Populations

Fig. 3.5. Mean ‘Number of trill notes’. Populations are clustered into Siberut, And Sipora & South Pagai

In discriminant function analysis (2) for Siberut, and the Sipora & South Pagai group, three variables are now the principal components of the discriminant function analysis for inter-island diversity, despite the fact only one function is created: ‘Trill duration’, ‘Notes/second in pre-trill’ and ‘Duration of 1st note’. The variables ‘Trill duration’ and ‘Notes/second in pre-trill’ are different on both islands in that none of the population means overlap between islands (Fig. 3.6).


Mean Trill Duration of each Population on Siberut and Sipora

Mean Notes per Second Pre-trill of each Population on Siberut and Sipora

Fig. 3.6. Clustered bar chart of mean ‘Trill duration’ and mean ‘Notes/second in pre-trill’. Populations are clustered into Siberut, and Sipora & S.Pagai

‘Trill duration’ also has a strong positive correlation with ‘Number of trill notes’ ($p<0.01$, $r = 0.829$) which further supports this new discriminant function analysis because the removed variable is still indirectly represented.

The alteration in classification when discriminant function analysis (2) is used is because mean ‘Number of trill notes’ is removed from the variables for analysis (Table 3.8). Original classification has classified correctly 87.5% of cases, and after cross validation this is reduced to 79.2% of cases. A Cohen’s κ test statistic shows inter-rater reliability is highly significant ($p<0.003$, $\kappa = 0.589$) within the cross validated classifications. 90% of individuals from Sipora & South Pagai are correctly assigned. Siberut has a 71.4% correct predicted assignment for individuals from the island, suggesting a slight overlap with the Sipora individuals.

Table 3.8. Discriminant Function Analysis (2) Classification Results for the Siberut Group and Sipora & South Pagai Group

	Group	**Predicted Group Membership**		**Total**	**% of individuals correctly classified**
		Siberut	**Sipora & S.Pagai**		
Original classification					
Count	Siberut	11	3	14	
	Sipora & S.Pagai	0	10	10	
	Total	11	13	24	
%	Siberut	78.6	21.4	100.0	78.6
	Sipora & S.Pagai	0.0	100.0	100.0	100.0
	Total				87.5
Cross-validated classification [a]					
Count	Siberut	10	4	14	
	Sipora & S.Pagai	1	9	10	
	Total	11	13	24	
%	Siberut	71.4	28.6	100.0	71.4
	Sipora & S.Pagai	10.0	90.0	100.0	90.0
	Total				79.2

4. DISCUSSION

4.1. INTRA-INDIVIDUAL DIVERSITY

Intra-individual diversity is moderately low, with all twelve variables having a Coefficient of Variation (CV) of 18.3% or less. The most consistent variable is ‘Frequency of 2nd note’. From the second note of the great call phrase until the end of the trill element, frequency tends to fluctuate very little and therefore this variable represents more than the second note. The variable’s consistency implies the whole of the pre-trill element after the first note, and the trill element, are consistent in frequency. Although this variable is consistent within females and would thus appear the most useful for discriminating between individuals, frequency is the most consistent feature at all levels of grouping (i.e. individual, population, island, ESU) because of the nature of sound propagation (Whitten, 1981; Richards & Wiley, 1978). The least consistent variables are those related to the first note of the great call. This implies that the first note is not important in proclaiming identity of an individual and is therefore not subject to stringent control of its emission.

The low intra-individual diversity supports the possibility of individual recognition potential between conspecifics, because, if an individual is to be recognised by the great call, that call must be consistent within the individual (Fenton *et al.*, 2004; Jordan *et al*, 2002; Dallmann & Geissmann, 2001a,b; Friedl & Klump, 2001; Lengagne, 2001; Reby *et al.*, 2001).

The reason for the intra-individual diversity that does exist may be environmental fluctuations, however, great calls from females were recorded during a single song bout, which lasts ~20mins. Although most environmental fluctuations would seem unlikely in this short amount of time, some factors fluctuate fast enough to influence the variation. A change in wind strength/direction would encourage the female to alter her phrases to compensate for differences in the sound window (Whitten, 1981). Temperature also alters the way sound carries, and temperature gradients, such as those between the forest floor and the forest canopy, refract sound. At the time females sing, temperature will be gradually increasing and this could create a similar refraction effect. The effect of this could be tested in future research by examining the change in great calls over time within single song bouts, whilst measuring variations in temperature. Therefore, environmental fluctuations may be a contributing factor but are not influential enough in the given time frame to be the ultimate source of all variation. Physiological and psychological state of the individual can likewise be ruled out as a major factor due to an insufficient amount of time available for this to change.

The intra-individual diversity could be a function of age and related level of experience, whereby, the less experience a female has, the more likely that female will have difficulty in reliably reproducing the species song. Age has been noted as a function of variation in chimpanzee vocalisations, however, the level of genetic influence in chimpanzee vocalisations is thought to be less than in gibbon vocalisations and therefore this information is applied to this work with species differences in mind (Arcadi, 1996; Mitani *et al.*, 1992; Marler & Hobbett, 1975 cited in Mitani *et al.*, 1999). The CV results (Appendix II) clearly show that one individual has a high CV for every variable, and so by this implication would be a young, inexperienced female. Gibbon song is of genetic basis (Cheyne & Brule, 2002; Geissmann, 1984; Tenaza, 1984) and the age function described would be expected in species where learning is involved in vocalisations. Perhaps in hylobatids, a genetic basis provides the vocalisation that will be sung at adulthood after a necessary period of ‘practice’. Barbary macaques follow such a pattern, exhibiting a fixed structure of vocalisation that has an element of plasticity (Fischer *et al.*, 1998). In addition, the song of gibbons is a complex vocalisation in comparison with other mammals adding further support to the idea of necessary period of ‘practice’. Also, females sing to declare and protect territory (Cowlishaw, 1992), and therefore the gibbon can afford this period of practice before a territory of its own is held and requires maintenance. In contrast to this idea, Gittins (1978) suggests female gibbons sing to declare ‘ownership’ of their mate, however, the article which implies this is mostly speculation and not the result of detailed analyses. Therefore, the function proposed by Cowlishaw (1992) is the function I accept in the writing of this report.

CONCLUSION FOR INTRA-INDIVIDUAL DIVERSITY

Therefore, in conclusion, the null hypothesis that there will be no significant intra-individual diversity, can be accepted. The proposed reason for low intra-individual diversity is the potential it provides for individual recognition of conspecifics. The small amount of diversity that does exist is most likely to be a function of age and related experience in maintaining a consistent great call.

4.2. INTER-INDIVIDUAL DIVERSITY

The four populations vary greatly in the amount of inter-individual diversity they contain, demonstrated by the discriminant function analysis which assigned great calls to individuals with a varying success rate. Despite the variation, it does seem that from the results, overall, individuals can be distinguished by their great calls. This is supported by the Kruskal Wallis analysis of variance within each population, where at least three variables differ significantly between individuals in a population. In Haimoff & Tilson's (1985) study, twelve of the fifteen variables tested for variance between Kloss's gibbon females differed significantly. This inter-individual diversity is higher than Simabuggai and South Pagai, but lower than Sikabei and Saureinu. Unfortunately, a difficulty exists in comparing the Haimoff and Tilson (1985) study to this work because of the variation in significance between populations, however, their results do further illustrate the large difference between populations which is discussed in Section 4.3. The authors argue the strongest differences found between Kloss's gibbon individuals are in duration and not in frequency of various elements in the great call phrase. The results of the Haimoff & Tilson (1985) must be treated prudently because only four females were used in the entire analysis and therefore the high inter-individual diversity could be a function of small sample size rather than illustrating actual diversity.

Whitten (1981) describes a 'sound window' used by the Kloss's gibbon which is determined by sound attenuation in the heterogeneous forest environment. Amplitude modulation (e.g. the trill element) is also an adaptation to sound propagation in a forest environment (Richards & Wiley, 1978). Many birds and insects in the Mentawai Islands use amplitude modulated structures in the sounds they produce (pers. obs.) so it is highly possible there are specific characteristics of Mentawai forests which favour this form of sound propagation. Trills are the most acoustically diverse variable between individuals, therefore the trill element would be used for individual recognition among Kloss's gibbon females.

Trills are used by animals in long-range territorial and/or mate attraction (Elemens *et al.*, 2004; Radford & du Plessis, 2004; Rogers & Cato, 2002; Doutrelant *et al.*, 2000). Male leopard seals (*Hydrurga leptonyx*) vary between individuals in duration more than frequency in long-range trill calls (Rogers & Cato, 2002). Watkins & Schevill (1979) suggest that increased length of a call may increase the calls detectability at a distance. Ring doves (*Strepopelia risoria*) possess special “superfast” muscles used in trilling (Elemens *et al.*, 2004), demonstrating that this is of such importance that anatomy has been altered at a cost to other structures to allow trills.

On the basis of trill properties, the territorial behaviour of the Kloss’s gibbon and the nature of being the only hylobatid on the Mentawai Islands, I propose the following three hypotheses to explain inter-individual diversity: (1) Trilling as a handicap, (2) Neighbour-stranger discrimination, (3) Relaxed selection.

4.2.1. HYPOTHESIS (1) TRILLING AS HANDICAP

In sexual selection, individuals of some species chose a mate due to their performance of a certain behaviour or for a particular physical attribute, which may not be adaptive in terms of natural selection but does increase the number of offspring an individual has, and therefore is deemed ‘sexual selection’. Zahavi’s Handicap Principle (Zahavi, 1975) states that mates will be chosen on their ability to cope with a characteristic that otherwise hinders fitness.

The trill has been proposed to be a handicap in male Kloss’s gibbons in concordance with Zahavi’s Handicap Principle (Whitten, 1984b). This was applied to the male because it sings more often than the female, however, the trill may also act as a handicap for the female. Trilling is energetically costly, therefore an individual that can trill for a long time (long trill duration or long song bout) can demonstrate a high level of fitness/stamina (Dallman & Geissmann, 2001b). Trill duration has significant diversity within every population in this study, thus supporting this idea.

Some suggest that if a characteristic indicates fitness, that characteristic should vary over time as fitness varies (Puglisi & Adamo, 2004; Lengagne, 2001). However, a characteristic with a genetic basis such as gibbon song would remain stable whilst still acting as an indicator of genetic fitness. It is therefore reasonable to assume intra-individual differences indicate fitness on a temporal scale whereas inter-individual differences are indicative of fitness on a genetic scale. Brockelman (1984) suggests communication of this type may be referred to as 'demonstrative communication' because it vocally demonstrates a genetic state.

However, it may be that the songs of gibbons are not concerned with information transmission. Brockelman (1984) questions the 'information paradigm' which he states as "…regards communication as information transmission." It is assumed any communication that does not serve an informative purpose will be filtered via natural selection because it wastes essential energy. Although disputed by some, I conclude that the 'information paradigm' makes intrinsic sense and that gibbon songs do convey important information. Brockelman himself points out no alternative explanations are available.

In contrast to the hypothesis of trilling as a handicap in females, the song of female gibbons has been proposed to function for territory defence and maintenance

(Cowlishaw, 1992), and therefore is not concerned, or only secondarily concerned, with mate attraction. However, the study that proposed this function attempted to encompass all hylobatid species within the explanation, and this may be diluting the specific function of song within each species. It may be particularly inaccurate in the case of Kloss's gibbons because of the lack of duets.

4.2.2. HYPOTHESIS (2) NEIGHBOUR-STRANGER DISCRIMINATION

Neighbour-stranger discrimination relies on the ability to recognise conspecifics. Conspecific recognition has been demonstrated in many taxa (Fenton *et al.*, 2004 - African bats; Friedl & Klump, 2001 – tree frogs; Jordan *et al*, 2002 – cotton top tamarins; Lengagne, 2001 – eagle owls; Reby *et al.*, 2001 - red deer). Individual recognition over a long-range serves in territory defence and/or mate attraction/defence (Rogers & Cato, 2002) and can be achieved if intra-individual characteristics remain consistent while inter-individual diversity is apparent. The results from this work and from Haimoff and Tilson (1985) suggest Kloss's gibbons have the potential to differentiate between individuals within their population, however, Haimoff & Tilson's (1985) study did not analyse intra-individual variation and therefore the assumptions of a potential for individual recognition is extrapolated from this work.

Neighbour-stranger discrimination using vocalisations is applicable to animals which are either territorial and/or protect specific calling sites from conspecifics. The principle works because individuals become habituated to the vocalisation of their neighbour and therefore exhibit reduced aggression in reaction to the neighbour's song (Friedl & Klump, 2001). Decreased aggressive reactions to neighbours vocalisations saves time and energy, which can be used for other activities, such as foraging or attracting a mate. The individuals continue to react to strangers because they are not habituated to the strangers' vocalisations (Bee & Gerhardt, 2000). This stranger reaction is adaptive because strangers are usually more of a threat. The increased threat is because they are not likely to hold their territory and therefore are more likely to challenge existing territory owners.

The neighbour-stranger idea is applicable to gibbons because during border disputes, it is mostly the males which display aggressively whilst the females have a more subdued reaction (Cowlishaw, 1992). The female song is hypothesised to function in territory defence and the male song in mate defence, and therefore, a neighbour-stranger system is supported because during the border dispute a female will be aware that the rival female already owns a territory and therefore is not a threat. In further support, the male, who is not functioning as a territory defender but rather in defence of his mate, reacts aggressively because claims to females are more dynamic in nature and aggressive reactions are not already habituated by a neighbour-stranger system.

Despite the knowledge that individuals can potentially be recognised by conspecifics, this does not mean that recognition actually takes place. Playback experiments can provide confirmation of recognition. Mitani *et al.* (1985) conducted playback experiments with Műller's gibbons (*Hylobates muelleri*) but recorded no response to self, neighbour or stranger duets. This sheds doubt on the idea that gibbons employ neighbour-stranger discrimination strategies, however, it may be that such vocalisations and recognition is context dependent and playback experiments may not sufficiently replicate the natural context required.

4.2.3. HYPOTHESIS (3) RELAXED SELECTION

Closely related, sympatrically living species originate from (a) sympatric speciation, or (b) immigration of one species into the area already inhabited by the other species. In the case of gibbons, some sympatrically living species are thought to originate from the method (b) due to evidence from migration patterns and biogeography (Geissmann, 1993). For example,Műller's gibbons were thought to have diverged on Borneo whereas agile gibbons are thought to have diverged on Sumatra and colonised Borneo via a land bridge when sea levels were low. Now, both species co-exist sympatrically on Borneo. This means that in this case sympatry is not the cause of their species-specific song divergence but serves to maintain and reinforce the existing variation. This is advantageous and important in lieu of the 'recognition concept of species' (Paterson, 1985 cited in: Templeton, 1989).

The 'recognition concept of species' expresses that potential mates of a species can recognise each other by a particular recognisable characteristic, exemplified by vocalisations. A vocalisation would be specific to that species and therefore it is an evolutionary step to ensure an individual will only mate with a member of its own species (Templeton, 1989). There are criticisms of this species concept but in this context it is the most appropriate concept of species.

When a hylobatid does not live sympatrically with another hylobatid species, the pressure for a species-specific recognition system relaxes and individual recognition may become the priority. Relaxation of the selection pressures to keep the species song specific would allow random genetic drift to be able to have a greater effect on the song before its effect is removed via natural selection. Geissmann (2002) suggests duet-splitting evolved within the songs of the Kloss's gibbon and the Javan gibbon as a result of relaxed selection leading to a reduced need to prevent inter-species breeding. The song would still be subject to other selection pressures, such as the ability of the song to travel through the gibbons' environment (Richards & Wiley, 1978; Whitten, 1981), but the species discrimination pressure is relaxed. The three Mentawai monkeys also endemic to the islands have vocalisations that are too dissimilar to the gibbon to replace the selection pressure that would be provided by another hylobatid species (pers. obs.). Therefore the diversity found within populations serves no function but is merely a by-product of relaxed selection and subsequent random genetic drift.

There are exceptions to the idea of sympatry resulting in divergence. The mechanism underlying divergence is the lowered fitness of hybrids between the parent populations. If hybrids are produced and they do not exhibit a lower fitness than their parent species, the characteristics of the two species may merge. This is known to occur in agile/ Műller's gibbon hybrids in the hybrid zone in Kalimantan, Indonesia. Hybrids of the two species do not appear to show deleterious effects and their vocalisations are intermediary between the parent populations, demonstrating a merging of vocal characteristics (Short, 2005). Avian species have also demonstrated this merging effect but without the presence of hybrids (de Kort *et al.*, 2002). The assumption Kloss's gibbons would experience an increased pressure to diverge and stereotype their song in the presence of a sympatric hylobatid species is therefore unsubstantiated and the possibility of relaxed selection must be treated with caution.

CONCLUSION FOR INTER-INDIVIDUAL DIVERSITY

In conclusion, the null hypothesis that there will be no significant inter-individual diversity can be rejected. I propose that neighbour-stranger discrimination is the principle influence behind significant inter-individual diversity, with relaxed selection contributing a smaller influence, particularly in non-trill elements of the great call.

4.3. INTER-POPULATION DIVERSITY

The most diverse variables between populations are variables concerned with the first and second notes of the great call and the number of trill notes. Mean 'Number of trill notes' for South Pagai and Sikabei is the same, but in Sikabei this variable is less consistent intra-individually and inter-individually. One individual at Sikabei has a particularly low number of trill notes (range 25 – 43), and this affects the overall mean of the group. This individual may be particularly young and/or unfit and so could have produced a sub-optimal song. The individual's rate of notes per second in the trill is also unusually low. Removal of this individual from the population data does indeed bring the mean number of notes in the trill closer to the Simabuggai population. Nonetheless, the CVs for this individual are high only in the 'Trill duration' and 'Number of trill notes' variables, and therefore do not support that the female was young and inexperienced unless the trill is the last element of the call to be mastered by a female due to its speed.

The discriminant function analysis for populations assigned individuals to the correct populations 58.3% of the time after cross validation and the assignment was significantly reliable. Therefore, populations must have a clear difference between them. Sikabei and Saureinu overlap in characteristics of vocalisations and as a result are the hardest populations to classify according to the discriminant function analysis. The variables chosen for functions in the discriminant function analysis may not have been the most appropriate because the first two variables were very diverse intra-individually and therefore, concluding real differences between them at a higher group level is problematic. F_3 does not display such a problem, however, this function only accounted for 6.9% of total variation between the populations and was not accounted for on the canonical discriminant functions graph. The discriminant function analysis for populations must therefore be treated with caution.

4.3.1. SIKABEI AND SAUREINU RELATIONSHIP

I propose a tentative hypothesis to explain why Sikabei and Saureinu are more similar than Sikabei and Simabuggai (the Siberut populations). The hypothesis focuses on the known effect of rivers acting as boundaries to gibbon distribution (Morris, 1943), and the knowledge that the two Siberut populations are separated by two rivers. In addition, the Sikabei population is located on a section of island only connected to the rest of Siberut by a 2km wide area (Fig. 4.1). Rivers continue to flow when sea levels drop because precipitation will continue and therefore, when sea levels last dropped to the extent that the Mentawai Islands were all connected, the rivers would still separate the Siberut populations. In this event, Sikabei is unobstructed from the exposed land between Siberut and Sipora, and Saureinu, located in the Northern half of Sipora, may be equally unobstructed. These two populations would therefore be able to mix in such an event, which last occurred 7,000 years before present (Whittaker, 2005) and thus would be more closely related than the two Siberut populations. The notion of rivers acting to facilitate the process of speciation is supported by a literature review of lemur research which admits more research is necessary but there is a distinct possibility it has occurred (Goodman & Ganzhorn, 2004).

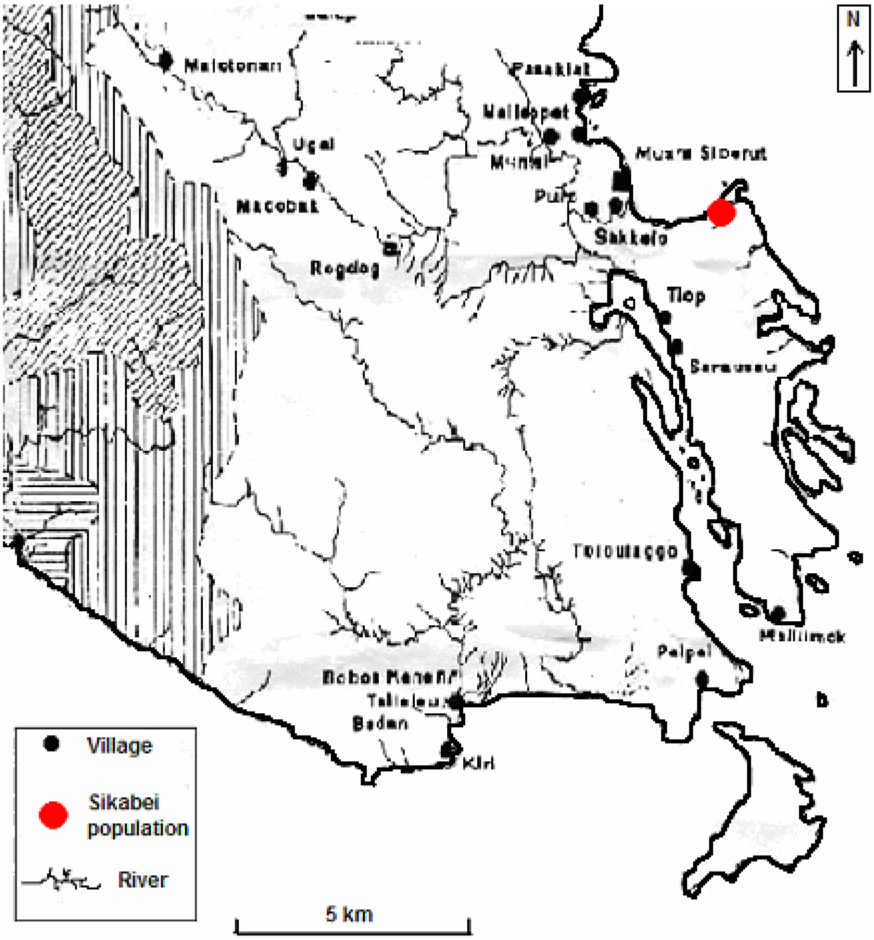


Fig. 4.1. Land Formation around the Sikabei Population.
(Adapted from the TNS Management Areas Map)

On the other hand, there are a number of criticisms to this hypothesis. Rivers alter their course over time and how different the Siberut river was 7,000 years before present compared to now is unknown. Also, maps presented by Voris (2000) depict the Mentawai Islands as separate from each other when the sea is 120m BPL (Fig. 1.3), however, Voris cautions the reader about large error margins in these maps. In spite of these criticisms, the hypothesis should be considered as an initial and tentative hypothesis to the problem.

4.3.2. INTER-POPULATION DIFFERENCES IN INTRA-POPULATION DIVERSITY

There is a large difference between the levels of diversity seen within each population. South Pagai shows the least amount of diversity and I suggest this is because the population lives within a logging concession. Whittaker (2005) estimates 210km^2 of suitable habitat remains in designated buffer zones, conservation zones and limited production zones. The area where I obtained recordings was in the limited production area where only small tracts of primary forest remained and these were usually fragmented strips (pers. obs.). Therefore, it is possible the population is reduced in this area to such a degree that diversity is also reduced. Fewer individuals means the population is more affected by stochastic events because the reproductive success of each individual is instrumental in which genes are passed on (Cowlishaw & Dunbar, 2000). Density of gibbon groups at this site was much higher where they did occur (pers. obs.) which also supports the idea of this population being subject to pressures from logging and loss of habitat. Kloss's gibbons are thought to show equal survival in logged and non-logged forest (Paciulli, 2004), however, the study that advocates this does not detail the level of logging at which survival is good.

The environment of South Pagai is more limiting than the environment of the other populations. It has a high elevation (~200m), is colder and experiences higher rainfall than the other populations. This could mean the individuals have to conform to a very specific fitness to be able to produce a vocalisation that will propagate sufficiently through the forest. Cold temperatures and heavy rain is known to inhibit Kloss's gibbons singing (Whitten, 1981).

Saureinu has very high intra-population diversity. I theorise this could be because only an estimated 10-15% of the island of Sipora is still forested, which in metric measurement is 84.5-126.8km² (Whittaker, 2005; Fuentes, 1996/7), and the individuals left could include immigrants from other areas of forest that were being logged. Therefore, the forest around Saureinu could be acting as a reservoir for the island's population. The area is recovering from logging 20 years earlier (Whittaker, 2005), so the gibbons which are resident there now may have come from other areas if it was inhabitable during the logging. The Siberut populations do not have any features of their environment which I can suggest for the cause of their diversity levels. Random genetic drift could account for the diversity seen between populations that cannot be accounted for by human intervention and subsequent habitat alterations.

CONCLUSION FOR INTER-POPULATION DIVERSITY

In conclusion, the null hypothesis that there will be no significant inter-population diversity can be rejected. Differences are proposed to be due to human influence on the local environment and random genetic drift.

4.4. INTRA-ISLAND DIVERSITY

Intra-island diversity could only be assessed within Siberut because only 1 population was studied on Sipora and on South Pagai due to lack of available field sites. The diversity within Siberut is low, with only one significantly diverse variable: 'Frequency modulation of 1st note'. The variable is concerned with frequency and this relates to the earlier discussion regarding sound propagation (Section 4.2) where it was suggested frequency is less variable than duration within vocalisations (Rogers

& Cato, 2002; Friedl & Klump, 2001; Lengagne, 2001; Whitten, 1981; Richards & Wiley, 1978). Therefore, the reason for the difference between the Siberut populations' great calls may be due to environmental differences in the structural properties of the forest. The Mann-Whitney U test shows this was in fact the only significantly diverse variable between the two populations, and therefore the nature of discriminant function analyses (i.e. looking for and exaggerating differences between populations) explains the result (Fig. 3.2).

Contrastingly, if the variable is significantly diverse because of structural differences, it would be expected that all frequency variables would be significantly diverse, which they are not. The first note was not considered important for individual recognition compared to the importance of the trill (Section 4.2). Therefore, if the variable is not an important functional part of the great call, the ability to transmit the first note through the forest environment would not be essential. This reduction of essential function would result in relaxed selection on this variable, leaving it susceptible to the actions of random genetic drift.

CONCLUSION FOR INTRA-ISLAND DIVERSITY

In conclusion, the hypothesis that there will be no significant intra-island diversity on Siberut can be rejected. In this case, the rejection of the null hypothesis is based only on one of the twelve variables and therefore does not account for the level of diversity. The level of diversity is extremely low and the only significantly diverse intra-island variable is proposed to be due to random genetic drift.

4.5. INTER-ISLAND DIVERSITY

Inter-island diversity is larger than intra-island diversity (Siberut) which is to be expected because more islands imply a larger gene pool. The trill element variables were not significantly diverse, which is also to be expected because if the trill is the most important element of the great call for individual recognition and its associated advantages, it would be subject to the strongest selection pressure of all the variables, expect perhaps for the frequency variables as previously discussed. A strong selection pressure means that an individual whose trill deviated far from the optimum would have reduced reproductive success and the deviation would eventually be lost in the population.

The discriminant function analysis for islands chose 'Duration of 1st note' as function one (F_1) and 'Notes/second in pre-trill' as function two (F_2) in the first classification. Both functions are linked with the pre-trill element of the great call, again adding support to the conservation of the trill element within the species. The discriminant function analysis correctly classified 70.8% of cases demonstrating significant reliability of being able to place an individual within its correct island. Sipora and South Pagai were less reliably classified than Siberut, with only 40% correct classification. Incorrectly assigned individuals from both Sipora and South Pagai were all assigned to Siberut, therefore suggesting each island's individuals are more closely related to Siberut than to each other. Sipora is geographically closer to Siberut (71km) than to South Pagai (121km) and thus it is reasonable incorrect assignments will be in the direction of Siberut. However, South Pagai is closer to Sipora than Siberut (192km), and so the result here is confusing. 'Notes/second in pre-trill' (F_2) is the factor that resulted in the incorrect assignment of South Pagai individuals because Siberut and South Pagai centroids are extremely similar on both islands for the factor. In contrast, the two island centroids are very different in 'Duration of 1st note' (F_1).

The canonical discriminant functions graph (Fig. 3.3) depicts a clinal relationship in F_1 ('Duration of 1st note'), showing the island centroids in the same order as the islands are geographically. There is even a gap in the graph where one could imagine a North Pagai population would fit. Unfortunately, it is likely the North Pagai population of Kloss's gibbons has disappeared due to logging on the island (Whittaker, 2005) and so could not be included in this work. Due to the link between F_1 and the island chain geography, and that F_1 represents a higher percentage of variation in the overall sample (F_1=63.3%; F_2=36.7%) I am inclined to conclude that F_1 is a better indicator of island than F_2 ('Notes/second in pre-trill'). Despite this, the variable 'Duration of 1st note' is the most diverse intra-individual variable and therefore is not a suitable variable for analysis at a higher level of grouping. Therefore the clinal relationship is not valid.

As a further point of conflict, a similar geographic relationship in tree frogs demonstrated an environmental influence (Ralin, 1977). The two species of tree frog were thought to have different vocalisations due to a genetic basis, however, it was discovered the species could converge in vocal characteristics when in the same environment. The likelihood of this being the case in gibbons is small because the gibbon song is far more complex than that of tree fogs, however, it must be considered that influences other than genetics may exist.

CONCLUSION FOR INTER-ISLAND DIVERSITY

In conclusion, the null hypothesis for no significant inter-island diversity can be rejected. The inter-island diversity initially implies a clinal relationship between the islands, which corresponds to their geographic relationship. However, this relationship is dismissed on consideration of further evidence.

4.6. A SIBERUT GROUP, AND A SIPORA & SOUTH PAGAI GROUP

The motivation for a combined Sipora and South Pagai to be compared to Siberut was to assess whether Kloss's gibbons can be recommended for classification simply as a species, or as a species consisting of Evolutionarily Significant Units (ESUs). Siberut and the other three islands would be most likely to have this division between them, because the Mentawai monkeys are all separated into two subspecies or species along this division. The Mentawai langur and the snub-nosed pig-tailed langur were both classified into two subspecies by Chasen and Kloss (1927) on the first expedition to the Mentawais to classify animals. Both langurs were described as being one subspecific form on Siberut and a different subspecific form on Sipora and the Pagais. The Mentawai macaque has recently been elevated to two species, one on Siberut and one on the other three islands (Roos *et al.*, 2003).

4.6.1. EVOLUTIONARILY SIGNIFICANT UNITS (ESUS)

The results section shows contrasting discriminant function analyses for classification into the Siberut group or into the Sipora & South Pagai group. The first classification, which used all the variables, predicts the classification of individuals unreliably (62.5% of cases correctly assigned). This would suggest there is no significant difference in vocal characteristics between the two groups and is provided further support by the inter-island diversity already discussed (Section 4.5). Contrastingly, the second classification, which removes just one variable (number of trill notes) has a significantly reliable classification of individuals to their islands (79.2% of cases correctly assigned). What this difference means is unclear but two main possibilities exist: (1) The first classification is overshadowed by the variable ‘Number of trill notes’ and therefore misses other important features, (2) There is no difference between Siberut and the Sipora & South Pagai group, and the results are simply an artefact of the highly variable data or of the statistical test.

Evidence for possibility (1) is found in the results (section 3.6). The variable used as the function for the first classification has the same mean in Sikabei and South Pagai which presents problems immediately obvious in classification, the two populations must overlap. The two functions which cover the largest amount of variation used in the second classification do not have this overlap problem suggesting they are the better variables for discriminating between the island groupings. The possibility of (2) is unlikely because of the inter-island classifications discussed in the previous section (Section 4.5). In consideration of the possibilities I suggest possibility (1) is the reason for such a dramatic increase in correct classification, however, the results must be treated with caution because of the subjective manipulation of the data.

The results in this work are comparable to that in Whittaker (2005) who studied the genetic phylogeography of the Kloss’s gibbon using the D-loop of mitochondrial DNA (mtDNA). The mtDNA did not provide significant evidence to support the Kloss’s gibbon species consisting of ESUs, however the sample was small and of poor quality due to difficulties in collection of faecal samples. Whittaker (pers.

comm.) suggests a trend towards divergence between Siberut and the other islands, despite the lack of significance.

In light of this evidence, I propose that the Kloss's gibbon is undergoing a speciation event whereby divergence between all islands is occurring, but that the level of divergence is not yet sufficient to classify the species as containing more than one ESU. Whittaker (2005) estimates the Mentawai Islands were last connected 7,000 years before present, however Mann (2005) notes that tectonic movements cause a constant rising and dropping of the Mentawai Islands and this brings the methods of estimation for the last connection event into question because they rely on the depth of sea between the islands and corresponding sea level drops. Despite this, 7,000 years is a very short time in primate speciation events. To put this time in perspective, the various species in the genus *Hylobates* evolved over a period of 800,000 (Chivers, 1977). Some speciation events can take longer, for example, three spider monkey (Ateles) species diverged from each other 3.27 million years ago and in the most recent divergence two subspecies of one of the afore mentioned species diverged 0.34 million years ago (Collins & Dubach, 2000).

The validity of the Mentawai monkey classifications should be questioned and should perhaps follow a similar classification to the Kloss's gibbon. The Mentawai langur was classified on the basis of just five specimens from Sipora and five from Siberut, and diagnostic characters were mainly colour differences (Chasen & Kloss, 1927). The problems are that with such a small sample, colour differences may simply be polymorphisms within the population. The snub-nosed pig-tailed langur subspecific classifications are based on a similarly small sample size (four individuals from

Sipora, three individuals from Siberut), the main difference of the Siberut species (*Simias concolor siberu*) being, "…like *S. concolor* from Sipora island, but darker, especially on the rump." (Chasen & Kloss, 1927). The authors even admit the Siberut female specimen cannot be distinguished from the Sipora specimens.

Mentawai macaques are currently classified as two species: one on Siberut and one on Sipora and the Pagais; as a result of genetic analyses (Roos *et al.*, 2003). However, the specimen base from Siberut is highly unreliable: twelve individuals in total, only five of which were actually sampled on Siberut. The rest are from Bukittinggi Zoo and Padang (presumably pets), both on the Sumatran mainland (Whittaker, 2005). Bukittinggi Zoo is in awful condition and it is very unlikely proper records are kept for their animals and owners of pet macaques in Padang do not often know the specific origin of their pets (pers. obs.). Further from this, the authors discuss the Siberut macaque (*Macaca siberu*) as being more genetically similar to the mainland form of the macaque (*Macaca nemestrina*), leading to the suggestion the origin of the 'Siberut' sample found on mainland Sumatra is not the Mentawais. Therefore, I do not believe this study was sufficient to alter the original classification of one species of Mentawai macaque to two separate species. ESUs for all Mentawai monkey species need further research to either substantiate or disregard the studies that have already taken place.

4.6.2. CONSERVATION IMPLICATIONS

The Kloss's gibbon species can be treated as a species with no ESUs, however, management strategies must also account for high levels of fragmentation of the species and the beginning of divergence on the different islands. Unfortunately, because the species is treated as containing no ESUs, focus may be put onto Siberut at the cost of the other island populations, because the Siberut population is more viable due to it being larger. Limited resources in conservation of the Mentawai Islands means that Siberut is most often targeted, so some effort should go towards highlighting Sipora and the Pagais before the Kloss's gibbon stops being endemic to the Mentawai Islands and is only endemic to Siberut.

CONCLUSION FOR SIBERUT, AND A SIPORA & SOUTH PAGAI GROUP DIVERSITY

The null hypothesis that there is no significant diversity between Siberut and a Sipora & South Pagai group can be accepted. Although, the null hypothesis is accepted, there is a trend towards divergence, with a boundary being between these two groups. The Kloss's gibbon is suggested to remain as a species with no ESUs, and the validity of the classifications of the Mentawai monkeys are challenged.

4.7. CRITIQUE AND FUTURE RESEARCH

The data collection resulted in a smaller sample size of females than was expected. This was because of the lack of a full pilot project in the Mentawai Islands, and that the available information presented females as singing every three to four days (Whitten, 1981). Time frames were set for each field site accordingly, however, females sang less frequently than was suggested, with some listening posts being visited for 7 days before a female was heard and recorded (pers. obs.). Future research should account for this unpredictability in singing behaviour.

Sipora and South Pagai were each represented by only one field site which was problematic because intra-island diversity could not be assessed for these two islands.

Inter-island diversity can only be assessed to a level of high reliability if it is pitched against intra-island diversity, because of the premise that inter-island diversity will be higher than intra-island diversity. This would have been of particular interest because of the high inter-population diversity observed within this work. The lack of these field sites was because of the logistical difficulties of finding new sites, and also because of the small amount of remaining forest, particularly on North Pagai where it is suggested the Kloss's gibbon no longer exists (Whittaker, 2005; Fuentes, 1996/7).

Analysis in this work could have been improved by increasing the number of variables measured/counted, however, it was useful to be able to directly compare this work with that of Haimoff & Tilson (1985). Future research could use the recordings already obtained and increase the number of variables examined. This would be useful because it may be that important differences have been missed in this study because they were not covered by the chosen variables. Research would also be improved if a larger sample size was gained because of the high diversity within this species. In addition, intra-individual diversity may be more constant if only females of an age whereby the song is fully 'practised' were recorded. Although this sounds good in principle, no Kloss's gibbon populations exist where the age of all individuals is known.

Inter-individual diversity among Kloss's gibbons raises the possibility of using vocalisations to monitor populations. If individuals can be distinguished, migration of individuals between groups can be tracked, and a full record of females in an area at any one time compiled. Vocal discrimination is not reliable enough to be used as the sole method of monitoring, but combined with visual observation, would be a powerful tool. The ability to monitor group composition changes would allow stability of groups to be assessed. Stability may be linked to stability in the environment and thus may indicate environmental changes and their effect on the species.

Although this work has shown individual diversity, it can infer no more than a potential for individual recognition. Playback experiments would help resolve whether this potential has been realised by the species and whether neighbour-stranger discrimination is used. Playback experiments could also be used to investigate the function of gibbon song, and so this can be applied to all hylobatids (Geissmann, pers. comm.). In theory this sounds reasonable because the solo songs of males and females would make it easy to separate functions of each sex's song. However, Kloss's gibbons have been observed in groups of up to fifteen (Whittaker, 2005). Duets are thought to reinforce pair bonds (Ahsan, 2001) so the lack of these duets combined with the presence of large groups means suggests that Kloss's gibbon pairs are not as tightly bonded as other hylobatid species.

5. SUMMARY OF DISSERTATION

(1) Intra-individual diversity was low and the null hypothesis was accepted. The diversity is likely a function of age and environmental fluctuations.

(2) Inter-individual diversity varied greatly between populations but was significant in all of the populations. Hypotheses to explain the inter-individual diversity are: (a) Trilling as a handicap, (b) Neighbour-stranger discrimination, (c) Relaxed selection. Neighbour-stranger discrimination is concluded to have the greatest influence, whilst relaxed selection contributes a small influence.

(3) Inter-population diversity was significant and different conditions on the islands are offered as explanations.

(4) Intra-island diversity in Siberut rejected the null hypothesis but is significant in only one variable.

(5) Inter-island diversity is significant and appears to suggest a clinal relationship, however, evidence directs the conclusion that this relationship is not valid.

(6) The Kloss's gibbon species should remain without ESUs but does show evidence of the beginnings of divergence and speciation. Conservation implications are discussed and reassessment of classifications is suggested for the Mentawai monkeys.

(7) Future research should focus on playback experiments and the importance of the 'recognition concept of species' in hylobatids, and population monitoring using vocalisations should be investigated for feasibility.

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APPENDIX I

GPS WAYPOINTS:

Simabuggai:	LP1	S 01º 22’ 29.9’’ E 098º 56’ 35.2’’	41m
	LP2	S 01º 23’ 13.5’’ E 098º 56’ 59.7’’	140m
	LP3	S 01º 22’ 26.7’’ E 098º 56’ 54.4’’	65m
	LP4	S 01º 22’ 37.0’’ E 098º 56’58.7’’	22m
Sikabei:	LP1	S 01º 37’ 07.1’’ E 099º 15’ 15.7’’	39m
	LP2	S 01º 36’ 36.7’’ E 099º 15’ 26.3’’	18m
	LP3	S 01º 37’ 20.1’’ E 099º 15’ 41.6’’	41m
	LP4	S 01º 36’ 44.8’’ E 099º 15’ 00.1’’	120m
S.Pagai:	LP1	S 02º 58’ 00.9’’ E 100º 17’ 15.5’’	215m
	LP2	S 02º 58’ 06.1’’ E 100º 18’ 12.6’’	221m
	LP3	S 02º 58’ 05.2’’ E 100º 17’ 45.1’’	269m
	LP4	S 02º 57’ 26.7’’ E 100º 18’ 35.6’’	194m
	LP5	S 02º 57’ 54.3’’ E 100º 18’ 38.8’’	231m
	LP5+	S 02º 57’ 59.3’’ E 100º 18’ 39.2’’	209m
Saureinu:	LP1	S 02 07’ 15.5’’ E 099 38’ 04.1’’	97m
	LP3	S 02 07’ 52.0’’ E 099 37’ 33.7’’	140m
	LP4	S 02 07’ 49.2’’ E 099 37’ 01.7’’	145m

APPENDIX II

Table A.1. Coefficients of Variation for all Variables in all Individuals and Means of each Variable

INDIVIDUAL				VARIABLES							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1	4.7	22.04	34.31	32.22	16.15	6.915	22.35	19.45	17.32	10.6	8.261	9.014
2	5.915	6.335	4.412	23.81	10.43	2.297	19.33	9.01	12.42	11.48	10.9	7.667
3	8.239	7.19	16.75	25.52	15.14	5.883	12.08	11.97	10.14	9.645	13.05	9.958
4	2.435	9.283	17.67	15.39	14.2	2.606	25.33	12.26	25.35	10.17	11.02	8.998
5	22.67	14.52	35.76	16.63	50.48	3.426	30.52	36.76	25.45	14.71	25.97	26.5
6	17.18	4.618	56.3	28.44	18.6	6.525	30.42	31.87	8.182	6.975	6.148	1.786
7	6.032	21.74	10.55	16.84	23.11	1.583	7.733	6.542	7.752	6.91	9.634	3.409
8	5.668	21.65	18.64	10.42	4.094	3.078	0	9.804	9.804	3.891	6.95	7.642
9	10.29	15.35	10.4	17.06	11.98	3.677	17.86	9.79	15.24	14.54	12.4	7.659
10	4.717	5.718	15.61	13.85	5.298	4.094	10.88	0.857	9.74	8.723	10.61	20
11	4.956	6.035	10.04	9.316	12.43	4.473	23.93	15.07	16	6.713	8.093	3.748
12	2.44	7.421	3.831	25.82	11.49	1.888	22.36	7.042	17.69	6.164	5.313	4.554
13	8.825	11.11	16.46	14.21	15.85	1.086	13.48	3.416	13.08	17.17	21.39	7.5
14	7.594	8.601	10	20.27	11.85	3.475	17.57	13.17	5.521	7.799	11.33	7.307
15	7.052	6.662	12.84	11.85	10.22	2.965	9.695	14.65	20.51	7.79	10.57	13.91
16	6.984	19.88	47.1	15.16	29.61	4.597	17.39	4.74	12.59	9.157	8.511	2.653
17	2.623	11.46	25.97	7.863	4.278	3.014	10.88	9.785	1.274	3.324	5.172	8.429
18	3.932	10.27	15.7	10.32	10.81	3.488	12.16	8.88	7.407	11.51	9.361	4.167
19	5.284	8.309	15.96	18.1	6.897	1.275	23.5	14.98	12.16	5.858	9.957	7.114
20	6.724	8.932	7.31	13.91	9.225	3.514	6.458	6.979	6.829	8.65	6.684	2.96
21	6.635	6.247	5.691	8.324	6.842	2.403	10.5	5.574	8.609	9.931	8.461	6.77
22	12.41	4.934	18.18	18.96	9.211	1.099	12.95	13.56	11.92	12.39	9.402	7.912
23	8.194	13.08	22.73	16.46	8.92	1.497	11.83	12.02	15.12	17.19	16.66	10.7
24	8.374	8.786	6.987	13.08	18.95	3.893	7.796	8.349	7.927	11.03	14.48	5.782
MEANS	**7.495**	**10.841**	**18.3**	**16.826**	**14.003**	**3.281**	**15.708**	**11.939**	**12.418**	**9.68**	**10.847**	**8.172**

APPENDIX III

Key to table: Island 1 – Siberut, 2 – South Pagai, 3 – Sipora
Pop. 1 – Simabuggai, 2 – Sikabei, 3 – South Pagai, 4 - Saureinu
Ind. = Individual
GC # = Great call number

Table A.2. Data set of all Variables from all Individuals and all Great Calls

Island	Pop.	Ind.	GC #	1	2	3	4	5	6	7	8	9	10	11	12
1	1	1	1	22.08	780	0.97	125	1.34	917	5	4.95	0.99	17.14	86	5.02
1	1	1	2	23.78	600	1.69	212	2.23	1103	9	9.57	1.06	14.21	91	6.40
1	1	1	3	22.66	540	1.45	180	2.08	1041	7	9.08	1.30	13.59	72	5.30
1	1	1	4	21.07	690	2.61	240	1.74	1109	6	8.20	1.37	12.88	78	6.06
1	1	1	5	21.22	930	2.69	297	1.92	1145	5	8.10	1.62	13.12	79	6.02
1	1	1	6	22.02	930	2.11	254	2.17	1060	8	9.06	1.13	12.97	78	6.02
1	1	1	7	23.53	960	2.78	360	1.99	1079	7	9.71	1.39	13.82	88	6.37
1	1	2	8	18.54	840	2.54	510	2.27	1199	6	8.98	1.50	9.55	61	6.39
1	1	2	9	18.86	780	2.64	339	2.21	1145	7	9.23	1.32	9.63	58	6.03
1	1	2	10	19.63	720	2.80	240	1.89	1229	4	7.41	1.85	12.23	70	5.72
1	1	2	11	20.75	840	2.93	297	1.75	1187	7	9.57	1.37	11.17	79	7.07
1	1	2	12	20.80	740	2.71	360	2.23	1169	5	8.58	1.72	12.23	73	5.97
1	1	2	13	21.90	840	2.74	330	2.08	1169	6	9.26	1.54	12.64	72	5.69
1	1	2	14	20.45	780	2.70	360	2.36	1169	7	9.87	1.41	10.58	64	6.05
1	1	3	15	20.83	840	2.47	382	2.07	1103	6	9.01	1.50	11.82	56	4.74
1	1	3	16	22.15	870	1.86	270	2.16	1049	7	10.51	1.50	11.64	55	4.73
1	1	3	17	22.21	810	2.48	420	1.72	1169	7	11.20	1.60	11.01	56	5.09
1	1	3	18	18.64	720	2.27	270	1.61	1169	7	8.66	1.24	9.99	52	5.21
1	1	3	19	17.74	870	2.18	420	1.67	1079	6	8.63	1.44	9.11	41	4.50
1	1	3	20	19.93	750	1.75	300	2.20	990	6	8.41	1.40	11.53	44	3.82
1	1	3	21	20.36	840	1.62	210	1.54	1079	5	8.50	1.70	11.86	59	4.98
1	1	4	22	23.15	930	2.20	420	2.05	1139	5	9.80	1.96	13.36	60	4.49
1	1	4	23	23.96	840	1.69	420	1.55	1079	9	10.37	1.15	13.59	75	5.52
1	1	4	24	23.80	900	2.08	300	1.57	1079	6	7.77	1.29	16.04	76	4.74
1	1	4	25	22.74	750	2.62	420	1.60	1109	7	8.97	1.28	13.77	66	4.79
1	1	5	26	20.47	570	4.58	420	1.39	1139	4	8.50	2.12	11.97	40	3.34
1	1	5	27	20.30	630	2.08	450	1.28	1049	7	8.31	1.19	11.99	69	5.75
1	1	5	28	25.51	780	2.43	300	2.16	1109	7	9.93	1.42	15.58	54	3.47
1	1	5	29	32.15	750	3.53	390	3.58	1109	9	16.78	1.86	15.37	74	4.82
1	1	6	30	21.63	780	1.98	420	1.48	1199	9	9.48	1.05	12.15	61	5.02
1	1	6	31	18.30	810	1.33	300	1.42	1079	6	6.23	1.04	12.07	61	5.05
1	1	6	32	26.58	810	2.23	420	2.10	1049	13	13.74	1.06	12.85	66	5.14
1	1	6	33	26.35	870	4.61	600	1.86	1049	10	12.35	1.24	14.00	69	4.93
1	1	7	34	18.59	600	2.61	300	1.75	1079	8	9.23	1.15	9.36	56	5.98
1	1	7	35	19.65	750	2.41	420	2.53	1109	7	9.10	1.30	10.56	63	5.97
1	1	7	36	20.60	990	2.90	420	1.66	1079	7	9.72	1.39	10.89	69	6.34
1	1	7	37	21.38	933	2.30	330	2.56	1109	8	10.49	1.31	10.89	69	6.34

1	2	8	38	18.92	600	2.36	510	1.58	1229	5	7.53	1.51	11.39	44	3.86
1	2	8	39	17.85	960	2.14	420	1.77	1199	5	7.35	1.47	10.50	50	4.76
1	2	8	40	18.45	840	2.23	450	1.68	1169	5	7.60	1.52	10.86	51	4.70
1	2	8	41	18.26	660	1.93	480	1.73	1139	5	7.03	1.41	11.23	53	4.72
1	2	8	42	20.72	750	2.86	540	1.77	1199	5	9.12	1.82	11.61	54	4.65
1	2	8	43	17.97	540	1.66	420	1.75	1139	5	7.28	1.46	10.70	51	4.77
1	2	9	44	23.30	510	2.20	300	2.39	1049	10	11.84	1.18	11.47	58	5.06
1	2	9	45	27.52	510	2.81	420	2.65	1109	7	12.15	1.74	15.37	73	4.75
1	2	9	46	32.28	720	2.77	390	1.87	1049	8	14.59	1.82	17.69	84	4.75
1	2	9	47	28.20	600	2.56	480	2.43	1109	6	11.21	1.87	16.99	76	4.47
1	2	9	48	29.01	720	2.28	330	2.66	1139	7	11.63	1.66	17.38	74	4.26
1	2	9	49	28.76	630	2.36	360	2.51	1049	8	12.74	1.59	16.03	66	4.12
1	2	10	50	18.25	540	1.95	420	1.58	1079	6	8.25	1.37	10.00	54	5.40
1	2	10	51	19.75	594	2.52	540	1.51	1169	5	8.11	1.62	11.63	44	3.78
1	2	10	52	19.89	600	2.62	540	1.43	1109	5	8.16	1.63	11.73	47	4.01
1	2	11	53	18.89	930	2.80	660	2.10	1229	5	8.95	1.79	9.95	52	5.23
1	2	11	54	16.80	870	2.33	540	1.67	1289	5	6.43	1.29	10.37	55	5.31
1	2	11	55	18.86	900	3.01	540	1.94	1199	8	9.76	1.22	9.10	45	4.95
1	2	11	56	18.28	930	2.51	600	2.00	1139	5	8.00	1.60	10.27	50	4.87
1	2	11	57	18.96	1020	2.81	540	1.54	1229	5	8.00	1.60	10.96	55	5.02
1	2	12	58	17.68	870	2.45	510	1.46	1199	7	8.00	1.14	9.68	54	5.58
1	2	12	59	18.28	1020	2.65	480	1.19	1229	5	7.21	1.44	11.06	58	5.24
1	2	12	60	17.63	840	2.61	570	1.62	1169	5	7.59	1.52	10.03	53	5.28
1	2	12	61	18.68	870	2.73	600	1.65	1169	5	7.80	1.56	10.88	56	5.15
1	2	12	62	17.66	900	2.68	750	1.48	1199	4	7.48	1.87	10.18	50	4.91
1	2	12	63	18.27	960	2.53	330	1.47	1199	7	8.78	1.25	9.49	52	5.48
1	2	13	64	16.28	780	2.67	390	1.46	1229	8	8.50	1.06	7.77	29	3.73
1	2	13	65	14.99	960	2.32	480	1.63	1229	7	8.55	1.22	6.44	25	3.88
1	2	13	66	17.36	1050	2.22	540	1.96	1229	6	8.14	1.36	9.22	39	4.23
1	2	13	67	18.12	870	2.99	540	1.89	1259	6	8.34	1.39	9.78	43	4.40
1	2	13	68	18.79	960	1.97	570	2.22	1229	6	8.92	1.49	9.87	37	3.75
1	2	14	69	24.55	840	1.91	300	2.38	1049	7	11.75	1.68	12.80	62	4.84
1	2	14	70	22.39	670	2.25	360	1.88	1079	6	9.28	1.55	13.11	60	4.58
1	2	14	71	23.22	810	2.51	330	1.75	1049	6	10.24	1.71	12.98	62	4.78
1	2	14	72	24.54	870	2.16	300	2.18	1139	6	10.12	1.69	14.41	62	4.30
1	2	14	73	24.83	840	2.40	540	2.42	1020	7	11.38	1.63	13.45	59	4.39
1	2	14	74	24.37	930	2.20	390	2.17	1079	7	11.73	1.68	12.65	61	4.82
1	2	14	75	26.87	840	2.22	360	1.80	1079	9	13.55	1.51	13.32	72	5.40
1	2	14	76	28.74	840	1.80	420	2.28	1020	9	13.46	1.50	15.28	79	5.17
1	2	14	77	25.70	780	2.30	330	2.16	1079	6	10.24	1.71	15.46	75	4.85

2	3	15	78	16.35	870	2.00	480	1.86	1199	6	6.09	1.02	10.26	55	5.36
2	3	15	79	18.16	750	2.25	390	1.85	1139	6	8.34	1.39	9.82	49	4.99
2	3	15	80	19.71	810	1.64	339	1.92	1166	5	9.17	1.83	10.54	42	3.99
2	3	15	81	18.59	720	2.33	450	1.50	1199	6	8.76	1.46	9.84	56	5.69
2	3	15	82	19.05	750	2.44	450	2.16	1199	6	9.63	1.61	9.42	46	4.88
2	3	15	83	19.99	810	2.36	450	1.84	1169	5	9.88	1.98	10.11	54	5.34
2	3	15	84	20.19	750	2.26	480	1.88	1109	5	8.30	1.66	11.89	47	3.95
2	3	16	85	17.05	750	2.12	390	1.67	1229	6	8.43	1.41	8.62	43	4.99
2	3	16	86	19.58	540	0.87	360	1.87	1124	8	9.28	1.16	10.30	51	4.95
2	3	16	87	18.76	540	1.16	480	1.01	1199	6	8.86	1.48	9.90	47	4.75
2	3	17	88	19.39	780	1.65	420	1.84	1109	5	7.90	1.58	11.49	55	4.79
2	3	17	89	19.08	720	2.43	420	1.97	1169	5	7.92	1.58	11.16	58	5.20
2	3	17	90	20.08	900	2.84	480	1.82	1169	6	9.33	1.56	10.75	61	5.68
2	3	18	91	20.16	900	2.24	480	1.72	1139	6	9.82	1.64	10.34	50	4.84
2	3	18	92	20.08	810	2.54	390	1.86	1229	5	8.49	1.70	11.59	56	4.83
2	3	18	93	20.36	930	2.50	420	1.90	1229	6	10.09	1.68	10.27	47	4.58
2	3	18	94	22.20	960	2.29	510	2.11	1139	7	9.68	1.38	12.52	57	4.55
2	3	18	95	20.15	720	2.26	420	1.54	1199	7	11.21	1.60	8.93	45	5.04
2	3	18	96	20.66	840	1.56	480	2.00	1169	6	10.15	1.69	10.51	52	4.95
2	3	19	97	19.40	690	1.45	270	1.85	1199	4	6.98	1.74	12.42	66	5.31
2	3	19	98	20.58	780	2.15	420	1.82	1169	7	9.61	1.37	10.97	54	4.92
2	3	19	99	20.48	840	2.02	390	1.57	1169	6	8.36	1.39	12.12	54	4.46
2	3	19	100	22.06	810	1.88	390	1.73	1169	7	9.78	1.40	12.29	61	4.97
3	4	20	101	18.46	1020	3.23	570	2.47	1109	5	9.28	1.86	9.18	45	4.90
3	4	20	102	20.47	1050	3.60	630	2.42	1139	5	9.79	1.96	10.68	51	4.78
3	4	20	103	20.57	1140	3.60	570	2.74	1199	5	10.46	2.09	10.11	49	4.85
3	4	20	104	20.84	1110	3.48	480	2.77	1169	5	10.41	2.08	10.43	50	4.79
3	4	20	105	19.55	1110	3.81	480	2.31	1139	5	10.24	2.05	9.31	44	4.73
3	4	20	106	21.87	1110	3.02	450	3.04	1079	5	10.82	2.16	11.04	50	4.53
3	4	20	107	21.92	990	3.13	420	2.96	1079	6	11.43	1.90	10.50	51	4.86
3	4	20	108	21.99	870	3.40	450	2.76	1109	5	10.13	2.03	11.86	54	4.55
3	4	20	109	23.09	930	3.44	480	2.90	1139	5	11.54	2.31	11.56	53	4.59
3	4	21	110	18.50	900	2.31	450	1.64	1169	7	8.98	1.28	9.52	57	5.99
3	4	21	111	17.17	930	2.39	510	1.93	1199	6	8.38	1.40	8.79	47	5.35
3	4	21	112	17.49	840	2.63	420	1.85	1259	6	8.48	1.41	9.02	48	5.32
3	4	21	113	18.55	990	2.55	450	1.92	1229	5	8.32	1.66	10.23	51	4.99
3	4	21	114	18.96	885	2.27	420	1.85	1199	6	8.76	1.46	10.21	50	4.90
3	4	21	115	18.96	960	2.42	480	1.91	1259	6	9.24	1.54	9.72	52	5.35
3	4	21	116	20.03	900	2.67	450	2.21	1259	5	8.72	1.74	11.32	54	4.77
3	4	21	117	19.76	960	2.63	450	1.81	1229	6	9.18	1.53	10.58	51	4.82
3	4	21	118	19.59	900	2.35	450	1.88	1229	6	9.24	1.54	10.34	51	4.93
3	4	21	119	19.77	840	2.40	540	1.97	1199	7	9.98	1.43	9.79	52	5.31
3	4	21	120	21.75	810	2.47	420	1.90	1229	6	9.41	1.57	12.34	63	5.10
3	4	22	121	17.23	900	2.18	420	2.08	1109	5	8.39	1.68	8.84	39	4.41
3	4	22	122	17.55	900	1.76	300	2.24	1109	7	8.76	1.25	8.79	43	4.89
3	4	22	123	19.18	930	2.48	450	2.41	1109	7	9.89	1.41	9.29	38	4.09
3	4	22	124	17.50	900	2.20	390	2.15	1109	6	8.41	1.40	9.09	44	4.84
3	4	22	125	18.30	810	2.21	270	2.16	1109	6	9.82	1.64	8.48	41	4.83
3	4	22	126	23.41	930	3.02	390	2.65	1139	7	11.76	1.68	11.65	49	4.20
3	4	23	127	18.32	1050	2.14	390	2.21	1109	7	11.57	1.65	6.75	32	4.74
3	4	23	128	20.75	960	2.77	480	1.95	1079	5	10.47	2.09	10.28	43	4.18
3	4	23	129	18.49	780	3.05	330	2.21	1109	6	9.03	1.50	9.47	48	5.07
3	4	23	130	19.20	900	2.49	360	2.35	1079	6	8.88	1.48	10.31	51	4.95
3	4	23	131	22.11	780	3.85	330	1.92	1109	6	11.20	1.87	10.90	43	3.94
3	4	24	132	19.82	870	2.05	330	2.08	1139	6	10.44	1.74	9.38	43	4.58
3	4	24	133	23.81	1020	2.25	480	1.38	1109	7	11.72	1.67	12.09	57	4.72
3	4	24	134	25.08	870	2.37	420	1.99	1079	7	12.27	1.75	12.81	64	5.00
3	4	24	135	23.81	810	2.48	360	2.03	1199	7	10.80	1.54	13.01	63	4.84
3	4	24	136	22.09	870	2.43	390	2.35	1169	6	10.21	1.70	11.88	50	4.21
3	4	24	137	21.55	810	2.20	390	1.58	1109	7	9.96	1.42	11.60	54	4.66

APPENDIX IV

Key for table follows that in Appendix IV.

Table A.3. Means for all Variables for all Individuals. Means for all Variables in each Populaiton also included.

Island	Pop.	Ind.	1	2	3	4	5	6	7	8	9	10	11	12
1	1	1	22.34	775.71	2.04	238	1.92	1065	7	8.38	1.26	13.96	82	5.88
1	1	2	20.13	791.43	2.72	348	2.11	1181	6	8.99	1.53	11.15	68	6.13
1	1	3	20.27	814.29	2.09	324	1.85	1091	6	9.27	1.48	10.99	52	4.72
1	1	4	23.41	855.00	2.15	390	1.69	1102	7	9.22	1.42	14.19	69	4.89
1	1	5	24.61	682.50	3.16	390	2.10	1102	7	10.88	1.65	13.73	59	4.34
1	1	6	23.21	817.50	2.54	435	1.72	1094	10	10.45	1.10	12.76	64	5.04
1	1	7	20.05	818.25	2.56	367	2.12	1094	8	9.63	1.29	10.42	64	6.16
		Mean	**22.00**	**793.53**	**2.46**	**356.03**	**1.93**	**1104.29**	**7.07**	**9.55**	**1.39**	**12.46**	**65.53**	**5.31**
1	2	8	18.70	725.00	2.20	470	1.71	1179	5	7.65	1.53	11.05	51	4.58
1	2	9	28.18	615.00	2.50	380	2.42	1084	8	12.36	1.64	15.82	72	4.57
1	2	10	19.29	578.00	2.37	500	1.51	1119	5	8.17	1.54	11.12	48	4.40
1	2	11	18.36	930.00	2.69	576	1.85	1217	6	8.23	1.50	10.13	51	5.07
1	2	12	18.03	910.00	2.61	540	1.48	1194	6	7.81	1.46	10.22	54	5.27
1	2	13	17.11	924.00	2.43	504	1.83	1235	7	8.49	1.30	8.62	35	4.00
1	2	14	25.02	824.44	2.19	370	2.11	1066	7	11.31	1.63	13.72	66	4.79
		Mean	**20.67**	**786.63**	**2.43**	**476.88**	**1.84**	**1156.61**	**6.10**	**9.15**	**1.52**	**11.52**	**53.75**	**4.67**
2	3	15	18.86	780.00	2.18	434	1.86	1169	6	8.60	1.56	10.27	50	4.89
2	3	16	18.47	610.00	1.38	410	1.52	1184	7	8.86	1.35	9.61	47	4.90
2	3	17	19.52	800.00	2.31	440	1.87	1149	5	8.38	1.57	11.13	58	5.22
2	3	18	20.60	860.00	2.23	450	1.85	1184	6	9.91	1.62	10.69	51	4.80
2	3	19	20.63	780.00	1.88	367	1.74	1177	6	8.68	1.48	11.95	59	4.91
		Mean	**20.03**	**806.67**	**2.10**	**417.02**	**1.82**	**1176.73**	**5.91**	**9.06**	**1.55**	**10.97**	**53.26**	**4.87**
3	4	20	20.97	1036.67	3.41	503	2.71	1129	5	10.45	2.05	10.52	50	4.73
3	4	21	19.14	901.36	2.46	458	1.90	1224	6	8.97	1.51	10.17	52	5.17
3	4	22	18.86	895.00	2.31	370	2.28	1114	6	9.50	1.51	9.36	42	4.55
3	4	23	19.77	894.00	2.86	378	2.13	1097	6	10.23	1.72	9.54	43	4.58
3	4	24	22.69	875.00	2.29	395	1.90	1134	7	10.90	1.64	11.79	55	4.67
		Mean	**20.29**	**920.41**	**2.67**	**420.68**	**2.18**	**1139.90**	**6.02**	**10.01**	**1.68**	**10.28**	**48.59**	**4.74**