Agile Gibbons
(*Hylobates agilis albibarbis*):
Vocalisations as an Indicator
of geographical isolation

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Abstract

The primary aim of this study was to discover if there are differences in call characteristics of agile gibbons (*Hylobates agilis albibarbis*) between genetically isolated gibbon populations over a small geographical distance compared to gibbon groups over a large geographical distance without major physical barriers to population migration (ie rivers). This was done by recording six areas separated by three rivers in Central Borneo, Indonesia.

The study found that agile gibbon song has a particular social structure and is both genetically determined and learned by listening to other individuals. It was discovered that there was differences between female great calls in inaccessible and linked populations. Also discovered was the difference in call characteristics between individuals inhabiting the same area. The study suggests that gibbon's call individuality is a major factor in maintaining accurate communication with groups of the same population. If the gibbons do not have to opportunity to come into contact with one another, then they have no need to distinguish their song as they don't need to maintain individuality. If the opportunity of meeting does occur then they must maintain individuality to ensure accurate communication.

Contents

1.0 Introduction

1.1 Taxonomy and Classification

Gibbons are small, arboreal apes with a specialised social structure which is maintained by a complex communication system of sex and species-specific calls unknown to any other primate species. Both species of Bornean gibbon (*Hylobates agilis albibarbis,* and *H. muelleri spp*) are classified Low Risk/near threatened by the World Conservation Union (IUCN) and listed on CITES Appendix 1. Indonesia harbours the highest number of threatened mammals in the world (135 species) and birds (115 species; IUCN, 2004). Population size of agile gibbons is currently estimated at 50,000 individuals (S, M Cheyne, 2005, pers comm) and has been steadily declining over the years due to many factors such as habitat fragmentation and degradation, illegal logging, the illegal pet trade, forest fires, the expansion of the palm oil industry and human population pressure. The decentralisation of government makes law enforcement difficult, which is essential for the survival of this species.

This particular sub-species (see figure and table 1.1) is only found on the island of Borneo, Indonesia. The island is also home to the Mueller's gibbon (*Hylobates muelleri*) which inhabits the northern part of the island, shown in figure 1.2.

Kingdom	Animalia
Phylum	Chordata
Class	Mammalia
Order	Primates
Family	Hylobatidae
Genus	*Hylobates agilis*
Species	*Hylobates agilis albibarbis*
Common name	Bornean agile gibbon

Table 1.1 Classification of species

Fig 1.1 *Hylobates agilis albibarbis*

A hybrid (*Hylobates agilis* x *H. muelleri*) population exists in the forests around the headwaters of the Barito river, Central Kalimantan. Populations of Mueller's and agile gibbons are restricted by the Joloi, Busang and Murung tributaries but narrowing in the river has resulted in hybridisation between the species (Mather, 1992).

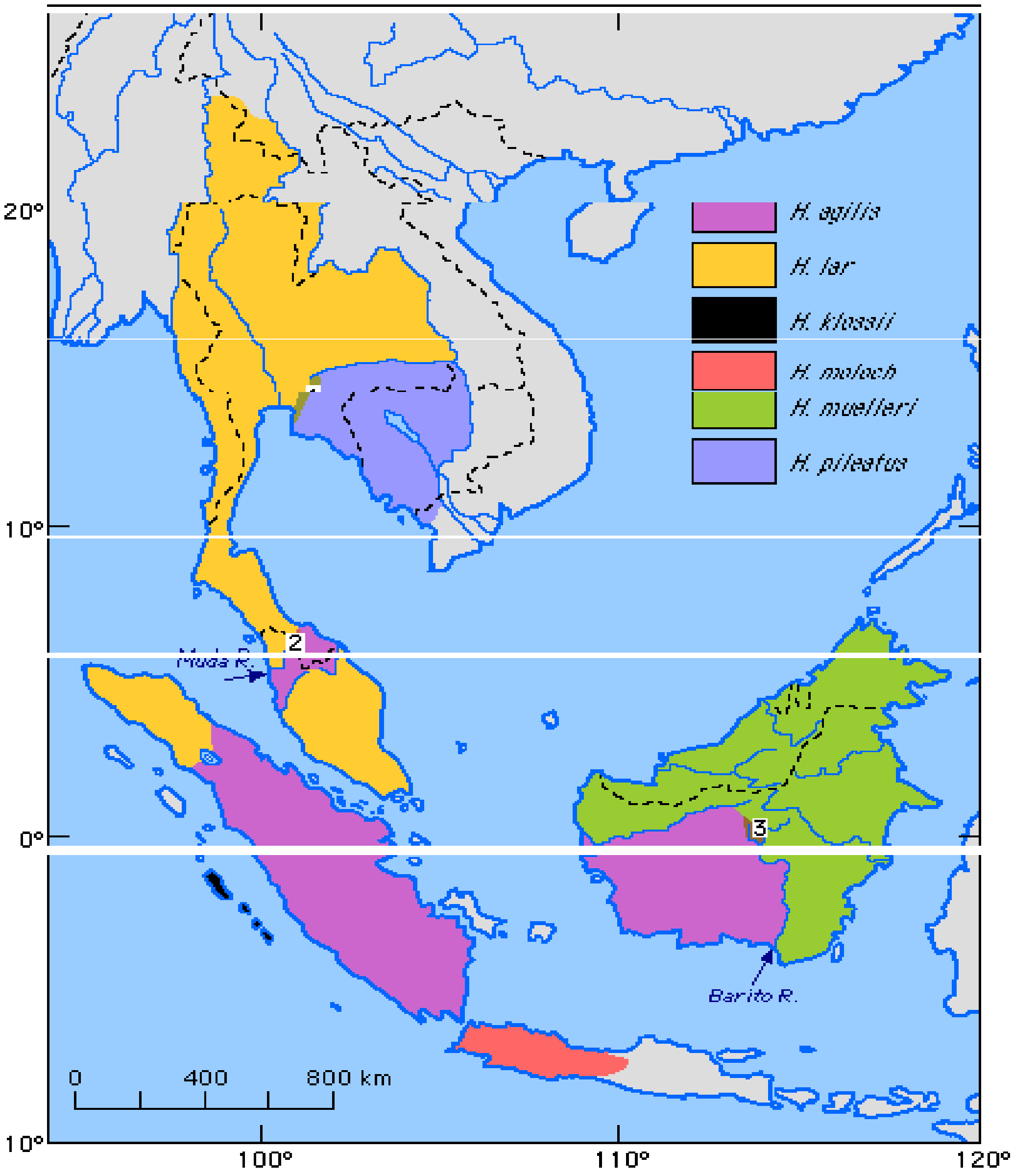

Fig 1.2 Map showing distribution of six of the gibbon species throughout S.E Asia.

1.2 Behaviour and Habitat

Agile gibbons inhabit a range of forest types including the primary and secondary tropical peat swamp, low and tall pole and karangas. Gibbons live in monogamous, territorial family groups characteristically consisting of a mated pair and up to three immature offspring (Dallmann and Geissmann, 2001). They are highly mobile members of the forest through the use of brachiation as their main form of locomotion when moving in the upper canopy (Gittins, 1983). This adaptation provides them with a swift and direct movement, enabling them to exploit scattered food sources and defend a large territory.

Territory is the area within the home-range, which is used exclusively by the group and defended against conspecifics. Gibbons have classical territories, meaning that mating, feeding, and raising young all occur in this defended space. The suggested home-range size of agile gibbon groups ranges between 16.5 and 43 hectares, seventy-five percent of which is defended and is considered its territory. This is also dependant on the size of the group and the quality of the forest they inhabit (Chivers, 1984). Gibbon home ranges can overlap as much as 64 percent with neighbouring gibbon home ranges; as a result, aggressive intergroup encounters are common (Reichard and Sommer 1997). Overlapping can also occur in extensively logged forest habitats where the animals are being forced to move into each other's territories. This can cause higher levels of stress and aggression and an increase in alarm calling.

The topography of an area must also be taken into account; whether the area is flat or there are hills present will affect how frequently the gibbons sing. Inhabitants of hilly landscapes were observed to sing less due to echoing intensifying the sound of their calls (pers obser). Gibbon song is an important part of their behaviour as duetting advertises the mated status of the pair and defends the exclusive reproductive access to the mate (Leighton 1986).

Exclusive reproductive access is however, not always the case, as with the black-crested gibbon (*Hylobates concolor*) where extra-pair copulations have been observed (Delacour, 1933). It is important in establishing, strengthening and maintaining pair bonds. This however must be accompanied with other behaviours such as grooming, and foraging for food. Newly mated pairs will sing more frequently in order to synchronise duetting, as it is more difficult for unfamiliar individuals to adjust to each other's idiosyncrasies (Mather, 1992).

1.3 Calls

All gibbon species produce long, loud and complex song bouts at specifically established times of day, usually in the early morning. The evolution of their song emerged from the last common ancestor of gibbons (Muller *et al,* 2003). They produced duets that probably evolved from a song common to both sexes that later became separated into male/female specific parts (Geissmann, 2002). Most species call in the form of well-coordinated duets, however in the *Hylobates klossii* and *H.*

moloch species, duetting is absent but female solo songs are common (Geissmann, 2002).

Duetting in agile gibbons are structured in three distinctive sequences 1) the introductory sequence, occurring at the start of the song bout, followed on by 2) the organising and 3) the great call sequences which are produced in irregular succession throughout the remaining song bout. Duet bouts of all species are produced and organised in this particular way, with the least unpredictable and most obvious characteristic being the female great call (Haimoff and Gittins 1984).

The emphasis for this study will be on the female great call as it is the most genetically conserved part of the song; therefore the best place to look for differences between populations (Haimoff, 1984). It is also the most stereotypical song phrase generated by female gibbons (Dallmann and Geissmann, 2000). There are five main sections of phases, shown in figure 1.2, compromising the great calls of the agile gibbon females; these include the introductory, inflective, climax, post-climax and terminal phases (Haimoff and Gittins 1984). The variables selected for this analysis in this study are presented in the methods section.

Once the female's great call is completed, the males produce a series of notes called the 'coda'. This sequence of notes was originally believed to be as distinguishing and consistent as the female great call (Marshall and Marshall 1976). However, Haimoff and Gittins (1984) later discovered the male's codas was variable in all aspects, therefore it was concluded that it has a different function to the great calls and is not suitable for evaluation and analysis of individuality.

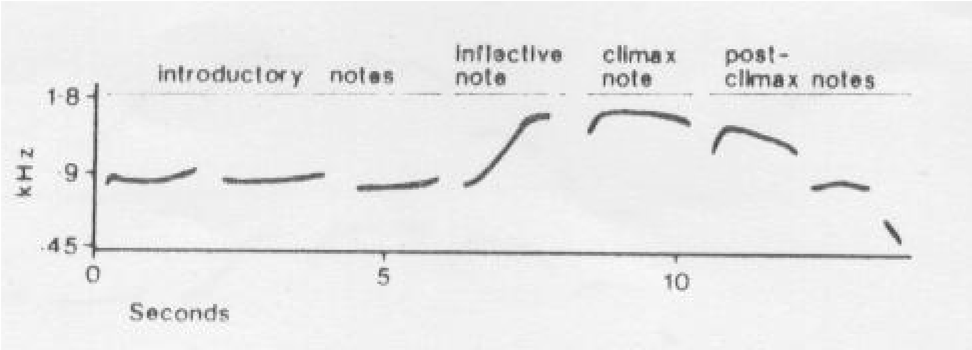

Fig 1.2 The five main phases of a female agile gibbon's great call

All gibbon species have call sequences of different frequencies and phrases that are organised specific to each species (Haimoff 1984). These songs show evidence of individual, species and sex specific characteristics (Dallmann and Geissmann, 2000). Individual call characteristics are one of the main mate choice criteria; this reduces the likelihood of inbreeding through recognition of family-specific calls. Playback experiments have been carried out on various bird species, who recognise, and occasionally respond to the songs of other species, for example closely related competitors. They are also able to learn to songs of their neighbours and distinguish between unfamiliar individuals of the same species and neighbours. This suggests song has a broad range of functions and assists recognition of a diversity of significant things, including: sex, kin, species, mate and other individuals such as territorial neighbours (Catchpole and Slater, 1995).

1.4 Aims and Hypothesis

The aim of this study is to discover if there are differences in call characteristics between genetically isolated gibbon populations over a small geographical distance compared to gibbon groups over a large geographical distance without major physical barriers to population migration (ie rivers). It is predicted that there will be evidence of both genetic inheritance and learning; a combination of both attributes that make up the production of song.

Null hypothesises:

1. There are no significant differences between the great calls of female gibbons in isolated and connected populations.
2. There are no significant differences between individual's great calls within an area.

2.0 : Methods

2.1: Experimental Design

This study was designed to analyse differences in call characteristics between different locations of gibbon groups. The study was carried out in central Borneo, Indonesia where six locations were chosen to perform the study, either side of three major rivers. Refer to figure 2.3.3 for the distances between which areas used in comparisons and appendix 5 for satellite images of the area. The sample size was three groups per area, and six female great calls per group to examine both individual repertoire and dialect within a location. In area C – Sabangau, seven groups were recorded as opposed to the usual three. These recordings were obtained purposely to determine if individual repertoire has significant variation within an area and if the area's dialect should be taken into account rather than specific individual repertoire. The dependant variable would be the call characteristics, with the independent being the location of the population.

2.2 : Study site

This study encompassed three sites each with two locations per site. They included areas 1: **Katingan River**, 2: **Sabangau River** and 3: **Kahayan River.** These three study sites all contained different tropical mixed peat swamp forest sub-types such as, low pole, tall pole and karangas, shown in table 2.2.1.

Area	**Forest type**	**Topography**	**Quality of forest**
1. Katingan river			
A. Bankonan	low and tall pole forest	flat land	logged extensively
B. Musang	tall pole forest	flat land	logged extensively
2. Sabangau River			
C. Sabangau	mixed peat swamp	flat land	minor logging
D. Mega Rice Project	mixed peat swamp	flat land	logged extensively, fragmented forest.
3. Kahayan River			
E. Hibongan	low and tall pole forest	hills present	logged extensively
F. Bawan	karangas	hills present	some logging

Table 2.2.1 Different forest types in each area

2.3 Forest Types

Tropical mixed peat swamp forest – A little known, relatively inaccessible habitat, yet remarkably diverse and home to 50% of the remaining population of wild orang-utans in Borneo. Some distinct habitat sub-types can be identified there; varying in the structure and vegetation composition from the depauperate, wet, **low pole** forest to the diverse, dry, deep peat **tall pole** interior forest on the watershed. The latter is unique and remarkably diverse, standing on peat 13m deep and 20,000 years old, see figure 2.3.1.

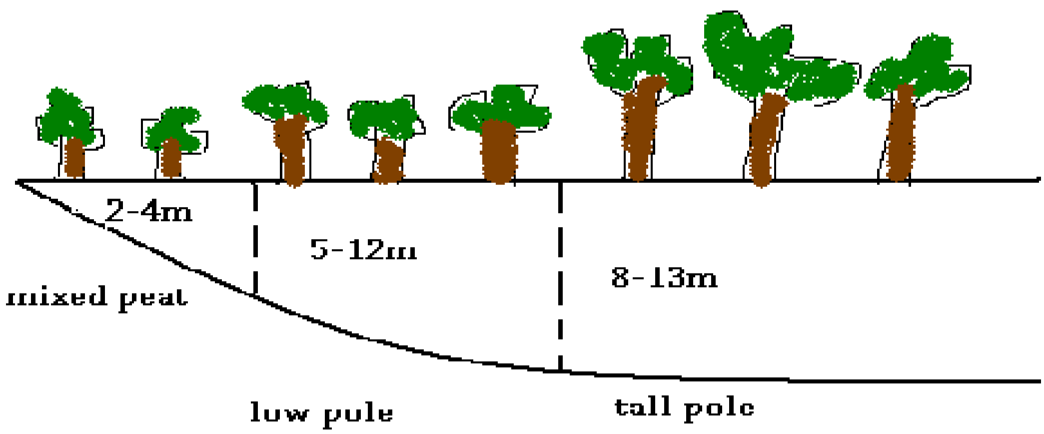

Fig 2.3.1 Depth of peat in a tropical mixed peat swamp forest

Karangas forest – A distinctive characteristic of Karangas forest is the white sand floor, which is dried up peat. It is the part of the forest that outskirts it's tropical tall pole interior, see figure 2.3.2.

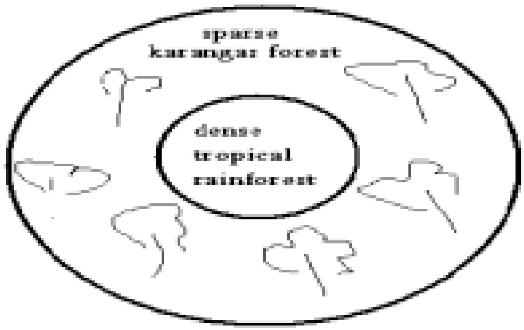

Fig 2.3.2 Karangas and tropical rainforest

These forests support a wide diversity of plant and animal life and is home to endangered tree species such as ramin (*Gonystylus bancanus*) and swamp meranti (*Parashorea densiflora*) which are exported all over the world to be used for furniture and things such as pool cues. Ramin can reach prices of up to $1000. Since 2001, ramin has been registered on the endangered species list of CITES and classified 'zero quota' (IUCN, 2000). Nine species of primate can be found there, including the Bornean orangutan (*Pongo pygmaeus pygmaeus*), agile gibbon (*Hylobates agilis albibarbis*), slow loris (*Nycticebus coucang*) and the pig-tailed macaque (*Macaca nemestrina*). There is also a wide range of mammal species, including; the sun-bear (*Ursus malayanus*), bearded pig (*Sus barbatus*), sambar deer (*Cervus unicolour*), clouded leopard (*Neofelis nebulosa diardi*), marbled cats (*Pardofelis marmorata*), civets (*Diplogale hosei* and *Viverra tangalunga),* pen-tailed tree shrews (*Ptilocercus lowi*), water monitors (*Varanus salvator*), several species of snake, over 200 species of bird and a diverse invertebrate community.

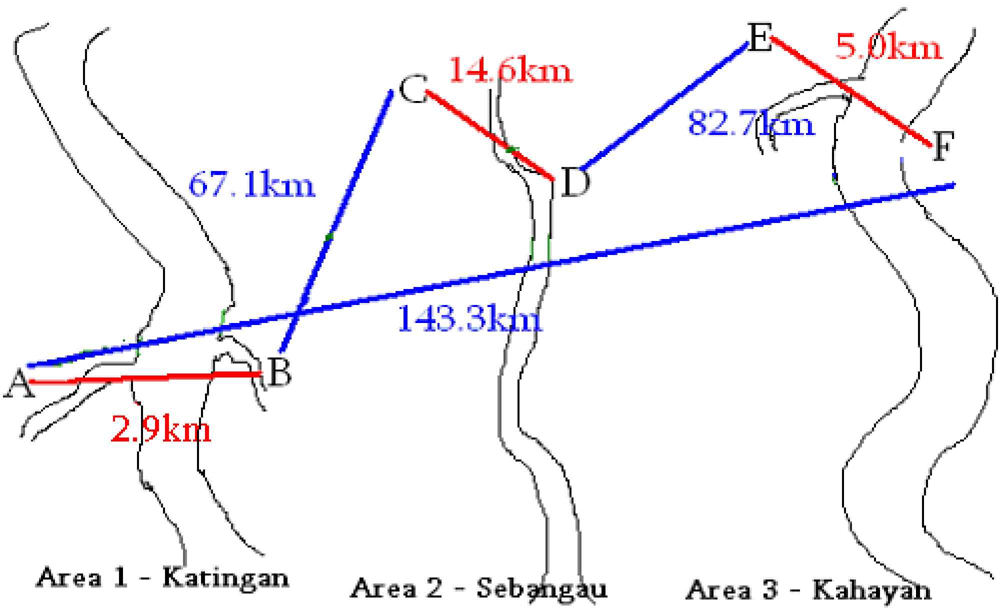

Fig 2.3.3 Distance (km) between each area studied (not to scale)

2.4 : Recording protocol

The great calls were recorded opportunistically at various times depending on the topography of the area, environmental conditions and individual group preference. On average the gibbons would begin singing at approximately 5.25am but ranged from 4.20am to 6.30am. Recording was assisted by up to two people. I requested and applied the knowledge of the local village chief in order to locate the whereabouts of the gibbons and employed the help of local villagers to act as counterparts in the forest. Visits to the local police were compulsory to obtain permission to undertake research in the area.

In total six locations were chosen for recording, either side of three rivers; two locations per river. It was decided three gibbon groups per location, with six great calls per group (with the exception of the Sabangau area) was a sufficient sample size to study. The emphasis was on the female great call as it is the most genetically conserved part of the song; therefore the best place to look for differences between populations (Haimoff 1984). In the Sabangau area seven groups were recorded to justify the similarity between calls within the same area. The individual groups were identified by the territory they inhabited. Territory is the area within the home range that is used exclusively by the group and defended against conspecifics. The suggested home range size of gibbons ranges between 16.5 and 43 hectares depending on the size of the group (Chivers 1984).

Recording consisted of getting within as close as possible proximity to the gibbon groups. This was not always straightforward as some parts of the forest were densely overgrown and no grid system was available. Also, getting too close would disturb the animals and may have resulted in alarming them into moving away. The equipment was used every day and set up using standard audio cassettes. The date, time, companion and whereabouts were given to avoid confusion at a later date when analysing the calls. The microphone was held as close as possible to the sound and the tape left running to obtain all of the song. Battery life was checked at regular intervals. The equipment used to record included:

- Sony directional microphone – ECM-M5907
- Sony Walkman Professional Dolby B-CNR
- Sennheiser HD 474 headphones
- Audio cassette tapes

2.5 : Song analysis

The computer programme 'Canary 1.2.4' was used on an Apple personal computer to analyse the calls and demonstrate whether or not dialect exists between populations inhabiting an area. Figure 2.5.1 shows an example of the canary working environment. Spectrograms are available to distinguish the female great call, even if the male is performing a duet. Spectrograms generate measurable records of complicated muscular movements involved in the production of sound. These records permit detection of breakdown or alteration of individual patterns with greater confidence than is possible with different kinds of behaviour measurements adjustable to primates. The descriptions of the variables can be found in table 2.2. Variables used to analyse the song included:

1. Duration of great call (sec)
2. Frequency exploitation/range (kHz)
3. Duration of climax note (sec)

4. Peak frequency of climax note (kHz)
5. Lowest frequency (Hz)
6. Note/duration (number of notes/duration of great call)
7. Number of post-climax notes
8. Duration of post-climax phase

Variable	**Description**
1. Duration of great call (secs)	Time interval between start of first note until the end of the last note
2. Frequency range (kHz)	No. 4 minus no. 5
3. Duration of climax note (secs)	Time from the beginning of the climax note until the end
4. Peak frequency of climax note (kHz)	The highest frequency in the entire great call
5. Lowest frequency (Hz)	The lowest frequency in the entire great call
6. Number of notes	Number of notes between the first and last note of the great call
7. Number of post-climax notes	Number of notes after the climax note
8. Duration of post climax phase (secs)	The time from the start of the note after the climax note until the end of the last note

Table 2.5.1 Descriptions of the variables analysed

Certain problems arose whilst analysing the calls. A distinct beginning and end of the great call had to be established. This starts on the first long note of the call and ends as the frequency gets lower and the female stops the great call. The male will reply with his song – called a coda but this fragment is not analysed. Some of the great calls are interrupted by the male coda of either the same or a different group. This adds difficulty to the analysis of the great call but the decision was made to continue to measure the call up until the female ends the great call. The frequency is sometimes hard to measure as there is always background noise of birds and insects; however the program can filter out other sounds to some extent. Once the calls had been analysed the results were entered into SPSS 11.0 and the one-way analysis of variance (ANOVA) statistical test was run and Tukey's post-hoc test was performed to test for multiple comparisons.

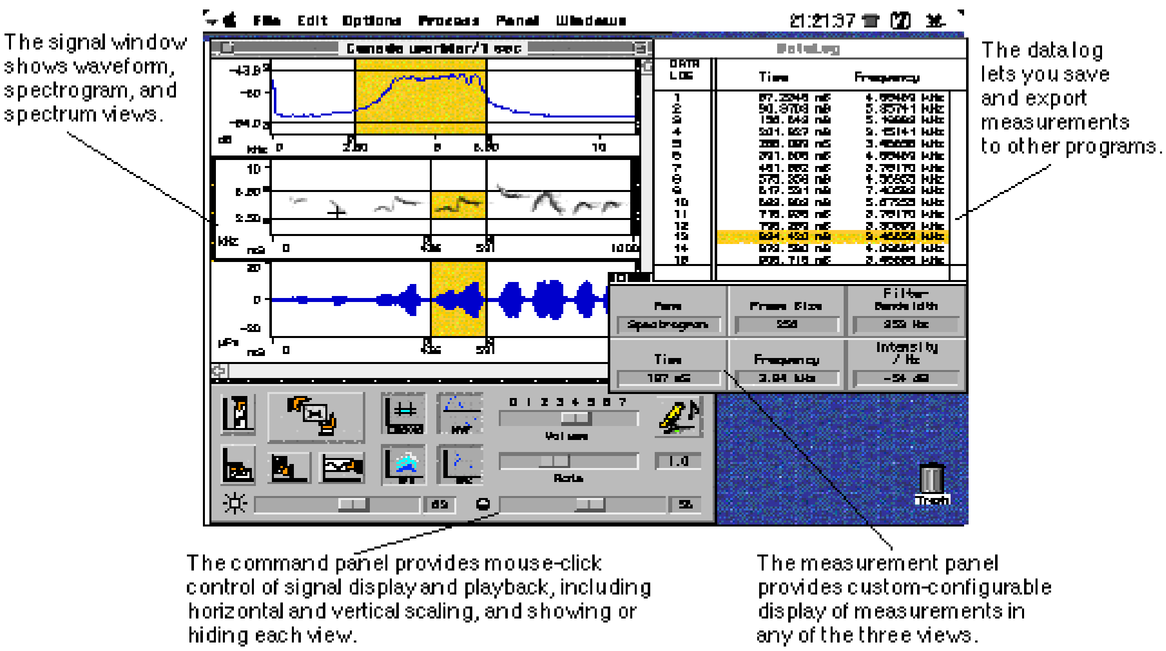

Fig 2.5.1 The Canary working environment, showing a signal window, the command panel, measurement panel, and data log (Canary, 2005)

2.6 Spectrograms

Figures 2.6.1 – 2.6.6 shows examples of great calls from each area. Figure 2.6.7 shows an example of an alarm call due to the presence of a chainsaw.

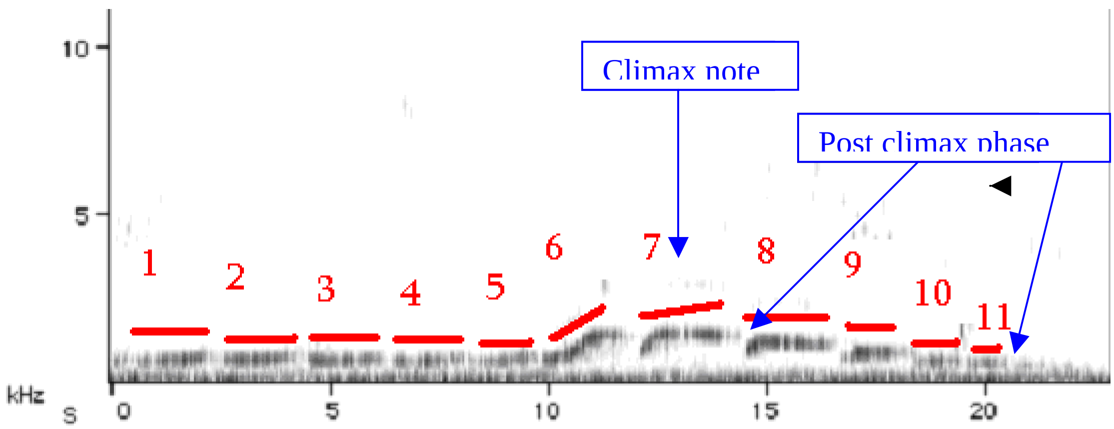

Fig 2.6.1 Area A – Bankonan

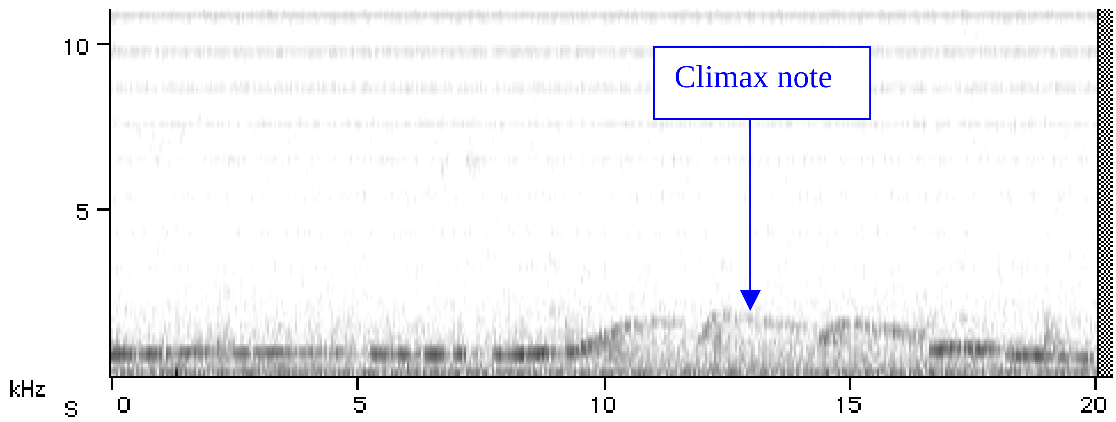

Fig 2.6.2 Area B – Musang

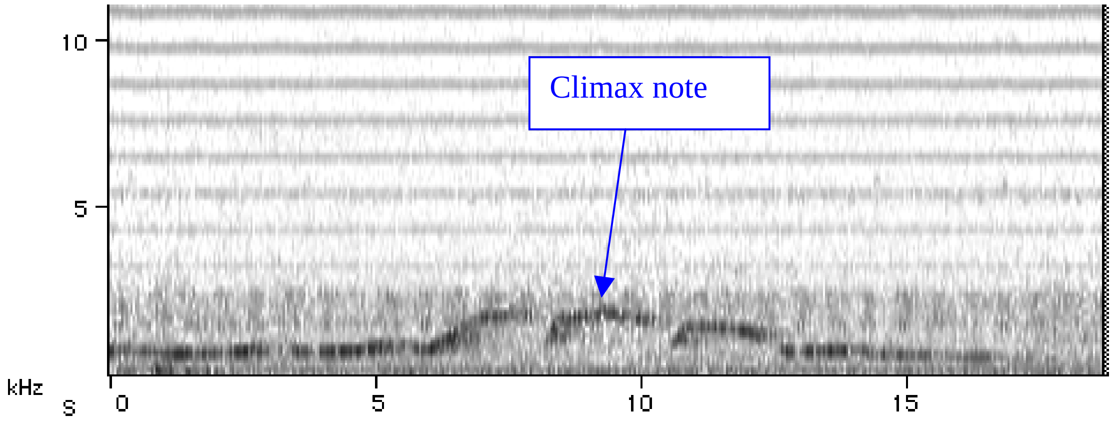

Fig 2.6.3 Area C – Sabangau

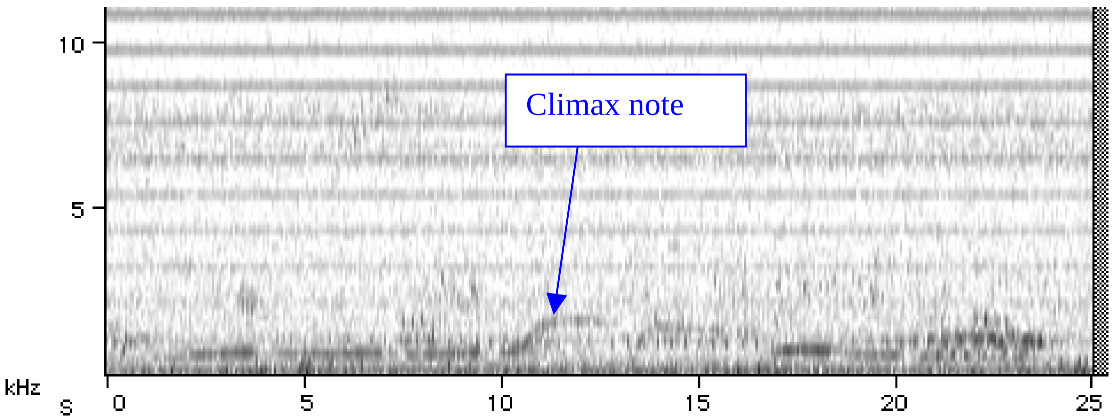

Fig 2.6.4 Area D – Mega Rice Project

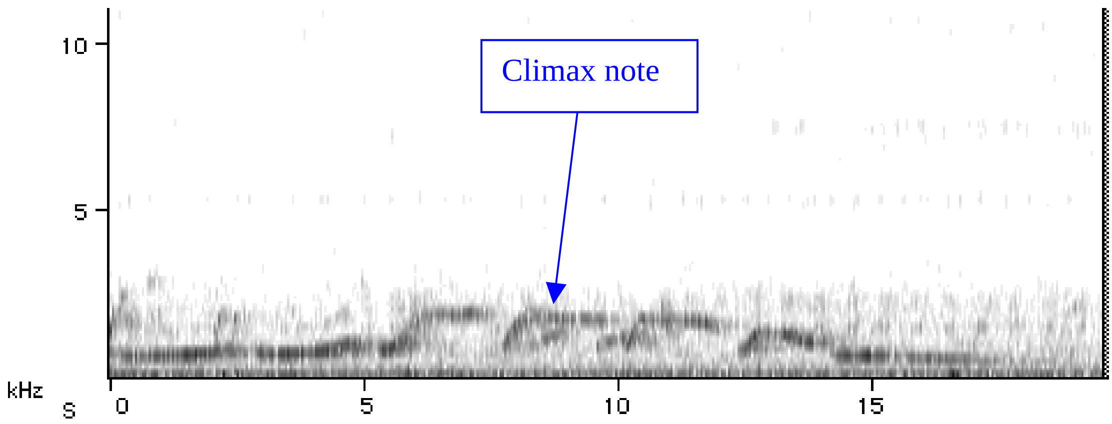

Fig 2.6.5 Area E – Hibongan

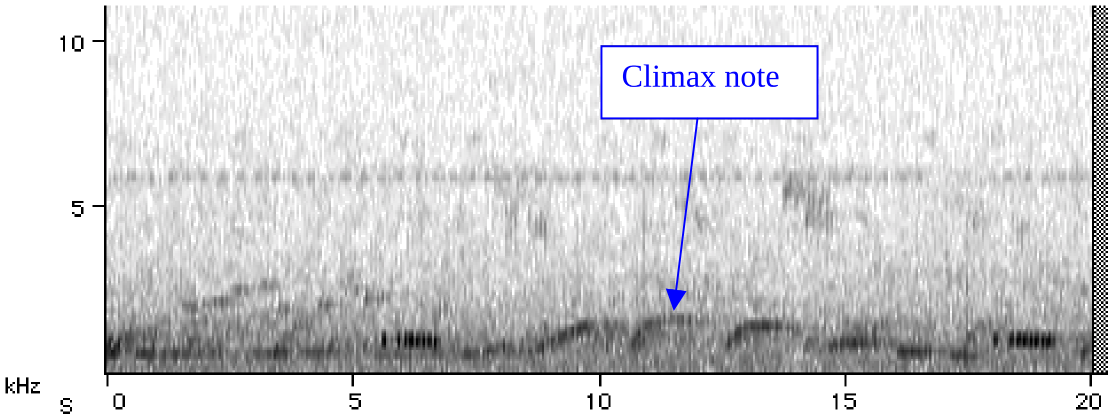

Fig 2.6.6 Area F – Bawan

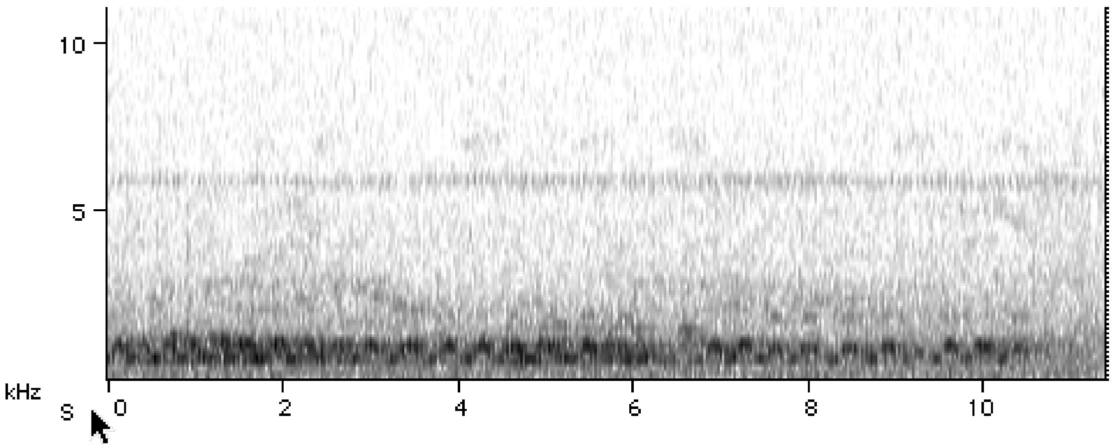

Fig 2.6.7 Alarm call

3.0 Results

3.1 Comparison across all areas

For the purpose of this study all individual group recordings within each area will be treated as replicates, which assume ‘group’ is not a meaningful division of population. The areas will be compared as follows: **A – B, C – D**, **E – F, B – C, D – E** and **A – F.** The one-way analysis of variance (ANOVA) statistical test was run, shown in appendix 3, and Tukey’s post-hoc test was performed to test for multiple comparisons.

Variable	P Value
1. **DURCALL** (duration of great call)	0.000
2. **FRERANG** (frequency range)	0.000
3. **DURCLIM** (duration of climax note)	0.270
4. **PEAKFREQ** (peak frequency)	0.000
5. **LOWESTFR** (lowest frequency)	0.000
6. **NO.NOTES** (number of notes)	0.000
7. **NO.POSTC** (no. of post climax notes)	0.000
8. **DURPOSTC** (duration post climax)	0.000

Table 3.1.1 One-way ANOVA results, significant if $P \leq 0.05$

Table 3.1.1 shows the overall significant differences of areas **A – F** according to each variable. The level of significance is shown in table 3.1.3 and the sample size for each area is shown in table 3.1.4. The sample size ranges from 18-57 and this will have affect on the results. By looking at the ratios in table 3.1.2 it is simple to see where the significant differences between the areas lie. Areas that can be combined together are: **A-B**, **B-C** and **D-E** with significant differences and **C-D**, **E-**

F and **A-F** with no significant differences, see figure 3.1.1. Therefore the first null hypothesis; that there are no significant differences between the great calls of female gibbons in isolated and connected populations is rejected.

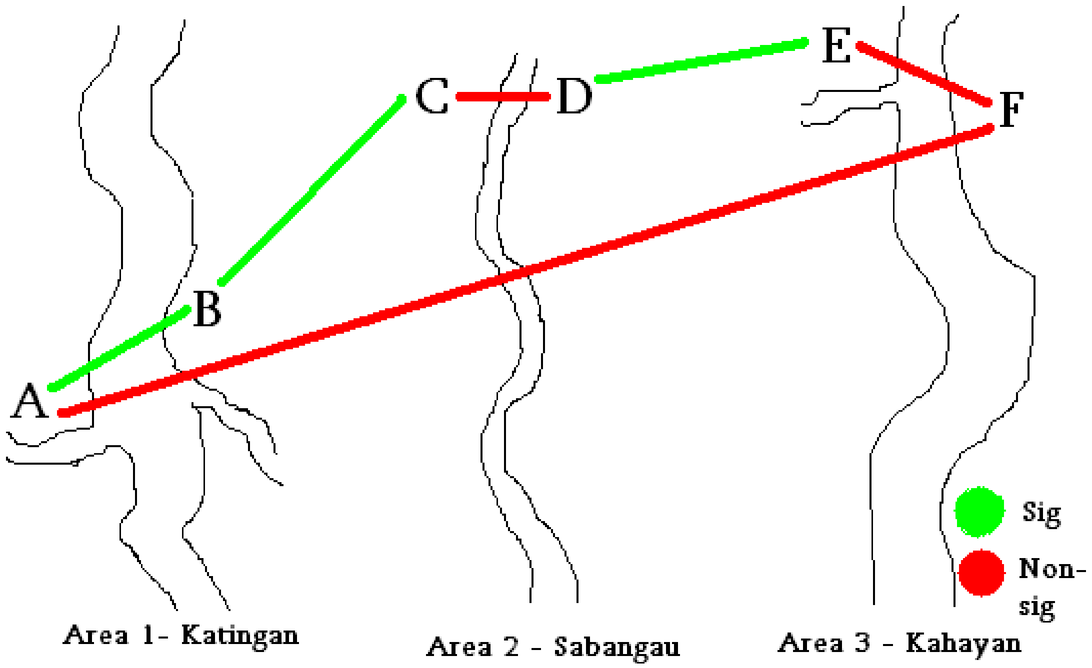

Fig 3.1.1 Areas that can be combined through significant or non-significant differences.

Variable	Is there significant difference between areas:					
	A -B	C -D	E -F	B -C	D -E	A -F
1. DURCALL (duration of great call)	yes	no	no	yes	yes	no
2. FRERANG (frequency range)	yes	no	no	no	no	no
3. DURCLIM (duration of climax note)	no	no	no	no	no	no
4. PEAKFREQ (peak frequency)	yes	no	no	yes	no	no
5. LOWESTFR (lowest frequency)	no	yes	no	yes	no	no
6. NO.NOTES (number of notes)	no	no	no	no	yes	no
7. NO.POSTC (no. of post climax notes)	no	no	no	yes	yes	yes
8. DURPOSTC (duration post climax)	yes	no	no	no	yes	no
Ratio yes : no	4:4	1:7	0:8	4:4	4:4	1:7

Table 3.1.2 Significant differences between areas

Variable	Level of significance between areas:					
	A-B	C-D	E-F	B-C	D -E	A -F
1. DURCALL (duration of great call)	0.002	0.793	0.257	0.000	0.000	0.547
2. FRERANG (frequency range)	0.001	0.953	0.432	0.780	1.000	1.000
3. DURCLIM (duration climax note)	0.677	0.998	0.999	0.776	1.000	0.434
4. PEAKFREQ (peak frequency)	0.009	0.903	0.585	0.033	0.983	0.998
5. LOWESTFR (lowest frequency)	0.062	0.000	0.996	0.001	0.443	0.271
6. NO.NOTES (number of notes)	0.994	0.717	0.983	0.821	0.000	0.570
7. NO.POSTC (no. post climax notes)	1.000	0.156	0.207	0.031	0.000	0.001
8. DURPOSTC (duration post climax)	0.003	0.999	0.970	0.486	0.000	0.737

Table 3.1.3 Levels of significance, significant if $P \leq 0.05$

Area	Sample size
A	18
B	57
C	50
D	18
E	18
F	18

Table 3.1.4 Sample size of great calls per area

3.2 Summary of results across all areas

Figures 3.2.1– 3.2.8 show significant differences of each variable across all areas. The two variables, duration of great call (No.1) and duration of post climax phase (No.8) proved most conclusive as they provided the most number of significant differences, as demonstrated in table 3.1.2 and figures 3.2.1 and 3.2.8. Duration of the climax note (No. 3) is the only non-significant variable, as is demonstrated in table 3.1.2. Statistical graphs confirming significant differences for all areas can be found in appendix 1 (figures 1.1 – 1.8).

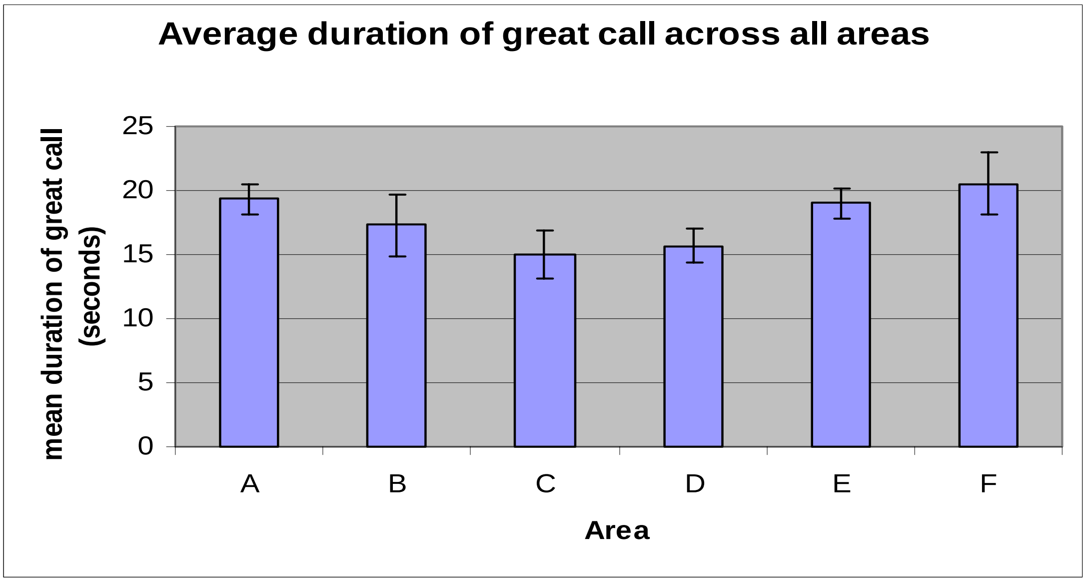

Fig 3.2.1 Bar graph demonstrating the average duration of great calls across all areas

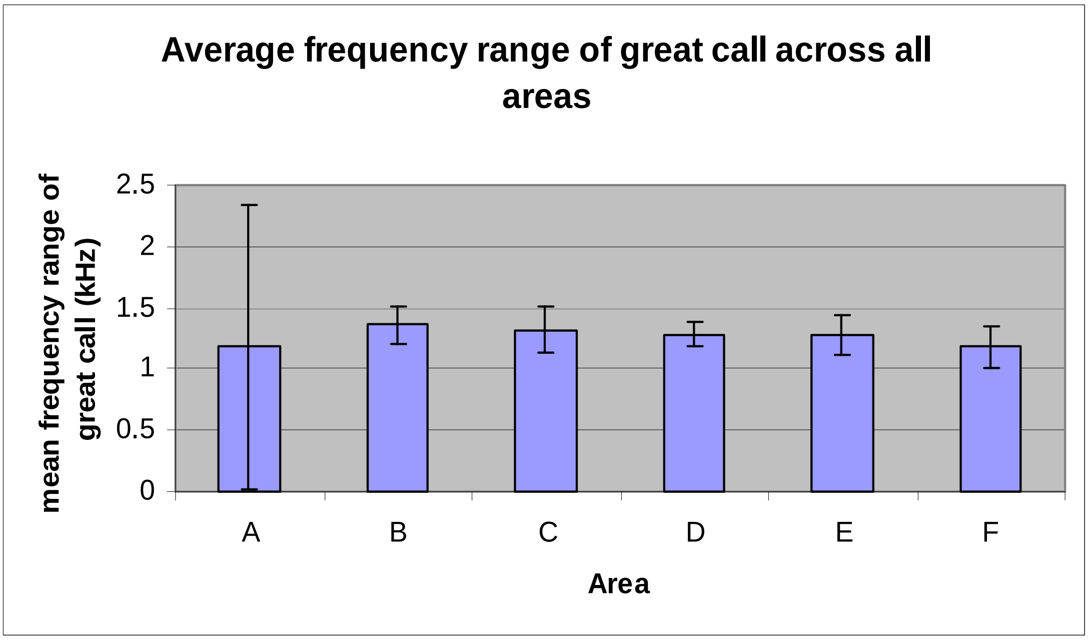

Fig 3.2.2 Bar graph demonstrating the average frequency ranges of great calls across all areas

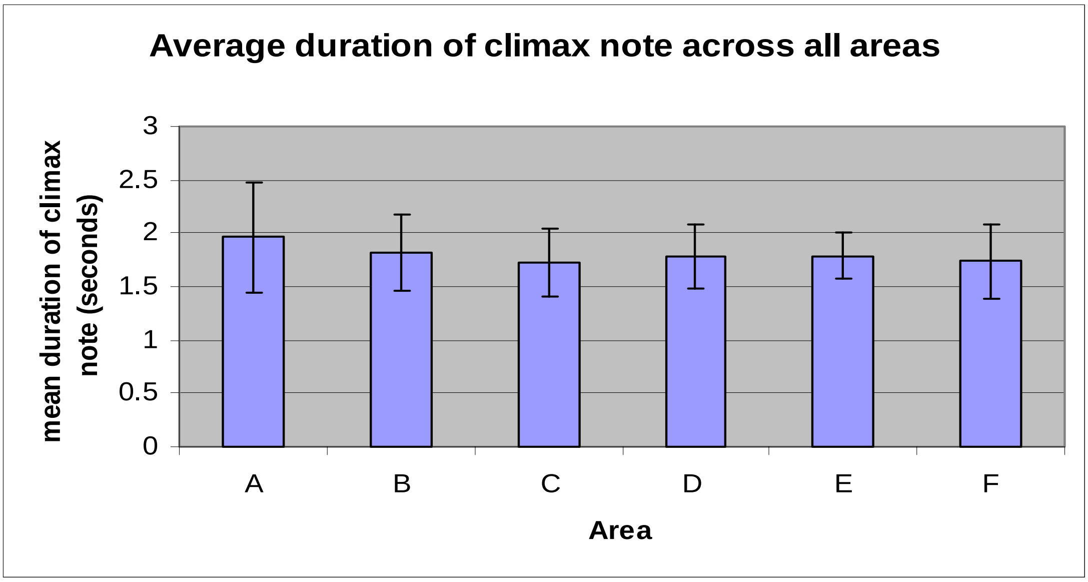

Fig 3.2.3 Bar graph demonstrating the average duration of the climax note across all areas

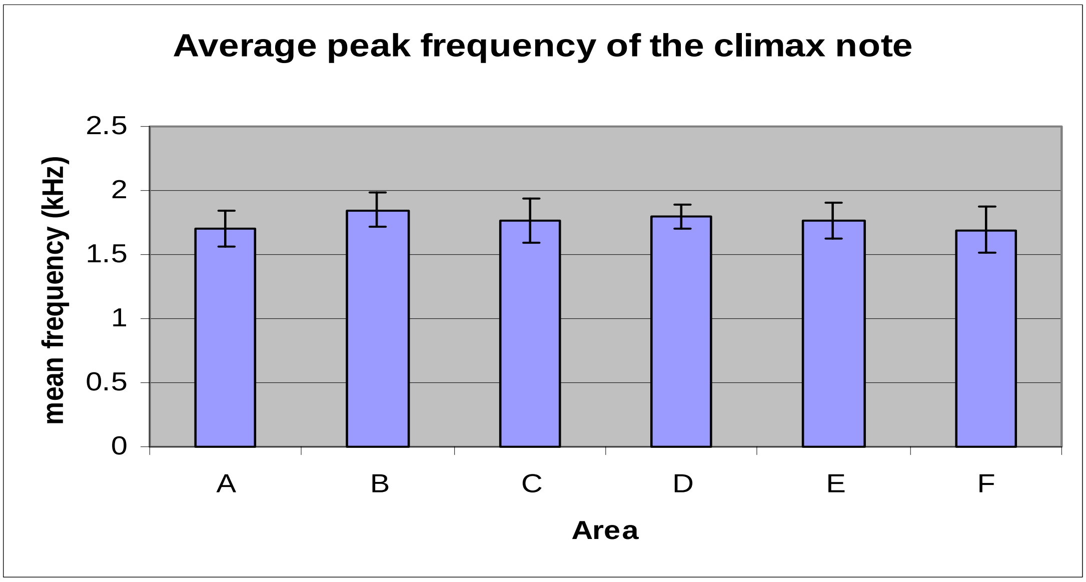

Fig 3.2.4 Bar graph demonstrating the average peak frequency of the climax note

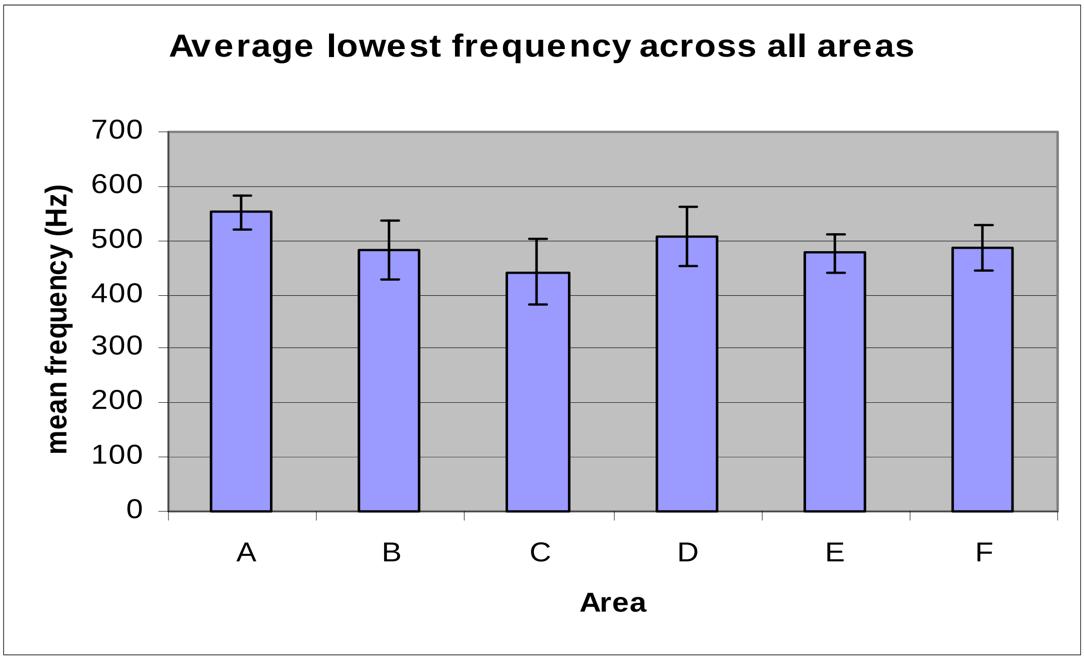

Fig 3.2.5 Bar graph demonstrating the average lowest frequency across all areas

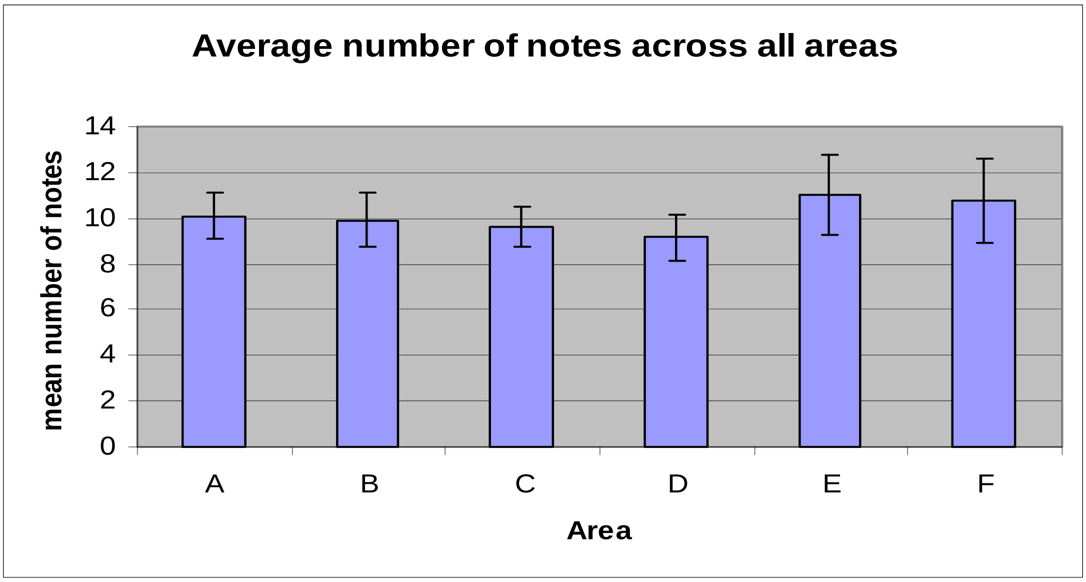

Fig 3.2.6 Bar graph demonstrating the average number of notes across all areas

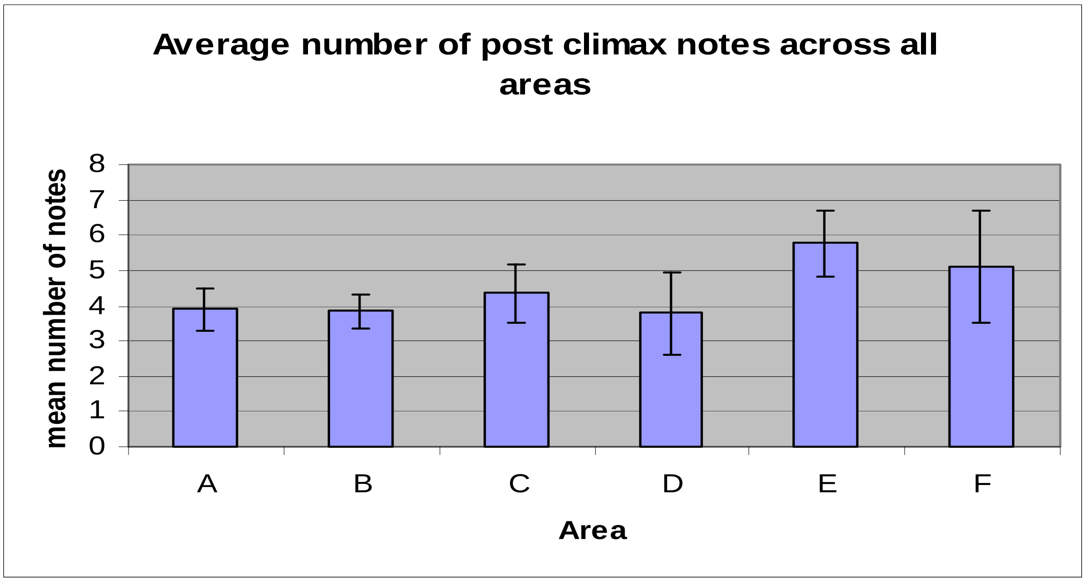

Fig 3.2.7 Bar graph demonstrating the average number of post climax notes across all areas

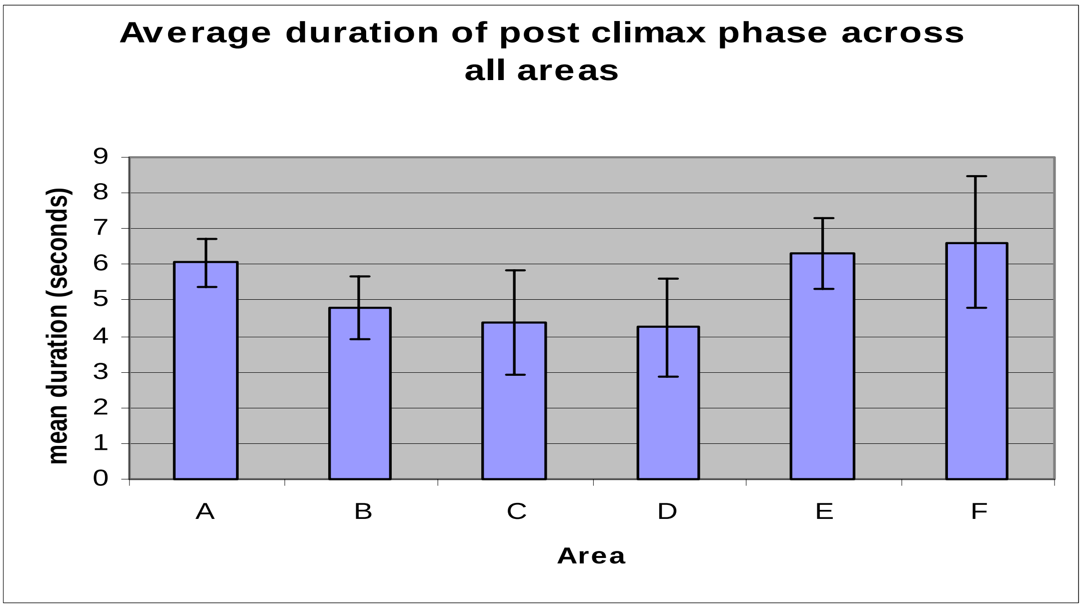

Fig 3.2.8 Bar graph demonstrating the average duration of the post climax across all areas

3.3 Comparison of individuals within Area C

These data come from Area C – Sabangau. In total seven groups, each with one female producing a great call, were recorded here in order to justify a small sample size for the other areas. However, significant differences were found between these groups and were analysed using the one-way analysis of variance (ANOVA) statistical test, shown in appendix 4. The second null hypothesis; that there are no significant differences between individual's great calls within an area is therefore rejected.

Variable	P Value
1. DURCALL (duration of great call)	0.002
2. FRERANG (frequency range)	0.003
3. DURCLIM (duration of climax note)	0.000
4. PEAKFREQ (peak frequency)	0.093
5. LOWESTFR (lowest frequency)	0.000
6. NO.NOTES (number of notes)	0.296
7. NO.POSTC (no. of post climax notes)	0.247
8. DURPOSTC (duration post climax)	0.016

Table 3.3.1 One-way ANOVA results, significant if $P \leq 0.05$

Table 3.3.1 shows the overall significant differences of groups 1-7 according to each variable. The only variables that showed no significant difference were; peak frequency (No.4), number of notes (No.6) and number of post climax notes (No.7). This would produce a ratio of significant : non-significant of 5:3. The sample size of great calls for each group is shown in table 3.3.2 and a summary of whether there is significant difference or not is shown in table 3.4.1. The significant differences between the groups are shown in figures 3.4.1 – 3.4.8 and statistical error bar graphs to confirm these results can be found in appendix 2 (figures 2.1-2.8). A Tukey's post-hoc test was performed to test for multiple comparisons.

Group	Sample size
1	40
2	41
3	53
4	11
5	22
6	6

7	6

Table 3.3.2 Sample size of great calls recorded in each group

3.4 Summary of results for individuals within Area C

Are there significant differences between groups?

Group	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1	no	yes	no	no	yes	no	no
2	no	no	no	no	no	no	no
3	no	no	no	no	no	no	no
4	yes	yes	yes	no	no	no	no
5	yes	yes	yes	no	no	no	no
6	no	no	no	no	no	no	no
7	yes	yes	no	yes	yes	no	no

Table 3.4.1 Significant differences between groups

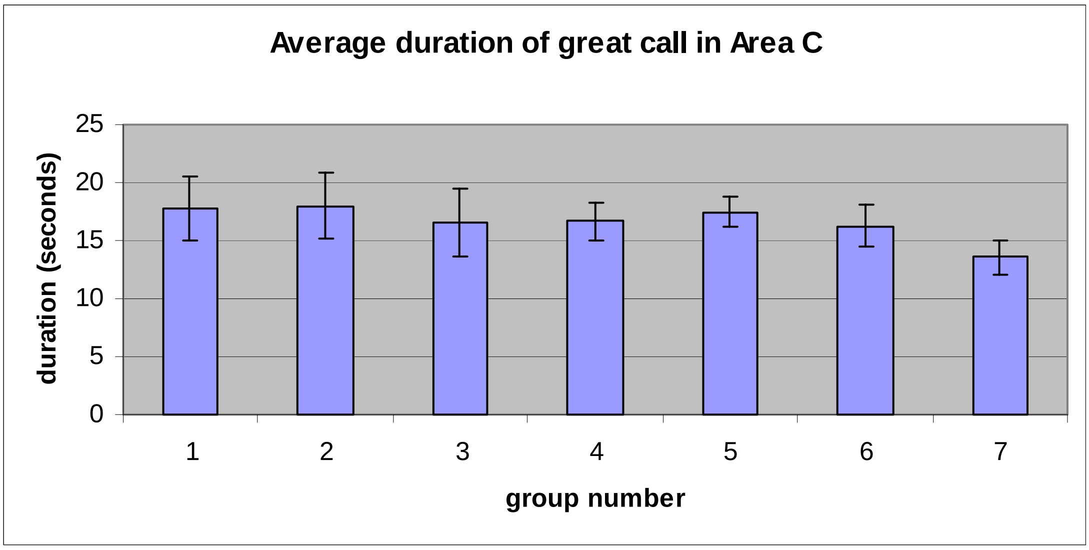

Fig 3.4.1 Bar graph demonstrating the average duration of great call in Area C

Group 7 was the only significantly different group presented here. It was significantly different from groups 1, 2 and 5. This was expected as the sample size for group 7 is substantially lower than groups 1, 2 and 5. Sample size is an important factor in assessing results; as the groups with a smaller sample size obviously have less variation in their calls due to the fact recordings could not be obtained from these groups very often. This affects the results as the data has less range from the highest to lowest number and therefore less variation is expected. If a large sample size was taken there would be more range and more variation, therefore producing a more accurate, conclusive result. The ratio of significant : non-significant (5:3) is also conclusive as it shows there are still some non-significant differences between groups within an area. Figures 3.2.1 – 3.2.9 show which groups are significantly different to each other. The majority of them are not significant to each other. The groups that are significantly different to each other have smaller sample sizes in almost all cases, the exception being figure 3.2.3 (duration of climax note) where group 1 is significantly different from group 2. This supports the original assumption of individuality within an area being not significantly different is still maintained and groups within an area will still be treated as replicates for the purpose of this study.

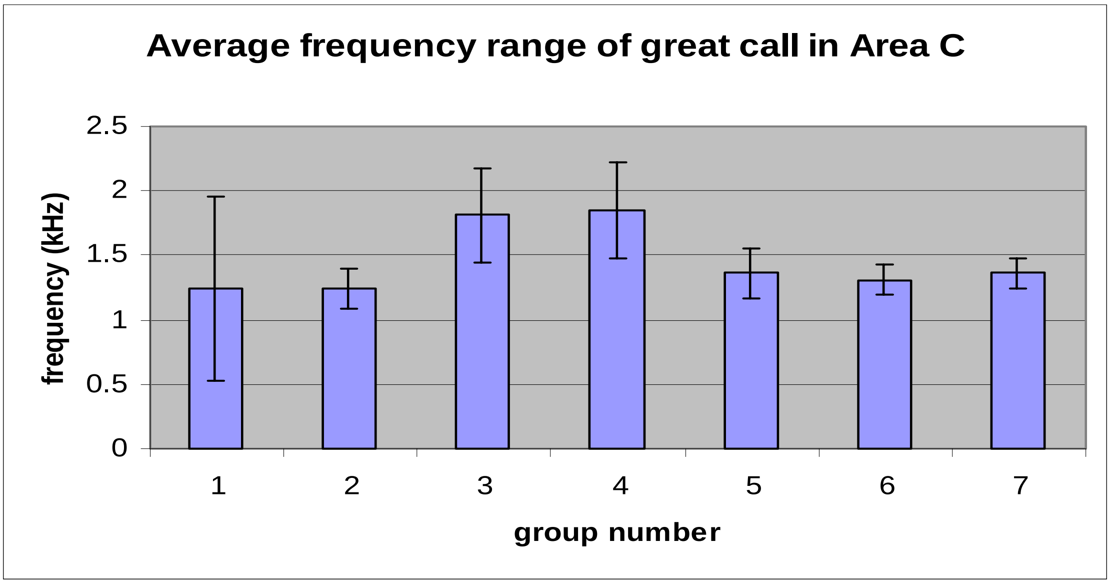

Fig 3.4.2 Bar graph demonstrating the average frequency range in Area C

This graph shows group 4 is significantly different only to groups 1 and 2. The sample size for group 4 is lower than for groups 1 and 2.

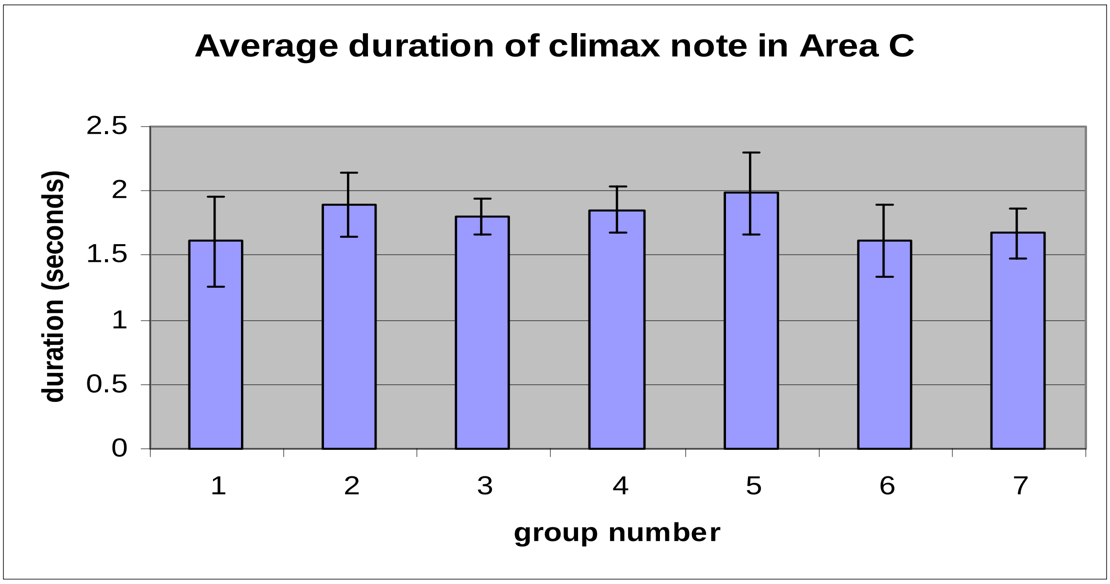

Fig 3.4.3 Bar graph demonstrating the average duration of climax note in Area C

Group 1 is significantly different only from groups 2 and 5. The sample size for group 2 is higher than groups 1 and 5, however only higher by 1 sample compared to group 1 and 19 samples for group 2.

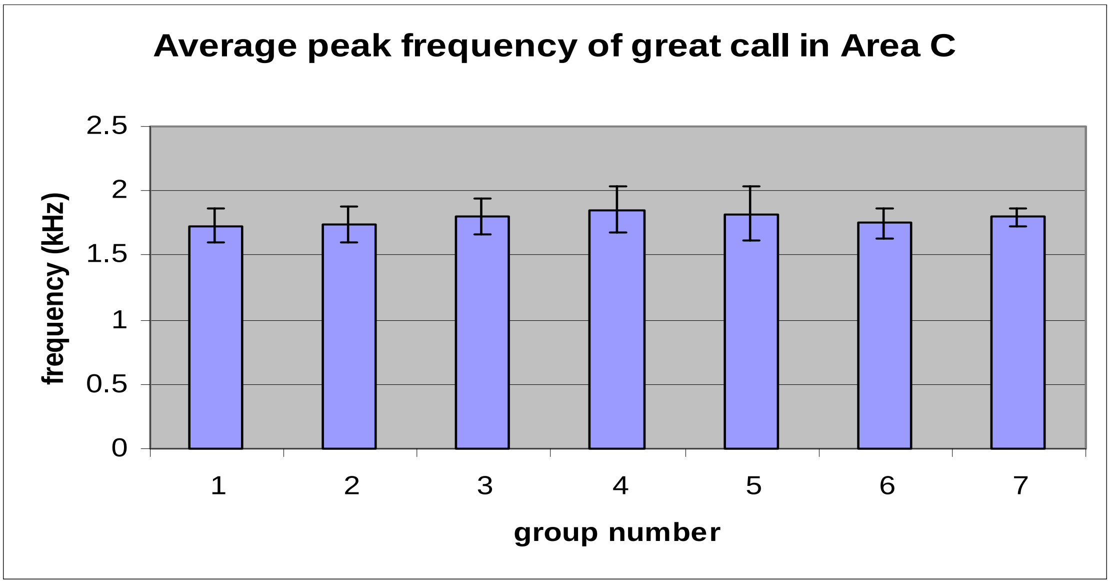

Fig 3.4.4 Bar graph demonstrating the average peak frequency of climax note in Area C

There are no significant differences between any groups for this variable.

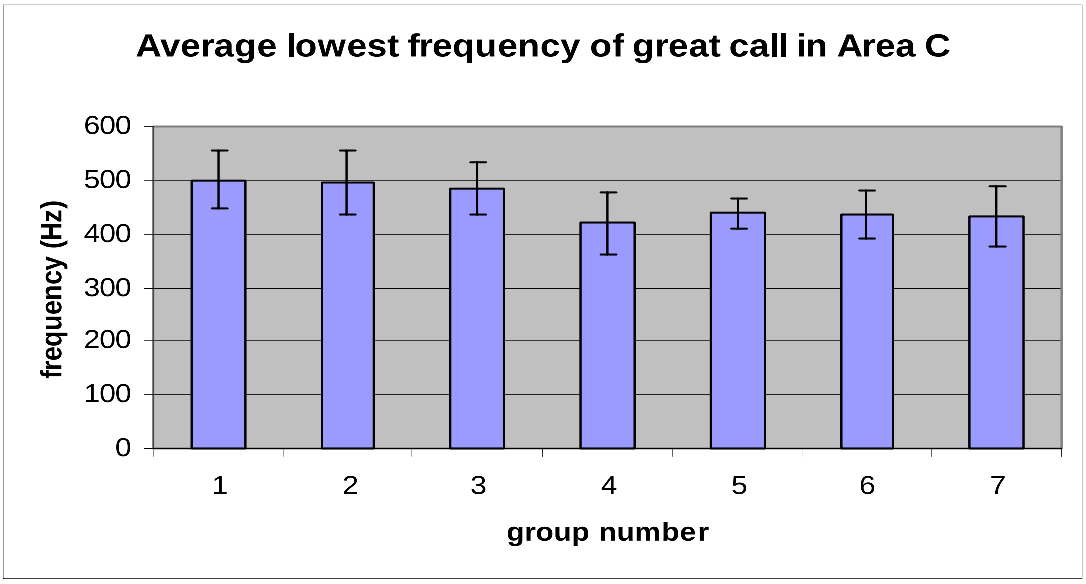

Fig 3.4.5 Bar graph demonstrating the average lowest frequency of great call in Area C

Group 7 is significantly different from group 1 and groups 4 and 5 are significantly different from groups 1, 2 and 3. This is the variable with the highest occurrence of significant differences. All groups that are significantly different have a lower sample size to groups they are compared to.

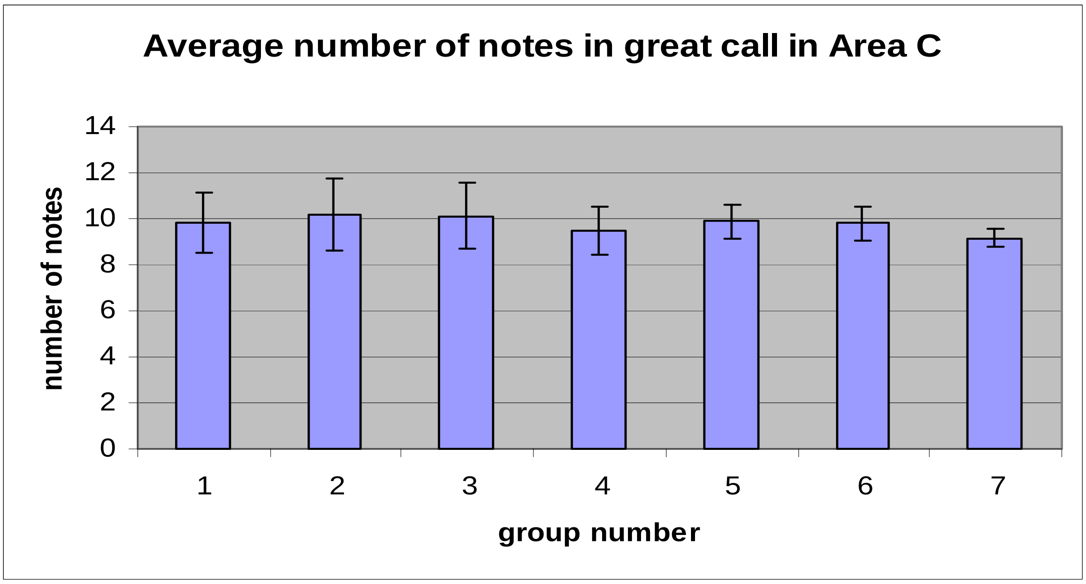

Fig 3.4.6 Bar graph demonstrating the average number of notes in Area C

There are no significant differences between any groups for this variable.

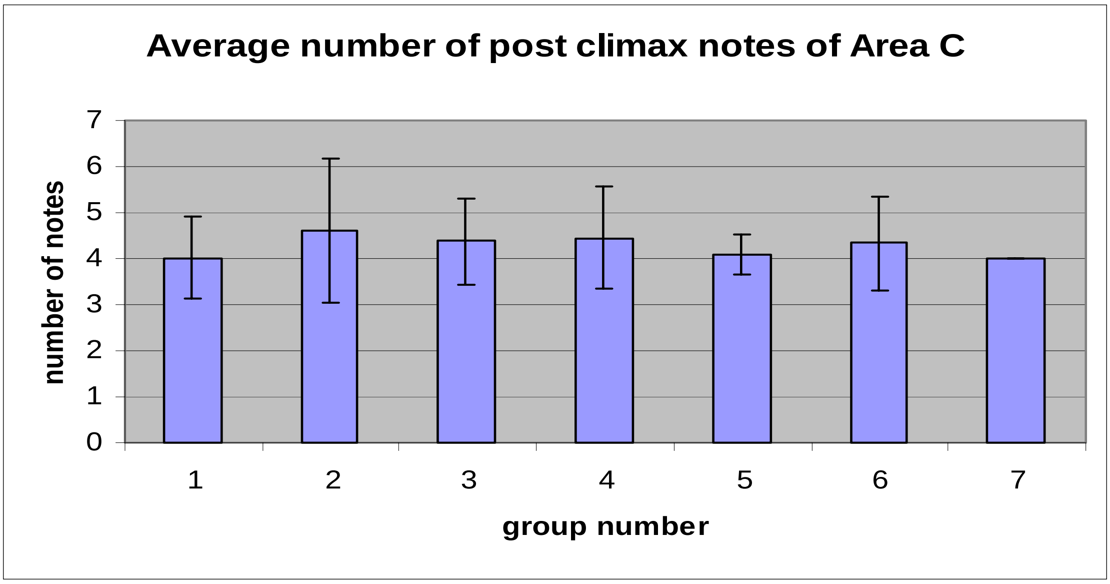

Fig 3.4.7 Bar graph demonstrating the average number of post climax notes in Area C

There are no significant differences between any groups for this variable.

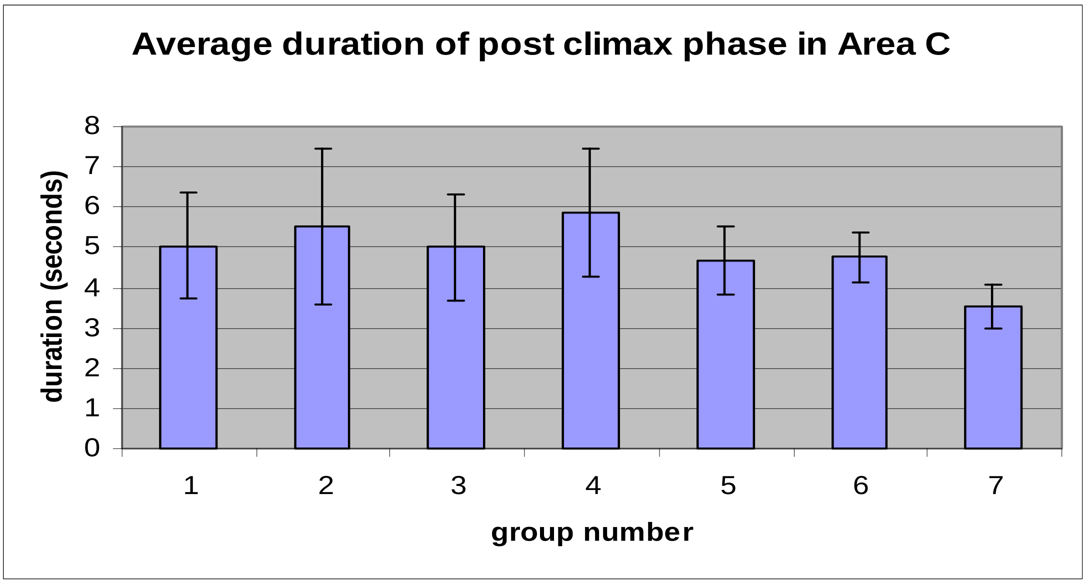

Fig 3.4.8 Bar graph demonstrating the average duration of post-climax phase in Area C

Group 7 is significantly different from groups 4 and 2. The sample size for group 7 is much lower than groups 4 and 2.

4.0 Discussion

4.1 Individuality within calls

It has been suggested that the role of gibbon song acts as a spacing mechanism and deters conspecifics from intruding upon an occupied territory (Haimoff and Gittins, 1984). Field playback experiments carried out on a number of gibbon species support this theory (Chivers and Mackinnon, 1977). Haimoff and Gittins (1977) suggested that the female song showed evidence of regular individuality throughout great calls and that the most important role of the song is to broadcast an individual's identity and the fact they occupation a certain territory. However, to fully confirm this statement further playback experiments on a range of gibbon species will be required.

If gibbon song acts as a means of inter-group communication then natural selection must have favoured individuality as well as kin and individual recognition, in addition to the transmission of other important information. It would be beneficial for individuals to distinguish amongst songs of other individuals, as then the gibbon would be able to make a distinction between songs involving a vocal reply, eg. from a bordering neighbour, and songs that do not require a response, eg. a non-bordering neighbour (Haimoff and Gittins, 1984). Haimoff and Gittins (1984) carried out research on individuality in gibbon song and recognized it was worth mentioning that the measured variables in the introductory phase had significantly lower amounts of variation within females than other phases in the great call. In one instance, with the variable – number of introductory phase notes, there appeared to be no variation whatsoever within females. Similar discoveries have been made for wild lar gibbons where it was anticipated that the variation within the introductory phase permits individuals to determine their identity preceding the production of the great calls climax note (Raemaekers and Raemaekers, 1985). It is important to recognise that individuality is a major factor in inter-group communication and therefore a major factor in inter-group spacing and the ability to successfully defend a territory.

4.2 Social spacing

Gibbons have the ability to uphold their territories mainly because their food sources are defendable. Fruit and other food sources are generally in ample supply in all forest types, but are not overly abundant. They are distributed in an even way, which means it is simple for a gibbon group to protect a specific area of its own. These food sources are in continuous supply, which makes defending a territory around them advantageous to all members of the group (Leighton 1986).

A reason explaining why gibbons live together in family groups is that their territory is just the right size to supply an ample amount of food for a mated pair and their offspring (Raemaekers and Raemaekers 1985). Territories that are big enough to hold more individuals and more food sources would be too big for one family group to defend. Another aspect contributing to the gibbon territory is intrasexual aggression expressed by females. Territories are important in the fact they have a role in the distribution of females, therefore meaning less contact and consequently less aggressive behaviour. The males monitor and protect the area around the female, which establishes a territory based on the female distribution, which in turn is based on the location and availability of food resources. Males defend females who defend access to food sources.

There are no established dominance relationships between neighbouring males, because every male normally dominates and surrenders to every other male after encounters at some time in their lives. Groups usually instigate encounters when they are aware of the existence of other groups within 100-150 metres (Reichard and Sommer 1997).

An intergroup contest starts with the male and female both producing territorial calls, after which the male typically directs the group toward the rival group (Islam and Feeroz, 1992). The male will complete the majority of the territorial defence, whilst the female will call or supplement her mate for a while during a dispute, after which she normally returns to the territory (Raemaekers and Raemaekers 1985). Sub-adult offspring will also assist in maintaining the territorial home-range by way of defence (Leighton 1986).

4.3 Location of areas

The location of the areas in which the calls were recorded must first be taken into account as they have a remarkable affect on the results. Each forest type is shown in table 2.1 along with the quality and topography of the land. It is important to recognise whether the area of land the gibbons inhabited was fragmented or not, as this is a key factor in the explanation of the areas having significant differences.

Area A – The Musang area was logged extensively and contained many groups being forced to the outskirts of the forest. There is possibility of hearing only area **B** and no possibility of genetic interaction with populations from any other area.

Area B – The Bankonan area was also logged extensively and the gibbons of the area experienced the same problems as in area **A**. There is possibility of hearing only area **A** and there was possibility of genetic interaction with area **C** when the areas were once connected, however the present day makes it impossible for genetic interaction to take place with area **C.**

Area C - The Sebangau area suffered from minor logging, the forest was not fragmented and it sustained a healthy density of 2.2 gibbon groups per square km (Buckley, 2004). There is no possibility of hearing any gibbons from any other areas and a possibility of genetic interaction only with area **B,** however, this would have been in historical times, when the forests were connected and would be impossible in the present day.

Area D - Mega Rice Project was exceptionally fragmented, as the forest existed in a sparse area of land where one million hectares of forest had been cleared in 2001. The forest here did not border the river and therefore the individuals had no way of hearing gibbon groups from area **C.** There is a possibility of genetic interaction as the animals live for over twenty-five years and would have been, before the fragmentation, genetically linked to area **E.**

Area **E** – The Hibongan area was a tributary running off from the main river. It was logged extensively and was situated on uneven land. There is no possibility of hearing any areas as the site was too far away from area **F** and obviously **D.** There is a possibility of genetic interaction with area **D** only.

Area **F** – Bawan village experienced minor logging and was situated on extremely uneven land. There no possibility of hearing gibbons from any area and no possibility of any genetic interaction from any area.

Deforestation is a major contributor to the declining numbers of gibbons in Borneo. Extensive logging is illegal under law by the Indonesian government; however illegal logging continues to claim 3% of Borneo's forests each year (B. Galdikas, pers comm., 2004). This has affected the populations of gibbons and this study has proved it can cause affect on their call characteristics in the long term. Areas **B, C, D** and **E** would once have been connected before the widening of the Sebangau river, a major town, general human interference (road building, etc.) and the Mega Rice Project which claimed one million hectares of forest in order to plant rice fields. This project was however, not successful and the rice failed to grow due to high acidity in the soil. It left small fragments of forest, still inhabited by gibbons and many other animals. This affects the level of individuality that the gibbons have to maintain. It has been stated above that individuality is a key factor in ensuring accurate communication between conspecifics inhabiting the same area (Haimoff and Gittins, 1984).

4.4 Comparison of areas with significant differences

The results were split into the areas with significant differences and the areas without. Areas that are significantly different to each other include: A – B, B - C and D – E. The explanations for these results will be discussed individually.

The gibbons inhabiting areas B – C have the chance of meeting and passing on genetic information through the migration of generations. The individuals therefore have the need to maintain individuality so as to ensure accurate communication between conspecifics. If they did not maintain the same dialect they would have problems with communication and may result in the evolution of a subspecies many years from now.

The gibbons inhabiting areas D – E logistically had the possibility of meeting in historical times, if it weren't for the 82.7km divide and the Mega Rice Project, amongst other physical barriers. However, the gene flow between these two areas was more likely than groups inhabiting areas either side of a major river where there is no possibility whatsoever of crossing. The gibbons of Area D have no chance of interbreeding with any other area in the present day. The individuals of this area therefore do not need to maintain a high level of individuality and their call characteristics must not differ too much from their conspecifics that inhabit the same area. As the area is smaller the level of individuality is kept constant through communication in order for them to successfully defend their territory and reproductive access to their mate (Leighton 1986). Some studies suggest that song in gibbons is a way of maintaining pair bonds and is highly typical of social, especially monogamous animals. Studies carried out on hybrids discovered that hybrid gibbons have to sing more frequently in order to adjust to each other's idiosyncrasies. As a result of increased time spent singing they expend more energy and therefore spend less time mating, which explains the lower reproductive rate of hybrid gibbons (Mather, 1992).

The gibbons inhabiting areas **A – B** are an across river group, however still show significant differences between areas. This is due to the populations reaching up to either side of the river banks, therefore having the likely possibility of hearing each other as the river narrows substantially in places. Gibbons are animals with an aversion to water and have not been known to enter water of any sort (Chivers, 1984). As both these areas were extensively logged this resulted in an echoing effect, which may have increased the amount of great calls produced in the area. Area **B** did produce the largest sample size of great calls (57), simply because they sung more in order to defend their territory and the great calls were in high abundance and therefore easier to obtain. It would be essential for each gibbon group to have high levels of individuality to compensate for the lack of space, as each group would have to encroach into their rival's territory. There is more pressure on groups neighbouring each other as they need to defend territory and this could not be achieved without the correct form of communication. Call characteristics must be familiar for all individuals within a population to understand. Dominance or fighting over mates or food resources may occur more frequently in small areas with large populations. This would also explain why they need to maintain their individuality as they are still within hearing distance of each other and communication is still essential for the transmission of information.

4.5 Comparison of areas with no significant differences

Areas that are not significantly different to each other include: **A – F, C – D** and **E – F.** The explanations of these results are discussed as follows.

The gibbons inhabiting areas **A – F** have no chance of meeting as they live 143.3km away from each other and are also restricted by the three rivers. Therefore there is no chance of either genetic interaction, or learning by listening to other individuals. This suggests that the evolution of gibbon song has evolved from a common ancestor (Geissmann, 1984). The populations inhabiting these two areas have no need to differentiate call characteristics because there is no need to maintain individuality with populations not involved in direct communication.

The gibbons inhabiting areas **C – D** have no chance of meeting, now or historically as the populations are separated by a river. However, they did have the chance of hearing one another in historical times. Before the Mega Rice Project, area **D** would have bordered the river and the populations of both sides would have been within hearing distance of each other. However, in the present day they have no chance of hearing each other due to the Mega Rice Project fragmenting the forest such that it encloses the inhabitants of the forest, restricting migration to any other areas. The animals here no do not require the maintenance of a high level of individuality as they will never meet other populations and only need to communicate with the individuals inhabiting the same forest area as they are.

The gibbons inhabiting areas **E – F** have no chance of coming into contact with one another as they are divided by a major river. Area **E** is a tributary river and the population here could not hear the population inhabiting area **F.** Therefore they are not significantly different as they have no need to differentiate characteristics of song or to maintain individuality with groups of incommunicable distance that inhabit another population.

4.6 Comparison of individuals within Area C – Sebangau

In this area, seven groups were recorded, as opposed to three in all the other areas. This was intended to be a justification of small sample size for other areas. The results demonstrate a ratio of significant : non-significant difference of 5:3. These data represent a range of sample sizes from 41 – 6. This difference of 35 samples has affected the results dramatically. This has however been justified as the majority of groups are not significantly different to each other and the ones that are significantly different have been proved to have a smaller sample sizes in all cases except one, shown in figure 3.2.3.

The concept of sample size is undoubtedly related to the total number of recordings taken, however this number can be deceptive when considering how adequate the sample is for drawing conclusions from. The main concept in understanding how adequate the sample size is for a certain purpose is to consider the variability contained within the data. For recordings with low variability, the number of recordings for adequate sampling would be much lower than for recordings with high variability.

In this study as many recordings as possible were collected from each group and it was due to collecting more recordings in more accessible locations that made the sample sizes vary so much. This could have been rectified by obtaining a constant, high number of sample sizes for each group. It would be expected to be so if further studies were to take place.

5.0 Conclusion

These results provide evidence to support the theory that song is both genetically inherited and learned by listening to other individuals. The importance of maintaining individuality must be expressed as it is a key factor in maintaining pair bonds, territories, and plays a big part in territorial disputes and in communicating with other pairs.

Individuality needs to exist not only across neighbouring populations, but also within the same population. Individual gibbon groups must be able to communicate effectively within their population (Dallmann and Geissmann, 2001). Without effective communication all sorts of problems can occur; solitary males may not understand the transmission of a mating call, territory defence may be jeopardised by mistaken communication, therefore increasing the occurrence of aggressive behaviours (Leighton, 1986). Reproductive rates are also threatened as mated pairs need to maintain a high level of communication in order to stay monogamous. The study by Mather (1992) on hybrid gibbons proved that the reproductive success was significantly lower in hybrids compared to pure-breds. This was because more energy was expended on learning each others song idiosyncrasies and therefore less time was spent mating or feeding, which decreases the likelihood of producing offspring.

Conclusions drawn from this study:

Female great call individuality is a key factor in maintaining good communication with neighbouring groups within a population.

If the gibbons have no chance of meeting they have no need to differentiate their song because they have no need to maintain their individuality.

If there is a chance of meeting (now of in historical times) they need to maintain their individuality so as to ensure accurate communication.

This study provides an insight into what the options are for further studies of this sort to take place. A similar study could be carried out over a larger geographical distance, with similar physical barriers. This would perhaps provide more conclusive results and it would be interesting to see if the differences occur between similar areas to the ones found in this study. A study on the vocal repertoires of hybrid gibbons compared to the two species they were hybridised from would further increase knowledge into how gibbons acquire their song and obtain a wider understanding of the distinctive repertoire and dialect differences between the two species.

5. 0 References

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Appendix 1

In figures 1.1-1.8 the black lines represent areas that are not significantly different from each other.

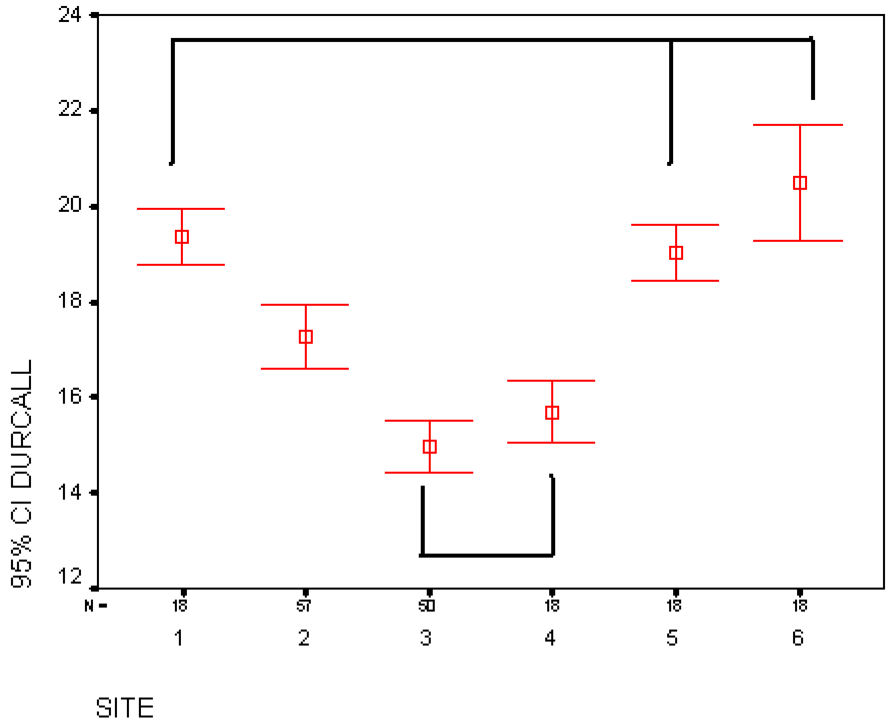

Fig 1.1 Duration of great call

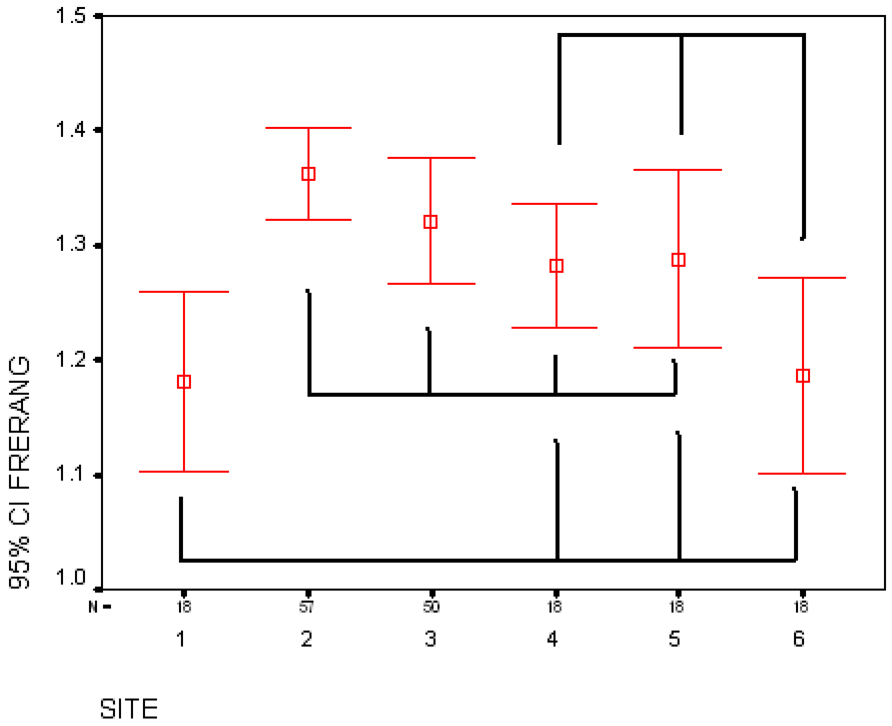

Fig 1.2 Frequency range

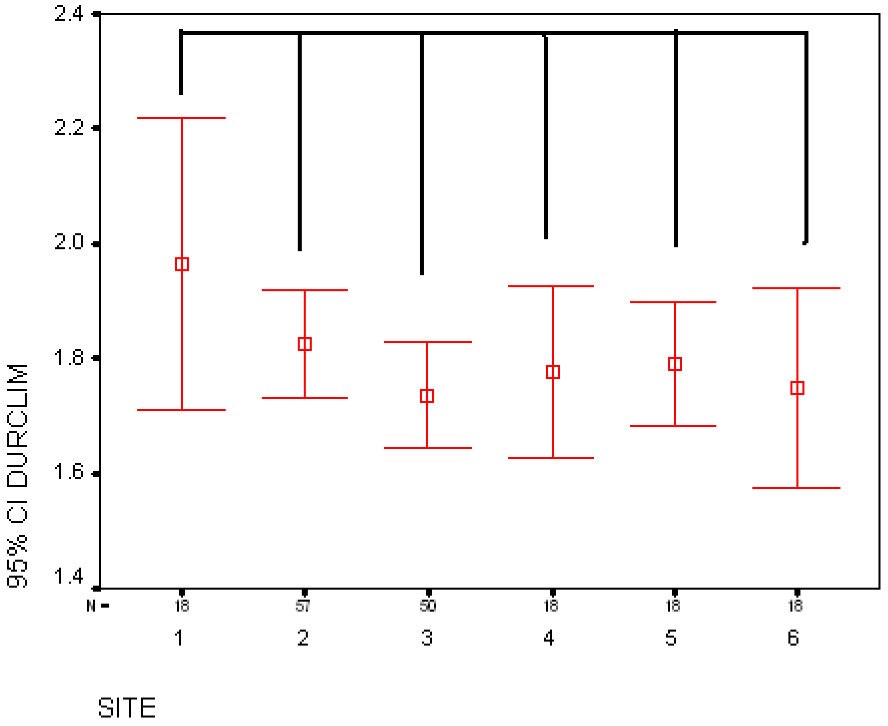

Fig 1.3 Duration of climax note

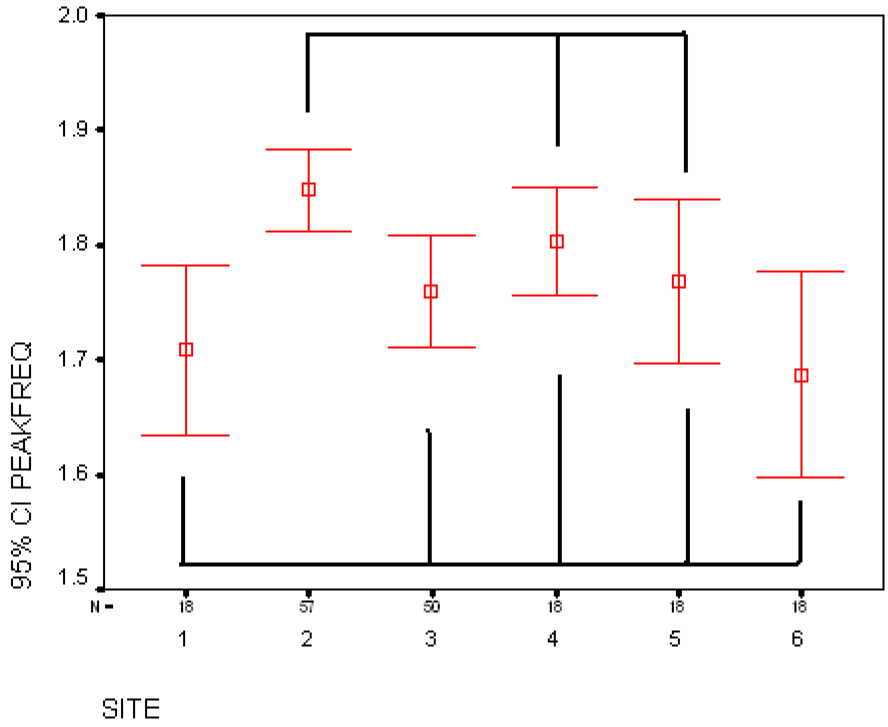

Fig 1.4 Peak frequency

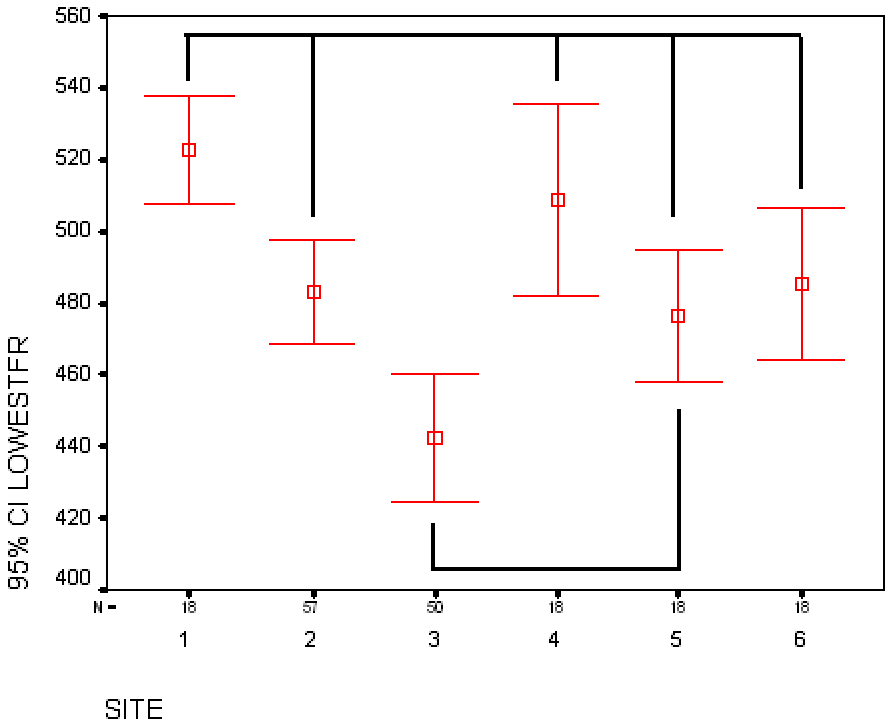

Fig 1.5 Lowest frequency

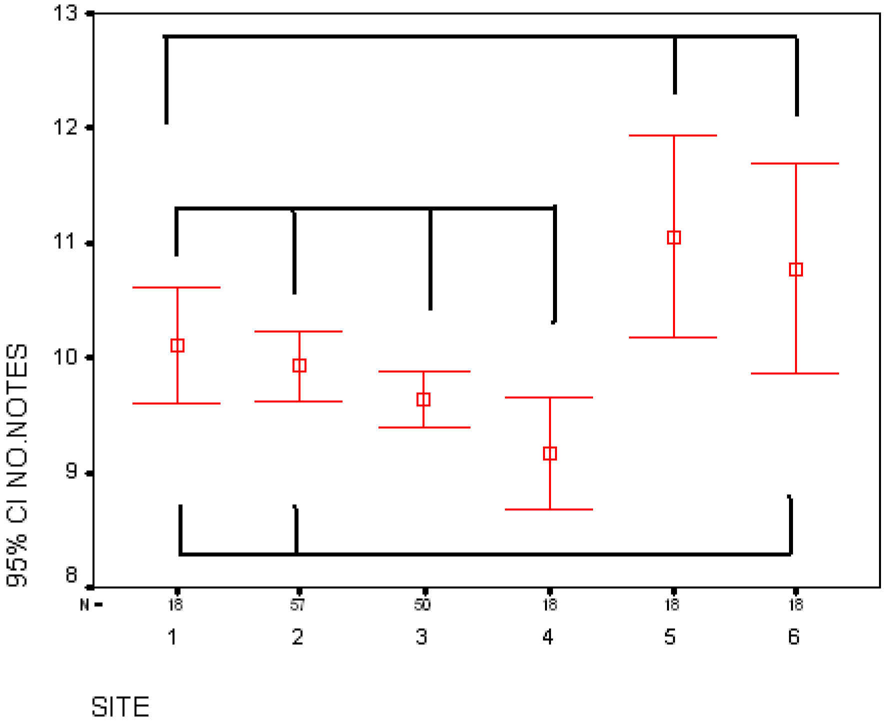

Fig 1.6 Number of notes

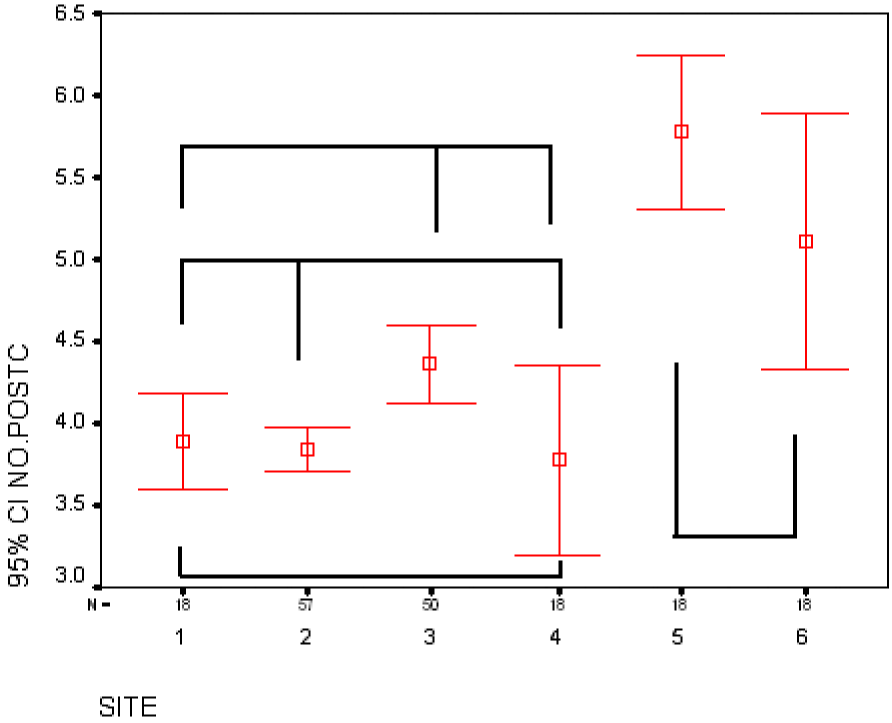

Fig 1.7 Number of post climax notes

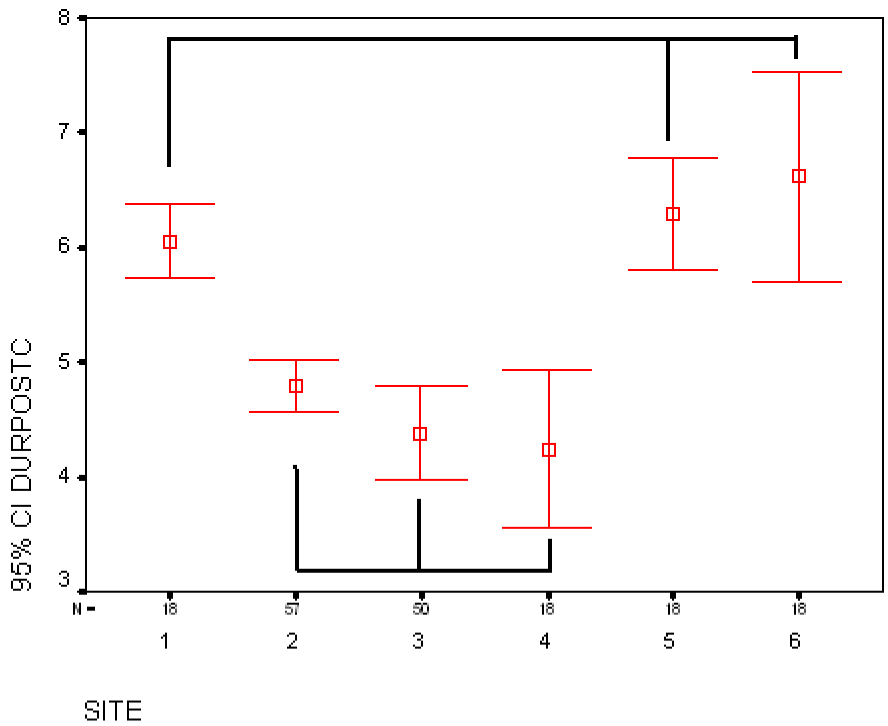

Fig 1.8 Duration of post climax phase

Appendix 2

In figures 2.1-2.8 the lines represent the mean of each variable in groups 1-7 from Area C – Sebangau.

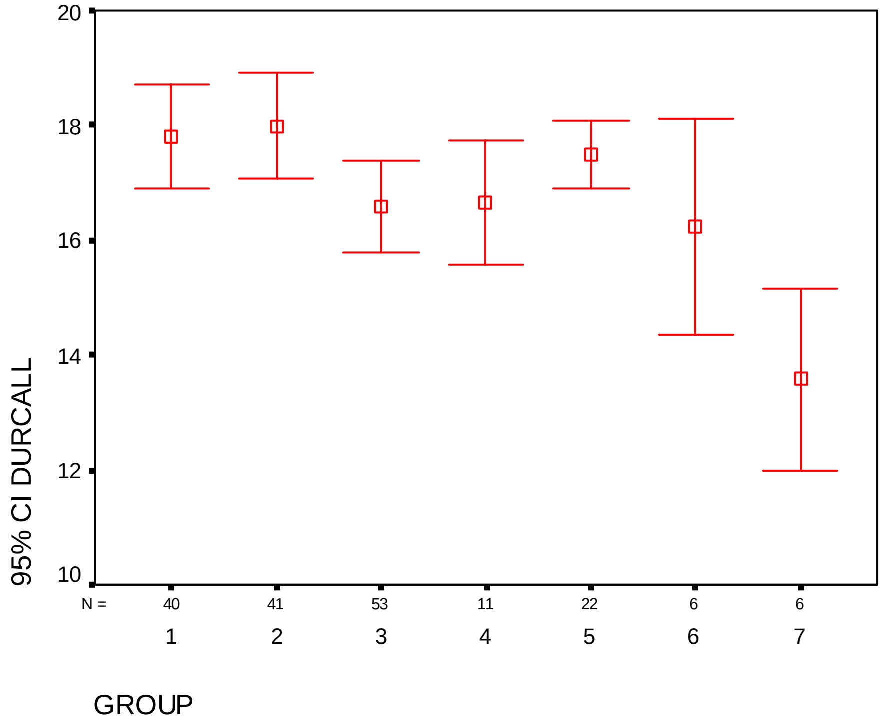

Fig 2.1 Duration of great call

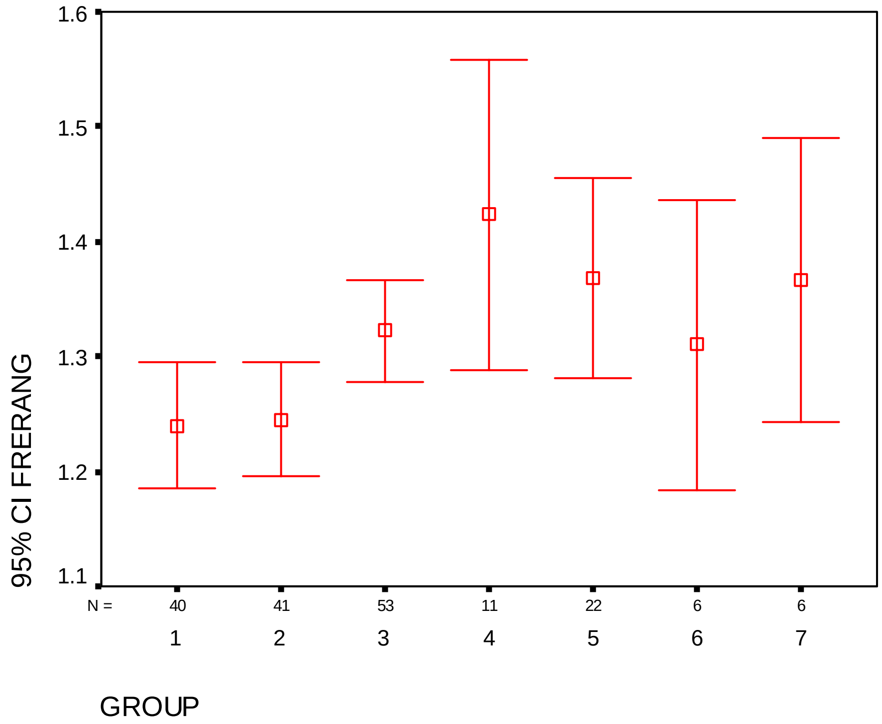

Fig 2.2 Frequency range

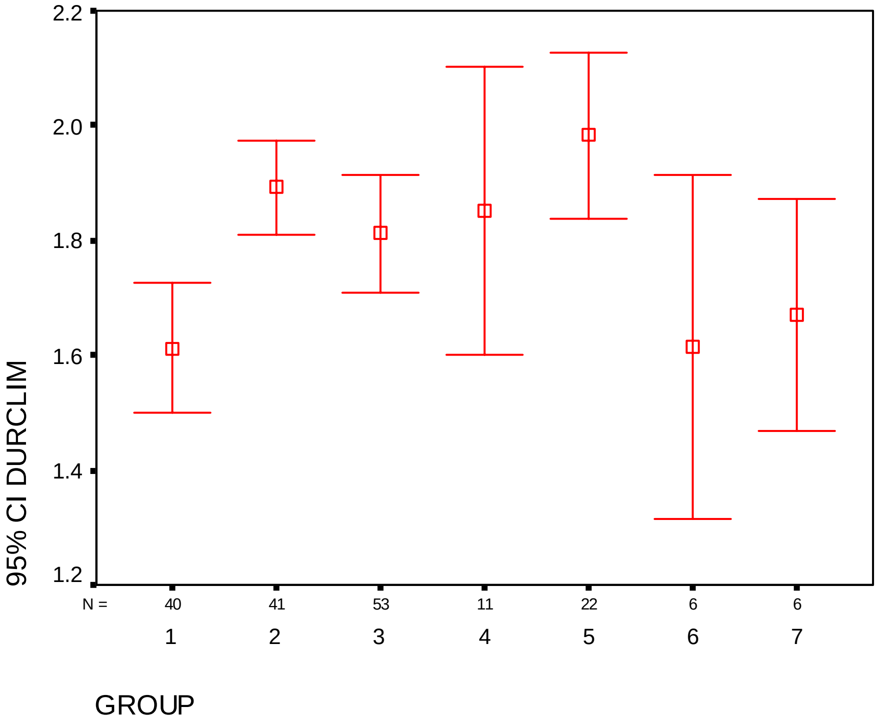

Fig 2.3 Duration of climax note

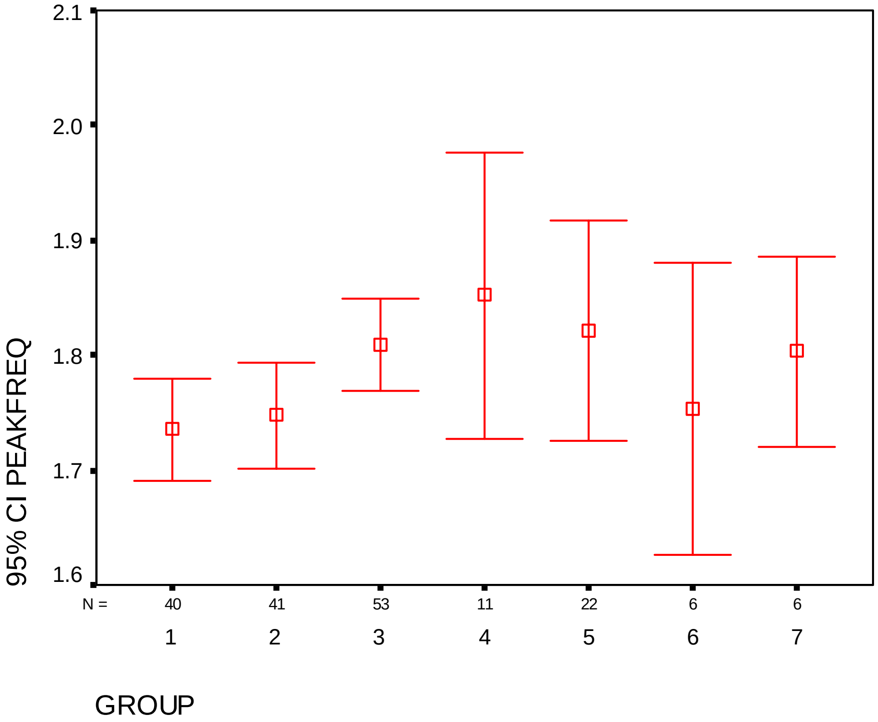

Fig 2.4 Peak frequency

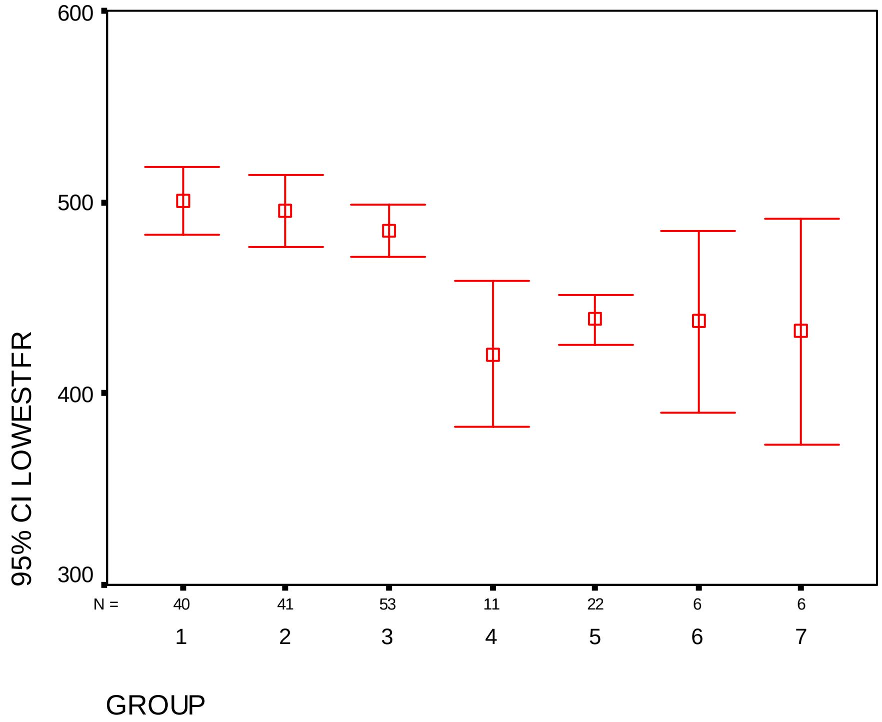

Fig 2.5 Lowest frequency

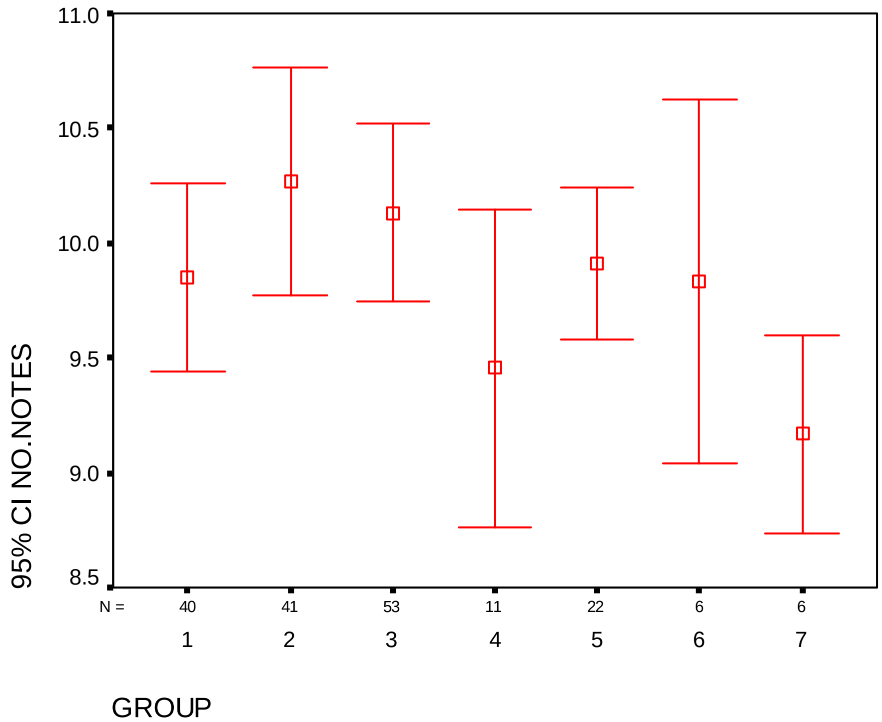

Fig 2.6 Number of notes

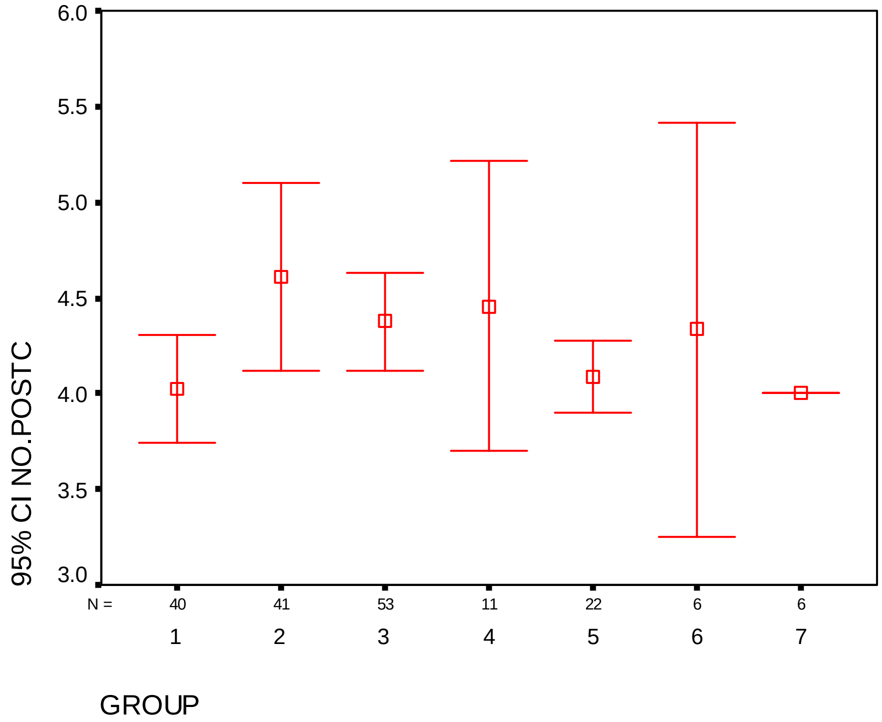

Fig 2.7 Number of post climax notes

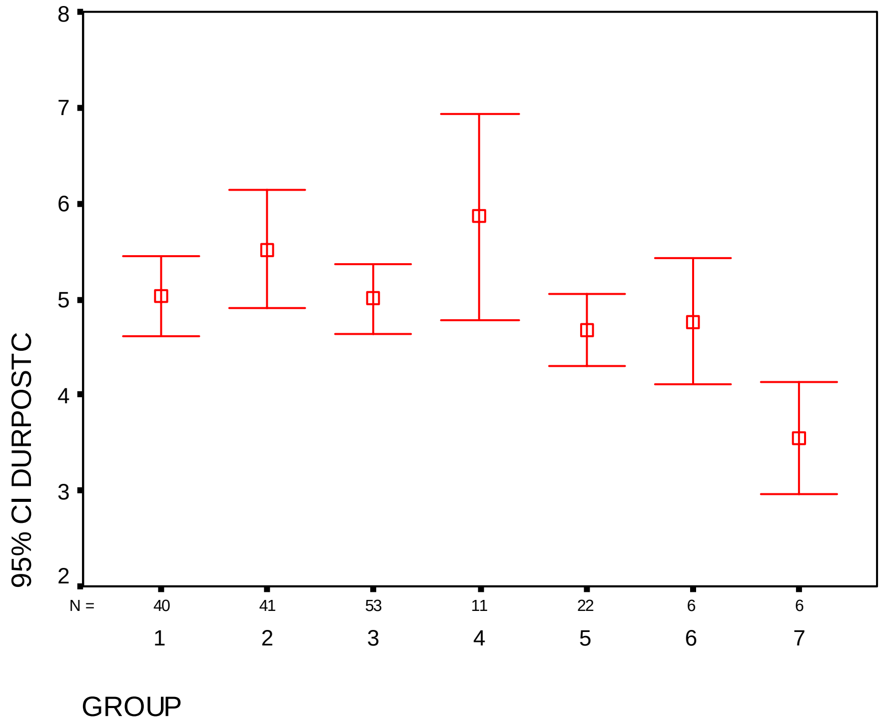

Fig 2.8 Duration of post climax phase

Appendix 3

Figures 3.1 – 3.8 show the results for each variable from the ANOVA statistical test for results across all areas.

ANOVA

DURCALL

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	628.409	5	125.682	30.856	.000
Within Groups	704.660	173	4.073		
Total	1333.069	178			

Fig 3.1 Duration of great call

ANOVA

FRERANG

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	.742	5	.148	5.508	.000
Within Groups	4.662	173	.027		
Total	5.405	178			

Fig 3.2 Frequency range

ANOVA

DURCLIM

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	.785	5	.157	1.290	.270
Within Groups	21.051	173	.122		
Total	21.836	178			

Fig 3.3 Duration of climax note

ANOVA

PEAKFREQ

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	.542	5	.108	4.822	.000
Within Groups	3.891	173	.022		
Total	4.433	178			

Fig 3.4 Peak frequency

ANOVA

LOWESTFR

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	118297.1	5	23659.410	8.578	.000
Within Groups	477180.6	173	2758.269		
Total	595477.6	178			

Fig 3.5 Lowest frequency

ANOVA

NO.NOTES

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	50.405	5	10.081	6.824	.000
Within Groups	255.573	173	1.477		
Total	305.978	178			

Fig 3.6 Number of notes

ANOVA

NO.POSTC

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	71.224	5	14.245	18.546	.000
Within Groups	132.877	173	.768		
Total	204.101	178			

Fig 3.7 Number of post climax notes

ANOVA

DURPOSTC

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	128.316	5	25.663	17.209	.000
Within Groups	257.992	173	1.491		
Total	386.308	178			

Fig 3.8 Duration of post climax phase

Appendix 4

Figures 4.1 – 4.8 show the results for each variable from the ANOVA statistical test for results in area C - Sabangau.

ANOVA

DURCALL

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	149.842	6	24.974	3.630	.002
Within Groups	1183.227	172	6.879		
Total	1333.069	178			

Fig 4.1 Duration of great call

ANOVA

FRERANG

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	.591	6	.099	3.521	.003
Within Groups	4.813	172	.028		
Total	5.405	178			

Fig 4.2 Frequency range

ANOVA

DURCLIM

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	2.834	6	.472	4.275	.000
Within Groups	19.002	172	.110		
Total	21.836	178			

Fig 4.3 Duration of climax note

ANOVA

PEAKFREQ

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	.268	6	.045	1.845	.093
Within Groups	4.165	172	.024		
Total	4.433	178			

Fig 4.4 Peak frequency

ANOVA

LOWESTFR

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	128363.7	6	21393.955	7.878	.000
Within Groups	467113.9	172	2715.778		
Total	595477.6	178			

Fig 4.5 Lowest frequency

ANOVA

NO.NOTES

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	12.541	6	2.090	1.225	.296
Within Groups	293.436	172	1.706		
Total	305.978	178			

Fig 4.6 Number of notes

ANOVA

NO.POSTC

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	9.038	6	1.506	1.328	.247
Within Groups	195.063	172	1.134		
Total	204.101	178			

Fig 4.7 Number of post climax notes

ANOVA

DURPOSTC

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	33.285	6	5.547	2.703	.016
Within Groups	353.023	172	2.052		
Total	386.308	178			

Fig 4.8 Duration of post climax phase

Appendix 5

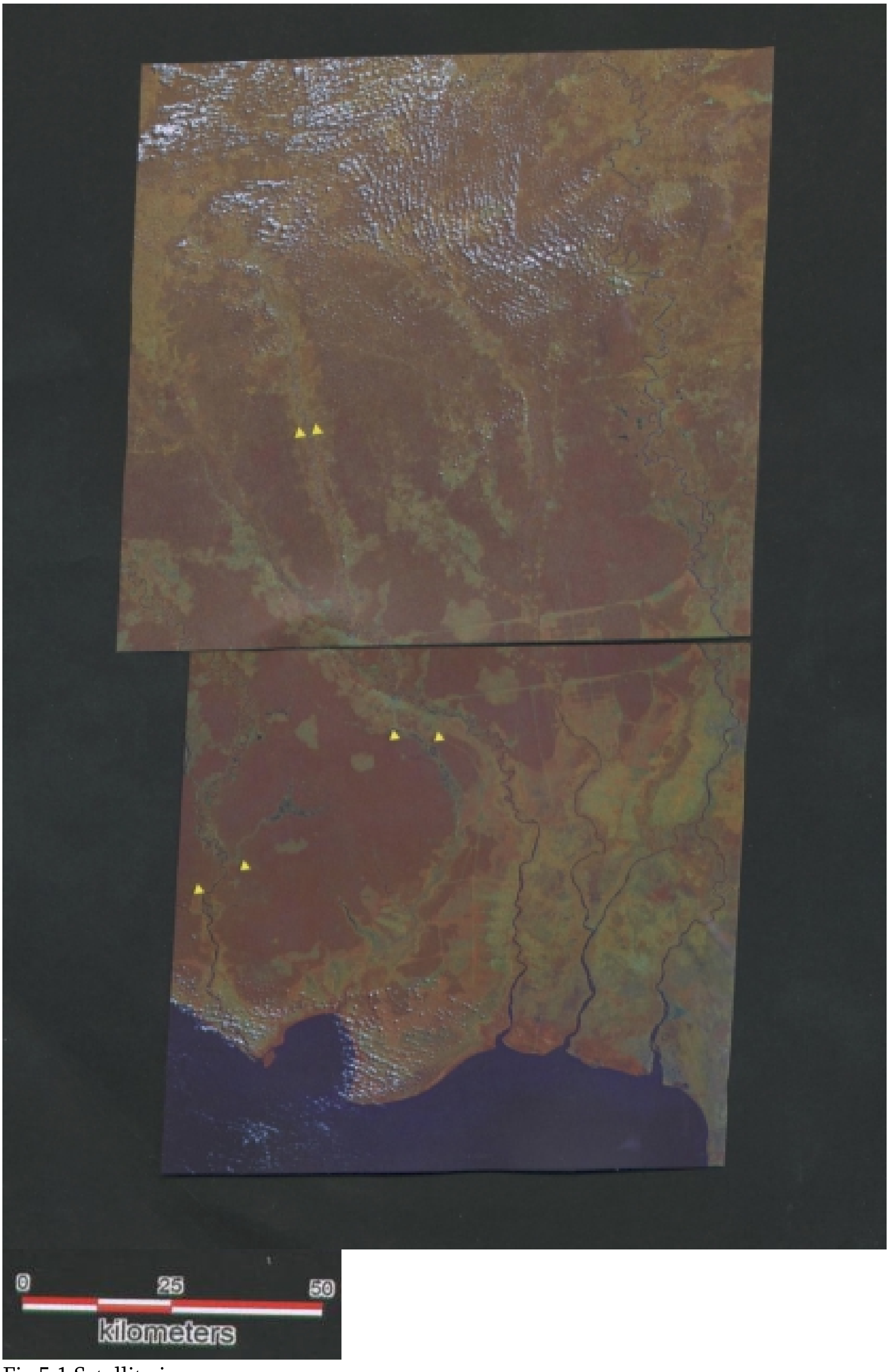

Fig 5.1 Satellite images

Fig 5.2 Position where images were taken from