Social Behaviour and Duetting in Hoolock Gibbons in Gibbon Wildlife Sanctuary, Assam

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By

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Certificate

This is to certify that Ms. Sumithra Sankaran has carried out an original piece of research in partial fulfilment of her M.Sc (Wildlife Science) Degree of the Saurashtra University, Rajkot. The topic of her dissertation is "Social Behaviour & Duetting in Hoolock Gibbons in Gibbon wildlife Sanctuary, Assam". The investigations were carried out in the Wildlife Institute of India, Dehradun under our supervision from November 2008 to June 2009. We hereby certify that this work has not been submitted for any degree of any university.

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SUMMARY

The hoolock gibbon (*Hoolock hoolock*), only anthropoid primate found in India, is a pair-living, territorial species, which duets extensively. Various hypotheses regarding the function of this behaviour in monogamous primates include territory advertisement, pair-bonding, mate defense, resource defence and group cohesion. This study aimed to understand the nature of social behaviour of this species, and how duetting fits into the repertoire of social behaviour seen in this animal.

Three groups of Hoolock gibbons were habituated and studied intensively over a three month period. Relationships between the different group members were explored, alongside time budgets of various activities of the adult pair, the synchrony in their behaviour and frequency and nature of all affiliative and agonistic behaviours. Relationships between territory sizes, group sizes, frequency of duetting and nature of other social interactions have been examined in detail.

A considerable amount of individual difference were found between the different study animals in their interactions with other group members. These animals display complex affiliative interactions with rare displays of aggression. It was found that although the proportion of time spent in social interactions was comparable between the three groups, the proportioning of this total time among different social interactions may vary considerably. The primary difference was found to be in allogrooming interactions with the proportion of time time spent increasing with increase in group size. The study also found considerable evidence for the possible existance of male-care in this species.

The study was able to find a fair amount of evidence against the group-cohesion hypothesis for the function of duetting behaviour. Maximum evidence was found in favour of the pair-bonding hypothesis. As duetting may be a complex behaviour serving more than a single function, long term studies with large sample sizes would be required to fully understand the role of this behaviour in the social repertoire of this monogamous species.

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CHAPTER 1

Introduction

Evolutionary and ecological pressures are believed to have led to the grouping of individuals, among social animals. Social systems are defined by three components(Kappeler and van Schaik 2002):

- Social organisation, (spacing, composition and cohesion of the groups),
- Social structure (nature of interactions between the members of the group), and the
- Mating system .

Both the mating system and the social structure have evolved in response to the social organisation (Dunbar and Shultz 2007). The mating system is constrained by the spacing of individuals and the social structure has evolved as a means of maintaining the social organisation. This is because the relative advantages of grouping are limited by ecological factors, such as competition for resources (Isbell 1991). Five fundamental types of social organizations have been recognized in primates - solitary and neighbourhood, pair-living or monogamy, uni-sex group living, uni-male multi-female group living and multi-male multi-female group living (Kappeler and van Schaik 2002).

Monogamy in primates always involves territoriality and close spatial association of the pair. The wide dispersion of females in response to food distribution makes it impossible for a male to monopolise more than a single female. This, coupled with the risk of infanticide, makes it more beneficial for the male to remain with a female and protect his offspring (Haimoff 1986). Monogamous primates usually exhibit close inter-individual social bonds, often accompanied by a characteristic behaviour known as duetting (Geissmann and Orgeldinger 2000).

The hoolock gibbon (*Hoolock hoolock*), the only anthropoid primate found in India, is a pair-living, territorial species, which duets extensively (van Schaik and Dunbar 1990). This study aims to understand the nature of social behaviour of this species, and how duetting fits into the repertoire of social behaviour seen in this animal. This would enable us to unravel the conditions that may have led to the evolution of this form of social organisation in this species, and the functions of specific behavioural mechanisms in maintaining the same.

1.1 Background

Hoolock gibbons, like other gibbons, are diurnal, canopy dwelling apes. They are frugivore - folivores with fruits constituting 51-89% of their diet (Tilson 1979, Islam and Feeroz 1992, Kakati 2005). Home range size of hoolock gibbons vary from 14-55 hectares depending on the habitat. Average distance travelled in a day ranges from 0.6 - 1.6 km (Islam and Feeroz 1992, Kakati 2005). These animals are known to bask in winters, preferring leafless tall trees, located in the centre of their territories for basking sites (Leighton 1987). Previous studies have shown seasonal fluctuations in their activity patterns, particularly in their day range and activity budget. They duet less frequently in winters spend more time feeding and less time travelling (Islam and Feeroz 1992). This shows that the ecological pressures faced by these animals differ across seasons, and result in consequent shifts in behavioural patterns.

Hoolock gibbons are known to be the closest to the common ancestor of all the gibbons, which is known to have been monogamous and to have displayed duetting behaviour (Takacs et al 2005). It is also believed that there is no sexual dimorphism in the vocal repertoire of this species, and display maximum synchrony in its duet songs (Geissmann 1993). Duetting involves simultaneous vocalization by two individuals in a coordinated manner and has been suggested to be a mechanism of bonding (Geissmann and Orgeldinger 2000), of territory advertisement (Mitani 1985) and of pair-bond advertisement (Cowlishaw 1992). Although these phenomena are common to all social primates, duetting is unique to monogamous primates (van Schaik and Dunbar 1990). Other hypothesis include resource defence and group cohesion. Social behaviour and duetting has, however, never been studied intensively in wild hoolock gibbons so far. Duetting behaviour has also not been examined in relation to other social behaviours or under different demographic conditions in this species.

Primates are known to invest time and effort in maintaining and reinforcing social relationships. Social bonding mechanisms vary between different primate species with regard to type and relative time investment (Mccomb and Semple 2005). This is because the nature of conflict between individuals differs with the type of social organisation. While numerous studies have looked into the intricacies of interactions among individuals in group living primates such as macaques (Bovet and Washburn 2003), few studies have looked into such interactions in gibbon societies, particularly in wild populations. This is an exploratory study of the social interactions between the different individuals of the gibbon groups. Relationships between adult pairs and between each adult and other group members have been examined in detail to gain an understanding of their respective roles in the social organisation.

As the Gibbon Wildlife Sanctuary, Jorhat, Assam supports one of the highest densities of the western hoolock gibbons in India (Sharma 2009), this area is an ideal study site for the intensive study of intra and inter-group interactions in gibbon groups with appropriate differences in composition. This study has explored relationships between ranging patterns, time activity budgets, feeding ecology and behaviour of three groups of gibbons in an attempt to identify proximate and ultimate correlates of their social behaviour, particularly duetting.

1.2 Objectives

1. To examine in detail the social behaviour of the adult males and females with primary focus on –
   - The time spent in social activities relative to that spent in other activities.
   - The proportioning of the time spent in social activities between different social interactions
   - Differences between the sexes in their allogrooming, affiliative and agonistic interactions with other group members.
   - Differences between the three groups in the interactions between the adult pair
2. To study the function of duetting behaviour in the social repertoire of these animals
   - To explore the relationship between duetting and other activities of the animal
   - To examine the social interactions between the participating individuals during this activity
   - The examine the frequency and time spent in this behaviour by different individuals

CHAPTER 2

Study Area

Gibbon Wildlife Sanctuary (GWLS), (26°40'-26°45' N, 94°20' - 94°25' E. and Alt 100-120m), was constituted in 1997. It comes under the district of Jorhat within the state of Assam and covers an area of 2098.6 ha. The sanctuary is surrounded by tea estates and villages. This forest fragment was once contiguous with large forest tracts that extended to Nagaland state. Presently, the nearest forest areas of Dissoi Valley Reserve Forests of Nagaland are separated by 8km of tea gardens.

The sanctuary is home to one of the highest density populations of gibbons in Assam. The other primate species found here include the capped langur (*Trachypithecus pileatus*), pigtailed macaque (*Macaca nemestrina*), assamese macaque (*Macaca assamensis*), rhesus macaque (*Macaca mulatta*), stump tailed macaque (*Macaca arctoides*) and the slow loris (*Nycticebus coucang*).

This P.A falls in the North-East India Biogeographic zone (9), and N.E Brahmaputra valley biogeographic province (9A) (Rogers and Panwar 1988). The temperature ranges from 90°C (Dec-Jan) to 31°C (June-August) (Duruah and Saikia 2008). The average rainfall recorded in the area is 2400m, with a 400mm/month average during the monsoon period (Duruah and Saikia 2008). The seasons can be divided into three distinct phases of pre-monsoon (March - May), monsoon (June - October) and winter (November - February).

As per the Champion and Seth (1968) classification scheme, the forest type in the GWLS is Assam Plains Alluvial Semi Evergreen Forests (1/2/2B/C) sparsely interspersed with wet evergreen forest patches. The vegetation is composed of several canopy layers, most of the components of which are evergreen in character (Hazarika .R. and Gupta .A.K). The top canopy (25- 30 m) is dominated by *Dipterocarpus macrocarpus*, *Artocarpus chama*, *Castronopsis sp.* and *Tetrameles nudiflora*, and the middle canopy by *Mesua ferrea*, *Lagerstomia flos-reginae*, *Dysoxylum procerum*, *Canarium resiniferum*, *Aqualaria sp.*, *Dillenia indica* and *Vattica lanciafolia*. The lower canopy consist of evergreen shrubs and herbs, most common of which are *Teinosstachyum dullooa*, *Pseudostachyum polymorphum*, *Calamus sp.* and *Laportea cremulata*.

The forest is entirely composed of tall trees, Bamboos and Canes. Grassland and aquatic vegetation are completely absent. More than 75% of the P.A has undergone artificial regeneration, and the total area under plantations within the P.A is 1690Ha. The plantation species include *Dipterocarpus macrocarpus*, *Terminalia myriocarpa*, *Aqualaria sp.* and *Lagerstomia flos-reginae*.

The sanctuary is divided into 5 compartments. The compartment 1 of the sanctuary is isolated by a railway line from the adjacent compartment 2. The groups which were followed during this study ranged within compartments 2 (group I, III) and 5 (group II) which were 900 and 200ha in size respectively.

Figure 2.1: Location of Gibbon Wildlife Sanctuary in Assam

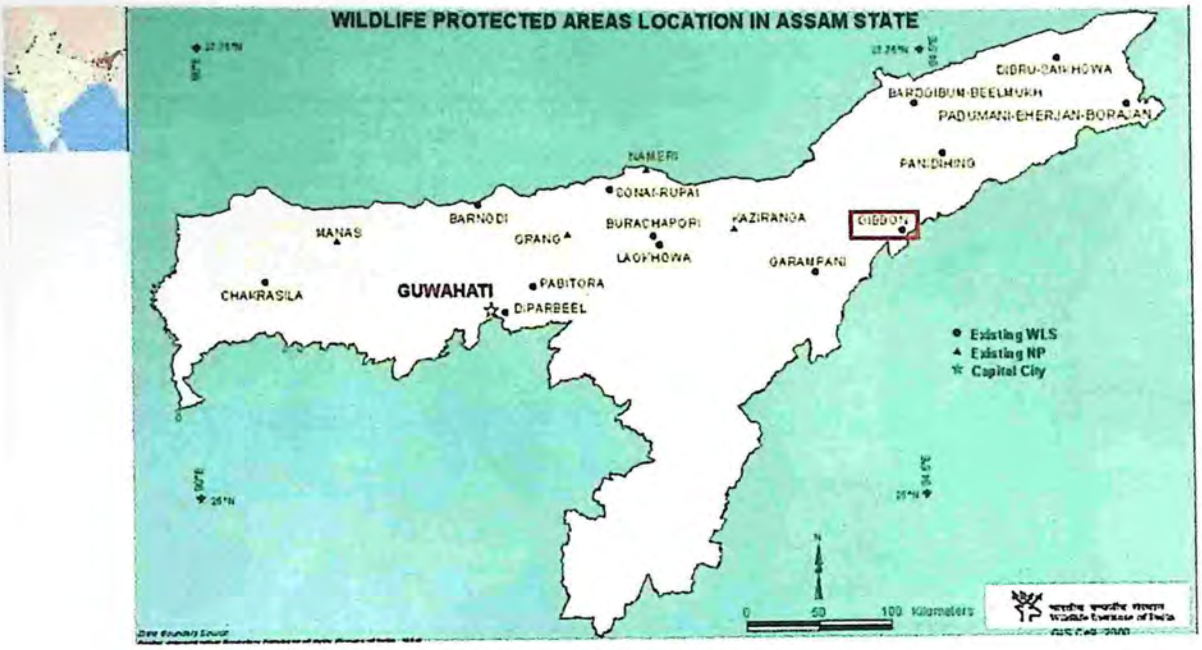


Figure 2.2: Location of Gibbon Wildlife Sanctuary with respect to surrounding tea estates and neighbouring forest fragments

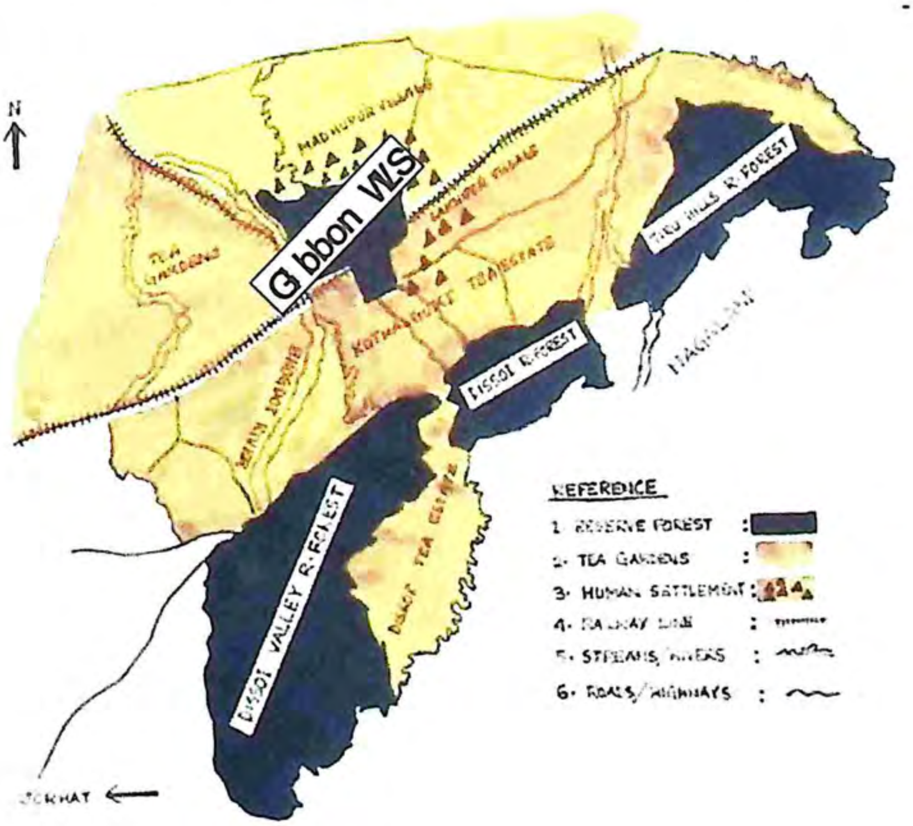
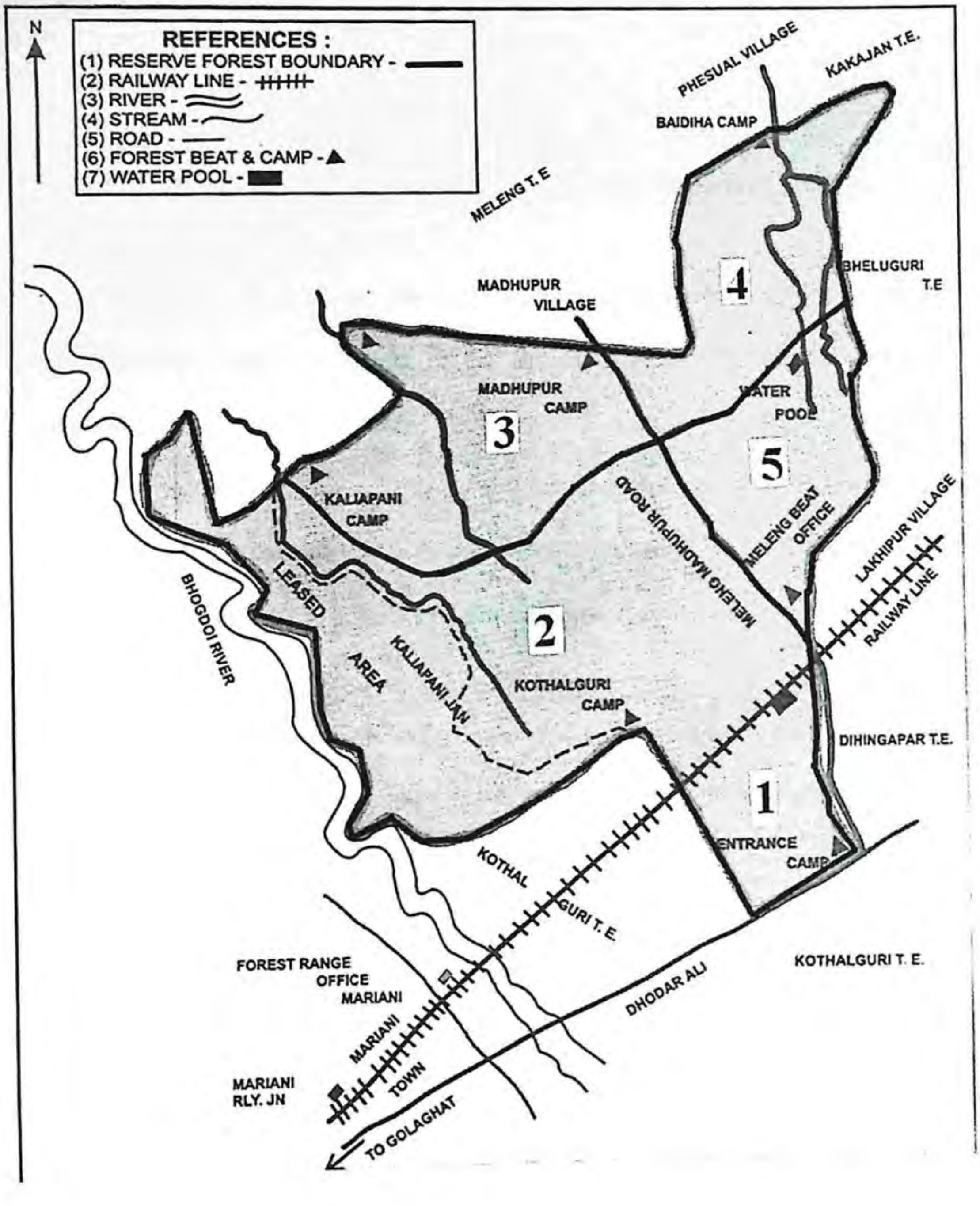


Figure 2.3: Boundaries of Gibbon Wildlife Sanctuary



CHAPTER 3

Methodology

3.1 Selection and habituation of study groups:

Three gibbon groups were selected on the basis of their differing demographic structure (presence/absence, number and age of the Sub adults and juveniles). Two of these groups were located in compartment II and one in compartment V. The study groups were chosen based on results from a rapid assessment of the gibbon groups in the entire area of the sanctuary which had been conducted in September 2008 (Sharma 2009). The troop compositions are given below-

- GROUP 1 (Compartment II) - Adult male, adult female, subadult female and juvenile male.
- GROUP 2 (Compartment V) - Adult male, adult female and subadult female.
- GROUP 3 (Compartment II) - Adult male and adult female.

40 days were spent in habituating these three groups, till they were approachable to within 5 meters without causing the animal any alarm. All observations were carried out as close as possible, with an average observation distance of about 20 meters in length, as often observations from directly under the tree obscured vision. During this period, an ethogram of their behaviours was prepared, and the behaviours were categorised into 7 different behavioural states. 26 different behavioural events were recognised as part of the social interactions between these individuals (Refer

Appendix). This period was also used to standardise sampling procedures and determine suitable durations of sampling bouts and intervals between them.

3.2 Behaviour data collection procedures:

3.2.1 Time activity budgets

The time-activity budget of each of the study individuals in the different groups was recorded by instantaneous sampling (Altmann 1974) of the individuals' behavioural states, at 10 minute intervals from dawn till the group lodged at their sleeping tree. Except when preceding sleeping, social interactions rarely lasted more than 20 minutes and the numbers of occasions were very few in a day. It was therefore decided that 10 minutes was the minimum possible interval between 2 consecutive instantaneous samples, in order to capture the time spent in social interactions relative to other activities. The synchronicity in behaviour among the different individuals of the group, and inter-individual distances between them was also recorded by instantaneous sampling at the same 10 minute intervals.

During these instantaneous observations, data was also collected on the location (tree species), height and plant species and part consumed (if the individual was found to be feeding). This data was used to test if activity centres in the home range were essentially resource centres and whether the relative amount of feeding (in terms of time spent feeding) on any particular food species had an influence on the interactions between the individuals.

3.2.2 Ad-libitum sampling of calls of solitary individuals

During the full day follows of these troops, data was also collected opportunistically on the number of group calls and the number of calls of solitary individuals heard from the vicinity of the groups home range..

3.2.3 Social Interactions

Focal animal sampling (Altmann 1974) of 7 minutes duration at 10 minute intervals, of each of the pair of study individuals (chosen at random) was carried out, to examine the behavioural profile of these individuals, with emphasis on the frequency and direction of different interactive behaviours displayed.

3.2.4 Ranging behaviour

Location co-ordinates in the daily path of the gibbon groups were taken every 5 minutes and every 20 meters during the group follows, using a GPS (Garmin etrex-H). These points were plotted on a 50/50mt grid map to identify grids of activity concentration, to then check for associations with locations of duets in the home range.

It was attempted to follow each of these groups for 5 full continuous days before shifting to the next, and to complete 3 such cycles over the entire study period. However this was not always possible, as sampling was at times interrupted by external factors such as the presence of elephant herds within the home range of the gibbon group under study. As a result, behavioural sampling of the three groups was done over three phases, but of unequal number of days, and during these full day follows, instantaneous and focal animal sampling of the individuals was carried out. In addition, their duetting behaviour was also recorded by sequence sampling (Altmann 1974) of activity states and inter-individual distances of the participating individuals, with sampling commencing with commencement of the call.

Table 3.1: Sampling descriptives

Group ID	Sampling Days	Male Instantaneous Samples	Female Instantaneous Samples	Male focal Samples	Female Focal Samples	Total observation hours
I	16	540	547	273	293	112
II	15	541	572	309	312	105
III	12	427	399	222	247	90

3.3 Statistical Analysis

3.3.1 Time activity budgets

Descriptive sums and averages of behavioural states were calculated using MS Excel V. 2003 (Microsoft Corporation) and used to graphically represent the proportion of time spent in different activities. This was done individually for each of the three groups. Chi-square analysis was carried out to examine differences between the sexes and between the three groups in the time activity budgets. 14 activity states were recognized, which were broadly categorized into five states [Appendix A].

3.3.2 Ranging

Daily path lengths were calculated by adding up the distances between the recorded GPS locations, for each group and home range areas of the three groups were calculated by the minimum convex polygon (Mohr 1947) method using ARCVIEW 3.02 (ESRI Inc.). A 50/50 m grid was laid over the home ranges of the three groups. Intensity of foraging activity in each of the grids was calculated by pooling in repeatedly used foraging points within the ranging areas and represented as bubble graphs. Visual comparison was used to check for overlap between activity centres and duetting locations. Further, the distances between these points of foraging activity and each of the duet locations of the study groups was plotted to examine patterns of association.

3.4 Social interactions

3.4.1 Dyadic interactions

Interactions between pairs in the group with primary focus on frequencies of affiliative and durations of allogrooming interactions were tested for equality between pairs as well as between the individuals involved using a non-parametric Wilcoxons signed rank test (Zar 1994). Affiliative interactions [Appendix B] have been considered to be mutual interactions while allogrooming has been considered as a directed interaction.

3.4.2 Hinde's Index

The responsibility for initiating and terminating interactions between two individuals is an important aspect of the relationship between them. The Hindes index (Hinde 1970) was used to assess the relative responsibility of the two individuals in maintaining the relationship between them.

The Hindes index is calculated by:

$$Hinde's\ Index = \frac{N_{AB}}{N_{AB} + N_{BA}} - \frac{n_{AB}}{n_{BA} + n_{AB}}$$

where N_{AB} = No. of friendly approaches by individual A to B

N_{BA} = No. of friendly approaches by individual B to A

n_{AB} = No. of departures from friendly interactions with individual B by A

n_{BA} = No. of departures from friendly interactions with individual A by B

This varies on a scale of -1 to +1, and if an individual A shows an index value of .68 towards B, then individual B automatically shows the corresponding negative value. However, if a single individual is responsible for a majority of the interactions in a dyad the Hindes index may not be a suitable assessment of that individuals responsibility for the interactions. Therefore, this proportion has also been calculated and presented.

CHAPTER 4

Results

4.1 Time Activity Budgets

4.1.1 Differences between sexes in proportioning of time between different activities

No significant difference was found between the adult males and adult females of the three groups in the poroportion of time spent daily in the five broad activity states (Table 4.1.1). No significant difference was found in the proportioning of total time spent in social activities among different social interactions, between the adult males and females of the three groups (Table 4.1.2).

Table 4.1.1: Chi–sq values for differences in relative time activity budgets (df = 5)

Group 1	Group 2	Group 3
4.4723 ($p < 0.50$)	4.4389 ($p < 0.50$)	4.0300 ($p < 0.50$)

Table 4.1.2: Chi–sq values for differences in relative time budgets of various social activities (df = 5)

Group 1	Group 2	Group 3
5.7704 ($p < 0.25$)	3.1599 ($p < 0.50$)	—

Figure 4.1: Time Activity Budget of various activities of the adults for the three study groups.

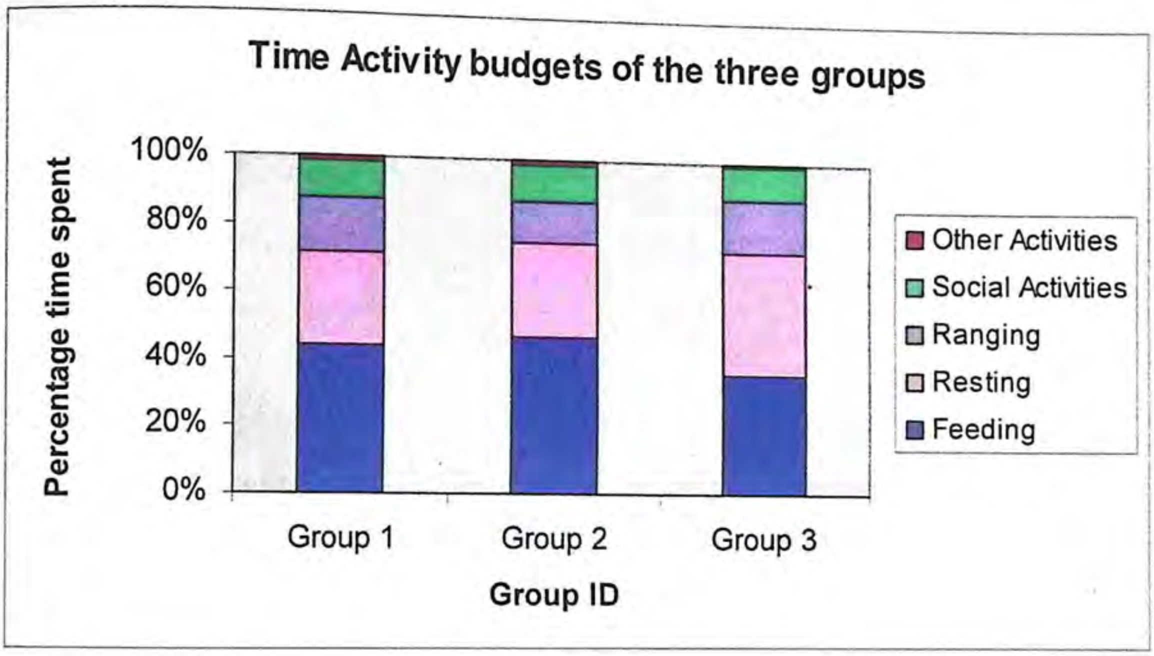
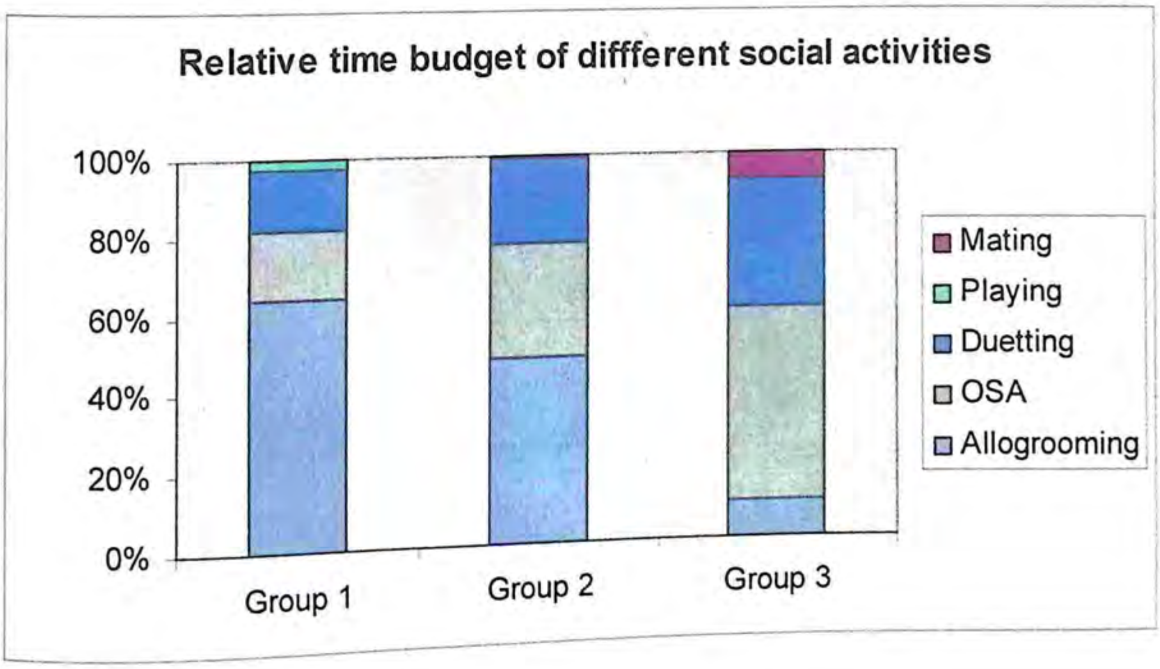


Figure 4.2: Contribution of different interactions to the total time spent in social activities by the adults of the three study groups.



4.1.2 Differences in the time activity budgets of the three groups

As it was found that there was no significant differences between the time activity budgets of the adult males and females, the instantaneous samples of activity states of the adult male & female were pooled for each of the three groups, and between group comparisons were carried out. Significant differences were found between the three groups in their proportioning of time between the five broad activity classes (Chi-sq = 39.7, df = 8, $p < 0.0001$), as well as in the proportioning of total time spent in social activities among different social interactions (Chi-sq = 61.6, df=6, $p < 0.0001$). For this analysis, the proportion of time spent in mating was not taken into account, as only 1 group was found to devote a considerable proportion of time spent in social activities in mating interactions. Despite this, as stated above, the results were found to be significant.

The difference appeared to be contributed largely by group III, which was seen to vary in the proportion of time spent in feeding and resting activities (Fig 4.1). Although the three groups were found to spend a comparable amount of their daily time budget on social interactions (Fig 4.1), the proportioning this time between different interactions was different, with proportion of time spent in allogrooming interactions increasing with an increase in group size, and the proportion of time spent in other social interactions varying in concordance between the three groups (Fig 4.2).

4.2 Social Interactions

4.2.1 Hinde's Index

Table 4.2.1: Hinde's Index values for dyadic interactions between the adults and the different group members of the three study groups.

Group 1		Group 2		Group 3	
M → F	0.15	M → F	0.04	M → F	$\boxed{0.42}$
M → SA	0.03	M → SA	0.08		
M → J	0.01	F → SA	0		
F → SA	$\boxed{-0.39}$				
F → J	$\boxed{-0.42}$				

The adult male-female relationships appeared to be of equal interest to both participating individuals except in the case of group III where the male was observed to show a disproportionately higher amount of contribution than the female. The female of group I was seen to show a negative interest in the relationship with both the Sub-adult as well as the juvenile. The adult males were seen to share a more or less equal relationship with all the non-adult group members.

4.2.2 Allogrooming interactions of the adult males and females with other group members

Table 4.2.2: Wilcoxon's paired signed rank test results for relative time spent grooming in dyadic interac- tions of the adults with other group members for the three groups.

Male – Female
F → M > M→ F

Group 1	T = -2.934 P < 0.05
Group 2	T = -2.310 P < 0.05
Group 3	T = -.314 P > 0.05

Adult male
with sub-adults

SA → M > M→ SA

Group 1	T = -2.934 P < 0.05
Group 2	T = -2.429 P < 0.05

Adult female
with sub-adults

F → SA > SA→ F

Group 1	T = -.031 P > 0.05
Group 2	T = -2.512 P > 0.05

Adult male
with juveniles

J → M Vs M→ J

Group 1	T = -0.135 P > 0.05

Adult female
with juveniles

F → J > J→ F

Group 1	T = -1.956 P < 0.05

In the case of adult male – adult female allogrooming interactions, the adult male was observed to receive grooming significantly more than he groomed the female , except in the case of group III where no significant difference was found.

In terms of interactions of the adult individuals with other groups members, it was found that adult males receive significant more grooming from the subadults than vice-versa. However, no significant differences were found between the amount of time spent grooming the subadults by the adult-females and the amount of time spent allogrooming the adult females by the subadults.

While no significant difference was found between between the adult male and juvenile in the amount of time spent grooming each-other, it was observed that the adult female grooms the juvenile significantly more than vice-versa.

4.2.3 Affiliative Interactions

Table 4.2.3: Wilcoxons paired sign-rank test results for difference in frequencies of mutual affiliative interactions between males and other group members Vs females and other group members.

Adults with sub-adults

SA ←→M Vs F←→ SA

Group 1	T = -0.445 P > 0.05
Group 2	T = -0.220 P > 0.05

Adults with juveniles

F ←→ J > J←→ M

Group 1	T = -1.726 P > 0.05

No significant difference was found in the frequency of affiliative interactions between the Adult females with other groups members and the adult males with the other group members.

One occurrence of play behaviour was observed between the adult male of group I & Subadult female of group I (freq. 0.03139), and 38 occurrences between adult male of group 1 & Juvenile male of group I (freq. 1.1930). Three occurrences of play behaviour was observed between Adult male of group II and subadult female of group II (freq.0.0824). Play behaviour was never observed in the case of any of the adult females of the three study groups.

4.3 Duetting Behaviour

The total number of calls observed per group were five, six and seven of groups I, II and III respectively.

Direct and indirect observations of individual gibbon calls over the entire study duration were nil.

In all occasions of duetting by the three study groups the calls were initiated by the female vocalising from a particular tree where the male was observed to join her in response to her vocalisation. The female continued vocalising in all the cases until the male had reached her, and after few seconds they were observed to begin calling in unison. The call was also terminated in all occasions by the female leaving the duetting tree. Three different species of trees were used by Group I as duet trees for a total of 5 duets, 4 for a total of 6 duets by group II and 4 for 7 by group III, all contributing 7 different species in a total of 18 duets observed of the three groups. All the duetting trees were measured to be 25 - 30 meters tall, which corresponds with the highest canopy layer in gibbon wildlife sanctuary.

4.3.1 Duetting - Pair Bonding, Group Cohesion & Mate Defence.

The duets were observed to be highly synchronous. Synchrony in activity state of the adult pair over the course of the duet was near perfect in all cases. % Synchrony in activity states for the adult pair of Group 1 was 97.48% (S.E. 0.1666), for Group II was 94.8% (S.E. 2.0407) and for group III was found to be 95.03% (S.E. 1.9798). Average interindividual distances over the course of the duet for group I was 1m (S.E 0.0122), 1.02 (S.E 0.0085) for group II and 0.957143 (S.E..0059) for group III.

Duetting behaviour appears to be exclusive to the pair bonded adults

- Subadult female of group I & juvenile male of group I were observed to participate in 0% of all the duets of the adult pair of group 1.
- Out of the 6 duets of group 2, subadult female of group II was found to participate for 14% & 9% in two duets and 0 % in the remaining.

Table 4.3.1: Frequency of duets and group size of the three study groups

GROUP ID	FREQUENCY DUETS	GROUP SIZE
GROUP 1	0.0446 hours	4 INDIVIDUALS
GROUP 2	0.0571 hours	3 INDIVIDUALS
GROUP 3	0.0833 hours	2 INDIVIDUALS

It can be seen from the above table that with more number of individuals in the group, duetting frequency does not increase, and in fact shows an inverse relationship. This suggests that this behaviour may not function as a means of achieving group cohesion.

In two out of four inter-group encounters of group III and one out of two inter-group encounters of group II duetting was observed by one of the two encountering groups. Further, the pattern of response was found to correspond closely with that observed in a study on white-handed gibbons which was of much longer duration and with much larger sample sizes where conclusive evidence for this hypothesis was found (Brockelman 1998).

4.3.2 Duetting - Territoriality & Resource Defence

Minimum Convex Polygon home range sizes of the three groups were prepared and the results are depicted in the following table.

Table 4.3.2: Average daily path length and the total home range area

Group ID	I	II	III
Average Daily path length (m)	1012.899	973.5956	1421.422
STD DEV	292.3512	300.7186	391.6246
STD ERROR	9.135975	8.353295	13.05415
HOME RANGE AREA(ha)	23.54435	57.96797	43.92391

Group II was observed to have the largest home range. However, Group II did not most frequently duet amongst the three groups and therefore no relationship could be found between homerange sizes and frequency of calls.

Table 4.3.3: Mann-Whitney U test results for differences in day range paths between days on which duetting was observed and days on which duetting was not observed for the three study groups.

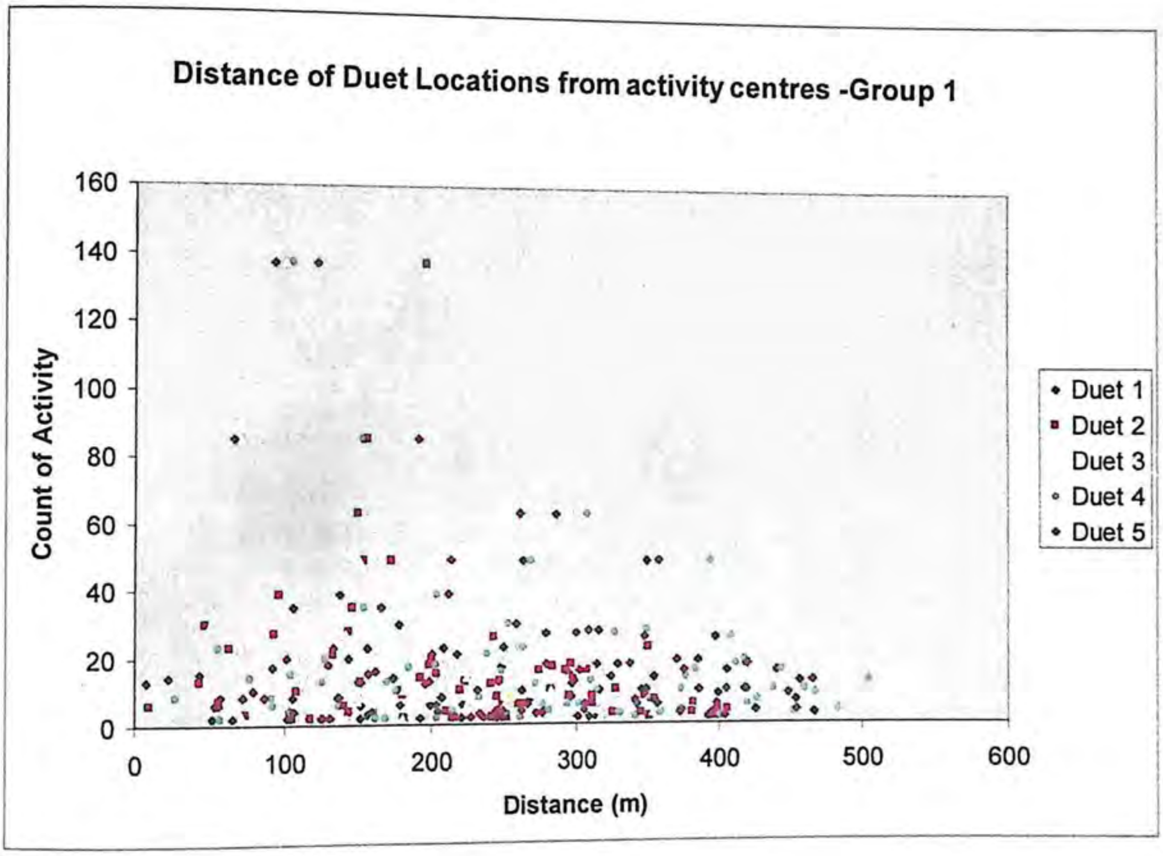
Group 1	$U = -31.934$ $P > 0.05$
Group 2	$U = -12.310$ $P > 0.05$
Group 3	$U = -19.314$ $P > 0.05$

No significant differences were found

Activity Centres Vs. Duetting Locations

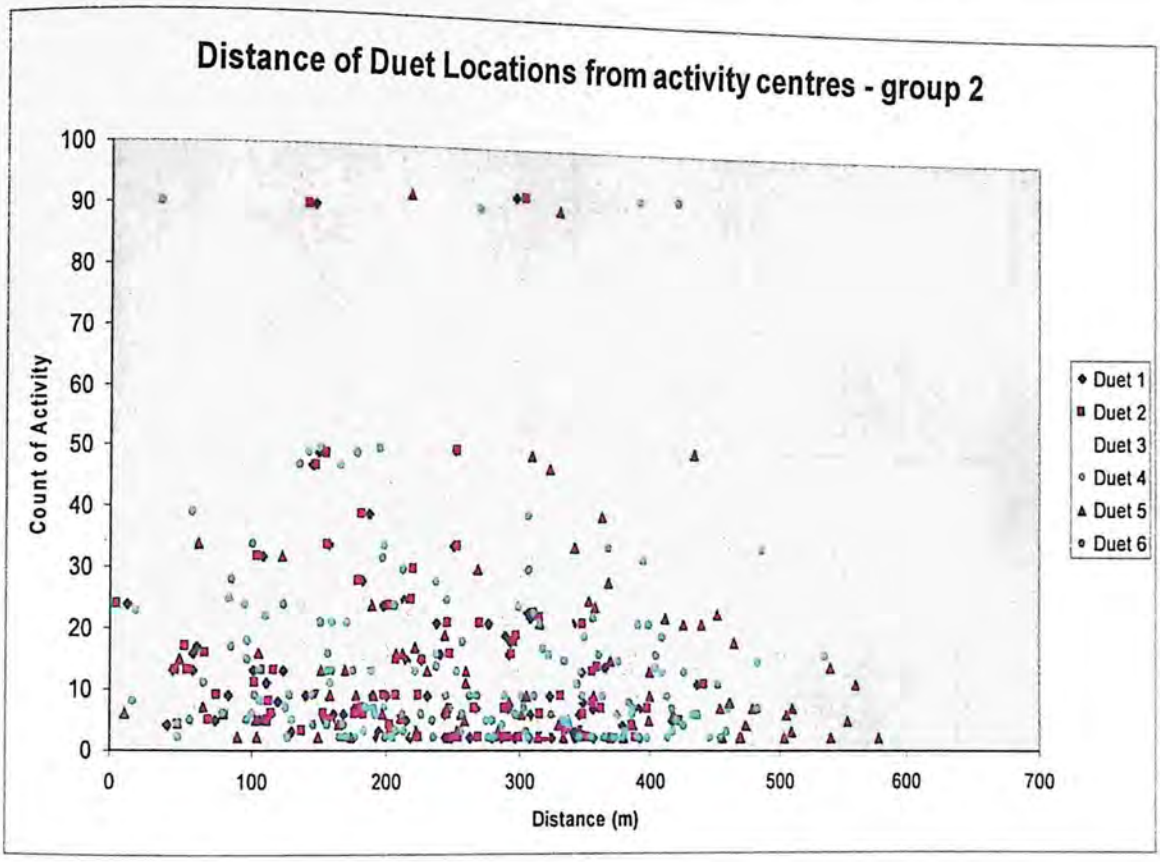
Visual comparisons of activity centres of the three groups showed little or no overlap with those of the recorded duetting locations (fig. 4.5,4.6,4.7). There was also no indication of favourite or repeated duet locations which could be discerned during the study period.

Fig 4.3: Relationship between intensity of foraging and distance from the duet location of the activity points in the home range area of group I



No consistent pattern of association between the foraging centres and the duet locations was discernable (Fig 4.3, 4.4). Spatial association was checked at a limit of 50m (Brockelman 1998, Fan et al 2009).

Fig 4.4: Relationship between intensity of foraging and distance from the duet location of the activity points in the home range area of groups II & III



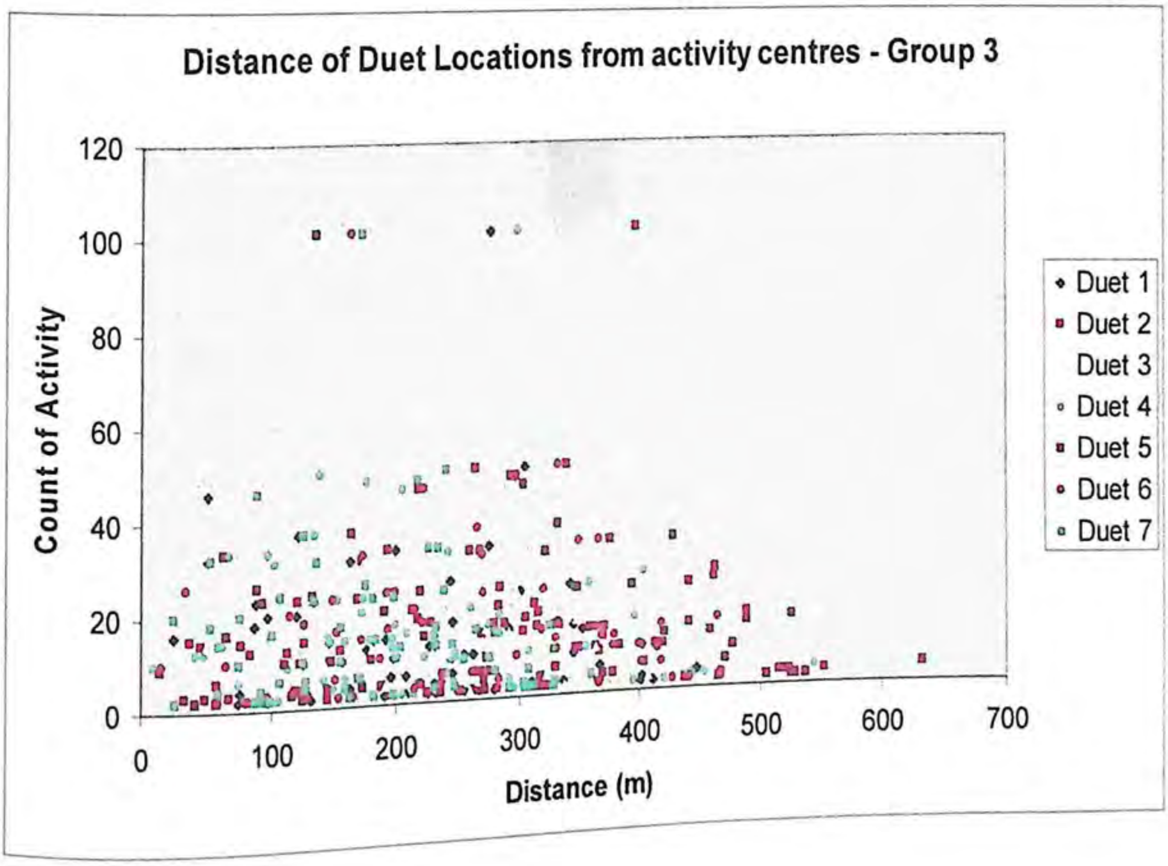


Figure 4.5: Duetting Locations for Group 1

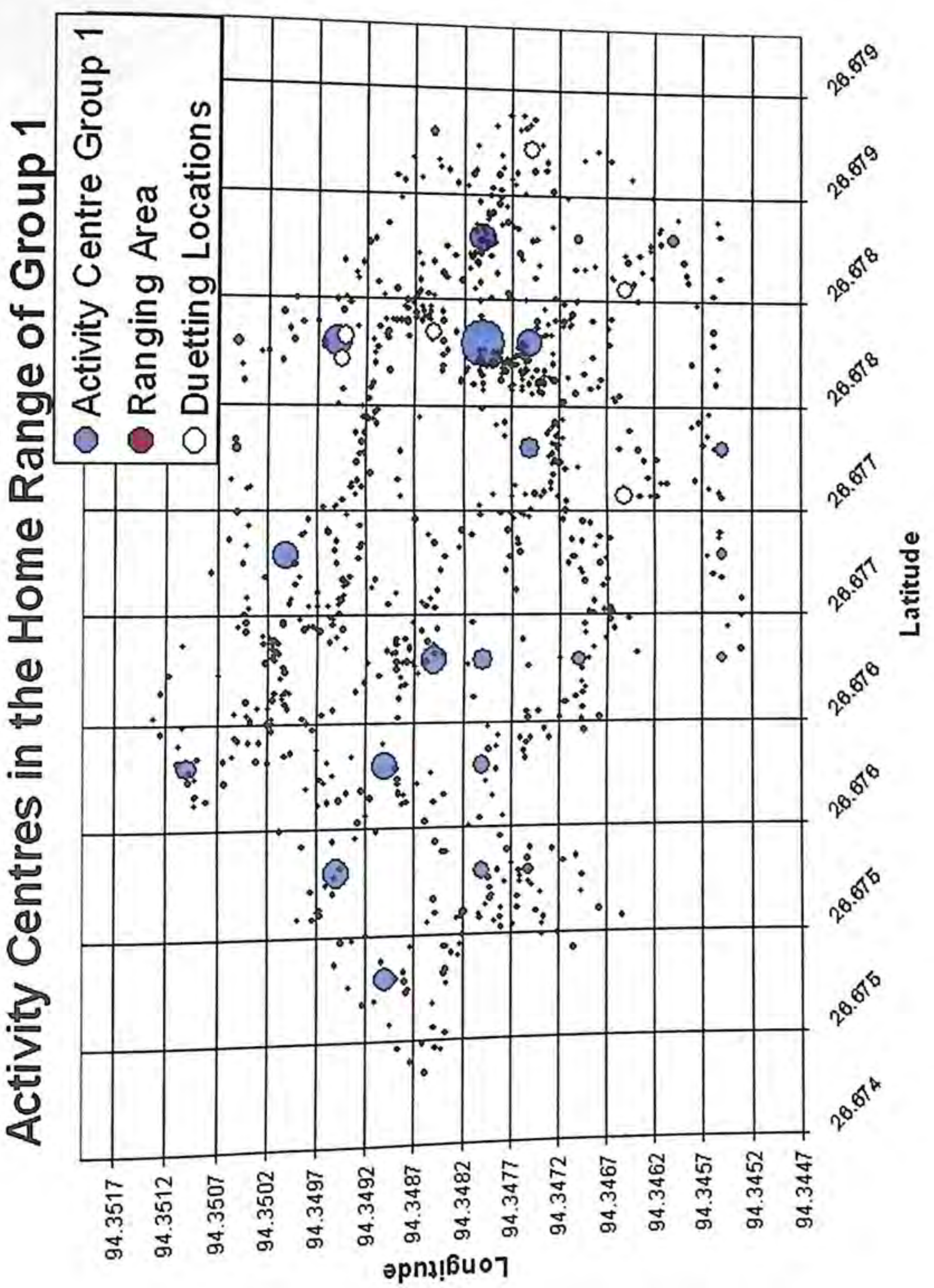


Figure 4.6: Duetting Locations for Group 2

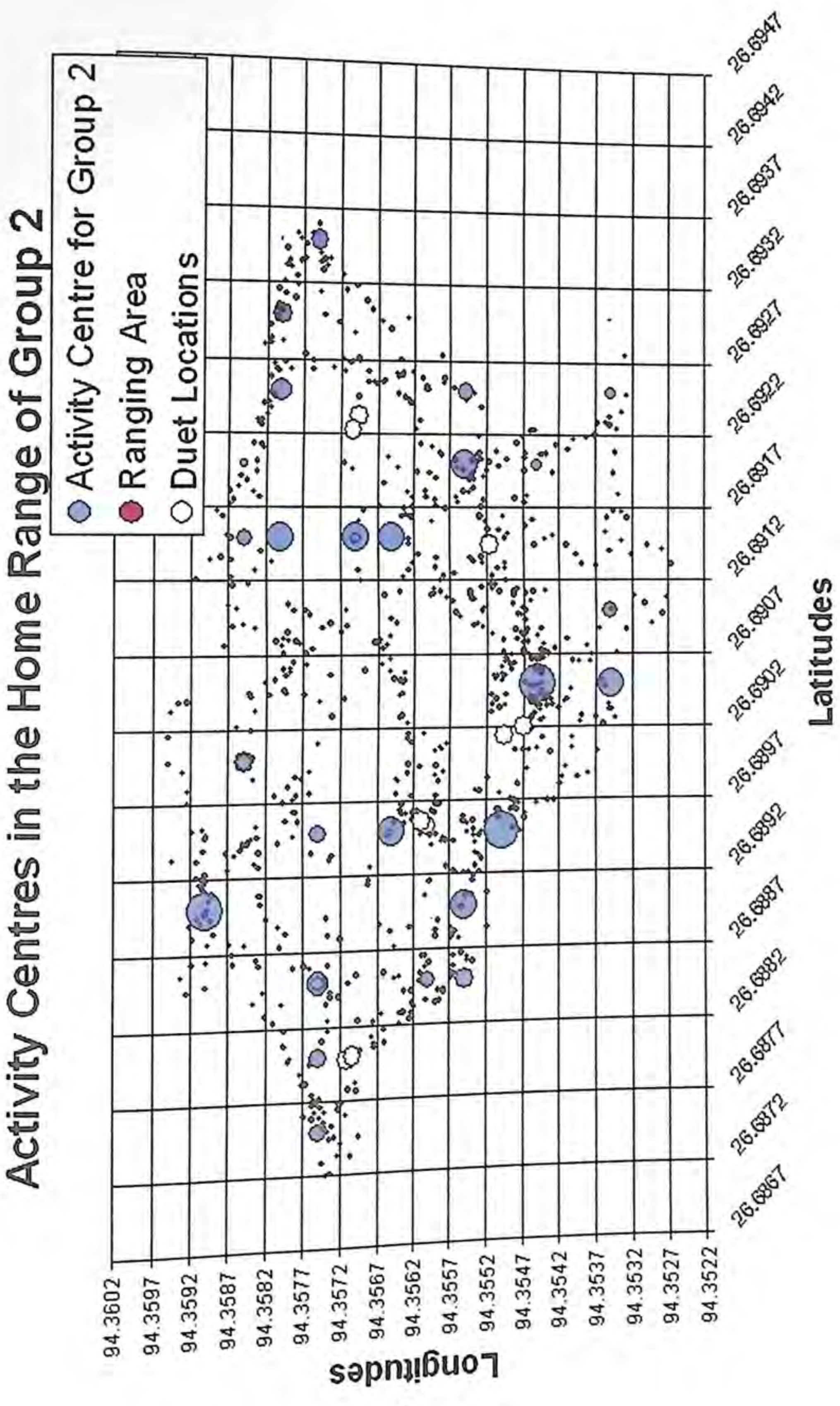
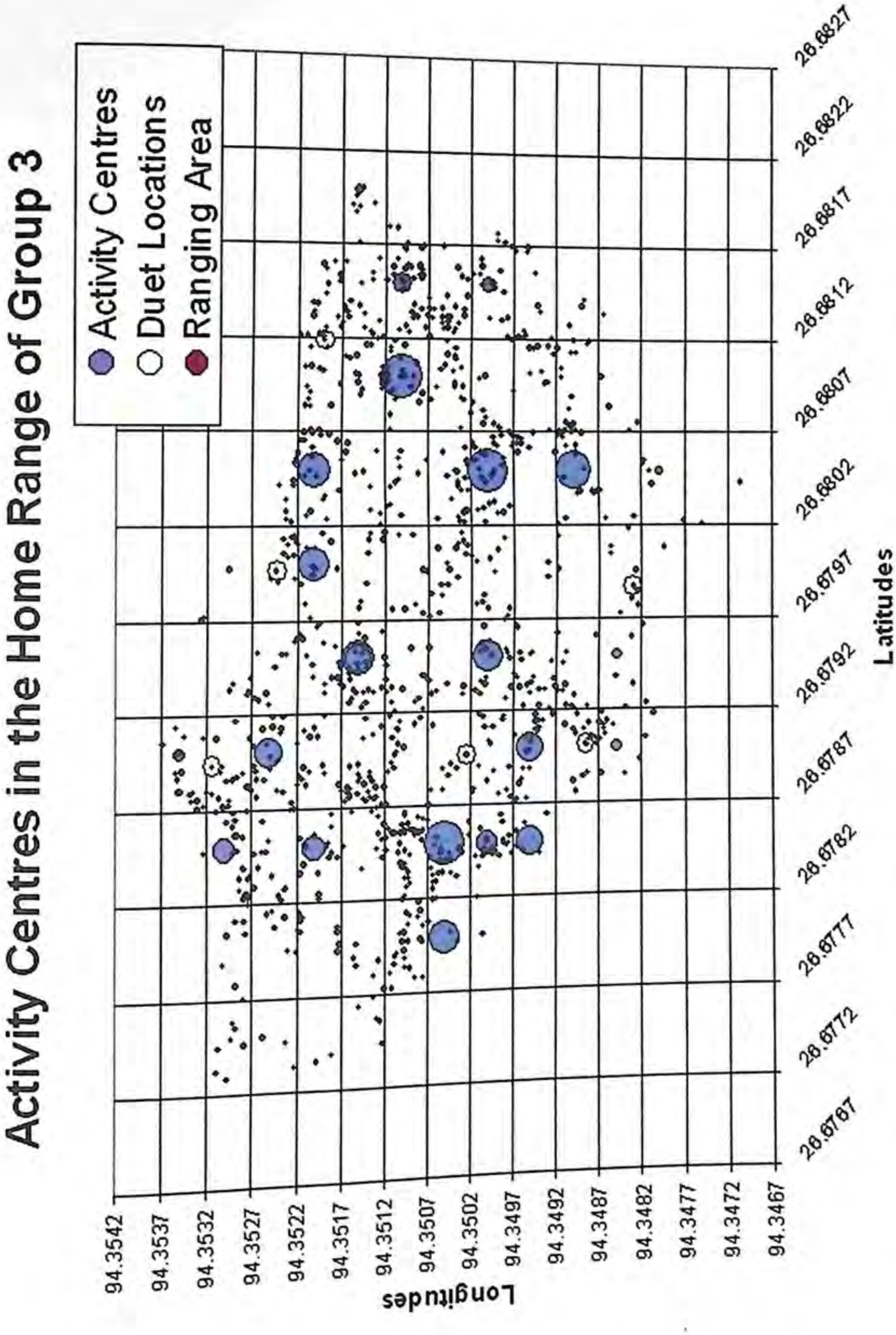


Figure 4.7: Duetting Locations for Group 3



CHAPTER 5

Discussions

5.1 Social Behaviour

The type and availability of food resources has a strong relationship with the activity patterns in primates (Stone 2007), and therefore the proportion of time spent feeding may influence the proportion of time spent resting. The three groups were found to show variable relationships between proportions of the day spent feeding and resting, and no direct or inverse relationship could be discerned. This may be because the habitat or rather the nature of resource distribution in the home ranges of the three groups may be an important mediating factor in their time activity budgets. Allthough the adult pairs of the three groups were found to spend comparable proportions of their activity budget on social activities, the different groups were observed to proportion their social interactions differently. The Proportion of time spent allogrooming decreased with the decrease in the number of group members. Allogrooming has been recognised to be an important means of bonding in social primates (Geissmann & Orgeldinger 2006). Our results suggest that there may be a certain amount of allogrooming time than necessarily has to be devoted to each of the other members of the group in these closely associated groups.

It is noteworthy that although the female of group I was seen to show a negative interest in her relationship with the juvenile, she was observed to spend more time allogrooming the juvenile than vice-versa. However, in the case of group III, although the male showed a highly positive hinde's index toward the adult female, it was he who was observed to allogroom the female more than vice-versa. And again, in the relationships of the adult males & the adult females with the subadults, the hinde's index and relative time spent allogrooming showed variable relationships. These results stress the subtleties of social relationships among these animals, and no single measure of affiliation can fully capture the intricacies of these interactions.

Three instances of feeding aggression directed by the adult male of group I at the sub-adult female of group I were observed. This sub-adult is very near to adulthood, and this suggests that it is possible that she is slowly being ousted by the group. Interestingly, unlike the expected pattern of the same sex adult turning agonistic toward the sub-adult eventually leading to sub-adults dispersal from the group, in this case all the aggression observed was only from the male. This could also explain the extent of disproportion in the sub-adults grooming interactions with the male as it is known in primates for subordinate individuals to groom the dominant individual in order to communicate affiliation.

Grooming in the gibbons in two instances was also observed to serve as a means of reconciliation. These observations were both of group II. In one instance when the sub-adult interrupted the mating of the adults, she was observed to subsequently come to each adult and groomed the individual for a brief period. The other instance was when the female of group two pushed the sub-adult away when attempting to forage on insects in the same tree hollow. She immediately began to groom the sub-adults head and after a very brief period moved away to leave to sub-adult to feed on the insects.

Among the small apes, only siamang males are known to display extensive paternal caretaking behaviour (Clemens et al 2008). The results of the relative frequencies of affiliative interactions between the male and non-adult group member in comparison to female and non-adult group members are suggestive of a certain extent of male care. More over the male was observed to play with the juvenile on numerous occasions, while the frequency for the female-juvenile play interactions was 0. Male care has also been reported from a study of a group of captive lar gibbons (Clemens et al 2008). These results suggest that male involvement in offspring care may be more variable among gibbons than previously believed.

5.2 Duetting Behaviour

5.2.1 Duetting Tree Choice

No species specificity was observed in the choice of tree species as duet locations by the female. The heights of the chosen trees were however always in the range of 25-30m. The taller trees would facilitate better voice transmission. Such selection of the tallest trees in the home range has also been observed in Klosss gibbons (Whitten 1984), Moloch gibbons (Kappeler 1984) and Black crested gibbons (Fan et al 2009). The choice of tall trees as singing sites does suggest that calling is a form of advertisement. However, this could also be a means of reducing predation risk as leopards are a potential predator on gibbons in Gibbon wildlife sanctuary.

5.2.2 Territory and Resource Defence

Duet calls of gibbons could be heard until a distance of 1.5km. The need for loudness in the call suggests that it could function as a means of advertisement. If duetting does indeed serve as a means of territory advertisement, one might expect that groups with larger home ranges may duet more frequently. However, animals also are known to actively patrol their territories as a means of defence. No relation- ship was found during the study between the size of home ranges and frequency of duetting. Nor was any significant difference found in the day range length on days when the study group was observed duetting and days when they were not, as would be expected, if active territory patrolling also takes place. Also no associations were found between feeding centres within the home range and the distribution of duet locations. However, given the loudness of the calls, these animals may not need to actually locate their calls at resource centres. Seasonal variation in call frequency has been demonstrated by previous studies, with frequen- cies peaking during the periods of maximum rainfall. Tropical rainforests which are the primary habitat of these lesser apes are known to vary in their seasonal produc- tivity with it peaking during the wet season. This suggests that the resource defence functionality of duetting cannot be disregarded.

5.2.3 Mate defence, Group cohesion and Pair-bonds

Behavioural observations of inter-group encounters during this study offer some support towards the mate defence hypoth- esis. A previous study on white handed gibbons found strong evidence in favour of this hypothesis (Brockelman et al 1998). In all the 6 inter-group encounters (group II - 2 and group III - 3 occasions) observed during the course of the study, the females were observed to be the first to vocalize, however it was the males and sub-adults who ventured toward the other groups. The females were observed to maintain distance and continuously vocalize, and in one of the four encounters of group III, the pair was observed to call, while group II was observed to call in one out of the two. All the four encounters of group III was with the same neighbouring group consisting of 4 individuals - the adult pair, a sub-adult male and a juvenile, and during one of the encounters only, did the other group call. Group III encountered 2 different groups - one adult pair and another with an adult pair and a sub-adult. In no occasion were both the encountering groups observed to call.

Of a total of 5 duets observed of group I, the sub-adult was never observed to participate. Of the 6 duets observed of group II, the sub-adult was observed to participate only twice, once for 1/6th of the call and the next for 1/10th. This suggests that this behaviour is exclusive to the paired adults. There is a great deal of synchrony between the adults in vocalization, movement and activity state over the entire course of the duet. While movement is 100% synchronized, the average distance between the male and female while duetting for all three groups was approximately 1m. The level of coordination and close spatial association required by this activity does suggest that it may well serve as a means of bonding. Moreover, studies on captive siamangs have found a strong correlation between strength of pair-bonds and frequency of duetting (Geissmann & Orgeldinger 2006). The inter-individual distances, frequency of allogrooming interactions between the pair and frequency of affiliative interactions were taken as measure of bonding. In this study the average inter-individual distances between the paired adults was not compared across groups, as the spatial association of individuals in primate groups in the wild is largely governed by the distribution and abundance of resources. Given that the groups are monogamous, and of differing compositions, such a measure of the strength of the adult male adult female pair bond may not be valid. Primates have highly evolved social cognitive skills and there is a great deal of variation among individuals in their social behaviours. It might therefore be useful to study relationships between the extent of affiliation and the frequency or time spent duetting in the same groups over extended periods of time.

Over the entire sampling period no evidences of calling behaviour from solitary individuals was found. This suggests that pairing is integral to the function served by this behaviour.

On one occasion group III male was observed to range away from the group III female toward a solitary young adult female. After a brief period of time, during which the male and the intruder repeatedly approached and retreated from each other, the group III female began to call. The individuals then called in unison for 1 minute 34 seconds. The call consisted entirely of short broken-barks. The calling stopped when the new female began to move away. The male then chased her for a short distance and returned to the group III female. During this time the group III female was carrying an infant and made no attempt to approach the young adult female intruder.

On another occasion when the male and the sub-adult of group II were ranging away from the female, the female began to vocalize. The male vocalized in response, and this exchange continued for 9 minutes 16 seconds, after which the female began to call. She was over 150 metres away, and the call consisted entirely of short broken barks that were audibly different from the regular duet call. The male and sub-adult immediately responded by calling, with a similar vocalization. This lasted 27 minutes 5 seconds, during which the male and sub-adult were seated at the canopy of a 26m tall tree and called continuously directing their vocalization towards the female. None of the common behaviours such as brachiating or sitting in contact with each other, or any synchronized movement was observed. On termination of the call, the male and sub-adult moved back to the female and joined her at a feeding tree.

Another interesting observation during the study was of a crested serpent eagle (*Spilornis cheela*) attempted to attack the juvenile of group I. The juvenile was observed to urinate, and the other three members of the group immediately began to call in perfect unison and rushed towards him. The call consisted of a single great call which lasted exactly 33 seconds and ended as abruptly as it had begun. All three individuals participated for its entire duration, and huddled with the juvenile who repeatedly broke contact and attempted to move away.

These variations in the context of the behaviour and the corresponding variations in the behaviour suggests that duetting in gibbons is a complex behaviour that could possibly serve more than a single function. Long term studies involving intensive observations of variation in this behaviour among different individuals and populations could throw up interesting revelations about the social lives of these animals and requirement for this behaviour in monogamous social primates.

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APPENDIX A

List of Behaviours

A.1. Activity States that were Instantaneously Sampled

Behaviour Activities

RE = **resting**; period of inactivities, sleeping, basking.

FE = **feeding**; manipulating a food item and bringing it to mouth, foraging (breaking branches or inspecting leaves in search of insects).

R = **ranging**; movement between the trees.
SA = Social activities
OA = Other activities

Social Activities

PL = playing

GR = allogrooming

AG = aggression

SA = sexual activities

VO = vocalisations

OSA = other social activities such as sitting together, sleeping with

Other Activities

OA = other activities, which are not associated with other categories like masturbating, defecating, traveling, autogrooming (grooming self), traveling (walking bipedal, leaping, brachiating, climbing, movement up and down in a single tree)

A.2 List of Social Behaviours that were Focal Animal Sampled

Autogrooming = GR00000

allogrooming = AG

brief grooming = BG

arrive = AR

soliciting grooming = SG

low throaty vocalisation = VO

ho call call = HO

double ho call = H2

triple ho call = H3

quadraple ho call = H4

sit together = ST

come to friendly approach = CM

approach = AP

submissive vocalisation = SQ

lunge without vocalisation = LG

lunge with vocalisation = LV

ignore = IG

push away = PA

cuddle = CD

huddle = HD

touch = TC

nuzzle =NZ

move away = MA

playing = PL

retreat without sb vocalization = RT

retreat with sb vocalization = RV

sexual approach = SA

mount = MT

move away = MA

present = PR

copulate with copulatory thrusts = CT

APPENDIX B

Frequencies of Different Interactions Betwee

Study Animals and Other Group Members

The following table contains the different interactions between study animals and other group members.

	Frequencies of different dyadic interactions between the Male and Female											
	TOTAL	AFF	MAGNF	FAGNM	MRTF	FRTM	MAGF	FAGM	MCMF	MMAF	FCMM	FMAM
Group 3	1.36	0.75	0.04	0.02	0.02	0.02	0.17	0.24	0.36	0.09	0.23	0.41
Group 2	0.46	0.13	0	0	0	0	0.06	0.06	0.15	0.07	0.07	0.21
Group 1	0.46	0.13	0	0	0	0	0.07	0.21	0.06	0.06	0.15	0.07
	TOTAL	AFF	SAGNF	FAGNS	SRTF	FRTS	SAGF	FAGS	FCMS	FMAS	SCMF	SMAF
Group 2	2.16	0.64	0	0.03	0	0	0.72	0.61	0.08	0.08	0.25	0.25
Group 1	51.02	6.12	0	0.03	0	0	18.78	17.14	1.63	5.31	4.08	2.45
	TOTAL	AFF	MAGNS	SAGNM	MRTS	SRTM	MAGS	SAGM	MCMS	MMAS	SCMM	SMAM
Group 2	2.16	0.64	0	0.03	0	0	0.72	0.61	0.08	0.08	0.25	0.25
Group 1	2.1	0.44	0.09	1.1	0.06	0	0	0.09	0.22	0.19	0.25	0.25
	TOTAL	AFF	FAGNJ	JAGNF	FRTJ	JRTF	JAGF	FAGJ	FCMJ	FMAJ	JCMF	JMAF
Group 1	1.41	0.40	0	0	0	0	0.31	0.59	0.03	0.11	0.34	0.11
	TOTAL	AFF	MAGNJ	JAGNM	MRTJ	JRTM	MAGF	MAGJ	MCMJ	MMAJ	JCMM	JMAM
Group 1	2.61	1.63	0	0	0	0	0.53	0.35	0.16	0.13	0.72	0.66

M	Male
F	Female
S	Subadult
J	Juvenile
AFF	Affiliative behaviour
AGN	Agressive Behaviour
RT	Retreat
AG	Allogrooming
CM	Come to
MA	Move away