Chapter 1

Introduction

1.1 Vocal communication in primates

Research on communication in primates has been conducted using field observations and experiments using captive groups. After several decades of studies, we now know that primates may use vision, gestures, hearing, olfaction and touch to transmit to and receive signals from conspecifics or individuals of other species, often as multimodal communication (Leavens, 2003). For example, gorillas combine vocalisations and gesture to communicate (Pika et al., 2003; Poss et al., 2006). Chimpanzees may vocalise and hit tree trunks or shake the branches of trees at the same time (Arcadi et al., 2004). Chimpanzees and orang-utans are known to use facial expressions in addition to vocalisations to express particular emotions (Kaplan & Rogers, 2000; Parr et al., 1999)

A growing number of studies have assessed the content of vocal communication in primates (Arnold et al., 2008; Arnold et al., 2006a; Bezerra et al., 2008; Gros-Louis et al., 2008; Pfefferle et al., 2008). For instance, vocalisations of primates can contain gender information as has been found to be the case across different primate species (*Pongo spp*.: Delgado, 2007; *Papio ursinus*: Ey et al., 2007; *Callithrix jacchus*: Norcross et al., 1993; *Saguinus oedipus*: Weiss et al., 2001). Furthermore, some studies of primate species have shown that vocalisations contain individual signatures (*Hylobates agilis*: Haimoff et al., 1985; Oyakawa et al., 2007; *Callithrix jacchus*: Jones et al., 1993; *Pongo pygmaeus*: Lameira et al., 2008).

Using a new approach in 1975, Waser was one of the first to conduct successful playback experiments in primate research (Marler et al., 1988). These playbacks demonstrated that researchers could not assume functions of vocal communications in primates by only observing their behaviour (Marler et al., 1988). Playback experiments, which have been used in avian studies for decades, allow researchers to determine functions of vocalisations, especially by using edited recording of vocalisations. Using playback in natural conditions, it was possible to determine the functions of vocal communication (Maurus et al., 1988; Snowdon, 1988). Such approaches have been used in recent years to determine the functions of vocalisations in many primate species, including great apes (Crockford et al., 2005; Lameira et al., 2008), New World and Old World monkeys (Ceugniet et al., 2004; Lemasson et al., 2005; Miller et al., 2005; Soltis et al., 2002; Weiss et al., 2001) and lemurs (Fichtel, 2007).

Primates produce vocalisations over a wide range of frequencies and they vary in duration, depending on the environment in which the species lives (Brown et al., 1988). For instance, Savanna primate species tend to retain visual contact with each other and therefore may use vocalisations in combination with other modes of communication, such as visual signals (e.g.

Papio cynocephalus ursinus: Fischer et al., 2004). Forest species can more readily lose sight of each other and, in these cases, vocalisations tend to be the dominant mode of contact (Brown et al., 1988). Vocal communication plays an important role in both great and small apes, since all apes, including gibbons, are forest species, although the ecological factors are clearly not the only reason determining the type of vocal communication.

Some studies have shown that animal vocalisations provide information about objects and events in the environment (Seyfarth et al., 1997). Since vocal communication has been understood as a two-way process, it is important that a) the caller is able to produce vocalisations carrying various types of information and b) the receiver is able to recognise the information that is signalled by the caller by being able to discriminate some particular aspects of either physical acoustic features or different sequences of the vocal elements. Such differences in vocalisations may not need to be extreme if the vocalisation provides a series of parameters between which the receiver can discriminate (Hammerschmidt et al., 1995).

1.1.1 Limitation on gibbon research

Gibbons, the small apes, have generally been studied relatively little even until quite recently, whereas there is a very large body of research literature available on great apes. Studies of great apes has included specific topics, for example, social organization (van Schaik et al., 2003), vocal and non-vocal communication (Crockford et al., 2005; Pika et al., 2003; Pika et al., 2005) and cognition (Tomasello et al., 2004). Geissmann (2002b) took the trouble to count the distribution of papers presented on apes at the Congress of the American Society of Primatologists that was held in 2001 and found that a total of 54 papers were presented on great apes, but none on gibbons. At the International Congress of the Primatological Society in 2008, fifteen studies on small apes were reported, compared to 181 papers on great apes. There may be a number of possible reasons for the dearth of studies on gibbons. One may be the greater number of gibbon species resulting in a wider spread of studies. There are only six species of great apes, including the mountain gorilla (*Gorilla beringei*), lowland gorilla (*Gorilla gorilla*), chimpanzee (*Pan troglodytes*), bonobo (*Pan paniscus*), Sumatran orang-utan (*Pongo abelii*) and Bornean orang-utan (*Pongo pygmaeus*), but there are sixteen classified gibbon species published by IUCN (2008). Moreover, great apes now tend to have a very limited distribution and there are also long-established research sites. Protected areas in South-East Asia tend to be of a more recent date than research sites in Africa where much of the research on great apes has been carried out.

Crested gibbons (genus *Nomascus*), the subject of this study, are currently found in southern China, Cambodia, Laos and Vietnam (Groves 1972; Dao 1983; Ma et al.1988; Geissmann et al. 2000). Due to the historical unstable political situations in some Indochinese countries, researchers have often found it very difficult to obtain permission to conduct research.

Moreover, the species occurring in some countries are listed as critically endangered or endangered (IUCN, 2008) and their small population makes it more difficult for researchers to find and observe them in the wild.

1.2 Vocal behaviour in gibbons

Gibbons are arboreal species and usually stay at canopy heights of around 20-30 m. Consequently, it is difficult for a human observer to see them. It appears that their vocal communication is highly developed as an adaptation to living in this habitat. For instance, when Baldwin & Teleki (1976) discussed lar gibbons taking into account Carpenter's (1940) and Ellefson's (1968) results, they reported at least nine types of main vocalisations. Lan (1993) noted that black-crested gibbons produce two types of alarm calls called "whuit youw" and "e,e". However, all gibbon species, as already mentioned, have an additional important vocal behaviour known as "song" and expressed usually pre-dawn or in the morning (Geissmann, 2002a).

Among these relatively low number of studies done on gibbons, song behaviour is the most common focus of studies on gibbon vocal behaviour, since Carpenter's (1940) pioneering study of lar gibbons (*Hylobates lar*) conducted in northern Thailand. This may be so because song in gibbons is a very special vocal behaviour that is not common in other primates. The song of gibbons consists of a series of long, loud and complex calls, particularly in mated pairs (Haimoff, 1984a; Marshall et al., 1976), where is not common to be observed on other ape species.

Research concerning the vocal behaviour of white-cheeked crested gibbons (*Nomascus leucogenys*) has been sparse. Song organisation and patterns have not been recorded in detail despite the fact that general song phrases have been identified. Those few who have studied vocal behaviour have included song phrases and song organisation but not their function and the studies were conducted in captive groups (Goustard, 1984; Schilling, 1984). Few are studies available on the vocal behaviour of closely related species, such as black-crested gibbons (*Nomascus concolor*) and yellow-cheeked crested gibbons (*Nomascus gabriellae*) in the wild (Lan, 1993; Rawson, 2004) and in captivity (Anderson et al., 2008; Haimoff, 1984b; Merker et al., 1999). The two general studies of wild white-cheeked crested gibbons (*Nomascus leucogenys*) that have been conducted did not include vocal behaviour (Hu et al., 1989; Yang et al., 1988). The exact role and development of song in crested gibbons has, therefore, not previously been fully investigated.

The songs can transmit over long distances, even up to 2 or 3 km (Haimoff et al., 1987; Rawson, 2004). Hence, researchers can use the gibbons' songs to locate them in some habitats where visual contact is difficult. Adult paired gibbons usually sing every day. The song period can last from several minutes to one hour depending on the species (Gittins, 1984a). Although gibbons produce songs nearly every day, several factors can affect their call rate. The rate of singing is affected by the number of neighbours. Gibbons sing less often when they have fewer neighbours and more often when they have more neighbours (Brockelman et al., 1993). The weather is also a factor influencing song. Gibbons may sing less frequently or even not sing at all on rainy days (Gittins, 1984a). Having said this, researchers still tend to disagree on call rates. Gittins (1984a) reviewed different studies and suggested that the average call rate of gibbons is between 0.6-1.9 bouts per group per day, except for the siamangs which has 0.18-0.35 bouts per group per day. However, Jiang & Wang (1997) observed that the average call rate of western black-crested gibbons is only 0.5 bouts per group per day and suggested that western black-crested gibbons may not use song as territorial defence. Yellow-cheeked crested gibbons in Cambodia also showed a low rate of calling (Rawson, 2004). It appealed that calling rate in *Nomascus* species may differ from *Hylobates* species.

Researchers use song for discriminating species (Geissmann, 2002a; Geissmann, 2002c), social behaviour (Gittins, 1984a; MacKinnon et al., 1984) and even for population estimates (Jiang et al., 1999). However, using gibbon song to estimate populations can sometimes be inaccurate if researchers do not understand the effects of factors such as weather, call rate, group size and possible changes in calls in the same individual. Brockelman and Srikosamatara (1993) suggested that larger sample sizes can reduce the bias of singing frequency in gibbons and estimate the population more accurately because the study may thus cover more singing groups. If individual information can be ascertained through gibbon song, population survey may be even more accurate.

1.2.1 Song structure and organization

It has been known for some time that all gibbon species produce species-specific songs (Marshall et al., 1976). The songs have complex structures and differences can be shown to exist across all gibbon species (Geissmann, 2002a; Marshall et al., 1976). However, there are some structural elements that they have in common. For instance, the song of all gibbon species consists of distinct sequences (Geissmann, 1993; Haimoff, 1984a). Haimoff (1984a; 1985) suggested that the general structure of gibbon song can be divided into three parts: 1) the "introductory" sequence, which is produced only once in the beginning of the whole song bout;

2) the “organizing” sequence, which produces the most variable part of the sequence, and 3) the “great-call” sequence, which is produced as a strong, intensive and distinct vocalisation during the whole song.

Geissmann (2002a) found that most gibbon species share some common types of song phrases between males and females during the duet song. This may not be true of crested gibbons as their song is so dimorphic as to have no overlap between call phrases of both sexes when performing their duet song (Geissmann, 2002a). Haimoff (1984a) addressed the concolor group (genus *Nomascus*) which has a different song organization than other gibbon species. They only have male song phrases and female great call phrases contained in the duet song sequence. Schilling (1984) described the possible variations and rules of song phrases in male white-cheeked crested gibbons and suggested that the male song phrases should follow these main rules:

1. The number of “mb-elements” contains of a maximum up to 14 elements within one “mb-element” phrase.
2. The “mc-elements” contain up to six elements within one “mc-element” phrase (whereas Goustard (1984) found that the multi-modulated call phrases may contain one to four elements).

3. The “mc-elements” contain up to six modulations, and the modulation occurs only in the first three elements. Geissmann et al. (2000) suggested that some *N. siki* may modulate only in the second element, whereas the *N. leucogenys* modulated in the second and third elements.

Schilling (1984) also suggested a possible sequence of male song phrases. However, among all theoretically possible sequences, “ma-ma”, “mb-mb”, and “mb-ma” sequences were never found in songs of white-cheeked crested gibbons, as far as observed (Schilling, 1984).

The song phrases of female white-cheeked crested gibbons are also relatively simple. Haimoff (1983) found no pre-great call phrases (phrases preceding great call), as is the case in other gibbon species. However, some incomplete great call phrases [termed “aborted great-calls” by Haimoff, (1983)] were observed as an uncommon event of observed individuals, whereas another study included both great-call phrases and incomplete great call phrases into call phrases [termed “f-elements”by Schilling (1984)]. Since both authors have noted this call phrase, it will be necessary to investigate whether incomplete great call phrases differ from great call phrases.

1.3 Vocal individuality

Individual vocalisations may vary in primates even if when the type or the structure of calls is similar. A caller may produce vocalisations that carry specific information, and the receiver may acquire information that the caller did not intend to send (Seyfarth et al., 2003). An individual's behaviour may, therefore, be affected by the vocalisations it hears. It has been shown repeatedly that it is important for animals to recognise the information conveyed via vocalisations (Insley, 2000; Miller et al., 2006; Wanker et al., 1998; Weiss et al., 2001). The more accurately an individual can process auditory information or "decode" it, the more benefits it can derive from the communication.

One of the important aspects of vocal communication in non-human primates is individual recognition. Since most primate species live in social groups, individuals should benefit from the ability to identify each member within the group or outside of the group (Snowdon, 1986). Snowdon (1986) proposed that primate species should be able to detect individual differences by assessing a number of acoustic parameters. Many studies have investigated individual differences in terms of acoustic structure of vocalisations in a wide range of primate species (*Macaca fuscata*: Ceugniet et al., 2004; *Pongo spp.*: Delgado, 2007; *Papio cynocephalus ursinus*: Fischer et al., 2001; Fischer et al., 2002; *Macaca Sylvanus*: Hammerschmidt et al., 1995; *Callithrix jacchus*: Jones et al., 1993; *Callithrix kuhli*: Jorgensen et al., 1998; *Pan troglodytes*: Mitani et al., 1996; *Lemur catta*: Oda, 2002). All studies that have analysed vocalisations, which is either variable (e.g. dusk calling in *Macaca Sylvanus*) or stereotyped, which defined that the call structure of vocalisations was distinct and had little variation, (e.g., phee calls in *Callithrix jacchus*) have found individual differences (Jones et al., 1993). In other primate species, this question has now been investigated and there is a growing literature documenting individual differences in the vocalisations of primates (Cheyne et al., 2007; Delgado, 2007; Lameira et al., 2008; Oyakawa et al., 2007).

1.3.1 Individual differences in gibbon song

An observation by Tenaza (1976) on Kloss's gibbons (*Hylobates klossii*) suggested that female great call phrases may be individually different. Gittins (1984b) and Haimoff et al. (1985) investigated variations in female great call phrases in agile gibbons (*Hylobates agilis*) found that the female's great-call sequence in agile gibbons contains individual differences, particularly in the introductory notes of the great-call sequence.

In the last decade, the techniques for sound analysis have improved greatly and these changes (also including software programs) make it considerably easier to establish such vocal differences and do so more accurately since early 00's. Several studies on vocal individuality in gibbons have also been published since then. For instance, a study of female Javan gibbons (*Hylobates moloch*), and two studies of agile gibbons have found acoustic differences in the great call phrase of females (Cheyne et al., 2007; Dallmann et al., 2001b; Oyakawa et al., 2007). However, to reiterate, these studies focused exclusively on females, presumably because they produce more distinct vocal features than males in their call phrases. Geissmann et al. (2005) first examined the song of eight male Javan gibbons and found that the order of song phrases and acoustic features of call elements were individually different although, for most of the individuals in this study, only one song was analysed.

However, all these studies concerned only *Hylobates* species. None have shown this in any other genus, such as *Nomascus*. It is unclear if such differences occur in *Nomascus* species at all and, indeed, specifically in white-cheeked crested gibbons, the species studied in the current thesis. Indeed, their vocal structure and organization have been found to be different from *Hylobates* species (Geissmann, 2002a; Haimoff, 1984a; Schilling, 1984). Therefore, it cannot be assumed that such individual differences in vocal behaviour found in *Hylobates* are necessarily applicable to the genus *Nomascus.* The study reported in the current thesis has investigated vocal differences, i.e., individuality (see Chapter 3).

1.4 Vocal development in juveniles and sub-adults

A question is regarding the development of vocalisations between infant and adulthood of an individual. Studies in several species of New World monkeys found that individuals can produce the full range of their species-specific vocal repertoire before they reach adulthood although some particular types of vocalisation, such as loud calls or long calls, were produced only by sexually mature individuals (Snowdon, 1986). For example, studies on common marmosets (*Callithrix jacchus*) and squirrel monkeys (*Saimiri sciureus*) (Hammerschmidt et al., 1995; Pistorio et al., 2006) found that the structure of vocalisations changed through an individual's development. Seyfarth and Cheney (1997) reviewed 34 studies of 14 different primate species and then proposed three general features of vocal communication in primates: 1) Vocal production, defined as an individual delivering a set of acoustic features within vocalisations; 2) vocal usage, defined as specific calls produced and used in certain social or ecological circumstances, and 3) vocal responses, defined as how an individual processes the vocalisations of others. They suggested that, of the three features, vocal production in primates is mostly innate and fixed, vocal usage may be partially fixed and vocal response can be flexible through development. Seyfarth and Cheney's model is used as a useful guide in the current thesis (see Chapter 4).

1.4.1 Song development of juvenile gibbons

Studies on the vocal development of gibbons primarily focused on factors influenced gibbon songs. Early studies observed the vocal patterns of hybrid gibbons compared to the calls of normal gibbons. Some studied noted that the vocal patterns of hybrid individuals in captivity and in the wild are intermediate song patterns between paternal and maternal song (Brockelman et al., 1984a; Geissmann, 1984; Tenaza, 1985). A study of a hybrid siabon (*Hylobates muelleri* x *Symphalangus syndactylus*) showed that this individual gradually changed the usage of song pattern from that of the paternal species to that of the maternal species during the fourth and fifth year (Shafer et al., 1984). Brockelman and Schilling (1984a) also found that the great call pattern of the hybrids could be predicted on the basis the colour of their pelage. They concluded that the song production is under strong genetic control, and not likely to be modified by learning.

However, studies of yellow-cheeked crested gibbons found that juvenile female yellow-cheeked crested gibbons gradually changed their great call phrases to become similar to those of adult females (Anderson et al., 2008; Merker et al., 1999). Thus, an infant or juvenile may produce vocalisations similar to adults with a high level of variability in term of acoustic features and then gradually modify this to become a full adult type of vocalisation. Merker & Cox (1999) concluded that yellow-cheeked crested gibbons might develop their fine song phrases particularly between six to thirty months of age. However, both available case studies concentrated on song development in females only. There is no information regarding the development of male song. Moreover, it is unclear whether such a time-frame proposed by Merker & Cox (1999) for song development can be applied to other gibbon species, but it is also still not known what specific factors may influence the development of gibbon song.

1.5 Vocal plasticity in adults

Primates spend more of their life as adults than they do in any other developmental stage (infants, juveniles and sub-adults). It is necessary to investigate whether their vocalisations have largely crystallised by the time the animals are juveniles or whether some plasticity is retained to adapt changes of social conditions. Seyfarth and Cheney (1997) suggested that some types of vocal production in some primates (e.g., the great calls of gibbons, all calls of Japanese macaques (*Macaca fuscata*), and J-calls in pygmy marmosets (*Callithrix pygmaea*) undergo no modification through vocal development and that evidence of vocal plasticity is very limited in primates, although more evidence to the contrary has come to light. For instance, vocalisations in adult primates may be modified by change of social context as was found in a study of pygmy marmosets, that modified their trill calls after they had been paired (Snowdon et al., 1999). Likewise, Japanese macaques modified their coo calls to match playback coo calls (Sugiura, 1998), and adult female Campbell's monkeys (*Cercopithecus campbelli*) changed acoustic features in their contact calls when the group composition changed (Lemasson et al., 2005).

Although Seyfarth and Cheney (1997) proposed that vocalisations in gibbons remained fixed during development, the evidence supporting their hypothesis is limited to a few *Hylobates* species. Moreover, since more evidence regarding vocal plasticity has been found in other primate species as mentioned previously, it would be premature to assume that no gibbon species modifies its vocalisations. The current studies reported in this thesis investigate whether there is any evidence of adult white-cheeked crested gibbons modifying or changing their vocalisations in structure or patterns if, for instance, they change social status.

1.5.1 Sex-specificity in gibbon song

All gibbon species, except Kloss's gibbons (*Hylobates klossii*), have sex-specific differences in their songs. Geissmann (2002a) pointed out that the song repertoire in gibbons has different levels of overlap. However, the research showing this has not included crested gibbons. Generally, males of all gibbon species produce various types of call phrases in their song, and these song phrases are different in terms of species. Studies that have described the vocal repertoire in songs of crested gibbons (Deputte, 1982; Deputte et al., 1978; Goustard, 1984; Haimoff, 1984a; Haimoff, 1984b; Schilling, 1984) have found three types of call phrases in white-cheeked crested gibbon males. Females have generally fewer types of song phrases, but all females in this genus produce a loud, distinct song phrase, known as “great call” phrase (Deputte et al., 1978; Goustard, 1984; Haimoff, 1984a; Haimoff, 1984b; Schilling, 1984).

Three studies have also noted that both sexes of juvenile crested gibbons often sing female great-call like phrases along with the adult female at the same time when the adult female produces her great call phrases (Geissmann, 2002a; Goustard, 1984; Schilling, 1984). Schilling (1984) even found that one adult male produced female great call phrases when he was moved from his enclosure together with his partner. Another study had also found in female crested gibbons that adult females also produce song phrases of the opposite sex under some circumstances (Chen et al., 2008). The results showed that, although crested gibbons are sex-specific when they produce duet song, they may still retain the ability to produce song phrases of the opposite sex.

1.5.2 Gibbon social structure and its relation to vocal plasticity

In early studies, it was suggested that gibbons were monogamous (Brockelman et al., 1984b; Chivers et al., 1980; Leighton, 1987) and many observations in the wild have found that lar gibbons may maintain their pair bond for a long time (Chivers et al., 1980). Results from studies of song behaviour in *Hylobates* species and siamang (*Symphalangus syndactylus*) have been used as evidence to support the view that gibbons live in monogamous groups and that they use song also to defend their territory (Carpenter 1940; Ellefson 1968; MacKinnon and MacKinnon 1984; Mitani 1987a; Leighton 1987). Fuentes (1998) pointed out that the term "monogamy" in primates generally involves two basic elements: one adult male/one adult female coupling and a long-term pair bonding (Anzenberger, 1992; Wittenberger et al., 1980).

Recent studies, however, have provided more evidence that the social structure of gibbons can be more flexible than once thought. A long-term study of lar gibbons in Khao Yai National Park, Thailand, for instance, found that lar gibbons may not only live in pairs. A social group may consist of introduced males and a family group (Brockelman et al., 1998). A series of studies in south China showed that western black-crested gibbons may form large social groups consisting of one adult male and multiple adult females (Haimoff et al., 1987; Jiang et al., 1999; Jiang et al., 2006; Lan, 1993; Sheeran, 1994). Such complexities in social structure in gibbons may also influence their vocalisations or, at least, correlate with them. Studies reported in the present thesis, therefore, investigated whether adult white-cheeked crested gibbons change their vocalisations in terms of acoustic features or song organisation when social status changes (see Chapter 4).

1.6 Functions of gibbon song

As said before, many studies on gibbons have been concerned with the functions of gibbon song because it is the most distinct and important vocal behaviour in gibbons. There are three potential functions that are recognised: territorial defence, pair bonding and possibly mate attraction, and several authors have addressed all three functions (Geissmann, 1999; Haimoff, 1984b; Leighton, 1987; MacKinnon et al., 1984). Mate attraction, however, is very rarely discussed in gibbon species because it is not easy to demonstrate only by observation, but some playback experiments have been conducted. Mitani's experiments (1984; 1987b) showed that Müller's gibbons (*Hylobates muelleri*) and agile gibbons (*Hylobates agilis*) approached playback songs that were recorded from their conspecific neighbours, but showed no responses to the calls of other species (e.g.: orang-utan vocalisations). Haraway et al. (1988) and Maples et al. (1988) also found that captive Müller's gibbons responded to their own species' song rather than to other gibbon species' song. Although Mitani (1987a) proposed that agile gibbons may not be able to recognise individuals from their songs, Haraway et al. (1988) suggested that Mueller’s gibbons may not initially identify the songs of conspecific neighbours, but may do so after they become aware of their neighbours’ songs (Maples et al., 1988). This suggests that Müller's gibbons may have the ability to learn to identify individual differences through repeated listening. They also found that Müller's gibbons respond preferably to the dawn song than to songs sung during other periods of the day.

These findings suggest that song behaviour is a specific type of social interaction in some gibbon species. However, such experiments have been limited to *Hylobates* species and siamangs (*Symphalangus syndactylus*) only. There are no publications dealing with this aspect of social behaviour in crested gibbons or in white-cheeked crested gibbons. Therefore, it needs to be tested whether white-cheeked crested gibbons show the same behavioural patterns as do *Hylobates* species when they hear another conspecific individual’s songs. This aspect is investigated in this thesis (see Chapter 5).

1.6.1 Territorial defence

Observations in the field have suggested that territorial defence may be a primary function of gibbon song (Brockelman & Srikosamatara, 1984; Mitani, 1987b). Raemaekers & Raemaekers

(1985) describe how adult gibbons approach and make alarm calls or exhibit aggressive behaviour toward the source of the playback. They found that lar gibbons respond to the sound source when it is positioned in the centre of their territory, but not when it is in the borderline of the territory. Gibbons respond to playback by trying to evict an intruder when they hear the songs of stranger or neighbouring conspecifics in their own territory (Raemaekers & Raemaekers, 1985). Another study also observed that gibbons produce duet songs for a longer duration if they have heard another gibbon's duet song previously (Brockelman & Srikosamatara, 1984).

Song in crested gibbons may have a different primary function compared to that of other gibbon species. Gittins (1984b) reviewed different gibbon studies and indicated siamangs which had no conspecifc neighbours produced lower calling rate than other gibbon species. As Gittins (1984b) suggested the observed siamangs produced low singing rate because they may not need to use song to defend their territory. A recent study also found that song of western black-crested gibbons does not elicit song in their neighbours (Fan et al., 2007), whereas a study of white-cheeked crested gibbons in captivity found that a newly introduced female individual may elicit song in another female (Dooley et al., 2007). These various results found in crested gibbons indicated that the further study of primary song function in crested gibbons is needed.

1.6.2. Pair bonding

Several studies using playback experiments have shown that agile gibbons and Muller's gibbons respond to the vocalisation of same-sex individuals (Haraway et al., 1988; Maples et al., 1988; Mitani, 1984; Mitani, 1987b; Raemaekers et al., 1985). In testing their pair bonding, researchers used male solo, female solo and duet song playback presentations to examine the gibbons' responses in captivity and in the wild. Several studies have shown that paired female lar and agile gibbons approach when the playback consists of the songs of a solitary strange female and they then display aggressive behaviour. By contrast, males may approach the solitary female song but then remain silent (Mitani, 1984; Mitani, 1987b; Raemaekers et al., 1985). Mitani (1987b) concluded that the differences between male and female responses show that females maintain the pair-bonding by preventing the opportunities for males to mate with other females. A study in siamang also showed that when siamangs change partners, they produce more incomplete songs at least 20 days after the change of partner (Geissmann, 1999). The degree of integrating duet songs may reflect the strength and duration of the relationship of pairs although there is no direct relationship proven in this study. Another further study of siamangs indicated that the song activity is positively and highly correlated with grooming activity (Geissmann & Orgeldinger, 2000). Hence, siamangs may strengthen their pair-bonding by using song behaviour, as well as social behaviour, or they may express the strength of the bond by vocalisations.

Given above mentioned studies, one may argue whether same primary function of song may apply to all gibbon species. Geissmann and Orgeldinger (2000) also propose that gibbon songs in all species may not serve the same function. For example, in wild western black-crested gibbons, that have a low calling rate, song behaviour was not elicited by neighbouring conspecifics (Fan et al., 2007; Jiang et al., 1997), which indicates that territorial defence may not be the primary function of song in crested gibbons. It is unclear whether vocal behaviour patterns of white-cheeked gibbons have any similarity with those of black-crested gibbons or with other gibbon species in the wild, although Dooley and Judge (2007), after observing the change of singing rate in an adult paired female, suggested that functions of song in white-cheeked crested gibbons may be inter-group spacing and possibly territory defence.

It is not known whether and how white-cheeked crested gibbons maintain their pair bonding. However, playback experiments may be able to shed some light on this question. If the primary function of song in white-cheeked crested gibbons is different from that of *Hylobates* species, the responses to the playback sound samples may differ from the responses observed in *Hylobates* species. The details of the playback response are discussed in Chapter 5.

1.7 Research aims and original contribution of this thesis

The research reported in the current thesis focuses on the vocal behaviour of white-cheeked crested gibbons (*Nomascus leucogenys*). The aim of this thesis is thus to establish details of singing in white-cheeked crested gibbons and to ascertain, as far as possible, the function of song, particularly of duetting, in this endangered gibbon species. Literatures have been proposed possible song structure and rule of song in crested gibbons (Haimoff, 1984a; Schilling, 1984). However, the lack of study in the vocal production and usage of white-cheeked crested gibbons under the social effects may not cover the whole image of white-cheeked crested gibbon song. There is a need to investigate the precise vocal structure and features of song in crested gibbon before assuming that the overall patterns proposed in other gibbon species apply to crested gibbons. The vocal behaviour of crested gibbons has not yet been investigated as the review of the literature in the earlier part of this chapter has revealed. Moreover, with increasing evidence of the function of song behaviour in *Hylobates* and *Symphalangus* species, whether these findings apply to crested gibbons needed the further investigation.

The research reported in this thesis has studied captive white-cheeked crested gibbons in order to answer the following questions:

- Do white-cheeked crested gibbons express vocal individuality within their song?

- Is song in white-cheeked crested gibbons subject to any changes and if so, what factors might be responsible?

- Is territorial defence the primary function of song in white-cheeked crested gibbons, as suggested to be the case in *Hylobates* species?

Previous sections of this chapter have mentioned that gibbon song contains a series of consecutive call phrases. If, as Snowdon (1986) proposed, individuals are able to express vocal individuality to their partner or other conspecifics, individual differences in the song of white-cheeked crested gibbons should also be present. In the current thesis, it is hypothesised that plasticity in the song of white-cheeked crested gibbons may be found in their vocal production or vocal usage of the song. If change of vocal usage can be found in white-cheeked crested gibbons, then it may serve the function of communicating with other members of the group rather than with the members outside of the group because most of tested gibbons have no conspecific neighbours. This is possible because such change of vocal usage affects song production directly by coordinating duet song with the partner or group members. Therefore, if this proves to be the case, song behaviour in white-cheeked crested gibbons serve the primary function in relation to their partner or group members rather than using the song to defend territory.

It is recognised that findings about song function may be limited by studying the gibbons in captivity because of lack of social contacts between conspecific neighbours. It was not possible to determine the detailed social interaction within groups or between groups partly because of housing and partly because most of studied gibbons had no conspecifics with whom they could directly interact. The study reported in the current thesis also used playback to test vocal response to strangers' songs of white-cheeked crested gibbon and other gibbon species gain an insight into song function because playback experiment may be simulated as possible conspecifics to these studied gibbons. This may provide a basic comparison between individuals with and without conspecifics. Despite this limitation, it may at least start to investigate the possible vocal and non-vocal response of the white-cheeked crested gibbons to the playback song. Hence, the basic song function of white-cheeked crested gibbon may begin to be established.

The studies reported in the current thesis provide an insight on vocal individuality may be expressed on so-called "stereotyped" or "fixed" song of adult white-cheeked crested gibbons. It also gains an extended understanding on the development of song in various age groups and what possibly causes these changes. Furthermore, the possible primary song function of white-cheeked crested gibbons is determined in the study of the current thesis.

As vocalisations of white-cheeked crested gibbons and related acoustic analysis from a major part of work in this thesis, Chapter 2 discusses the definition of components of song and related acoustic measurements. Background information of tested individuals and general statistical methods are also discussed in this chapter.

Vocal individuality expressed in the level of duet song phrases, acoustic features and song context was discussed in Chapter 3 Songs of ten adult individuals were recorded and analysed. All possible vocal individuality were analysed in both males and females, separately. This is aimed to determine whether vocal individuality of adult individuals expressed, and if so, what can be identified.

Vocal development in sub-adult and juvenile individuals of white-cheeked crested gibbons is investigated in Chapter 4. Three juveniles and four sub-adults were observed and analysed their vocalisations across three time-points. Vocal plasticity was also observed in four sub-adults and a further three adults when their social conditions were changed in this chapter. This also tested whether vocal development of white-cheeked crested gibbons fit the hypothesis which was suggested by Snowdon (1986) and Seyfarth & Cheney (1997) suggested

Playback experiments on pairs or family groups were presented in Chapter 5. This experiment is aimed to investigate the possible primary song function in white-cheeked crested gibbons. Non-vocal behaviour and vocal behaviour were observed and scored prior to conduct playback experiments. These results provide a baseline for understanding their behaviour when they heard other strangers' song.

Chapter 2

General Methodology

An important part of this research was to make a detailed record of any song from all available (*N. leucogenys*) individuals and pairs held in zoos in Thailand and the rescue centre in Vietnam, and establish the context and development of each song. The captive environment provided a preferable method to conduct this research because white-cheeked crested gibbons are difficult to find and see in their natural habitat. Moreover, in order to test the hypothesis of this thesis it was essential to be able to observe each individual clearly and identify each vocalisation of each individual. By identifying song phrases of each individual, it was hoped to establish precise song patterns of each white-cheeked crested gibbon and, in juveniles, also trace the development of their song patterns. General methods used in all observations and the playback experiment are outlined in this chapter. Other specific methods are described in later chapters as they apply to each experiment.

2.1 Study sites

The site research was conducted between 13th August 2006 and 30th April 2008 and three overseas research visits were arranged (Aug 13th –Nov 8th 2006, Mar 15^{2h} –Jun 21st 2007 and Nov 14th 2007 -Apr 30th 2008). Six different research sites were established including five zoos in Thailand and one rescue centre in Vietnam (Fig. 2.1). Each site except KhaoKheow Open Zoo (2) and Chiangmai Night Safari (5) was visited three times at between three to six months interval in order to record the change on song of juvenile and sub-adult individuals. KhaoKheow Open Zoo and Chiangmai Night Safari were visited twice to collect the song sample and conduct the playback experiment. Each visit lasted 10 to 16 days, depending on the need of experiments.

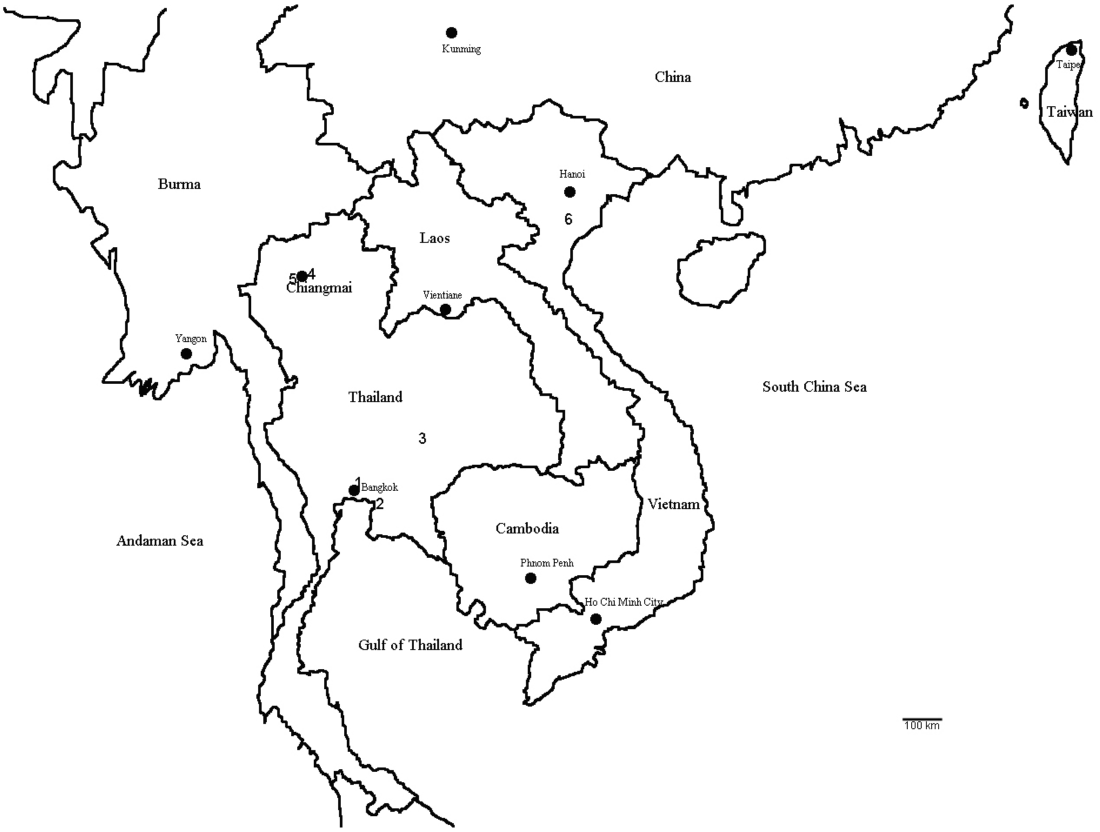

Figure 2.1: Map of South-East Asia and the location of the six research sites. Numbers 1 to 6 represent the location of each site as follows 1: Dusit Zoo, Bangkok (3); 2: KhaoKheow Open Zoo, Chonburi (2); 3: Nakornratchasima Zoo, Nakornrachasima (3); 4: Chiangmai Zoo, Chiangmai (3); 5: Chiangmai Night Safari, Chiangmai (3) and 6: Endangered Primate Rescue Center, Cuc Phong (3). The number in brackets indicated the number of visits to each site.

2.2 Subjects

2.2.1 Sample size and species

Nineteen northern white-cheeked crested gibbons (*N. leucogenys*) (11 Male; 8 Female) were used in the study (Table 2.1) although three females died due to different kinds of accidents before the second site visit. Data collected from these females were still included in the study.

Until recently, it was thought white-cheeked crested gibbons consisted of two sub-species: *N. l. leucogenys* and *N. l. siki*. However, recent studies in *Nomascus* taxonomy suggest that white-cheeked crested gibbons should be recognised as two independent species: the northern white-cheeked crested gibbon (*N. leucogenys*) and the southern white-cheeked crested gibbon (*N. siki*) (IUCN, 2008). Scientists have now also considered that there may be two sub-species of *N. siki* based on studies of vocalisation and mtDNA (Ruppell 2007; Monda et al. 2007). One study has suggested that the two species of white-cheeked crested gibbons may differ in their song repertoire (Geissmann et al., 2000), but this hypothesis has not been proven. Therefore, as far as possible, confounding factors of the subspecies or species were minimised in this study by using only the northern white-cheeked crested gibbons (*N. leucogenys*). Seventeen individuals were identified as belonging to the northern white-cheeked crested gibbons (*N. leucogenys*) by following the species identification guideline (Geissmann, 1995; Mootnick, 2006). Details of species identification of white-cheeked crested gibbons are presented in the Section 2.2.2. Preliminary DNA analysis suggests one of the adult males housed in Vietnam (Endangered

Primate Rescue Center) found differences may not belong to either the *N. siki* or *N. leucogenys* (T. Nadler, personal communication). Some research indicated this kind of individual may be the sister group with *N. leucogenys* although the status needs further study to clarify (Thinh et al., 2010a; Thinh et al., 2010b). Consequently, the total sample size included seventeen *N. leucogenys* and two individuals from sister group of *N. leucogenys*.

2.2.2 Identification of sex and age

Sex identification in adult individuals is straightforward because adult male and female white-cheeked crested gibbons have differently coloured pelages. Males have black fur, except for a white patch on the cheek (Fig. 2.2A), whereas females are uniformly light yellow but have a small patch of black fur on the top of their head (Fig. 2.2B). Females also have very light-yellow to white fur on the face, the so called “face-ring” (Geissmann, 1995; Mootnick, 2006).

Some individuals were rescued after being confiscated and their exact birth date is unknown. However, the age of these individuals could be estimated using the following rule: Newborn infants have a light yellow coat until the end of their first year. Then, fur colour of the male and the female juveniles will change to black, which is similar to that of adult males. Females at maturation change colour to light yellow, whereas the males remain black (Geissmann, 1995;

Geissmann, 2003; Mootnick, 2006). This colour change provides a reliable clue for identifying the age, particularly in the early life stages.

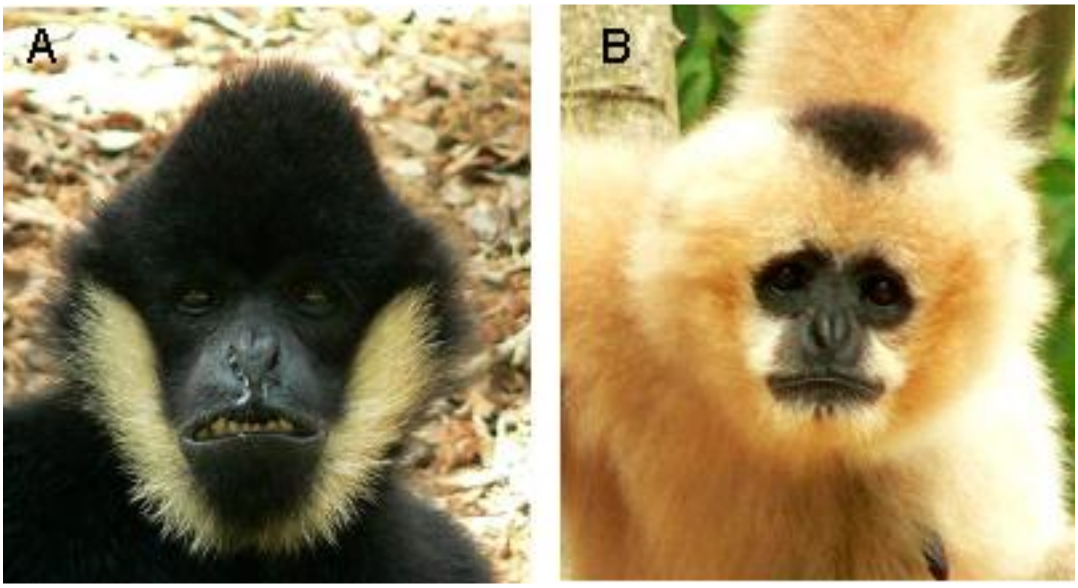

Figure 2.2: The appearance of male and female white-cheeked crested gibbons. A represents an adult male white-cheeked crested gibbon. B represents an adult female white-cheeked crested gibbon.

Table 2.1: Information on study animals. The arrival date refers to the individual's date of birth or the beginning date of its housing in captivity. The location refers to the current location of housing of the pair or family group (i.e. the current location may not be the place where individuals were originally housed). Cage refers to a net cage built with metal tube. The island refers to an enclosure with vegetation were surrounded by a water barrier. The hill refers to a natural hill surrounding by a fence.

Sex	Individual	Age stage	Origin	Location	Housing condition	Enclosure type	Arrival Date	Note
M	M1	Adult	Wild born	Dusit Zoo (Thailand)	Family group (n=3)	Cage	17/02/1985	
M	M2	Adult	Wild born	Night-Safari (Thailand)	Pair	Island	4/3/1995	
M	M3	Adult	Wild born	Endangered Primate Rescue Center (Vietnam)	Family group (n=4)*	Cage	11/10/1994	
M	M4	Adult	Wild born	Nakhonratchasima Zoo (Thailand)	Family group (n=3)	Island	4/3/1995	
M	M5	Adult	Wild born	Chiangmai Zoo (Thailand)	Pair	Cage	2/7/1995	
M	M6	Adult	Wild born	KhaoKheow Open Zoo	Pair	Island	01/03/1993	
M	M7	Sub-adult	Captive born	Dusit Zoo (Thailand)	Family group (n=3)	Cage	10/8/1999	
M	M8	Sub-adult	Wild born	Endangered Primate Rescue Center (Vietnam)	Group	Hill (semi-natural)	11/19/2004	
M	M9	Sub-adult	Wild born	Endangered Primate Rescue Center (Vietnam)	Single	Cage	10/3/2000	
M	M10	Sub-adult	Captive born	Nakhonratchasima Zoo (Thailand)	Family group (n=3)	Island	9/8/1998	
M	M11	Juvenile	Captive born	Endangered Primate Rescue Center (Vietnam)	Family group (n=4)*	Cage	17/12/2002	
F	F1	Adult	Wild born	Dusit Zoo (Thailand)	Family group (n=3)	Cage	17/02/1985	
F	F2	Adult	Wild born	Night-Safari (Thailand)	Pair	Island	4/3/1995	
F	F3	Adult	Wild born	Endangered Primate Rescue Center (Vietnam)	Family group (n=4)*	Cage	18/09/1993	
F	F4	Adult	Wild born	Nakhonratchasima Zoo (Thailand)	Family group (n=3)	Island	4/3/1995	Died on 16 Mar 2007
F	F5	Adult	Wild born	Chiangmai Zoo (Thailand)	Pair	Cage	3/6/1995	
F	F6	Adult	Wild born	KhaoKheow Open Zoo	Pair	Island	1/3/1992	
F	F7	Juvenile	Wild born	Endangered Primate Rescue Center (Vietnam)	Group	Hill (semi-natural)	5/28/2002	Died in August 2007
F	F8	Juvenile	Wild born	Endangered Primate Rescue Center (Vietnam)	Group	Hill (semi-natural)	5/28/2002	Died in August 2007

*: This group contained four individuals including one infant. This infant was excluded from this study as it was difficult to maintain visual contact of the infant when they produce song.

2.3 Housing

The gibbons were housed in different types of enclosures. One type of enclosure is an island-type exhibit (Fig. 2.3). The size of each island varies from 10m x 2m to 10m x 10m (length x width). Vegetation planted on the islands is varied. Some plants were over 15 m high for the gibbons to use. Other gibbons were housed in large cages (8m x 6m x 6m or 10m x 3m x 4m).

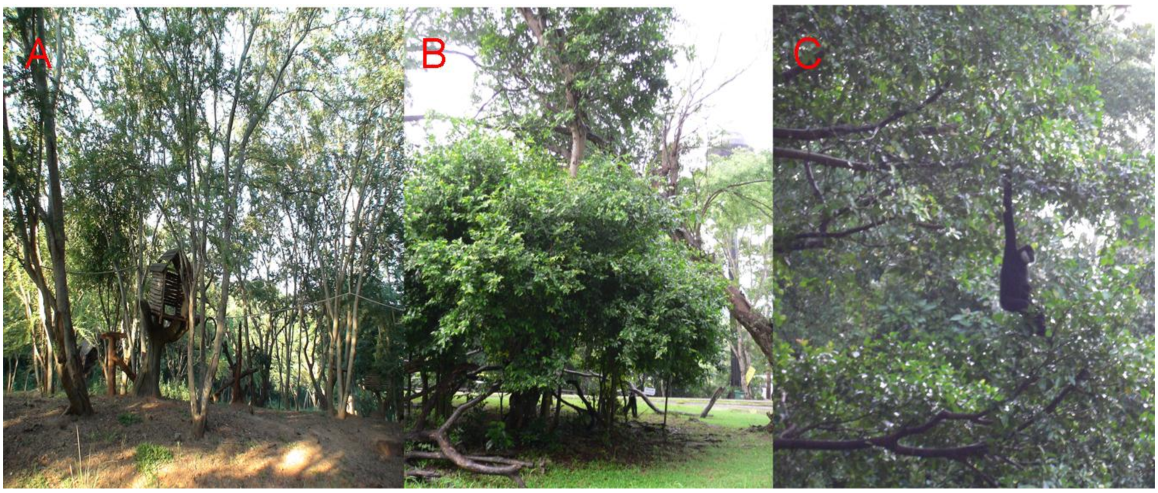

Figure 2.3: The island enclosure of white-cheeked crested gibbons. A and B represent different kinds of island enclosures with various vegetation and structures. C represents an example that how white-cheek crested gibbons use the vegetation in the exhibit.

Housing groups consisted of various numbers of individuals and they had formed different kinds of social groups (Table 2.2). The housing groups were defined as follows:

1) family: a group containing one adult male and one adult female with at least one offspring.

2) pair: a group containing only one adult male and one adult female.

3) solitary: an individual housed alone without any available direct social and physical contact with other conspecifics. However, visual and auditory contacts may still be present for these solitary individuals.

Table 2.2: Group composition of observed individuals.

Housing type	Location	Enclosure type	Adult(s)	Sub-adult(s)	Juvenile
Group 1	Dusit Zoo	Cage	M1, F1	M7	
Group 2	Endangered Primate Rescue Center	Cage	M3, F3		M11
Group 3	Nakhornratchasima Zoo	Island	M4, F4	M10	
Group 4	Endangered Primate Rescue Center	Semi-natural hill		M8, F7, F8	
Pair 1	Night-Safari	Island	M2, F2		
Pair 2	Chiangmai Zoo	Cage	M5, F5		
Pair 3	KhaoKheow Open Zoo	Island	M6, F6		
Individual	Endangered Primate Rescue Centre	Cage		M9	

2.4 Husbandry

All of gibbons used in this study that were observed in captivity and had been housed in an enriched environment for many years. They also had habituated to visitors and general human activities taking place in front of them. The keepers fed the gibbons two to three times a day (varied by the routine in place at each site) by providing various kinds of food, including fruits, leaves, vegetables, boiled eggs and mineral supplements.

Annual physical examinations were conducted routinely by veterinarians. If a gibbon suffered from an illness, a veterinarian administered medical treatment or removed it from its housing area to the animal hospital for further diagnosis. The adult female housed in KhaoKheow Open

Zoo suffered an injury in October 2006 and was moved to the animal hospital for three months before she returned to the enclosure. The adult male and female housed in Nakhornratchasima Zoo contracted pneumonia in March 2007. The male returned to the enclosure from the animal hospital after he recovered. The female, however, died.

2.5 Data collection

Initially, it was important to collect song samples from all individuals used in this study. A song bout is defined as one continuous set of vocalisations and it ends when singing stops for more than 5 minutes. A total of 178 song bouts were collected, including solo song (n= 96) and duet song (n= 82). The number of songs collected from each individual ranged from 3 to 18 songs. Details of songs recorded, analysed and presented in each chapter are listed in the Appendix. All vocal recordings were taken from 0500h to 1100h on each day of observation because several studies of crested gibbons also suggested that they are more likely to produce their song before dawn to early morning (Geissmann, 2002a; Lan, 1989; Rawson, 2004). All procedures of data collection were approved by the Animal Ethics committee at the University of New England (AEC06/118 and AEC07/125) with the accompanying research permission issued by Zoological Park Organization of Thailand, Chiangmai Night Safari and Endangered Primate Rescue Centre.

2.5.1 Vocalisation recording

A directional microphone (Sennheisser ME-66) and a digital recorder (Marantz PMD-670) were used to record the songs. Recording distances between equipment and subjects ranged from two metres when the animals were in a cage to 25 metres when they were in island or semi-natural enclosures. All animals did not demonstrate a response to the presence of the equipment and the observer as they have been housed in the enclosures for a long time and were habituated to the presence of visitors.

2.5.2 Vocalisation analysis

All recordings were digitised in 16-bit quantization and 44.1kHz sampling rate. Sound analysis software (Raven Pro 1.3, Lab of Ornithology, and Cornell University) was used to analyse the song samples to visualise the sound. The sonograms were computed by Fast-Fourier-Transformation (FFT) and a window was configured to display the spectrum in the following setting (Window size: 2048 samples with Hamming function; 3dB filter bandwidth: 30.5Hz; frequency resolutions: 2048 sample with 23.4Hz grid spacing; Time resolution: 512 samples with overlap 75 %). The terms used to describe the gibbon song in this study followed the definition by Haimoff (1984a). A *song bout* was defined as a series of consecutive call phrases with an identified sequence, and this sequence may last several minutes and can be either *duet song*, which defined as a song produced together by a pair or two mated individuals in the family group or *solo song* that produced a single individual with no mated partner. The length of each song bout was at least five minutes. If the individual stops producing any single call phrase longer than five minutes from its last call phrase, this was treated as a single song bout. A *note* refers as the single continuous sound made within an inhaled or exhaled breath (Fig 2.4A). A *phrase* refers a collection of notes identified as a single vocal activity (Fig 2.4B-C).

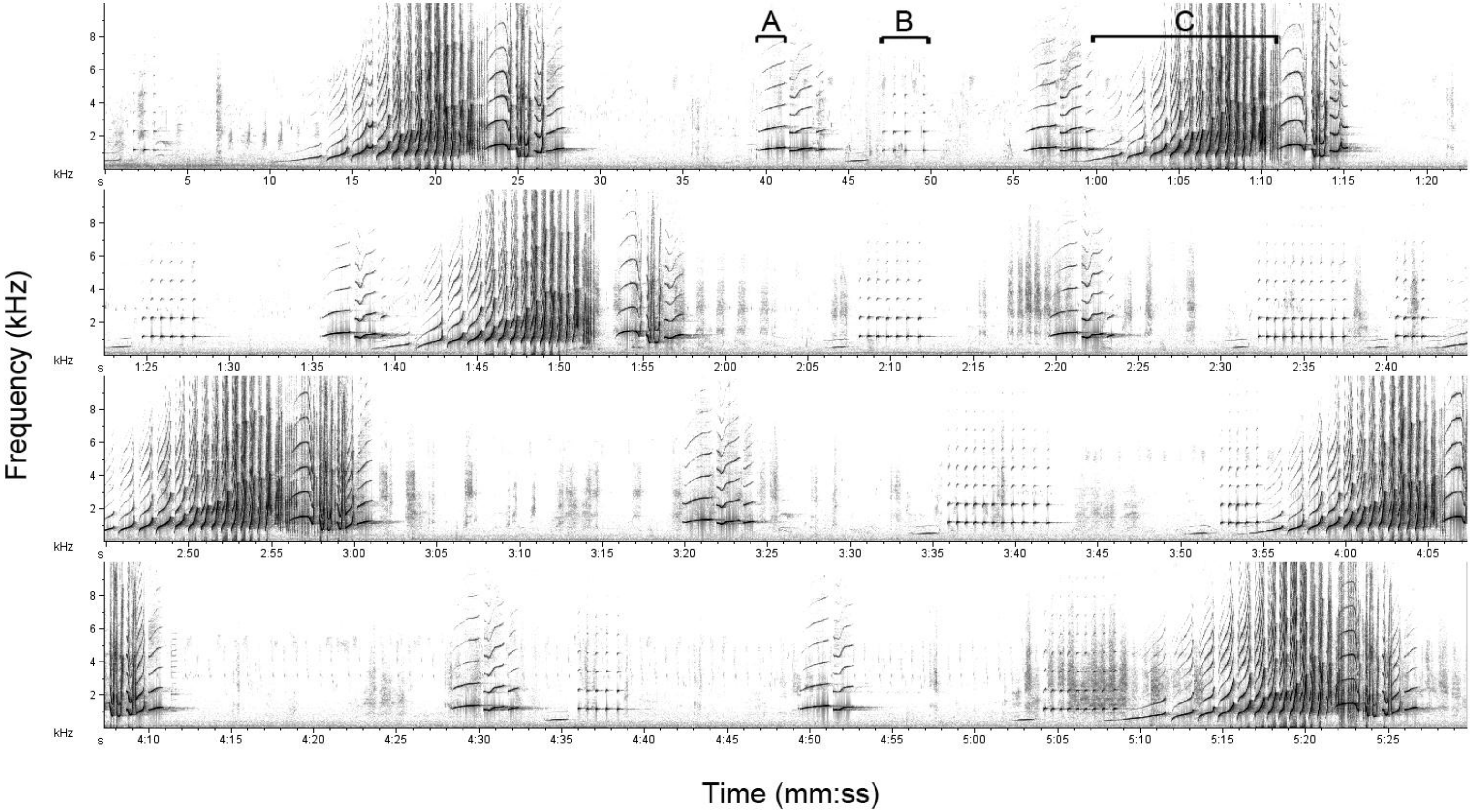

Figure 2.4: The sonogram of a complete duet song sung by a pair of white-cheeked crested gibbons. A represents a single note. B and C represent an example of male and female call phrases, respectively. All vocalisation recorded with visual identification of singers in this study.

2.5.2.1 Analysis of vocalisations made by males

Three types of song phrases were identified in males as follows:

1) Boom call phrases (Haimoff, 1984b) [or “ma-elements”, as lebelled by Schilling (1984)], consisting of a single note with a duration of 1.0-1.5 seconds and a fundamental frequency of approximately 600 Hz (see A in Fig. 2.5).

2) Staccato call phrases (Geissmann et al., 2000), [also termed “mb-elements” by Schilling (1984) or “aa” notes by Haimoff (1984b)], contain several short notes, each ranging 0.2-0.3 seconds with a frequency ranging 1.0 - 1.3 kHz (see B in Fig. 2.5).

3) Multi-modulated call phrases (Haimoff, 1984b) [or “mc-elements” as lebelled by (Schilling, 1984)], containing a series of notes of long duration (0.3-1.5 each) (see C in Fig. 2.5). These notes may have up to six modulations. These modulations can rise up to 4 kHz.

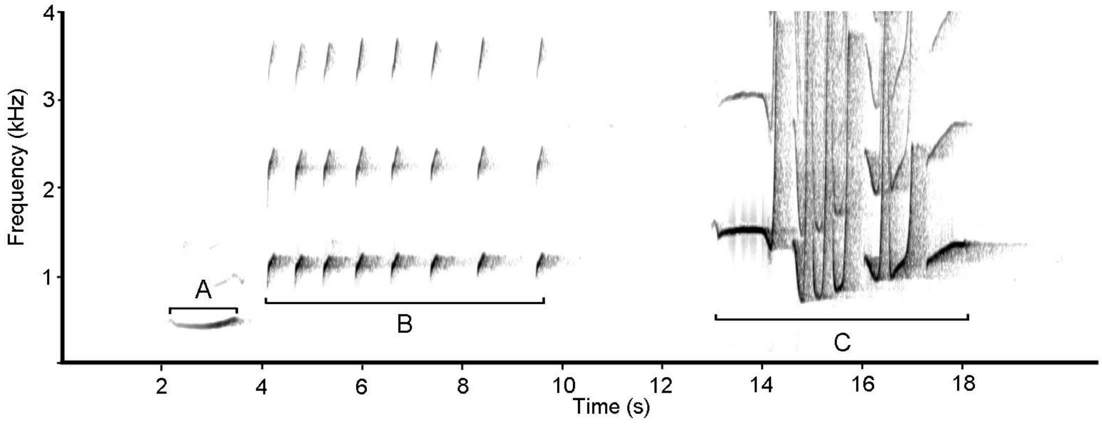

Figure 2.5: The examples of song phrases in male white-cheeked crested gibbons recorded in this study. (A) – (C) represents boom call phrases, staccato call phrases and multi-modulated call phrases, respectively.

Three feature measurements were used to identify boom call phrases (Fig. 2.6A) and staccato call phrases (Fig 2.6B) because these two call phrases have a very distinct structure. The measures were a) start frequency, b) peak frequency, and c) duration.

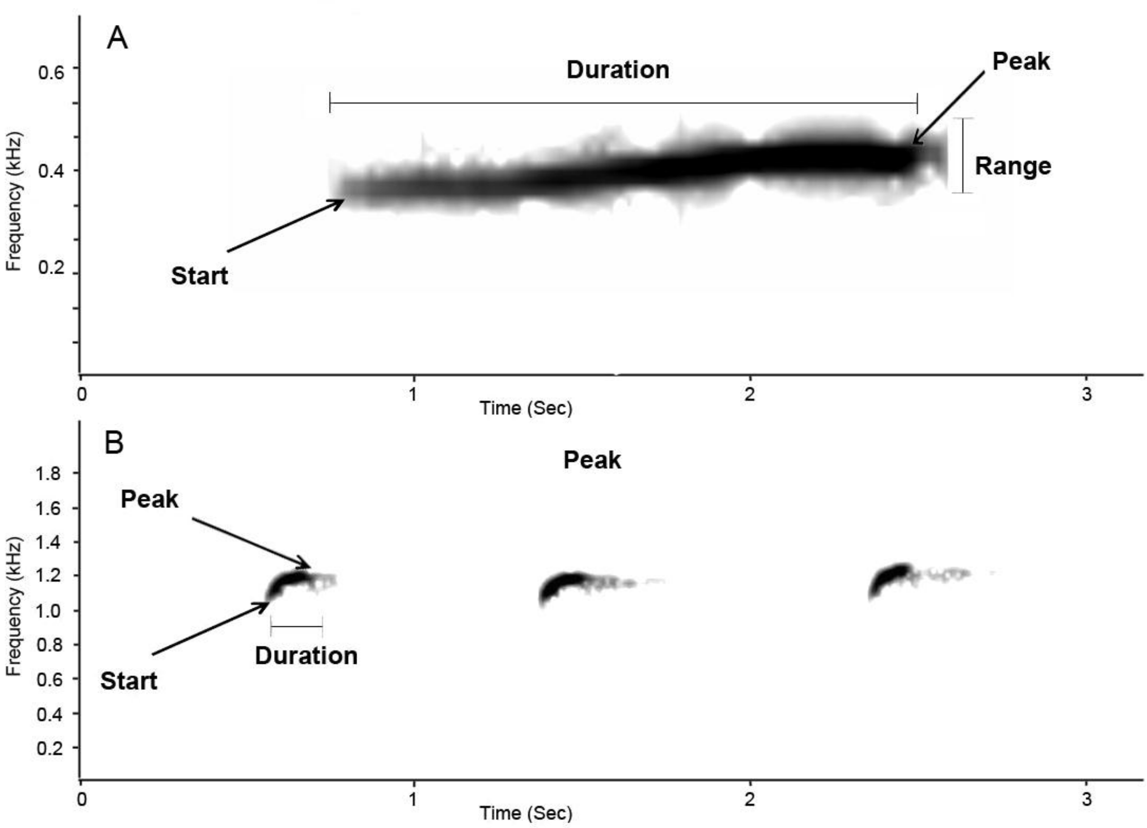

Figure 2.6: The acoustic measurements made of boom call (A) and staccato call phrases (B). Arrows point where the frequency was measured and the horizontal line represents the duration measure. The sonogram presented here are only the fundamental frequency of the phrases.

Multi-modulated call phrases were further sub-categorised in this study as suggested by Schilling (1984) described the possible variations and rules of song phrases in male white-cheeked crested gibbons and suggested that the male song phrases should follow these main rules: the physical characteristics of multi-modulated call phrases can be very different one from another. Schilling (1984) had observed suggested that captive white-cheeked crested gibbons have a maximum number of modulations is six within one multi-modulated call phrase. In order to explore whether there are any differences in these multi-modulated call phrases, the multi-modulated call phrases were sub-catalogued according to the number of modulated and the number of notes contained within one call phrases.

Each multi-modulated call phrase contains one to six notes as mentioned in the previous paragraph. In order to standardise measurement, only the first note of each multi-modulated call phrase was analysed (Fig. 2.7). All parameters were only measured on the fundamental frequency, which is the lowest frequency of a periodic waveform and majority of the energy source of vocalisations. Analysis of call notes was thus conducted according to several criteria:

1) The *start frequency* was defined as the start frequency of the call note. The peak frequency of the first note was not measured because frequency of this call note increased rapidly and frequency may not able to be measured precisely. It is thus not a reliable measure (Ruppell, 2007b).

2) The *lowest* frequency was defined as the lowest frequency point of this call note.

3) The *call duration*: defined as the duration between start frequency and lowest frequency. Further classification criteria of multi-modulated call phrase are described in Chapter 3.

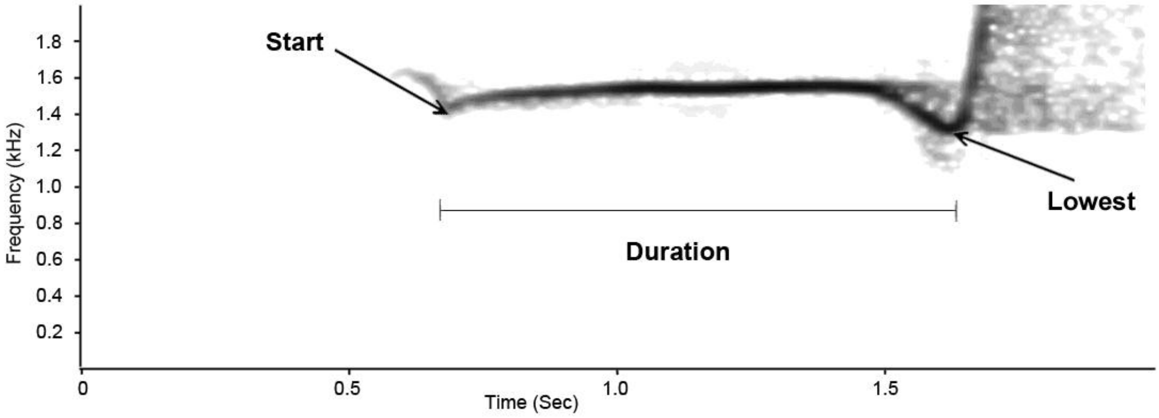

Figure 2.7: The acoustic measurements in the first note of multi-modulated call phrases. Arrows point to the frequency measure and the horizontal line represents the duration measure. The sonogram here only represents the fundamental frequency of the call note.

2.5.2.2 Analysis of vocalisations made by females

Great call phrases began with a note of long duration (up to 2.5 seconds) and a low start frequency which also defined as utter notes (350-600 Hz), followed by varying numbers of barking notes, terminating with one or more twitter (or trill) notes (Fig. 2.8) (Goustard, 1984; Schilling, 1984).

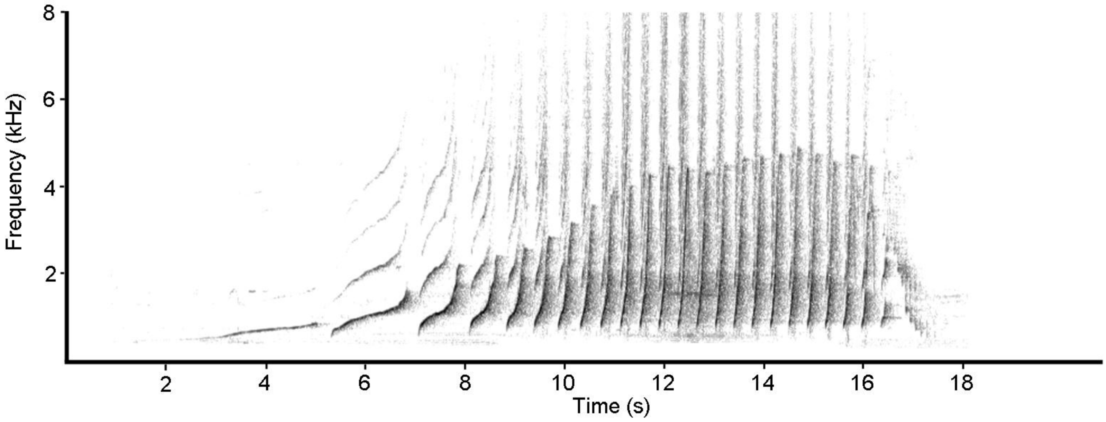

Figure 2.8: An example of a great call phrase in female white-cheeked crested gibbons.

Because the number of notes within each great call phrases varied, only the first note of each great call phrase was analysed. The start frequency, peak frequency and the duration of the first note of great call phrases were all measured (Fig. 2.9).

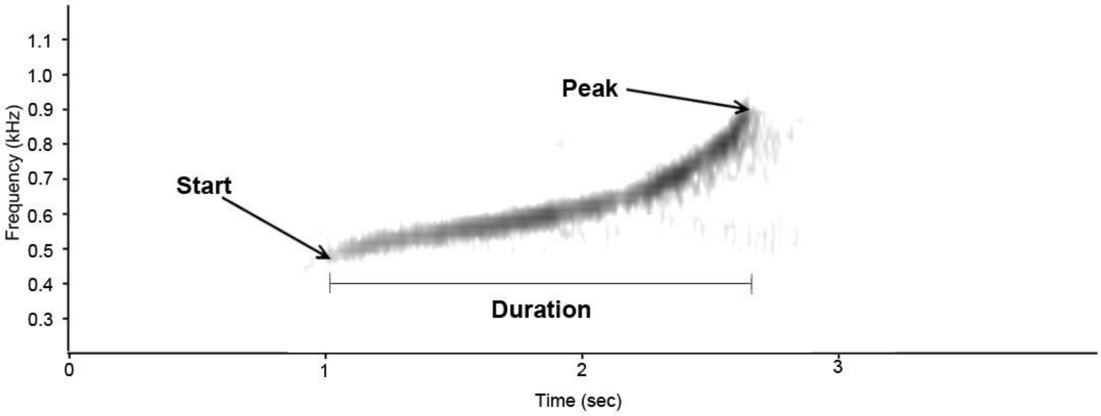

Figure 2.9: An example of first note of female great call phrase. The sonogram here only represents the fundamental frequency of the call note.

2.6 Statistics

For all measured data, the Shapiro-Wilk test was used to check the normality before any analyses were conducted (significant level was set at .05). Data that were not normally distributed were transformed by using log transformation with the aim of attempting to achieve normality before any hypothesis testing analyses were conducted. Data were usually analysed using the general method of analysis of variance (One-way, repeated-measures ANOVA). If the transformed data were still not normally distribution, one of a selection of non-parametric tests (Friedman test, Cochran’s Q test, Wilcoxon signed rank test and McNemar test) was employed in the analysis. Unless otherwise stated, all tests were two-tailed.

One-way, repeated-measures ANOVA was used in a number of instances to test for differences in relation to age groups or social context across different sampling periods. This form of analysis was also applied to determine whether or not acoustic features changed during development of an individual's song.

Multivariate analysis in the form of discriminant function analysis was used to test the individual differences in acoustic features of various songs. Further detail regarding the use of this statistical method is given in Chapter 3. Other tests applied to specific results will be described separately in the methods section of each chapter. All analyses were conducted using either SPSS 16.0 SPSS Inc. (SPSS, 1999) or Minitab version 13.1 (McKenzie et al., 1999).

Chapter 3

Vocal Individuality in White-cheeked Crested Gibbons (*Nomascus leucogenys*)

3.1 Introduction

Studies of several species of gibbons have found that *Hylobates* song repertoire contains a high degree of variability (Baldwin et al., 1976; Dallmann et al., 2001a; Gittins, 1984b; Mitani et al., 1989), whereas the song of crested gibbon species (genus *Nomascus*), has been reported to be less variety (Goustard, 1984; Haimoff, 1984b; Schilling, 1984). If the song of crested gibbons does not have any intra-species variations, or individuality (i.e., if there are no individual differences), crested gibbons would have difficulties in distinguishing one individual from another through song. It would be a surprise if that such an important function, especially in a visually restricted environment, would have been lost in crested gibbons but retained in other gibbon species (*Hylobates*). It is possible, however, that crested gibbons may use relatively stereotyped song phrases but show some individuality among different aspects of song, as has been suggested in *Hylobates agilis* (Haimoff et al., 1985; Oyakawa et al., 2007) and *H. mooloch* (Dallmann et al., 2001b; Geissmann et al., 2005). Schilling (1984) noted that none of male adults in the study produced same types of multi-modulated call phrases. These call phrases were different in the types and number of notes within call phrases, which may be sub-categorised. Various sub-categorised types of multi-modulated call phrases may be individually different in males although the call structure of call phrases was relatively distinct.

This kind of variation of patterns in the male call phrases has also been found in Kloss's gibbons (*H. klossii*), which produce individually different call phrases by using a number of "wa", "oo-was" and "trill" notes, as they are termed by Haimoff (1983) and Tenaza (1976). Therefore, the similar kind of vocal individuality may be found in white-cheeked crested gibbons.

Most studies that investigated vocal individuality in gibbons were restricted to female gibbons (Dallmann et al., 2001b; Haimoff et al., 1985; Oyakawa et al., 2007). There is only one study that has investigated male gibbons, though only one song bout was collected from the tested animals (Geissmann et al., 2005). As mentioned before, the call phrases of *Nomascus* species are more stereotyped compared to other gibbon species. It is possible to assess individual acoustic features of both sexes on white-cheeked crested gibbons.

Several questions need to be answered in order to address song individuality in white-cheek crested gibbons. If individuality is expressed, can it be identified in both male and female gibbons? If it can, are there any consistent and recognisable individual phrases in song of adult white-cheeked crested gibbon pair? Moreover, does vocal individuality only express on their call structure or even the usage of their call phrases in song?

The current study was aimed to investigate whether vocal individuality of white-cheeked crested gibbons can be identified on the both sexes. Moreover, call structure and usage of call phrases in the song were also be analysed to identify individual differences of white-cheeked crested gibbons.

3.2 Method

3.2.1 Subjects

Ten adult white-cheeked crested gibbons (*N. leucogenys*) (five males and five females) were housed as pairs in captive environments in Thailand and Vietnam (Table 3.1). All individuals were originally taken from the wild and had been housed in the current enclosures for at least four years. The exact age of these individuals was unknown. According to the record of the arrival date of each individual, the minimum age of these individuals was 13 years old and the maximum age would have been up to 25 years old.

Table 3.1: Information about the five observed pairs. The arrival date is listed here as the first day when the individual was housed in captivity. The location refers to the current location of housing of the pair or family group. (i.e. the current location may not be the place in which individuals were originally housed).

Pair	Individual	Location	Enclosure type	Arrival Date
1	M1	Dusit Zoo (Thailand)	Cage	17/02/1985
	F1	Dusit Zoo (Thailand)	Cage	17/02/1985
2	M2	Night-Safari (Thailand)	Island	4/03/1995
	F2	Night-Safari (Thailand)	Island	4/03/1995
3	M3	Endangered Primate Rescue Center (Vietnam)	Cage	11/10/1994
	F3	Endangered Primate Rescue Center (Vietnam)	Cage	18/09/1993
4	M4	Nakhonratchasima Zoo (Thailand)	Island	4/03/1995
	F4	Nakhonratchasima Zoo (Thailand)	Island	4/03/1995
5	M5	Chiangmai Zoo (Thailand)	Cage	2/07/1995
	F5	Chiangmai Zoo (Thailand)	Cage	3/06/1905

3.2.2 Procedures

This study was conducted in Thailand and Vietnam between 22nd August, 2006 and 25th April 2008 by visiting each of the five study sites two to three times (Table 3.2). For each individual, the aim was to collect a total of ten song bouts per pair over all visits combined. Note that there was one pair for which only nine duet songs could be collected owing to the death of the female. All sound recordings were taken from 0500h to 1100h on every observation day.

Table 3.2: The visit period and days for collecting duet song bouts in the pair of white-cheeked crested gibbons

Country	Study site	Visiting period	Total visiting Days
Thailand	Dusit Zoo (Bangkok)	Oct 2006, Apr 2007	14
Thailand	Night-Safari (Chiangmai)	Apr 2007, Dec 2007	17
Vietnam	EPRC (Cuc phong)	Jun 2007, Jan 2008, Apr 2008	24
Thailand	Nakhornratchasima Zoo (Nakhornratchasima)	Oct 2006, May 2007	10
Thailand	Chiangmai Zoo (Chiangmai)	Nov 2007, Mar 2008	24

* The female died on 16th March 2007, which occurred prior to my second field trip.

3.2.3 Sound analysis

Male white-cheeked crested gibbons modulate up to the first four elements of their multi-modulated call phrases. The criteria used to define the sub-catalogued multi-modulated call phrases were based on the number of modulations and the location of modulation in each element of multi-modulated call phrases. Twelve types of multi-modulated call phrases were identified and catalogued based on the number of modulation in each multi-modulated call phrase (Fig 3.1). Further description of each sub-catalogued types of multi-modulated call phrases was listed in Table 3.3. Note that type A call phrases classified in this study showed no modulation within any notes. Early studies termed this as the "long call" (Deputte, 1982) or "mc-element" (Schilling, 1984). Recent studies have suggested these un-modulated call phrases are precursors of modulated call phrases (Geissmann et al., 2000; Ruppell, 2007b). One of the authors of this study suggested these un-modulated call phrases should still be termed as multi-modulated call phrases (Geissmann, personal communication). Therefore, type A call phrases were included as part of multi-modulated call phrases.

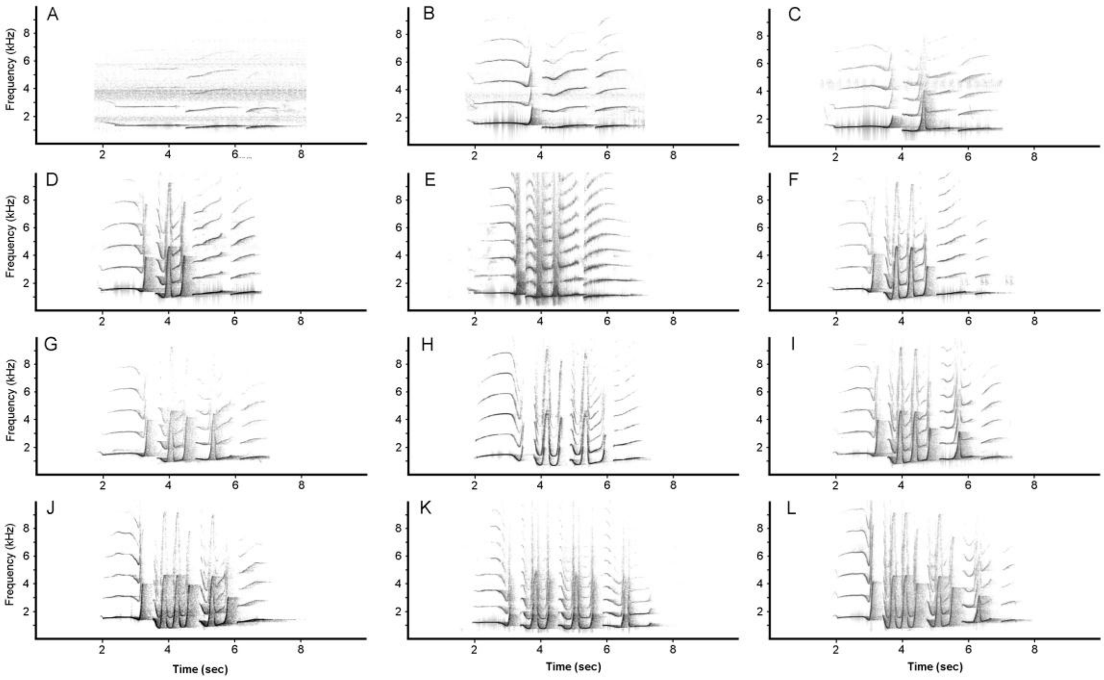

Figure 3.1: The sonogram of twelve types of sub-catalogued multi-modulated call phrases in male white-cheeked crested gibbons.

Table 3.3: The subcategories multi-modulated call phrases in male white-cheeked crested gibbons. The number of total modulation in one multi-modulated call phrase represents the number of times that male white-cheeked crested gibbons modulated the note up and down. If the white-cheeked crested gibbons modulated the note both up and down, it was counted as one episode of modulation. If the individual modulated any of the notes only up or down, it was counted as half of a modulation.

Type	Total Number of modulation in one multi-modulated call phrase	Number of modulations in each note			
		First	Second	Third	Fourth
A	0	0	0	0	0
B	1	1	0	0	0
C	2.5	1	1.5	0	0
D	3	1	2	0	0
E	3.5	1	2.5	0	0
F	4	1	3	0	0
G	4.5	1	2	1.5	0
H	5	1	2	2	0
I	5.5	1	3	1.5	0
J	6	1	3	2	0
K	6.5	1	2	2	1.5
L	7.5	1	3	2	1.5

The organization and structure of song including the number of call phrases produced by each individual, the duration of each song sequence and calling rate were analysed. Other physical structures of each of the call phrases were also analysed. The details and description of selected variables were listed in Table 3.4. To clarify differences between individuals of both sexes, the duet song was divided into male and female phrases.

Table 3.4: The description of variables of general song structure and acoustic features measured.

Type	Subject	Variable No.	Code	Description
General structure	Pair	1	DP	Total duration of duet song
		2	NP	Total number of call phrases produced in a duet song
		3	RP	The calling rate of call phrases in a duet song. It defined as number of call phrases produce per minute
		4	DF	Total duration of female song phrases. This period is defined as the time between the first note of first call phrase and the final call note of the last call phrase.
	Female	5	NF	The number of total call phrases produced by a female in a duet song
		6	NGF	Total number of great call phrases produced by a female in a duet song
		7	NNF	Total number of non-great call phrases produced by a female in a duet song
		8	RF	The calling rate of call phrases in a duet song. It defined as number of call phrases produce per minute within female song duration
	Male	9	DM	Total duration of male song phrases. This period is defined as the time between the first note of first call phrase and the final call note of the last call phrase.
		10	NM	Total number of call phrases produced by a male in a duet song
		11	RM	The calling rate of call phrases in a duet song. It defined as number of call phrases produce per minute within male song duration
		12	NMM	The number of total multi-modulated call phrases produced by a male in a duet song
		13	NBM	The number of total boom call phrases produced by a male in a duet song
		14	NSM	The number of total staccato call phrases produced by a male in a duet song
Specific Acoustic features	Female	15	SNGF	Start frequency of first note in non-great call phrases
		16	PNGF	Peak frequency of first note in non-great call phrases
		17	DNGF	Duration of first note in non-great call phrases
		18	SGF	Start frequency of first note in great call phrases
		19	PGF	Peak frequency of first note in great call phrases
		20	DGF	Duration of first note in great call phrases
	Male	21	SMM	Start frequency of first note of multi-modulated call phrases
		22	LMM	Lowest frequency of first note of multi-modulated call phrases
		23	DMM	Duration of first note of multi-modulated call phrases
		24	SBM	Start frequency of boom call phrases
		25	PBM	Peak frequency of boom call phrases
		26	DBM	Duration of boom call phrases
		27	SSM	Start frequency of first note of staccato call phrases
		28	PSM	Peak frequency of first note of staccato call phrases
		29	DSM	Duration of first note of staccato call phrases

3.2.4 Statistical analysis

For all measured data, the Shapiro-Wilk test was used to check normality (level at .05) before any analyses were conducted. Percentage data was root-arcsine transformed before analysis was conducted.

All tests used in this study were two-tailed. A one-way variance analysis (ANOVA) on transformed or raw data with repeated measures was applied to assess the pair and individual differences in terms of duration, total call phrases and call phrase rate in each pair and in each individual. Because the number of great call and non-great call phrases recorded was different for each individual, the mean of each measurement was used for each type of phrase to weight it equally. The mean of start, peak frequency and duration in each individual was used to carry out ANOVA to explore any differences between these two types of call phrases in females. A Kurskal-Wallis test was used instead of ANOVA if a set of data is not normally distributed after data transformation had been performed. Pearson correlation was also used to investigate the associations between the duration of song, the number of call phrases, and the calling rate in pairs, females and males, respectively.

Multivariate analysis (MANOVA) was used to test whether or not there were individual differences among acoustical features. Discriminant function analysis (DFA) was applied to examine which acoustic factors most contributed to the ability to identify individuals within male and female groups (Manly, 1986). Only the first 100 cases of each variable of each male were selected in order to standardise variables. In females, only the acoustic features in great call phrases were used to run DFA because the number of cases of non-great call acoustic features did not reach the minimum requirement of DFA design. ANOVA was conducted using Minitab version 13.1 (McKenzie & Goldman, 1999). The rest of analysis was conducted using SPSS 16.0 (SPSS Inc., 1999).

3.3 Results

3.3.1 General description of song phrases

Forty-nine completed song bouts were collected from the five groups of adult white-cheeked crested gibbons. A total of 4,382 call phrases were obtained. Each individual produced various numbers of call phrases (Table 3.5).

Table 3.5: The number of call phrases that were collected and analysed by each individual. Each column refers to each type of call phrases produced by males or females. The number of non-great call phrases refers to one-note or incomplete great call phrases (number of notes is < 5 and no twitter note contained). The types of call phrases produced by white-cheeked crested gibbons are sex-specific in duet song.

Sex	Location	No. of Multi-modulated call phrases	No. of Boom call phrases	No. of staccato call phrases	No. of Great call phrases	No. of Non-great call phrases	Total
Male	Dusit	352	221	189			762
	EPRC	332	185	192			709
	Safari	339	228	212			779
	Chiangmai	267	119	128			514
	Korat	400	258	193			851
Female	Dusit				71	173	244
	EPRC				64	22	86
	Safari				143	8	151
	Chiangmai				59	67	126
	Korat				38	122	160
Total		1690	1011	914	375	392	4382

3.3.1.1 Duration of duet song in pairs

The duration of duet song produced by each pair was ranged from 524.10 ± 25.34 to 873 ± 50.72 seconds. The length of song was stable within a pair but different among pairs (Duration: $F_{(4,34)}$= 20.50, p<0.001; Fig 3.2).

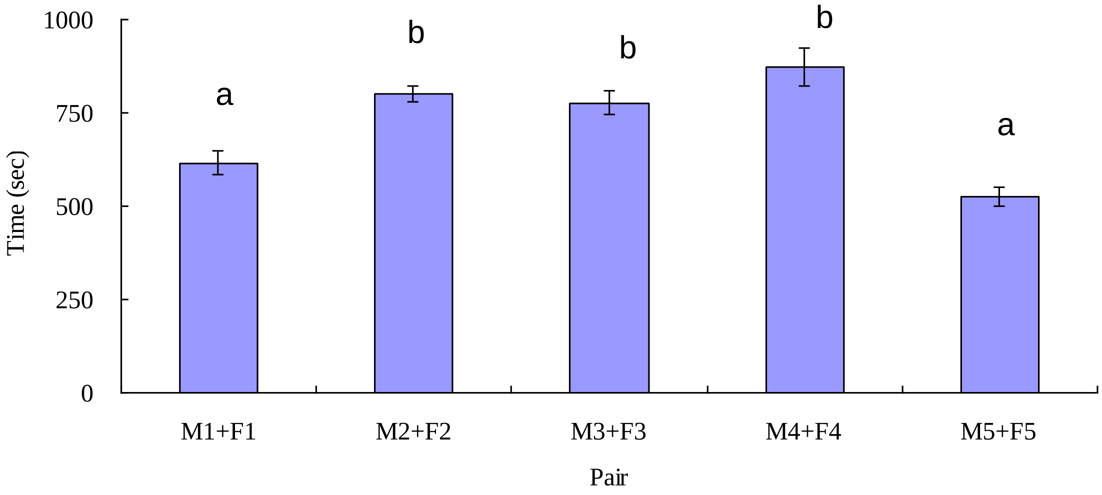

Figure 3.2: The mean duration of duet song produced by white-cheeked crested gibbons. Each bar (mean ± sem) shows the duration of duet song produced by each pair. 1 to 5 represents the pair housed in 1(Dusit Zoo), 2(Night-Safari), 3(Endangered Primate Rescue Center), 4 (Nakhornratchasima Zoo) and 5 (Chiangmai Zoo). a and b differ at a significant value of .05 level in post-hoc (Turkey's HSD test) comparisons.

3.3.1.2 Total of call phrases of duet song in pairs

The number of call phrases produced in each duet song was ranged from 62.8 ± 2.56 to 112.33 ± 5.52 (mean ± sem) call phrases per song (Fig. 3.3). Each pair produced significantly different the number of call phrases from one and another (total call phrases: $F_{(4,34)}$= 24.46, p<0.001).

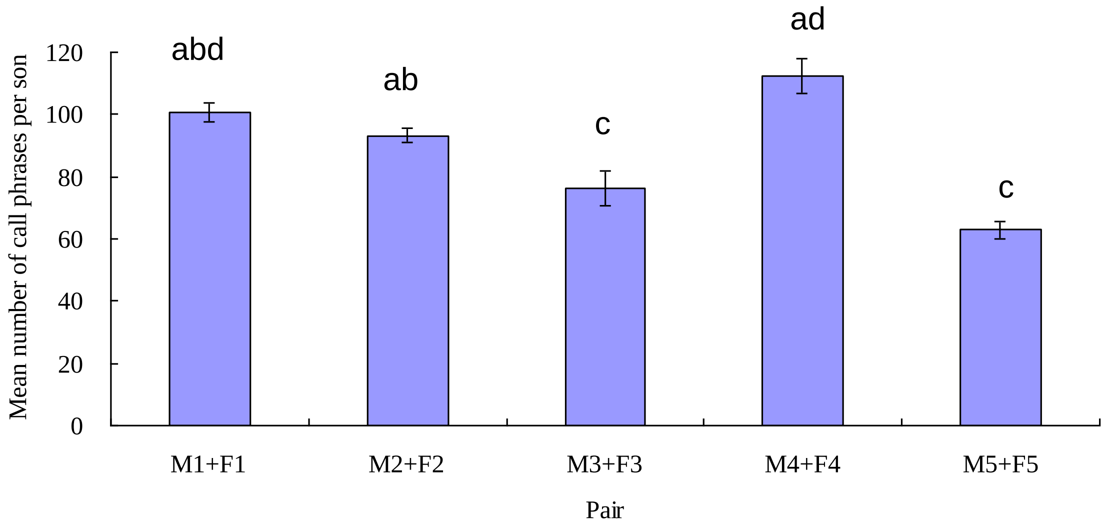

Figure 3.3: The mean call phrases contained in the duet song of white-cheeked crested gibbons**.** Each bar (mean ± sem) shows the duration of duet song produced by each pair. 1 to 5 represents the pair housed in 1(Dusit Zoo), 2(Night-Safari), 3(Endangered Primate Rescue Center), 4 (Nakhornratchasima Zoo) and 5 (Chiangmai Zoo). a, b, c and d differ at a significant value of .05 level in post-hoc (Turkey's HSD test) comparisons.

3.3.1.3 Calling rate of the duet song

Since the duration and the number of call phrases produced varied in white-cheeked crested gibbons, it was interesting to see whether or not each pair organises its duet song to have the same or very similar calling rate. The results showed that the calling rate varied in terms of pairs, ranging from 5.83 ± 0.25 to 9.91 ± 0.25 call phrases per minute (Fig. 3.4). Pairs organised their duet significantly differently from one another (Call phrase/min: $F_{(4,34)}$= 45.97, p<0.001).

There was no significant association among different duets in terms of the duration or the number of call phrases and the calling rate in the duet song (duration x the number of call phrases: r=0.63, p=0.258; duration x the calling rate: r= -0.26, p=0.57; the number of call phrases x the calling rate: r= 0.52, p= 0.37, two-tailed).

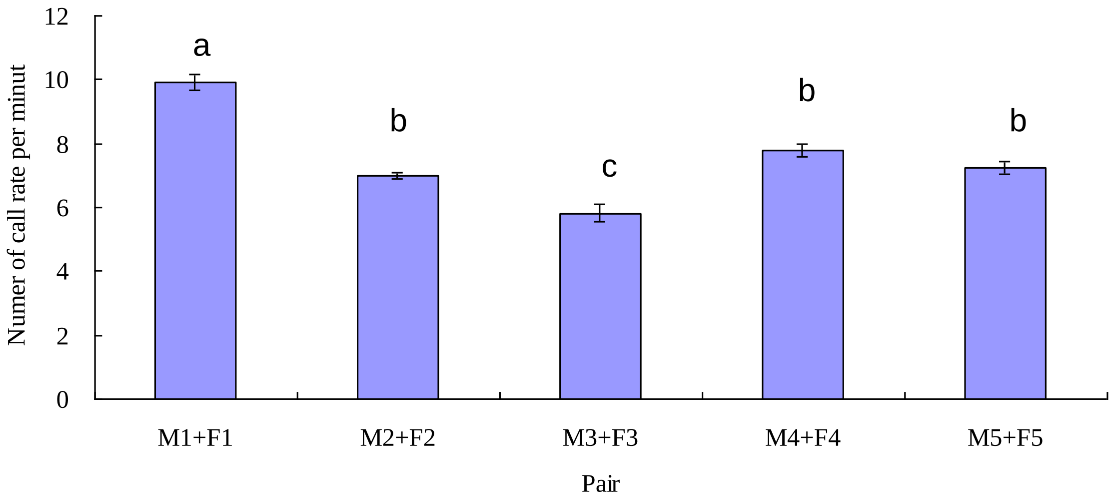

Figure 3.4: The mean number of call phrases produced per minute by the pair during the duet song. Each bar (mean ± sem) indicates the mean total number of call phrases produced by a pair of white-cheeked crested gibbons per song. 1 to 5 represents the pair housed in 1(Dusit Zoo), 2(Night-Safari), 3(Endangered Primate Rescue Center), 4 (Nakhornratchasima Zoo) and 5 (Chiangmai Zoo). a, b and c differ at a significant value of .05 level in post-hoc (Turkey's HSD test) comparisons.

3.3.1.4 Male song phrases

The duration of male song phrases also showed significant differences between individuals (Duration: $F_{(4,34)}$= 18.34, p < 0.001; Fig 3.5). The total number of call phrases produced by male white-cheeked crested gibbons was individually different (Total phrases: $F_{(4,34)}$=21.69, p<0.001; Fig 3.6), and the number of three types of call phrases were associated with each other (Multi-modulated x Boom: r= 0.97, p=0.006; Boom x Staccato: r=0.92, p =0.03; Multi-modulated x Staccato: r=0.817 p=0.091, two-tailed).

The proportion of three types of call phrases used by each individual was different (Multi-modulated $F_{(4,34)}$=5.99, p=0.001; Boom $F_{(4,34)}$=11.01, p=0.001; Staccato $F_{(4,34)}$=5.47, p=0.001). Figure 3.7 shows that the male from Chiangmai Zoo was different from the other males. This individual was paired with his partner for only four months before the recording was made. This pair may not have been as stable as other pairs. Therefore, the individual differences in the proportion of call phrases used was re-assessed by excluding this particular individual. The results showed that the proportion of boom and staccato call phrases used by each individual was different. However, there was no significant difference in the proportion of multi-modulated call phrases used among these males (Multi-modulated: $F_{(3,26)}=1.34$, $p=0.282$; Fig 3.7)

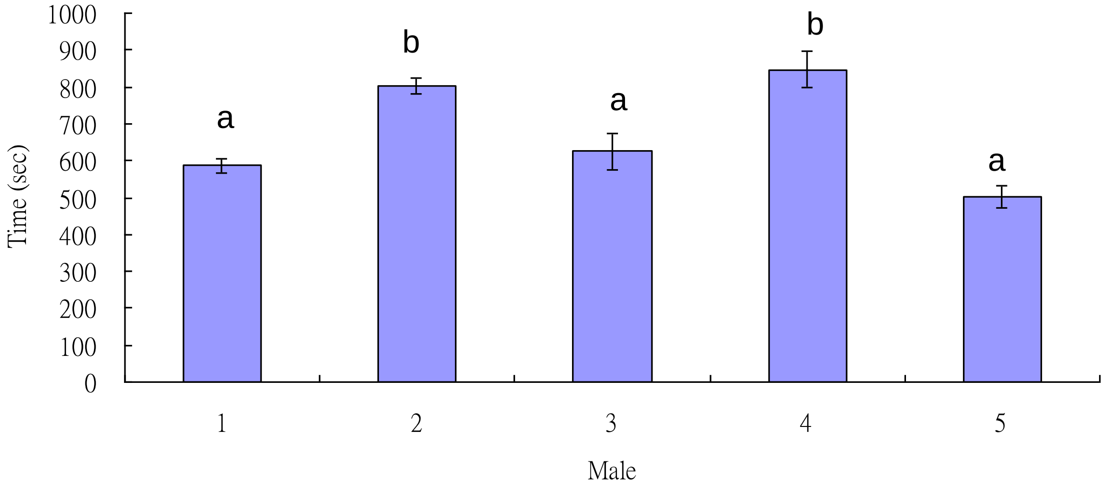

Figure 3.5: The mean duration of male song phrases. Each bar represents the mean length of song phrases (mean ± sem) in male white-cheeked crested gibbons. 1 to 5 represents the male individual of the pair housed in Dusit Zoo, Night-Safari, Endangered Primate Rescue Center, Nakhornratchasima Zoo and Chiangmai Zoo, respectively. a, and b differ at a significant value of .05 level in post-hoc (Turkey's HSD test) comparisons.

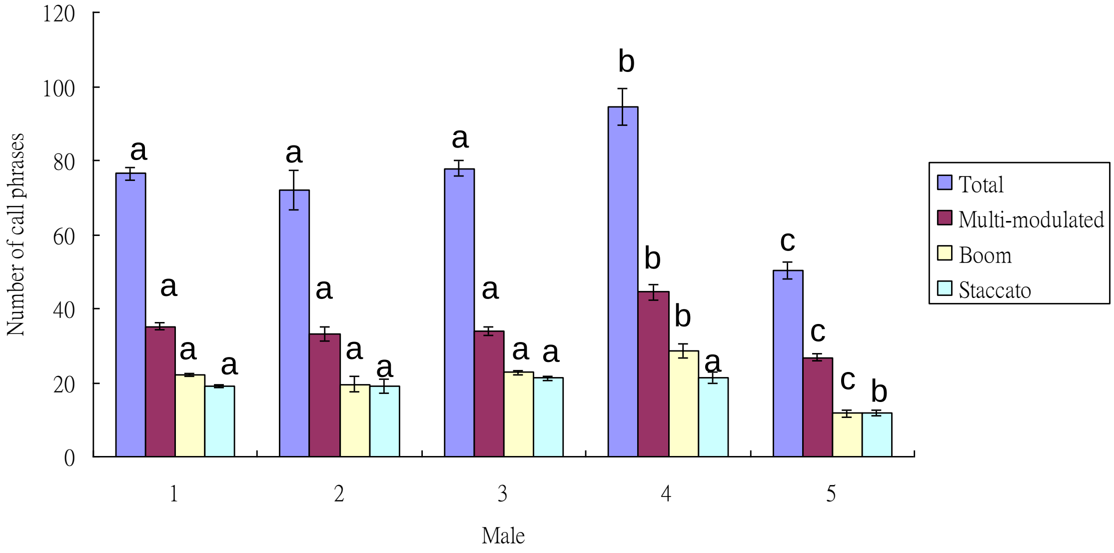

Figure 3.6: The number of male song phrases produced in male white-cheeked crested gibbons. Each grouped bar shows a mean number of call phrases produced per song in each individual (mean ± sem). 1 to 5 represents the male individual of the pair housed in Dusit Zoo, Night-Safari, Endangered Primate Rescue Center, Nakhornratchasima Zoo and Chiangmai Zoo, respectively. a, b, c and d differ at a significant value of .05 level in post-hoc (Turkey's HSD test) comparisons.

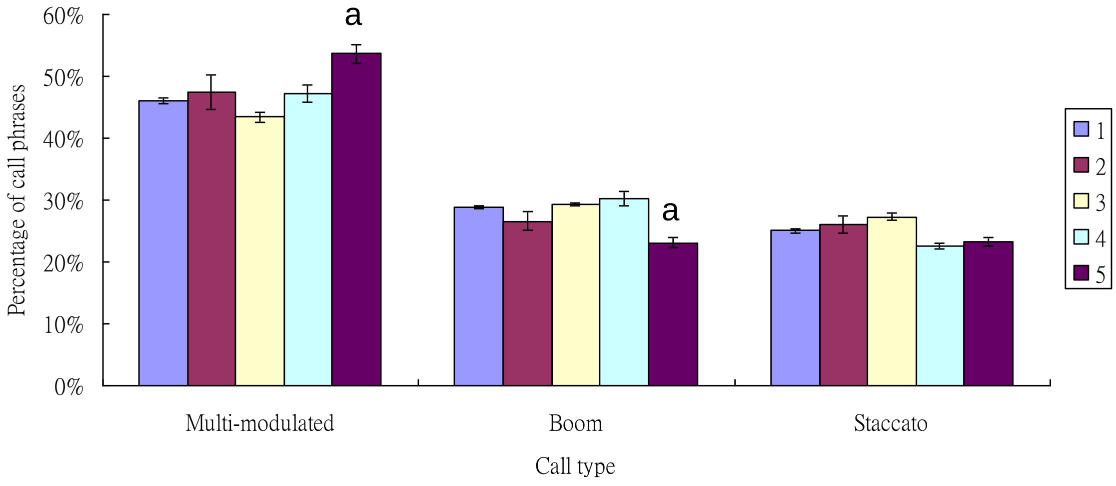

Figure 3.7: The percentage of each type of call phrases produced by male white-cheeked crested gibbons. Each grouped bar shows a mean percentage of call phrases used in each type of call phrase (mean ± sem). 1 to 5 represents the male individual of the pair housed in Dusit Zoo, Night-Safari, Endangered Primate Rescue Center, Nakhornratchasima Zoo and Chiangmai Zoo, respectively. a refers to significant value at .05 level of post-hoc (Turkey's HSD test) comparison.

3.3.1.5 Female song phrases

Result showed that females produced songs that were significantly different from each other, varying in duration ranging from 411.53 ± 30.03 seconds to 753.43 ± 20.3 seconds ($F_{(4.34)}$= 12.81, p<0.001; Fig. 3.8).

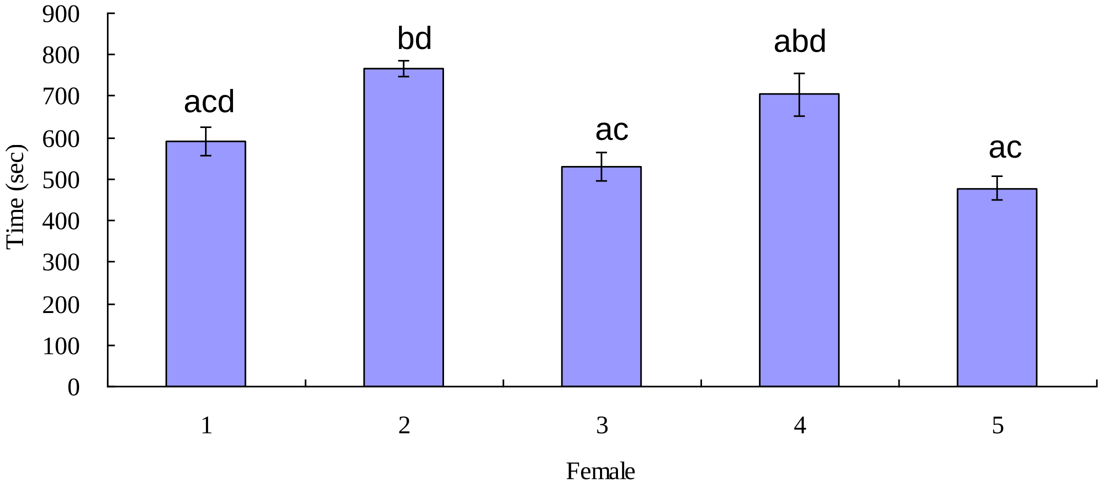

Figure 3.8: The mean duration of female song phrases. Each bar represents the length of song phrases (mean ± sem) in female white-cheeked crested gibbons. 1 to 5 represents the female individual of the pair housed in 1(Dusit Zoo), 2(Night-Safari), 3(Endangered Primate Rescue Center), 4 (Nakhornratchasima Zoo) and 5 (Chiangmai Zoo). a, b, c and d differ at a significant value of .05 level in post-hoc (Turkey's HSD test) comparisons.

Although the literature suggests that females produce only great call phrases, and not other calls, and occasionally abort great call phrases during song, some individuals in this study regularly produced call phrases containing only a few notes, which are not great call phrases. Combined with the number of great call phrases produced by female white-cheeked crested gibbons, the total call phrases varied in each individual (Fig. 3.9). The total number of call phrases, the number of great calls and the number of non-great call phrases were individually different (total call phrases: $F_{(4,34)}$=30.04, p<0.001; great call: $F_{(4,34)}$=90.80, p<0.001; non-great call: $F_{(4,34)}$=58.13, p<0.001). The singing speed of each individual was also investigated and the result showed each individual had significantly different singing rate in the number of call phrases per minute ($F_{(4.34)}$=91.87, p<0.001; Fig. 3.10).

There was no significant correlation between the duration of song produced by females and the number of total call phrases, great calls or non-great call phrases. (duration x total call phrases: r=-0.72, p=0.170; duration x great-call: r=0.33, p=0.586; duration x non-great call: r=-0.76, p=0.133). The number of great calls was not associated with the number of non-great calls (great-call x non-great call: r=-0.560, p<0.326).

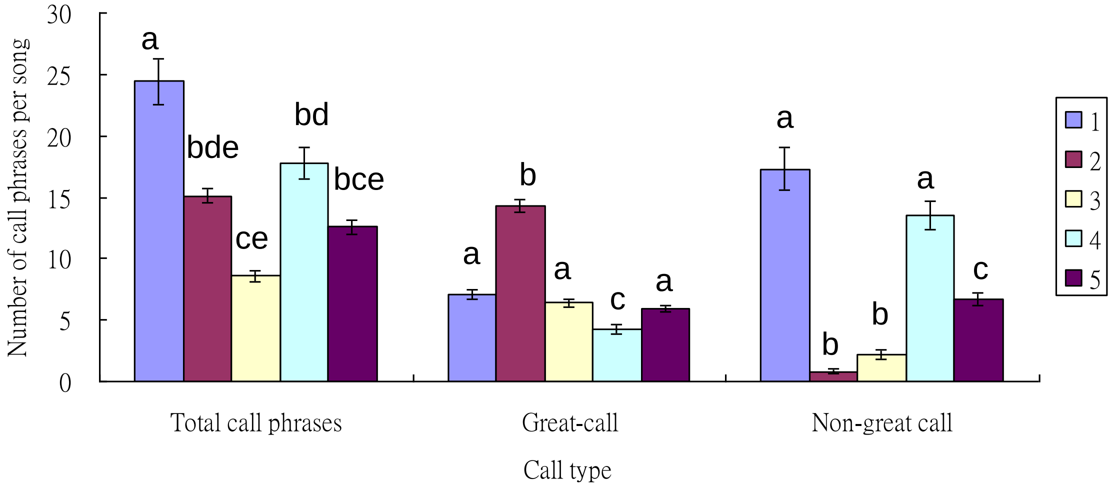

Figure 3.9: The number of female song phrases produced in female white-cheeked crested gibbons. Each group bar shows a mean number of call phrases (mean ± sem) produced per song in total, great-call and non-great call phrases. 1 to 5 represents the female individual of the pairs housed at Dusit Zoo, Night-Safari, Endangered Primate Rescue Center, Nakhornratchasima Zoo and Chiangmai Zoo, respectively. a, b, c, d and e differ at a significant value of .05 level in post-hoc (Turkey's HSD test) comparisons.

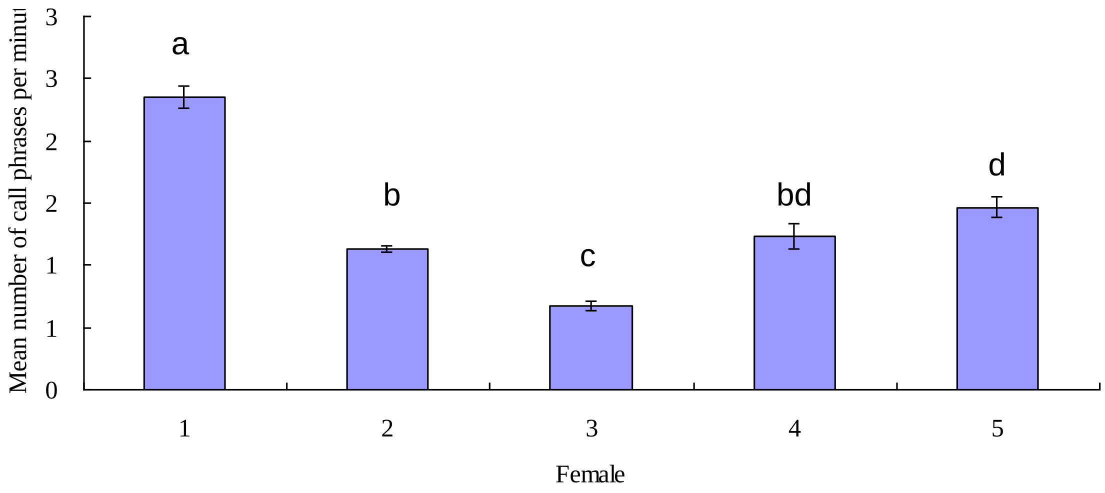

Figure 3.10: The mean number of call phrases produced per min during the duet song. Each bar (mean ± sem) represents the calling rate of female white-cheeked crested gibbons during female song phrases. 1 to 5 represents the female individual of the pairs housed at Dusit Zoo, Night-Safari, Endangered Primate Rescue Center, Nakhornratchasima Zoo and Chiangmai Zoo, respectively. a, b, c and d differ at a significant value of .05 level in post-hoc (Turkey's HSD test) comparisons.

3.3.2 Acoustic features of call phrases

3.3.2.1 Male call phrases

Multivariate analysis (MANOVA) was used to test whether or not the three types of call phrases were used differently among male individuals. The results of the MANOVA indicated significant individuality in acoustic features (Wilks's lambda = 0.004, $F_{(36,1826)}$=165.91, p<0.001). Nine acoustic variables (variables 21-29) were measured from three types of call phrases produced by the male white-cheeked crested gibbons. All acoustic variables exhibit significant difference (p <0.0001) indicating all measured acoustic parameters contributed to the differences of vocal individuality. However, this test did not provide enough results to assess which parameters contributed the most to individual recognition.

In order to explore what acoustic variables contributed the most to individual differences, a discriminant function analysis (DFA) was used to rank them. This test was able to assess the relative importance of the independent variables in classifying the dependent variable. Therefore, the result of DFA may reveal which parameters were able to identify the vocal individuality in male white-cheeked crested gibbons. The results of Wilks' lambda showed that out of all discriminant four functions have significant effects on identifying the individuality in male white-cheeked crested gibbons (chi-square $_{(36,\ 500)}$ = 1676.21, p <0.001). This indicated that the discriminant model could identify vocal individuality of white-cheeked crested gibbons. The eigenvalues showed that 77% of total variance arose from in the first functional group. A total of 93.5% of total variance accounted for by the first and second functions. This means the result of DFA could be explained by looking through the acoustic variables contained within the first two function groups. In other words, the vocal individuality of white-cheeked crested gibbons may be identified through acoustic parameters in the first two function groups, which were consisted of start frequency and peak frequency of boom call and staccato call phrases (function group 1) and lowest frequency of multi-modulated call phrases.

Table 3.6 shows the within-group correlations between acoustic features and the discriminant functions as well as the standardized weights. The first discriminant function has a strong correlation with peak and start frequency of boom and staccato call phrases, which were the most dominant acoustic features in identifying individuals of males. Lowest frequency had the strongest correlation in the second discriminant function. This suggests that the frequency variables measured in boom and staccato call are the primary features in identifying males, while the lowest frequency of first note of multi-modulated call phrases are the second most important feature in identifying males.

Table 3.6: Standardised coefficients and correlations of acoustic measurements with the four discriminant functions.

	Correlation Coefficients with Discriminant Functions				Standardized Canonical Discriminant Function Coefficients			
	Function				Function			
Acoustic Measurements	1	2	3	4	1	2	3	4
Peak frequency of boom call (PBM)	**.697**	-0.275	0.403	-0.409	0.620	-0.424	0.421	-0.467
Peak frequency of staccato call (PSM)	**.573**	0.146	-0.541	0.322	0.307	0.356	-0.510	-0.173
Start frequency of staccato call (SBM)	**.557**	-0.214	-0.375	0.393	0.394	0.11	0.256	0.135
Peak frequency of boom call (SSM)	**.376**	-0.01	0.08	0.268	0.241	-0.418	-0.043	0.338
Lowest frequency of multi-modulated call (LBM)	0.211	**.780**	0.12	-0.097	0.172	0.356	-0.51	0.173
Duration of boom call (DBM)	0.035	0.268	**.467**	-0.039	0.169	-0.048	0.122	0.332
Duration of multi-modulated call (DMM)	-0.036	0.085	**.275**	0.193	-0.042	0.287	0.199	0.426
Start frequency of multi-modulated call (SMM)	0.282	0.386	-0.393	**-.586**	0.118	-0.424	0.421	-0.467
Duration of staccato call (DSM)	0.049	-0.097	0.034	**.377**	0.095	0.322	0.536	0.097

Bold font refers to the largest absolute correlation between each variable and any discriminant function

When all nine acoustic measurements were considered, a correct assignment of 95.8% was achieved in cross-validation analysis. A correct assignment of 94.6% was still achieved in cross-validation when four acoustic variables (PBM, PSM, SBM, SSM), which contribute the most in identifying individuals were considered.

The plot of measured frequency variables of boom and staccato call phrases (Function 1) versus the lowest frequency of multi-modulated call phrases (Function 2) shows distance between each group in classification (Fig 3.11). M1 (housed in Dusit Zoo), M3 (housed in Endangered Primate Rescue Center) and M4 (housed in Nakhornratchasima Zoo) were distinct from each other in the frequency difference of boom and staccato call phrases, whereas M2 (housed in Night-Safari) and M5 (housed in Chiangmai Zoo) had closer characteristics, although over 90 % of correct assignments in both of these latter individuals was still achieved.

The lowest frequency variable of multi-modulated call phrases (Function 2) showed that the M4 (housed in Nakhornratchasima Zoo) had higher scores than other individuals, and this indicated that the lowest frequency of the first note of multi-modulated call phrases in this individual may differ significantly from others.

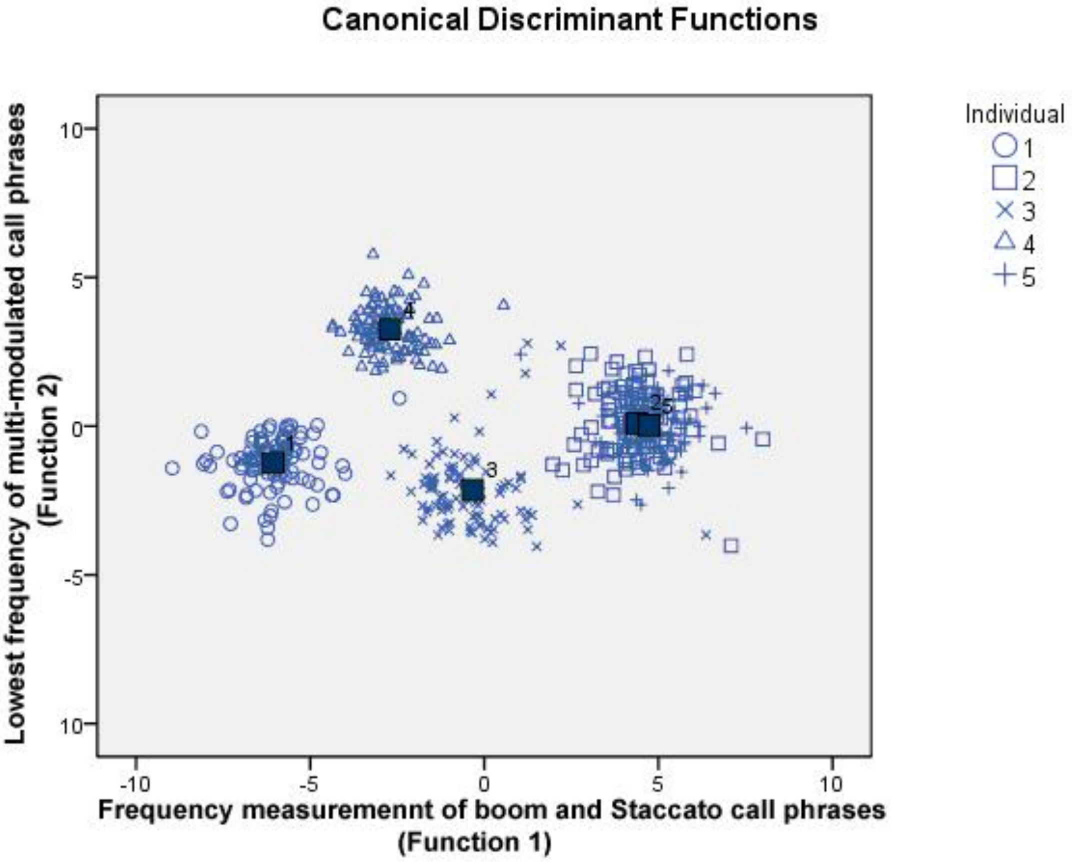

Figure 3.11: The plot of canonical discriminant functions in function 1 versus function 2. The score of measurements of each individual was plotted by different shape. The blue square represents the mean score of each individual.

Although the results of the DFA suggested that all acoustic features may have significant effects on identifying the individuals, the analysis was not able to provide an answer as to which minimal acoustic features would be sufficient to identify individuals. Therefore, the nine acoustic features were divided into three groups according to three features (Start frequency, Peak/lowest frequency and duration) and a re-run of DFA was performed. The results showed that the features of start frequency and the features of peak/lowest frequency of male call phrases were able to identify individuals correctly with accurate percentage of 86% and 94.6%

of total assignments, respectively. However, the duration of call phrases allowed the correct individual identification with only 46.6% overall.

3.3.2.2 Female song phrases

Female song phrases were simpler than male song phrases in terms of the types of call phrases produced. The acoustic features of the great call and of non-great call phrases varied in terms of the individual, but each individual remained consistent (Fig 3.12). Peak frequency between the first note of great call and non-great call phrases was significantly different in females (peak $F_{(1,4)}$=21.51, p=0.01). The mean difference of start frequency between the great call and non-great call phrases produced by females was significantly different. There is no difference in the duration between great call and non-great call phrases in females (duration: $F_{(1,4)}$=1.15, p=0.34).

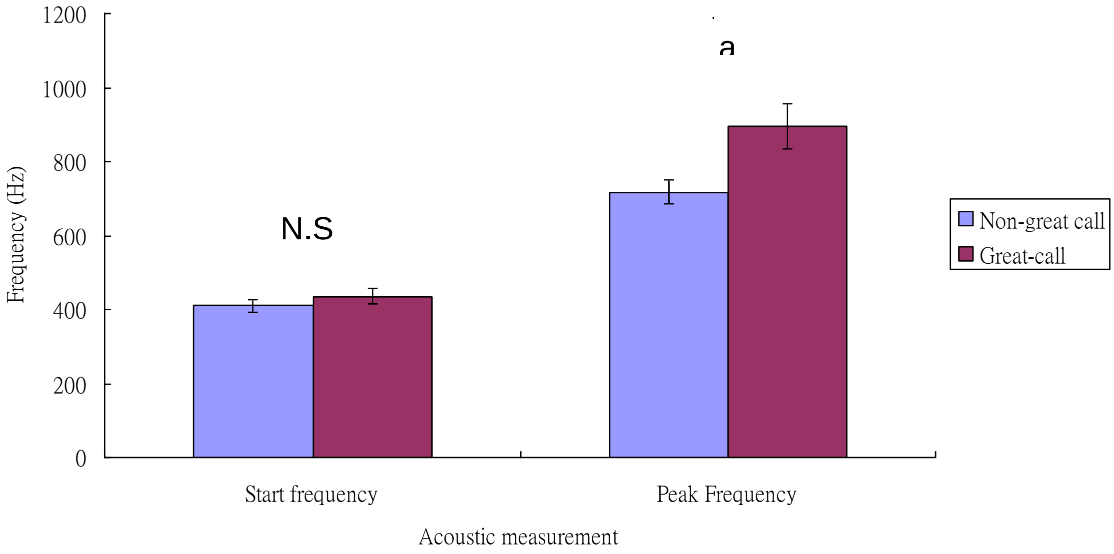

Figure 3.12: The start frequency and the peak frequency (mean ± sem) of great call and non-great call phrases**.** a refers to significant value at .05 level. N.S refers no significant value.

Multivariate analysis (MANOVA) was conducted on measurements in the great-call call phrases. The results indicated a significant difference in acoustic features (Wilks's lambda = 0.171 $F_{(12,973)}$=76.99, $p<0.001$) in these five females.

DFA was applied to determine which factors contributed the most to the difference between individuals. The results showed that females initiated their first note of great call phrases differently from one another. The duration of the first note, unlike those of male individuals, is actually the main acoustic feature (function 1) in female call phrases. Start frequency of the first note of great call contributed to the second discriminant function (Table 3.7). The plot of duration of the first note of great call phrases (function 1) versus the start frequency of great call phrases (function 2) shows these two acoustic variables were unable to discriminate well between individuals (Fig 3.13). It also resulted in the low percentage of group classification which achieved only 75.5% of overall correct assignments in cross-validation analysis, and the percentage of correct assignment varied from 47.4 % to 91.6 % in terms of individuals in cross-validation results.

Table 3.7: Standardized coefficients and correlations of acoustic measurements with the three discriminant functions.

Acoustic measurements	Correlation Coefficients with Discriminant Functions			Standardized Canonical Discriminant Function Coefficients		
	Function			**Function**		
	1	2	3	1	2	3
Duration of great call (DGF)	**0.980**	-0.025	-0.199	0.967	0.493	-0.329
Start frequency of great call (SGF)	-0.277	**0.846**	0.455	0.037	1.175	0.034
Peak frequency of great call (PGF)	0.339	-0.038	**0.940**	0.187	-0.464	0.977

Bold refers to the largest absolute correlation between each variable and any discriminant function

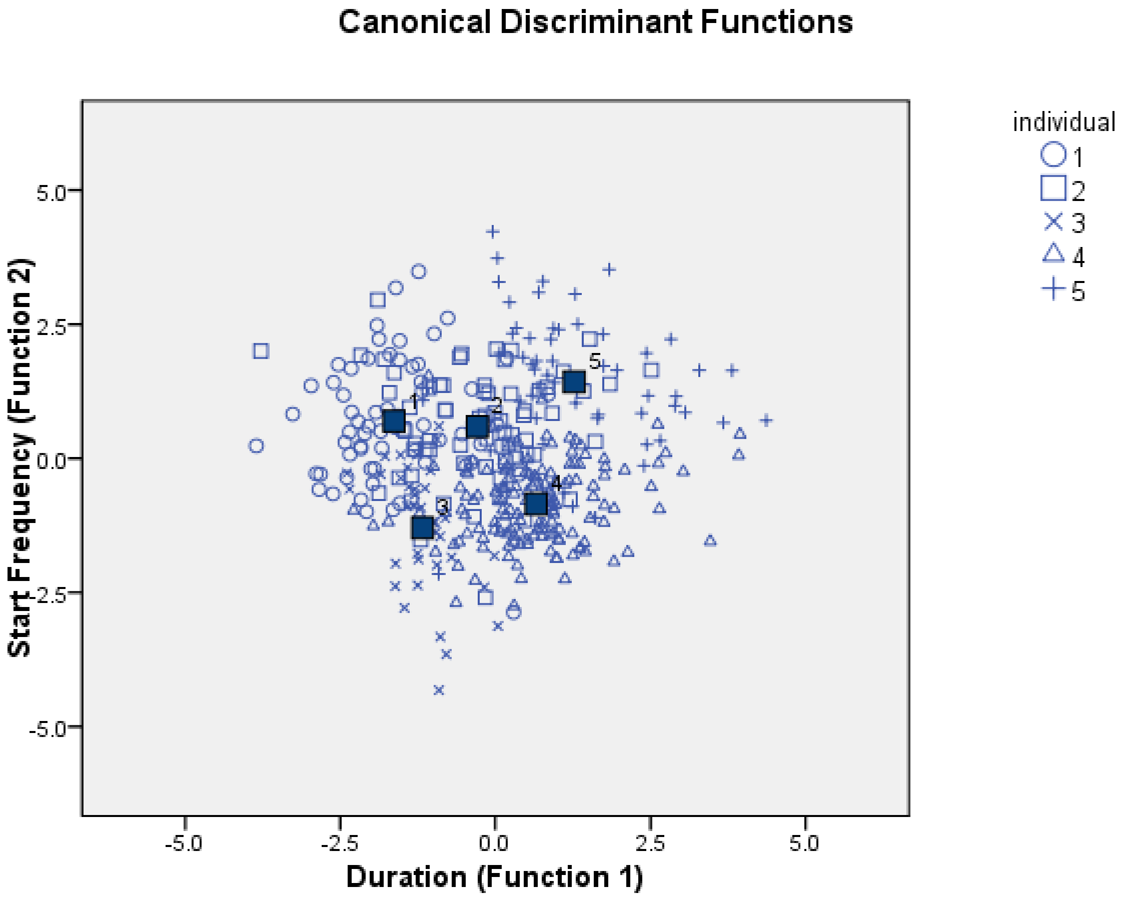

Figure 3.13: The plot of canonical discriminant functions in function 1 versus function 2. The score of measurements of each individual was plotted by different shape. The big square represents the mean score of each individual.

3.3.3 Context and structure of song

The duet song produced by the observed pairs of white-cheeked crested gibbons confirmed the general description of duet song as described in the literature. However, the results also showed that there is some variability in terms of structure of call phrases in both male and female song, which indicates that the context of the duet songs may have varied.

3.3.3.1 Male song phrase

The maximum number of notes achieved in one staccato call phrase differed significantly among individuals ($F_{(4,34)}=8.20$, $p<0.001$). The range of maximum number of notes produced by each individual was also different (Table 3.8). In three of the recorded males produced staccato call phrases that contained more than 14 notes (see example Fig 3.14)

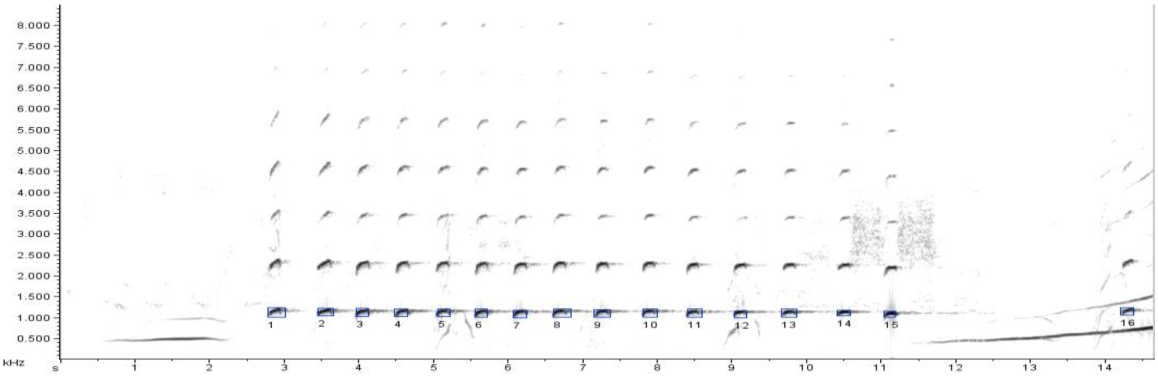

Figure 3.14: An example of a staccato call phrase produced by a male white-cheeked crested gibbon (M2) that contained more than 14 notes**.** This sample was recorded in Chiangmai Night Safari, Thailand on 5th April 2007.

Table 3.8: The maximum number of notes in one staccato call phrase made by male white-cheeked crested gibbons

Individual	Max number of notes in one staccato call phrase (Mean ±sem)	Range
1	9.90 ± 0.96	6-16
2	13.30 ± 0.50	10-16
3	7.10 ± 0.55	4-9
4	12.22 ± 1.41	6-20
5	9.80 ± 0.65	7-13

When the multi-modulated call phrases were sub-catalogued into 12 types of call phrases, a variety of call phrases used in terms of individuals emerged. Male 1 used more types of call phrases than other individuals (Friedman Test: Chi-square=19.56 df=4, p=0.001). Although the four individuals used a similar number of sub-types of multi-modulated call phrases, each individual selected individually different sub-types of multi-modulated call phrases. Moreover, the proportion of call types used by each individual was also different ($F_{(4,44)}$ =31.379, p=0.0001) (Fig. 3.15).

Table 3.9: The number of sub-catalogued multi-modulated call types used within a song of white-cheeked crested gibbons (n=10)

Individual	Number of sub-catalogued multi-modulated call phrases	Range
1	8.40 ± 0.27	7-10
2	4.80 ± 0.20	4-6
3	6.00 ± 0.15	5-7
4	5.67 ± 0.41	4-7
5	5.70 ± 0.30	4-7

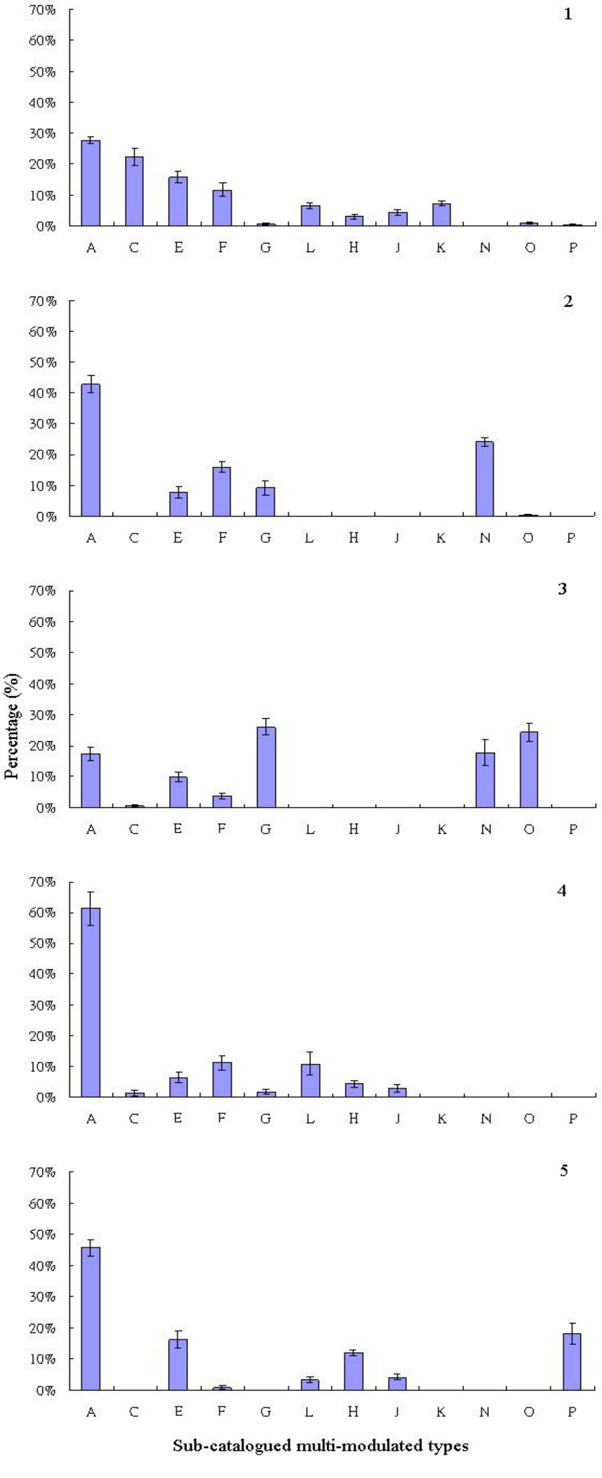

Figure 3.15: The percentage of sub-catalogued multi-modulated types in male white-cheeked crested gibbons. 1 to 5 represents the male individual of the pairs housed at Dusit Zoo, Night-Safari, Endangered Primate Rescue Center, Nakhornratchasima Zoo and Chiangmai Zoo, respectively.

3.3.3.2 Female song phrase

Although females mainly produced great-call phrases, great call phrases differed from each individual in terms of their number of notes and the order of great call phrases (Fig 3.16). The number of notes within a great call phrase was individually different (Kruskal-Wallis test Chi-square=197.64 N=372, $p<0.001$) (Fig 3.17). Most individuals, except for the individual housed in Dusit Zoo, produced great call phrases containing 11-15 notes.

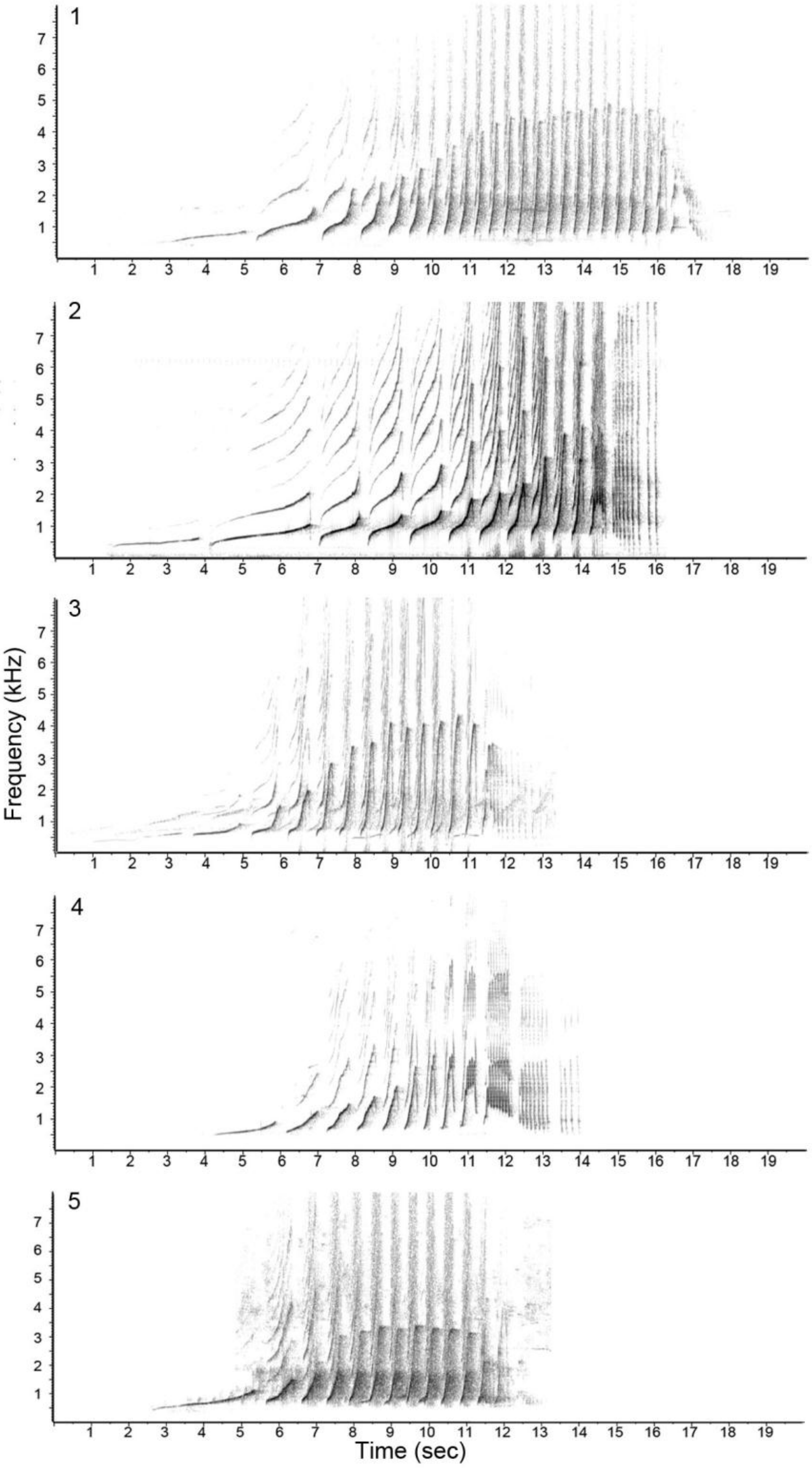

Figure 3.16: Representative great call phrases of the five subject females. 1 to 5 represents the female individual of the pairs housed at Dusit Zoo, Night-Safari, Endangered Primate Rescue Center, Nakhornratchasima Zoo and Chiangmai Zoo, respectively.

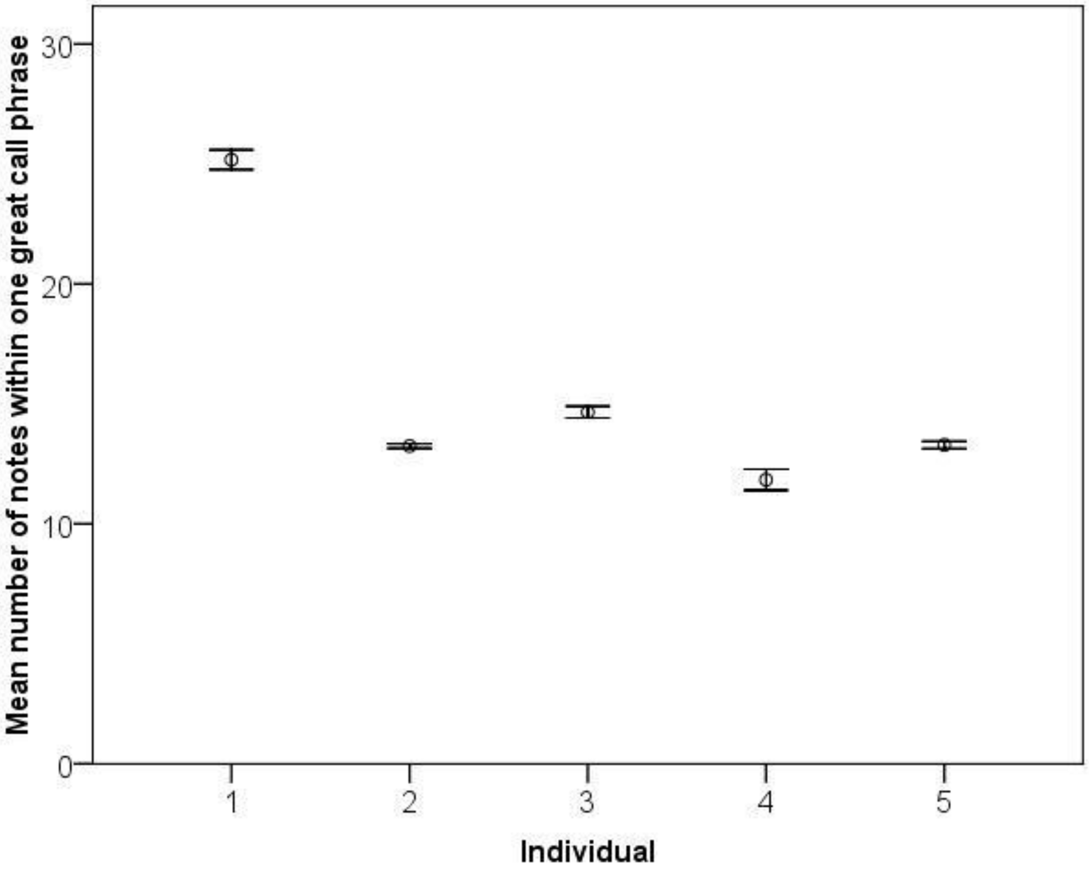

Figure 3.17: The mean number of notes within one great call phrase produced by each female individual. Individual 1 to 5 represents the female individual of the pair housed in Dusit Zoo, Night-Safari, Endangered Primate Rescue Center, Nakhornratchasima Zoo and Chiangmai Zoo, respectively.

3.4 Discussion

Duet song in gibbons is said to be highly coordinated between pairs (Geissmann, 1993). The coordination alone may have resulted in each pair's duet song being different because the preference of individuals may be different between pairs. My study found that five pairs of white-cheeked crested gibbons produced duet song that was distinguishable from one another in terms of duration (10-15 minutes) and was similar to the time-frames found by previous studies of crested gibbons in captivity and in the wild (8-40 minutes; Fan et al., 2007; Jiang et al., 1997; Rawson, 2004; Schilling, 1984; Sheeran, 1994). Indeed, each pair produced less intra-pair variability than inter-pair variability of the duration of duet song. It may be argued that song production may be affected by other individuals or pairs and this stability in each pair song was a consequence of isolation of pairs from other conspecifics. If this was the case, duration of the song produced by the pair housed in Vietnam should be affected by the conspecific individuals.

Only one pair that was able to maintain visual and audio contact with conspecifics. There are no available data in white-cheeked crested gibbons regarding this question. The study in wild eastern black-cheeked crested gibbons (*N. concolor jingdongensis*) found that song behaviour is unlikely to be elicited by other neighbouring groups (Fan et al., 2007). Moreover, It has been also found that newly paired siamang (*Symphalangus syndactylus*) pairs produce more poorly coordinated songs than a long-time pair (Geissmann, 1999). The duration of duet song thus may have little to do with other conspecifics and may, indeed, be mainly determined by the coordination within a pair.

Since duet song might be exclusively coordinated by a pair, it is interesting to investigate whether there are some particular rules in developing duet song in white-cheeked crested gibbons. The results found that the number of male call phrases may vary, but the proportion of call phrases used, especially in multi-modulated call phrases, was similar in adult paired males except for a newly paired male. It is possible that male white-cheeked crested gibbons may adjust their singing behaviour to match the singing behaviour of their partner.

Gibbon song was thought to be sex- and species-specific. Recent studies, which have investigated the intra-species variations, or individuality, in *Hylobates* species, found that vocal individuality of *Hylobates* species in acoustic features could be observed in the wild and in captive environments (Cheyne et al., 2007; Dallmann et al., 2001b; Geissmann et al., 2005; Oyakawa et al., 2007). Previous studies, excepting Geissmann et al. (2005), were only investigating female call phrases, but Geissmann et al. (2005) did not examine male individual differences in their acoustic features. My study has investigated both sexes of white-cheeked crested gibbons and found that such individuality expressed, in acoustic features, can be identified in *Nomascus* species.

The results of the DFA in my study found that frequency factors of call phrases in males were most useful in determining individuality, whereas the duration of the first note in female great call phrases was more heavily in discriminating between individuals. Such findings are noticed because both sexes produce relatively stereotyped call phrases in terms of structure. In males, the duration of three types of call phrases varied significantly, with less variation to duration of call phrases as a measure of exhibiting individuality. Instead, males may express more individuality by producing different call frequencies to advertise themselves.

In female white-cheeked crested gibbons, the very first note of great call phrases may identify individuals because differences were found in terms of this aspect of acoustic structure. It was similar to other studies in other *Hylobates* species (Dallmann et al., 2001b; Haimoff et al., 1985;

Oyakawa et al., 2007). Moreover, the results of DFA found that the duration of the first note was more useful than frequency factors in discriminating female individuals. Oyakawa et al. (2007) found that duration of the inflective and climax part in great call phrases produced by agile gibbons (*H. a. agilis*) showed strong acoustic individuality. It is possible that female great call phrases of white-cheeked gibbons were more stereotypic than agile gibbons in their call structure. Therefore, call notes of female agile gibbons may reveal individuality more by changing the duration of the note than the frequency. The same study of Oyakawa et al. (2007) also suggested that vocal individuality may also appear in the frequency of introductory and climax parts of great call phrases. In white-cheeked crested gibbons, the literature has suggested the great call phrases can be divided into “utter”, “barking” and “trill” parts (Schilling, 1984), and such acoustic structures of female great call phrases in white-cheeked crested gibbons differs from *Hylobates* species. In any sample, the number of notes contained in the great call phrases varies in terms of individuals. This may compromise attempts to the methodological difficulty to find the precise climax part of the great call phrases in each female white-cheeked crested gibbon. Although less information may be provided in the single call note of great call phrases in females, the overall structure of great call phrases may provide an alternative way to distinguish individuals.

Geissmann et al. (2000) suggested one great call phrase of female white-cheeked crested gibbons may vary between eight to thirty notes. All females in my study did not produce any great call phrases contained the number of notes outside of the range. However, the present study the number of notes within great call phrases was relatively stable in each individual. Each individual produced significantly different number of notes contained in the great call phrases, and such difference may therefore represent an individual signature which may assist conspecifics to recognize an individual.

Twelve sub-categorised multi-modulated call phrase were found among these tested male white-cheeked crested gibbons, but none of them produced all 12 sub-types of multi-modulated call phrases. Similar findings have also been made in male Javan gibbons (*H. moloch*) that do not produce all kinds of notes in the vocal repertoire in every individual (Geissmann et al., 2005). The question is whether such individual differences are actually due to geographic variation as the origins of these subjects were unknown. A study in wild and captive *H. albibarbis* found that although different populations may have dialects in their song, a high level of variability may still be presented within a population (Cheyne et al., 2007). Therefore, vocal individuality may be expressed regardless of possible geographic variation in all species.

Another noticed finding of the present study concerns the maximum number of notes in one staccato call phrase and the number of modulations in multi-modulated call phrases. So far, research has indicated that one staccato call phrase contained up to 14 notes, and modulation occurred only in the first three notes of multi-modulated call phrases (Goustard, 1984; Haimoff, 1983; Schilling, 1984). None of other studies indicated any exceptions. However, in the present study of a total of five male white-cheeked crested gibbons, three male individuals produced more than 14 notes within one staccato call phrase. Indeed, one individual even produced up to 20 notes within one staccato call phrase. Moreover, four individuals modulated their fourth note of multi-modulated call phrases. Findings of my study suggested that previous rules of song phrases in male white-cheeked crested gibbons may not be accurate. Geissmann et al. (2000) suggested that the differences in multi-modulated call phrases may reflect different sub-species. However, the difference between the two sub-species was based on the second and third note of multi-modulated call phrases. This could not adequately explain why the white-cheeked crested gibbons in the present study modulated in the fourth note. More, the multi-modulated call phrases were identified in 8 of 12 sub-types in these studies (Deputte, 1982; Schilling, 1984), but the white-cheeked crested gibbons scored in the present study produced more complex multi-modulated call phrases than those that were studied more than two decades ago. If above mentioned differences simply reflect the different sub-species, some similar results should be recorded through the wild survey conducted within last two decades. It is unknown what factors influence the complexity of male multi-modulated call phrases. Further study is needed to determine what possible factors may have been operating here.

Chapter 4

Song Change and Vocal Plasticity in White-cheeked Crested Gibbons (*Nomascus leucogenys*)

4.1 Introduction

Vocal development has previously been reported in several studies of primates (Hammerschmidt et al., 2001; Pistorio et al., 2006; Snowdon et al., 2001). Most of these studies investigated the change of vocal repertoire and acoustic features between age groups (e.g., infants, juveniles, sub-adults and adults). Although gibbons are well known for their special song behaviour, very little is known regarding the structural and organisational development of their vocalisations. A few studies of gibbon vocalisations have described changes in terms of vocal usage and physical structure of vocalisations in infants and juveniles (Anderson et al., 2008; Goustard, 1984; Merker et al., 1999; Shafer et al., 1984). Shafer et al. (1984) studied a female siabon (siamang-gibbon hybrid) and found that her vocalisation appeared *Hylobates*-like in the first three years, but then changed to a siamang-like vocal repertoire in the fourth and fifth year. Merker & Cox (1999) and Anderson & Bercovitch (2008) found that great call phrases produced by juvenile female yellow-cheeked crested gibbons (*N. gabriellae*) gradually approximated the great call phrases produced by adult female individuals.

All studies on the vocal development of gibbons concentrated on the early stage of the gibbon life-span (age <5 yrs old). There are no available data regarding possible changes in vocal repertoire from the age of five onwards to adults. Moreover, previous studies mainly investigated changes in the vocal repertoire of females, although two studies also mentioned vocal changes in males that with no details (Goustard, 1984; Uchikoshi, 2006). It is arguable whether these few studies can be regarded as conclusive of the actual vocal development of gibbons. By investigating young individuals only, and largely females, the question remains open as to whether or not vocal changes continues throughout adulthood.

Of all gibbon species, crested gibbons produce the highest diversity of song repertoire in adults (Geissmann, 2002a). Some circumstances juveniles and adults may produce song phrases of the opposite sex. Several studies have suggested that young crested gibbons produce some female-like great call phrases during their parents' duet song (Geissmann, 2002a; Geissmann, 2003; Goustard, 1984). Geissmann (2003) proposed such imitating song behaviour may be related to sexual maturity, but a study of a male juvenile agile gibbon (*Hylobates agilis*) showed that the male stopped producing female vocal repertoire about one to two years before the average age of sexual maturity (Uchikoshi, 2006). Moreover, some studies have found that male adult crested gibbons occasionally produce some female-like great call notes (Geissmann, 2002a; Schilling, 1984). Chen et al. (2008) also found that adult female crested gibbons produce male song phrases under some circumstances (e.g. housing alone or with same-sex partner). If such a process of song-switching is a general pattern in crested gibbons, it becomes a very interesting question as to why crested gibbons reproduce the song of the opposite sex at any age. Moreover, it is important to investigate whether this kind of process is related only to maturation or to other possible factors such as social context.

All of gibbon song was thought to be species-specific, and song of some species was also thought to be sex-specific (Geissmann, 2002a; Marshall et al., 1976), and thus quite stereotyped. However, the results in the previous chapter have already shown that both male and female white-cheeked crested gibbons express vocal individuality in terms of song elements used.

Studies of several other non-human primate species have found that vocal patterns or acoustic features may be modified even in adulthood. Snowdon & de la Torre (2002) suggested that conspecifics may influence an individual's vocalisations. A series of studies in pygmy marmosets (*Cebuella pygmaea*) found that they modified their call structure in relation to the change of social status (de la Torre et al., 2002; Elowson et al., 1994; Snowdon et al., 1999). Similar results were also found in other new world primate species (*Callithrix jacchus*: Norcross et al., 1999; *Callithrix kuhlii*: Rukstalis et al., 2003; *Saguinus oedipus*: Weiss et al., 2001) and other non-human primates such as Campbell's monkeys (*Cercopithecus campbelli*) and chimpanzees (*Pan troglodytes*) (Lemasson et al., 2005; Marshall et al., 1999). The results of these studies indicate that social factors may influence vocal communication in primates.

Song in gibbons has been recognized to play an important role in communication. It would be surprising if there was no flexibility in the acoustic features or vocal usage of gibbon song. Therefore, it is important to investigate, whether social context affects acoustic structure and song usage.

4.2 Method

4.2.1 Subjects

Ten white-cheeked crested gibbons (*N. leucogenys*) were used in this study, of which three were juvenile (1M, 2F) and four sub-adults (4M). These individuals represent all the juveniles and sub-adults that were available in Thai Zoos and the Endangered Primate Rescue Center (EPRC) in Vietnam at the time of the conduct of this study (Table 4.1). Three adult individuals (2M, 1F) were also included in this study because their social context changed during the course of this study and hence offered an opportunity to see whether the changes affected their song.

Individuals M7, M10 and M11 were captive-born and housed with their parents. Individual M9, another sub-adult, was housed alone. Individuals M8, F7 and F8 were housed together in a semi-wild hill area. These four individuals (M8-9 and F7-8) were originally taken from the wild, had been moved as infants and had been housed in their current enclosure for at least four years (Table 4.1). Their exact ages were not known but, as mentioned before (see Chapter 2), the fur colour of infants is so distinct that the estimated age is, therefore, close to their actual age. Of individual M4, M5 and F5, all were adults, M5 and F5 were paired while individual M4 lost his female partner during the course of this study and thus remained housed with his male offspring only.

Table 4.1: Personal information for each individual white-cheeked crested gibbon used in this study.

Age stage	Sex	Individual	Location	Birthday	Housing condition	Note
Juvenile	Male	M11	Endangered Primate Rescue Center	17/12/2002	A	Captive born
	Female	F7[1]	Endangered Primate Rescue Center	2001	B	Wild
	Female	F8[1]	Endangered Primate Rescue Center	2001	B	Wild
Sub-adult	Male	M7	Dusit Zoo	8/10/1999	A	Captive born
	Male	M8	Endangered Primate Rescue Center	1999	C	Wild
	Male	M9[1]	Endangered Primate Rescue Center	1999	B	Wild
	Male	M10	Nakhornratchasima Zoo	8/9/1998	A	Captive born
Adult	Male	M4	Nakhornratchasima Zoo	unknown	C[2]	Wild
	Male	M5	Chiangmai Zoo	unknown	B[2]	Wild
	Female	F5	Chiangmai Zoo	unknown	B[2]	Wild

A: The individual is housed together with its parents.
B: The individual is housed alone.
C: The individual is housed together with individual of the opposite sex.

[1]: The two females had died in July 2007 before the second field site visit. The male was then housed alone

[2]: The housing changed during the observation. The housing condition presented here is the original housing condition before the study conducted

4.2.2 Procedures

4.2.2.1 Development in juvenile and sub-adult white-cheeked crested gibbons

The study was conducted between 12 October 2006 and 25 April 2008 in four study sites located in Thailand and Vietnam. Individuals were sampled at three time points, with each time point being about three to six months apart from the next. Each individual was observed for a block of five days during each visit and his/her song recorded daily at pre-dawn or early to late morning (0500h-1100h) (Brockelman et al., 1993; Duckworth, 1998; Rawson, 2002).

A directional microphone (Sennheisser ME-66+K6) and a digital recorder (Marantz PMD-670) were used to record their song. All equipment was placed in front of the gibbons one day before the first recording started to habituate gibbons to the equipment.

4.2.2.2 Vocal plasticity in adult white-cheeked crested gibbons.

Three adult white-cheeked crested gibbons housed in Chiangmai Zoo (M5 and F5) and Nakhornratchasima Zoo (M4) were observed before and after the change of their social group. Individuals M5 and F5 (one adult male and one adult female) had been housed separately (no visual and auditory contacts) before they were paired (Table 4.1). The first recording was taken one week before they were paired. The second sampling period coincided with the time immediately after they had been housed together, and the third set of recordings were taken three months after they had been paired.

Individual M4 was initially housed together with his female partner and their one offspring. The first recordings were taken five months before the death of the adult female, the second recording point is one month after the death of the adult female and the third sampling point is one year after the death of the adult female. Each individual was observed and recorded for five consecutive days at each recording period.

4.2.3 Sound analysis

Song was analysed in two parts. In the first part of the analysis, all collected song phrases were analysed in terms of the parameters of song phrase usage. The parameters for analysis selected in males were 1) the total number of call phrases, 2) the duration of song, 3) the number of multi-modulated call phrases, 4) the number of boom call phrases, 5) the number of staccato call phrases, 6) the maximum number of notes within one staccato call phrase, 7) the number of types of sub-catalogued multi-modulated phrases used and 8) the number of “female-like” great call phrases (as illustrated in Fig. 4.1A). Female songs were analysed according to 1) the number of great call phrases and 2) the number of non-great call phrases, which was included single note call phrases and incomplete great call phrases (call notes were fewer than five within one call phrase).

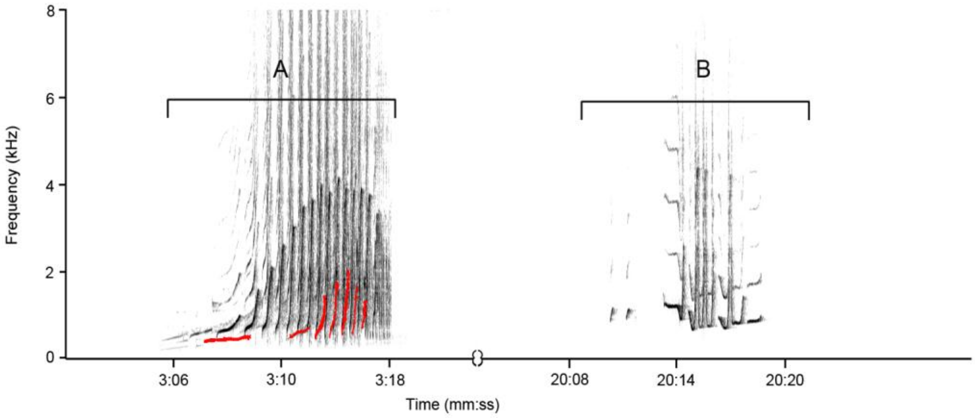

Figure 4.1: A represents the example of a female great call and male “female-like” great call phrases. The black call patterns represent the female great call phrases. The red colour call patterns represent the male juvenile’s “female-like” great call phrases. B represents the example of male song phrases produced by this juvenile. The contrast and color of the graph was modified to present the call patterns of two individuals. Both song sequences were taken from the same song. The x-axis represents the actual times in the complete song bout recording.

The second part of the analysis assessed acoustic features in the same manner as vocalisations of adult individuals were analysed in the previous chapter. These acoustic measures consisted of frequency and duration of each first note of the call phrases. The detailed description of each of these parameters was provided in the previous chapter (see Chapter 3, Table 3.5).

4.2.4 Statistics

All data were checked for normality using the Shapiro-Wilk test (significant level at 0.05). One-way repeated-measures analyse of variance (ANOVA) were used to determine whether or not the parameters of song usage and the acoustic parameters of song phrases changed across in any way the three sampling times. If the result of a test was significantly ($p<0.05$) different, then a post-hoc comparison (Turkey's HSD test) was undertaken. Measurements of acoustic features of each call phrase may have shown slight differences owing to variations in the condition of recording. When testing the differences in physical structure of vocalsiations, in order to avoid Type I error the probability for rejecting the null hypothesis was set at 0.01. Friedman-ranked test was used to test whether or not offspring produced their song before or after adult males sing the song.

4.3 Results

In total, 130 song bouts were collected from the three juveniles, four sub-adults and three adults. A total of 9,719 call phrases were obtained, with substantial variations in the number of call phrases used per individual (Table 4.2).

Table 4.2: The number of call phrases collected and analysed in each individual.

Age stage	Sex	Individual Number	No. of great call phrases	No. of non-great call phrases	No. of female-like great call phrases	No. of multi-modulated call phrases	No. of boom call phrases	No. of staccato call phrases	Total
Juvenile	Male	M11			55	694	232	260	1186
	Female	F7	6	40					46
	Female	F8	1	42					43
Sub-adult	Male	M7			12	629	147	142	918
	Male	M8			0	605	833	800	2238
	Male	M9			0	530	325	321	1176
	Male	M10			1	705	543	426	1675
Adult	Male	M4				599	458	320	1377
	Male	M5				464	218	218	900
	Female	F5	63	97					160
Total			70	179	68	4226	2756	2487	9719

4.3.1 Vocal development in juvenile white-cheeked crested gibbons

4.3.1.1 Development of acoustic features in the case of a juvenile male white-cheeked crested gibbon.

At the time of the first visit, this male juvenile (M11) was 4.5 years-old and produced only female-like great call phrases during the first two days of recording (Fig 4.1A), followed by male song phrases from the third day onwards of song recording. After he started to produce male song phrases, this individual produced either male song phrases, female-like great call phrases or both types of song phrases within the same song (Fig 4.1).

The number of multi-modulated call phrases of this juvenile increased significantly in song usage with increasing age ($F_{(2,5)}$=6.58, p=0.04) (Fig. 4.2A). However, there were no significant differences in the number of boom call phrases ($F_{(2,5)}$=2.26, p=0.20) or staccato call phrases ($F_{(2,5)}$=2.06, p=0.22). Duration of song also increased ($F_{(2,5)}$=6.14, p=0.045) (Fig 4.2B). No significant differences were found in the number of total call phrases ($F_{(2,5)}$= 3.83, p=0.098), the maximum number of notes within one staccato call phrase ($F_{(2,5)}$=3.88, p=0.096), or the number of sub-catalogued multi-modulated call phrases ($F_{(2,5)}$=3.6, p=0.108). It was to note that with regard to all parameters of song usage, variability in the early sampling point was much greater than it was in the later sampling points.

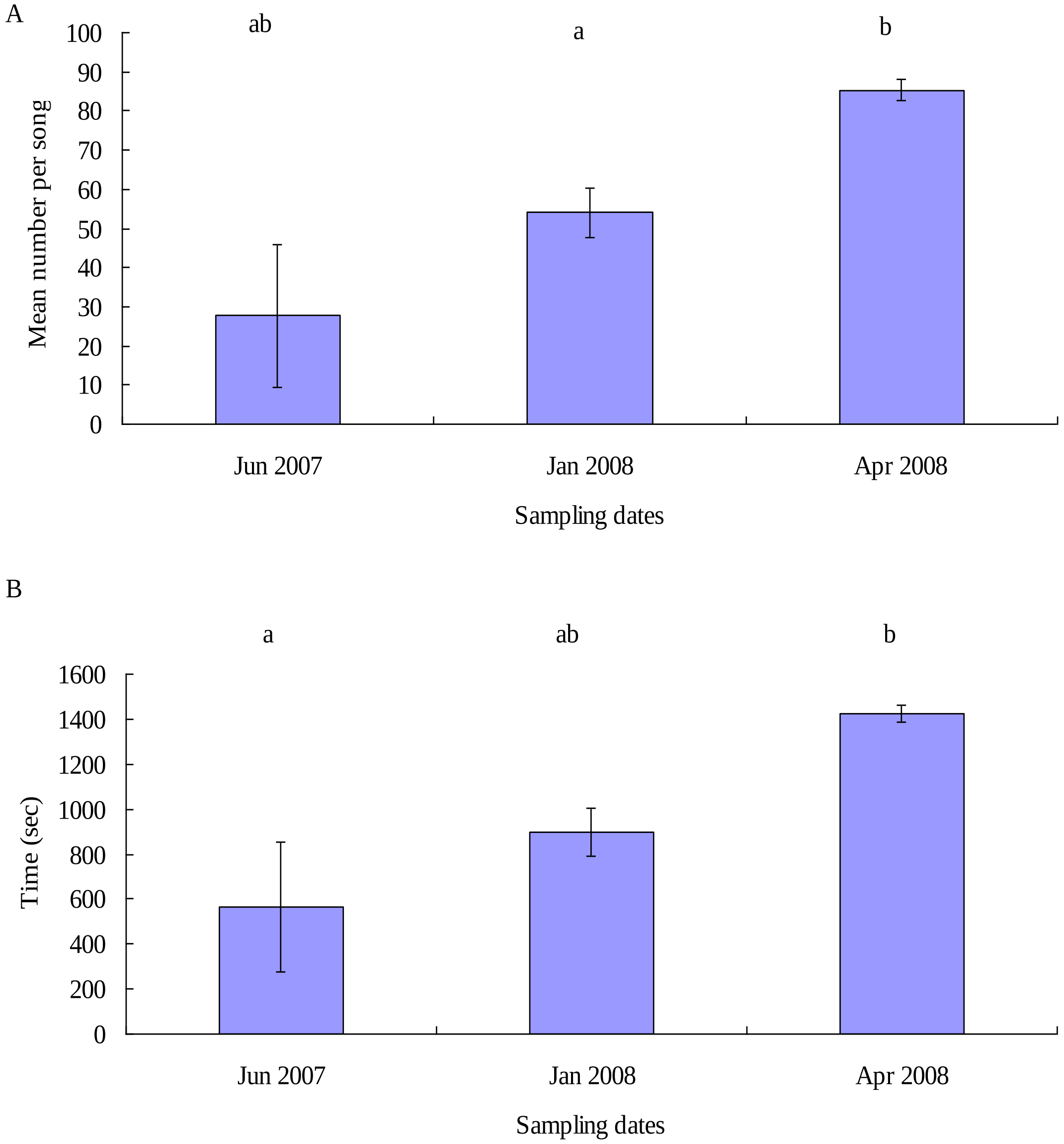

Figure 4.2: Changes of song parameters on the juvenile at different sampling time points. A represents the mean number of call phrases in the multi-modulated call phrases at different sampling time points. B represents the duration of song produced by the juvenile in different times. The bars represent the call phrases recorded in June 2007, January 2008 and April 2008, respectively. a and b differ at a significant value of .01 level in post-hoc (Turkey's HSD test) comparisons.

The acoustic features of the calls produced by the male juvenile in Endangered Primate Rescue Center (Table 4.2) also showed a significant change in the start frequency of multi-modulated, boom and staccato call phrases (multi-modulated: $F_{(2,238)}=70.46$, $p= 0.001$; boom: $F_{(2,115)}=5.66$, $p=0.005$; staccato: $F_{(2,84)}=24.67$, $p=0.001$) and the lowest/peak frequency of multi-modulated and staccato call phrases (multi-modulated: $F_{(2,238)}$=157.54, p=0.001; staccato: $F_{(2,84)}$=10.50, p=0.001) (Fig 4.3A-C). The peak frequency of boom call phrases showed no significant difference across the three sampling points ($F_{(2,115)}$=3.96, p=0.022). Similarly, the duration of all three types of call phrases produced by this juvenile showed no differences across the three sampling points (multi-modulated: $F_{(2,238)}$=1.32, p= 0.27; boom: $F_{(2,115)}$=1.37, p=0.26; staccato: $F_{(2,84)}$=4.64, p=0.12) (Fig. 4.3D).

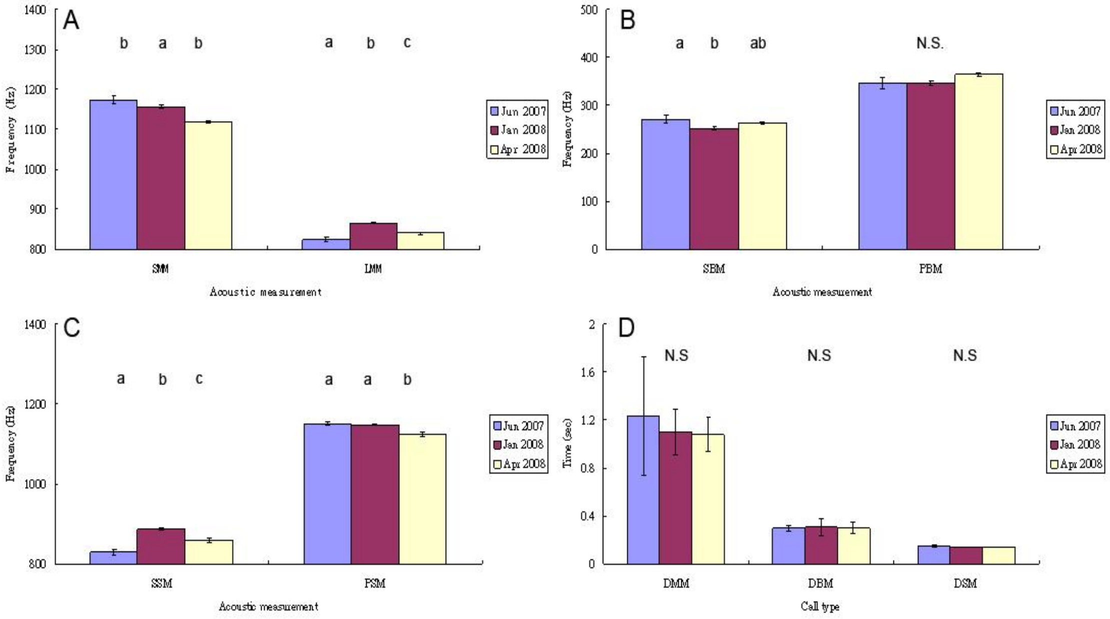

Figure 4.3: Changes of call parameters on the juvenile at different sampling time points. A) The start frequency (SMM) and lowest frequency (LMM) of multi-modulated call phrases, B) the start frequency (SBM) and peak frequency (PBM) of boom call phrases, C) the start frequency (SSM) and peak frequency (PSM) of staccato call phrases and D) the duration of multi-modulated (DMM), boom (DBM) and staccato (DSM) call phrases in the juvenile in EPRC at different sampling points. Each bar represents the call phrases recorded in June 2007, January 2008 and April 2008, respectively. a, b and c differ at a significant value of .05 level in post-hoc (Turkey's HSD test) comparisons.

4.3.1.2 *Comparison between two female juvenile white-cheeked crested gibbons*

Two female juveniles (F7 and F8: Table 4.1) that had been housed in the same enclosure since they arrived at the rescue center produced similar lengths of song ($F_{(1,2)}$= 0.52, p=0.55). The number of total call phrases and non-great call phrases produced by both individuals were also similar (total call phrases: $F_{(1,2)}$=3.00, p=0.23; non-great call phrases: $F_{(1,2)}$=0.57, p=0.53). However, one female produced a significantly lower number of great call phrases during the observation time ($F_{(1,2)}$= 25, p=0.038) (Fig. 4.4) than the others. Actually, this individual produced only one great-call phrase during the entire period of observation.

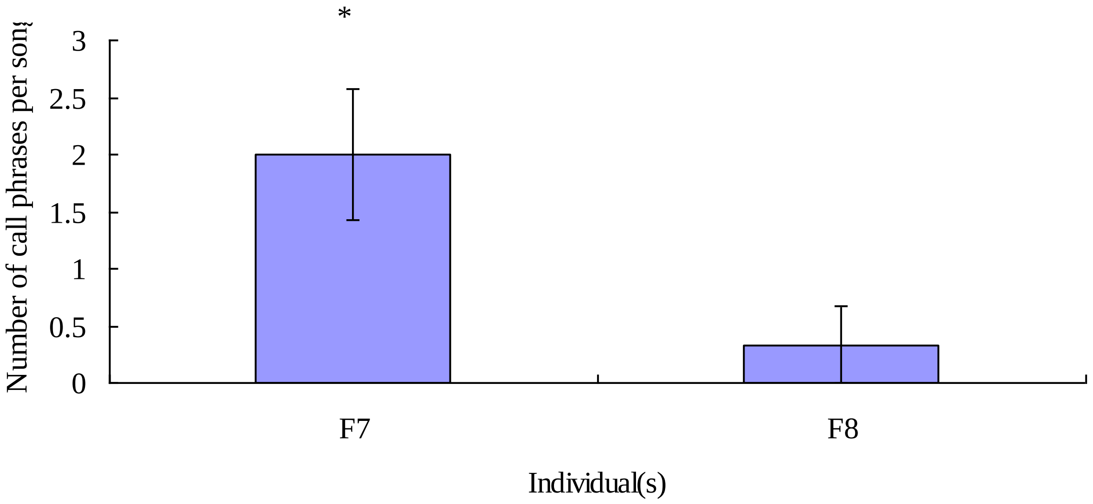

Figure 4.4: The great call phrases produced between two female juvenile white-cheeked crested gibbons in EPRC. Each bar represents the number of great call phrases produced by female individual F7 and female individual F8, respectively. Asterisk refers to significant value at .05 level.

4.3.2 Development of acoustic features in four male sub-adult white-cheeked crested gibbons

The social context of four sub-adults is varied. Female-like great call phrases and male song phrases were compared among the four sub-adult males to clarify the relationship of their song usage.

4.3.2.1 Female-like great call phrases of the four sub-adult males

Two of the observed sub-adult males (M7 and M10) produced female-like great call phrases at the first recording, but not in later visits. These two sub-adults were housed together with their parents. In contrast, the other two sub-adults (M8 and M9) which were not housed with their parents, produced no female-like great call phrases during any of the three site visits.

4.3.2.2 Comparison of male song phrases of four male sub-adults

Although these four sub-adult males were of a similar age, there were changes in song use that varied between individuals. Two sub-adults (M8 and M10) experienced changes in their social group. The females in both groups had died before my second visit, but both the sub-adult males showed a significant change in almost every parameter of song use compared to the first recording (M8: number of boom call phrases: $F_{(2,7)}=4.75$, $p=0.05$; number of staccato call phrases: $F_{(2,7)}=4.79$, $p=0.049$; number of total call phrases: $F_{(2,7)}= 4.99$, $p=0.045$; maximum number of notes within one staccato call phrases: $F_{(2,7)}=10.65$, $p=0.008$; M10: the number of multi-modulated call phrases: $F_{(2,8)}=9.57$, $p=0.008$; the number boom call phrases: $F_{(2,8)}=7.65$, $p=0.014$; the number of staccato call phrases: $F_{(2,8)}=7.89$, $p=0.013$; the number of total call phrases: $F_{(2,8)}=8.68$, $p=0.01$; the maximum number notes within one staccato call phrase:

$F_{(2,8)}$=4.98, p=0.039; duration of the song: $F_{(2,8)}$=6.24, p=0.023; calling rate: $F_{(2,8)}$=37.43, p=0.001) (Table 4.3). The sub-adult (M8) housed with two juvenile females (F7 and F8) in the semi-natural enclosure also changed the types of sub-catalogued call phrases used after the death of the two females (Table 4.4). Several complex sub-catalogued types (type E, F, I, L) of multi-modulated call phrases disappeared and changed to other types of sub-catalogued types (type G, H, K) of multi-modulated call phrases.

Table 4.3: The list of acoustic parameters measured for two sub-adult males. Mean±sem of each measured parameters was presented in each column. **Asterisk refers** significant value at .05 level.

Individual	M8		
Sampling point	First	Second	Third
Multi-modulated call phrases	37 ± 2.42	34 ± 1.60	35 ± 1.92
Boom call phrases	***22 ± 1.83**	**23 ± 3.56**	**21 ± 2.36**
Staccato call phrases	***22 ± 2.16**	**22 ± 4.09**	**20 ± 2.56**
Total phrases	***80 ± 5.75**	**79 ± 8.98**	**76 ± 5.88**
Max no. of notes within one staccato call phrase	***9 ± 0.37**	**14 ± 2.35**	**12 ± 1.14**
Duration of the song	644 ± 30.42	622 ± 50.07	594 ± 51.67
calling rate	7 ± 0.38	8 ± 0.35	8 ± 0.41
Individual	M10		
Sampling point	First	Second	Third
Multi-modulated call phrases	***59 ± 4.47**	**29 ± 4.02**	**54 ± 4.53**
Boom call phrases	***44 ± 4.92**	**21 ± 2.55**	**44 ± 4.66**
Staccato call phrases	***37 ± 4.19**	**14 ± 2.71**	**34 ± 3.86**
Total phrases	***139 ± 13.11**	**64 ± 9.03**	**132 ± 12.78**
Max no. of notes within one staccato call phrase	***7 ± 0.20**	**5 ± 0.63**	**6 ± 0.00**
Duration of the song	***1,008 ± 80.76**	**528 ± 92.77**	**961 ± 97.15**
calling rate	***4 ± 0.12**	**8 ± 0.65**	**3 ± 0.08**

Table 4.4: The types of sub-catalogued multi-modulated call phrases produced by the male adult in EPRC at the different sampling points. The three sampling points of social contexts are: i) before absence of the females (one month before the death of the two female conspecifics); ii) following the 5 months absence of the female adult (five months after the death of the two female conspecifics) ; iii) eight months after the two female conspecifics. Each column represents whether each type of sub-catalogued multi-modulated call phrases produced by the male during the observation period (five days).

Type of sub-catalogued multi-modulated call phrase	Before absence of female conspecifics	Following five months absence of female conspecifics	Eight months after absence of female conspecifics
A	○	○	○
B	○	○	○
C	○	○	○
D	○	○	○
E	○	X	X
F	○	X	X
G	X	○	○
H	X	○	○
I	○	X	○*
J	○	X	X
K	X	○	○
L	○	X	X

* There is only one call phrase of I-type multi-modulated call phrases recorded during five days of recording.

The other two sub-adults (M7 and M9) that had undergone no changes between visits showed only slight changes in their call usage. One sub-adult (M7) at Dusit Zoo only increased the number of staccato call phrases across the time points from 4±2.09 to 13±1.01 staccato call per song ($F_{(2,8)}$=4.74, p=0.044) and the solitary sub-adult in EPRC (M9) changed the maximum number of notes within one staccato call phrase from 7±0.63 to 5±0.37 notes per one staccato call phrase ($F_{(2,8)}$=4.78, p=0.043). No significant changes were found in the number of types of sub-catalogued multi-modulated call phrases in each song bout within each individual across the sampling times.

4.3.3 Comparison of song length and onset of song between adult males and their offspring (one male juvenile and two sub-adult males)

The relationship between the song produced by the male juvenile (M11) and the two sub-adults males (M7 and M10) and their father was investigated. The three male offspring showed a greater variability of song duration than the adult white-cheeked crested gibbons over the nine months to one year of observation (Fig 4.5). The juvenile in EPRC (M11) produced a significantly longer song than its father (adult: 682.5±32.79 sec per song; offspring: 990.9±125.48 sec per song)(Age: $F_{(1,18)}$=4.81, p=0.042), whereas the length of song produced by the other two sub-adults showed no significant differences compared to their father(s) (Dusit: $F_{(1,24)}$=0.05, p=0.82; Nakhornratchasima: $F_{(1.24)}$=1.12, p=0.23) (Fig 4.5).

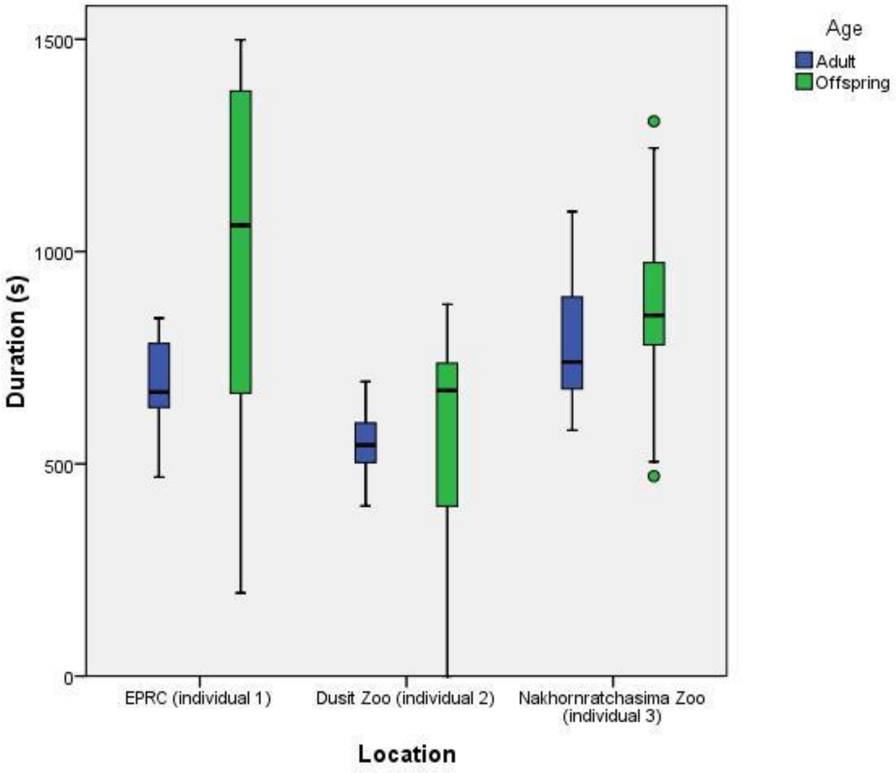

Figure 4.5: Boxplot of song duration, showing song duration of the male adult and its offspring in Dusit Zoo, EPRC and Nakhornratchasima Zoo, respectively. The blue bar represents the adult and the green bar represents the offspring.

The timing of onset of song between one juvenile and two sub-adults and that of the co-housed fathers were also compared. The results showed that both offspring in EPRC and Dusit Zoo rarely produced the song before the relevant adult male initiated it (Friedman rank test: EPRC X^2= 8.33 N=12, p=0.004; Dusit: X^2=11.27 N=15, p=0.001). However, the other male sub-adult (in Nakhornratchasima Zoo) often initiated the song before his adult father commenced singing, although no significant difference was found in comparison to the father (Friedman rank test: X^2=3.27, N=15, p=0.071; Fig 4.6). As mentioned before, the adult female in Nakhornratchasima Zoo died before the second visit and this affected the song usage of the sub-adult male individual. After exclusion of this recording period, the results showed that the sub-adult produced the song significantly earlier than the adult (Friedman rank test: X^2=6.40, N=10, p=0.011).

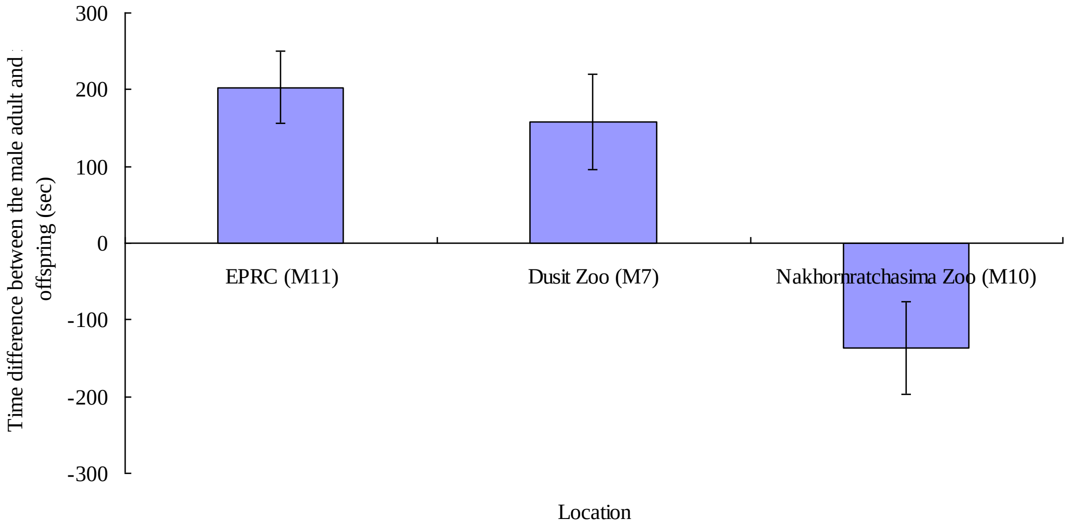

Figure 4.6: The mean initial singing timings of onset song of the juvenile and sub-adult white-cheeked crested gibbons compared to their parents. The zero time point was set as the time point when the adult male of the group starts to produce the song. Each bar represents the mean start singing time point of the white-cheeked crested gibbons.

Onset of song made by these offspring was assessed whether there were any changes over time. The results showed that, although the juvenile individual in EPRC produced the song much later after the adult male initiated the song, it gradually changed and across the recording sampling period (EPRC $F_{(2,5)}$=6.48, p=0.041), whereas other two sub-adults showed no significant changes between the sub-adult and its adult (Dusit $F_{(2,8)}$=3.15, p=0.098; Nakhornratchasima: $F_{(2,8)}$=2.01, p=0.20) (F4.7)

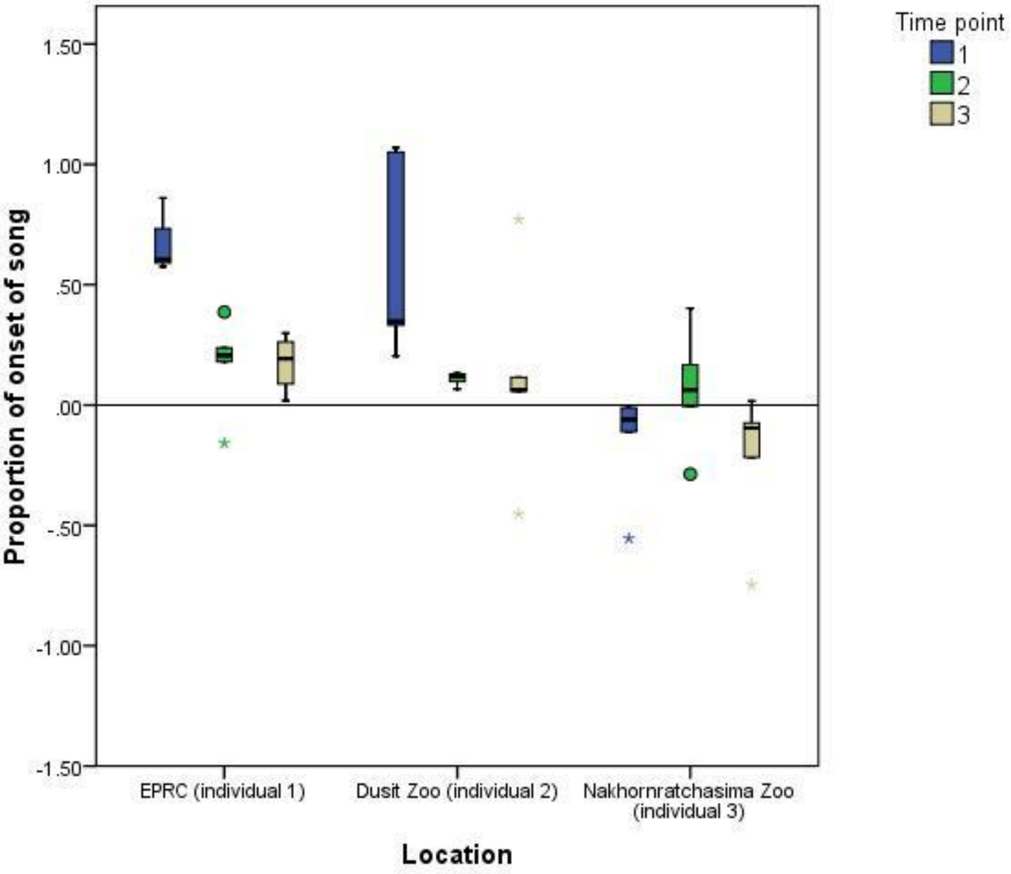

Figure 4.7: Boxplot of onset of song of the juvenile and sub-adult white-cheeked crested gibbons in Dusit Zoo, Nakhornratchasima Zoo and EPRC across three time points. The blue, green and yellow bars represent the first, second and third recording time point, respectively.

4.3.4 Vocal plasticity in adult white-cheeked crested gibbons

4.3.4.1 Vocal plasticity in adults before and after pairing

Two adult white-cheeked crested gibbons (one male and one female) were observed before, immediately after and three months after the pairing. The results of song phrases in adult males showed a significant change before and after pairing and this change remained three months after the pairing. The number of call phrases produced by the males actually increased after pairing from 26±14.43 to 75.6±8.29 phrases per song ($F_{(2,7)}$=21.64, p=0.001). Moreover, the variability in the number of song phrases produced became shrank as the pairing duration lengthened. A significant change of the number of song phrases was also found in multi-modulated call phrases ($F_{(2,7)}$=7.35, p=0.002), boom call phrases ($F_{(2,7)}$=25.52, p=0.001 and staccato call phrases ($F_{(2,7)}$=24.6, p=0.001). These three types of song phrases had the same trend of change after this male paired with the female.

The duration of the song also showed a significant change after pairing ($F_{(2,7)}$=9.23, p=0.011), and the variability in the song duration also decreased. The male white-cheeked crested gibbon increased the calling rate after being paired ($F_{(2,7)}$=8.83, p=0.012). However, although the number of song phrases and duration of song changed after pairing, the calling rate did not change once paired with the female. Additionally, the number of sub-catalogued multi-modulated call phrase types increased after pairing ($F_{(2,7)}$=4.58, p=0.053). The maximum number of notes within one staccato call phrase showed no significant changes before or after pairing ($F_{(2,7)}$=1.11, p=0.38). The male also produced two additional complex sub-catalogued multi-modulated call phrases after pairing (Table 4.5), and one additional simple type of sub-catalogued multi-modulated call phrase was found three months after the pairing.

Table 4.5: The types of sub-catalogued multi-modulated call phrases produced by the male adult in Chiangmai Zoo at the different sampling points. The three sampling points of social contexts are: i) before pairing (five days before the male moved to house with the adult female together); ii) after pairing (the fourth days after housing together); iii) three months afer (three months after two individuals housing together). Each column represents whether each type of sub-catalogued multi-modulated call phrases produced by the male during the observation period (five days).

Type of sub-catalogued multi-modulated call phrases	Before pairing	After pairing	Three months after
A	○	○	○
B	X	X	X
C	○	○	○
D	X	X	○
E	○	○	○
F	X	○	○
G	○	X	X
H	X	X	X
I	○	○	○
J	X	○	○
K	X	X	X
L	X	X	X

The female (F5) did not produce any call phrases during the observation period before the male was housed together with her. The female started to produced call phrases four days after pairing, although the results showed no significant changes in the total number of call phrases or non-great call phrases produced immediately after pairing, or three months after pairing (total call phrases: $F_{(1,7)}$=2.67, p=0.16; non-great call phrase: $F_{(1,7)}$=0.07, p=0.80). However, the female increased the number of great call phrases significantly even up to three months after pairing ($F_{(1,7)}$=17.09, p=0.009) (Fig 4.8). The duration of song phrases produced by the female did not change in the period from several days after pairing and three months after pairing ($F_{(1,7)}$=0.74, p=0.43).

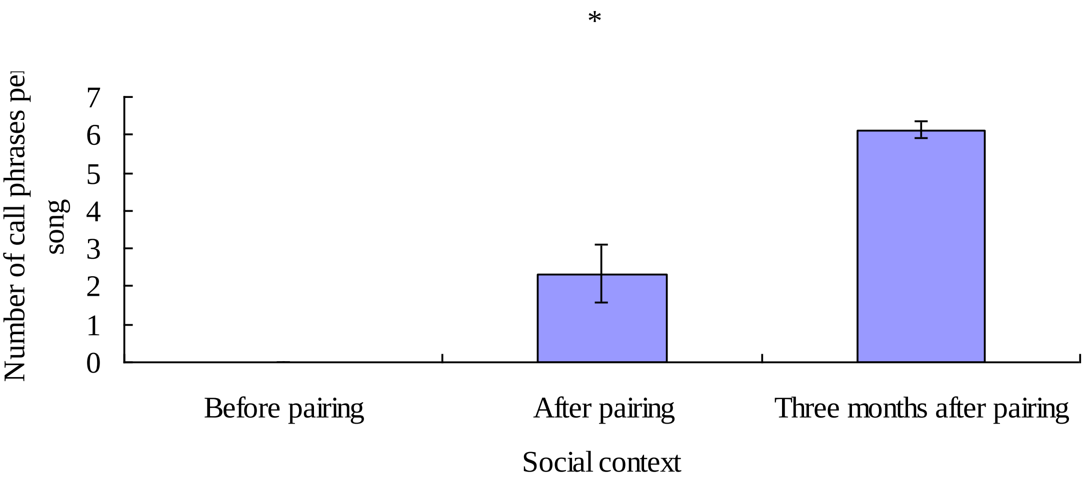

Figure 4.8: The number of call phrases produced by the female adult in Chiangmai Zoo before, after and three months after the pairing. Each bar represents the social status changes before and after the three months after pairing, respectively. Asterisk refers to significant value at .05 level.

4.3.4.2 Vocal plasticity in the adult male before and after the death of his female partner

The adult male housed in Nakhornratchasima Zoo (M4) reduced the number of each type of call phrases he produced after the death of the adult female, although no statistical differences were found between the sampling periods (multi-modulated call phrases: $F_{(2,8)}$=2.69, p=0.13; boom call phrases: $F_{(2,8)}$= 3.70, p=0.07; staccato call phrases: $F_{(2,8)}$= 0.46, p=0.646; total call phrases: $F_{(2,8)}$= 1.85, p=0.22; maximum notes within one staccato call phrase: $F_{(2,8)}$= 0.29, p=0.75; duration: $F_{(2,8)}$= 2.58, p=0.14; calling rate: 1.96, p=0.203). However, the male used a significantly fewer types of sub-catalogued multi-modulated call phrases in his song after the female had died ($F_{(2,8)}$= 4.98, p=0.039) (Fig 4.9). Table 4.6 shows the change of the types of sub-catalogued multi-modulated call phrases the male produced in Nakhornratchasima Zoo before, immediately after and one year after the death of his female partner. The result shows that this male did not produce any of his most complex multi-modulated call phrases (type J) after the death of the female.

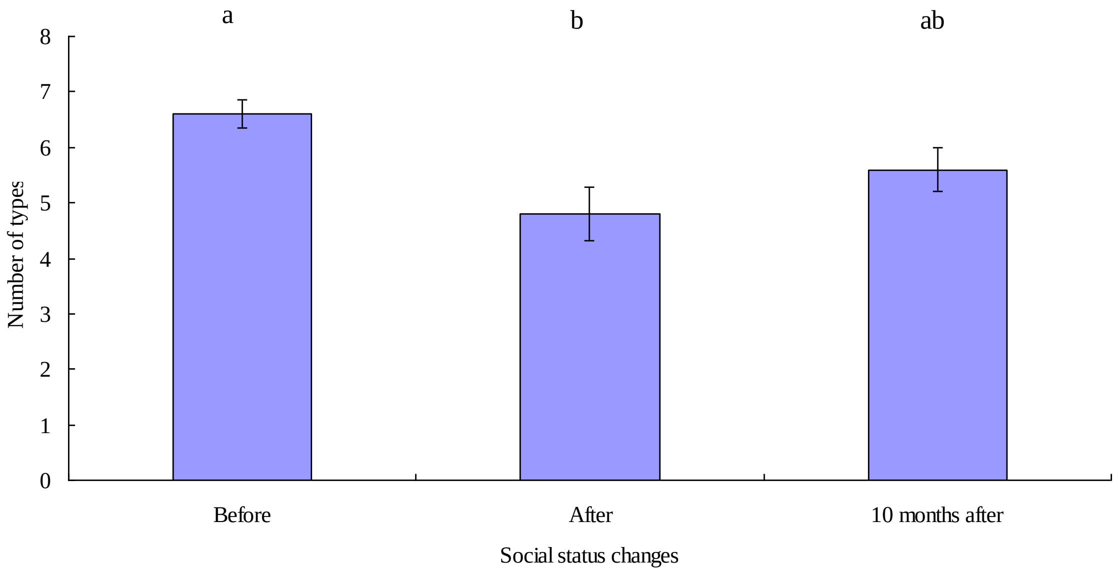

Figure 4.9: The number of sub-catalogued multi-modulated types produced by the white-cheeked crested gibbons before and after the change of social status. Each bar represents the number of types per song by the white-cheeked crested gibbon in the different social status. (A) and (b) differ at a significant value of .05 level in post-hoc (Turkey's HSD test) comparisons.

Table 4.6: The types of sub-catalogued multi-modulated call phrases produce by the male adult in Nakornratchasima Zoo at the different sampling points. The three sampling points of social contexts are: i) before absence of the female adult (six months before the death of the female); ii) after absence of the female adult (one month after the death of the female adult); iii) one year afer (one year after the death of the adult female). Each column represents whether each type of sub-catalogued multi-modulated call phrases produced by the male during the observation period (five days).

Type of sub-catalogued multi-modulated call phrases	Before absence of female conspecifics	After absence of female conspecifics	One year after
A	○	○	○
B	○	○	X
C	○	○	○
D	○	○	○
E	X	X	X
F	○	○	○
G	○	○	○
H	X	X	○
I	○	○	○
J	○	X	X
K	X	X	X
L	X	X	X

4.4 Discussion

Vocal development in gibbons has received very limited attention, with a few notable exceptions (Anderson et al., 2008; Merker et al., 1999; Uchikoshi, 2006). These published accounts report that development of the physical call characteristics occurs before the age of five, and propose that crested gibbons may produce a call structure similar to adults by two years of age. Results in the present study indicate that the acoustic features in the male juvenile showed no significant changes over nearly one year of observation. This result also supported with Seyfarth & Cheney's (1997) proposition that call production in gibbons may not be modified after early development.

This raises another question as to whether the usage of gibbon song can be modified in adulthood and Seyfarth & Cheney (1997) proposed that vocal production of gibbons is innate and is not modified during development. Snowdon et al. (1997) suggested that, to avoid missing all aspects of vocal development, studies in vocal development in humans, in non-human primates and in birds needed to consider all three aspects proposed by Seyfarth & Cheney (1997): vocal production, usage and response Previous theories on vocal development in gibbons were based exclusively on the results of experiments dealing with vocal production.

By taking account of the results of gibbon song use, rather than simply production, vocal development of gibbons may be different as what has been suggested in the literature with the data shown in the present study. The results here have demonstrated that “use” in gibbon song, at least in white-cheeked crested gibbons, continues to change even if individuals were considered mature. Males were found to produce female song phrases in early life as infants and juveniles and started to express male song phrases as early as four years of age. In my samples, the proportion of female song phrases declined while the proportion of male song phrases increased. This was observed even when the individuals reached the eight years of age. Such a shift is not exclusive to white-cheeked crested gibbons. However, the period of vocal development may vary from one gibbon species to another. For instance, in both *H. lar* and *H. agilis* males stop producing female song phrases before the age of five (Uchikoshi, 2006), whereas the individuals in the present study were found to produce female song phrases up to the age of eight. Uchikoshi (2006) also documented that males in both *H. lar* and *H. agilis* produce female-like great call phrases before the age of one year. These two individuals were hand-reared. They did not live with their biological mother until they were two years old, and have no chance to hear the great call produced by their biological mother. If the process of producing female-like great call phrases requires the learning from their mother or other adult females. These male infant gibbons should not be able to produce these female like great call phrases. This indicates that the development of song repertoire in the early stages may be independent of social contexts.

Females were found not to have the same vocal features as one another in the present study, although this may have been an experimental artifact, and may have been a consequence of not having been able to conduct the same amount of observations in females compared to males. Unlike males, females showed no song switching and spent more time in the development of their own sex-specific song phrases. Merker & Cox (1999) noted that the great call structure in young yellow-cheeked crested gibbons becomes increasingly similar to the great call produced by adult females by age of two. If this were the same for to white-cheeked crested gibbons, one might expect that the two female white-cheeked crested gibbons observed in the present study would produce complete great call phrases frequently. However, both females in EPRC rarely produced complete great call phrases in the songs recorded when they were five years old. It may be argued that the development of song phrases in white-cheeked crested gibbons may not be completed in the early stage (two-years old) as the literature has suggested. From the results it appears that song development in female white-cheeked crested gibbon juveniles may take at least five years. In fact, the whole process may not be completed within such a short period. Moreover, such development may be not only related to the age. Other factors may be involved with the process of development.

One question that remains regarding the process of song development in white-cheeked crested gibbon is how an individual develops the song completely. Although Snowdon et al. (p 237, 1997) proposed four models in the development of vocal production in primates, it did not include discussion on the possible development of call usage. Song behaviour was thought to be common in avian species, but not in non-human primates (Geissmann, 2000). The model proposed in birds, therefore, may be able to explain the vocal development in gibbons. Nelson & Marler (1994) proposed that song development in birds may follow two possible models. One model is that an individual may gradually increase the repertoire and usage of song with increasing age by acquiring elements from a tutor. The other model is that an individual expresses its full vocal repertoire and usage in early age and slowly shapes the usage and reduces the variability by practising it. The literature and my results showed that male *H. lar* and *H. agilis* are capable of producing a full repertoire by as young as 5 years old (Uchikoshi, 2006). This can occur even if individuals have no experience of living with their l fathers or other male conspecifics from birth to two years of age. This indicates that gibbons, at least in some *Hylobates* species, develop and express their song repertoire without acquiring elements from parents or conspecifics. The results of the male juvenile white-cheeked crested gibbon recorded in the present study showed that he first expressed a wide range of usage with high variability in song usage. After that, although the acoustic features of the call structure showed no significant changes over the period of observation, he gradually reduced the variability of song usage and the song he produced became more stable. This may indicate that the white-cheeked crested gibbon song may actually follow the second model that Nelson & Marler (1994) proposed.

Age may not be the only factor to affect the development of juvenile or sub-adult song. Four sub-adult males of similar ages were compared in the present study. Two of them (M7 and M10) had same housing conditions, whereas the other two (M8 and M9) had different housing conditions. Results of these two individuals (M7 and M9) showed no significant changes in their song usage over time although their housing conditions were different. In contrast, song usage had changed for the other two individuals (M8 and M10) whose social life had changed dramatically. If maturation is the main factor to affect song usage, the four sub-adults should have shown patterns of song similar to each other. These results therefore suggest that song usage in male white-cheeked crested gibbons may not only be affected by age, but also by changes of social conditions.

It is also to note the results in the timing of song produced in the offspring. The juveniles or sub-adults generally do not produce song before the parents initiate the song. Uchikoshi (2006) documented that infant gibbons (*H. lar* and *H. agilis*) who were hand-reared by human carers elicited their call when they heard the calling from the carer. After being returned to their mother at age of two, they still produce the vocalizations after hearing song or sounds made by their mothers, conspecifics and the human carer. In the present study, offspring do not initiate song until the age of eight.

It is not clear what makes sub-adults gradually modify the timing of their song within a group and start initiating their song. Two possible reasons have been hypothesized. First, studies in several *Hylobates* species showed that solitary males sang their solo song up to three hours earlier than the adult pairs produce their duet song (Geissmann, 2002a). They may do so to advertise themselves more successfully by choosing a time with less sound competition from paired individuals. Another possible reason is related to tolerance of adult males. Aldrich-Blake & Chivers (1973) suggested that an adult male siamang reduced his tolerance to the song of a sub-adult as sub-adult matured. In contrast, Sheeran (1994) found increased antagonism between the sub-adult and his natal group in western black-crested gibbons. There were no any agonistic or aggressive behaviour between sub-adult and adult males during the entire observation period. Thus, the result of the present study may support the hypothesis regarding the function of self-advertising, rather than the hypothesis relating to the reduction in conflict with adults. Further details regarding the primary function of song in white-cheeked crested gibbon will be discussed in the next chapter.

As discussed in the previous chapter, call use in adults was less variable than in other age groups in white-cheeked crested gibbons. This does not mean that there is no flexibility in their song use. In fact, two studies of *Hylobates* species have found that levels of plasticity in the song use change according to social context (Clarke et al., 2006; Inoue et al., 2008). The result from our study of the newly paired white-cheeked crested gibbons also showed significant change in call usage. Such change may not be completed over a few days period. It may actually take a relatively long period to adjust song usage. Similar findings have been observed in siamang, showing that newly paired individuals sing more incompletely than the beginning of pair formation (Geissmann, 1999) and that the family members have a better coordination of singing activity when they stay together longer (Aldrich-Blake et al., 1973; Maples et al., 1989). If these findings could be applied also to white-cheeked crested gibbons, it would be expected that white-cheeked gibbons should organise or modify their song flexibly in terms of social context or situation within the species-specific song repertoire. Two studies in *H. lar* and *H.*

muelleri found flux of the sequence of call elements or the timing of call phrases in association with different kinds of social events (Clarke et al., 2006; Inoue et al., 2008). In the present study, I was unable to test whether white-cheeked crested gibbon modify the sequence in the same way as *Hylobates* species. However, both males in the present study changed in the types of sub-catalogued multi-modulated call phrases after their social context had changed. This effect may be very quick as the adult male changed his call usage after pairing. The paired female also started to produce the great call sequence after hearing the male song phrases. In fact, this female stopped producing any great call or non-great call phrases after the individual has been relocated to the new housing place a year ago. A similar finding was also found in the adult male that underwent the loss of his female partner. The number of multi-modulated call phrases had reduced significantly, whereas boom and staccato call phrases showed no differences after the death of the female white-cheeked crested gibbons. Therefore, the change in the number of multi-modulated call phrases produced by the male white-cheeked crested gibbons may play a significant role in expressing their social context. Such changes may take effect quickly and may take time to reach a relatively stable stage; as shown in our study in both cases of male white-cheeked crested gibbons. Janik & Slater (2000) suggested that individuals were capable of responding to the partner’s call in the exact timing when they were duetting may have involved with usage learning. It is unclear whether such kind of learning process was applied to the coordination of duet song on white-cheeked crested gibbons. Further investigations on this topic were needed.

Overall, the present study has provided evidences on the change in song usage of the different social context in white-cheeked crested gibbons. This kind of changes may be involved with both age and social factors. Moreover, the length of usage change may take time to reach its stability. A certain level of vocal plasticity has been observed on white-cheeked crested gibbons, especially in males. Long term study is needed to investigate further details of song usage in association with interaction between maturation of individuals and changes of social context.

Chapter 5

Primary Function of Song in White-cheeked Crested Gibbons (*Nomascus leucogenys*)

5.1 Introduction

The roles of gibbon song have been discussed for several decades. Several possible functions, including territory defense, pair-bonding and mate attraction have been suggested in previous studies (Chivers et al., 1977; Mitani, 1987a; Mitani, 1987b; Raemaekers et al., 1985). However, the interaction between different groups has rarely been observed in the wild (1985a). Mitani (1990) suggested that using audio playback may simulate group interactions. Several studies have played back calls to gibbons in the wild (Mitani, 1984; Mitani, 1985a; Mitani, 1987a; Mitani, 1987b; Raemaekers et al., 1985) and in captivity (Haraway et al., 1988; Maples et al., 1988) to explore the function of song in different settings.

Previous studies using field observations and playback experiments have uncovered several patterns when gibbons hear other gibbons' song. A study on lar gibbons (*Hylobates lar*) found that they tend to sing longer when other individuals are singing simultaneously (Brockelman & Srikosamatara, 1984). Another experiment on a captive male Mueller's gibbon (*H. muelleri*) also found that the captive male increased singing rate when the playback frequency of the playback sound samples of other gibbons was increased (Maples et al., 1988). Studies in *H.*

species suggested that they tend to respond to the same species song rather than other gibbon species song (Haraway et al., 1988; Mitani, 1987a). Mitani (1987a) found that wild agile gibbons (*H. agilis*) do not respond to the song of Mueller's gibbons (*H. muelleri*), but do respond to songs of other agile gibbons from other regions. Haraway *et al.* (1988) also found that captive Mueller's gibbons tend to respond to their own species' song rather than other species. Thirdly, sex-specific song tends to stimulate same sex individuals other than individuals of the opposite sex in *H. agilis* and *H. lar* (Mitani, 1984; Raemaekers et al., 1985).

All previous studies relating to song function in gibbons have been conducted on *Hylobates* species. There is no clear evidence to suggest that the playback procedures used in these studies would produce similar results in crested gibbons. Some observations conducted in wild western black-crested gibbons (*N. concolor*) showed that their song may not necessarily elicit song from conspecific neighbours. A preliminary playback test on two pairs of white-cheeked crested gibbons housed in the same zoo was no vocal responses (Ruppell, 2007a). These results suggest that the song function of *Nomascus* species may be different to that of *Hylobates* species.

Another failing of the previously-mentioned gibbon studies was that they tested the gibbons only when they were not singing. As mentioned above, the observation in lar gibbons was that they produced longer songs when other conspecifics were singing. Given these results, it may therefore be interesting to test whether the playback sample affects the vocalisations or other behaviour of white-cheeked crested gibbons while they are singing.

Three questions were asked relating to the song function of white-cheeked crested gibbons: 1) Do white-cheeked crested gibbons express any behaviour changes before, during and/or after their song? 2) Does song of conspecifics, other gibbon species or other animals affect the song context or behaviour of white-cheeked crested gibbons when they are singing? 3) Do playback samples elicit a vocal or non-vocal response? If so, what kind of playback sample is most likely to elicit a response?

Because of the limitations of the captive environment of our study animals, the present study did not aim to determine the precise function of song in white-cheeked crested gibbons. Such limitations mean that the white-cheeked crested gibbons I studied had fewer opportunities to express social interaction than other groups. However, while acknowledging these constraints, the present study was designed to explore the possible functions of song in white-cheeked crested gibbons.

5.2 Materials and Methods

5.2.1 Materials

Five pairs of white-cheeked crested gibbons housed in Thai zoos and Endangered Primate Rescue Center, Vietnam, were selected for the present study (Table 5.1). Two of the pairs lived with their offspring, and the other three pairs were housed only with their partner. The duration of pairing of these gibbons ranged from four months to ten years. All adult individuals were wild caught. The group of gibbons in Vietnam was housed with conspecific members with which they had visual and audio contact. In contrast, the other pairs of gibbons were not in the vicinity of other groups of conspecifics.

Table 5.1: Housing, duration of pairing and presence of offspring in the tested groups.

Group	Offspring	Housing condition	Pairing period (years)
Dusit Zoo	1	Cage	15
Chinagmai Night-Safari	None	Island	10
Endangered Primate Rescue Center	2	Cage	14
KhaoKheow Open Zoo	None	Island	2
Chiangmai Zoo	None	Cage	0.3

5.2.2 Playback song selection

Five different kinds of song samples were selected to playback in two sections. Unlike previous studies on other *Hylobates* species, white-cheeked crested gibbons do not have other sympatric gibbon species in the wild. Yet the present study also aimed to test whether white-cheeked crested gibbons express similar species-specific responses to the song. The song of lar gibbons, one of the most common gibbon species, was also included in the playback study. Additionally, Mitani (1990) suggested that calls from non-gibbon species need to be included in the playback sample as a control to check whether the response of the animal was affected by the playback procedure and apparatus. Haraway et al (1988) also followed a similar procedure while testing a captive gibbon. Therefore, a control playback sample (bird song) was also included in the present study.

The *duet song*, *male solo song* and *female solo song* sample of white-cheeked crested gibbons were recorded from a pair of wild caught white-cheeked crested gibbons housed in Melbourne Zoo (Melbourne, Australia) in October 2007. This pair had been together since 1983 and had had two offspring. A sample of *duet song* included one song section containing all necessary elements included all three types of male song phrases: 1) boom call, 2) staccato call, 3) multi-modulated call phrases and 4) the female great call phrase.

The sample of *male solo song* contained a sequence of boom, staccato and varied kinds of multi-modulated call phrases. The sequence of the song followed the rule that the boom call phrase was produced first, followed by the staccato call phrases and multi-modulated call phrases proposed by Haimoff (1983).

Female solo song sample included one to two call phrases containing two non-great call phrases and several great call phrases. Haimoff (1984a) suggested that females mainly contribute great call phrases to the duet song. This great call phrase may serve an important function within song because males tend to produce a multi-modulated call phrase in response to this great call phrase (Geissmann, 2002a). In addition, females also produce some call phrases containing one or two call elements. These features were included in the sample of female solo song.

The sample of *lar gibbon duet song* was recorded at Khao Kheow Open Zoo (Chonburi, Thailand) in March 2007. The edited sample contained a sequence of male song phrases, female great call and a male song response, as known as “coda”. All tested gibbons except for those housed in Vietnam have been exposed to lar gibbon song as they had lar gibbon conspecifics housed in the same zoo.

The *control* sample was taken from a recording of a native bird species, *Eudynamys scolopacea*, distributed broadly to South-East Asia (Fig 5.1). The frequency of call structure ranged from 0.95 to 1.47 kHz, and the duration was between 0.63 to 1.02 seconds. The interval between two song elements was 2.02 ± 0.08 (n = 20) seconds. Their song contained only one simple but loud element. This pattern presented the clearly different pattern to the gibbon song. Therefore, it could be used to assess whether white-cheeked crested gibbon simply responded to all playback samples or they could actually discriminate the type of playback.

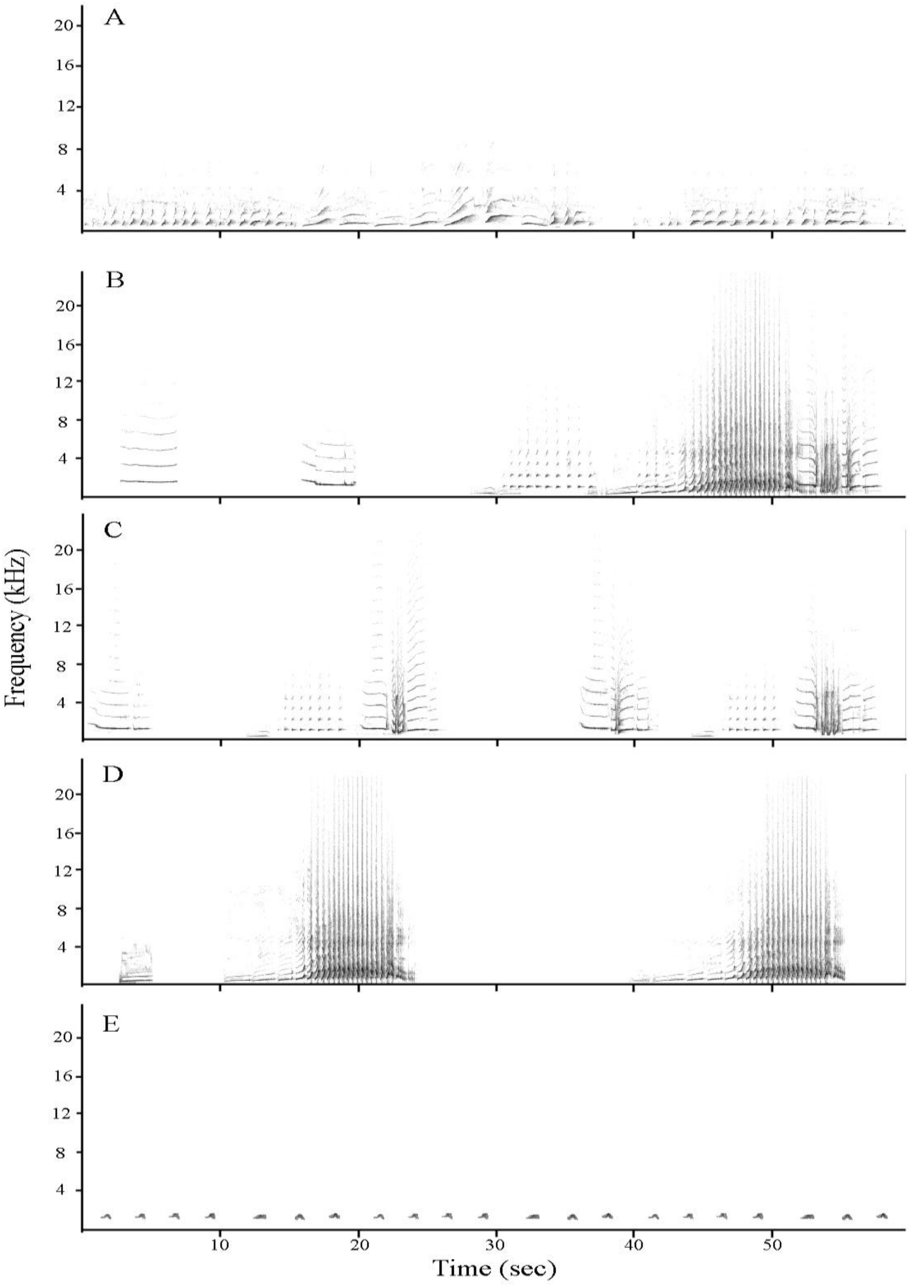

Figure 5.1: The sonogram of playback samples. A, lar gibbon song. B, white-cheeked crested gibbon duet song. C, male solo song of white-cheeked crested gibbon. D, female solo song of white-cheeked crested gibbon. E, the control sample (bird song). The sonogram sample here is only 1 minute long, but this represents the detail of the entire song sample as the context of the second minutes is the same that of as the first minute.

5.2.3 Procedure

5.2.3.1 Pre-playback experiment observation

The current experiment was conducted from 22nd August 2006 and 17th June 2007. Behaviour of each observed individual was scored before, during and after they produced the song. Pre- and post-singing sessions were scored for ten minutes in each session, and the during-singing session depended on the actual singing time for each gibbon pair made. The observation starting time was 30 to 60 minutes earlier than the gibbon actual singing time, so the exact ten minutes pre-song period can be calculated. Vocalisations and non-vocal behaviour listed in section 5.2.4 were scored. All scored behaviours were transformed into percentages to standardise the variable singing time in each singing session.

5.2.3.2 Playback experiment observation

The playback experiment was conducted from 23 December 2007 to 31 March 2008. Samples were played back in two sessions: 1) during and 2) after the testing gibbon song on each testing day. An additional control sample (bird song) was played back in the second session. There was only one sample selected randomly to playback in each session. Two sessions were performed every testing day. There was a two hours interval between two sessions in the same day. Each pair of white-cheeked crested gibbons was tested with a total nine of treatments over a one week period.

A portable audio player (Sony CFD-F17CP) was used to play selected song samples back and was placed about 10 meters from gibbons’ gibbons. The amplitude of playback samples was set at the peak level of 70-80 dB (measured by Precision Sound Level Meter Type 2206, Bru¨el & Kjær,Nærum, Denmark, fast sample, A frequency). The five selected song samples were 1) male song; 2) female song; 3) duet song; 4) other gibbon species song (Lar gibbons) and 5) a control song sample (native avian species). Each sample lasted two minutes and contained sequences similar to those gibbons produced. The only exception was the female solo song, which had shortened the interval between two great call phrases from 2-3 minutes to 15 seconds to standardise the length of playback song sample. The order of the playback samples was randomised.

Session 1: This playback was conducted after gibbons had begun to produce their song behaviour. Behaviour was scored ten minutes before gibbons produced song. Once the female gibbon completed her first great call phrase and the male responded to the great call phrase, the sample was played back to the pair. The song sample was played back in a two minute period. If the gibbons did not stop singing when they heard the playback song sample, the behavioural observation was continued until they finished singing and scored another ten minutes as the post-song stage. If gibbons stopped singing during or after playback, the behaviour observation was continued only for the following ten minutes.

Session 2: This playback was conducted two hours after the gibbons completed their first song of the day. Behaviour was scored ten minutes before playing back the sound sample. The song sample was played back in a two minute period. If gibbons did not stop singing, the behavioural observation was continued until they finished their singing and scored their behaviour for another ten minutes as the post-song stage. If gibbons stopped singing during or after playback, the behaviour observation was continued only the following ten minutes.

Visual and vocal behaviour was scored including 1) attention (defined as an individual turning its head to the sound source, while the body position remained the same or movement froze), 2) approach (defined as an individual move toward the sound source), 3) agonistic behaviour (defined as an individual presenting its teeth or shaking a branch) and 4) singing. The number of individuals paid attention or approached the sound source were also recorded.

5.2.4 Behaviour recording

White-cheeked crested gibbons performed a series of different types of behaviour. Most behaviour observed in captivity was related to the individual itself although a few types of behaviour involved social interaction. The definitions of scored behaviours are listed in Table 5.2.

Table 5.2 The definition of each scored behavior catalogued and recorded before, during and after white-cheeked crested gibbons produced a song.

Behaviour	Definition
Brachiation	An individual moves itself mainly by using its hands. This behaviour particularly occurred when an individual moved around the tree branches and it sometimes may involve use of the legs.
Hanging	An individual maintains its position by using only its hand.
Walking	An individual moves itself on the branches of a tree or on the ground by using only its legs. Any movements combined with using hands do not score as walking.
Sitting	An individual sits on the branch or ground, and the individual did not use its hands to assist with balance.
Grooming	An individual uses its hands, legs or mouth to groom any part of its body or another individual.
Feeding	An individual intakes any food in the enclosure where it lives.
Social contact	An individual shows any kind of attempt, excepted for grooming, to interact and receives response from another individual.

5.2.5 Statistics analysis

A Friedman test was employed to determine whether or not gibbons expressed behaviour differently according to the stage of singing (before, during and after song). A Wilcoxon signed-rank test was then employed to test whether the behaviour was expressed differently between the first and second playback sessions of a day. A Cochran test was applied to test whether gibbons have different kinds of response to different playback samples (Mitani, 1987a). A McNemar test was employed to test the difference between two playback samples if the result of Cochran test was significant (Mitani, 1987a).

5.3 Results

5.3.1 Behaviour observation before, during and after song without sound playback

All duet songs were produced in the early morning. The earliest time the gibbon pairs were observed to produce song was at 0455h, and the latest time that they started to produce the duet song was at 0734h.

There was no discernable stimulus event that prompted the gibbons to produce their song. The observed pair of white-cheeked crested gibbons housed in the Endangered Primate Rescue Center, Vietnam, was the only pair housed with other conspecifics remained audio contact. This pair never initiated their duet song until other groups of gibbons started singing.

Seven catalogued behaviours were scored (Table 5.3). The white-cheeked crested gibbons spent more than 70% of observation time sitting. Three types of locomotion behaviour (brachiation, hanging and walking) ranged from 7% to 18% before, during and after singing. Grooming and feeding behaviour occupied less than 5% of time in each recording section. Individuals had little or no social contact between group members before, during and after song. Therefore, social contacts were excluded as it was not possible to conduct statistical analyses on these data.

Table 5.3: Each scored behavior expressed by the gibbons before, during and after singing (mean ± sem)

	Recording sessions		
Scored Behaviour	Before	During	After
Brachiation	6.4 ± 1.1	5.0. ± 1.9	8.0 ± 2.5
Hanging	4.2 ± 1.7	1.5 ± 0.7	7.9 ± 2.2
Walking	1.3 ± 0.5	0.3 ± 0.2	2.2 ± 1.0
Sitting	79.5 ± 3.2	89.8 ± 3.0	71.8 ± 4.9
Grooming	3.6 ± 1.6	1.8 ± 0.5	5.3 ± 1.5
Feeding	4.0 ± 1.3	1.6 ± 0.7	4.7 ± 1.6
Social contact	1.1 ± 1.0	0.0 ± 0.0	0.1 ± 0.1

The gibbons spent significantly more time sitting while they were singing than following completion of singing (Wilcoxon signed rank test, z= 2.191, p= 0.028). Hanging behaviour also increased significantly after singing (Wilcoxon signed rank test, z= 2.395, p= 0.017; Fig. 5.2). No statistical differences were found for other scored behaviours although the amount of time spent was increased after completing singing.

Although the gibbons reduced various behaviour other than sitting, it was noted that all gibbons tended to move to the canopy of trees or the top of cages when they started to produce the song. None of the individuals were found to produce the song on the ground of the enclosure. The individuals started to leave their position after they had finished singing.

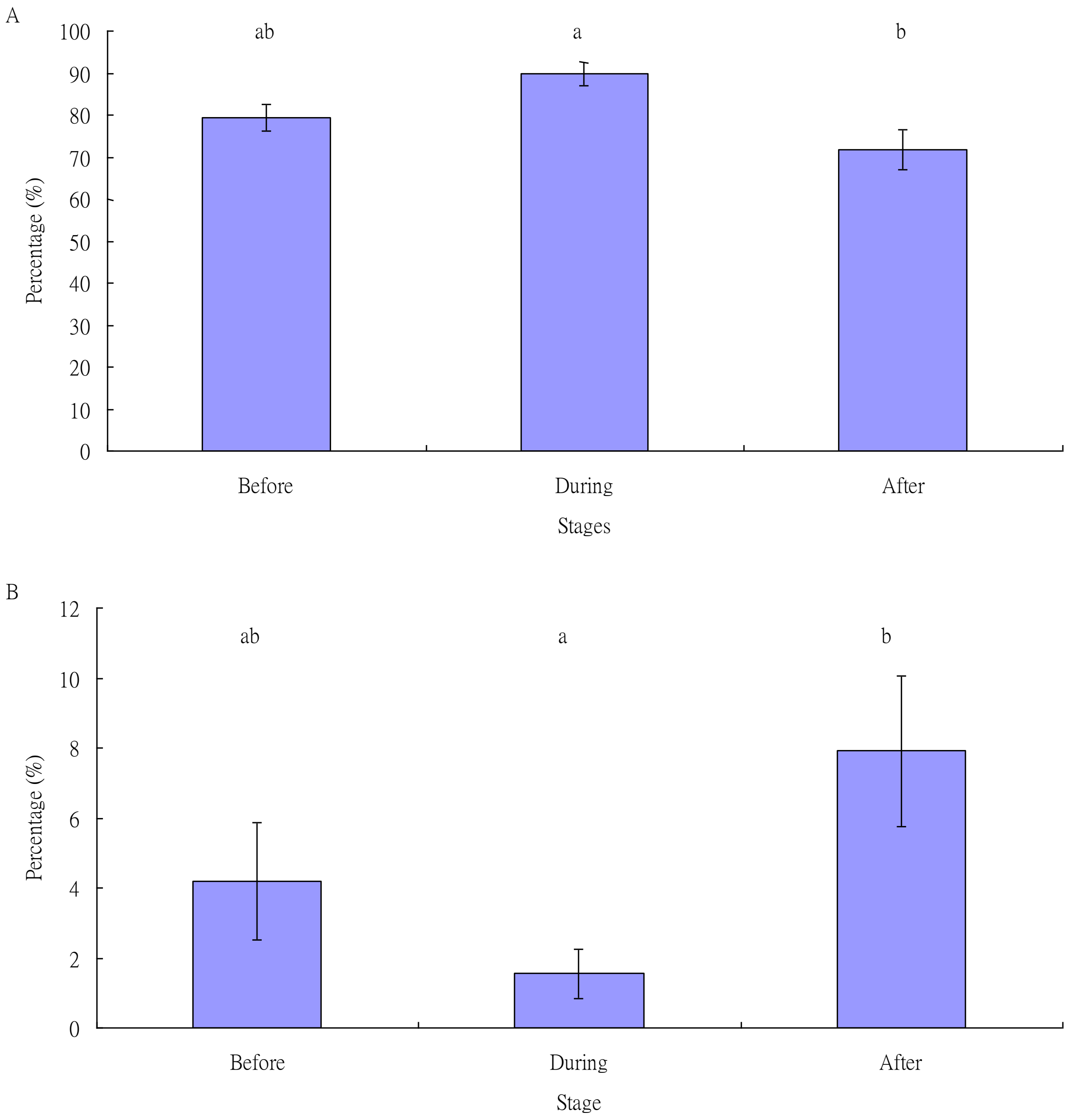

Figure 5.2: Behaviour of white-cheeked crested gibbons changes before, during and after sing. (A) represents the percentage of sitting behaviour changed before, during and after singing (mean + sem). (B) represents percentage of hanging behaviour changed before, during and after singing (mean + sem). a and b refer to significant difference at .05 level of Wilcoxon signed rank test.

5.3.2 Vocal and non-vocal response to playback samples

None of the tested gibbons stopped singing or were interrupted by playback samples equally. No agonistic or vocal responses other than song behaviour were expressed in response to playback samples. Most of the pairs (four of five testing pairs of white-cheeked crested gibbons) paid attention to the playback duet song rather than to other playback samples. There were no significant differences to each scored response in terms of playback samples (first attention: Cochran's Q= 4.00, p= 0.750; second attention: Cochran's Q= 6.00, p= 0.250; first approach: Cochran's Q= 6.00, p= 0.156; second approach: Cochran's Q= 6.00, p= 0.250) (Table 5.4).

Table 5.4: Attention and approach of white-cheeked crested gibbons to the different playback sound samples, while the white-cheeked crested gibbons produced their song. Five playbacks per sample were conducted.

	Playback Samples			
	Lar gibbon duet song	White-cheeked crested gibbon Duet song	Male white-cheeked crested gibbon solo song	Female white-cheeked crested gibbon solo song
First individual attention	2	4	3	3
Second individual attention	0	4	2	1
First individual approach	2	2	1	2
Second individual approach	0	0	0	0

Similar results of response to the playback samples were also found in Section 2. Among the five playback samples, the sample of bird song did not elicit any responses during and after the playback (Table 5.5). Three pairs paid attention to the lar gibbon song, but of these only two approached the sound source. All individuals paid attention to all white-cheeked crested gibbon song samples, regardless of the context (duet song, male solo or female solo song). However, only the sample of duet song elicited one of the individuals in each pair to approach the sound source. Duet song and female solo song of white-cheeked crested gibbons triggered the three of five tested pairs to produce the song. Male solo song of white-cheeked crested gibbon and lar gibbon duet song elicited two and one song, respectively. It was to note that the pair that gave song in response to the lar gibbon playback song sample, was newly paired and also produced song in response to all gibbon song playback samples. Moreover, all elicited song was initiated by adult individuals only.

Table 5.5: Attention, approach and song producing of white-cheeked crested gibbons to the different playback sound samples two hours after the white-cheeked crested gibbons produced their song. Five playbacks per sample were conducted.

	Playback Samples				
	Lar gibbon duet song	White-cheeked crested gibbon Duet song	Male white-cheeked crested gibbon solo song	Female white-cheeked crested gibbon solo song	Bird sound
First individual attention	3	5[a]	5[b]	5[c]	0
Second individual attention	3	5[a]	5[b]	5[c]	0
First individual approach	2	5[a]	3	3	0
Second individual approach	1	0	2	0	0
Song producing	1	3	2	3	0

[a]: $p < 0.03$, one-tailed McNemar test for changes in response between white-cheeked crested gibbon duet song and bird song playbacks.

[b]: $p < 0.03$, one-tailed McNemar test for changes in response between male white-cheeked crested gibbon solo song and bird song playbacks.

[c]: $p < 0.03$, one-tailed McNemar test for changes in response between female white-cheeked crested gibbon solo song and bird song playbacks.

Three of the five pairs produced the song after the sample of white-cheeked crested gibbon duet song was played back. The results showed hanging, sitting and grooming behaviour were expressed differently in the three recording stages in section 2 when the duet song sample was played back (Friedman test: Hanging: $X^2=7$, df=2, p=0.03; Sitting: $X^2=8.33$, df=2, p=0.016; Grooming: $X^2=8.33$, df=2, p=0.016). The Wilcoxon signed-rank test showed that these individuals reduced the percentage of time sitting in the same position after they produced their song, whereas hanging and grooming behaviour increased significantly (z = 2.201, p=0.031 two-tailed; Fig. 5.3A-B).

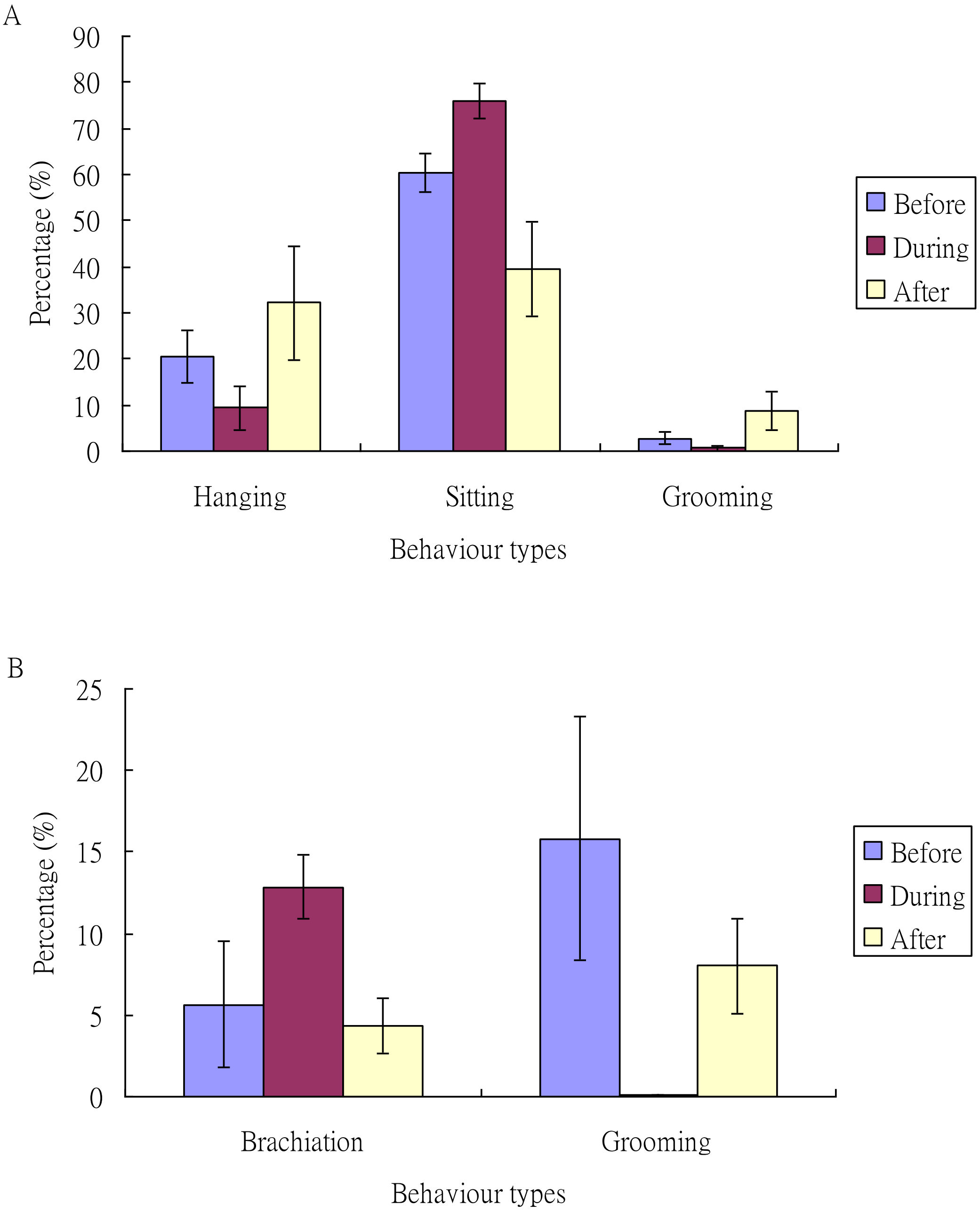

Figure 5.3: Responses to white-cheeked crested gibbon duet song playback sample. A, the proportion of scored behaviour expressed by the white-cheeked crested gibbons before, during and after song eliciting by the playback sample of duet song. B, the proportion of scored behaviour expressed by the white-cheeked crested gibbons before, during and after song eliciting by the playback sample of female solo song. Only behaviours with significant changes present in the figure. The purple, read and yellow bars represent before, during and after song producing elicited by the playback sample of white-cheeked crested gibbon duet song.

The context of song produced by the white-cheeked crested gibbons in different sessions was assessed (Fig 5.4A). The tested gibbons did not change their singing whether they heard playback song samples or not (Friedman test: $X^2 = 5.440$, df = 4, p = 0.245). However, gibbons did respond differently to the playback samples in the second session of the day. The duration of song elicited by the duet song samples was significantly shorter than these song produced spontaneously (Wilcoxon signed rank test. Z = 2.023, p = 0.043 two-tailed).

The number of call phrases contained in the song between the first and the second session was also assessed (Fig 5.4B). The results showed that white-cheeked crested gibbons produced significantly lower numbers of call phrases when their song was elicited by duet song and female solo song samples compared to the song produced spontaneously (Wilcoxon signed rank test. duet song: Z = 2.023, p = 0.043, female solo song: Z = 2.023, p = 0.042 two-tailed).

The calling rate was also compared between the first and the second session in each playback sample (Fig 5.4C). The results showed that white-cheeked crested gibbons sing slower when their song was elicited by the playback samples than when they sang spontaneously (Wilcoxon signed rank test duet: Z = 2.023, p = 0.043; male solo song Z = 2.023, p = 0.043; female solo song: Z = 2.023, p = 0.043 two-tailed). There were no significant differences in the calling rate when they produced the song with or without hearing playback samples (Wilcoxon signed rank test duet: Z = 405, p = 0.686; male solo song Z = 1.753, p = 0.08; female solo song: Z = 0.135, p = 0.893, two-tailed).

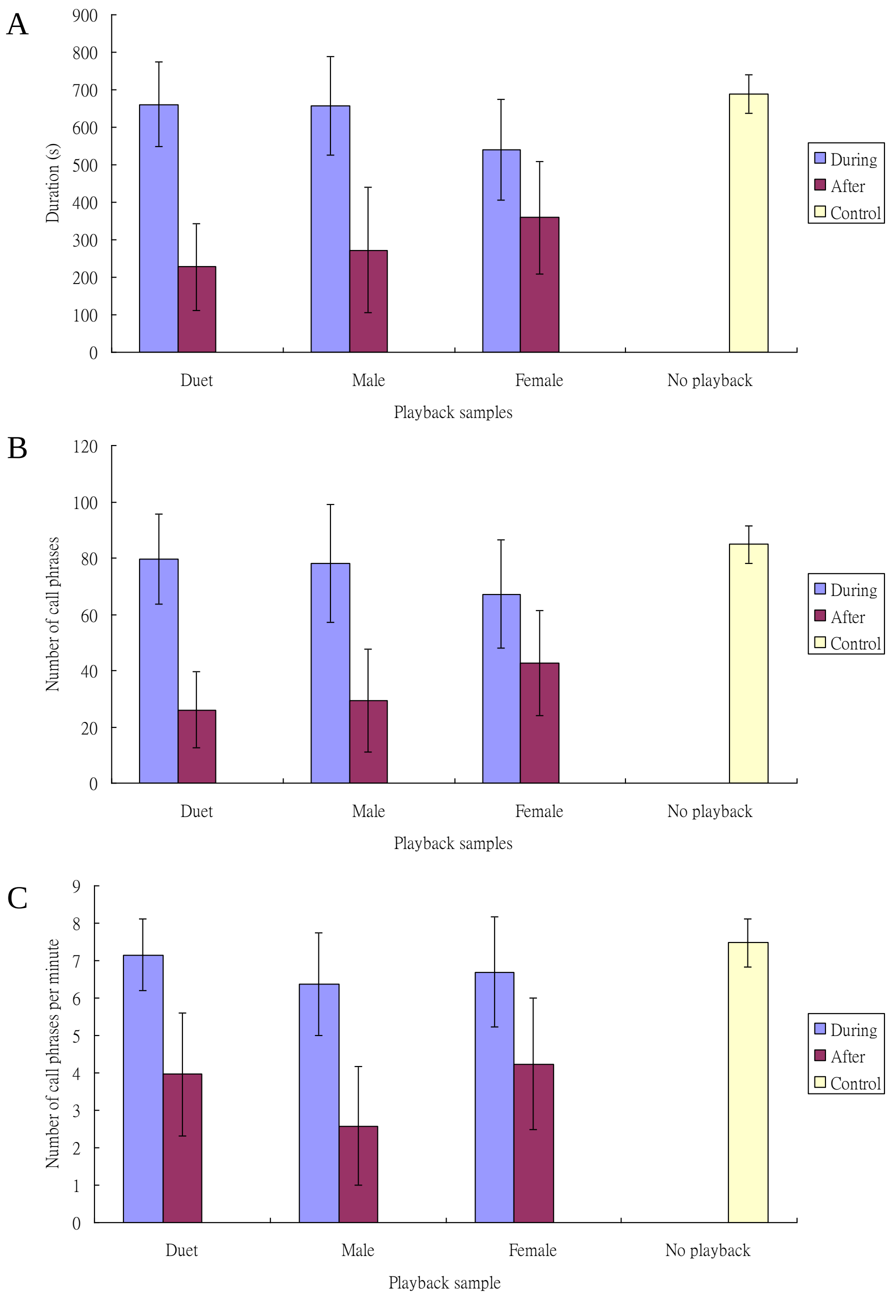

Figure 5.4: Results of playback testing white-cheeked crested gibbons. A, The duration of song produced by the testing white-cheeked crested gibbons. B, The number of call phrases produced within a song. C, the calling rate of the song. Three different playback samples (duet song, male solo song and female solo song of white-cheeked crested gibbons) were played back to five testing pairs while they produced the song (during) and two hours after they finished their song producing (after). Control refers to the song they produce without any playback sample conducted. *: $p < 0.05$, two-tailed Wilcoxon signed rank test for difference in response to the playback between during the song producing and two hours after the song finishing.

5.4 Discussion

Several functions of gibbon song have been proposed in the literature (Cowlishaw, 1992), and a common question is what factor elicits singing. Mitani (1985a) observed wild Mueller's gibbons (*H. muelleri*) and found that 42% of song was elicited when other neighbour's were singing or had just finished singing. However, Mitani (1985a) also found that nearly half of song bouts elicited had no association with specific stimuli. Schilling (1984) noted that captive white-cheeked crested gibbons may produce song in response to various kinds of stimuli, including loud sounds (bells, police sirens and singing of other gibbons) or presence of the keeper, but these stimuli do not always elicit song. Both studies indicated that there were no conclusive events or stimuli to elicit gibbon song. These results match those of previous findings in the study of Fan (2009a). In the present study, four of the five observed pairs have no conspecifics housed around and they produced song without hearing the conspecific song or particular stimuli. The only pair that was housed with other conspecifics never produced song before their conspecifics start to sing. Therefore, the present study revealed no general factor that can elicit song of white-cheeked crested gibbon.

Non-vocal behaviour may be an indicator of the possible function of gibbon song. Cowlishaw (1992) reviewed the relationship between allogrooming, defined as an individual gives or receives grooming to/from another individual, and duet song in *Hylobates* species and found no correlations. White-cheeked crested gibbons in the present study expressed infrequent social contacts or grooming behaviour. These two kinds of behaviour may not directly correlate with their song behaviour. During my observations, there were very few occasions that white-cheeked crested gibbons expressed allogrooming. The most frequently scored grooming behaviour was self-grooming. Observations of *Hylobates* species have found that most observed gibbons in the wild spend less than 3% of daily activity budget on allogrooming (Chivers, 1984; Gittins, 1979; Leighton, 1987; Srikosamatara, 1980). Similar results have also been found in western black-crested gibbons (*N. concolor*). Lan (1989b) observed a group of wild western black crested gibbons and only found eight occasions of allogrooming behaviour in 120 hr of actual of observation. Since they do not spend lots of time on allogrooming, it may be argued that the amount of time white-cheeked crested gibbons spend on allogrooming represent the quality of the pair-bonding.

Playback experiments conducted in *Hylobates* species showed that gibbons express agonistic behaviour toward the sound source if it is in the centre of the territory (Mitani, 1985a; Mitani, 1987b; Raemaekers & Raemaekers., 1986). However, that seems to not be the case in white-cheeked crested gibbons. My study showed that playback samples did not elicit any kind of agonistic behaviour as shown in *Hylobates* species. Moreover, the white-cheeked crested gibbons did not elicit any alarm calls. Although the sample size of testing pairs in my study was limited, this clear trend may indicate that song behaviour in white-cheeked crested gibbons is not used primarily to defend territory. Cowlishaw (1992) proposed that gibbons may discriminate the quality of the song to identify the strength of the pair-bonding and avoid further conflict. If this is applied to white-cheeked crested gibbons, newly paired gibbons should produce less or no song when they hear song of other conspecifics to avoid further conflict. In the present study, the newly paired gibbons responded to all playback experiments, whereas the pair with two offspring housed in Vietnam did not produce any song to playback samples. This result does not match what Cowlishaw (1992)'s proposal and may suggest the quality of pair-bonding in white-cheeked crested gibbons may not correlated with the response they expressed when they heard the song of other gibbons.

It was to note that there are another seven groups of northern (*N. leucogenys*) and southern (*N. siki*) white-cheeked crested gibbons housed with the group of white-cheeked crested gibbons who never produced any vocal responses to the playback song samples in Vietnam. These seven groups of white-cheeked crested gibbons did not respond vocally to the playback samples played in the present study. None of these gibbons produced any song at least one hour after the playback experiment. Haimoff and Gittins (1985) suggested that *H. agilis* is able to discriminate the song of neighbours and intruders and decide whether to respond vocally to the song or not. Since the tested group of white-cheeked crested gibbons in Vietnam only initiated their song after hearing songs of conspecific groups. Gibbons housed in Endangered Primate Rescue Center may possibly identify between the song produced from the neighbours and the strangers, and decide whether to respond to the song vocally or not. Further study is needed clarify this question.

One previous study has reported the vocal behaviour of groups of black-crested gibbons in response to songs produced by neighbouring groups (Fan et al., 2007). A common response is that the groups of gibbons begin to sing first and then withdraw their duet. The result of the playback experiment in my study showed that tested white-cheeked crested gibbons paid attention to the playback song samples while they were still singing. The behavioural responses to their own species duet song, male and female solo song samples were similar. Although they had less response to lar gibbon’s song, there was no significant difference between the response to lar gibbon song and to white-cheeked crested gibbon song, possibly due to the limited sample size. Despite of the modest overall sample size, the result indicated that white-cheeked crested gibbon may not discriminate between intra- and inter-species song. Studies in wild *H. agilis* showed that they may not discriminate well between inter-species song (Mitani, 1987a) and the similar finding has also been found in captive *H. Muelleri* (Mitani, 1985b). Indeed, studies in Sulawesi macaques showed that *M. tonkeana* may not be able to discriminate between the loud calls of its own species and other close species (Muroyama et al., 1998). This may suggest that such discrimination may not be necessary. However, Haraway *et al.* (1988) found that a male Muller’s gibbon (*H. mulleri*) can respond selectively to the song of his own species rather than lar gibbon song after hearing playback samples for three months. The white-cheeked crested gibbons may respond to their own species song stronger after playing samples back for a longer period. Further study is therefore required here to clarify this uncertainty due to time limitation of the present study.

None of the tested white-cheeked crested gibbons stopped producing their song after they heard playback samples. This finding is quite different to those of Minita (1985a) who conducted a study on wild *H. muelleri* nor the observation conducted on *N. c. jingdongensis* (Fan et al., 2007). Previous studies in white-cheeked crested gibbon suggested that singing may be more like a ritual (Goustard, 1984; Schilling, 1984). Therefore, it may be more important for white-cheeked crested gibbons to continue to coordinate their song than withdraw it when they heard the song of neighbours or strangers. This may explain why the song of white-cheeked crested gibbons is neither stopped nor interrupted by playback samples.

The duration of song produced by the white-cheeked crested gibbons in my study was also of interest. Previous studies have found that some *Hylobates* species produce longer songs when they encounter singing from conspecifics groups (Mitani, 1985a; Tenaza, 1976). However, when compared with natural singing, songs produced by playback samples in the present study were not significantly longer. This indicates that the song produced by the strangers did not influence the song of white-cheeked crested gibbons.

The playback conducted after the white-cheeked crested gibbon finished the song showed another interesting pattern. All tested pairs appeared to notice the playback of their own species song regardless of the context of the song. Three of five pairs also appeared to notice the playback of lar gibbon song. None of them appeared to notice the bird song playback. These results suggest that white-cheeked crested gibbon can at least discriminate the context contain songs according to species. The results here also concur with previous studies (Mitani, 1985b; 1987a), in that they may not distinguish the difference between lar gibbon song and white-cheeked crested gibbon song.

Although it appeared that white-cheeked crested gibbons expressed some non-vocal responses such as paying attention or approaching the playback samples, the level of responses was not strong. There were no other vocal response-like alarm calls as found in *H. lar, H. agilis* and *H. muelleri* (Mitani, 1985a; Mitani, 1987a; Mitani, 1987b; Raemaekers et al., 1984). This may suggest that the function of song in white-cheeked crested gibbons may be different to the functions proposed in *Hylobates* species.

Geissmann (2000) proposed that the function of song may differ between gibbon species. From my study, it would be not possible to determine conclusively the function of song in white-cheeked crested gibbons, because the sample size of the tested gibbon pairs. However, the vocal and non-vocal responses expressed by the white-cheeked crested gibbons while they were singing or after they had finished singing strongly suggests that the function of song may not involve territory defence. Rather, it appears to serve the function of enhancing group cohesion and maintaining pair-bonds.

Chapter 6

General Discussion

6.1 Individuality

Seyfarth and Cheney (1997) advocated the vocal development of non-human primates has different level of flexibility in terms of their vocal production, usage and response. Development of vocal production has lest modification, whereas vocal usage and response have partially and full flexibility. Some studies also suggested that production of gibbon song may be innate (Brockelman & Schilling, 1984; Geissmann, 1984), but no data presented in their vocal usage and response. The results of my study here shown that song in gibbons, at least in white-cheeked crested gibbons, can involve considerable flexibility in its production, usage and response. Vocal individuality of gibbons may present under such flexibility. By a using similar song repertoire, each individual of both sexes performs the song differently from each other.

Studies on new world monkeys have found that vocal individuality even when vocalisations are stereotyped (Jones et al., 1993; Jorgensen et al., 1998). Results of my study on white-cheeked crested gibbons supported these findings Both male and female white-cheeked crested gibbons expressed individual differences according to the acoustic parameter analysis of their distinct song. Moreover, acoustic parameters used to identify the individual may differ from males and females. For example, frequency-related factors help to identify the individuality of males, whereas duration of the first notes of female great call is important in identifying females.

The usage of song in white-cheeked crested gibbons also shows great variation. This provides the capacity for white-cheeked crested gibbons to adjust their song and thus express individuality. However, several questions remain about variation of song usage. It is not clear which factors have caused this variation. Most previous studies have investigated the acoustic features of vocalisation in primates but only a few primate species were found to produce combination vocalisations (Arnold et al., 2006b; Crockford et al., 2005). Gibbons have been recognised as one of the primate species to use combined vocalisations (song) to communicate (Clarke et al., 2006; Inoue et al., 2008). Thus, it is possible that crested gibbons may also express their vocal individuality through their song usage. A study of male Javan gibbons (*Hylobates moloch*) showed that each individual used different kinds of notes in their song within a limited level of song repertoire (Geissmann et al., 2005). The results of my study showed the number of call phrases or notes within a call phrases produced by white-cheeked crested gibbons differed from one and another. This suggested that white-cheeked crested gibbons, in both sexes, express vocal individuality by changing the number of notes in the call phrases or types of call phrases.

The very question here is whether variations in call usage results from only physical differences in vocal production (genetic component), or only from self-selection of usage (social component) or both. Seyfarth & Cheney (1997) proposed that production of gibbon song is innate and undergoes no modification throughout development. Each type of sub-categorised multi-modulated call phrase produced by adult male white-cheeked crested gibbons was found on more than one individual, but none of them produced any unique call phrases beyond twelve sub-categorised multi-modulated call phrases. This means that although white-cheeked crested gibbons in the present study expressed variation in call usage between individuals, the outcome of the vocalisations were still within the species-specific repertoire’s range. The results of the present study have shown that the white-cheeked crested gibbons form their vocal individuality under the species-specific call repertoire. Moreover, the production of each call phrase in males is stereotyped. Juveniles and sub-adults produce their call with the same structure as adults do. This matches the findings from other *Hylobates* species (Brockelman & Schilling et al., 1984; Geissmann, 1984) and supports the idea proposed by Seyfarth and Cheney (1997) that characteristics of call phrases in gibbon song may be genetically inherited.

Despite these findings, the usage of song may not be exclusively determined by genetic components. The results in the present study showed that the number of notes used in the great call phrases varied among individuals, whereas other gibbon species (e.g., *Hylobates agilis*) are more stereotyped in the number of notes produced in female great call phrases (Haimoff et al., 1985; Oyakawa et al., 2007). The number of notes of female great call phrases produced by white-cheeked crested gibbons ranges from eight to thirty notes per call phrase (Geissmann et al., 2000). Theoretically, each female should be able to produce similar numbers of notes in great call phrases; the number of notes contained in one call phrase should not be limited by the female's physical ability. However, each female tends to produce a stable number of notes rather than vary the number of notes in each great call phrase. This suggests that female white-cheeked crested gibbons have the ability to adjust the number of notes they express.

One question raised here is how well do songs need to be discriminated between individuals? The results of the experiments on acoustic features and song usage in white-cheeked crested gibbons indicate that patterns of vocal communication are far more flexible than has been proposed in the past. These results support Snowdon et al. (1997) argued, i.e. that reports of inflexible communication in nonhuman primates may primarily reflect a lack of appropriate quantitative data.

6.2 Development and plasticity

6.2.1 Development

Snowdon et al. (1997) investigated vocal production, usage and response in birds, humans and non-human primates, and suggested that they all follow a similar process of vocal development. Most studies, however, have only investigated the vocal development of non-human primates in terms of vocal production (Elowson et al., 1992; Ey et al., 2007; Hammerschmidt et al., 2001; Pistorio et al., 2006; Seyfarth et al., 1986). There is no exception in gibbon studies. There have been very few studies of vocal development in gibbons. Two studies investigated acoustic changes in the great call of *N. gabriellae* (Anderson et al., 2008; Merker et al., 1999) and found young female yellow-cheeked crested gibbons can produced great call phrases with similar call structure as adults once they are three years old. However, it is not clear what factors are involved in vocal development of white-cheeked crested gibbons.

The development of vocal production may not require learning (Owren et al., 2008). Rather, it may simply develop via intrinsic natural ability. The vocal production and call types of gibbons may be influenced by genetic effect, as suggested in *Hylobates* species (Brockelman & Schilling 1984; Geissmann, 1984; Shafer et al., 1984). In *Nomascus* species, previous literature indicated that male white-cheeked crested gibbons produced female-like great call phrases as both juveniles and adults (Goustard, 1984; Schilling, 1984). However, lack of results in female crested gibbons made this question difficult to resolve. The findings from my study indicate that female crested gibbons can produce male call phrases, thereby providing some evidence that cross-sex call mimicry does occur (Chen et al., 2008) Thus, it appears that white-cheeked crested gibbons may produce all possible call phrases which used to be thought as sex-specific in the song.

Genetic factors may take great effects on influencing the development of vocal production in white-cheeked crested gibbons. However, this may not be the only factor influencing the usage of song in white-cheeked crested gibbons. Individuality found in adult white-cheeked crested gibbons in my study showed that such individual differences can be found in the physical call structure and the usage of call phrases in the song. Thus, development of song usage may also be influenced by other possible factors such as social factors.

Practising (i.e. learning) is one of possible factors that may affect the development of song patterns, as stated in Chapter 4. The difference in the number of call phrases produced between the adult and juvenile males showed that young juveniles may express all possible call phrases. They may gradually reduce the types and number of call phrases produced until they reach the more simplistic general patterns expressed by most adults. The questions raised by this hypothesis are 1) when is the turning point that a white-cheeked crested gibbon starts to reduce the number and patterns of call phrases? 2) what is the peak number of call phrases that a white-cheeked crested gibbon can produce? and 3) what kind of event (if any) causes a white-cheeked crested gibbon to change their song patterns from juvenile to adult stage? The results of my study provided some evidence to assist in answering these questions. From the recordings of the gibbons in my study, it emerged that the possible turning point may occur between 8 year and 15 years of age (Fig 6.1). The peak number of call phrases produced in each song may not be less than 210 call phrases per song in juveniles. Newly paired individuals and individuals who lost their partners or family members changed the usage of their call phrases in their song. This suggests that changes in social condition have a great influence in the vocal development of white-cheeked crested gibbons.

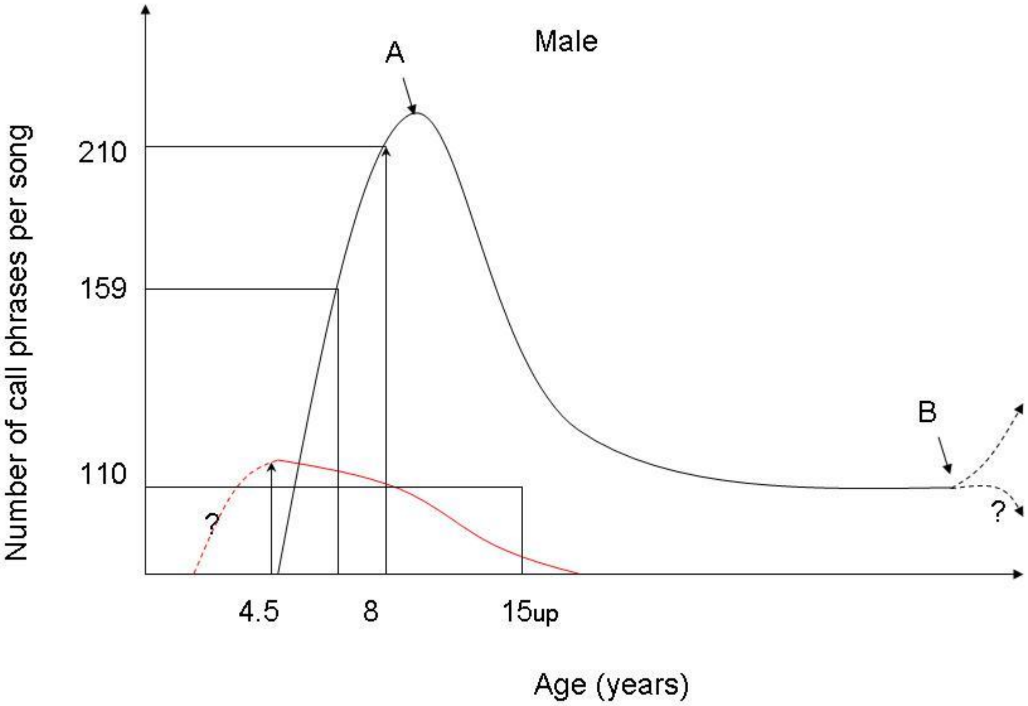

Figure 6.1: The relationship between the age of the individual (X-axis) and the number of call phrases produced per song (Y-axis) in male white-cheeked crested gibbons in the present study. Black line represents the number of male call phrases. Red line represents the female-like call phrases. The dotted line indicates the period of no available data. A represents the turning point of the number of call phrases produced. B represents possible events that may cause the change of number of call phrases produced.

6.2.2 Plasticity

The stability of song is affected mainly by the partner or the group members rather than conspecifics of other groups in white-cheeked crested gibbons. Both males and females adjust their song usage through the process of coordinating the pair-bond (see Chapter 4), and similar findings have been found in siamangs (Geissmann, 1999; Maples et al., 1989). My study also found that a change of social context can lead to a similar effect on song usage in males. These results may indicate that such dynamic change occurs within group members rather than between group members.

Similar results also emerged for the male multi-modulated call phrases of white-cheeked crested gibbons in my study. Twelve sub-catalogued multi-modulated call phrases were identified in the present study. One sub-adult (individual M8) changed his sub-catalogued multi-modulated call phrases dramatically after the death of his female conspecifics. Similar results were also found in other adult males. Two adult males (individual M4 and M5) changed the number of call phrases and the sub-catalogued multi-modulated call phrases after both individuals underwent a change in their social context. If the usage of song phrases were affected only by inheritance, the usage or types of call phrases should be fixed, as suggested in the vocal production.

6.3 Primary song function

6.3.1 Ability of discrimination

Vocal recognition plays an important role in vocal communication in primate species (Snowdon, 1986). However, it is unclear how white-cheeked crested gibbons to communicate each other if they cannot distinguish between their own song and others'. White-cheeked crested gibbons did not respond to playback samples of male, female stranger solo song and stranger duet song.

Mitani (1985b) conducted playback experiments on *Hylobates muelleri* and found no significant differences that discriminated the songs from different individuals. He suggested that the apparent lack of song discrimination may be related to the population density, as those species (e.g., *H. lar* and *H. agilis*) who expressed stronger responses to playback of song had a higher population density. There is no available population data for white-cheeked crested gibbons, and it was believed that the current wild population is well below its original population density (B. Rawson, personal communication). However, studies in other crested gibbons showed that they have a lower density of population compared to *Hylobates* species (Brockelman et al., 1998; Cowlishaw, 1992; Jiang et al., 1999). It is possible that white-cheeked crested gibbons may not identify the stranger song well as they have fewer opportunities to encounter conspecifics.

Although the study of Maple et al. (1988) conducted on *H. muelleri* showed that gibbons can identify and respond to their own species' song after hearing the song repeatedly. This may indicate that reinforcement may be involved in song discrimination in this case. All experiments conducted in the present study were in the captive environment, so all tested individuals had fewer opportunities to listen to other conspecifics' song compared to the wild population. All playback song samples excepted for the control sample were never heard by any of these individuals in my study. Moreover, the individuals in my study only heard the playback sample once. The possibility of reinforcement or learning is not likely to have had a significant effect in the present study. Thus, the current results describing minimal song discrimination may match what Mitani (1985b) proposed that lower population density may result in the lack of ability to discriminate song of different individuals.

6.3.2 Primary song function

Song functions in crested gibbons are still unclear. A field study of black-crested gibbons (*N. concolor jingdongensis*) found that this species' behaviour seems to support partly the possible hypotheses of song function playing a role as territory defence and group cohesion, but none of these hypotheses can be exclusive (Fan et al., 2009b). My study could not provide a conclusive answer to this question. Results of the playback experiments reported in Chapter 5 do not fully support any of the song function hypotheses. This may suggest that white-cheeked crested gibbon song may simply have multiple functions as previous researchers have proposed for other gibbon species (Fan et al., 2009b; Geissmann, 1999; Geissmann et al., 2005; Geissmann et al., 2000).

Despite the uncertainty regarding the function of gibbon song, the results of my playback experiments suggest that white-cheeked crested gibbons may not use song primarily in territory defence, in contrast to other gibbon species such as *Hylobates* species. Reactions of white-cheeked crested gibbons to playback promote the need for further study. Based on the observations of duet song and the results of playback experiments, it seems that the songs of white-cheeked crested gibbons elicited no particular responses. This finding is similar to those for black-crested gibbons, where the song of one group may not elicit song from neighbouring conspecific groups (Fan et al., 2007). Results of my playback experiments also showed that none of the playback samples can interrupt other on-going gibbon song. This evidence suggests that such song behaviour of white-cheeked crested gibbons mainly serves an intra-family group function rather than inter-family group function. There were no clear patterns that indicated which particular individual chiefly initiated song, but results showed that the adult individual in tended to initiate the song in the family group. The result also indicated that the partner or other family members join the song once the song was initiated by the adult individual. The adult pair achieves the best coordination among the family members, while other family members (e.g., the offspring) produce the song with less coordination. Therefore, by considering the evidence above, songs of white-cheeked crested gibbons may chiefly play a role in the maintenance of the pair bond.

6.4 Limitation of the current project

Some findings were still managed despite some limitations in the current study. Small sample size and captive environment may limit further outcome of the current study. The number of tested individuals was relatively low in this study due to the available number of individuals. It may be argued whether some results of this study applied to the large population. The results with small sample size did provide the evidence that changes in song usage of white-cheeked crested gibbons occurred. The only question was whether such changes can be found in other groups in captivity or in the wild. Further study in wild population may provide a better answer for this question.

Most of tested individuals excepted for gibbons housed in Vietnam had no conspecific neighbours. Social behaviours between two neighbouring groups were unable to be observed in the current study. There were no available data on inter-group behaviour of white-cheeked crested gibbons in the wild. A study in black-crested gibbons showed that group interactions may only account for less than 1.6% of activity budget (Fan et al., 2008). It may be assumed that lack of inter-group behaviour may not have a major effect to the current study.

6.5 Conclusion

The present study has added substantially to our understanding of vocal usage, plasticity and function of song in white-cheeked crested gibbons. It has shown that white-cheeked crested gibbon song is not stereotyped, as earlier studies have suggested. White-cheeked crested gibbons expressed vocal individuality in both sexes, and could be identified through their call structure and the vocal usage. Indeed, the context and plasticity of song suggest that social factors also have a great influence to the change of song. The change of the song, therefore, may involve some learning process. Further studies are therefore required to investigate how learning affects the ultimate characteristics of this species' song and what kind of events influences it. Although the results of playback experiments could not prove the conclusive function of gibbon song in white-cheeked crested gibbons, it is suggested the song of white-cheeked crested gibbons may serve the primary function for the intra-group members rather than inter-group members. By further exploring the process of vocal development and conducting playback experiments in the wild, it may be possible to reveal the precise function of song phrase produced by the white-cheeked crested gibbons.

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APPENDIX

List of song recording detail

Number	Recording detail				Data analysed and presented		
	Date	Location	Type	Individual(s)	Chapter3	Chapter4	Chapter5
1	2006/10/23	Dusit Zoo	Duet	M1, F1	3	4	
2	2006/10/23	Dusit Zoo	solo	M7		4	
3	2006/10/24	Dusit Zoo	Duet	M1, F1	3	4	
4	2006/10/24	Dusit Zoo	solo	M7		4	
5	2006/10/25	Dusit Zoo	Duet	M1, F1	3	4	
6	2006/10/26	Dusit Zoo	solo	M7		4	
7	2006/10/26	Dusit Zoo	Duet	M1, F1	3	4	
8	2006/10/27	Dusit Zoo	solo	M7		4	
9	2006/10/27	Dusit Zoo	Duet	M1, F1	3	4	
10	2007/3/28	Dusit Zoo	solo	M7		4	
11	2007/3/28	Dusit Zoo	Duet	M1, F1	3	4	
12	2007/3/29	Dusit Zoo	solo	M7		4	
13	2007/3/29	Dusit Zoo	Duet	M1, F1	3	4	
14	2007/3/30	Dusit Zoo	solo	M7		4	
15	2007/3/30	Dusit Zoo	Duet	M1, F1	3	4	
16	2007/3/31	Dusit Zoo	solo	M7		4	
17	2007/3/31	Dusit Zoo	Duet	M1, F1	3	4	
18	2007/4/1	Dusit Zoo	solo	M7		4	
19	2007/4/1	Dusit Zoo	Duet	M1, F1	3	4	
20	2007/12/28	Dusit Zoo	Duet	M1, F1			5
21	2007/12/30	Dusit Zoo	solo	M7		4	
22	2007/12/30	Dusit Zoo	Duet	M1, F1		4	5
23	2008/1/1	Dusit Zoo	Duet	M1, F1			5
24	2008/1/3	Dusit Zoo	solo	M7		4	
25	2008/1/3	Dusit Zoo	Duet	M1, F1		4	5
26	2008/1/3	Dusit Zoo	Duet	M1, F1			5
27	2008/1/5	Dusit Zoo	solo	M7		4	
28	2008/1/5	Dusit Zoo	Duet	M1, F1		4	
29	2008/1/9	Dusit Zoo	solo	M7		4	
30	2008/1/9	Dusit Zoo	Duet	M1, F1		4	
31	2008/1/11	Dusit Zoo	solo	M7		4	
32	2008/1/11	Dusit Zoo	Duet	M1, F1		4	
33	2007/4/5	Night-Safari	Duet	M2, F2	3		

Number	Recording detail				Data analysed and presented		
	Date	Location	Type	Individual(s)	Chapter3	Chapter4	Chapter5
34	2007/4/6	Night-Safari	Duet	M2, F2	3		
35	2007/4/7	Night-Safari	Duet	M2, F2	3		
36	2007/4/8	Night-Safari	Duet	M2, F2	3		
37	2007/4/9	Night-Safari	Duet	M2, F2	3		
38	2007/4/11	Night-Safari	Duet	M2, F2	3		
39	2007/11/30	Night-Safari	Duet	M2, F2	3		
40	2007/11/30	Night-Safari	Duet	M2, F2			5
41	2007/12/3	Night-Safari	Duet	M2, F2	3		
42	2007/12/3	Night-Safari	Duet	M2, F2			5
43	2007/12/3	Night-Safari	Duet	M2, F2			5
44	2007/12/5	Night-Safari	Duet	M2, F2			5
45	2007/12/7	Night-Safari	Duet	M2, F2	3		
46	2007/12/7	Night-Safari	Duet	M2, F2			5
47	2007/12/7	Night-Safari	Duet	M2, F2			5
48	2007/12/9	Night-Safari	Duet	M2, F2	3		
49	2007/6/11	Endangered Primate Rescue Center	solo	M9		4	
50	2007/6/11	Endangered Primate Rescue Center	Duet	M3, F3	3		
51	2007/6/12	Endangered Primate Rescue Center	solo	M8		4	
52	2007/6/13	Endangered Primate Rescue Center	solo	M11		4	
53	2007/6/13	Endangered Primate Rescue Center	solo	M8		4	
54	2007/6/13	Endangered Primate Rescue Center	solo	F7		4	
55	2007/6/13	Endangered Primate Rescue Center	solo	F7		4	
56	2007/6/13	Endangered Primate Rescue Center	solo	M9		4	
57	2007/6/13	Endangered Primate Rescue Center	solo	M9		4	
58	2007/6/13	Endangered Primate Rescue Center	Duet	M3, F3	3	4	
59	2007/6/14	Endangered Primate Rescue Center	solo	M11		4	
60	2007/6/14	Endangered Primate Rescue Center	solo	F7		4	
61	2007/6/14	Endangered Primate Rescue Center	solo	F8		4	
62	2007/6/14	Endangered Primate Rescue Center	solo	M9		4	
63	2007/6/14	Endangered Primate Rescue Center	Duet	M3, F3		4	
64	2007/6/14	Endangered Primate	Duet	M3, F3	3		

Number	Recording detail				Data analysed and presented		
	Date	Location	Type	Individual(s)	Chapter3	Chapter4	Chapter5
		Rescue Center					
65	2007/6/15	Endangered Primate Rescue Center	solo	M11		4	
66	2007/6/15	Endangered Primate Rescue Center	solo	M8		4	
67	2007/6/15	Endangered Primate Rescue Center	solo	M8		4	
68	2007/6/15	Endangered Primate Rescue Center	solo	F8		4	
69	2007/6/15	Endangered Primate Rescue Center	solo	F8		4	
70	2007/6/15	Endangered Primate Rescue Center	solo	M9		4	
71	2007/6/15	Endangered Primate Rescue Center	Duet	M3, F3		4	
72	2007/6/15	Endangered Primate Rescue Center	Duet	M3, F3	3		
73	2008/1/16	Endangered Primate Rescue Center	Duet	M3, F3			5
74	2008/1/17	Endangered Primate Rescue Center	solo	M11		4	
75	2008/1/17	Endangered Primate Rescue Center	Duet	M3, F3		4	
76	2008/1/18	Endangered Primate Rescue Center	solo	M8		4	
77	2008/1/18	Endangered Primate Rescue Center	solo	M9		4	
78	2008/1/18	Endangered Primate Rescue Center	Duet	M3, F3			5
79	2008/1/19	Endangered Primate Rescue Center	solo	M11		4	
80	2008/1/19	Endangered Primate Rescue Center	solo	M9		4	
81	2008/1/19	Endangered Primate Rescue Center	Duet	M3, F3		4	
82	2008/1/19	Endangered Primate Rescue Center	Duet	M3, F3			5
83	2008/1/20	Endangered Primate Rescue Center	solo	M11		4	
84	2008/1/20	Endangered Primate Rescue Center	solo	M9		4	
85	2008/1/20	Endangered Primate Rescue Center	Duet	M3, F3		4	
86	2008/1/20	Endangered Primate Rescue Center	Duet	M3, F3			5
87	2008/1/21	Endangered Primate Rescue Center	solo	M9		4	
88	2008/1/22	Endangered Primate Rescue Center	solo	M8		4	
89	2008/1/22	Endangered Primate Rescue Center	solo	M9		4	

Number	Recording detail				Data analysed and presented		
	Date	Location	Type	Individual(s)	Chapter3	Chapter4	Chapter5
90	2008/1/23	Endangered Primate Rescue Center	solo	M8		4	
91	2008/1/24	Endangered Primate Rescue Center	solo	M11		4	
92	2008/1/24	Endangered Primate Rescue Center	Duet	M3, F3		4	
93	2008/1/25	Endangered Primate Rescue Center	solo	M8		4	
94	2008/1/26	Endangered Primate Rescue Center	solo	M11		4	
95	2008/1/26	Endangered Primate Rescue Center	solo	M8		4	
96	2008/1/26	Endangered Primate Rescue Center	Duet	M3, F3		4	
97	2008/1/26	Endangered Primate Rescue Center	Duet	M3, F3	3		
98	2008/4/18	Endangered Primate Rescue Center	solo	M11		4	
99	2008/4/18	Endangered Primate Rescue Center	solo	M8		4	
100	2008/4/18	Endangered Primate Rescue Center	Duet	M3, F3	3	4	
101	2008/4/19	Endangered Primate Rescue Center	solo	M11		4	
102	2008/4/19	Endangered Primate Rescue Center	solo	M8		4	
103	2008/4/19	Endangered Primate Rescue Center	solo	M9		4	
104	2008/4/19	Endangered Primate Rescue Center	solo	M9		4	
105	2008/4/19	Endangered Primate Rescue Center	Duet	M3, F3	3	4	
106	2008/4/20	Endangered Primate Rescue Center	solo	M11		4	
107	2008/4/20	Endangered Primate Rescue Center	solo	M8		4	
108	2008/4/20	Endangered Primate Rescue Center	Duet	M3, F3	3	4	
109	2008/4/21	Endangered Primate Rescue Center	solo	M8		4	
110	2008/4/21	Endangered Primate Rescue Center	solo	M9		4	
111	2008/4/22	Endangered Primate Rescue Center	solo	M8		4	
112	2008/4/22	Endangered Primate Rescue Center	solo	M9		4	
113	2008/4/22	Endangered Primate Rescue Center	Duet	M3, F3	3		
114	2008/4/23	Endangered Primate Rescue Center	solo	M11		4	
115	2008/4/23	Endangered Primate	solo	M9		4	

Number	Recording detail				Data analysed and presented		
	Date	Location	Type	Individual(s)	Chapter3	Chapter4	Chapter5
		Rescue Center					
116	2008/4/23	Endangered Primate Rescue Center	Duet	M3, F3	3	4	
117	2006/9/2	Nakhornratchasima Zoo	Duet	M4,F4	3		
118	2006/9/3	Nakhornratchasima Zoo	Duet	M4,F4	3		
119	2006/9/4	Nakhornratchasima Zoo	Duet	M4,F4	3		
120	2006/9/22	Nakhornratchasima Zoo	Duet	M4,F4	3		
121	2006/10/11	Nakhornratchasima Zoo	solo	M10		4	
122	2006/10/11	Nakhornratchasima Zoo	Duet	M4,F4	3	4	
123	2006/10/12	Nakhornratchasima Zoo	solo	M10		4	
124	2006/10/12	Nakhornratchasima Zoo	Duet	M4,F4	3	4	
125	2006/10/13	Nakhornratchasima Zoo	solo	M10		4	
126	2006/10/13	Nakhornratchasima Zoo	Duet	M4,F4	3	4	
127	2006/10/14	Nakhornratchasima Zoo	solo	M10		4	
128	2006/10/14	Nakhornratchasima Zoo	Duet	M4,F4	3	4	
129	2006/10/15	Nakhornratchasima Zoo	solo	M10		4	
130	2006/10/15	Nakhornratchasima Zoo	Duet	M4,F4	3	4	
131	2007/5/3	Nakhornratchasima Zoo	solo	M10		4	
132	2007/5/3	Nakhornratchasima Zoo	solo	M4		4	
133	2007/5/5	Nakhornratchasima Zoo	solo	M10		4	
134	2007/5/5	Nakhornratchasima Zoo	solo	M4		4	
135	2007/5/6	Nakhornratchasima Zoo	solo	M10		4	
136	2007/5/7	Nakhornratchasima Zoo	solo	M4		4	
137	2007/5/8	Nakhornratchasima Zoo	solo	M10		4	
138	2007/5/8	Nakhornratchasima Zoo	solo	M4		4	
139	2007/5/9	Nakhornratchasima Zoo	solo	M10		4	
140	2007/5/9	Nakhornratchasima Zoo	solo	M4		4	

Number	Recording detail				Data analysed and presented		
	Date	Location	Type	Individual(s)	Chapter3	Chapter4	Chapter5
141	2008/3/3	Nakhornratchasima Zoo	solo	M10		4	
142	2008/3/3	Nakhornratchasima Zoo	solo	M4		4	
143	2008/3/4	Nakhornratchasima Zoo	solo	M10		4	
144	2008/3/4	Nakhornratchasima Zoo	solo	M4		4	
145	2008/3/5	Nakhornratchasima Zoo	solo	M10		4	
146	2008/3/5	Nakhornratchasima Zoo	solo	M4		4	
147	2008/3/6	Nakhornratchasima Zoo	solo	M10		4	
148	2008/3/6	Nakhornratchasima Zoo	solo	M4		4	
149	2008/3/7	Nakhornratchasima Zoo	solo	M10		4	
150	2008/3/7	Nakhornratchasima Zoo	solo	M4		4	
151	2007/11/19	Chiangmai Zoo	solo	M5		4	
152	2007/11/20	Chiangmai Zoo	solo	M5		4	
153	2007/11/21	Chiangmai Zoo	solo	M5		4	
154	2007/11/22	Chiangmai Zoo	solo	M5		4	
155	2007/11/28	Chiangmai Zoo	Duet	M5, F5		4	
156	2007/11/30	Chiangmai Zoo	Duet	M5, F5		4	
157	2007/12/4	Chiangmai Zoo	Duet	M5, F5		4	
158	2007/12/6	Chiangmai Zoo	solo	M5		4	
159	2007/12/8	Chiangmai Zoo	Duet	M5, F5		4	
160	2007/12/10	Chiangmai Zoo	solo	F5		4	
161	2007/12/12	Chiangmai Zoo	solo	F5		4	
162	2008/3/19	Chiangmai Zoo	Duet	M5, F5	3	4	5
163	2008/3/19	Chiangmai Zoo	Duet	M5, F5			5
164	2008/3/21	Chiangmai Zoo	Duet	M5, F5	3	4	5
165	2008/3/21	Chiangmai Zoo	Duet	M5, F5	3	4	5
166	2008/3/23	Chiangmai Zoo	Duet	M5, F5	3	4	5
167	2008/3/23	Chiangmai Zoo	Duet	M5, F5		4	5
168	2008/3/25	Chiangmai Zoo	Duet	M5, F5	3	4	5
169	2008/3/25	Chiangmai Zoo	Duet	M5, F5			5
170	2008/3/27	Chiangmai Zoo	Duet	M5, F5	3	4	
171	2008/3/29	Chiangmai Zoo	Duet	M5, F5	3	4	
172	2008/3/31	Chiangmai Zoo	Duet	M5, F5	3	4	
173	2008/4/1	Chiangmai Zoo	Duet	M5, F5	3	4	
174	2008/4/1	Chiangmai Zoo	Duet	M5, F5	3		

Number	**Recording detail**				**Data analysed and presented**		
	Date	Location	Type	Individual(s)	Chapter3	Chapter4	Chapter5
175	2007/12/19	KhaoKheow Open Zoo	solo	M6			5
176	2007/12/21	KhaoKheow Open Zoo	solo	M6			5
177	2007/12/23	KhaoKheow Open Zoo	solo	M6			5
178	2007/12/25	KhaoKheow Open Zoo	solo	M6			5