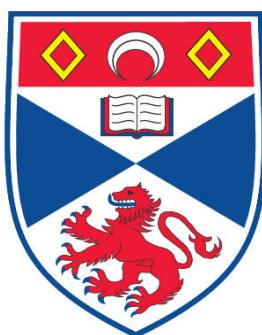


**THE VOCALISATIONS AND ANTI-PREDATORY BEHAVIOUR  
OF WILD WHITE-HANDED GIBBONS (HYLOBATES LAR) IN  
KHAO YAI NATIONAL PARK, THAILAND**

**Esther Anne Elizabeth Clarke**

**A Thesis Submitted for the Degree of PhD  
at the  
University of St. Andrews**



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**The Vocalisations and Anti-predatory Behaviour  
of Wild White-handed Gibbons (*Hylobates lar*) in  
Khao Yai National Park, Thailand**

**By: Esther Anne Elizabeth Clarke**

**Submitted for the higher degree of Doctor of Philosophy**

**June 2010**

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## **ABSTRACT**

The loud songs of gibbons (*Hylobatidae*) usually consist of a duet by the mated pair delivered each morning. These songs can transmit over a kilometre through dense forest habitat and therefore presumably play a role in long-distance communication. There is some evidence to suggest that gibbons use song in contexts other than their daily duets, such as predation, but these songs have not been well studied. Close-range communication is also relevant for gibbons, but these quieter calls have completely escaped any detailed observation.

The responses of wild white-handed gibbons (*Hylobates lar*) to simulated visual and acoustic predators (tiger, clouded leopard, reticulated python and crested serpent eagle) were studied in Khao Yai National Park, Thailand to address the lack of empirical data about these important events. Little is known about gibbons' anti-predatory behaviour in general, and simulated predator encounters provided an opportunity to investigate these responses as well.

Results showed that gibbons used song as part of their anti-predator strategy and that subtle combinatorial changes were meaningful to conspecifics. They also showed marked behavioural changes in the short-term, and some evidence of longer-term changes as well. Quiet calls were also part of the gibbons' response repertoire with the *hoo* call being particularly relevant. Hoos were used as a prelude to singing both normal duets and predator songs, but there were consistent differences between each context. Hoos were also delivered independently in a number of other contexts

outside predation. When analysed, these hoos showed consistent contextual differences in a number of spectral parameters.

Within the duet context, important contextual subtleties were evident also revealing a remarkable vocal plasticity. In addition, gibbons voluntarily attended to specific vocal elements of other gibbon duets, indicating that certain sequences are more pertinent than others.

Results suggest both gibbon song and gibbon hoos are powerful communication tools that reliably reference external objects and events; this ability is also a critical feature of human language.

## **CHAPTER 1. Introduction**

Comparing human and non-human cognition has been a fascinating scientific journey. Emotion, once thought the exclusive property of humans is now known to be present among other animals (Aureli 1997; Aureli et al. 1999) as is deception (Byrne and White 1985; Anderson et al. 2001; Held et al. 2002), thinking, reasoning and knowledge (Griffin 1991; Cheney et al. 1995; Beran et al. 1998; Zuberbühler 2000; Watve et al. 2002; Griffin and Speck 2004; O'Connell and Dunbar 2005), tool use (Beck 1980; Boesch and Boesch 1990), culture (Boesch 1995; Whiten et al. 1999) and complex auditory (Marler 1977; Marler and Tenaza 1977) and gestural communication (Hostetter et al. 2001; Pika et al. 2003; Liebal et al. 2004; Pika et al. 2005). In fact, there is little ground left uncovered, and therefore we must either change the definition of what it is to be human, or at least blur the lines that separate humans and other primates.

In addition, we can try to trace the evolutionary origins of human and non-human cognitive traits. The comparative approach is based on the assumption that cognitive capacities have an evolutionary history, just like physical traits. Convergent evolution is always a possibility, but as the process of evolution is generally conservative, this is a relatively rare outcome, especially among more closely related species. Therefore, by examining the behaviours of species closely related to humans, namely other primates, we can potentially source the derivation of specific human behaviours, and infer some of their evolutionary history.

Communication is one such behaviour that has a rich and complex evolutionary tale. Defining communication is problematic because there is a huge array of different forms of communication (Hurford 2007), but since this thesis is concerned with primate vocal behaviour, the definition can be restricted to describing acoustic interactions between animals of the same species. Thus, it may be described as the exchange of information between two or more individuals, or more specifically as the transmission of signals between a sender and a receiver. This makes communication a necessarily social event; senders of acoustic signals rarely do so in the absence of a potential receiver, and signals have evolved to be tailored to the exact needs of the receiver (Seyfarth and Cheney 2003). Similarly, listeners have evolved to extract maximal information from a call. Human communication includes language, with its infinite capacity for transmitting novel pieces of information. Does anything similar exist among our close relatives? Approximately five million years separate us from our closest living relatives, the common chimpanzee and the bonobo, but how much of our language developed during that time? Unfortunately, none of the other hominid species that spanned that five million year gap are still around today, for surely they would have been able to answer that question better than anyone. All that remains is a fossil record, which offers some clues to early human cultures and behaviours - but unfortunately, neural tissue does not fossilise well. Thus, we are left with mostly fragmented information about our direct human ancestors, as well as a wealth of information from today's living primate species. Though we cannot directly communicate with them, we can observe their communication and assess the underlying cognitive processes.

Some researchers have attempted to determine the linguistic capacities of non-human primates: the earliest research endeavoured to enculturate non-human primates into human society to teach them human language-like systems. These studies produced some interesting examples of non-human primates learning to use human symbols and signs to communicate effectively their wants and desires (Premack 1970; Gardner and Gardner 1975; Patterson 1978), but were limited by their reliance on specifically human symbols and paradigms. A more recent approach has been to study animals in their natural habitats, and to focus on intra-specific communication. These studies have proved very fruitful, and if we break language down into its constituent parts (Hurford 2007), we find language pre-cursors that are readily found among living primate species. Simple grammar and syntax - the rules by which human language is governed - have been described for several species (Fitch and Hauser 2004; Crockford and Boesch 2005; Arnold and Zuberbühler 2006). Functionally referential signals, which pertain to the labelling of objects and events in the environment in a way that other individuals can recognise and understand, are also being described in more and more species (Di Bitetti 2003; Slocombe and Zuberbühler 2005; Kirchhof and Hammerschmidt 2006).

However, the question remains: just how much can research on primate communication tell us about the evolution of these traits and indeed language itself? We now know that many primate species display similar cognitive traits to us, and presumably the neural pathways underlying these traits evolved somewhere earlier in the primate lineage. For example, correlate brain structures thought important in language development and use have been found in other primate brains, such as Wernicke's and Broca's areas – asymmetric regions of the brain with larger analogues

present in the left hemisphere than in the right (Gannon et al. 1998; Cantalupo and Hopkins 2001). In general, however, the neural pathways underlying language in humans and their primate analogues are poorly understood. An alternate approach is to abandon direct comparisons between humans and other primates, and look instead within extant primate families to understand how their communication has evolved during the last few million years. Humans belong to the super-family *Hominoidea* along with the other apes (chimpanzees, gorillas, orangutans and gibbons). The chimpanzees are part of the *Pan* genus and can be split into two extant species: the common chimpanzee, and the pygmy chimpanzee (bonobo), who diverged about one million years ago. Gorillas are part of the *Gorilla* genus and can be separated into the Eastern and Western gorilla. Similarly, the orangutans, part of the *Pongo* genus can be separated into two surviving species: the Bornean and the Sumatran orangutan. Only one extant species remains in the case of the human genus *Homo*. However, the last member of the *Hominoidea* super-family, the *Hylobatidae* are different; gibbons and siamangs, are represented by four genera with twelve extant species (Takacs et al. 2005) as well as several sub-species. These animals therefore offer a unique opportunity to study the evolutionary relationships between living apes.

Gibbons live in Southeast Asia, and can be found in Bangladesh, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Thailand, and Vietnam. They are famous for their loud calls, often referred to as *songs*. For the purposes of this thesis, songs are defined as loud calls that are pure in tone and musical in nature. Furthermore, animal songs are distinct from other vocalisations because they must consist of repetitive vocal utterances that display syllabic diversity and temporal regularity, not unlike human music. For gibbons, songs include duets and solos that echo across the

dense forest. These songs have been the subjects of research for decades (Carpenter 1940; Ellefson 1974; Haimoff 1984; Raemaekers et al. 1984; Mitani 1985; Mitani 1988; Geissmann 2002). Behaviourally, gibbons have also been well studied (Carpenter 1940; Ellefson 1974; Brockelman et al. 1998; Geissmann and Orgeldinger 2000; Bartlett 2001, 2003; Barelli et al. 2007; Barelli et al. 2008; Cheyne 2008) but cognitively they have been almost completely ignored (Hyatt 1998; Ujhelyi et al. 2000; Myowa-Yamakoshi and Tomonaga 2001, 2001). Though suggestions have been made that their vocal repertoire is much larger than just their songs (Ellefson, 1974; Raemaekers et al., 1984), there has been very little research on it, with no detailed empirical studies - much of the gibbons' vocal behaviour and subsequent cognitive ability remains unknown.

The following chapters represent a study of these unknown gibbon vocal traits and hope to answer several questions: what is the gibbon's vocal repertoire? What functions do their various vocalisations have? Do these vocalisations encode specific semantic information, and if so, do conspecifics comprehend this information and respond in ways that illustrate their understanding? The white-handed or lar gibbon (*Hylobates lar*) in its natural habitat is the subject. Included is a review of gibbon vocal behaviour as far as our current knowledge permits (chapter 2), followed by a chapter devoted to the study site and the subjects therein (chapter 3). Next comes an observational study of song repertoire (chapter 4), which is in turn followed by an empirical study of long-distance calls given in response to potential predators in comparison with those performed as part of the normal daily routine (chapter 5). Predator encounters are presumably highly emotive events with potentially life-threatening consequences; by investigating the gibbons' responses to these and other

non-threatening contexts, one can determine whether each of these very different events are distinctly labelled vocally and also behaviourally. Therefore, following this chapter is an empirical study of gibbon behavioural responses to potential predators (chapter 6). This is followed by a detailed analysis of gibbon intra-group *hoo* calls (chapter 7). These intra-group calls have received little attention for over twenty years, and provide clues to the social relationships and social cognition of these apes. The thesis ends with an overall conclusion discussing the white-handed gibbons' vocal and behavioural repertoire, its' possible functions and cognitive implications (chapter 8).

Other animals are often faced with the same communication challenges as we are, revolving largely around attaining food and mates and evading danger, but they may solve them in different ways. By understanding each species on its own terms and in its natural habitat, we may be able to decipher the evolutionary relationships between them and obtain a better understanding of how communication, and the underlying cognition, has evolved over the millennia. This, fascinating in its own right, may also offer up clues as to how human language originated.

Finally, it is hoped that these studies will ensure that gibbons be better preserved. Unfortunately many species are threatened by extinction and may not be around much longer according to a number of assessments (Rylands et al. 2008). Recently, an entire population of white-handed gibbons was wiped out from China's Yunnan province (Holden 2008). They face constant threat from logging, poaching and the pet trade; it is therefore imperative that all individuals that remain are protected.

Each species is an exceptional creation of natural selection. Each has an essential role to play in its ecosystem. Eradicating even a single species has profound effects - the natural world is complex, and well functioned but also fragile. Preserving biodiversity has many benefits: economic, recreational, health (pharmaceutical), and protecting the human rights of indigenous peoples. In addition, biodiversity has intrinsic value. Gibbons, like other animals and plants, including humans, are a valued part of a bigger whole – an integral link in the web that nature has woven.

## **CHAPTER 2. Gibbon vocal behaviour and socio-ecology**

### ***Abstract***

Gibbon vocal behaviour is particularly interesting because it represents a rich and complex system. As such, it has received much scientific attention. All gibbon species produce loud sex-specific songs, which are audible to neighbouring as well as non-neighbouring conspecific groups, and therefore presumably play a role in inter-group communication. This review details the current thinking on the evolutionary origins of gibbon songs and the phylogenetic relationships of these apes, which are relevant to the evolution of primate vocal behaviour in general. Moreover, it highlights the contemporary view of gibbon phylogenetics which considers there to be a plethora of extant species, with the study species, *Hylobates lar*, being one of the most derived. Gibbon socio-ecology is also reviewed and reveals that gibbons are extremely well adapted for their mostly arboreal lifestyle. They have relatively long life spans and do not display the sexual dimorphisms common among other primates. Behavioural studies suggest a degree of co-dominance between the sexes who are often cited as being united by a pair bond, evidenced by their daily song bouts.

The most famous of the gibbon songs is the duet, performed by a paired adult male and female, but not all species perform duets. This review reveals that current thinking considers the duets the ancestral form, with non-duetting species appearing later in the gibbon lineage. The function of duets is up for debate, possibilities

include: pair bond advertisement or strengthening, territory advertisement or defence, and songs as reliable signals of health or fertility. In addition, the structure of song sequences examined in the lar species revealed six different basic units or notes that combine into structures that are more complex and culminate in song. The duet songs have a very rigid sequence, but there are other songs that do vary in structure depending on context. The terminology used in the literature to describe these songs and their constituent vocal elements is also discussed.

## **The gibbons**

Gibbons are found throughout Southeast Asia and are mostly frugivorous, lesser apes of the family *Hylobatidae* (figure 1).

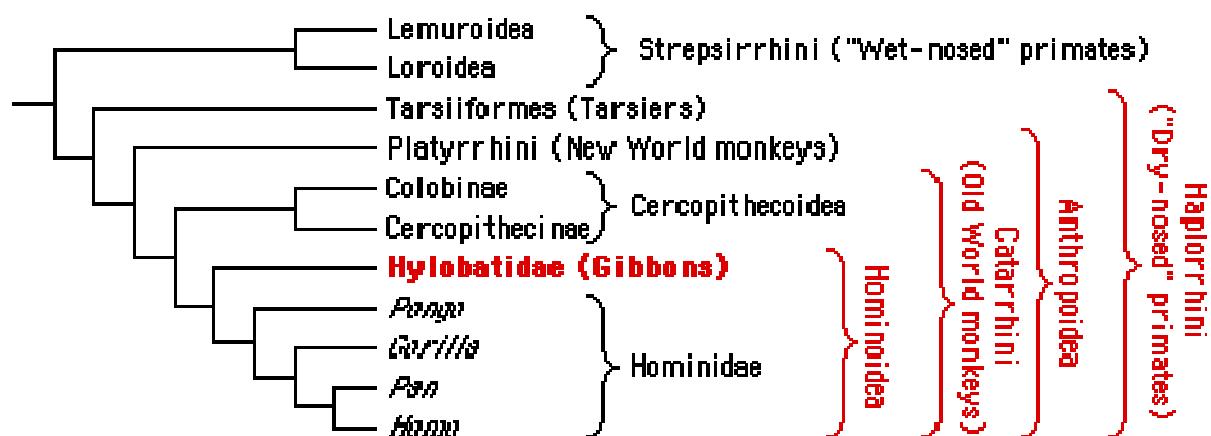


Figure 1. Gibbons occupy a basal position in Hominoidea phylogeny, which makes them interesting for evolutionary comparative studies (reproduced from Thomas Geissmann, [www.gibbons.de](http://www.gibbons.de) with permission).

Weighing between just five and twelve kilograms, they are the smallest of the ape species, and the most specialised for an arboreal lifestyle (Geissmann 2005). Long upper limbs and a graceful brachiating locomotion place them among the fastest and nimblest creatures in the trees. They typically inhabit the middle and upper stories of deciduous monsoon and evergreen rainforests, and have a lifespan of between 30 and 40 years. They live in home ranges that overlap considerably with other groups, although each has their own exclusive use area. These home ranges are often referred to as territories, but strictly speaking, only the exclusive use portions can be defined as such (see chapter 3). Nevertheless, the terms “home range” and “territory” are used somewhat interchangeably throughout this thesis since much of the older literature is based on the premise of the gibbon as a territorial ape. Gibbons’ small family groups usually comprise of one breeding pair, and their dependent offspring, although non-nuclear family compositions are not uncommon. Female gestation is approximately seven months, resulting in a single infant every two to four years (Col 1996).

Males and females are monomorphic in size, but may be dimorphic in pelage colour, depending on the species. Most of the literature also regards them as co-dominant, however there is some evidence that females lead group progression more often than males, and have priority over access to food (Barelli et al 2008a).

Gibbons make up the most diverse extant phylogenetic family of all the apes, and are thus extremely valuable for studies of evolution within the primate taxa (Geissmann 2005). The most recent classification systems agree on four genera of gibbon species:

*Hylobates*, *Bunopithecus*, *Nomascus* and *Sympalangus* (Geissmann 2002; Takacs et al. 2005) where the *Hylobates* genus are the most derived (figure 2).

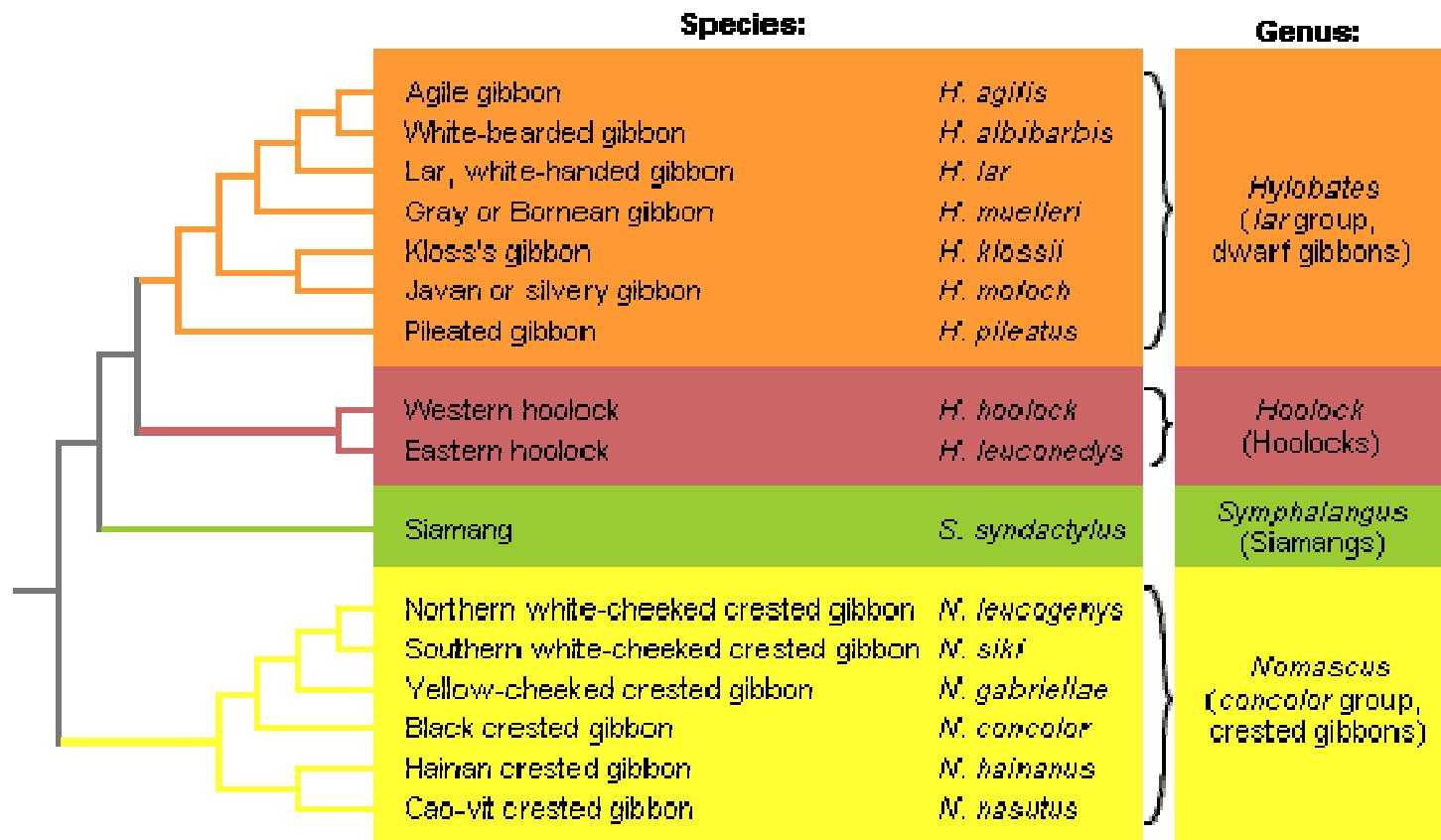


Figure 2. Gibbon phylogenetic tree (reproduced from Thomas Geissmann, [www.gibbons.de](http://www.gibbons.de) with permission). *H.alibarbis*, *H.leuconedys*, *N.siki* and *N.hainanus* are extinct.

## **The pair bond**

Hylobatids and some other animals, most notably birds, are often described as being *pair bonded*, a term coined in the 1940's that can be defined as "the temporary or permanent association found between a female and male animal during courtship and mating" (The American Heritage Dictionary of the English Language 2004), or as: "A strong affinity that develops in the same species between males and/or females in a pair, potentially leading to breeding" (The American Heritage Dictionary of the English Language 2004).

The first definition allows the bond to be temporary or permanent and the second allows it to be an affinity that can develop between either members of the same or opposite sex. This association or affinity does not preclude individuals from engaging in the extra-pair copulations seen among gibbons.

Just what is a "bond" then? Consider the two-part definition below:

"a) A substance or agent that causes two or more objects or parts to cohere,  
b) The union or cohesion brought about by such a substance or agent" (The American Heritage Dictionary of the English Language 2004).

This definition is devoid of all affect; for the purposes of this thesis, gibbon pairs are bonded simply because of their physical proximity to one-another, specifically in sharing a home range, and their union, which in this sense excludes others. However, gibbons do seem to choose their partners and exhibit behaviours exclusive to the pair unit, which can aid in designating two gibbons as bonded, see below.

A study conducted by Palombit (1994) described the mating histories of several Hylobatid groups over a six-year study period and asserted that there are certain social

behaviours, such as duetting, grooming, and coordinated defense of territory that are diagnostic of hylobatid pair bonds. He also postulated that mated individuals of both sexes regularly deserted their partners, not because of an instability in the original pair bond, but because of a need to exploit renewed reproductive opportunities. Indeed, he stated that “members of a monogamous pair are likely to be continually assessing their mates and reproductive prospects in light of current opportunities and conditions...these animals are active decision makers whose lifetime reproductive options demand greater scrutiny and quantitative analysis” (89). However, his work revealed that gibbon pair bonds did show remarkable short-term stability, potentially to aid in the rearing of young animals.

In this thesis therefore, the pair bond is defined as an affinity or cohesion, usually between adult male and female gibbons, that have chosen each other using reproductive decision-making skills. Their union should be stable though it may be of short or long duration; it should lead to the production of offspring, and be evidenced by joint active engagement in duetting, grooming and home range defense.

### **Gibbon song phylogeny**

Singing behaviour is the vocal utterance of musical tones, and to be musical requires some organisation in the sound produced. This type of vocalisation among non-human primates is not restricted to gibbons; it has also been observed in lemurs (*Indri*), tarsiers (*Tarsius*), and titi monkeys (*Callicebus*). In gibbons, songs consist of loud tonal vocal units and in fact, the term “loud call” is synonymous with “song” throughout this thesis (table 2). Often male and female individuals produce sex-specific sequences, which differ structurally between species. For example, female

gibbons often produce a loud call sequence known as the *great call* because of its distinctive configuration and placement within song bouts, but the acoustic structure of this sequence differs from species to species. It has been suggested that gibbon song is under strong genetic control because hybrid animals develop songs that consist of equal elements from both parents (Brockelman and Schilling 1984). But this finding has been disputed (Geissmann 1984), and gibbons are in fact able to exert some control over the order of notes in their duets (Raemaekers et al. 1984). In some species, individuals show considerable versatility in their singing behaviour (Haimoff 1984; Mitani 1988; Haraway and Maples 1998), suggesting that there is some volitional control over vocal utterances (Koda et al. 2007).

Although all gibbons sing on a more or less daily basis, they do not all perform duets. For example, neither silvery gibbons (*H. moloch*) nor Kloss' gibbons (*H. klossii*) produce duets (Geissmann, 2002, see figure 2). This distinction has led to a debate about how duetting has emerged through evolutionary time. Geissmann (2002) suggests that duetting represents the ancestral form, while non-duetting is the derived feature. He argues that the complexity of duets and their overall similarity between gibbon species belies the idea of convergent evolution of the two forms.

What follows is an account of Geissmann's ideas on gibbon song phylogeny:

Geissmann (2002) argues that, in the more ancestral gibbon, both sexes had similar vocal repertoires, which they coordinated in time. This behaviour is still seen in the extant Hoolock gibbon (*B. hoolock*) that does not have sex-specific calls. Later, these songs became separated into male and female specific parts, by a process known as *song-splitting*. Song-splitting is still found in the agile gibbon (*H. agilis*), the Bornean gibbon (*H. muelleri*), the pileated gibbon (*H. pileatus*), and the siamang

gibbon (*S. syndactylus*). In a further evolutionary step, males began to sing solos at different times and in addition to duets. This behaviour is still seen in the Western black crested gibbon (*N. concolor*), the Eastern black crested gibbon (*N. nasutus*), the yellow-cheeked gibbon (*N. gabriellae*), the white-cheeked gibbon (*N. leucogenys*) and the lar gibbon (*H. lar*), which all exhibit sex-specific duetting roles. Some species then underwent a further process that eventually led to segregated solo songs for males and females, known as *duet-splitting*. For example, the Kloss's gibbon and the silvery gibbon are the only extant species where females produce full solo songs. Geissmann attributes this final change to their island habitat, suggesting that isolation from others may have driven the derivation of a non-duetting form from a duetting one. An interesting observation of a female silvery gibbon duetting with a male lar gibbon, in which both parties actively contributed to a well-coordinated typical duet, is compelling evidence that the silvery gibbon species has secondarily abandoned its duetting behaviour (discussed in Geissmann 2002).

### ***The function of gibbon duet songs***

A traditional and frequently cited function of animal duetting behaviour is to strengthen the bond between the duetting partners. The bond between gibbon partners is transient since pairs often exchange mates and extra-pair copulations occur (see chapter 3). Nevertheless, newly mated pairs invest considerable time and energy in the practice of coordinating their respective song parts (Haraway and Maples 1998; Geissmann 1999) such that a singing relationship is built up over time. The pair bond strengthening theory has been corroborated by showing that the duetting intensity of captive siamangs (*Hylobates syndactylus*) is correlated with three measures of pair

bond strength: mutual grooming, behavioural synchronisation, and distance between mates (Geissmann and Orgeldinger 2000). However, whether distance between mates can be reliably measured within the confines of a captive environment is controversial, and studies in the wild are needed to confirm their ideas.

Overall, the pair bond strengthening hypothesis is an attractive explanation for gibbon song; it explains the evolution of complex and intricate coordination of song parts, both requiring a great deal of time and effort, and thus reflecting the investment of each individual in the union. At the proximate level, a recent study has shown that in many animals loud low frequency sounds, above the saccular threshold, stimulate pathways that lead to reward centres in the brain, suggesting that singing partners may thus find each other's vocal behaviour rewarding (Todd and Merker 2004). Gibbon duets could thus function as vocal courtship, by stimulating positive affective responses and making duetting a pleasurable experience. If singing together rewards both parties, this would explain the daily song bouts, and facilitate the building of a closer relationship between pairs. The idea that gibbon singing is an appetitive behaviour is further reviewed by Haraway & Maples (1998).

Because duets travel long distances, over one kilometre, through dense forest habitat (Mitani 1985) and reach neighbouring groups, they may function to advertise territory ownership (Geissmann 2002). Evidence for this idea comes from Bornean gibbons and lar gibbons that respond in a territorial manner to playbacks of neighbours' duets when broadcast from within their home range (Mitani 1985; Raemaekers & Raemaekers 1985), although this may not always be the case (Fan et al. 2007). Another possible function of duet songs is to advertise the pair bond itself; a study

published recently found that when a newly introduced captive female white-cheeked gibbon began to produce solo great calls, a neighbouring group significantly increased their duetting behaviour (Dooley and Judge 2007).

The more recent literature regards gibbons as polygamous with temporary and fluctuating partnerships between adult males and females who hold a territory together (see chapter 3). This newer picture of gibbon socio-ecology does not lend itself as easily to the idea of the pair bond or territory advertisement as functional explanations of gibbon song. However, this does not mean that these explanations should be disregarded altogether, only modified in the light of a more flexible mating and living system. Indeed, the data suggest that gibbon pairs do invest time and energy into their singing relationship, and a well-coordinated duet is something that has to be earned through diligent practice on an almost daily basis (Palombit 1994; Haraway and Maples 1998). Gibbons can and do make this investment with a single partner whom they may raise young and share a home range with for several years. However, an alternative functional explanation for gibbon song is that it acts as a reliable signal of health, fertility and ability to provide; songs serve as an advertisement of a gibbon's worth as a mate. Like all displays, these songs have a cost that makes performing them a handicap, which in turn is a testament to their truthfulness. These ideas are further discussed in chapter 4.

### ***The lar gibbon***

The lar gibbon (*Hylobates lar*), also known as white-handed gibbon, is by far the most vocally studied of all gibbon species. It is also the most abundant, found in Southern Burma, Thailand, the Malay Peninsula, North Sumatra and Indochina. Individuals

vary in fur colouration between light and dark morphs. The dark morph ranges from black to dark brown, the light one from buff to almost white. Colour differences are not sex-related. All are characterised by white fur on their hands and feet, and a white face ring (see figure 3).



Figure 3. Picture of a female dark morph lar gibbon (Photograph by Brendon Snyder, with permission).

Brockelman et al. (1998) proposed the following age classifications for wild lar gibbons, which are also adopted for this thesis: infants (zero to two years, carried by their mother during travel); juveniles (two to five years; tend to follow their mother); adolescents (five to eight years; larger than juveniles but not yet fully grown); sub-adults (over eight years; adult sized but not yet dispersed from natal group); adults (over eight years, mated, in possession of a territory and singing duets).

The lar gibbon, as in most other gibbon species, produces sex-specific and species-specific songs. A mated individual takes part in an elaborate vocal duet with his or her partner on most mornings. Both unmated and mated males also produce solo songs, often before dawn, while females are renowned for their great call, a common feature of the pair duet.

### ***Classification of lar gibbon song***

Carpenter (1940) carried out the first detailed work on wild gibbons. He described nine types of vocalisations in lar gibbons, along with their contexts and probable functions. Later work by Ellefson (1974) expanded on these definitions to distinguish between intra- and inter-group communications, including gestural communication. Raemaekers et al. (1984) described in detail the loud calls of the lar gibbon, categorising each element, and offering visual descriptions from spectrographic images. Haimoff (1984) developed a unified method for describing gibbon vocalisations so that they could be compared across species.

### **The lar duet**

Much of the literature on gibbon vocal behaviour has focused on the pair duet and its components (Cowlishaw 1992; Geissmann 1984, 2002; Haimoff 1984, 1985; Merker & Cox 1999; Mitani 1985). This is arguably the most spectacular and conspicuous of gibbon behaviours (Haimoff 1984). The duet sequences for the lar gibbon consist of the following three elements: (a) *Introductory sequence* (rhythmic series of calls given by both male and female); (b) *Great call sequence* (female great call followed by male reply); (c) *Interlude sequence* (most variable sequence often contributed to more by the male than the female). Songs invariably open with an introductory

sequence and thereafter the great call and interlude sequences alternate, and can terminate with either sequence (Raemaekers et al. 1984; see figure 4).

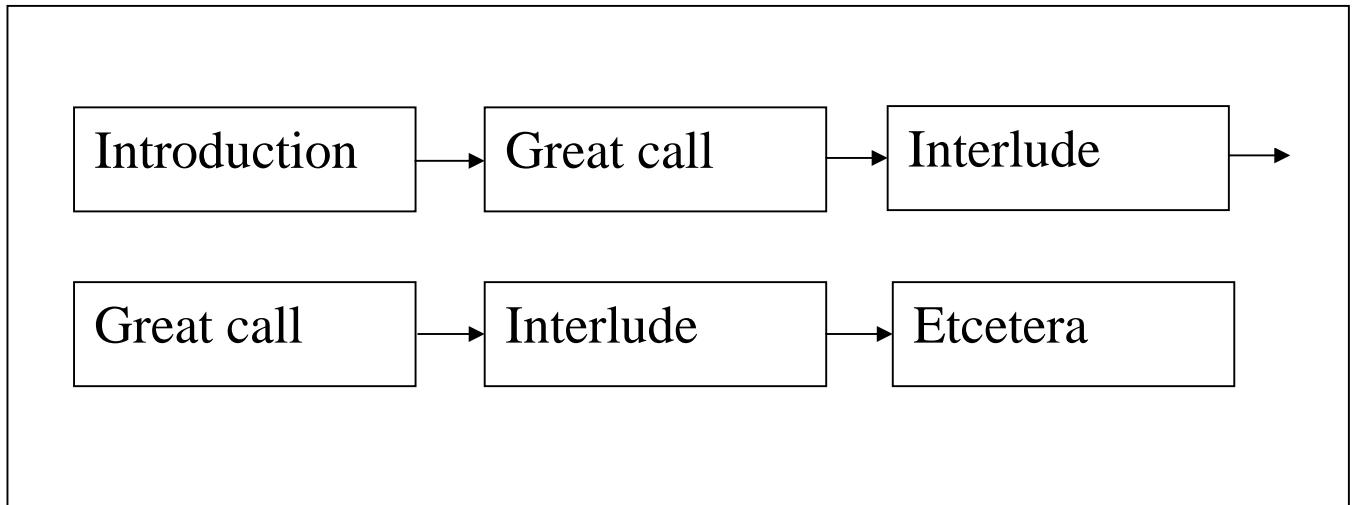


Figure 4. Schematic representation of sequence compositions in the lar duet, produced by Esther Clarke.

### Other lar gibbon songs

Lar gibbons also produce vocalisations in other contexts, for example in situations of alarm or disturbance, as well as during affiliative, playful and defensive circumstances (Carpenter 1940). Apart from the duets, the following call types have been identified (see table 1):

Table 1. Vocal patterns described in lar gibbons other than duet songs (after Raemaekers & Raemaekers 1985).

Call type	Caller	Description
The male solo	Mated and unmated males	Solos can last from a few minutes to up to 4 hours, and include a series of phrases
The female solo	Usually mated females	A single, (or occasionally more than one), great call is produced with no other singing prior to or following it
Territorial dispute calls	Adult and sub-adult males	These are given during group encounters at territory borders
Ooaa duets	All group members	Several bursts of ooaa are termed an ooaa duet, although they may also form part of a normal duet; calls are rare, but have an infectious property, such that it is usual for other surrounding groups to also sing ooaa in unison with the initiating group
Disturbed calls	All group members	These comprise of certain notes that are produced by all group members when encountering a disturbance of some kind (for example, a predator or tree fall)
Contact calls	All group members	These are bouts of intermittent calls by one or two individuals, apparently functioning to maintain contact with the rest of the group

## Terminology

What follows is an overview of the terminology used to describe the vocal behaviour of the lar gibbons in Khao Yai National Park, Thailand (table 2). This classification scheme is based on Haimoff (1984) and Raemaekers et al. (1984). Haimoff's terms were intended to describe the vocalisations of all species of gibbon and have been adapted to suit those of the lar gibbon.

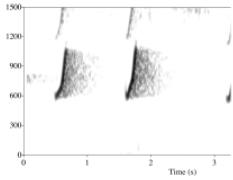
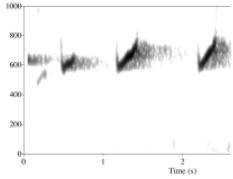
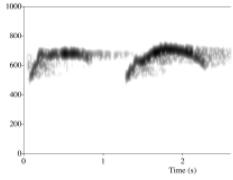
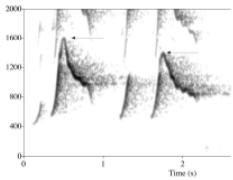
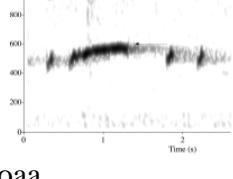
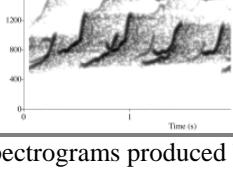
Table 2. Terminology used to categorise the vocal behaviour of lar gibbons.

Term	Description
Note	Any single continuous sound of any frequency
Noise	A variety of sounds which lack distinct frequencies and are irregular in amplitude and pitch, such as grunts, squeals and whimpers
Figure	A short set of notes produced in a set relationship and rarely heard individually
Phrase	A collection of notes and/or figures identifying a single vocal activity, such as the male coda (a distinctive reply made by the male to the female's great call during a duet); the pauses between notes within a phrase are necessarily shorter than pauses between phrases
Song	Sound that is pure in tone and musical in nature; song includes all calls that are high in amplitude ("loud calls"), including duets, and therefore serve as long-distance calls and probably function in inter-group communication
Song/call bout	The first to last note produced during a song/loud call; pauses in singing are no longer than ten minutes.
Duet	The song bout in which both sexes produce loud sounds and a mutually cooperative and coordinated display
Quiet calls	Calls that are relatively low in amplitude and short and simple in acoustic structure; they may be elicited by an external stimulus, for example preferred food, disturbance, distant group member, or territorial dispute and function as intra-group signals

## **Classification of note types**

Raemaekers et al. (1984) further discriminated between different types of notes in the loud calls of lar gibbons (table 3). Notes usually show a frequency range of 400-1600Hz, with male calls, on average, being pitched higher than female calls.

Table 3. Description of the lar gibbons' basic note types.

Note	Description	Type of loud call bout associated with
Wa	<p>This note is short uninflected and steeply rising, and is straight or slightly concave; it is the simplest and most common note, given by both sexes and includes hoos (short, breathy quiet notes)</p> 	Produced in all classes of loud call bout
Leaning wa	<p>This note is similar in shape to the wa, but longer in duration, so it leans more to the right; it is given by both sexes</p> 	Produced mostly in the introductory sequence to duets
Waoo	<p>This is an inflected note, which rises steeply to produce a flat line of varying length but may otherwise descend to produce a convex shaped note; it is a plaintive note sung by either sex</p> 	Produced in disturbed call bouts, introductory sequence of duets, and contact call bouts
Sharp wow	<p>This note rises steeply, and then falls steeply into a concave curve; a loud and penetrating note</p> 	Produced mostly in disturbed call bouts by adult and sub-adult males; occasionally it is found in the introductory sequence of duets
Oo	<p>This note is of a low, even pitch and is mainly given by the female, but occasionally by the male</p> 	Produced in the introductory sequence of duets and in disturbed call bouts
Ooaa	<p>This is a concave wa, a J shaped note, given by both sexes of adult and offspring</p> 	Typically given in rhythmical bursts during an "ooaa duet", which elicits reciprocation among neighbouring groups

Spectrograms produced by Esther Clarke.

There are also fine pitch modulations, which can be imposed on the shape of any note, see table 4.

**Table 4. Description of the lar gibbon's frequency modulations imposed onto the basic note shapes.**

Modulation	Description	Type of loud call bout associated with
Tremble	This is produced by both sexes and according to Raemaekers et al. (1984) is suggestive of a lack of voice control	Produced in all classes except the female solo; here pictured on a series of oo notes
Wobble	This is essentially a brief reversal or reduction in the rate of change of pitch, intermediate between the tremble and quaver	Produced in all classes except the female solo; here, it is pictured imposed on two waoo notes
Quaver	This is a deep, regular modulation, which signifies voice control and only the males produce true quavers; Raemaekers et al. (1984) suggest this (apart from the female great call) is the major difference between the vocal repertoire of the male and female of this species	All classes except the female solo; here pictured imposed on three male waoo notes, with the female's contribution underneath

Spectrograms produced by Esther Clarke.

## Classification of figures

Individual notes are produced as part of longer call sequences, some of which can be recognised as distinct figures (table 5).

Table 5. Description of the figures in lar gibbon songs.

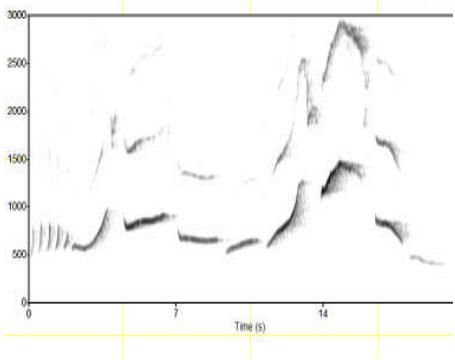
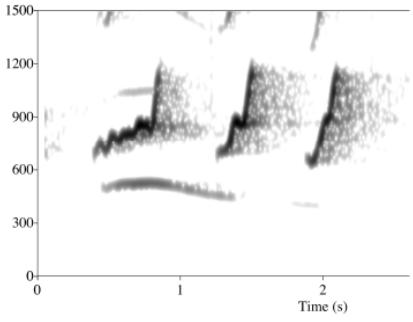
Figure	Description	Type of loud call bout associated with
Male trill	This is a rapid series of wa notes	This may form the beginning of a male structured phrase (see table 6) or part of the introductory sequence to a duet
Ooaa burst	This is a rhythmical series of ooaa notes, which often elicit the same calls in other neighbouring groups	Produced in the ooaa duet, and also sometimes the duet
Hoo-sigh	This is a low-pitched quiet figure encompassing both an inhalation and exhalation; this corresponds to the “hoo-oo” that Raemaekers et al. (1984) describe	This may function as an alarm call or signify aggression/frustration; can be present in duets, ooaa duets and alarm calls

Spectrograms produced by Esther Clarke.

## Classification of phrases

Finally, figures and notes can be combined into phrases, two of which are described in table 6.

Table 6. Description of some of the lar gibbon's phrase repertoire.

Phrase	Description	Type of loud call bout associated with
Great call phrase	<p>Only the female produces the great call and its basic two-humped shape is invariable; the notes given in this phrase are not given in any other calls or contexts and when part of a duet, it is usually followed by the male coda to form the great call sequence</p> 	The great call sequence is usually given in normal duets, ooaa duets; single great calls can also be heard during encounters with neighbouring groups
Male quaver phrase and male simple phrase	<p>The male quaver phrase is produced by the male only, but is much more variable than the female great call; the male simple phrase is the same as above, but there are no quavers, and it is less common than the quaver phrase</p> 	Both male phrases are the main constituents of the male solo, but are also given in normal, and ooaa duets, as replies to great calls (codas) and in the interlude sequences; they can be distorted however, and appear in disturbed call bouts and male dispute calling; here the end of the female great call is pictured below the male coda.

Spectrograms produced by Esther Clarke.

## ***Summary***

The lar gibbon vocal repertoire as described in this chapter is acoustically rich and structurally complex. Much is now known about the duet songs, but surprisingly little is still known about their other calls, and the contexts that elicit them. With such a diverse range of notes, figures and phrases, the combinatory possibilities are vast. Due to their unique position in Hominoidea phylogeny, gibbons are especially important in any comparative approach to understand the evolution of primate vocal communication, including human language.

## **CHAPTER 3. The white-handed gibbons (*Hylobates lar*) of Thailand's Khao Yai National Park**

### ***Abstract***

The studies included in this thesis take place in the forests of Northeastern Thailand. The study site itself is one to be admired for its picturesque landscape and abundance of animal and plant life. An understanding of the location and the relevant animals therein is essential in being able to formulate clear hypotheses to test regarding the behaviour of the study species. This chapter describes the flora and fauna focusing specifically on the socio-ecology, mating system, home range and predation risk of the white-handed gibbon. Reviews of the literature as well as time spent with the animals reveal that they live in small groups usually made up of an adult mated pair and their offspring, but partner exchanges are frequent and offspring are not always genetic relatives of both adults. Correspondingly, third adults are sometimes present, usually males. Annual temperature and rainfall graphs revealed a cold, dry season, a hot season, and a wet season. Fruit availability is dictated by these weather patterns, as is the gibbons' activity, with them moving more frequently from tree to tree when ripe fruit is abundant. Gibbons were observed and listened to over a period of 119 days, with most listening time concentrated between 6:00 AM and 2:00 PM on any given day. The pattern of group visitation was mostly random, though some groups were deliberately avoided for short periods when they were being closely followed by other researchers. A review of the literature demonstrated that gibbon predators were split into three classes: snakes, raptors and cats. They appear to counter predation risk

with a suite of anti-predatory adaptations such as swift locomotion, preference for the high canopy and early retirement to tall sleeping trees. They also adopt a mobbing strategy when predators are encountered, one which may aid in predator deterrence by advertising their agility and strength and/or literally harass the predator out of their home range. Justifications for the research presented in subsequent chapters are also discussed.

## ***Introduction***

Khao Yai National Park (literally translated from Thai as “big mountain”) is situated at 101°22’E, 14°26’N, 130 aerial km Northeast of Bangkok, Thailand. It was established in 1962, making it the first of over 100 national parks in the country today (figure 5). It was originally nicknamed “the jungle of the fire lord” due to local fears and superstitions, as well as the rampant malaria that afflicted all who entered. It covers a total area of 2,165 km<sup>2</sup>, and is therefore the third largest of Thailand’s national parks, extending across the four provinces of Saraburi, Nakhon Nayok, Nakhon Ratchasima and Prachin Buri. Most of the park lies on a sandstone plateau 600-1000 metres above sea level.



Figure 5. A map of Thailand showing the location of Khao Yai National Park in relation to the capital, Bangkok. Figure produced by Esther Clarke.

The park's vegetation can be split among five main types: grasslands, dry evergreen forest, tropical moist evergreen forest, mixed deciduous forest and hill evergreen forest. Around 60% of the park, including the study site, is tropical moist evergreen forest (WildAid 2002). Khao Yai is home to an abundance of animals including dholes (*Cuon alpinus*), wild boar (*Sus scrofa*), gaur (*Bos gaurus*), elephants (*Elephas maximus*), Asiatic black bears (*Ursus thibetanus*), Malayan sun bears (*Helarctos malayanus*), king cobras (*Ophiophagus hannah*), giant squirrels (*Ratufa indica*), binturongs (*Arctictis binturong*), hornbills (*Buceros bicornis*) and many more. There are over 340 species of bird, 70 species of mammal and 70 species of reptile. The fauna most relevant to this thesis are detailed in table 7. There are also 2500 species of plant, including the heavily poached “mai hom” or aloe wood tree (*Aquilaria*

*crassna*), whose bark and wood is used for its medicinal properties and also sold and used to manufacture perfumes and incense (Young 2001).

Table 7. Relevant fauna of Khao Yai National Park.

Vernacular name	Latin name	Detail
White-handed/lar gibbon	<i>Hylobates lar entelloides</i>	Study species
Pileated/capped gibbon	<i>Hylobates pileatus</i>	Sympatric gibbon species
Asiatic tiger	<i>Panthera tigris corbetti</i>	Potential gibbon predator
Clouded leopard	<i>Neofelis nebulosa</i>	Potential gibbon predator
Asian golden cat	<i>Catopuma temminckii</i>	Potential gibbon predator
Marbled cat	<i>Pardofelis marmorata</i>	Potential gibbon predator
Leopard cat	<i>Prionailurus bengalensis</i>	Potential gibbon predator
Reticulated python	<i>Python reticulatus</i>	Potential gibbon predator
Crested serpent eagle	<i>Spilornis cheela</i>	Potential gibbon predator
Changeable hawk eagle	<i>Spizaetus cirrhatus</i>	Potential gibbon predator
Black eagle	<i>Ictinaetus malayensis</i>	Potential gibbon predator
Mountain hawk eagle	<i>Spizaetus nipalensis</i>	Potential gibbon predator
Barking deer	<i>Muntiacus muntjak</i>	Shared prey*
Variable squirrel	<i>Callosciurus finlaysoni</i>	Shared prey*
Sambar deer	<i>Cervus unicolor</i>	Shared prey*
Oriental pied hornbill	<i>Anthracoboceros albirostris</i>	Shared prey*
Pig-tailed macaque	<i>Macaca nemestrina</i>	Shared prey*

\*Shared prey of gibbon predator.

Khao Yai receives about 2,270 mm of rainfall per year (see figure 10), most of which occurs during the rainy season from May to October. There is also a cold season from

November to February and a hot season from March to April. However, the annual mean temperature is 23°C. The park is also renowned for its splendid waterfalls, making it a popular tourist attraction especially among Thais. The highest waterfall is Heo Narok reaching 150 metres in total (figure 6).



Figure 6. The Heo Narok Waterfall. Photograph by Esther Clarke.

### ***The study site***

The Mo Singto study site was founded by Dr Warren Brockelman in 1979 and further developed by Dr Ulrich Reichard and colleagues. The site is located at 730-860 metres elevation, and bordered on one side by the Mo Singto reservoir. The Takhong

River divides it to the East (figure 8). Tourist trails run through several parts of the site, and are complemented by the trails made by previous researchers designed to cross the forest. There are three main entrances to the site; the first entrance is adjacent to the reservoir, the second by the visitors' centre, and the third at a tourist site called "Wang Jumpee." All three entrances are within ten to twenty minutes walk of each other. The researcher accommodation lies in the Forest Training Centre, and the closest entrance to the field site is approximately forty minutes walk away or ten minutes by car or moped.

### ***The study species***

The study site is heavily populated with more than forty groups of white-handed gibbons; thirteen of these groups range from being fairly to extremely well habituated to human presence (figure 7). These groups are named A, B, C, D, E, H, J, N, R, S, T, W and NOS. There are also groups of the closely related pileated gibbon present, and a hybrid zone exists between the two species. One of the study groups, group E, actually contained a male white-handed gibbon and a female pileated gibbon for much of the study period (table 9).

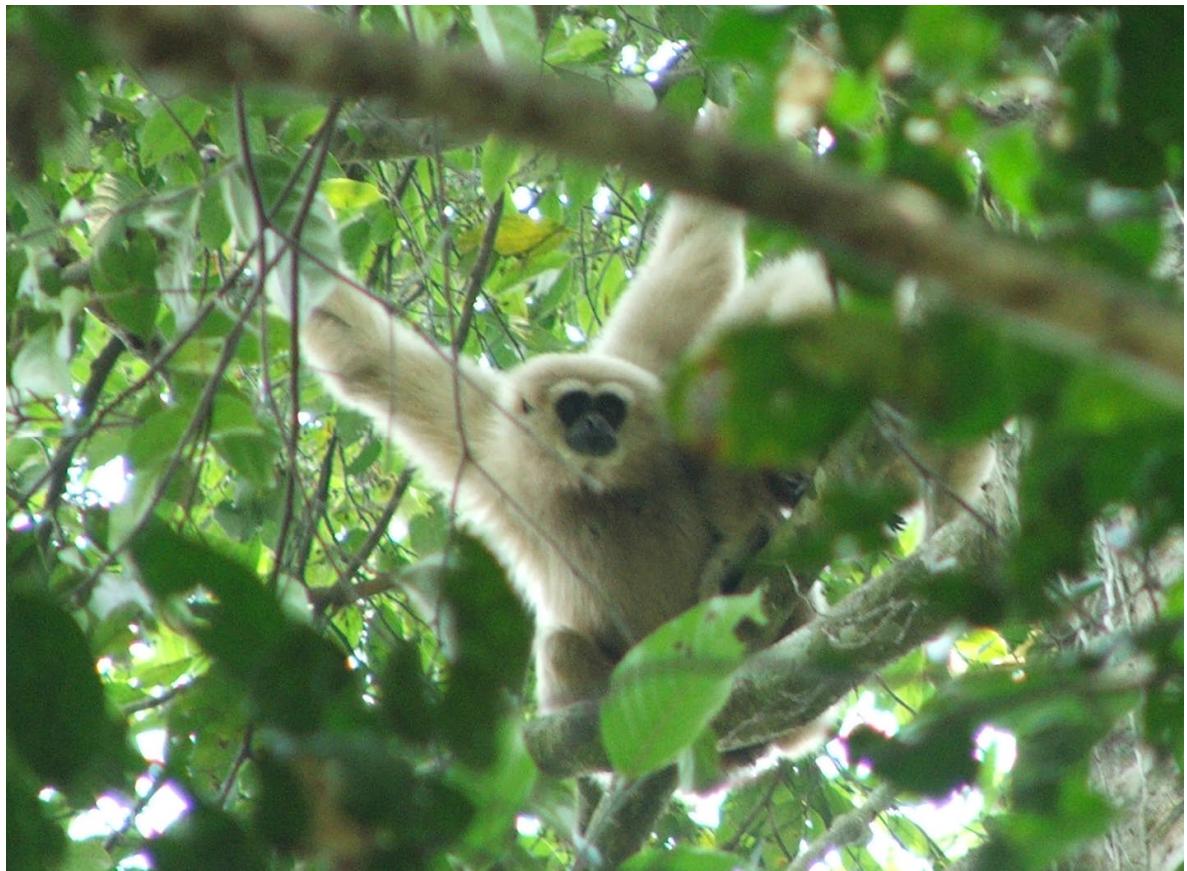


Figure 7. A light-phase male white-handed gibbon. Photograph by Esther Clarke.

The white-handed gibbons at the study site tend to live in groups in home ranges of between 400 and 500 metres in diameter; approximately every other day adult gibbons loosely defend these ranges against their neighbours (Reichard and Sommer 1997). Home ranges overlap extensively, though an exclusive-use core exists for each. This core usually represents about one third of the total area, and is the only part of the home range that can be labelled as a true territory (Sommer and Reichard 2000). Ranges support a small group of between two and six individuals, usually consisting of a mated pair and some offspring. The reason gibbons are not more gregarious in their grouping structure is probably because female gibbons will not tolerate competition from other females over resources. Thus the anti-predatory benefits of large group living are outweighed by the costs of maintaining physical

condition and optimising reproduction (Sommer and Reichard 2000). The classic literature describes these gibbons as fiercely territorial, with non-overlapping territories; they were seen as obligatorily monogamous apes that pair bond with a partner and live together until one dies, and were thought to live in nuclear family groups consisting of a mated pair and their dependent offspring. Traditionally these groups were created when a sub-adult left the natal group to found a new territory (Carpenter 1940; Ellefson 1974). More recently however, these claims have been opposed (Palombit 1994; Brockelman et al. 1998), and a more modern view is that adult lar gibbons disperse by displacing the adults of existing territories, thus creating non-nuclear families. The group compositions at Khao Yai can therefore be fairly unstable, although changes occur with relatively long time intervals (years). A study by Brockelman et al. (1998) reported seven sub-adult dispersals and subsequent displacements in the study site occurring over an eighteen-year period. They concluded that sub-adult gibbons dispersed at a mean age of ten years old (two years after maturity), and to an average distance of seven hundred and ten metres, which is relatively close to their natal territory. In fact, three gibbons dispersed to territories directly neighbouring their own. This means that neighbours are often closely related, a fact that has favoured the evolution of kin-selected behaviours, and explains the affection with which neighbours sometimes interact and the apparent intermittent nonchalance of adult males defending their territories against one another (E.C., pers. obs.). In a saturated environment such as that in Khao Yai, it may be advantageous to delay dispersal and support the adult pair in territory defence, help them with grooming, and assist in social play with juveniles.

In most cases, gibbons in Khao Yai exhibit grouping monogamy. It is important to distinguish between three levels of social systems here: grouping, mating and breeding. A pair of gibbons can be living together (monogamous grouping) but engaging in extra-pair copulations (polygamous mating) with the possibility that offspring are not full siblings or are not related to the adult male (polygamous breeding). The benefits of a monogamous group include higher survival rates for offspring. Males that stay with a single female to raise their young can protect them from infanticide; a rival male may kill an infant or juvenile in order to free up the mother's energy to conceive and care for his own young. The main cost of monogamous grouping is foregoing reproductive opportunities with other individuals. Males in particular lose out from this since they invest relatively little in reproduction and could conceivably travel from female to female. However, data from Khao Yai suggests that females are somewhat synchronised in their fertility, and as such males would find it difficult to ensure reproductive success with multiple females (Sommer and Reichard 2000). Nevertheless, polygamy is tolerated in a few instances, usually polyandry. Here, males may tolerate one another when a population reaches carrying capacity in the environment since reproductive success is higher with limited access to a polygamous female, than with access to no female at all. Few polygynous groups are found in Khao Yai; the groups that are present most often consist of one female lar gibbon and one female pileated gibbon living with a single male lar gibbon in the overlapping hybrid zone where the two species coexist. It may be that these females tolerate each other because they are different species, and in particular, they have different great calls, which may minimise friction within the group. The great call seems to have an important role in gibbon reproductive behaviour, and females of one species may not be able to sex females of another species by call alone (Raemaekers

and Raemaekers 1985). In terms of mating and breeding, monogamy is virtually non-existent (Sommer and Reichard 2000). Extra-pair copulations are fairly common among Khao Yai gibbons (Barelli et al 2008b) and other than improving individual fitness, these may act to forestall infanticide by new males looking for a new mate. If males have previously engaged in extra-pair copulation with a neighbouring female, they may be confused about the residing offspring's' true paternity. As such, groups may consist of a mixture of related and unrelated individuals, full- and half-siblings. The potential for family relation between groups is also present even when it cannot be confirmed because of the existence of extra-pair copulations. This also therefore has implications for the functions of gibbon songs, which traditionally are theorised as territorial and/or pair strengthening (see chapter 2). In sum, the picture of the monogamous ape has been radically challenged in recent years. The instability of family groups, regular pair exchange, extra-pair copulations and polygamous grouping, mating and breeding described for these gibbons creates a dynamic social structure – this structure impacts upon the concept of territoriality, subsequent territorial conflicts and song function.

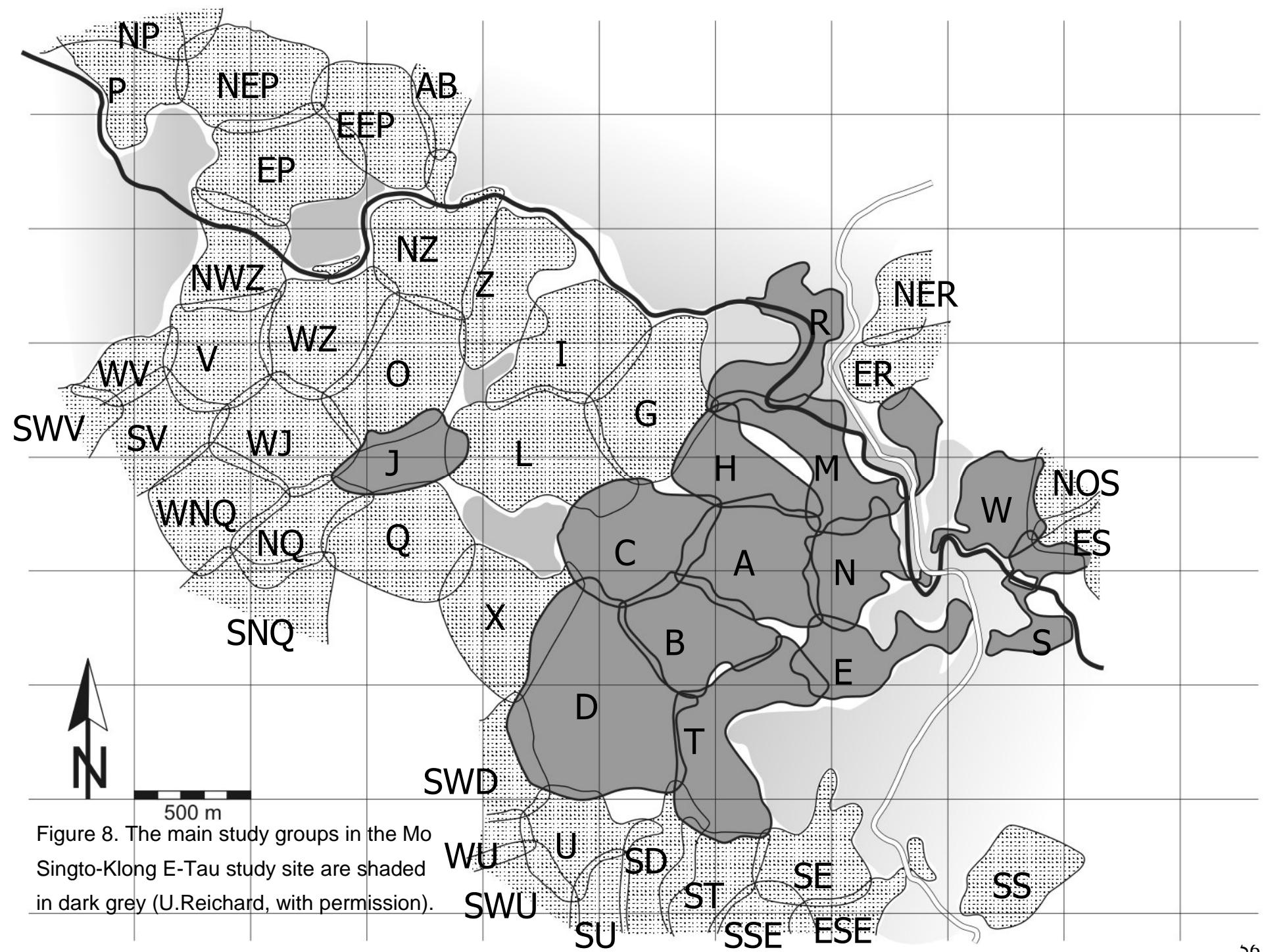


Figure 8. The main study groups in the Mo Singto-Klong E-Tau study site are shaded in dark grey (U. Reichard, with permission).

## **Study details**

Gibbons are known to live for several decades, and Uhde & Sommer (2002) postulated that at the time of their study, the adult female of group A was at least 35 years old. This female is still an active member of Group A today.

All the habituated gibbons at Mo Singto have common names, and after some time of acquaintance are recognisable through individual markings, behaviour, or features. Their distinctive dark or light pelage (unrelated to sex) can also be an aid in individual recognition among such small groups. Table 9 shows the group compositions and names at the time of the study. Four groups were polyandric - where one adult female lived with two adult males, neither of which were her genetic relatives - and three others contained adult male offspring of the current pair. In these multi-male groups, the primary males were defined as the ones who regularly copulated and duetted with the adult female, that is, were pair-bonded with the female. The other males were termed secondary males and they did not normally engage in copulation or duetting. These secondary (unrelated) males did sometimes copulate with the female, but these occurred significantly less often than copulations with the primary male (Barelli et al. 2008b). Table 8 shows the days that each group was visited during the study period. Figures 9 and 10 detail the mean monthly listening hours across all groups, and the diurnal listening hours across groups. Mean listening times were usually over seven hours per day, and the time of day spent listening peaked between 7:00 AM and noon on any given day.

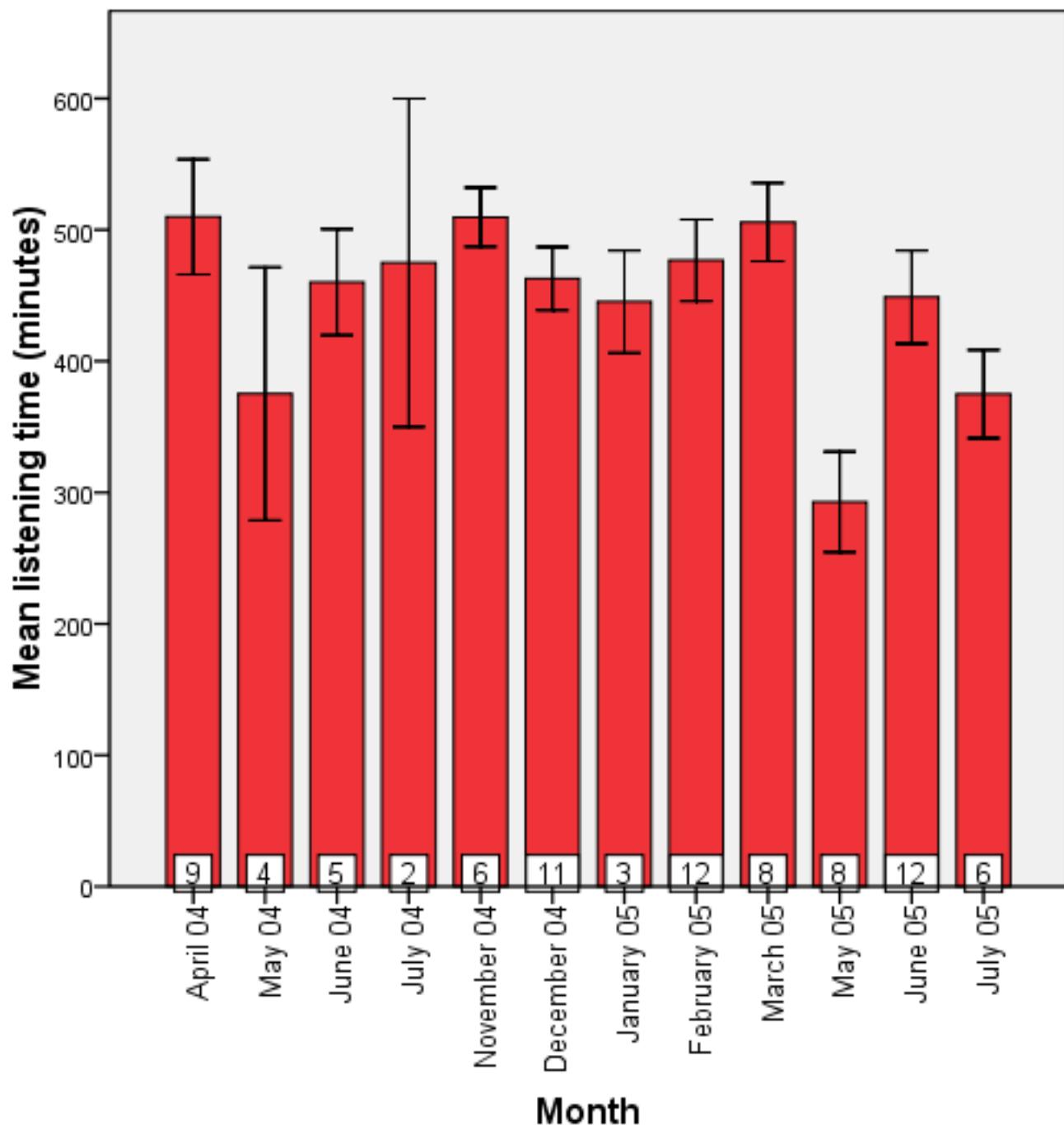


Figure 9. Mean (+- 1 SE) listening time during each month of the study period. Numbers in white boxes represent the actual number of days for which listening times were available.

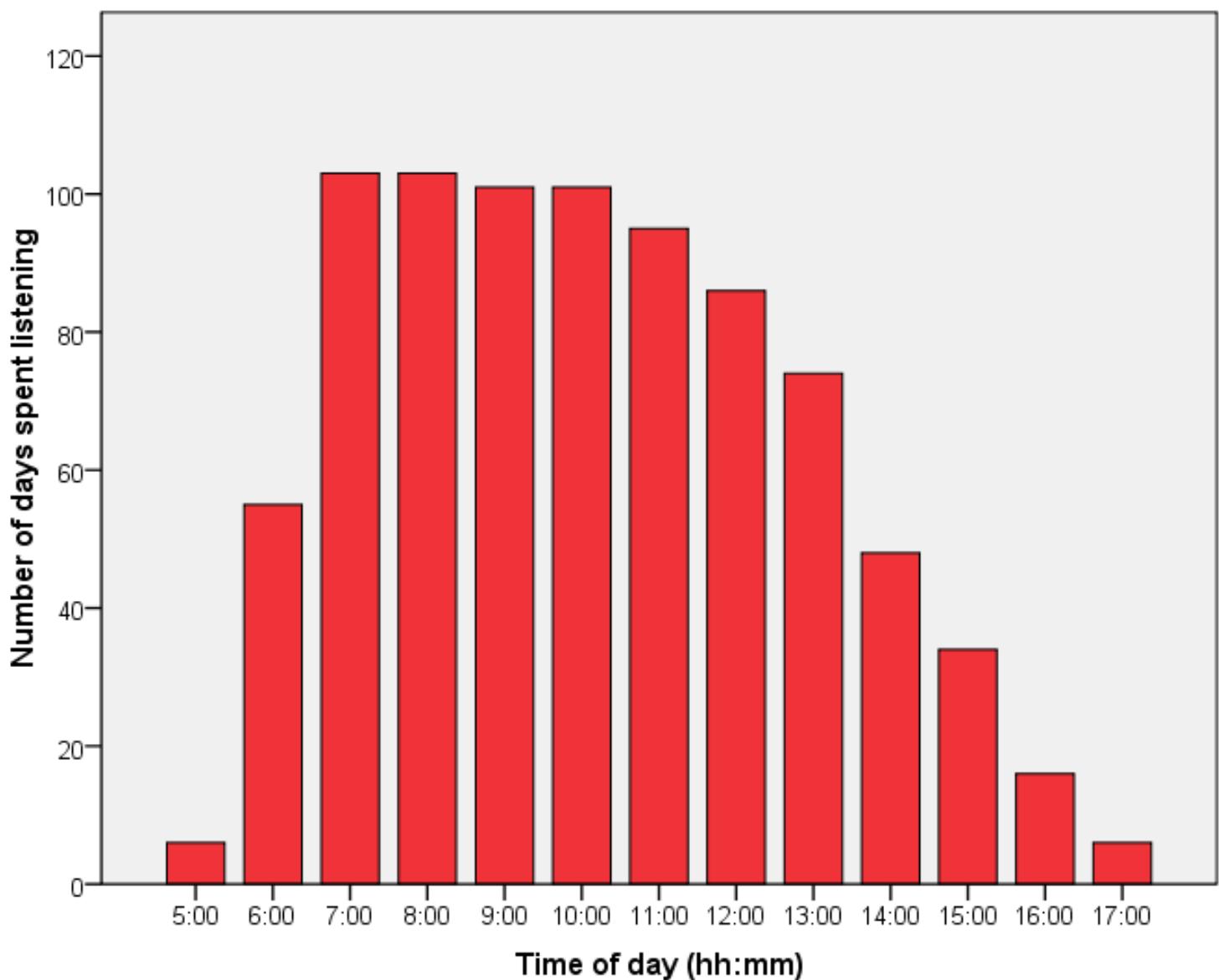


Figure 10. Diurnal listening times. Bars represent the number of days spent in the forest listening to gibbon groups at each hour of the day.

Table 8. Group visits during the study period. Numbers represent dates of the month.

Group	Date											
	April '04	May '04	June '04	July '04	Nov. '04	Dec.'04	Jan.'05	Feb.'05	March '05	May '05	June '05	July '05
B	17,24,28,29 30	1,21,22	26	2	5	9,16		5,16		30	11	4
C	13,22,23				3,10	6,17		15	5,6	24	9	14
D	15,16			3	16	15	7,8	8,9	7	19,20	18	20,23
E												25,27,28
H				6	2	4,5,14, 22			11	25		
J	16,21	23			4,12	8,18		10	9	27	19	
N				4	9	7,19	5	6,19,20				25,27,28
R	27				11,17			4,11,18	4	26	8	3
S			15,20, 22									
T	20	2,3,4	25,27,30							18	1	25
W	23				1		6	7,17	3,10	31	2,22,26	12
NOS										23,24,25	31	

Table 9. Group compositions at the end of the study period (July 2005).

Group	Number of individuals	Composition	Habituation
A^	5	2AM: <b>Christopher</b> and Cassius, 1AF:Andromeda, 1J/SAM: Chikyu, 1JM:Chu	***
B	3	1AM:Chet, 1AF:Bridget, 1SAM:Bua	***
C	2	1AM:Chanah, 1AF:Cassandra	***
D^	5	2AM: <b>David</b> and Diego, 1AF:Daow, 1JF:Dodo, 1I? *	
E†	3	1AM:Fearless, 1AF:Rung, plus 1AF pileated:Emmanuelle	***
H	4	2AM: <b>Felix</b> and Haley, 1AF:Hannah, 1JM:Henry	***
J^	5	2AM: <b>Joe</b> and Frodo, 1AF:Jenna, 1JM:Jojo, 1I?	*
N	4	2AM: <b>Claude</b> and Nithat, 1AF:Natasha, 1JM:Noi	***
R	3	1AM:Elias, 1AF:Brit, 1JF:Rak	***
S	4	2AM: <b>Samran</b> and San, 1AF: Sophie, 1IF	***
T	3	1AM:Amadeus, 1AF:Brenda, 1J?:Thala	***
W	5	1AM:Wotan, 1AF:Wolga, 1SAF:Waraporn,*** 1JM:William, 1I?	
NOS^	5	2AM: <b>Nostradamus</b> and Nissan, 1AF:Nassima,* 1JF:Nossi, 1JM:Noss	

<sup>^</sup>Polyandric group. Where there are two males the primary male's name is in bold, and is followed by the secondary male's name †Hybrid group (lar pair=primary pair), M=male, F=female, ?=sex unknown, A=adult (>8 years, mated, own territory), SA=sub-adult (5-8 years), J=juvenile (2-5 years), I=infant (0-2 years). Habituation status: \*\*\* well habituated (>4 years of regular observations by researchers or daily exposure to researchers or tourists. \*=partially habituated (<4 years of regular observations by researchers and exposure by tourists or researchers less than once per week).

## **Resources**

A gibbon's diet consists mainly of fruit, but is supplemented with leaves and occasional insects. Gibbons are largely frugivorous due to the energetic demands of their locomotion. Brachiation is an extremely efficient way to manoeuvre around peripheral sections of trees and between trees, without returning to the trunk or descending to the ground, but it is energetically expensive (Parsons and Taylor 1977); ripe fruit offers a rich source of calories, which are needed to sustain locomotion of this type. In addition, food distribution plays a key role in sustaining females and their offspring. A female's dietary needs seem to prevent her from aggregating with other females, and single home ranges are likely to support only one female at a time. As such, males are probably mapping themselves onto the spatial distribution of females (Reichard and Sommer 1998). Resource availability in the park alters throughout the year, with peaks in fruit availability in April and September. There is a marked reduction in fruit availability in the cold season from November to February. These changes are known to affect gibbon behaviour (Bartlett 2003), as an example, gibbons are much more active when ripe fruit is abundant. Accordingly therefore, their ranging patterns are reduced in the cold season when resources are low, and activity is somewhat diminished.

The temperature, rainfall and humidity at Khao Yai for most of the study period are detailed in figures 11 to 13. Data for portions of 2005 (March-July) are missing, and at the time of writing were unavailable.

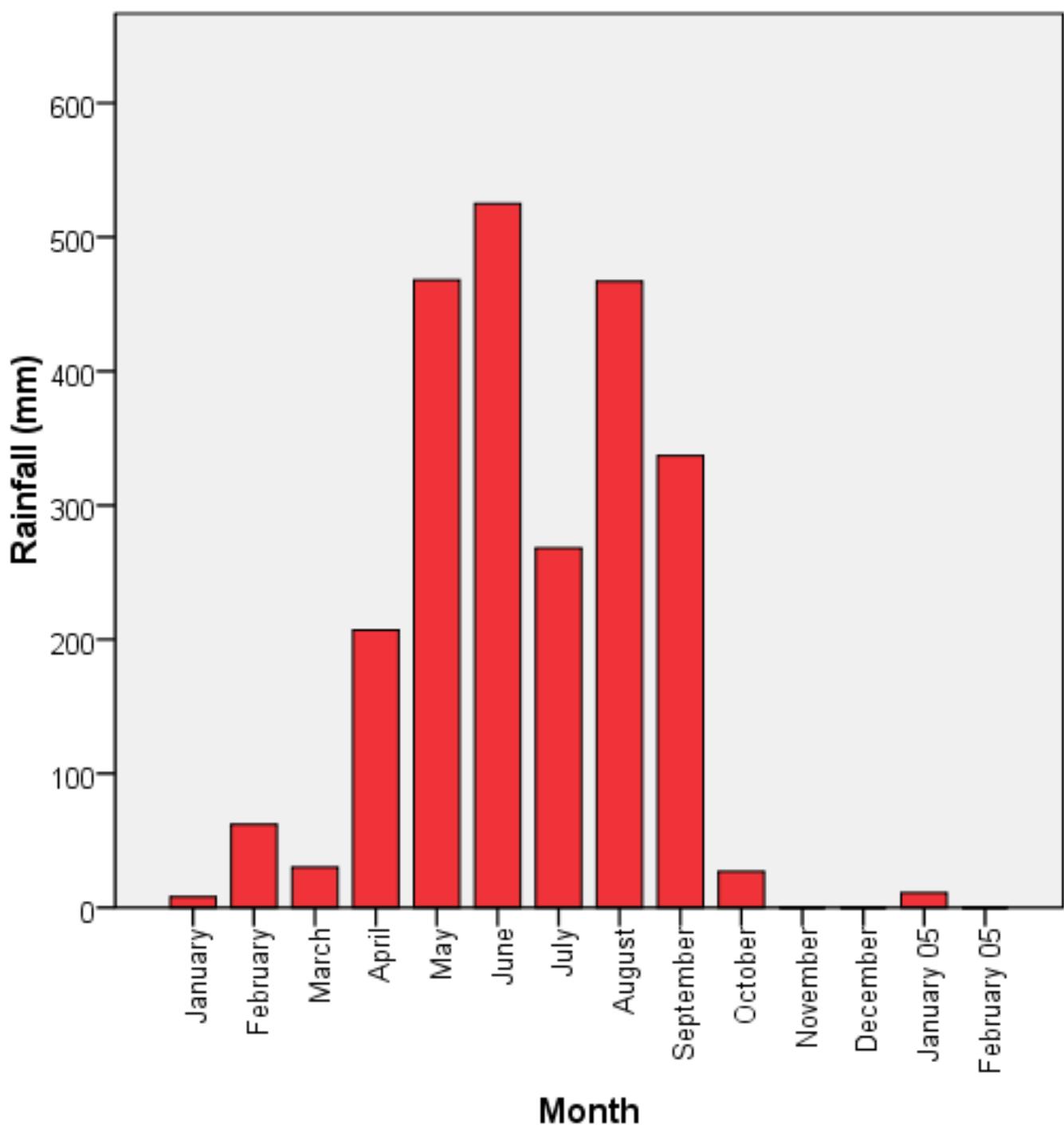


Figure 11. Monthly rainfall in the Khao Yai study site for all of 2004. January and February of 2005 are also included.

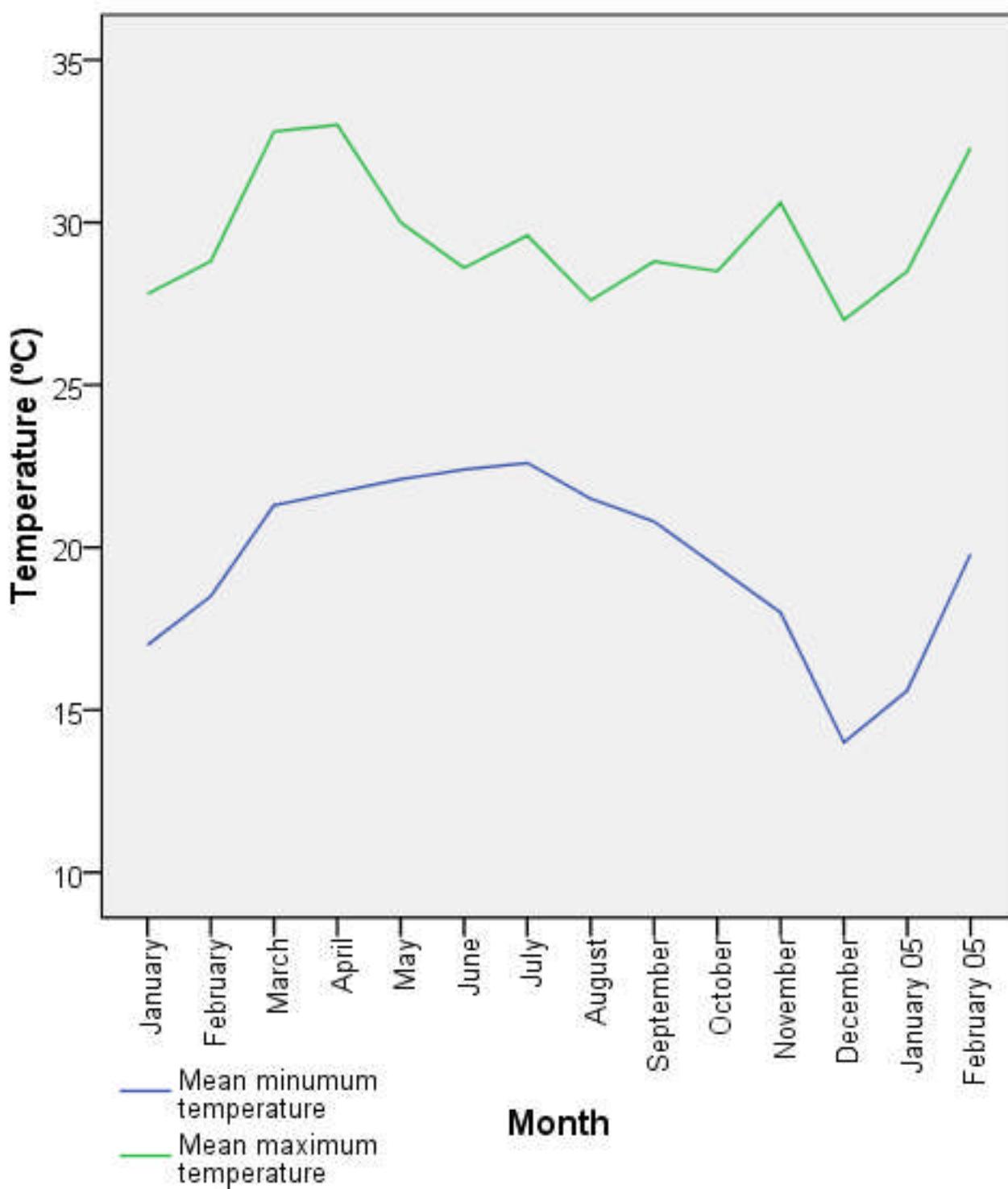


Figure 12. Mean monthly maximum and minimum temperatures throughout 2004. January and February 2005 are also included.

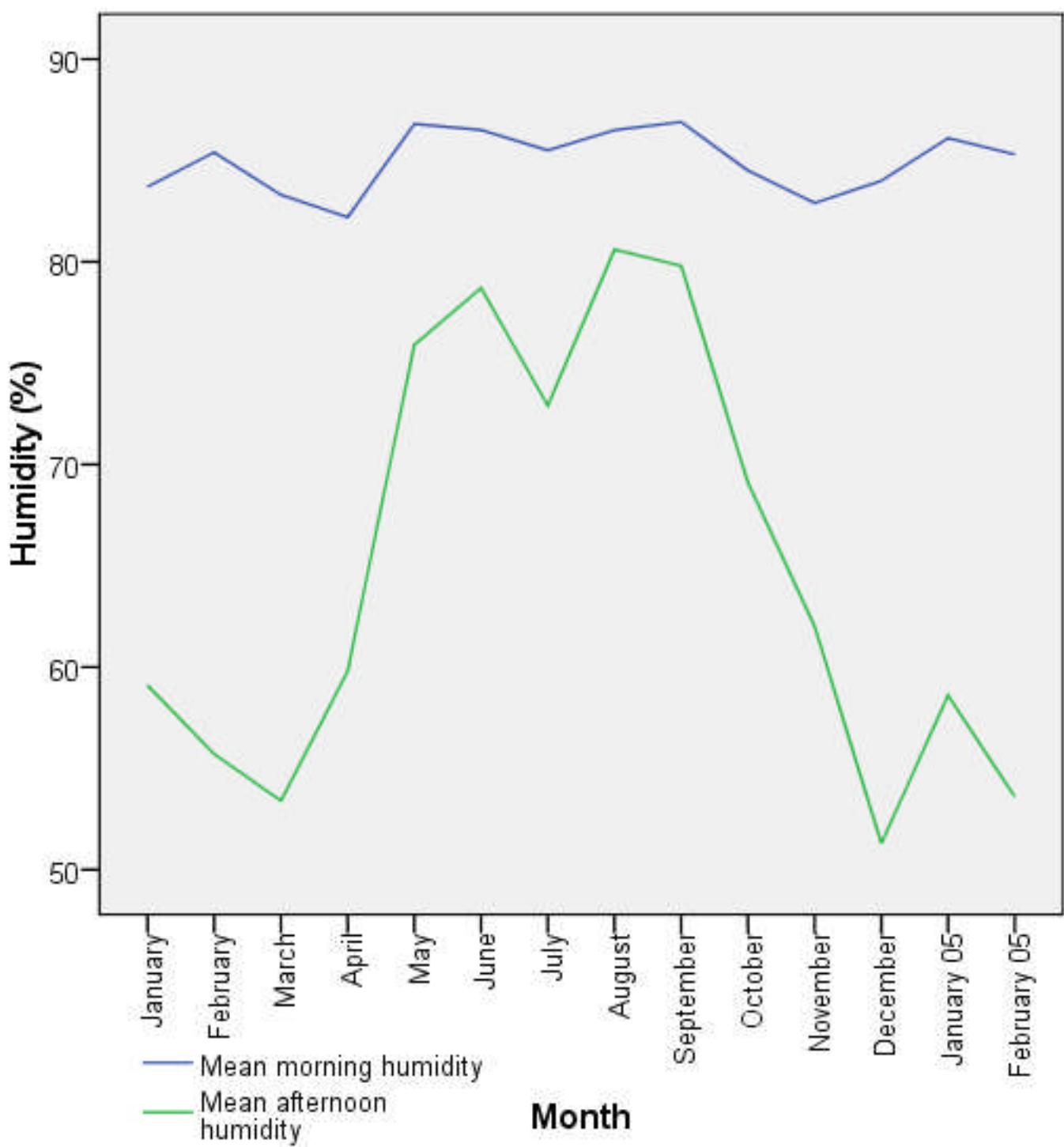


Figure 13. Mean monthly humidity in the morning (5:00 AM) and afternoon (5:00 PM) throughout 2004. January and February 2005 are also included.

## **Gibbon predation risk**

According to Carpenter (1940) and Ellefson (1974), gibbon predation risk is negligible. The gibbons' access to very high trees gives them good vantage points to spot danger from, as well as making it physically challenging for any land predator to get to them. Their high-speed locomotion is also thought to afford them with excellent escape tactics from predators that may try to pursue them in the canopy. Moreover, evidence of actual predation on gibbons is scarce - the discovery of lar gibbon remains in leopard (*Panthera pardus*) faeces is a rare exception (Rabinowitz 1989). However, gibbon behaviour towards potential predators suggests they are genuinely perturbed by their presence. For example, when a group of gibbons observe a python in a tree they will approach it closely, sometimes to within a metre or less (Reichard 1998). In addition, on occasion gibbons may physically interact with pythons, slapping them while excitedly emitting vocalisations (C.Neumann pers.comm.). In fact, gibbons are known to give calls to all three classes of potential predator, and have been seen to approach and mob in response to raptors, tigers and snakes (Uhde & Sommer 2002). Typically, vocalisations in response to an urgent threat from a predator are termed *alarm calls*; these usually evoke escape tactics among listeners, as seen in the vervet monkeys of Amboseli National Park, Kenya (Cheney and Seyfarth 1990). However, vocalisations that accompany predator approach and harassment are termed *mobbing calls*. Mobbing is an altogether different way of reacting to a predator at close-range and is thought to potentially deter its attack (Godin and Davis 1995). Gibbons emit vocalisations and brachiate wildly while harassing potential predators. These vocal and visual displays may act to discourage predators from attacking as well as informing conspecifics about imminent danger.

Gibbon social structure and behaviour also seems to point towards anti-predatory adaptation: they forage on ripe fruit at the very top of the forest, they do not build nests like other primates, they sleep dispersed except for mothers and infants, and they regularly change their sleep location but choose sleeping trees that are taller on average than other trees (Reichard 1998). Similarly, their behaviour just prior to retiring for the day is cryptic; they move stealthily and speedily to their night tree with little forewarning, presumably to hide its location from potential predators (Reichard 1998; E.C. pers. obs.). They also often go to sleep early in the day well before dusk, when their most formidable predators become active. Since these behaviours have evolved, it is reasonable to assume they have an important purpose, and that predation risk is largely responsible.

Gibbons may make themselves vulnerable to terrestrial predators, despite their arboreal nature, by coming to the ground on occasion to eat or play, albeit rarely. The paucity of data regarding this behaviour is probably due to the lack of habituation of groups in previous studies; nevertheless, being on the ground offers an opportunity for large felines to attack. Similarly, there have been reports of well-habituated gibbons spending time low in the canopy (Reichard & Sommer 1997; E.C. pers. obs.), and this may also increase their predation risk from terrestrial carnivores. The following section gives a brief introduction to the gibbons' main predators.

## ***Gibbon predators***

The gibbons' most notable predation risks come from three distinct predator classes: snakes, raptors and large cats (Uhde & Sommer 2002), each of which are briefly described below.

## **Snakes**

The reticulated python is likely to be the gibbons' only potential snake predator. It can be up to ten metres in length and is essentially terrestrial, although a good climber (see figure 14). It can overpower and constrict many mammals, ranging in size from a mouse to a deer or a pig (Cox et al. 1998). Pythons are prominent in the park, and are found both in the trees and on the ground. Gibbons are thought to respond with stronger anti-predator behaviour to those encountered in the trees (N.Uhde, pers.comm.). Pythons tend to coil themselves in tree forks, remaining quite still, at heights of only a few metres above ground. Here they pose a risk to gibbons feeding on low branches.



Figure 14. Reticulated python (*Python reticulatus*). Photograph by Jörg Hess, with permission.

## **Raptors**

There are four species of raptor present in Khao Yai that pose a potential threat, mainly to infant and juvenile gibbons. These are the changeable hawk eagle, black

eagle, mountain hawk eagle and crested serpent eagle (table 7). The most common of these in the study area is the crested serpent eagle (A. Pierce, pers.comm.).

- Crested serpent eagle

These birds feed mainly on reptiles, occasionally small mammals, and very rarely birds. Their hunting strategy is that of “sit and wait” and will sometimes remain still for hours on a perch before swooping in for the kill. Most prey is seized on the ground. They are regularly seen, often in pairs, circling high above the canopy and emitting a loud screaming “Kee kee ke” vocalisation. They are unlikely to be hunting when seen exhibiting this behaviour (Channing 2004; Haryana 2004), see figure 15, and this may be reflected in the way that gibbons respond to playbacks of their calls (see chapter 6).



Figure 15. Crested serpent eagle (*Spilornis cheela*). Photograph by Liz Leyden, with permission.

## Cats

There are five species of cat that may pose a predation threat to the gibbons of Khao Yai: the tiger, the clouded leopard, the Asian golden cat, the marbled cat, and the leopard cat (table 7). The most notable threats are likely to come from the tiger and the clouded leopard, since the other cats are mostly nocturnal and significantly smaller, approximating the size of a domestic cat.

- Tigers

The presence of the Asiatic tiger in Khao Yai is now disputed, although they were commonplace two decades ago. The last recorded sighting was in September 2002 by a park ranger (Wildaid 2002). According to a 2001 Final Report by the Wildlife

Conservation Society (WCS 2001), since January 1999, just two individuals were present. This was despite over 4000 trap-nights of sampling over the entire park. One of the confirmed individuals came from photo-captures from camera traps set up near the park headquarters, the other one from tracks found in the south of the park. From these disappointing findings, it was estimated that five to ten tigers, at most, still existed in Khao Yai, with the official estimate being three. However, fifteen to twenty years ago, tigers and their prints were regularly seen every week or two by park staff (Pennington 2000), and tourists at the Khao Yai watchtower. Since gibbons are known to live for several decades, it is highly likely that adults in the park today still have some recollection of this predator.

Tigers rarely climb trees and are mostly nocturnal hunters – two factors that may seem to preclude them from posing a real threat to the gibbons. However, they are extremely capable of tree climbing when provoked and in any case, gibbons may make themselves vulnerable to attack when they come to the forest floor to forage or play. In addition, tiger activity patterns are variable, and in habitats with little human impact, they have been seen to hunt at any time during the day or night. Tigers are known to consume fish, birds, monkeys, and mice, although the main bulk of their diet usually includes large prey like wild pig and deer (Sunquist and Sunquist 2002), see figure 16.



Figure 16. WCS camera trap photograph of an adult Indo-Chinese tiger (*Panthera tigris*). From [www.nfwf.org](http://www.nfwf.org) with permission.

- Clouded leopards

One of the most formidable of the cat predators is the clouded leopard, since it is well adapted to an arboreal lifestyle, and is therefore able to hunt and kill in the trees. It weighs 16-23 kg and is about the size of a small leopard, with a long tail and short legs. Its name comes from its distinctive cloud-shaped markings on its fur (see figure 17). Little is known about clouded leopards' natural history, since they are rarely seen in the wild; although they are fairly well represented in zoos, they are difficult to breed in captivity. Most wild sightings have occurred on the ground, and some believe that they use the trees as resting places during the day, and hunt mainly at night. Nevertheless, they are thought to prey on a variety of terrestrial and arboreal vertebrates including pigs, deer, monkeys and other smaller mammals (Sunquist & Sunquist 2002).



Figure 17. A captive clouded leopard (*Neofelis nebulosa*). Photograph by Anna Wilkinson, with permission.

Despite the rarity of actual evidence of predation, it is clear that predation avoidance is of real significance to these primates (Reichard 1998; Uhde & Sommer 2002), and their behavioural and vocal adaptations in particular warrant further investigation. The following chapters examine the gibbons' suit of anti-predatory behaviours and vocalisations with empirical data taken during interactions with dummy predators presented in their natural habitat.

## **CHAPTER 4. Song repertoire**

### ***Abstract***

The best known of the gibbon songs are the duets performed by mated pairs. The duetting behaviour of the white-handed gibbon has been well studied, and offers a platform for further study into this and other less well-documented call types. Duets and other call types of white-handed gibbons were recorded in Khao Yai National Park, Thailand, to provide a comprehensive account of their natural vocal behaviour. According to some important hypotheses, the main functions of gibbon songs are pair bond strengthening or advertising, and territory defence or advertisement. To address these hypotheses, the time of day for each singing event was recorded along with the calling location within the home range, and whether neighbouring groups were heard or seen. For all song types, the main acoustic features were investigated and measured, and then compared across contexts. Results showed that duets were given regularly one to two hours after sunrise each day, and male solos were also given regularly, but usually at or around dawn. All other song types were more randomly distributed in time. Duets were typically given from the core of the territory, and they did not necessarily elicit calling responses from other groups. When two neighbouring groups overlapped in their singing behaviour, callers voluntarily often interrupted their own singing until the neighbouring female finished producing her great call. This study demonstrates that inter-group communication is a major function of gibbon loud calls and largely refutes the idea that the gibbon duet is designed to strengthen the pair bond, or defend the territory. Instead, duets are proposed to primarily advertise the pair bond and contribute to same-sex exclusion.

## ***Introduction***

Lar gibbons produce a range of songs otherwise known as loud calls, which include the following (Raemaekers et al. 1984):

1. Duet songs
2. Male solo songs
3. Disturbed songs
4. Territorial dispute calls also known as inter-group encounter calls
5. Contact calls
6. Ooaa duet songs
7. Female solo songs, or great calls (see table 1 for a description of each song type)

Since most lar territories have a diameter of less than one kilometre (Reichard and Sommer 1997; see also map of group territories, figure 8), these long-distance calls will often reach non-neighbouring groups as well as neighbouring ones.

## **The function of duet and male solo songs**

Raemaekers et al. (1984) put forward an important functional hypothesis for duets; they argue that duet songs strengthen the pair bond and exclude other same- or opposite-sex individuals. Alternate hypotheses cite territorial defence (Raemaekers and Raemaekers 1985), territory advertisement and spacing (Mitani 1985), pair bond advertisement (Cowlishaw 1992) or pair bond strengthening (Geissmann and Orgeldinger 2000) as primary functions. These hypotheses are not mutually exclusive, as all explain why gibbon duets are frequent and carry over long distances. However, the hypotheses make somewhat different predictions concerning the spatial patterns of call production and the degree of contagion. One possible prediction of

the territory advertisement hypothesis is that callers should produce duets predominantly in peripheral areas of their home range, as opposed to core areas, if these calls serve as communication signals to specific neighbouring groups. If calls are addressed to specific neighbours, it might also be expected that duets trigger vocal responses in other groups but that these responses are not agonistic and do not elicit approaches from other groups at overlapping segments of home ranges (Mitani 1985). Therefore, neighbours should not normally be seen during duet songs.

If duet songs function to settle disputes over territory boundaries with neighbouring groups (territory defence), they should also be given from the periphery of home ranges, and in response to the presence of a specific group. In addition, they should trigger vocal responses from these neighbours. If calling is contagious, calling should be biased towards the early parts of the day and calling events should trigger responses within a limited time interval. Neighbours should also be seen during duet song bouts if territory boundaries are disputed.

On the other hand, if duet songs predominantly function to advertise a pair bond, then calling should be given from locations that reach the largest possible audience (i.e. the centre of the territory), calling should not automatically elicit vocal responses from other groups, and neighbours should not be seen.

If duets function primarily to strengthen the pair bond however, calling location and degree of contagion should be random, but as above, neighbours should not normally be seen.

According to Raemaekers et al. (1984), male solo songs function to advertise territory ownership and may even convey something about the male's vigour following the handicap principle (Zahavi 1975; Zahavi and Zahavi 1997), especially when combined with other call types. Males that can produce long and complicated calls may possess high fitness and carry genes that are desirable for females in the process of selecting a mate. Singing for extended periods demonstrates the male's ability to provide; he must be an efficient forager or have access to a rich territory if he can go so long without feeding. Some empirical support for this idea comes from the finding that sub-adult males call more frequently and for longer than adult males that are already mated (Raemaekers et al. 1984). Sub-adult males do not take part in duet singing, but may still have an interest in communicating to neighbouring individuals; perhaps they advertise their availability and prowess as a mate to females, or their ability to rival other males. If solo songs are given to target specific neighbours, then they should be given mostly in the periphery of the territory, and in response to the calls of other males. Males may be expected to seek each other out visually if songs function specifically in inter-male communication. If calls are addressed to females who are in a position to choose whether or not to attend, it is predicted that other gibbons will not normally be seen during song bouts and that singing will not elicit solos from other males, though songs may be clustered around the same time of day. In addition, if males are indeed communicating about their vigour, the findings of Raemaekers et al. (1984) should be upheld, and sub-adults should sing for longer than adult mated males. Moreover, primary males are expected to sing less frequently and for shorter durations than secondary males who may have more reason to advertise themselves. If however, male solos function in territory advertisement, adult mated primary males who hold a territory should produce most of them; they should be

emitted from the periphery of the home range, and neighbours should sing in response, but not normally be seen.

Hence, data on call start times, the spatial locations within the territory, and whether or not non-group members responded directly to each other, compared to simply calling in the same time window, will help to test these ideas.

### **The function of disturbed songs**

Disturbed calls are given to predators or other species alarm calls, during conflicts with other group members and sometimes during territorial disputes according to Raemaekers et al. (1984). The fact that these calls are loud and can carry over long distances suggests that they have an additional function of informing other groups about the presence of a predator or conflict within or between groups. Since these events can occur at any location and at any time, there should be no correlation between time of day, or location in the territory, and calling events. However, as potential indicators of predator presence, they may be expected to elicit similar calls in neighbouring groups, especially if such calling deters the predator (individual selection) or informs kin about the nature of the danger (kin selection) (Dunbar 2004). In terms of communicating with the predator, these songs could function to alert the predator to the gibbons' location as well as making it aware that it has been seen, and therefore may act as handicaps, and an honest testament to their ability to escape (Zahavi and Zahavi 1997). These types of songs are mobbing vocalisations as opposed to alarm calls, the difference being that alarm calls are emitted when prey are trying to escape a predator, and mobbing calls are given when prey approach and/or harass a predator (see chapter 3). As a result, alarm call structure is expected to

consist of high frequency calls, testament to the prey's excited and agitated state whilst trying to flee danger. Conversely, mobbing calls should be of lower frequency, associated with a relaxed state that truthfully communicates the prey's confidence in its' ability to fend off any attack. In this study, it is particularly relevant that neighbouring groups often consist of close relatives since dispersing lar gibbons tend to settle in territories close to their natal ones (Brockelman et al. 1998). This would favour the evolution of songs that alert gibbons in other groups to the presence of a predator. For example, gibbons in any one group in the study site often had immediate genetic relatives (sibling, parent or offspring) in several of the other groups: Group A, B and C all had relatives in each other's groups. Group E had relatives in groups H, J, T and R. Group N had relatives in groups C and A. Group R had relatives in groups E and B, and Group T had relatives in groups B, E, and A. In sum the predictions for disturbed songs are as follows: no specific location or time of day should be associated with these songs if their function is to delineate predator disturbances or conflict in the group, and they should elicit singing from neighbouring groups if they function to alert kin or deter potential predators. More specifically, though, if songs function to deter predators rather than alert kin to their presence, fewer neighbour response songs are predicted. This is because only neighbouring groups that are in close proximity to the area of predator encounter may be expected to sing in response to the target group's song, since the nearby predator would pose a direct threat to them also. On the other hand, if disturbed songs function to alert kin, then a greater number of response songs may be heard due to the great number of relatives present in surrounding gibbon groups.

### **The function of male dispute calls and contact calls**

Raemaekers et al. (1984) considered male dispute calls as loud call bouts. However, these calls are not audible over long distances, especially in comparison to the other songs considered in this study. Since these calls always involve direct visual and sometimes physical contact with another group, they usually occur at territory boundaries, with both groups' males calling. Such direct inter-group communication does not need to be audible over vast distances like the other songs and, in fact, advertising such a dispute to other neighbouring groups might be expected to increase the chances of these other groups entering the disputing groups' territories, and pillaging their resources. Indeed, other observers have labelled these calls as "conflict hoos" (Ellefson 1974:132), or "low-key hoot-sequences" (Reichard & Sommer 1997:1146). Sometimes prior to inter-group encounters, groups may "counter sing" back and forth with one another, or sometimes at the end of an encounter, one or both groups may sing. These songs may be better grouped along with the other disturbed calls that Raemaekers et al. (1984) describe. These are probably audible to neighbouring groups, but do not seem to occur during the actual encounter. Therefore, male dispute calls or as they are termed in this thesis "inter-group encounter calls" are classed separately along with other quiet calls (see chapter 7). Similarly, loud contact calls were heard infrequently and were difficult to define, so are not included in this analysis; quiet contact calls are discussed separately in chapter 7.

### **The function of ooaa duet songs and female solos**

Raemaekers and Raemaekers (1984) found that ooaa duet songs are highly contagious given mostly between the hours of 6:00 AM and noon, with a relative peak between

10:00 and 11:00 AM. However, they were unable to determine a common eliciting factor, and the function of this calling behaviour remains unknown. This study expects to corroborate Raemaekers and Raemaekers (1984) findings, and as such predicts that ooaa duets will elicit the same songs from surrounding groups. If ooaa duets function as a type of predator response (Reichard 1998), calling should not be biased towards any part of the day since predator encounters may occur at any time. If on the other hand, calling is biased towards the morning hours, as Raemaekers and Raemaekers (1984) found, then the function of this song is probably not anti-predatory. Since the ooaa note is rarely heard and can be combined with other notes in an otherwise normal duet, or given in isolation as a series or burst, it may have a specific referent-like function.

The female solo song may be given in response to separation from the male partner, signalling to neighbouring males that she is alone and potentially available for extra-pair copulation (Reichard and Sommer 1997). Male partners may be reluctant to answer female solos, since this would provide accurate information about their distance from the calling female as well as the fact that she is unguarded (Reichard & Sommer 1997). The handicap principle may apply to the female gibbon's song as well as the males, since it too requires an energetic investment that may be measured by listeners. The female great call is loud and protracted with a climactic ending, and may repeat every couple of minutes throughout the pair duet, or is sung in isolation as the female solo. This stereotyped sequence may reveal something about a female's identity (Dallmann and Geissmann 2001) as well as her age and fecundity. As such, a female that can reproduce the sequence in its entirety multiple times during a single song bout may signal to her mate and other neighbouring or roaming males that she is

fit, healthy and fertile. Thus, if the female solo acts to attract other males, it should only be given when the primary male is separated from the rest of the group. Consequently, it is predicted that a female solo should trigger silent and immediate return of the male to the female partner in order to guard her from intruding males.

Loud singing is a risky business. Not only energetically demanding, songs also divulge the callers' exact location; this information could be used by rival gibbons who may seek opportunities for extra-pair copulations or exploit resources in unused portions of a groups' home range, or indeed by predators who are planning an attack. In any case, the signals these songs convey must be reliable for them to impose such a handicap on the singers.

In sum, the main objective of this study is to investigate the function of the different types of lar gibbon songs. The time of day, the location of where calls are given, as whether neighbouring groups can be heard or seen during call bouts will help to determine the calling patterns, and address the main hypotheses put forward to explain the long-distance communication and advertisement features of some of their calls.

## **Methods**

### **Study site and subjects**

For a full account of the study site, see chapter 3.

The entire study site supported approximately 40-plus gibbon groups at the time of the survey (see figure 8, chapter 3), and some observations reported here come from some of the non-habituated groups that surrounded the main study groups.

## **Data collection**

Data were collected between April 2004 and July 2005. Each day, a different habituated study group was followed and all their songs noted, including call start and end time, call duration, call types and caller identity. If possible, the same data were collected for each song given by a neighbouring individual. Total observation time was 813 hours. Calls given by the study group were tape recorded with Sony DAT recorders, (TCD-D8 or TCD-D7), and Sennheiser directional microphones (MKH815T or ME66) with windshields. Recordings were transformed onto a PC for analysis using Cool Edit 2000. Raven 1.2 software was used to produce waveforms and spectrographic images. Recordings were sampled at 44,100 Hz, and 48,000 Hz and 16-bit resolution.

Each time a call was given by a focal group, it was noted whether other gibbon groups called simultaneously in the vicinity, and whether any of them could be seen in the vicinity (the fact that gibbons can probably detect other groups before an observer on the ground can notwithstanding). The ranges of each group were mapped before the onset of this study, and these maps were used to determine the callers' location in the core or periphery of their home range. Each range contained overlapping segments with neighbouring groups, which were considered part of the periphery. The core areas were assigned to the central parts that covered approximately 25% of the total area, including overlapping zones, although absolute sizes varied widely between groups. Song location was scored as either core or periphery, where core corresponded to the centremost areas of home range, and periphery the outermost areas, rather than as a measure of where the gibbons spent most of their active time,

which may have had more to do with seasonal fruit availability. Scale maps were used for each individual group to base these distinctions on: the total area of each home range was calculated from the maps' scale squares (one square = 100.0 m<sup>2</sup>). When an entire square was within the target group's home range it was assigned as the core. If any part of a square contained overlapping segments of home range or other substrate outside of the target group's range, it was labelled as periphery. This led to the innermost squares (that made up approximately 25% or more of the total territory) being assigned as the core area. The remaining home range was assigned as the periphery, see figure 18.

All other factors that were likely to trigger calling bouts were noted as well, including the presence or vocalisations of other animals such as elephants, or whether the song bout was just prior to or closely followed a group encounter.

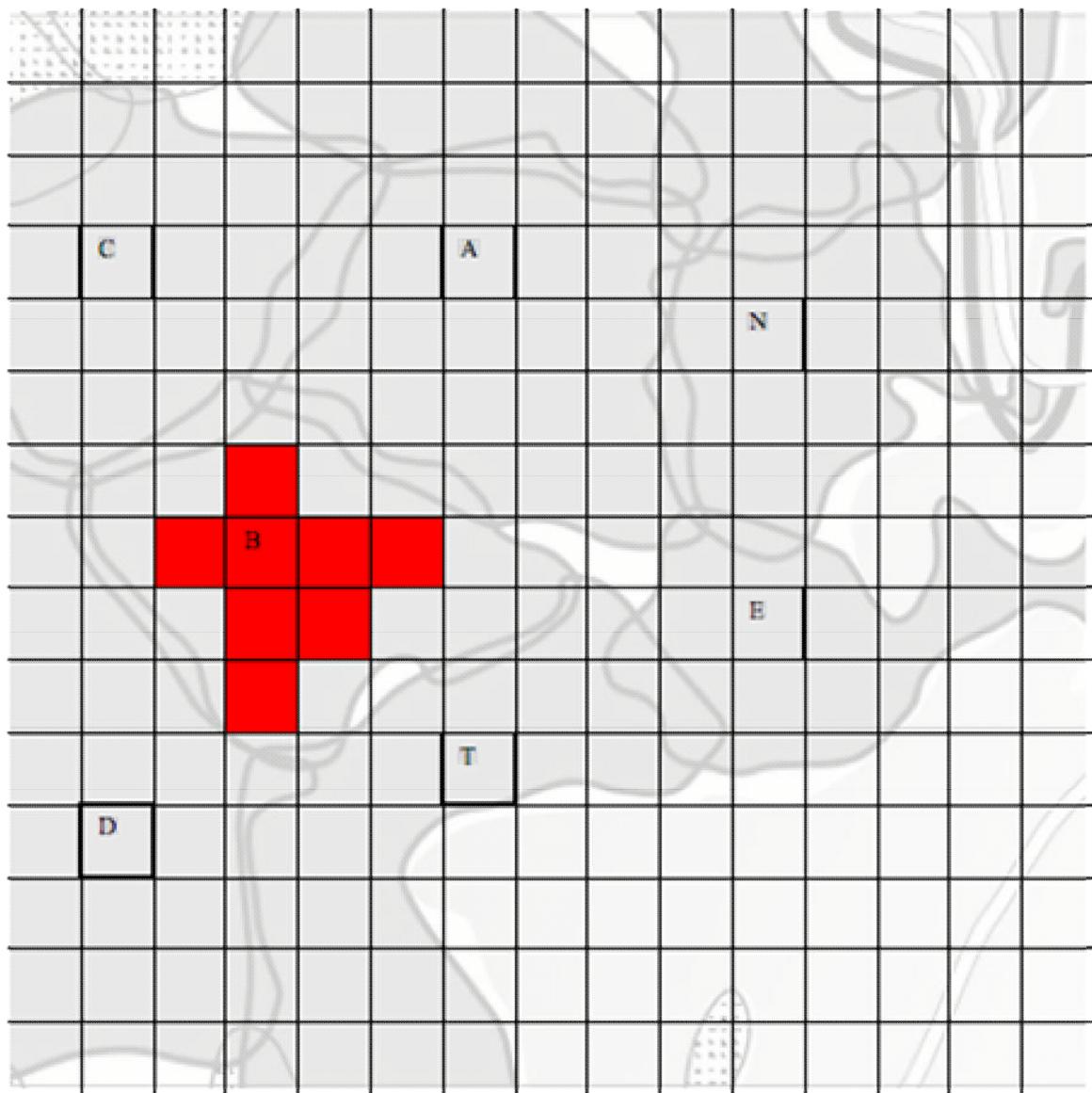


Figure 18. Grid map of the groups' home ranges. Ranges are shaded in grey and group names are shown in capital letters. Grid squares are  $100.0\text{m}^2$ . The red squares represent the core of group B's home range and the remaining squares represent the periphery. Figure produced by Esther Clarke and adapted from a map of group territories by U.Reichard, with permission.

## Analyses

Call rates for the different loud call types were calculated over the entire observation period. Variations in time of delivery between each call type were measured using a Timex stopwatch and analysed while paying attention to the number of hours that had passed since the sunrise of each day's observation. Differences in frequencies of the

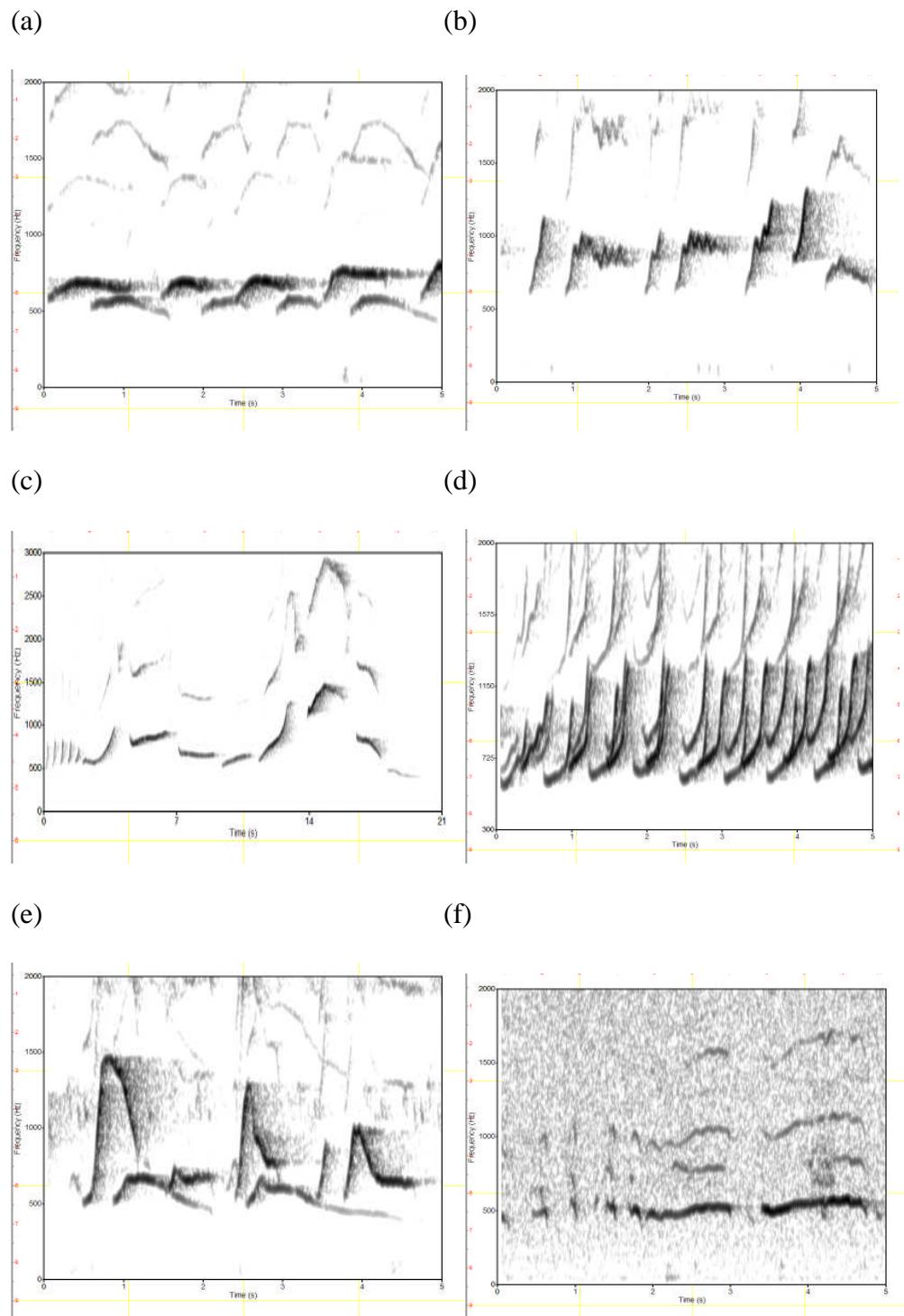
song types were compared with one-way Chi-square tests, although once converted to relative rates, data were analysed using Kruskal-Wallis, Mann-Whitney U and Fisher's Exact tests. The mean duration of each call was calculated from spectrograms or, if this was not possible, estimated from field notes. Duration data were log transformed (base e transform) to meet the normal distribution criterion necessary for parametric analyses of variance.

## **Results**

### **The song repertoire of lar gibbons at Khao Yai National Park**

Six song types were identified in this study, mostly in accordance with Raemaekers & Raemaekers (1985). (a) Duet songs were produced by the adult members of a bonded pair. They always included at least one great call sequence (figure 19a), which alternated with an interlude sequence. Great call sequences were often accompanied by locomotive displays by the mated pair. (b) Male solo songs were given by both adult and sub-adult males and consisted of several male phrases (figure 19b). (c) Female solo song usually consisted of only one great call with no male reply or other vocalisations, but may sometimes be followed by subsequent great calls. The great call has a two-humped shape, with the second hump also known as the climax (figure 19c). (d) The ooaa duets were given by most or all group members producing only ooaa notes; this is different from the Raemaekers & Raemaekers (1985b) description which includes otherwise normal duets containing ooaa elements (figure 19d). Raemaekers and Raemaekers (1985b) "disturbed songs" were separated into two different contexts in this study: (e) group conflict calls: given by most or all group members calling together. These call sequences differ from the ones given to

predators by the lack of low hoo notes at the start. Sequences contained sharp wow notes and few if any delayed great call sequences. There was usually no obvious external referent, and attention was not directed (figure 19e), (f) predator songs: most or all group members call together. Sequences were initiated by low frequency hoo notes, before culminating in full singing containing sharp wow notes and few, delayed great call sequences. Often the callers' attention was directed towards a specific area, where a potential predator or disturbance was located (figure 19f).



**Figure 19.** Spectrographic illustration of sections of the different call sequence types (a) Duet songs: The male's vocal contribution is higher pitched than the female's. (b) Male solo song: Individuals notes are often subject to marked frequency modulation. (c) Female solo great call. (d) Ooaa duet song, containing repeated J-shaped ooaa notes. (e) Group conflict call, containing high peaked sharp wow notes given by the male. (f) Predator songs, which typically begin with a series hoo notes before singing. X-axis denotes time (s); y-axis denotes frequency (Hz). Spectrograms produced by Esther Clarke.

## **Relative call rates**

Since listening time was somewhat biased towards the middle parts of the day (see figure 10), relative call rates were calculated by dividing the number of songs heard by the number of days in the forest listening to them for each hour of the day. This allowed for a comparable account of each song type's delivery rate for any given hour of the day, see figure 20 below. This calculation assumed that each and every song that was heard during the study period was made note of, and although efforts were made to do so, there were almost certainly songs that went unrecorded. Therefore, exact call rates may vary somewhat from that presented. Analyses revealed significant differences in relative call rate (Kruskal-Wallis Test, chi-square=15.7, df=5, p=0.008), with duets given at significantly higher rates than female solos (post-hoc Mann-Whitney U test, U=36.0, n<sub>duet</sub>=14, n<sub>female solo</sub>=14, p=0.002). Other comparisons showed that duets were given at higher rates than all other songs except male solos, though these were no longer significant after a Bonferroni correction (0.05/15) reducing the alpha level to 0.003.

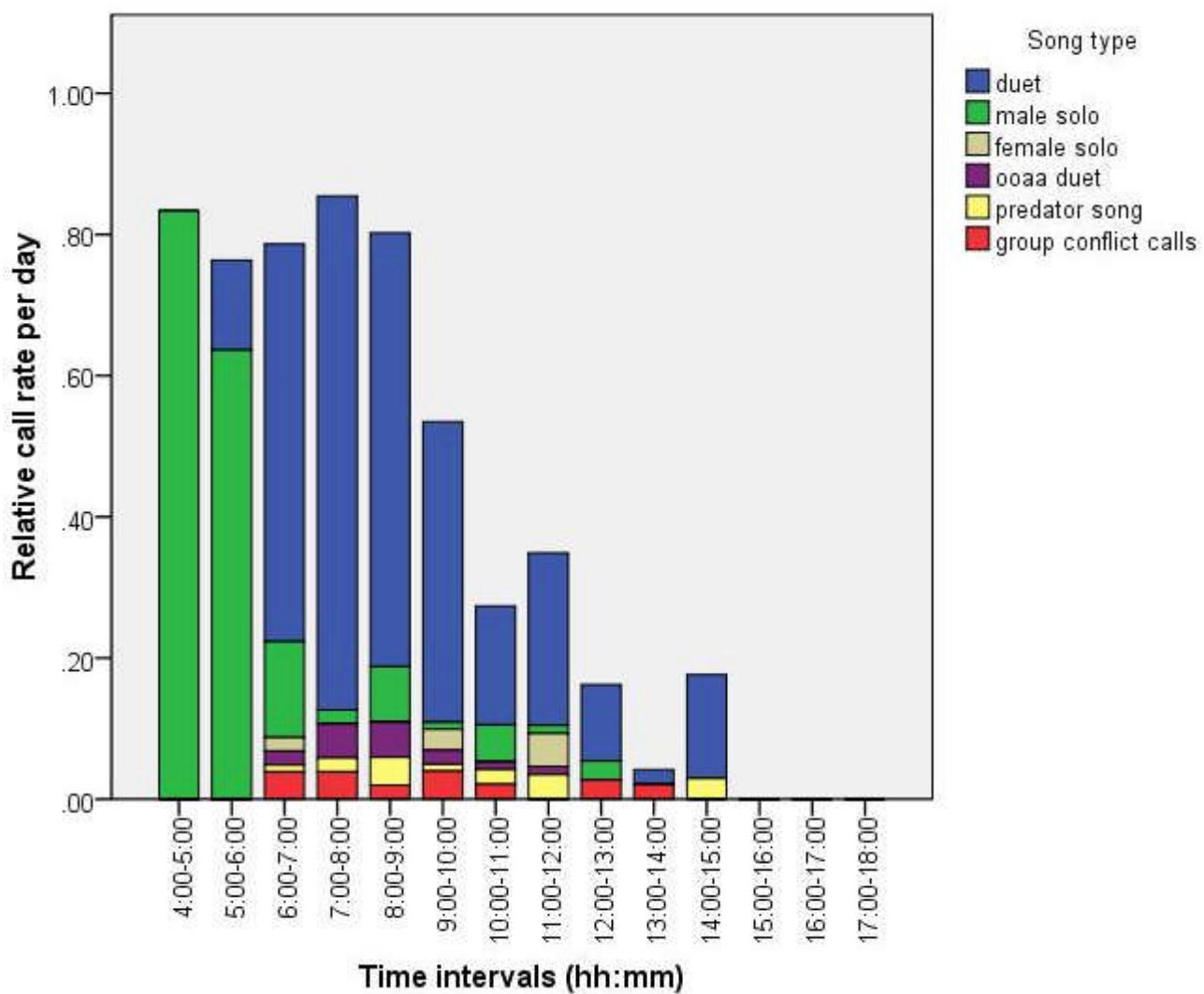
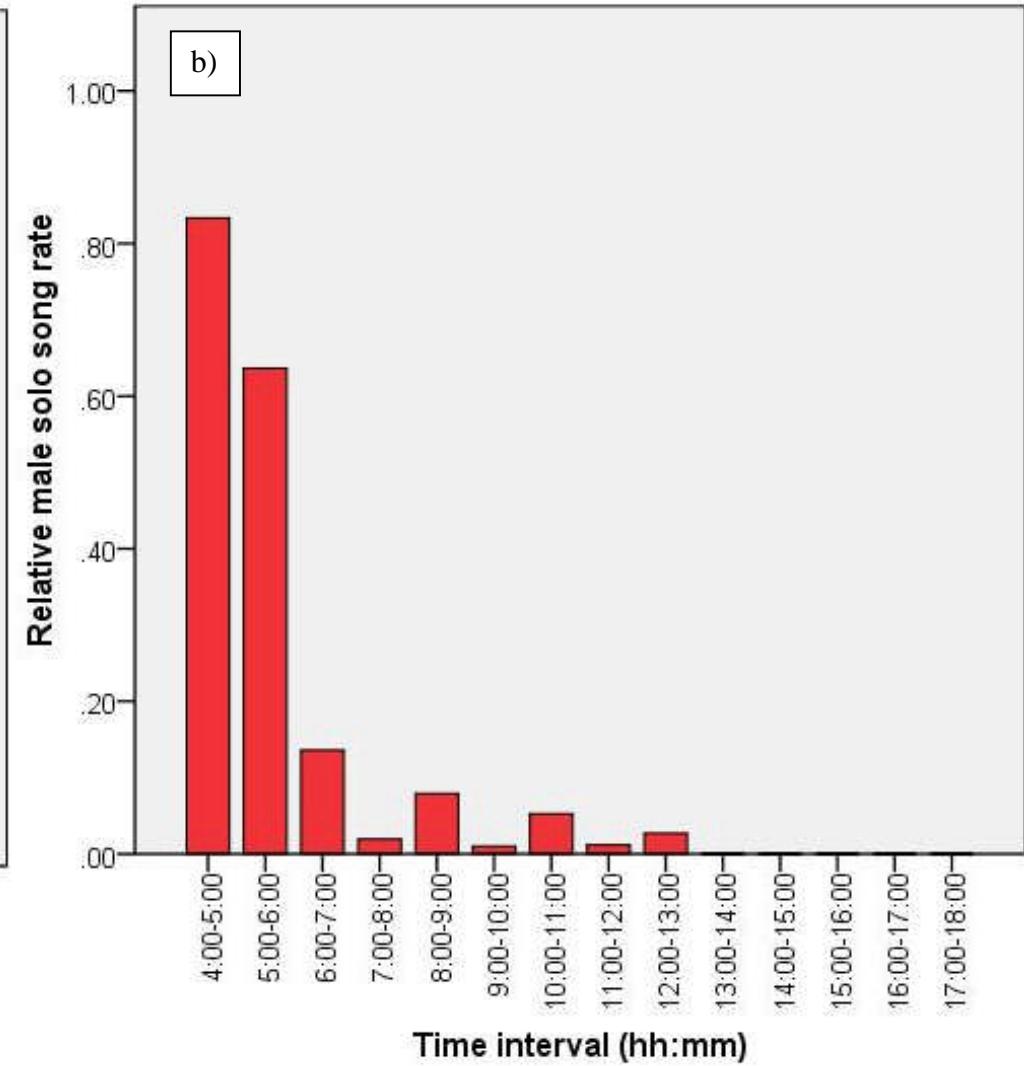
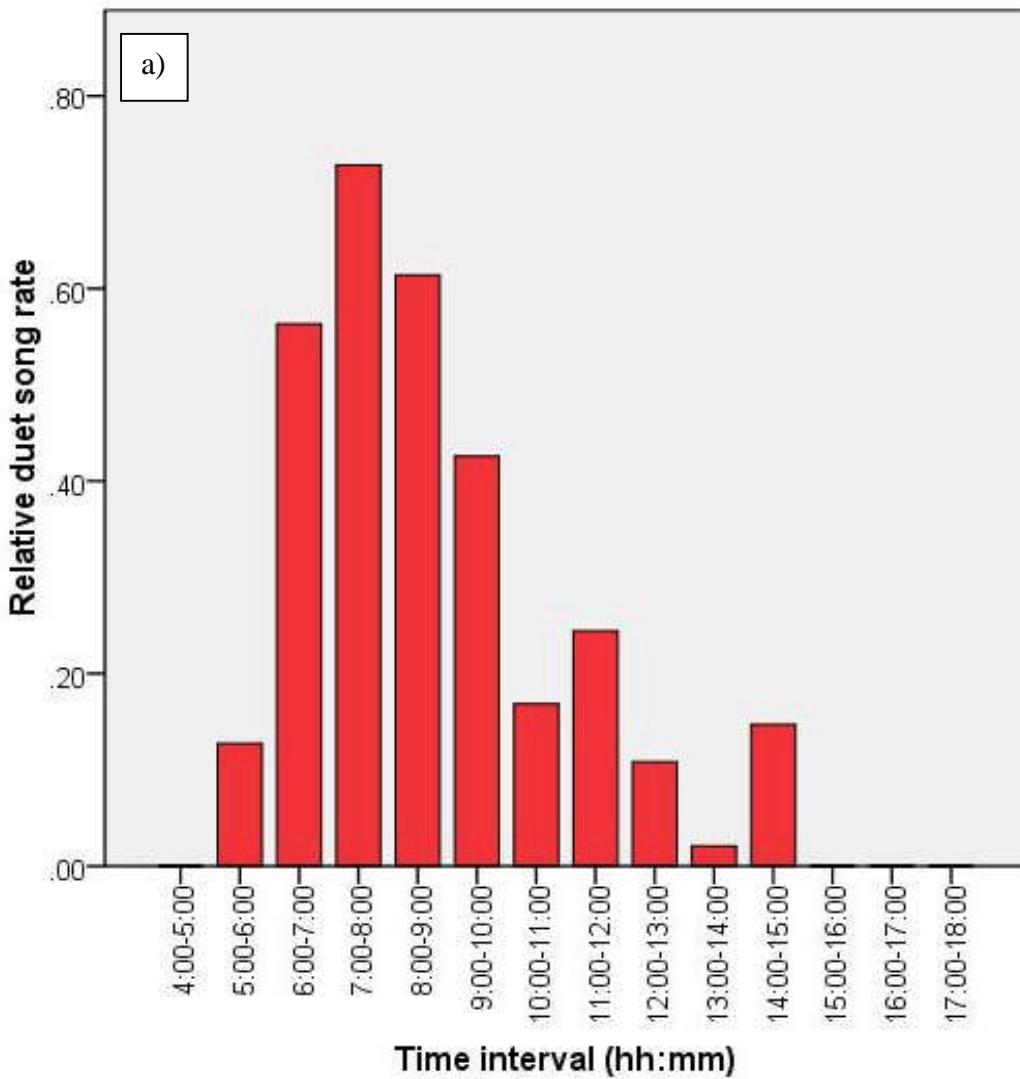


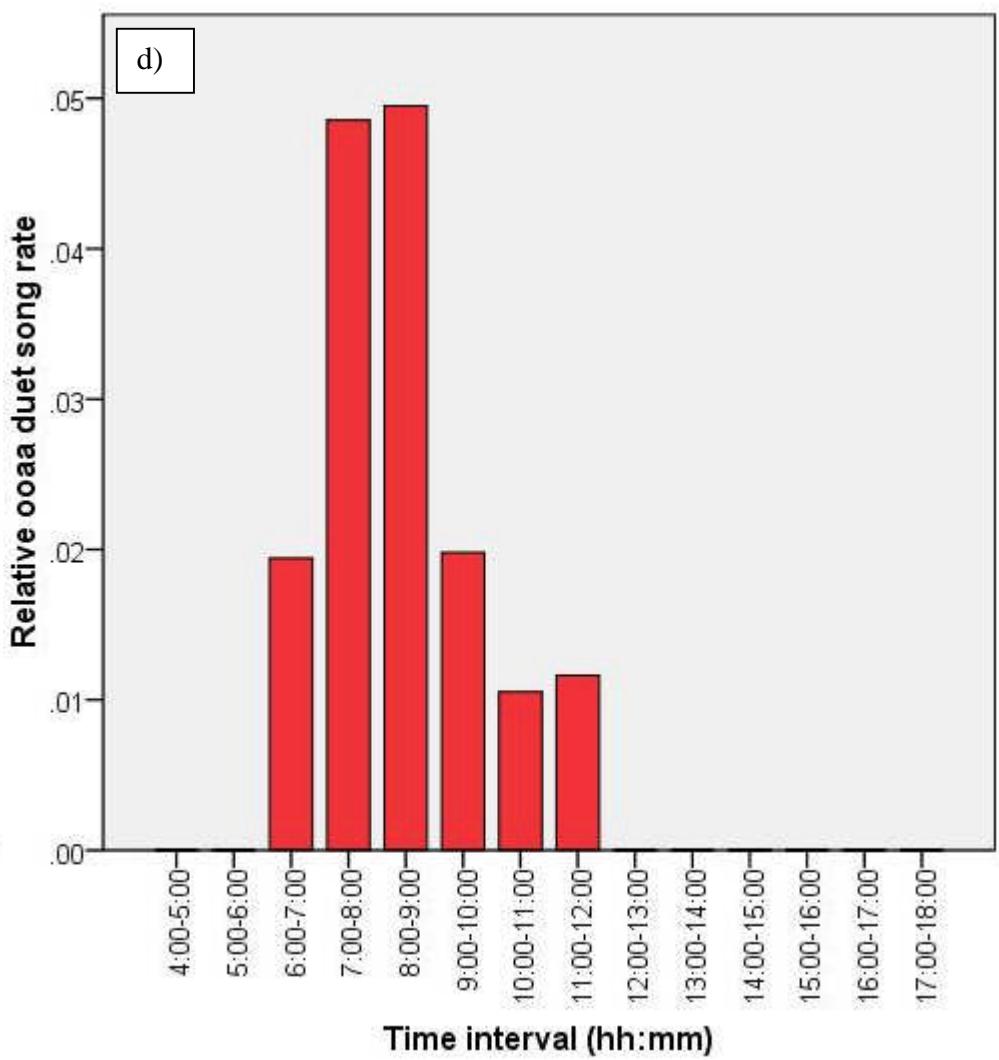
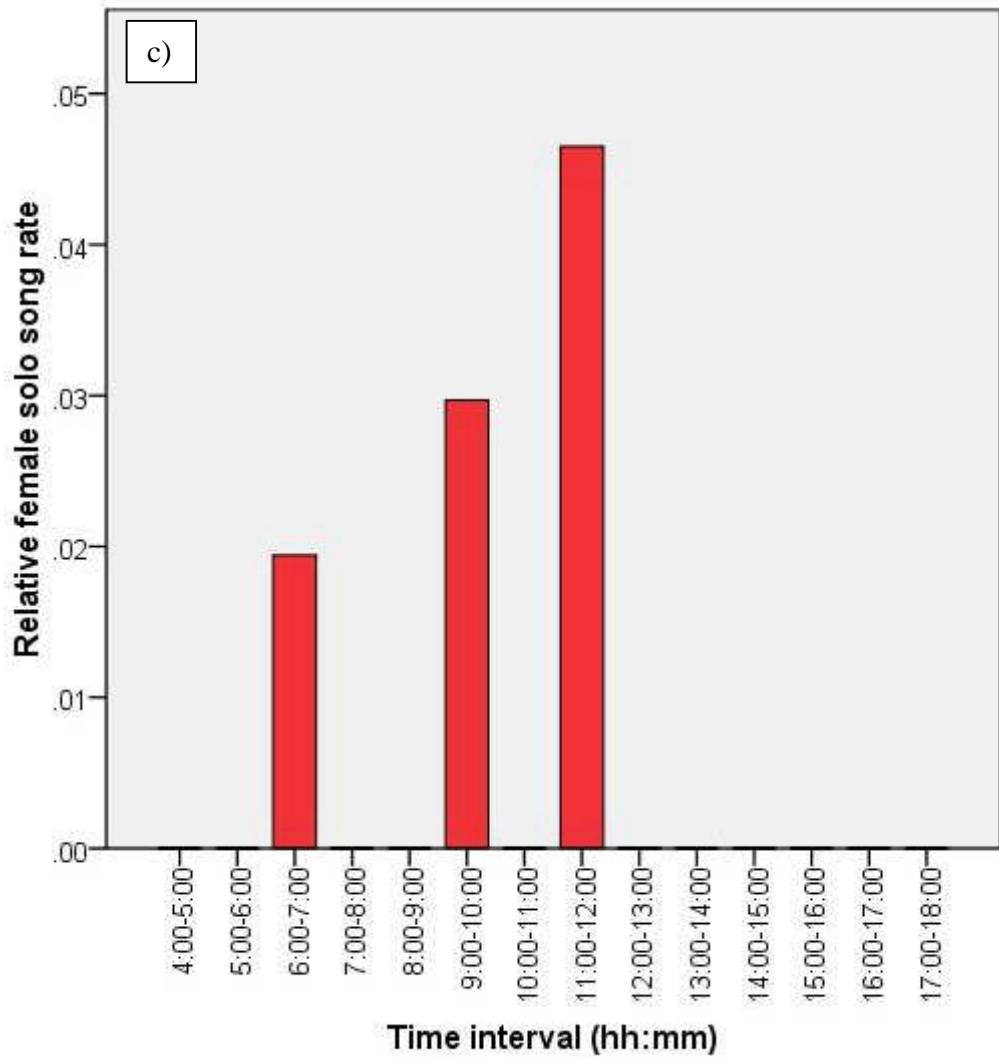
Figure 20. Relative call rate per day of different song sequences at different times of day.

### Diurnal calling patterns

Sunrise occurred between 5:15 AM and 6:12 AM for the duration of the study period. Most songs were delivered in the earlier part of the day between 4:00 AM and 9:00 AM, figure 20. Male solos dominated the earliest hours between 4:00 AM and 6:00 AM (the hours before and during sunrise), figure 21b. Between 6:00 AM and 9:00 AM, duet songs replaced these, figure 21a. The other song types were given at much lower relative rates spread throughout the day from 6:00 AM to 3:00 PM, figure 21c-f. Since relative rates were low, actual rate data from days when complete records

were available were used to analyse frequency distributions of duets and male solos from two different parts of the morning. There were six days when songs were listened to continuously from 4:00 AM to 8:00 AM. Data were split into two equal time frames: 4:00 to 6:00 AM and 6:00 to 8:00 AM, and results revealed a significant difference in the distribution of the two song types. Male solos were more likely to be sung between 4:00 and 6:00 AM, and duets were more likely to be sung between 6:00 and 8:00 AM (Fisher's Exact Test,  $p<0.001$ ,  $n_{duet}=6$ ,  $n_{male\ solo}=13$ ).





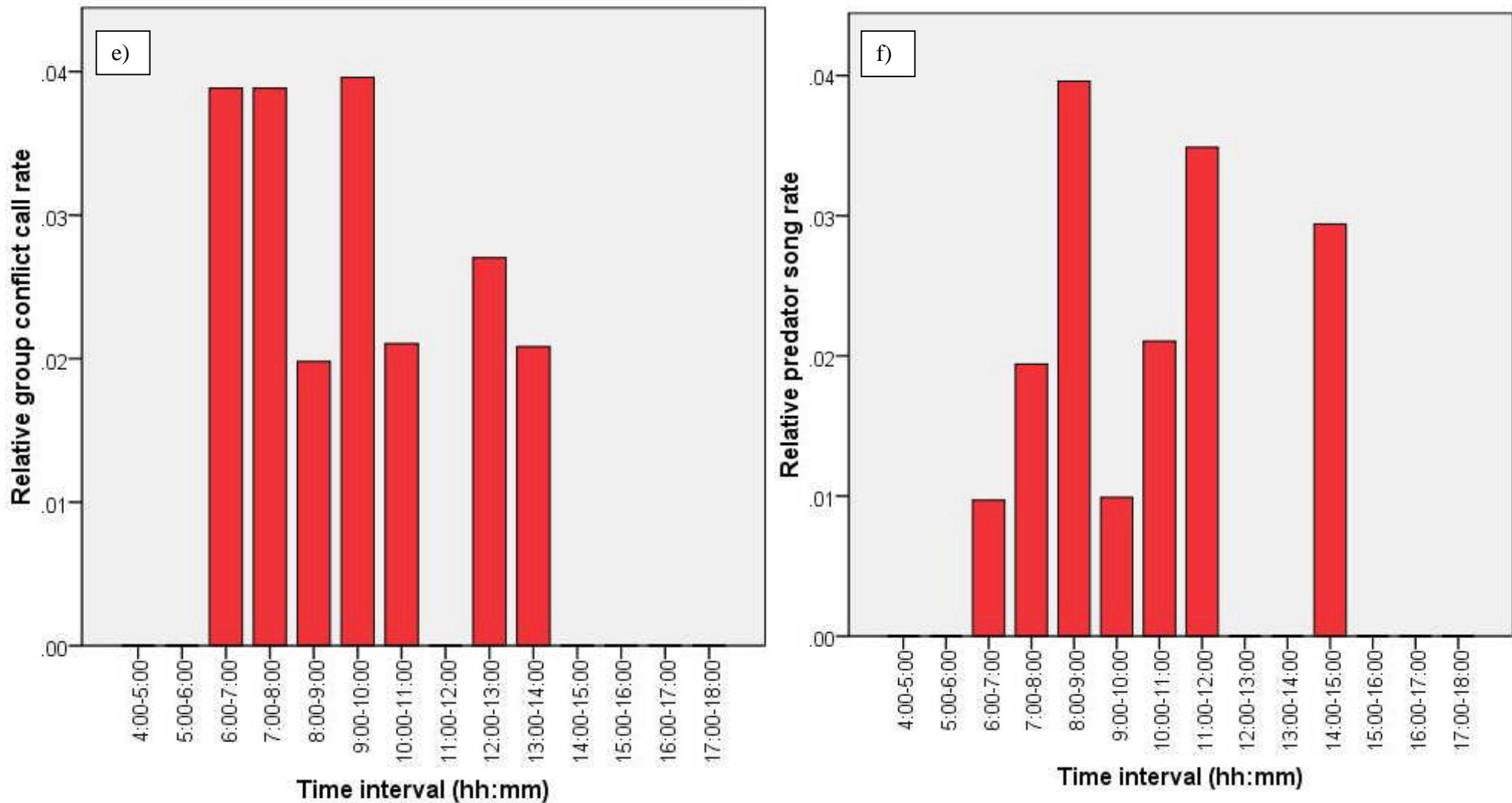


Figure 21. Relative diurnal distribution of (a) duet song rates (b) male solo song rates (c) female solo song rates, (d) ooaa duet song rates, (e) group conflict call rates and (f) predator song rates. Call rates throughout the daylight hours were measured from April 2004 to July 2005. Time axes represent the gibbons' total potential active time.

Sub-adult males produced the majority of male solo song sequences, though sample sizes proved too small for analysis, figure 22.

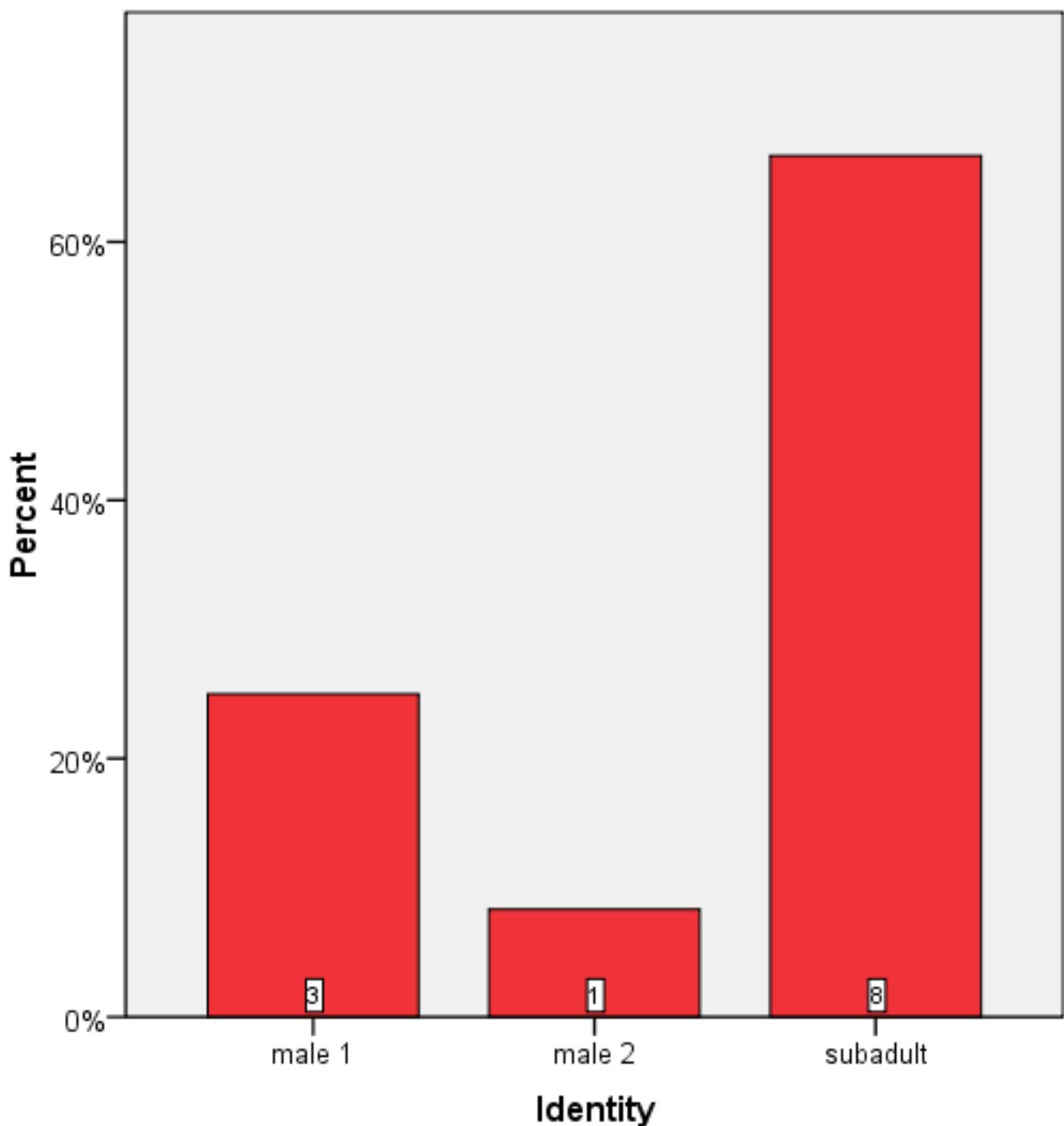


Figure 22. The percentage of male solos given by primary adult males ("male 1"), secondary adult males ("male 2") and sub-adult males. Numbers in boxes represent n-values.

## **Songs – duration**

The different types of song sequences also varied in overall duration. Male solos were the longest and they showed the most variation, while female solo great calls were the shortest (figure 23). All calls were significantly longer in duration than solo great calls (one-way ANOVA,  $f=9.8$ ,  $df=236$ ,  $p<0.001$ , Tukey post hoc test), but there were no significant differences in duration between the other five song types (Tukey post hoc test,  $p>0.05$ ).

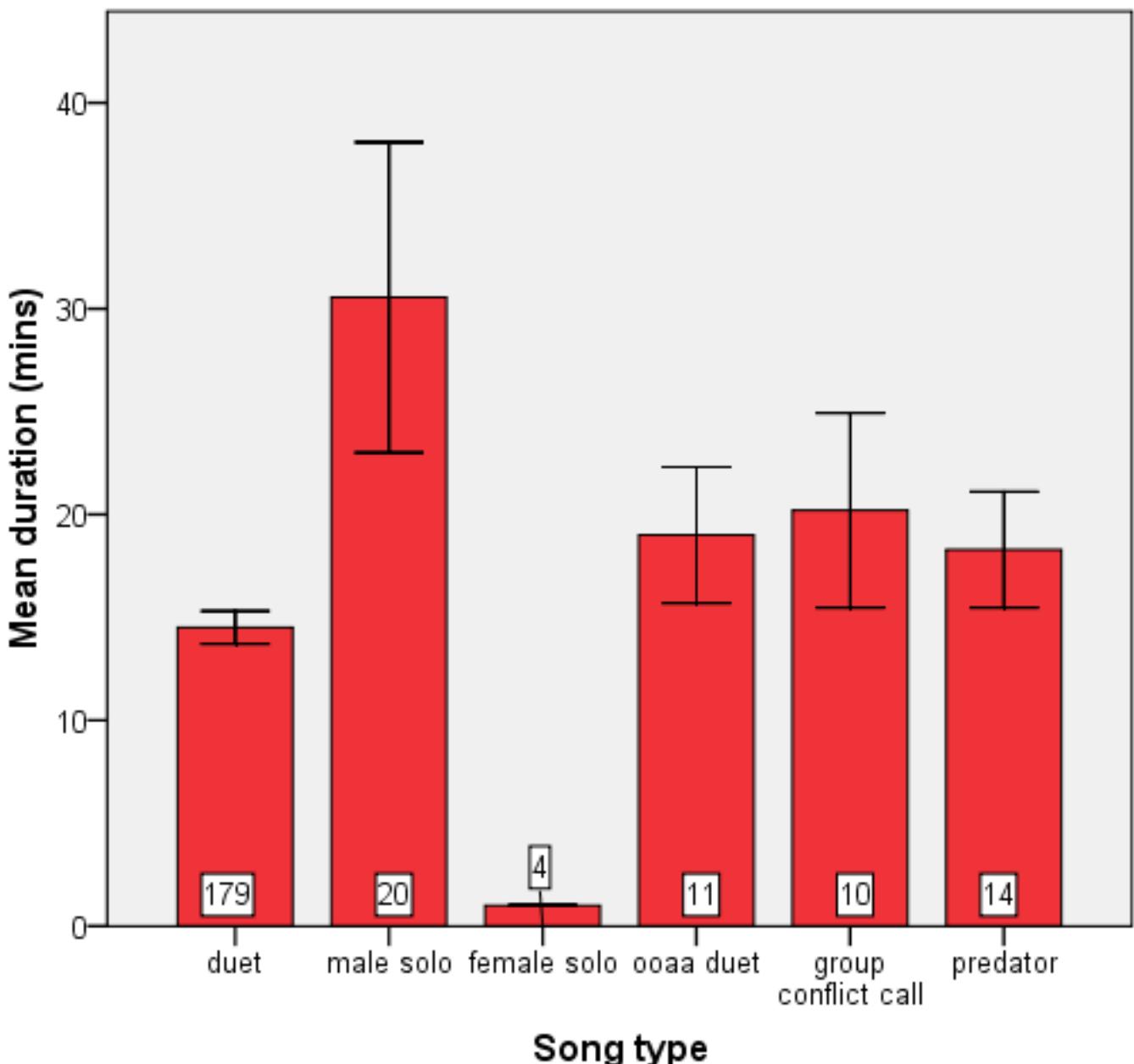


Figure 23. Mean duration ( $\pm 1.0$  SE) of all song sequences, recorded ad libitum. Numbers in boxes represent n values.

### **Songs – neighbours seen or heard**

Whenever a focal group produced a loud call, it was noted ad libitum whether a neighbouring group could be seen or heard. Instances where neighbours could be seen were generally rare: 8.3% for alarm calls, 1.8% for duets, 0.0% for male solos, and 10.0% for oooaa duets (figure 24). Neighbours were often heard, however: A significant proportion of oooaa duets (90.0%) were accompanied by a neighbour's song (Chi squared test, chi square=6.4, df=1, p=0.010). The

percentage of other call types where neighbours were heard showed no significant differences from what would be expected by chance: 25.0% for alarm calls (Chi squared test, chi square=3.0, df=1, p=0.083), 45.6% for duets (Chi squared test, chi square=0.4, df=1, p=0.508) and 33.3% for male solos (Chi squared test, chi square=1.0, df=1, p=0.317; figure 25). There were insufficient records of group conflict call sequences to be included in these analyses.

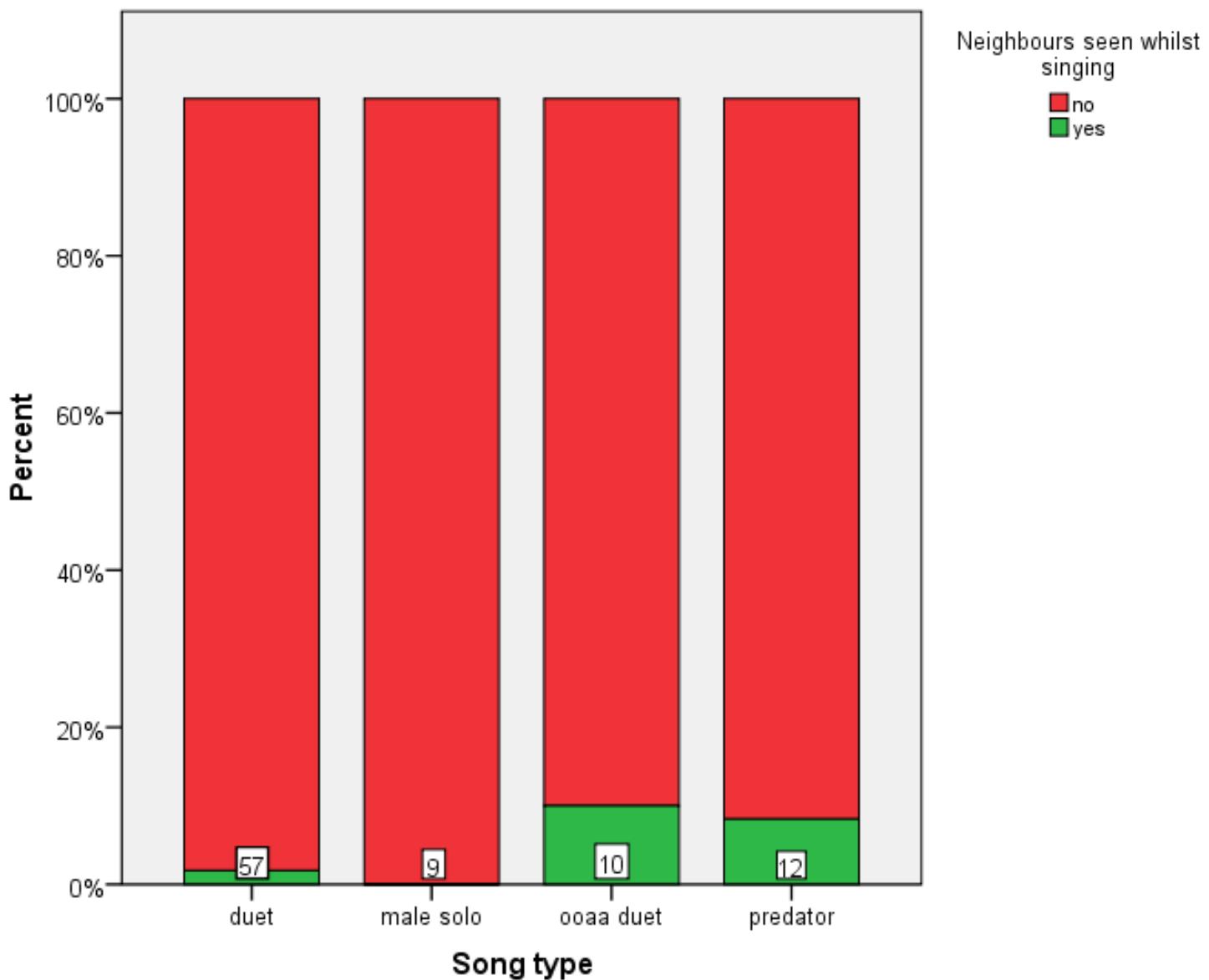


Figure 24. Percentage of calls where neighbours were seen whilst songs were emitted.

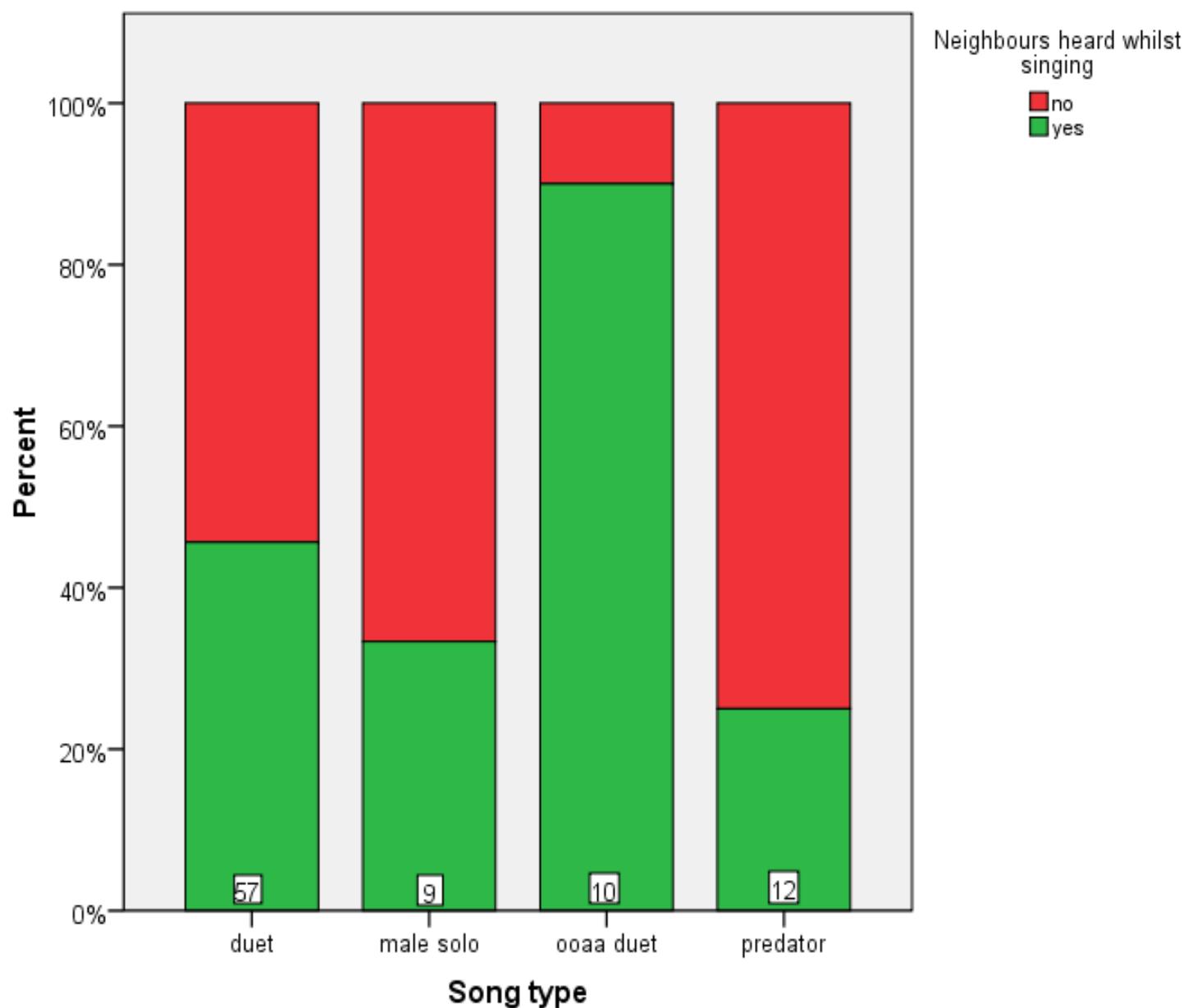


Figure 25. Percentage of calls where neighbours were heard whilst songs were emitted.

## **Neighbours' overlapping songs**

When neighbours called during tape-recorded duet bouts, it was possible to determine whether individuals interrupted their own singing in response to the calls of the other group. If such interruption occurred then the female great calls appeared to play an especially important role. Monitoring of 37 song bouts involving 11 different groups revealed the following pattern: in 18 of 37 cases, individuals interrupted their duets and paused their songs for the entire duration of the neighbouring female's great call. In 11 of 37 cases, duetting was interrupted but individuals partially sang over the neighbour's great call, usually only pausing for climax of the call (9 of 11 cases). On a few other occasions (4 of 37) the females of both groups gave their great calls simultaneously, while in the remaining cases callers seemingly disregarded their neighbours' great calls altogether. A one-way Chi Square test revealed a significant distribution (chi square=14.6, df=3, p=0.002; table 10).

Table 10. Group singing behaviour during neighbouring groups' great calls.

Groups	Duet interruption				Total
	No	Yes	Partial	Simultaneous	
T over E	1	3	1	1	6
E over T	0	4	1	1	6
W over S	0	1	0	0	1
? over C	0	2	2	0	4
C over ?	0	2	2	0	4
H over C	0	3	1	1	5
C over H	1	1	3	1	5
T over ?	0	1	1	0	2
? over T	0	1	0	0	1
D over ?	1	0	0	0	0
? over D	1	0	0	0	0
Total	4	18	11	4	37
Percent	10.8	48.7	29.7	10.8	100.0

?=unknown group; No=complete singing over great calls; Yes=no singing at all over great call; Partial=partial singing over great call; Simultaneous=great calls given by both females at the same time.

### Songs – location

If analysed together, singing behaviour was mostly recorded in the periphery, rather than the core area, of the home ranges (figure 26), but the difference was not statistically significant (Chi squared test, chi square=1.9, df=1, p=0.168). For individual song types there were no significant differences in location: 62.5% of predator songs were given in peripheral locations (Chi squared test, chi square=0.5, df=1, p=0.480), 53.0% of duets (Chi squared test, chi square=0.3, df=1, p=0.606),

77.0% of male solos (Chi squared test, chi square=3.77, df=1, p=0.052) and 50.0% of ooaa duets (Chi squared test, chi square=0.0, df=1, p=1.000; figure 27).

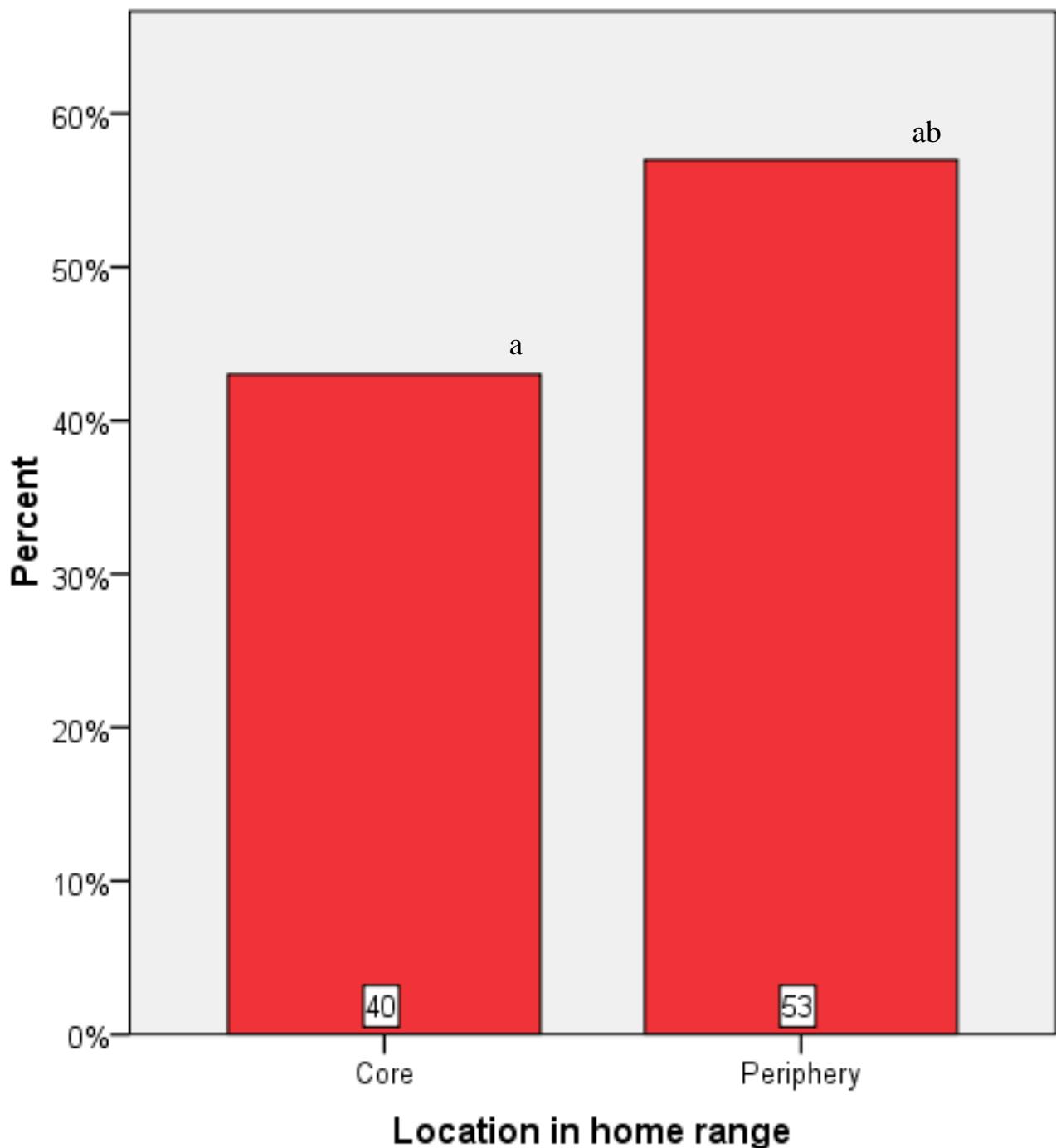


Figure 26. Percentage of all songs and the location of the gibbons within their home ranges when calling.

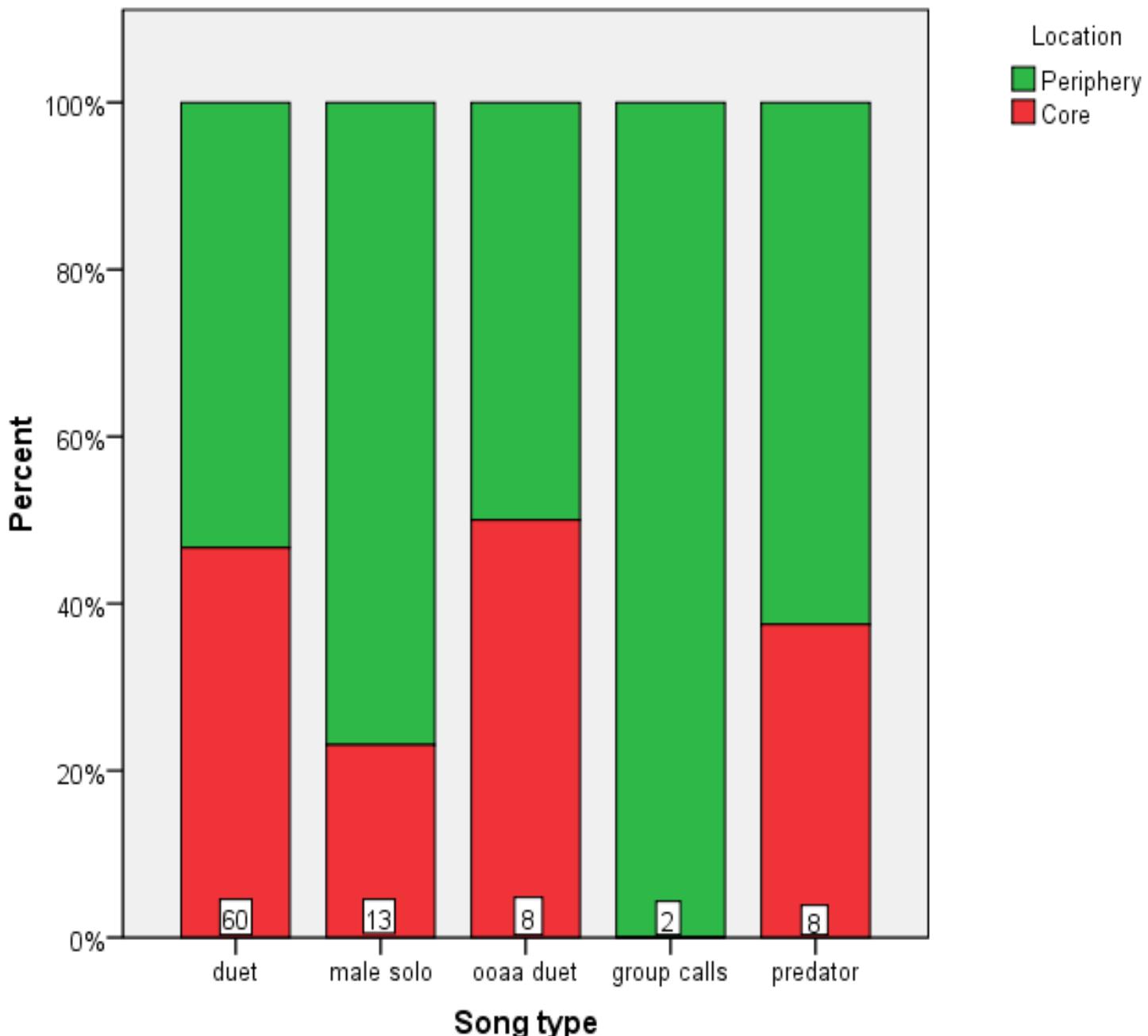


Figure 27. Percentage of different songs given in periphery or core locations in the home range.

Concerning the question of whether duets were more likely to elicit, or be elicited by, neighbours' calls there was no effect of other groups calling at the same time. In the periphery, 60.0% of duets were sung without neighbours heard in the vicinity, and 61.0% of duets were sung when neighbours could be heard in the vicinity (Chi squared test, chi square=0.1, df=1, p=0.746, figure 28).

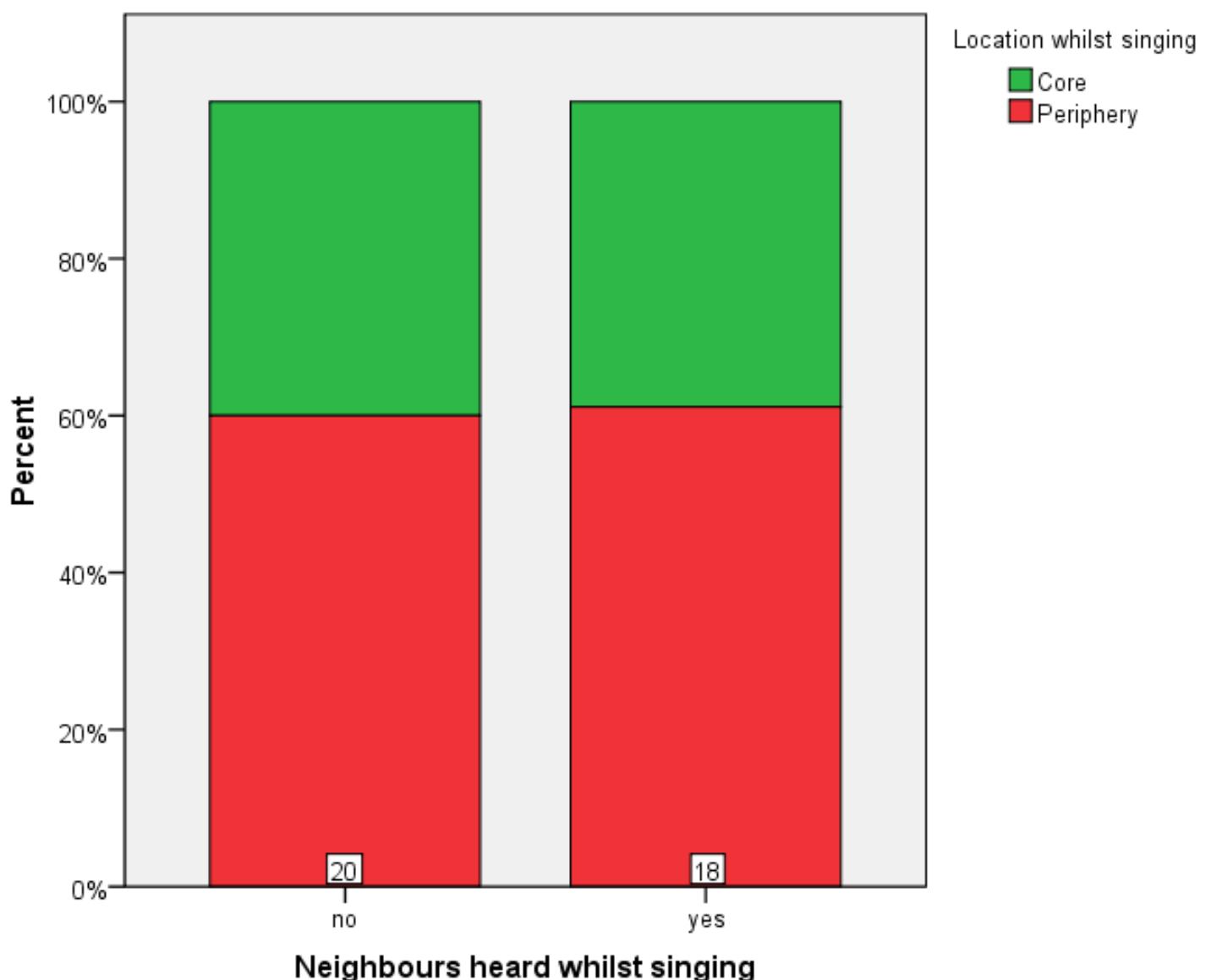


Figure 28. Percentage of neighbours heard whilst calling when duets were given from the periphery or core of the home range.

Since there was a sharp decrease in duetting frequency at around 10:00 AM (about four hours after sunrise, see figure 19a), it was of interest to check for differences in the structure of the early and late duets (those sung after 10:00 AM, or more than four hours after sunrise). There was no significant difference in duet duration between the earlier and later part of the day (one-way ANOVA,  $F=0.5$ ,  $df=1$ ,  $p=0.476$ ), and there was also no difference in whether neighbours were heard calling in the early morning more than later in the day (Chi squared test, chi square=0.0,  $df=1$ ,  $p=0.939$ ).

However, when duets were separated by call start time and by location, there were significantly more duets given in the core in the morning as opposed to the afternoon (Chi squared test, chi square=6.8, df=1, p=0.009). The reverse pattern was not seen in the periphery (Chi squared test, chi square=3.7, df=1, p=0.056).

## ***Discussion***

The aim of this study was to provide a comprehensive account of the different types of naturally occurring songs of white-handed gibbons in Khao Yai National Park, Thailand. Six types of song were identified: duets, male solos, female solos, ooaa duets, predator songs, and group conflict calls. Their temporal patterns were observed, along with gross acoustic features such as duration and presence of certain call elements. The context of each call was taken into account such that whether neighbouring groups could be seen or heard was noted, as was the location the groups were in when singing. It was expected that these measures would shed light on the functions of these calls in facilitating inter-group communication. Results revealed the following patterns:

Duets and male solos were the most commonly heard song sequences. The eliciting factor for duetting behaviour was not the songs of neighbouring groups, but the time of day – this contrasts with the findings of Raemaekers and Raemaekers (1985a), probably because their study differentiated between directly neighbouring and non-neighbouring groups, whereas this study classes all non-focal group duet songs as neighbour duets. The vast majority of duets were sung one to two hours after sunrise. Location was generally unrelated to calling behaviour, except in the case of these morning duets, which were significantly more likely to be sung in the core area of the

group's home range. This also contradicts the findings of Raemaekers and Raemaekers (1985a) study of lar gibbons and Mitani's (1985) study of Bornean gibbons, possibly because they did not separate duets by time of day, or by external referent. Mitani (1985) found that 46.0% of duets were "not associated with identifiable eliciting stimuli" (66). These spontaneous duets are termed "normal duets" in this thesis, and other duets with obvious external referents were excluded from the analyses. Perhaps by including duets in response to obvious external referents, such as those immediately preceding or following an inter-group encounter, the location data were biased, and a clear effect of location on morning duet could not be revealed. Judging from the results presented here, callers appeared to be more interested in reaching a large number of neighbouring individuals, rather than addressing their calls to a specific neighbouring pair. This finding therefore, is more in line with the predictions of the pair bond advertisement, rather than the territorial advertisement or defense hypotheses.

Reichard (1998) has shown that white-handed gibbon sleep sites are not limited to core areas and are often in the peripheral and overlapping segments of their territories, suggesting that duetting location is not just a byproduct of the location of the sleeping tree. Instead, callers appear to time their duetting and actively seek out core area locations in order to broadcast these morning calls. Core locations do not necessarily have increased resource availability, and in fact, neighbouring groups often share good feeding trees on overlapping segments of their territories (Reichard 1998).

By singing in the core area, a group is able to broadcast its song to all sides of their territory so that all neighbouring groups will be exposed simultaneously. In addition, neighbours are very rarely seen during song bouts. However, Raemaekers and

Raemaekers (1985b) found that playbacks of neighbours' duets played from inside other groups' territories always elicited approach and territorial behaviours from territory holders, although it is difficult to interpret these findings as they failed to replicate a natural event. Perhaps then, duetting from the core offers some kind of protection from intruding members of other groups. Morning singing in the periphery may entice unwanted gibbon visitors attempting to lay claim to overlapping segments of home ranges. This would suggest then that the morning duet's primary function is not to advertise territory or maintain boundaries (duets are not primarily sung at the periphery), nor to strengthen the pair bond (pairs actively seek out core locations to sing). Instead, duets appear to advertise the pair bond and contribute to same-sex exclusion (pairs broadcast their song on all sides, whilst avoiding intrusion of neighbours). This advertisement theory supports the newer notion of gibbon socio-ecology outlined in chapter 3. Building and maintaining the pair bond may be relevant functions of pair duetting in gibbons and other species, but the data presented here reveal another additional purpose.

A further important function of duetting is to communicate with other groups about group composition (identity of the pair), pair bond strength (as revealed by how well coordinated the pair sing together), and possibly the age of the partnership (how frequently the pair engage in duetting behaviours: newer pairs duet more frequently than well-established pairs) among perhaps other things. The handicap principle (Zahavi and Zahavi 1997) may also be applied here, and by its nature indicates the honesty of the signals. Other groups may listen and use the information delivered in these calls to keep tabs on dispersed kin and potential rivals' whereabouts and mating status. Sub-adults or lone individuals as well as paired adults may also use this information to determine which groups or home ranges are most vulnerable to

takeover. In a saturated environment such as that in Khao Yai, it may be more important to duet regularly to keep intruders out. It may be that populations in less saturated areas are less motivated to sing, or do not sing as long or as recurrently in a single day, or have a lower rate of great call delivery, since the threat of takeover may be much reduced: an idea that could be easily tested. The few duets given later in the day do not conform to the rules of those given earlier on, and may have a different function, perhaps related to the experiences a group has had that day, such as encounters with non-predatory animals or intense inter-group conflict. In addition, gibbons meet neighbouring gibbon groups on a very regular basis, averaging every other day (Reichard & Sommer 1997) and these encounters are characterised by their own unique set of vocalisations (see chapter 7). It is therefore proposed that gibbon males maintain territory boundaries during these encounters and use these rather than duets as a primary way of defending their resources and perhaps more importantly protecting their mates.

Gibbons pause their own singing to listen to the great call of another group's female at the same time. Therefore, although neighbouring groups' songs do not necessarily elicit singing, when there is overlap between songs, group members pay attention to a neighbouring female's great call and voluntarily inhibit their own singing, especially for the climax of the great call. This is similar to the duet overlap avoidance described by Raemaekers and Raemaekers (1985b), who also anecdotally report gibbons listening to the great call of neighbouring females. What information is transmitted by the great calls remains a mystery, although cues to identity, age, reproductive state and perhaps the strength of the pair bond are likely candidates (Dallman and Geissmann 2001). Great calls may thus serve as honest signals of a female's health and fecundity, especially regarding the female's ability to complete

the climax of the call, which may represent a handicap (Zahavi and Zahavi 1997). Reichard & Sommer (1997) suggest that aside from territorial conflict, group encounters may offer opportunities to “monitor reproductive options” (1165), since sub-adults displace same-sex rivals in neighbouring groups when they disperse, and adult partners sometimes end relationships and find new mates. The present study suggests that duets may function in a similar way since neighbouring groups have an active interest in and can potentially glean reproductive information from song, particularly the great call sequence. Raemaekers & Raemaekers (1985a) suggest the female great call may contribute to exclusion of outside females since when played back in the centre of target groups’ home ranges, the target females’ responses were exaggerated and always involved a higher rate of great call delivery than would be usual for a normal duet. Thus following the handicap principle, females under threat from a rival may use the great call as a deterrent, signaling to the intruder that they are physically able to see off any attempts to lay claim to their territory and their mate. It is possible therefore, that mated individuals can advertise their ability to fend off competitors during a typical duet song. Males in particular may give away the strength or duration of their current bond by the presence, quality and latency of their reply to the female great call, an idea that has yet to be tested.

Female solos are single great calls delivered outside the context of a normal song bout. They were not recorded frequently enough, or from close enough range, to determine whether the female was separated from her partner, as predicted by their general behavioural patterns (Reichard and Sommer 1997). However, these calls are often produced during a group encounter when males are engaged in border disputes and females usually remain separated inside their own ranges (Reichard and Sommer 1997). Reichard and Sommer (1997) suggest that female solo great calls may

increase the costs of male philandering and may act to attract neighbouring males, especially if the great call can convey information about a female's fecundity (see above). This could be the mechanism therefore for pair bond advertisement in a normal duet, whereby the great call and quickly following male reply act to announce the partnership to surrounding groups.

Male solos were sung almost exclusively at dawn by mostly sub-adult males, supporting the findings of Raemaekers et al. (1984). Of the male solos measured, 77.0% were sung in the periphery of the home range, which lent support to the hypothesis that calls targeted specific recipients in neighbouring groups. Unlike duets, which are broadcast in all directions, male solos are directed, possibly with a single recipient in mind. Since these songs do not necessarily cause other males to sing, it may also be the case that callers advertise themselves to the female of a neighbouring group. For example, the sub-adult male "Bua" of group B was observed to alternate the direction of his solo, once towards neighbouring group A, and on another occasion towards neighbouring group C, suggesting he communicated with more than one group. Neighbours were never seen during male solo bouts, also suggesting they may not be aimed at other males. However, an observer on the ground is likely to see less than a gibbon high up in a tree, and it's possible that males could indeed see each other, especially in the few cases where other males sang at the same time. An explanation for the male solos' lack of contagion may be that other males were simply listening to the solos and practicing overlap avoidance, as has been previously described for the duets (Raemaekers and Raemaekers 1985b). This could be an avenue for further research. Primary males did not sing less than secondary males, suggesting solos do not solely advertise vigour or availability. However, only one secondary male solo was recorded and therefore these songs may have been

grossly underreported. Since there were only four groups that contained secondary males as part of the study population, it is difficult to determine the true frequency of these types of call or make judgments about the communicative function of them. If on the other hand, male solos functioned to advertise territory, primary males, as the territory holders, should have sung more often and for longer than sub-adult males. The reverse pattern was found suggesting territorial advertisement is not a primary function of the male solo.

Predator songs and group conflict calls represented a category previously described by Raemaekers et al. (1984) as “disturbed” calls. In contrast to duet songs, all or most group members called simultaneously, generating a cacophony of notes in a disorganised arrangement. The main differences between predator song and group conflict song was that predator song sequences always began with a series of low frequency hoo notes, while callers were usually alert with their attention focused in a particular direction. Both song sequences included sharp wow elements and the female great calls were always delayed (chapter 5). This study found no correlation between predator song and the time of day or the location in which they were sung, as predicted. They did not however reliably elicit song from neighbours, as was predicted if they functioned primarily to inform kin in other groups. The function of alarm calls and mobbing calls is a topic of ongoing research. In some cases, calls deter predators by making them aware that they have been spotted and communicating about the prey’s ability to escape. In other cases, they alert kin of potential danger, thereby protecting them and increasing the callers’ inclusive fitness. In this case, gibbon predator song seems to function primarily to communicate with the predator. Neighbouring groups may also use this information of course and respond in kind when they feel threatened by the predator themselves, but these

response songs may also function principally to deter or harass the predator. The structure of predator song suggests that the female great call has functions mainly outside of this context since it was always delayed, but anecdotal evidence suggests that gibbon predator songs are loud and of high frequency implying the gibbons are in an agitated state as they sing them. This conversely favours the kin selection hypothesis over the pursuit-deterrance hypothesis for the evolution of alarm and mobbing vocalisations, since calls directed at the predator are expected to be of low frequency, presumably as they are designed to be testament to the prey's relaxed state and confidence at their ability to escape (Zahavi and Zahavi 1997). However, it seems plausible that songs of a high frequency may be more harassing or annoying to a potential predator than low frequency songs, and thus pursuit-deterrance could still be the driving force behind gibbon predator mobbing songs. The function of group conflict song sequences is less clear. There were too few instances recorded in this study to make reliable statements about the nature of the contexts in which they were given. However, given the plasticity of gibbon song it seems likely that these songs are adapted from predator songs, which they closely resemble. It is possible therefore, that group conflict calls denote that a predator has been seen earlier in the day or on the previous day; further study is needed to help elucidate their function further.

Ooaa duets finally, are very little understood. Results confirmed that they are extremely contagious, and did not occur regularly at a specific time of day, although they appeared somewhat clustered during the early morning, but they were not more likely to occur in a core or peripheral location. The initial eliciting stimulus for these calls remains unclear. Reichard (1998) describes an encounter with a mountain hawk eagle that elicited ooaa calls from white-handed gibbons, suggesting it may be a type of alarm call, but it's clustering in the morning belies this as a convincing explanation.

Using playback, Raemaekers & Raemaekers (1984) found that oooa duets were significantly more contagious than normal duets, but they were equally unable to identify an initial eliciting stimulus of naturally occurring call bouts. As a specific referent, oooa calls could function to label objects or events in the environment, and as such, playbacks under controlled conditions are needed to monitor behavioural responses to try and expound their meaning.

In conclusion, gibbon loud calls have many functions: they may act to deter conspecific intruders, attract individuals of the opposite sex, elicit within-group and between-group singing, advertise pair bonds, and serve as honest signals to rivals, mates, predators and other conspecifics. They may also provide clues to caller identity, and reproductive status in the case of females.

Further research is strongly indicated. Firstly, more complete follows are necessary to better discern call frequency and identity. Greater numbers of group conflict calls and natural predator songs are required to test ideas about their possible link to one another. Only a skilled observer can accurately differentiate between the gibbons' song types, since they overlap extensively in the types of call units included (see chapter 6), especially the duets. This study demonstrates there are clear differences in the functions of duets given before 10:00 AM and those given afterwards. Similarly, there were a number of instances where duets were recorded, apparently given in response to non-predatory animals such as elephants or bears, or before or after an inter-group encounter. Such duets were excluded from the analyses presented here because of their attachment to an obvious external referent. The duet then seems to be remarkably plastic in its function and further research may reveal structural differences to accompany these functions. In any case, it seems to be an important way of communicating between groups, about pair compositions, and about events

going on within the home range. Secondly, both within the duet song and in isolation, the female great call is an excellent candidate for future study regarding the reproductive hypothesis put forward above. Further long-term observation may give clues as to the types of information it conveys. Several females' calls could be recorded over time and compared with one another. Do older, less fecund females have predictably different great calls than younger ones? If so, do pregnant or cycling females sing differently? The ability to reach the climax of the call may decline with age, and thus provide honest clues to the reproductive potential of the singer. Thirdly, male solos could be investigated further. Like great calls they may be honest signals of fertility and in particular a males' potential ability to hold a territory. Similarly, long-term studies could provide clues as to whether age, disease or fertility affect a males' ability to produce complex phrases – something that listening females could take into account regarding extra-pair copulations, and listening males could take into account regarding possible cuckoldry or territory take-over. If solos are directed to specific groups or individuals as this study suggests, do they vary structurally between target audiences? Do the solos produced by mated males differ in any other way than duration from the solos produced by unmated or sub-adult males? Finally, oooaa duets need further clarification. This study confirmed their high degree of contagion but did not reveal their function. Long-term data are needed as well as controlled playbacks where listeners' behaviours are closely monitored.

## **CHAPTER 5. Vocal responses to predator models**

(Data published in Dec 2006; Clarke E, Reichard UH, Zuberbühler K (2006) The Syntax and Meaning of Wild Gibbon Songs. PLoS ONE 1(1): e73.  
doi:10.1371/journal.pone.0000073)

### ***Abstract***

Spoken language is a result of the human capacity to assemble simple vocal units into more complex utterances; these are the basic carriers of semantic information. Not much is known about the evolutionary origins of this behaviour. The vocal abilities of non-human primates are comparatively unimpressive, with gibbon songs being a rare exception. These apes assemble a repertoire of call notes into elaborate songs, which function to repel conspecific intruders, advertise pair bonds, and attract mates. A series of field experiments with white-handed gibbons showed that this ape species uses songs also to protect itself against predation. The acoustic structure of predatory-induced songs was compared with regular songs that were given as part of their daily routine. Predator-induced songs were identical to normal songs in the call note repertoire, but consistent differences were found in how the notes were assembled into songs. The responses of out-of-sight receivers demonstrated that these syntactic differences were meaningful to conspecifics. This study provides the first evidence of referential signalling in a free-ranging ape species, based on a communication system that utilises combinatorial rules.

## ***Introduction***

For some primates, there is good evidence for reference-like communication in their alarm calls given to predators. Referential communication is here defined as the ability to use communication signals to denote specific objects or events in the external environment, which are used by listeners to draw inferences about the occurrence of these objects and events. In nature, if signallers reliably produce acoustically distinct vocalisations to different classes of predators, then recipients often respond to them as if spotting the corresponding predator themselves. Very little is known about the psychological processes that drive call production, and hence the term “functionally” referential is often used to describe such cases. This is also to separate them from human speech, a communication system based on signallers and recipients understanding each other’s intentions (Grice 1969). For non-human primates, the default assumption is that callers do not vocalise to actively inform each other, but as a by-product of signallers responding to evolutionarily important events.

Somewhat strikingly, there is an almost complete lack of evidence for referential signalling from our closest living relatives, the apes. This is particularly puzzling in light of a substantial literature on referential signalling in various monkey species, such as vervet monkeys (Seyfarth et al. 1980), Diana and Campbell’s monkeys (Zuberbühler et al. 1997; Zuberbühler 2001), putty-nosed monkeys (Arnold and Zuberbühler 2006), and white-faced capuchin monkeys (Fichtel et al. 2005). Somewhat recently, it has been suggested that captive chimpanzees produce functionally referential calls in response to different types of foods, but it is not yet clear whether these calls serve as labels for specific food items

(Slocombe and Zuberbühler 2005; Slocombe and Zuberbühler 2006).

Gibbons small body mass makes them vulnerable to predation from large cats, snakes and birds of prey and perhaps because of this, gibbons almost exclusively reside in the upper canopy (van Schaik and van Hooff 1983; Leighton 1986).

Aside from their regular duet songs, gibbons sometimes also produce songs in response to predators (Raemaekers et al. 1984; chapter 4), but no systematic study has ever been conducted to investigate this phenomenon. Uhde and Sommer (2002) noted that white-handed gibbons sometimes give loud vocal responses to tigers, pythons, and large raptors as well as the alarm calls of barking deer, variable squirrels and oriental pied hornbills. The question remained to what extent white-handed gibbons produced songs in response to potential predators, and whether these songs differed from songs given as part of the daily morning routine, the duets. Differences between these songs may be in the overall temporal structure, the product of distinct individual call units, or in the ways in which identical call units are combined. The latter, if consistently governed by context, would represent a simple form of syntax, something that has yet to be demonstrated in any ape species.

## **Methods**

### **Study site and subjects**

See chapter 3 for a description of the study site and subjects.

### **Vocal behaviour**

(a) Single notes: Raemaekers et al. (1984) have described the basic vocal

behaviour of white-handed gibbons and, whenever possible, their terminology is used (see chapter 2, table 3). Individual vocal units are termed “notes”, of which seven different types can be distinguished: (1) *wa*, (2) *hoo*, (3) *leaning wa*, (4) *oo*, (5) *sharp wow*, (6) *wao*, and (7) *other*. The *hoo* was originally considered part of the *wa* group, but it was found that this class of call was consistently lower-pitched than *wa*, of lower amplitude, and usually covering a frequency range of less than 150Hz (mean frequency range = 73.8Hz ± 36.9, n=115). These three parameters allowed *wa* and *hoo* notes to be reliably discriminated from one another. Notes labeled “other” included any that could not be easily categorised as one of the previous six.

(b) Note combinations: As outlined in chapter 2, individual notes are rarely produced in isolation but normally assembled into more complex structures, so-called figures or phrases, to form a song (see tables 5 and 6). Two prominent examples of phrases are the relatively rigid female great call lasting on average 17.4 seconds ( $\pm 1.3$ , n=13, from duets and predator contexts), and the male reply, a coda sequence, which usually immediately follows the great call (table 6). When two group members produce songs in a coordinated way, this is termed a duet.

## **Data collection and equipment**

See chapter 4 for details of tape-recording equipment. Ad libitum sound recordings throughout the day resulted in a library of complete natural duet songs (n=14) from different groups, which were then compared with predator-induced songs. Natural predator encounters are very difficult to observe in rainforest habitats and systematic studies are almost impossible to conduct. Hence, songs were elicited experimentally by presenting realistic life-size visual predator

models, and by presenting acoustic models of predators to the different study groups.

### **Visual predator models**

The visual model predators were custom-made, to match photographs of the real predators, and positioned in their natural resting or hiding position (Sunquist and Sunquist 2002). Responses to the following predator types were tested: clouded leopard, tiger, reticulated python, and crested serpent eagle (see chapter 3, table 7 for Latin names). For the tiger and clouded leopard models, two different exemplars were used. Clouded leopard models consisted of fake-fur wrapped around an object, such as a large rucksack, positioned approximately one metre from the ground on a log or stone (figure 29b). Tiger models were displayed using an assistant who walked hunched under the group whilst covered in a fake tiger fur (figure 29a). A control model was a similarly sized print of a non-descript design on a brightly coloured fabric, presented in exactly the same way, to control for presentations of a conspicuous stimulus on the forest floor. The tiger and control stimulus were presented alternately so that five groups saw the tiger first and four groups saw the control first. The reticulated python model was made from several draught excluders of approximately ten centimetres in diameter, sewn together and painted, to make a tube of about four metres in length. The python was placed, usually coiled, at about one to two metres above the forest floor in a small tree, tree stump, or log (figure 29d). The crested serpent eagle model, finally, was made from chicken wire and papier-mâché, painted and feathered with feather dusters bought locally. It was hoisted four to ten metres into the trees with a rope, and positioned usually between two parallel branches as though perched on the lower branch. For this, an assistant shot a weight attached to a fishing line over an

appropriate branch with a catapult, allowing him to pull the rope over the branch for hoisting and positioning the eagle model into the canopy, figure 29c.

a) Tiger









Figure 29. Predator models used in the experiments a) tiger model (photograph by Esther Clarke), b) clouded leopard model (photograph by Brendon Snyder, with permission), c) eagle model (photograph by Esther Clarke), d) python model (photograph by Esther Clarke).

## **Acoustic predator models**

Acoustic models included: tiger growls, clouded leopard hisses, and crested serpent eagle shrieks (figure 31). Playback equipment was set up on the ground, except in the case of the eagle playback, where the speaker was hoisted into a tree at approximately four to six metres (figure 30). Playbacks took place approximately 40 metres from the group. Predator vocalisations were broadcast using a Bose 151 Environmental Speaker connected to a commercial car CD player/amplifier, powered by a customised laptop charger unit. The speaker was directed towards the group and angled slightly upwards to avoid ground sound absorption. The equipment was obscured from the animals' view with camouflaged cloth (figure 30).

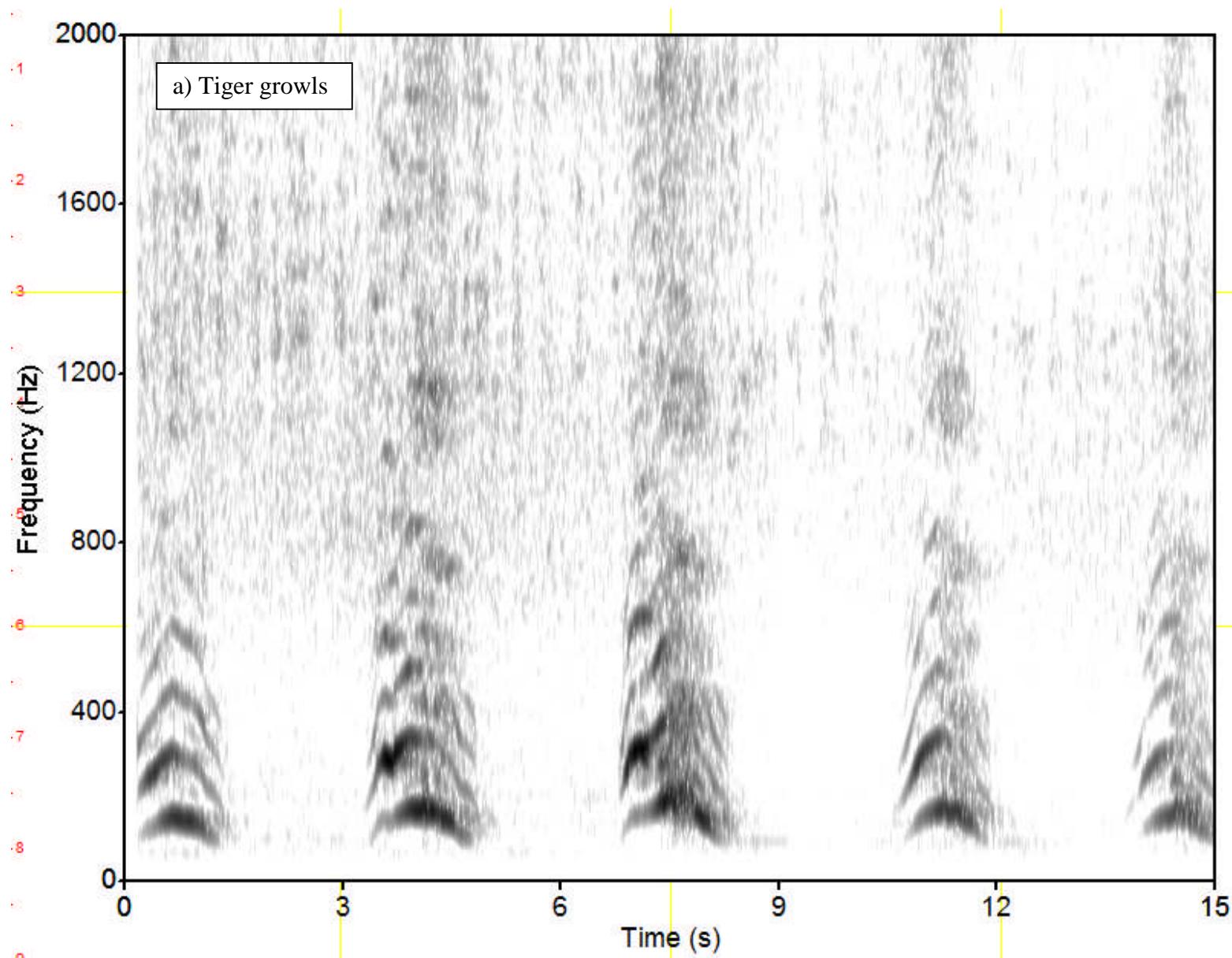


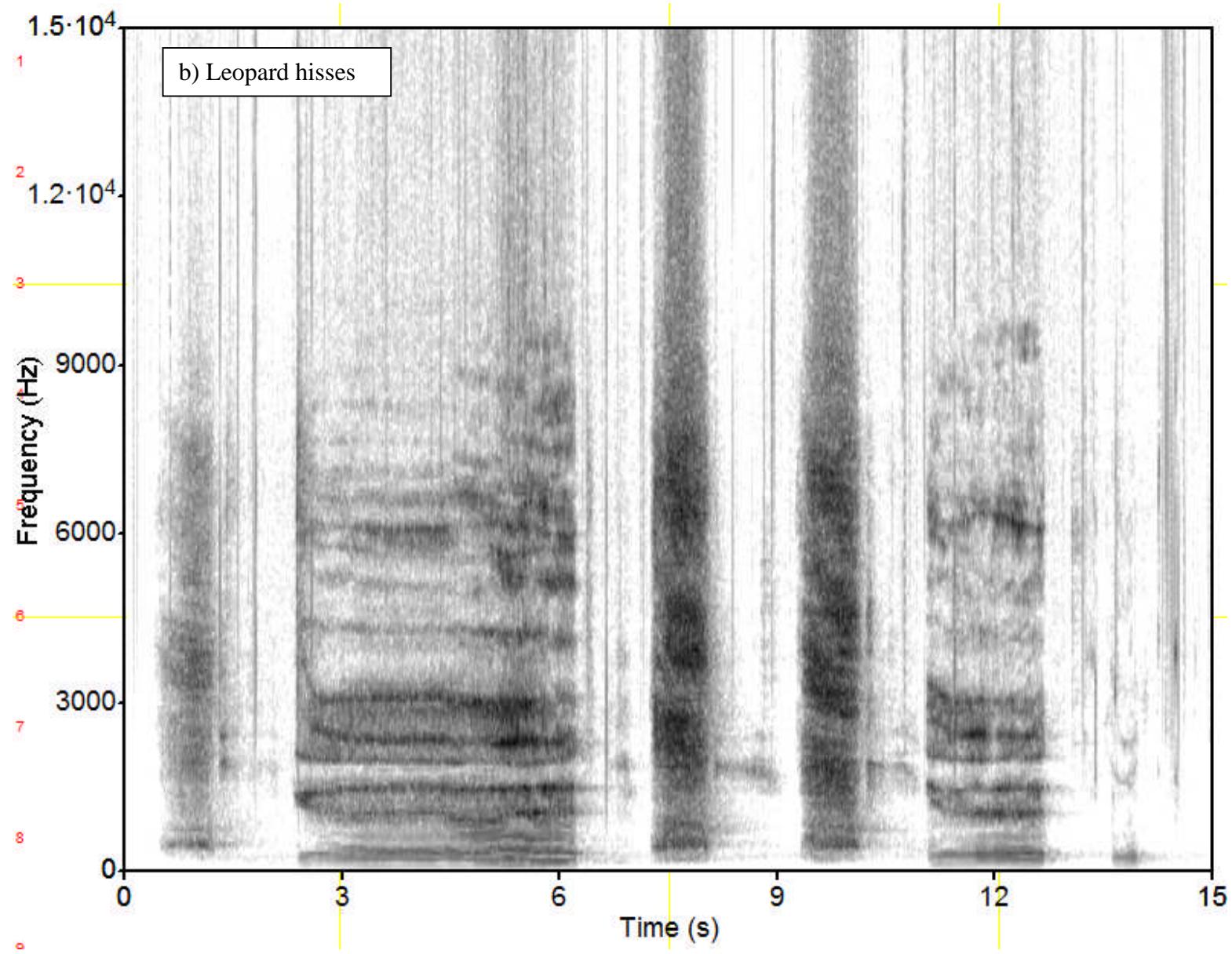
Figure 30. Illustration of how the predator models were presented to the gibbons. The camouflaged playback equipment was positioned near a group on the ground (left), or hoisted into a tree (right).

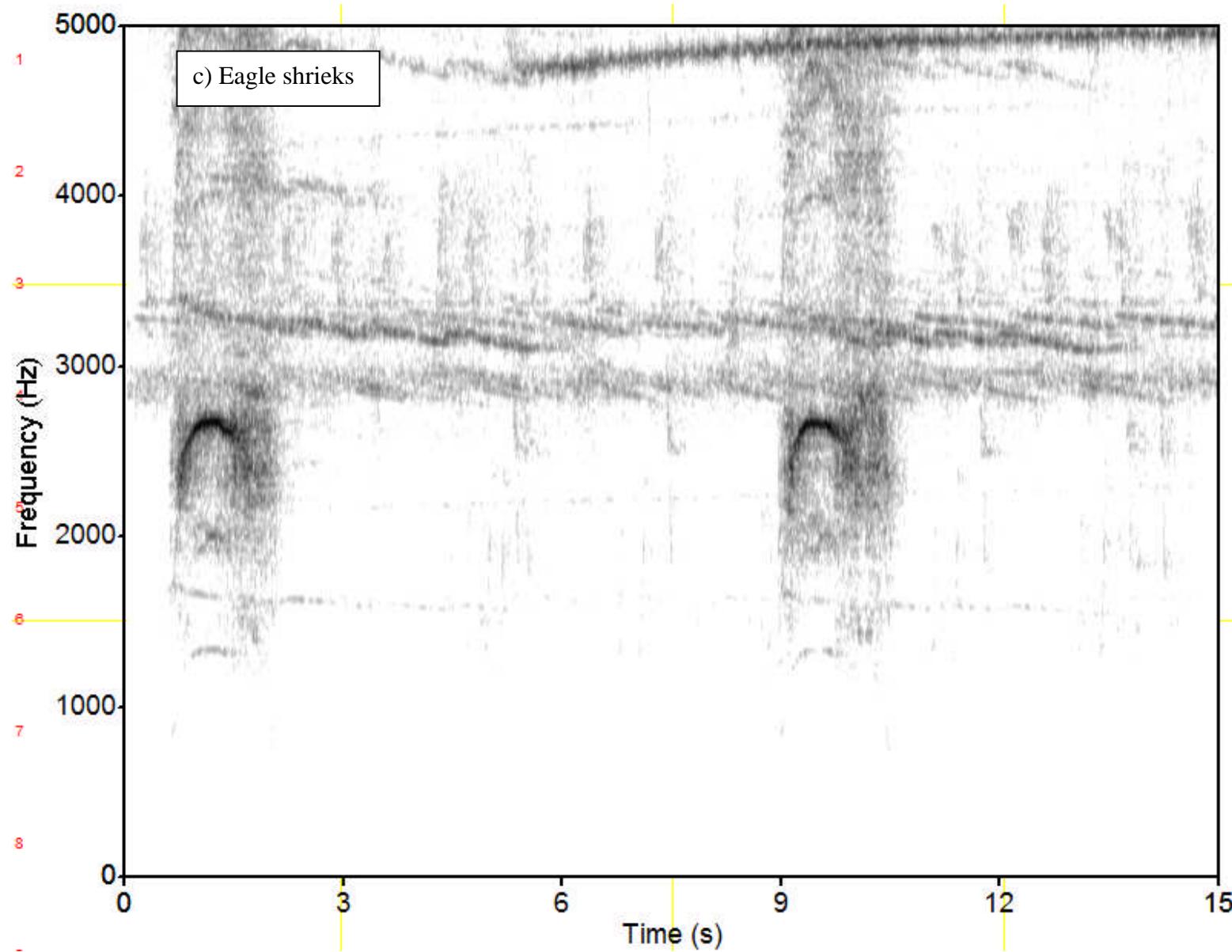
All predator vocalisations were obtained from the British Sound Library and then spliced into fifteen-second sections for playback. Each section was surrounded by five minutes of silence on either side to control for any noises emitted by the equipment itself. In addition, barking deer calls were presented as a control stimulus (figure 31). Barking deer barks are given in response to several disturbances,

including potential predators, but they are not thought to convey specific predator information (Midha 2001). These calls were recorded at the study site by the author, and presented as single barks in isolation or following the growls of a tiger or clouded leopard. This was to address whether gibbons were able to take context into account when responding to barking deer calls, a behavioural skill that has been observed in some monkey species (Zuberbühler 2000).

Playback stimuli were edited using Cool Edit software and burned onto CD for presentation. Sound pressure readings for each stimulus were taken at one metre from the playback speaker using a sound pressure meter. These were recorded in open forest habitat away from the study site and prior to them being presented to a gibbon group. Volume levels were adjusted so that all playback stimuli fell between 90-95 dB, to ensure that response differences could not be explained with differences in stimulus amplitude. Playback stimuli were presented in a random order. Barking deer playbacks that followed big cat playbacks were presented approximately ten minutes after any predator response behaviour had ended.







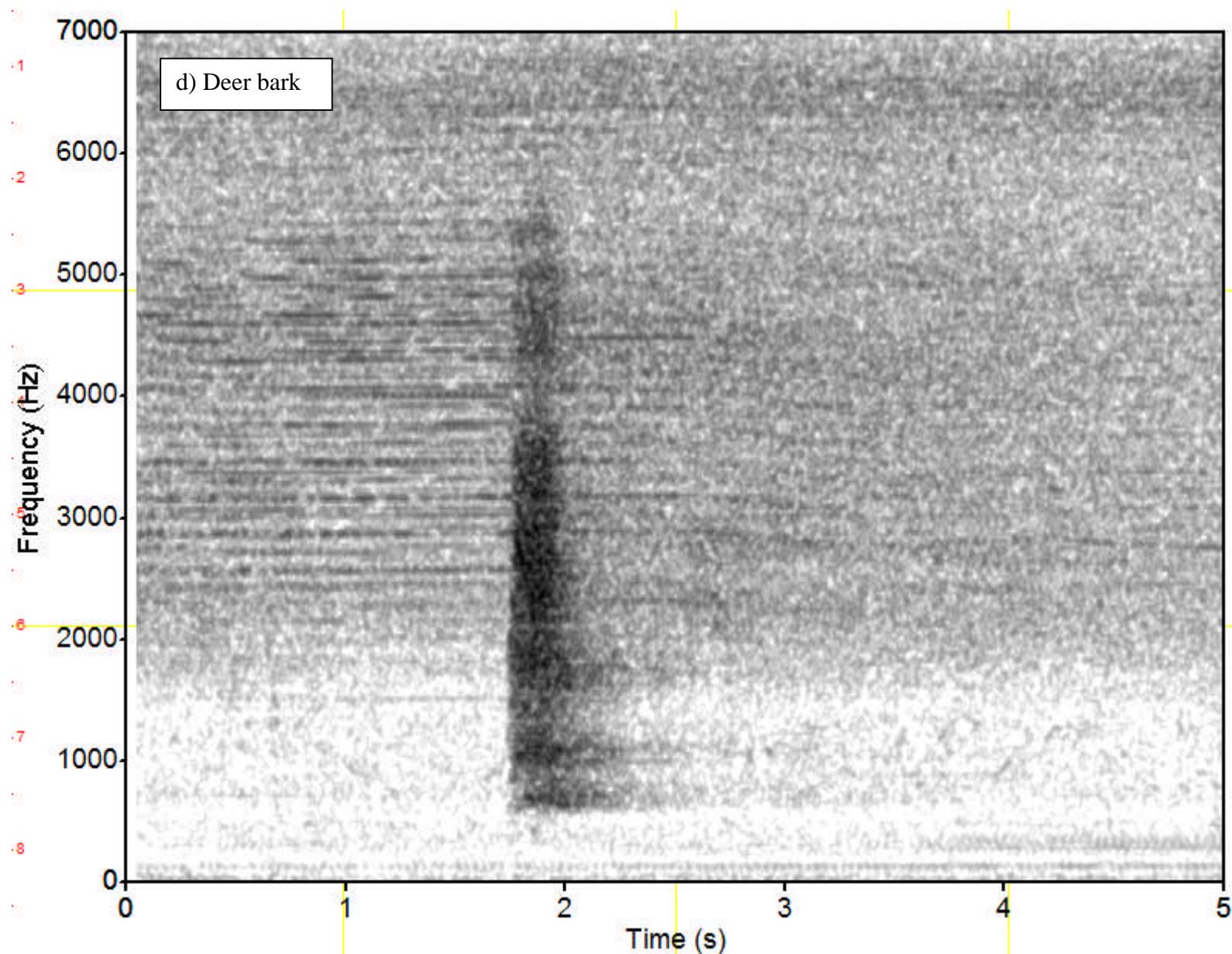


Figure 31. Playback stimuli: a) tiger growls, b) clouded leopard hisses, c) crested serpent eagle shrieks, and d) barking deer bark.

The overall aim was to keep stress for the study animals as low as possible. Some observations suggested that natural predation events could occur at a maximum rate of about one per three to four days. These observations were based on scoring any time that a gibbon group contacted a potential predator including indirect evidence of a predator such as the alarm calls of another species. No successful predation events were witnessed during this time. Predator models were presented at intervals of no more than one per week per group, much below the maximum observed rate. Each group was exposed only once, maximally twice, with a particular model type. Predator models were presented in open forest habitat, so that individuals always had open escape routes.

### **Experimental protocol**

Groups were located usually by their morning duets, or by identifying their sleeping site the night before. Once found, they were followed for at least two hours before a visual predator experimental trial was initiated, except in the case of the eagle model, which was presented opportunistically since the chances of the gibbons witnessing the placement of this model was greatly increased. In other cases, this two-hour period permitted the individuals to acclimatise to the presence of an observer and it provided baseline vocal and non-vocal data before model presentation. If no real predator was encountered during this two-hour period, a visual predator model was discretely positioned ahead of the gibbons predicted travel route and remained displayed for a period of about twenty minutes starting from when the gibbons had first detected it, and then removed. The group were usually observed for at least two more hours, or until the group reached their final sleeping site for the day. In the case of playbacks, the acoustic models were also

opportunistic in their presentation, largely because of the difficulty in transporting heavy equipment through the forest for extended periods. Throughout model presentation, the focal groups' behaviour was monitored continuously and recordings were made. The vocal responses of neighbouring groups were also recorded whenever they occurred.

## **Data analyses**

The structural differences of gibbon songs produced (a) as part of their early morning routine and (b) in response to predators were of particular interest. The responses to the visual tiger model were removed from the main analyses because of the difference in presentation between this and the other terrestrial predators, and because tigers are rarely seen in the park anymore (WCS 2001). Nevertheless, groups responded strongly to this predator model, in one case also triggering a vocal response from a neighbouring group. Table 12 details the call statistics for this predator.

Whenever neighbours responded to the focal groups' singing behaviour to a predator, these calls were analysed too. This provided a natural experiment: since the focal group had undoubtedly responded to a predator, the information their songs potentially transmitted to recipients in adjacent home-ranges, or to group members who were temporarily away from the group, could be determined. Visual tiger model responses were included for this analysis due to the low sample size. Similarly, when groups sang later in the day following a predator model encounter, these songs were recorded and analysed to see if earlier predator exposure would affect gibbon vocal behaviour in the long-term.

Calls were digitised using Cool Edit 2000 software. Spectrograms were made using Raven 1.2.1 with a Hanning window function, 8.7Hz filter bandwidth, 0.5Hz frequency resolution and 15s grid time resolution. Gibbons' singing is a crescendo of notes, particularly in response to predators. Vocal behaviour usually starts with a series of very soft hoo notes, initially only audible at close range, but rapidly grading into much louder units carrying over long distances. Hence, for each song its start was defined as the first loud non-hoo note. Then, the following were determined: (a) number of hoo notes and (b) duration of hoo sequence before song onset. After song onset, the following were determined: (c) presence of and (d) latency to first sharp wow note, (e) latency to first female great call and (f) latency to male reply, and (g) total duration of singing. In addition, a sequential analysis was conducted to compare the first ten notes per song in the duet and predatory contexts.

The identity of each gibbon's voice was distinguishable, and the order in which each group member called was noted at the time of predator presentation to facilitate analyses. Statistical analyses were conducted using SPSS software, mainly non-parametric procedures such as Mann-Whitney U tests and Fisher's exact tests.

## **Results**

### **Predator-induced songs**

Gibbons reliably sang in response to the visual terrestrial models, but not the

raptor. Predator visual models elicited singing as follows: clouded leopard (8/8 trials), tiger (9/9 trials), reticulated python (3/9 trials), crested serpent eagle (0/7 trials), suggesting that singing is a firm part of these primates' natural defence to ground predators. However, vocal responses to acoustic presentations of predators were much weaker, hardly ever eliciting singing. This meant that they could not be statistically compared with responses to visual models. Playback models elicited singing as follows: clouded leopard (0/5 trials), tiger (1/10 trials), crested serpent eagle (0/3 trials), barking deer (0/5 trials), barking deer after cat (1/15 trials). For this reason also, the two songs elicited by playback trials were not included in the main analyses along with other predator songs, but see table 11 for their call statistics.

### **Song composition: early differences**

Although there were no obvious overall differences between the songs given in duet contexts and those given in response to predators, a more detailed analysis revealed a number of subtle differences. As soon as an individual began to sing, (by producing loud non-hoo notes) the first ten notes for each song were compared between the two contexts, which is roughly equivalent to about fifteen seconds of singing (mean duration=12.5s, n=38). This initial song segment was particularly interesting because, if gibbons conveyed any information about external events, they should do so as early as possible to benefit conspecific and/or heterospecific recipients, particularly during predator encounters. Two main differences emerged. First, leaning wa notes were significantly less likely to occur in the predatory than the duet context (Fisher's exact test,  $p<0.001$ ). Second, there were significantly more hoo notes nested within the other call units in the predatory

than in the duet context, figure 32.

### Duet songs - fully habituated groups

Gp. ID	n1	n2	n3	n4	n5	n6	n7	n8	n9	n10
W AF	f	o	f			/	/		f	
	/	o		/			/		/	
C AF	-	-	-	-	-	f	f	f	f	f
	AM	f	f	f	/	/	/	/		/
T AF		/	f	o	/	o	o		o	
	AM	-	-	o	f	o	o	o	/	-o
T AF	/	f	f	f	o	f	-	f	/	/
	AM	f	o	-	X	f	f	o	f	f
C AF	/		o							
	AM	f	o	f	o	f		f		

### Duet songs - partially habituated groups

NO S	AF	/	-	-	f	f	f	f	f	o	f
	AM	f	f	f	f	f	f	f	f	f	f
D AF		o	o	o	o	o	o		o	f	f
	AM	f	f	f	-	f	f	f	f	-	
D AF	-	f	f	f	f	-	/	f	f	-	
	AM		o	-	f	/	f	f	f	f	f
NO S	AF	f	o	f	f	f	X	f	/	o	o
	AM	f	f	f	f	f	-	f	/	/	/

### Predator songs – visual clouded leopard model

Gp. ID	n1	n2	n3	n4	n5	n6	n7	n8	n9	n10
W AF	f	f	f	f	f			f	X	X
	/	o	o	o	o			o	o	o
B AF	f	f	f	f	f	f	f	o	o	
	AM	/	/					o	o	o
C AF	-	-	-	-	-	-	-	f	f	o
	AM	f	f	f	f	f	f	f	f	f
R AM	f	-	o	o	o	o	o	f	f	f
	N AF	f	f	-	o	o	-	o	f	-
H AF		X								f
	AM	/	f	f	f	-	o			
D AF	-	o	o	o	o	o	o	o	o	o
	AM	-	-	-	o	o	-	o	o	o
J AF	f	f	f	f	o	f	f	f	o	
	AM					f	f	X		

### Predator songs - snake model

R AF	/	o	-	o	o	o	o	o	o	o
AM	-	-	o	-	o	o	o	o	o	o
B AF	f	f	f	-	f	o	f	f	-	-
	AM	-	o	o	o	o	o	o	o	o
N AM	-	o	o	o	o	o	o	o	o	o
	AM	-	o	o	o	o	o	o	o	o

#### Key:

/	= leaning wa	o	= hoo	f	= wooo	-	= oo		= wa	~	= all other notes	X	= uncodeable
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Figure 32. Sequential analyses of the first ten song notes in both predatory and duet song contexts.

## **Song composition: overall differences**

Following the first ten notes, additional differences were found in song composition depending on context: sharp wow notes were significantly more common in predatory than in duet songs, appearing on average  $236.4 \pm 346.8$ s into a predatory song ( $n=11$ , figure 33). A few duet songs also contained sharp wows ( $n=6/14$ , mean latency =  $71.5 \pm 47.2$ s), but interestingly they were all given by groups that had not been fully habituated to human presence (groups D, J, and NOS; table 9). It is likely, therefore, that the sharp wows are notes given in response to any disturbance, which can be incorporated into regular duets and predator-induced songs.

Overall, songs given in the predatory context were significantly longer than songs in the duet context (predatory mean duration =  $2005.0 \pm 1560.0$ s,  $n=11$ , versus duet mean duration =  $625.9 \pm 450.7$ s,  $n=14$ , figure 34). Predator-induced songs were always introduced by a long series of soft hoo notes. The number of these notes differed significantly between the predatory and the duet contexts (predatory:  $100.9 \pm 110.9$ ,  $n=11$ ; duet:  $9.2 \pm 8.3$ ,  $n=14$ , figure 35). Correspondingly, the total duration of the hoo note series in the predatory context was significantly longer than in the duet context (predatory:  $158.7 \pm 290.6$ s,  $n=11$ ; duet:  $9.8 \pm 13.1$ s,  $n=14$ , Mann-Whitney U test,  $U=17$ ,  $p=0.001$ , figure 36).

The female great call, finally, is a stereotyped sequence of notes described as a phrase (Raemaekers et al. 1984), lasting on average  $17.4 \pm 1.3$ s ( $n=13$ ). Females produced great calls in both contexts, but during duets they were delivered significantly earlier compared to when responding to predators (duets:  $80 \pm 35.2$ s,

n=14; predatory:  $682.4 \pm 669.8$ s, n=9) with no overlap; great calls during the first two minutes were reliably linked with the duet context, whereas great calls given after two minutes were always associated with the presence of a predator (Fisher's exact test,  $p < 0.001$ , figure 37). Males usually replied to female great calls with a specific phrase, but these replies came significantly earlier in the predatory than in the duet context (predatory  $= -1.3 \pm 1.7$ s, n=9; duets:  $1.0 \pm 3.4$ s, n=14, figure 38). There were just two instances where a playback elicited singing from the gibbons. These songs could not be included in the above analyses due to low sample size, but upon inspection, they too appeared to have the hallmarks of a typical predator song, though were somewhat shorter in overall duration. Table 11 summarises these song statistics. Table 12 gives the mean song statistics for the visual tiger model response songs, which were excluded from the main analyses due to differences in model presentation. Nevertheless, they too showed the traits of a typical ground predator song.

**Table 11.** Playback response songs.

	Group W tiger playback response	Group D barking deer playback response (after clouded leopard playback)
Song duration (s)	937.3	404.5
Hoo duration (s)	107.2	26.9
Latency to first great call (s)	493.9	298.1
Latency to male reply (s)	0.4	6.7
Presence of sharp wows	yes	yes

**Table 12.** Tiger song statistics.

Measure	Value	N-value
Mean song duration (s)	1442.6	10
Mean number of introductory hoos	63	10
Mean hoo duration (s)	38.6	10
Mean latency to first great call (s)	984.4	8
Mean latency to male reply (s)	0.93	7
Presence of sharp wows	yes	9

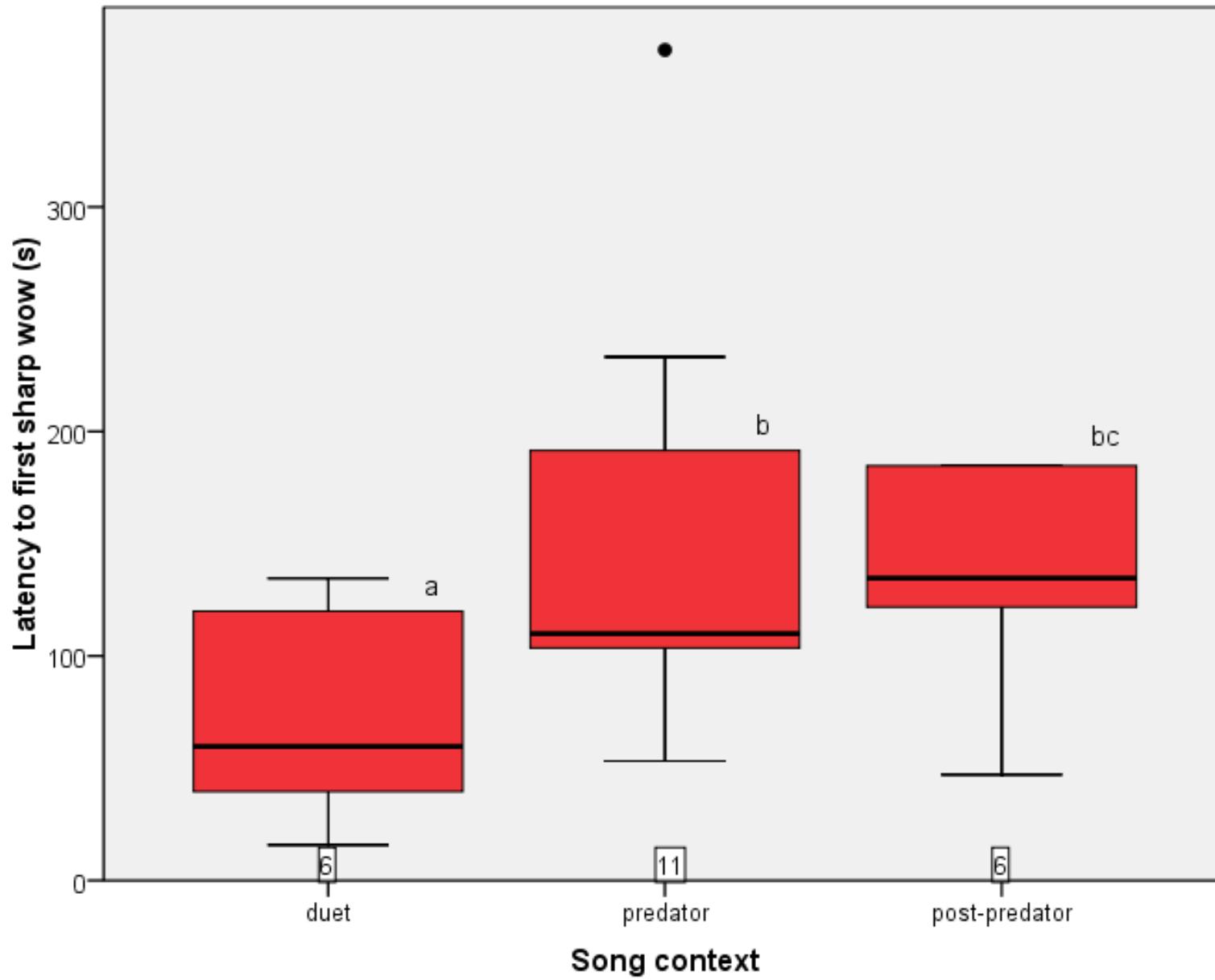


Figure 33. The latency to the first sharp wow note in the different song contexts. Box plots represent medians and inter-quartile ranges. Two extreme values were omitted from the graph but not the analyses. Numbers in white boxes are n values. Differing letters denote significant differences.

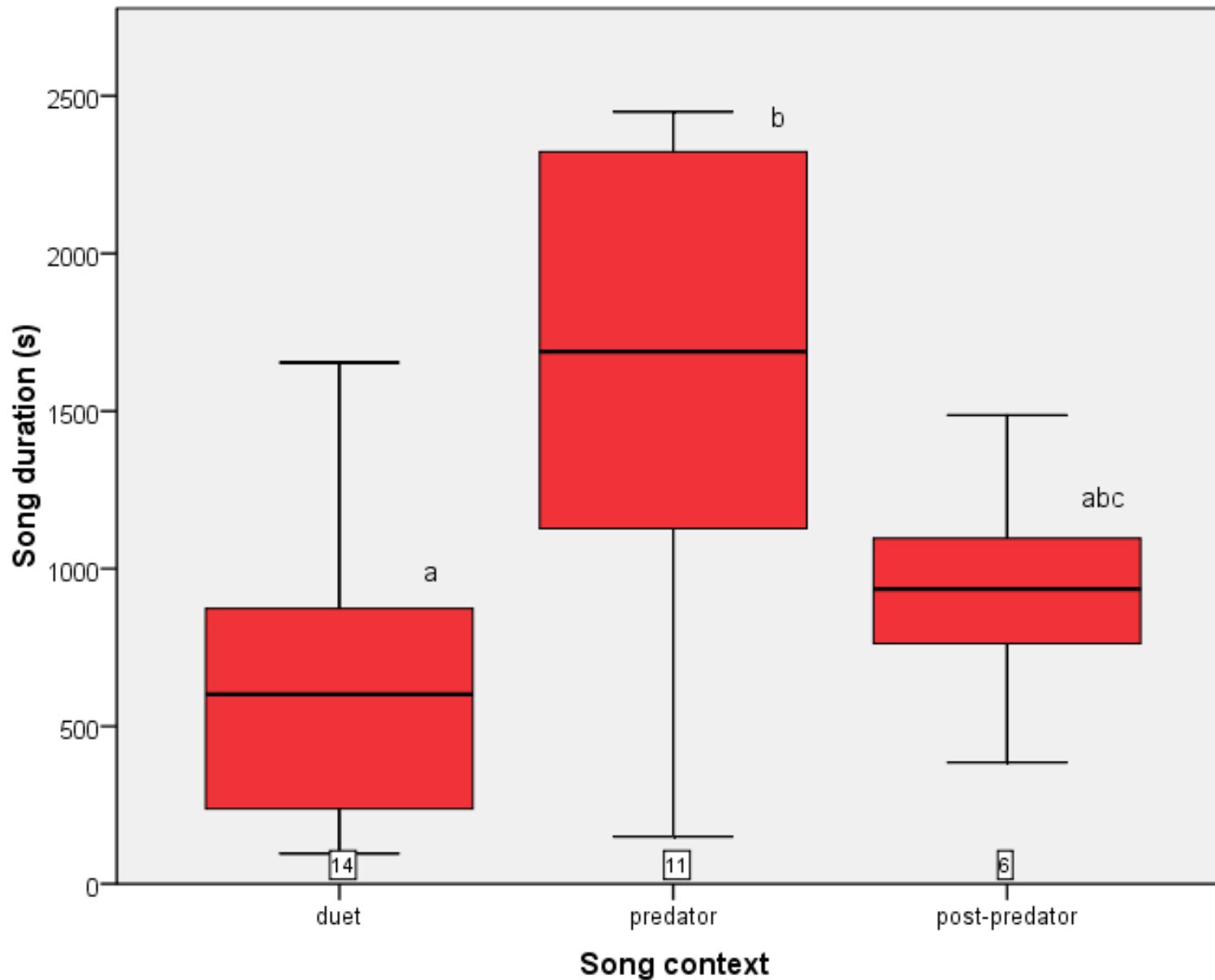


Figure 34. Song duration in the different song contexts. Box plots represent medians and inter-quartile ranges. Two extreme values were omitted from the graph but not the analyses. Numbers in white boxes are n values. Differing letters denote significant differences.

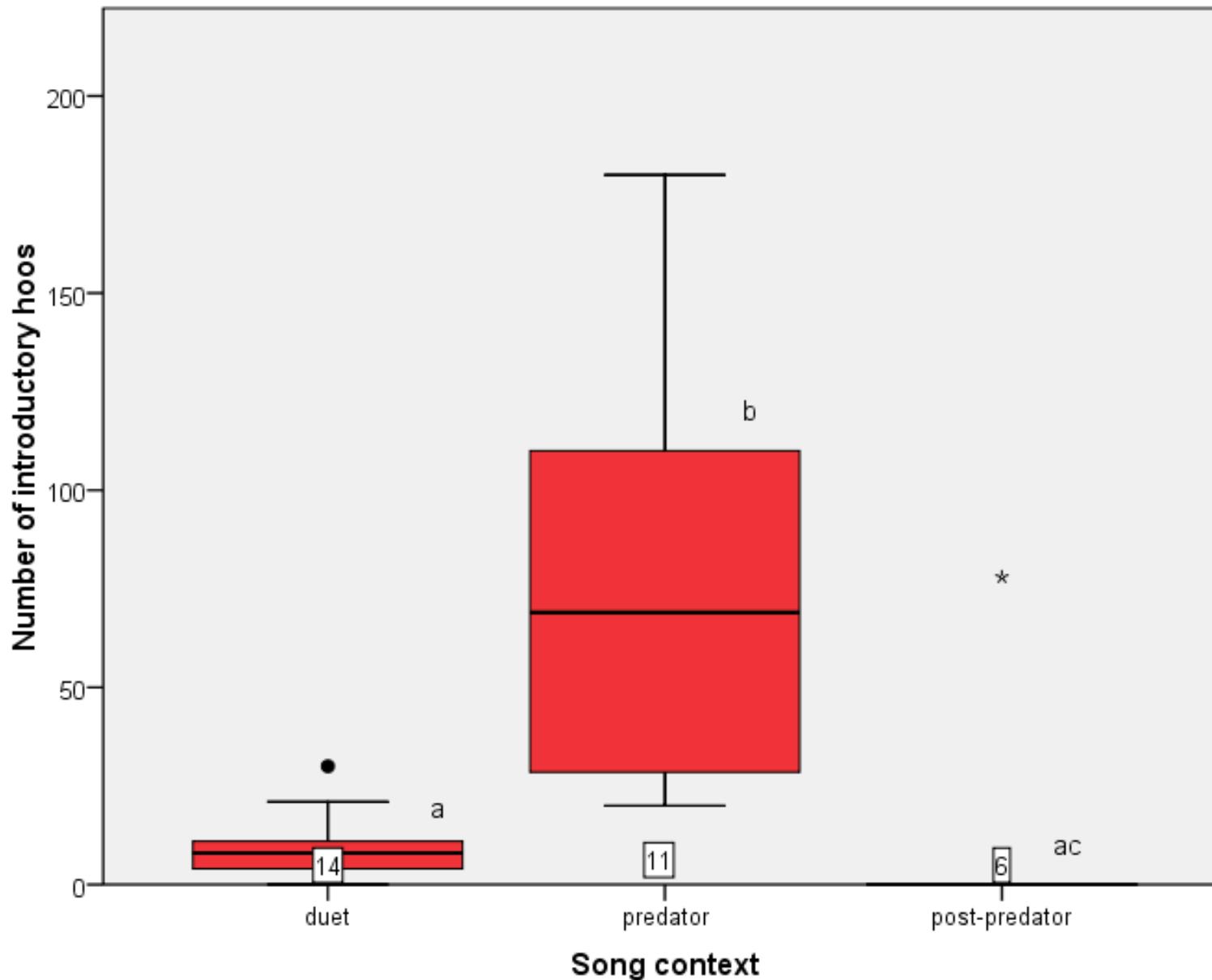


Figure 35. The number of hoo notes that introduced song in each different context. Box plots represent medians and inter-quartile ranges. One extreme value was omitted from the graph but not the analyses. Numbers in white boxes are n values. Differing letters denote significant differences.

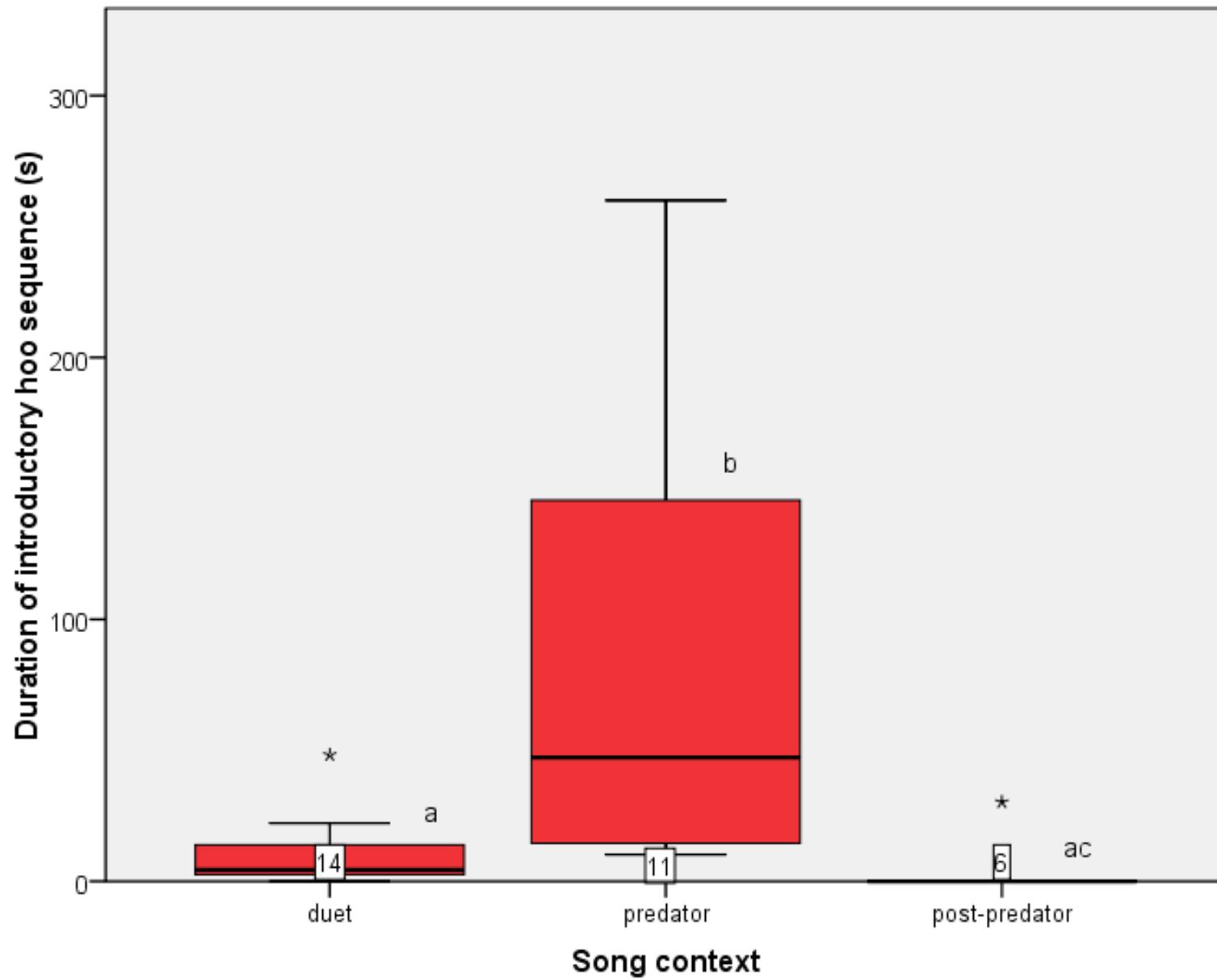


Figure 36. The duration of the hoo sequences introducing song in each context. Box plots represent medians and inter-quartile ranges. One extreme value was omitted from the graph but not the analyses. Numbers in white boxes are n values. Differing letters denote significant differences.

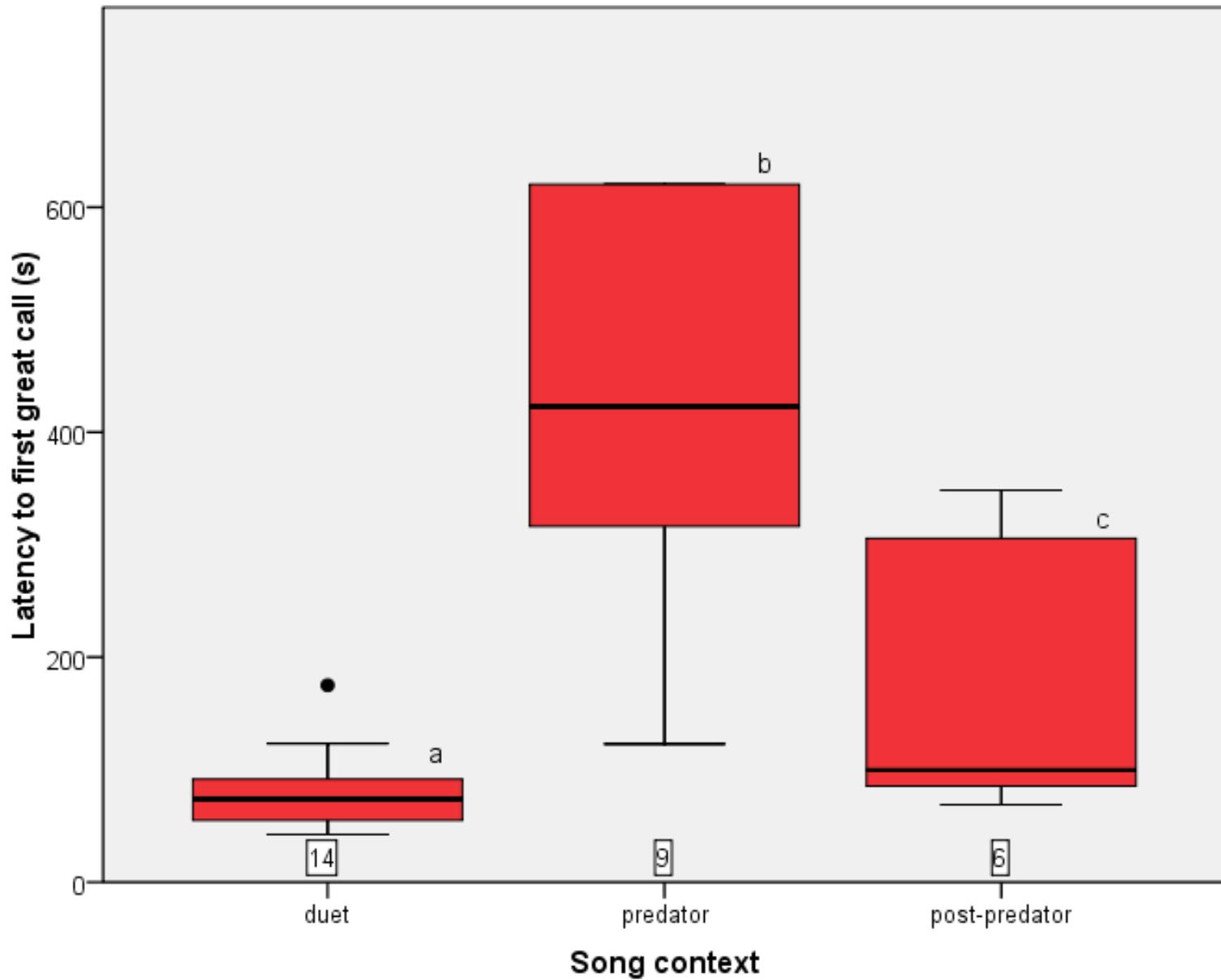


Figure 37. Latency to first female great call in the different song contexts. Box plots represent medians and inter-quartile ranges. Two extreme values were omitted from the graph but not the analyses. Numbers in white boxes are n values. Differing letters denote significant differences.

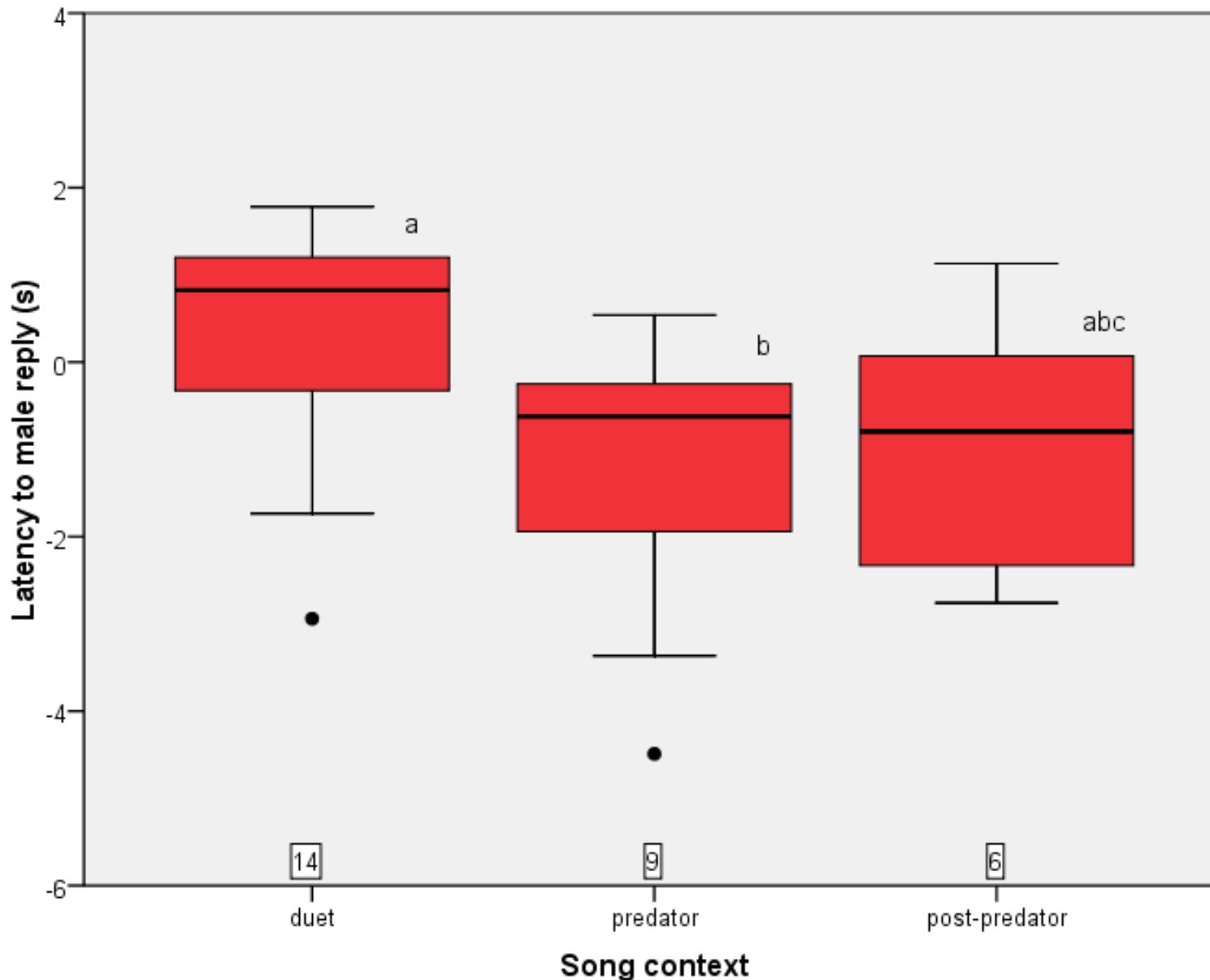


Figure 38. Latency to male reply after female great call in the different song contexts. Box plots represent medians and interquartile ranges. One extreme value was omitted from the graph but not the analyses. Numbers in white boxes are n values. Differing letters denote significant differences.

## **Conspecific responses to gibbon songs**

Sometimes, some individuals spend time away from the rest of the group. This happened on three occasions during clouded leopard model presentations (group H: primary adult male; group J: secondary adult male; group N: sub-adult male). In all cases, the absent individual responded with his own songs after hearing the groups' songs to the predator models, before reappearing to join the group again. This behaviour was never observed when the adult pair gave duet songs, despite the fact that in some groups the second males were often absent as well, suggesting that these individuals distinguished predator-induced from normal songs. During four other predator trials, a neighbouring group began to sing after the commencement of the study group's singing. Analyses of the structure of these calls with regards to two indicators of predator-induced songs: the presence of sharp wows and the delay of the female great call beyond two minutes, revealed that all response songs contained sharp wow notes ( $n=7$ ), suggesting that recipients perceived them as being given in response to a ground predator. In addition, in two of four neighbouring groups, the first female great call was delayed beyond the critical two-minute threshold, further suggesting that these groups perceived and responded to the songs of their neighbours with the correct matching songs.

A small number of songs that were given in response to the regular duets by a neighbouring group ( $n=4$ ) were also analysed. As predicted, in all cases, the first female great call was delivered during the first two minutes, indicating a normal duet context, and sharp wow notes were never recorded. Table 13 summarises the main results.

Table 13. Recipients' responses to predator-induced songs and duet songs.

Context	Focal group	Recipient	Sharp wows	Latency to 1 <sup>st</sup> great call*
Clouded leopard	B	Group A	present	883.9
Clouded leopard	N	Group H	present	35.7
Tiger	W	Group N	present	479.8
Snake	N	Group H	present	105.3
Clouded leopard	H	AM, Felix	present	---
Clouded leopard	J	AM2, Frodo	present	---
Clouded leopard	N	AM2, Nithat	present	---
Duet	D	Group ?	absent	48.9
Duet	T	Group ?	absent	65.4
Duet	W	Group S	(absent)	30.0
Duet	T	Group E	absent	41.1

\*Two minutes or more usually delays great calls in predator-induced songs. ()=incomplete recording.

### Post-predator songs

On six out of twenty-six occasions after responding to a predator model (tiger n=9; leopard n=8; snake n=9), the gibbons sang for a second time on the same day. These “post-predator” songs were different from both duet songs and predator songs in a number of ways. First, post-predator songs had significantly less introductory hoos than predator songs (Mann-Whitney U test,  $U=7.0$ ,  $p=0.008$ ,  $n_{\text{predator song}}=11$ ,  $n_{\text{post-predator song}}=6$ ). Secondly and accordingly, these introductory hoos were significantly shorter in duration in post-predator songs than in predator songs (Mann-Whitney U test,  $U=4.0$ ,  $p=0.003$ ,  $n_{\text{predator song}}=11$ ,  $n_{\text{post-predator song}}=6$ ). There were no significant

differences in the introductory hoos between duet songs and post-predator songs however. Thirdly, post-predator songs were significantly more likely to contain sharp wow elements than normal duets (Fisher's Exact Test,  $p=0.042$ ,  $n=20$ ). Fourth, although these post-predator songs contained female great calls like other songs, these were delivered significantly earlier than in a predator song (Mann-Whitney U test,  $U=11.0$ ,  $p=0.005$ ,  $n_{\text{post-predator song}}=6$ ,  $n_{\text{predator song}}=17$ ), but also significantly later than in a normal duet song (Mann-Whitney U test,  $U=18.0$ ,  $p=0.048$ ,  $n_{\text{post-predator song}}=6$ ,  $n_{\text{duet}}=14$ ). Finally, post-predator song contained sharp wows notes, but these were delivered significantly later than the ones found in normal duets (Mann-Whitney U test,  $U=5.0$ ,  $p=0.037$ ,  $n_{\text{post-predator song}}=6$ ,  $n_{\text{duet}}=6$ ). See figures 31 to 35. It is also worth noting that for three of the six post-predator song bouts, gibbons returned to the exact predator location to sing.

## ***Discussion***

Gibbon songs are of great interest because, aside from human speech, these vocalisations provide a remarkable example of acoustic sophistication and versatility in primate communication. Individuals combine a finite number of call units into structurally more complex sequences in rule-governed ways, illustrating a simple form of phonological syntax. These calls then function to convey different contextual situations. Field experiments revealed that white-handed gibbons of Khao Yai National Park, Thailand, were able to produce structurally different types of songs in the predator and duet contexts with the following differences.

First, significantly more hoo notes introduced predator-induced songs than duet songs. Second, overall song duration was longer in the predator context than in

the duet context. Third, the first female-specific great call was significantly delayed in a predatory song, although the acoustic structure of this phrase did not seem to differ between contexts. This suggests that the great calls' ontogeny and most important function is within the duet song. Fourth, males replied earlier to female great calls in the predation context than in duets, perhaps because of their reduced function in predator song. The absence of female great calls during the early part of a song, and hearing the male's hurried reply, in other words, are reliable indicators that the callers are singing in response to a ground predator. Fifth, predatory songs contained a smaller number of leaning wa notes and a higher number of hoo notes, than duet songs. The absence of leaning was and presence of hoos in the initial parts of a song, in other words, could function as further reliable early indicators of a predator encounter. This sequential analysis revealed that although note elements in predator and duet songs were identical, their arrangement was highly dependent on context. Notes were combined in predictably different ways, for example predator songs always nested several hoo notes among the other notes, whereas duet songs included much fewer and surrounded them with leaning wa notes. Finally, songs given to predators invariably contained sharp wow notes, while duet songs usually did not. If sharp wows were present in duets, then this was only in groups that were not well habituated to human observers (D, J, NOS; see table 9), suggesting that these duet songs encoded the presence of a human observer. In all other aspects, these songs were identical to normal duet songs, for example, the female great call appeared within the first two minutes and the male reply was normal, and the songs were not introduced by a series of quiet hoo notes. It was also observed that duet-based sharp wows were given earlier in the song than the ones that were part of the predator songs, making this note a particularly interesting candidate to convey information regarding environmental events and further illustrating the remarkable

flexibility underlying gibbon calling behaviour, not unlike that described for some passerine birds. Playbacks of gibbon predators and heterospecific alarm calls did not evoke the same kinds of vocal responses as the visual models. On two occasions, playbacks did elicit song though, and in both cases the songs began with quiet hoos, delayed the first great call until after the first two minutes, and contained sharp wow notes, all hallmarks of typical ground predator song. These two songs were however somewhat shorter than the visual predator songs, quite possibly because the length of exposure was significantly shorter: playbacks were just fifteen seconds in length, whereas visual models were displayed for twenty minutes at a time. This dichotomy could explain why gibbons seldom responded to playbacks at all. Differential responses to visual and acoustic representations of predators are further discussed in chapter 6.

Gibbon songs are highly complex acoustic structures, and it may well be possible that other important acoustic cues were overlooked. Whatever the perceptually relevant cues, observations also demonstrated that neighbouring groups were able to differentiate between songs given in the two contexts. In particular, a predator-specific delay in the production of the first great call was observed, as well as the inclusion of sharp wow notes in all cases in which neighbours responded to the predator-induced song. These patterns were never observed in the response songs of neighbours to normal duets. In all observed cases, absent males began to sing while returning to the rest of the group. Again, such behaviour was never observed during normal duets. The returning males' songs always included sharp wow notes, a convincing sign that they understood the meaning of the song produced by their group.

In addition, six post-predator songs were recorded, which in structure appeared to be intermediate between a typical predator song and a typical duet song. Strikingly, on three of the six occasions, the gibbons returned to the location of predator presentation to sing. These songs illustrate an extraordinary vocal plasticity: an ability to tailor different songs to suit different situations: something that has also been found in other primates (Brumm et al. 2004). In addition, gibbons exhibited the ability to recall a predator event and the exact location it occurred, which was on average some 45 minutes later. It may be beneficial for gibbons to revisit a prior predator location to ensure that the predator is no longer there and to alert the predator to their continued vigilance. The ability to connect an event with a precise location also suggests that gibbons possess a detailed mental representation of their environment similar to the cognitive maps that other primates use to avoid encounters with neighbouring conspecifics (Noser and Byrne 2004) and collect and reuse tools (Boesch and Boesch 1984).

Why did gibbons produce songs in response to ground predators? Chapter 4 describes two possible functions: firstly kin selection, that is, to alert related conspecifics to the presence of a predator (Maynard-Smith 1965; Tenaza and Tilson 1977). The gibbons at Khao Yai frequently change group compositions, and as a result, close relatives often live in neighbouring groups. For example, members of groups A and B are closely related, perhaps explaining group A's strong response to group B's song to the clouded leopard model. However, this may also have been a product of showing the model at an overlapping segment of both groups' home ranges, and/or that group A happened to be foraging nearby at the time of presentation. Either way their avid response may still have been designed to signal directly to the predator, supporting the second possible function of predator songs: pursuit-deterrence. In the case of large cats, empirical work has

shown that primate alarm calls and mobbing vocalisations have a direct deterring effect on hunting behaviour (Zuberbühler et al. 1999); loud vocalisations may irritate a predator as well as inform it of its detection, both of which may act to discourage pursuance of prey. This perhaps explains why it is adaptive to produce loud songs when hearing a neighbouring group singing to a predator also. Chapter 4's data on naturally occurring predator songs suggested that their main function was in fact predator deterrence, since they did not necessarily provoke singing from neighbouring groups that contained kin of the target group. This study too showed that neighbours did not always respond to a predator song. Interestingly when they did, response songs demonstrated an obvious understanding of the target groups' song, and established that predator songs did inform conspecifics about predator encounters, even if that were not their original purpose. Actually, gibbon song probably functions to do both: alert kin and deter predation. The quiet hoo note series, which reliably precedes a predator song, could announce to immediate group members the presence of a predator, and the louder, high frequency singing including piercing sharp wow notes, could act to bombard and harass a nearby predator, signaling its detection and confirming the futility of further hunting attempts. Another interesting finding was that the gibbons did not produce songs to raptor models, although other types of alarm calls are produced to real raptors and models, a topic of ongoing research (see chapter 7 for analysis of raptor response vocalisations).

Not unlike humans, gibbons assemble a finite number of basic call units into structures that are more complex in order to convey different messages. These are audible over long distances through dense vegetation, and the data presented here show that distant individuals are able to distinguish between different song types. This study thus offers first evidence of a functionally referential communication

system in a free-ranging ape species, which is entirely based on combinatorial rules.

These data could be supported by further research. Firstly, more snake responses are needed so that they can be compared with cat and raptor responses and potentially classified as acoustically distinct calls. This would also provide opportunity to test a theory that snake song is tailored to the snake hearing range, cat song is tailored to cat hearing range and that raptor hoots are designed to escape the hearing range of raptors (see also chapter 6). This is based on the idea that pursuit-deterrant signals are better aimed at ambush predators who rely on surprise, whereas cryptic signals are better used on sit-and-wait predators who can potentially move unnoticed through the forest. Second, all predator songs should be used in playback experiments; an elegant way to delve inside the minds of receivers, these procedures would provide further evidence for a functionally referential system of communication. This could also provide opportunity to measure receivers' response latencies more closely to better decipher which elements in the predator song first elicit response, and are therefore the most important carriers of semantic information. As a potentially interesting aside to this, songs could be experimentally altered to increase and/or decrease the number of salient units in the opening sequences of songs, such as the leaning wa and hoo notes. Could a duet song be turned into a predator song and vice versa based on alterations of initial song segments? The sharp wows also lend themselves to this kind of manipulation. Their presence in a song seems to indicate disturbance and could be used to transform an otherwise normal duet into an indicator of human attendance, or signal another type of predator encounter. Similarly, great call latency in a song seems to signal whether or not a predator is present. Carefully controlled manipulations of these song elements would allow the discernment of

optimally relevant notes, phrases or arrangements in communicating about these important events.

# **CHAPTER 6. Behavioural responses to predator models**

(Responses to visual predator models is submitted for publication)

## ***Abstract***

To investigate the role of predation in gibbons, and to study their anti-predator behaviour, visual and acoustic predator models were presented to thirteen groups of wild white-handed gibbons. Their responses were measured to four potential predators: tiger, clouded leopard, crested serpent eagle and reticulated python. Responses were generally more vigorous to visual than acoustic predator models. Subjects reliably approached all four predators. In response to tigers and leopards, they additionally produced predator-specific songs, defecated, and group cohesion increased. In response to eagles and pythons, gibbons also produced vocalisations, but this did not always include singing. Potential long-term effects of these simulated predator encounters were also monitored, but did not reveal any differences in overall activity or strata use. This study demonstrates that gibbons discriminate between different potential predators and respond to them with adaptive anti-predator behaviours, which include predator-specific vocal responses.

## ***Introduction***

Surprisingly little is known about the role of predation on gibbon evolution despite the fact that they have been studied in the wild for decades (Carpenter 1940). Similar sized monkeys are well within the prey spectrum of most large cats, eagles and snakes

(Gursky 2006). However, gibbons may be better protected from predation than other groups of primates with comparable body and group sizes due to their highly specialised rapid locomotion and preference for the high canopy. At Khao Yai National Park, Thailand, lar gibbons interact with ten potential predator species, see table 7 (Uhde and Sommer 2002). The same study also showed that estimated predation rates were very low, with few direct observations or indirect evidence of predation. Yet, evidence suggests that predation does affect gibbon behaviour (chapters 3, 4 and 5).

Gibbon songs possess an important function during predator encounters (Ellefson 1974; Uhde and Sommer 2002). Chapter 5 has demonstrated that predator songs produced by white-handed gibbons are different from regular duet songs in a number of consistent ways, especially with regards to the structural arrangement of the different song units. Anecdotal observations further suggested that after predator encounters gibbons increase group cohesion, sometimes engage in mobbing, and decrease foraging behaviour (Uhde & Sommer 2002).

In order to systematically investigate gibbon anti-predatory behaviour, a series of experiments were conducted that simulated real predator encounters. Both visual and acoustic predator models were used, by presenting live-sized predator dummies or by playing back recordings of typical predator vocalisations, respectively. Both immediate and long-term effects of a predator encounter were of interest, since both have significant adaptive consequences. Empirical studies with free-ranging monkeys have revealed that most species that have been tested possess a number of predator-specific defence responses. For example, savannah-living vervet monkeys (*Cercopithecus aethiops*) run into cover or descend a tree when an eagle flies overhead, or they climb into a tree if a leopard is in the vicinity (Struhsaker 1967;

Cheney and Seyfarth 1992). Likewise, Diana monkeys (*C. diana*) respond with temporary cryptic behaviour to the arrival of predatory chimpanzees or they generate conspicuous vocal and locomotor behaviour to a hiding leopard (Zuberbühler 2000).

At Khao Yai National Park, primates interact with aerial, terrestrial and arboreal predators. If predation risk is considerable for gibbons then predator encounters should increase group cohesion, vigilance, and scanning behaviour, but decrease routine activities such as foraging or social behaviour. Depending on the predator type, gibbons are expected to use different parts of the vertical strata use (for example, low canopy following exposure to an eagle model). Learning about the presence of a predator in the visual or acoustic mode may also generate different responses as seen in chapter 5. Both are salient cues of predator presence and both reliably elicit alarm calls in other primates (Zuberbühler 2001), but a vocalising predator is unlikely to be hunting, and this may warrant a different set of anti-predator behaviours.

## **Methods**

### **Study site and subjects**

See chapter 3 for a full description of the study site and subjects.

### **Immediate and long-term behavioural effects of predator encounters**

The types of behavioural responses measured to assess immediate effects of predator encounters are detailed in table 14. Predator-specific long-term behavioural effects are a good indicator that individuals have some knowledge about their predators' behaviour. Some predators may remain in an area for several days, and increased vigilance and other anti-predatory behaviours may be warranted for extended periods. Changes in vertical strata use and group cohesion may also be affected. Therefore a

series of basic behavioural effects were collected, some of which are part of their anti-predatory behaviours.

Table 14. Behavioural variables used to measure immediate and long-term effects of model predators.

Behaviour	Definition
Grooming	Cleaning fur using hands or mouth; includes both auto- and allo-grooming
Moving	Locomotor travel within a tree
Travelling	Locomotor movement between trees
Feeding	Cessation of locomotor movement and placing items in the mouth and chewing
Vocalising**	Engaging in the vocal production of sound; includes quiet and loud calls
Resting	Reclining, or sitting doing nothing with eyes closed
Playing	One or more individuals engage in chase behaviour or tickle and play bite; accompanied by “play face”: a relaxed open-mouthed grin
Sitting and Hanging	Sit or hang on a substrate excluding all other behaviours, (Uhde & Sommer, 2002)
Vigilant: Fixing**	Staring intently at a fixed point in space (the model) for at least five seconds
Vigilant: Scanning**	Attention directed at the inanimate environment; The head must rotate to the left and/or right by at least 45 degrees. A ‘sweeping motion of the head’ (Koenig, 1998)
Copulating	Engaging in sexual intercourse
Defecating**	Exuding faeces and/or urine
Looking*	Orienting head and/or body towards the stimulus
Branch shaking/breaking*	Any branch seen actively shaken by an individual during stimulus presentation and/or any branch fall during stimulus presentation;
Approach*	When the gibbons actively move towards the stimulus
Flee*	When the gibbons, upon detection of the stimulus, move away rapidly or seek cover; They may jump to a higher substrate, or drop to a lower one, move towards an adult or centre of tree top (Uhde & Sommer, 2002)
Remain or move away*	Remain in or move away from vicinity immediately after stimulus has been removed
Drop in canopy height*	A marked lowering in height - of approximately five metres or more -- during stimulus presentation
Other	Any other behaviour not described above

Behaviours marked with a single asterix (\*) are those that were measured for immediate effects, those marked with a double asterix (\*\*) are those that were measured for both immediate and long-term effects; all others were measured for long-term effects.

## **Data collection**

Data were collected from April 2004 to July 2005. Behavioural observations of immediate effects were recorded using one-zero sampling when performed by any individual in the group. If a behaviour occurred repeatedly, such as defecations and branch drops, exact counts were recorded. Changes in location in relation to the playback stimulus were estimated in metres. Long-term effects were assessed using focal animal sampling every five minutes. Scan samples of height and distance between adults were taken every ten minutes. Focal animals were the adult males or females of a mated pair; each was sampled for one hour before and one hour after stimulus presentation. The order of sampling was random.

## **Visual and acoustic predator models**

Figure 29 to 31 in chapter 5 show all the visual and acoustic stimuli. For a detailed methodology of these experiments, also see chapter 5.

## **Data analyses**

Statistical analyses were conducted with SPSS v.12 using non-parametric testing (Friedman's, Wilcoxon signed ranks, Cochran's Q, Mann-Whitney U and Fisher's exact statistical tests). All tests were conducted at the 0.05 level, except if multiple comparisons necessitated a Bonferroni correction. In these cases, the critical level was determined by the number of comparisons made.

## **Results**

### **Immediate responses to visual predator models**

#### *Defecations*

There were significant differences in the number of defecations across predator stimuli (Friedman's test, chi-square=11.4, df=3, p=0.010, n=6). Post hoc, Bonferroni corrected, Wilcoxon tests revealed significantly more defections to the leopard than the control model, ( $Z=-2.4$ ,  $p=0.016$ ,  $n=8$ ) and significantly more defecations to the snake than the control model, ( $Z=-2.2$ ,  $p=0.025$ ,  $n=8$ ).

The tiger model was excluded because there were not enough matching groups. No other significant effects were found.

#### *Branch shaking/dropping*

There were no significant differences in how often branch dropping was observed to the different predator stimuli: (Friedman's test, chi-square=6.0, df=3, p=0.112, n=6).

The eagle was excluded from this Friedman test because there were not enough matched eagle groups. A separate set of Wilcoxon tests showed no significant differences between the eagle and the other conditions.

#### *Vigilance*

Gibbons were significantly more likely to show vigilant behaviours, such as fixing and scanning, to a predator model than the control model ( $Q=20.0$ ,  $p<0.001$ ,  $df=4$ ,  $n=5$ ; control vs. tiger:  $p=0.008$ ,  $n=8$ ; control vs. leopard:  $p=0.008$ ,  $n=8$ ; control vs. snake:  $p=0.008$ ,  $n=8$ , control vs. eagle:  $p=0.063$ ,  $n=5$ ).

### *Drop in canopy height*

Gibbons were more likely to drop in canopy height when the leopard or eagle model was displayed than when a control model was shown ( $Q=13.8$ ,  $p=0.008$ ,  $df=4$ ,  $n=5$ ).

### *Distance moved*

Gibbons moved significantly further after seeing a tiger model than after seeing a leopard model, (Wilcoxon test,  $Z=-2.2$ ,  $p=0.028$ ,  $n=6$ ); all other comparisons were not statistically significant. However, there were a number of instances where data were collected from non-matched groups. Here unrelated-samples Mann-Whitney U tests were conducted, revealing some further effects of model type as follows. Gibbons moved significantly further after seeing the tiger model than the control model, ( $U=0.0$ ,  $p=0.003$ ,  $n_{\text{tiger}}=7$ ,  $n_{\text{control}}=5$ ), and they moved further after seeing the tiger than the eagle model, ( $U=4.5$ ,  $p=0.030$ ,  $n_{\text{eagle}}=5$ ,  $n_{\text{tiger}}=7$ ), although the effect was no longer significant after a Bonferroni adjustment. All other comparisons were not statistically significant.

### *Vocal behaviour*

Cochran's Q matched samples tests were used to determine whether the proportion of groups exhibiting several other behaviours was the same across the different predator conditions. These tests showed some highly significant differences in the *song response* ( $Q=23.4$ ,  $p<0.001$ ,  $df=4$ ,  $n=7$ ) and *hoo response* ( $Q=11.8$ ,  $p=0.019$ ,  $df=4$ ,  $n=6$ ). Post hoc McNemar tests with Bonferroni corrected alpha levels showed that gibbons were significantly more likely to respond with singing to the ground predator models compared with the control model (control vs. tiger:  $p=0.008$ ,  $n=8$ ; control vs. leopard:  $p=0.008$ ,  $n=8$ ). They were also significantly more likely to sing to the tiger or leopard model than the eagle model ( $p=0.016$ ,  $n=7$  for both). They were more

likely to give just hoos to the eagle model than the tiger or leopard model, although not significantly so after a Bonferroni correction ( $p=0.031$ ,  $n=7$  for both).

#### *Predator inspection*

There were no significant differences in how close gibbons got to the different predator models during presentation (Friedman's test, chi-square=1.1, df=2,  $p=0.568$ ,  $n=6$ ). The tiger and eagle conditions were excluded from this analysis because of small sample sizes ( $n=1$ ,  $n=4$  respectively).

Figures 39 to 42 provide summary information on the different anti-predator responses observed in the study groups.

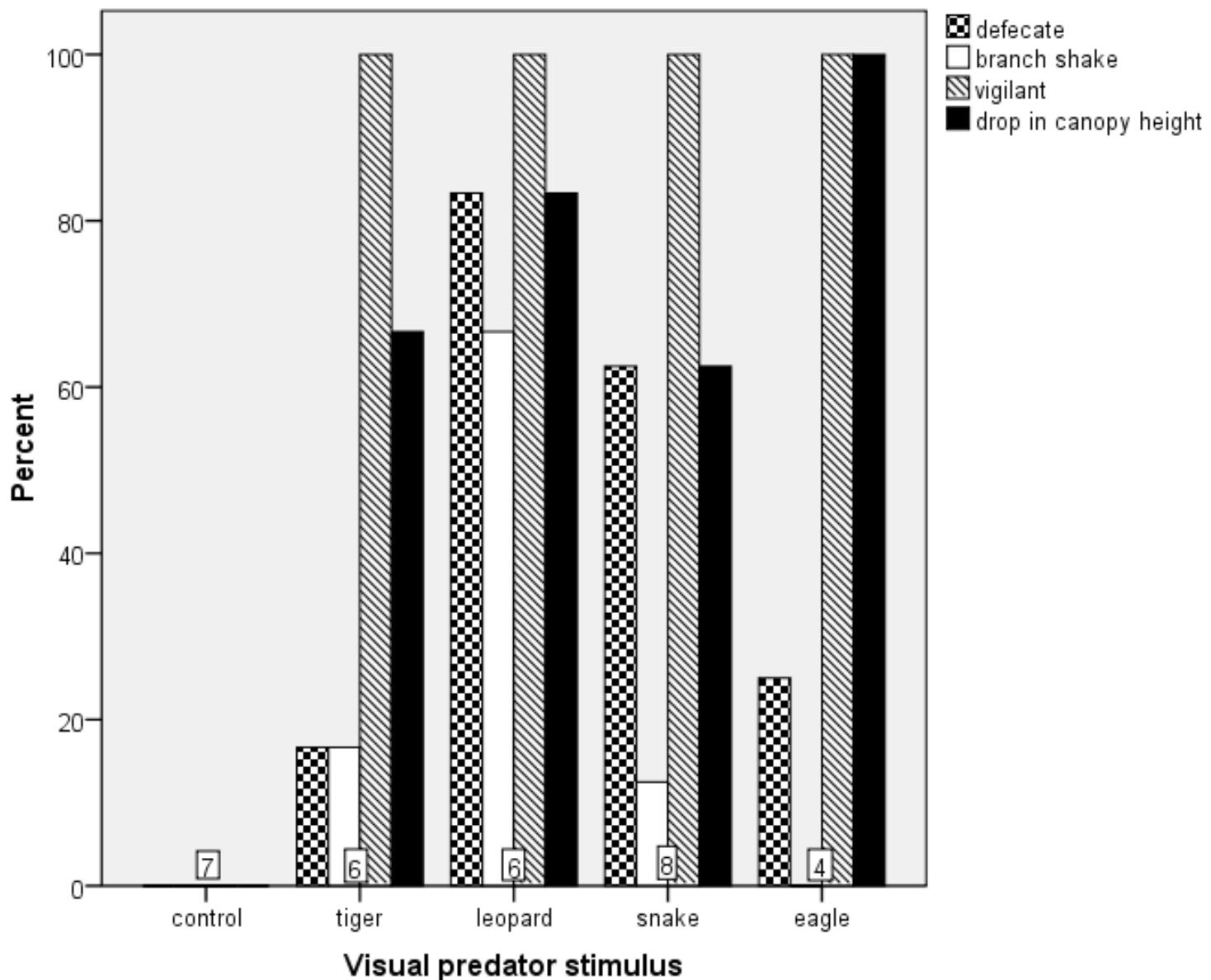


Figure 39. The percentage of trials in which different anti-predator behaviours were recorded in response to the different visual predator stimuli.

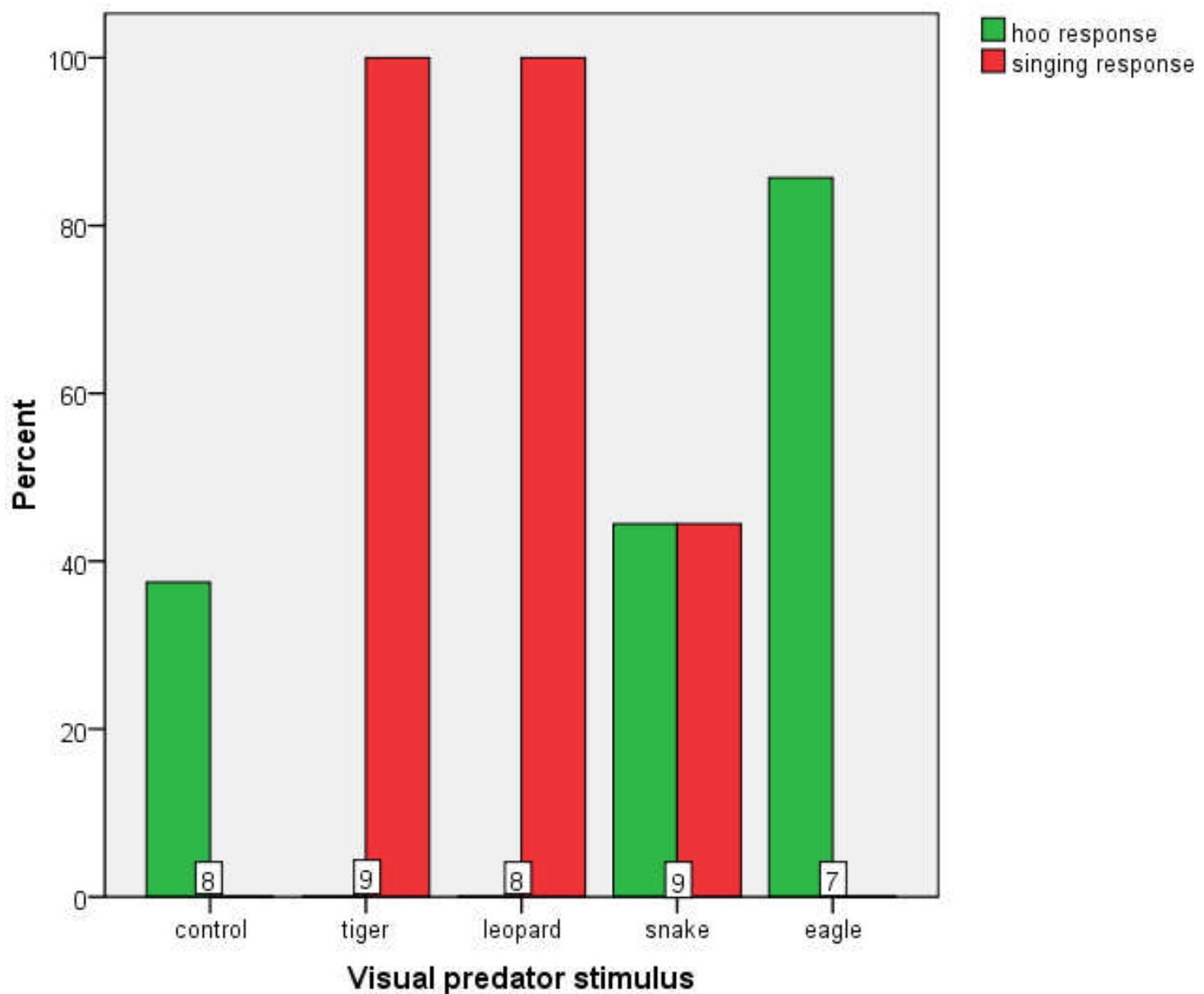


Figure 40. Percentage of trials in which a song or hoo response was recorded to the different visual predator stimuli.

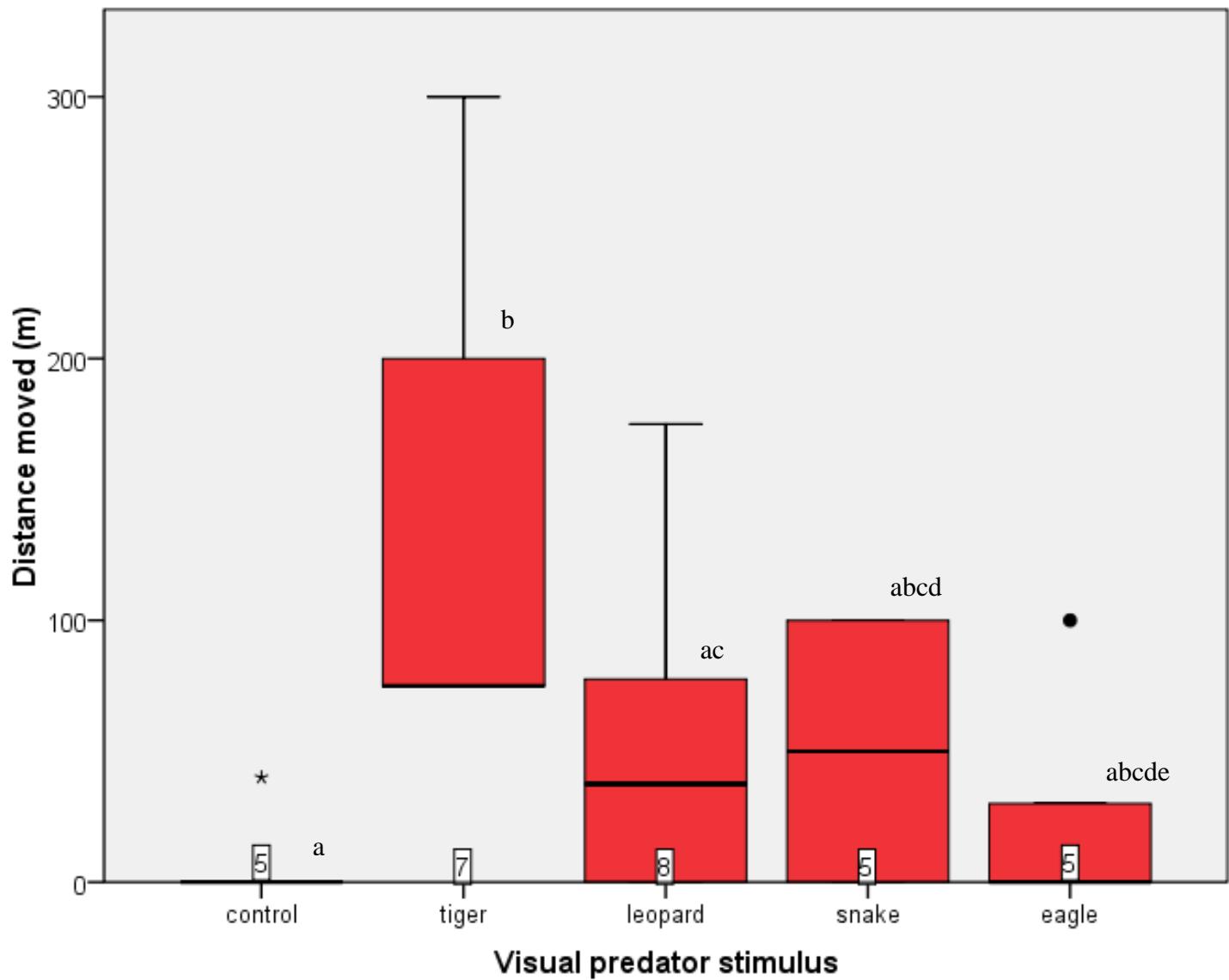


Figure 41. Median distance the different groups moved away from the site of predator presentation after presentation had ended. Box plots and whiskers represent medians and inter-quartile ranges. Numbers in boxes represent n values. Differing letters denote significant differences.

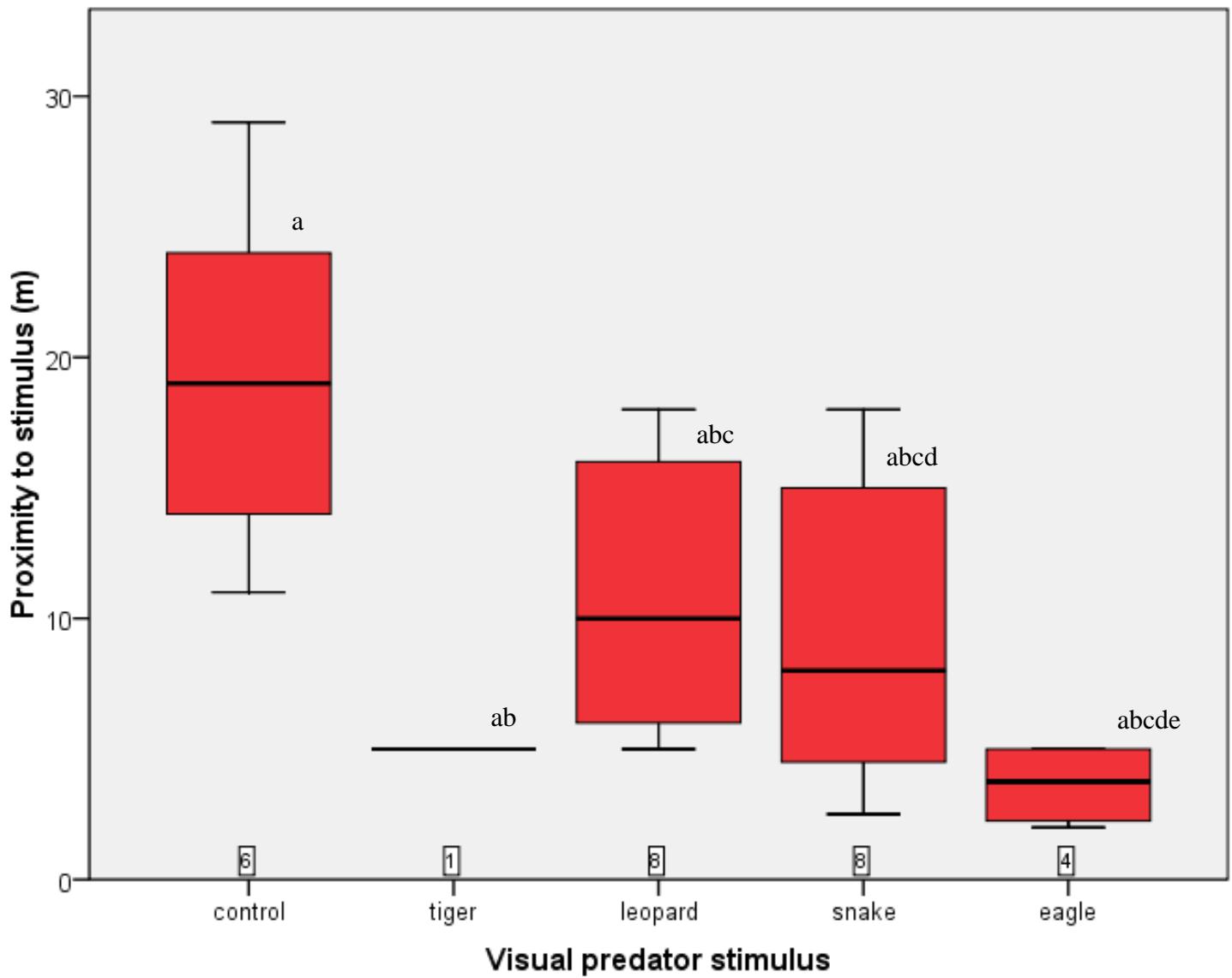


Figure 42. Predator inspection as measured in distance of the nearest group member to the predator model during presentation. Box plots represent medians and inter-quartile ranges. Numbers in boxes represent n values. Letters show no significant differences between contexts.

### Immediate responses to acoustic predator models

#### *Defecations*

A matched sample Wilcoxon test showed there were no significant differences in the number of defecations to the tiger playback and the deer after tiger playback ( $Z=-1.0$ ,  $p=0.317$ ,  $n=9$ ). Where there were not enough matched samples, a Mann-Whitney U test showed there were also no significant differences in defecation number between

the deer playback and the deer after the tiger playback ( $U=22.5$ ,  $p=1.000$ ,  $n_{deer}=5$ ,  $n_{deer after tiger}=9$ ). Small sample sizes prevented further comparisons.

### *Branch shaking/dropping*

There were no significant differences in the number of branches dropped between the tiger playback and the deer after tiger playback (Matched-samples Wilcoxon test,  $Z=0.0$ ,  $p=1.000$ ,  $n=9$ ). A separate Mann-Whitney U test on the remaining valid cases that were not matched samples revealed no significant difference in branch drop number between the deer playback and the deer after tiger playback ( $U=22.5$ ,  $p=1.000$ ,  $n_{deer}=5$ ,  $n_{deer after tiger}=9$ ). Other stimuli sample sizes were too small to conduct analyses.

### *Vigilance*

A matched-sample McNemar test showed there were no significant differences in vigilance behaviours observed between the tiger playback and the deer after the tiger playback ( $p=1.00$ ,  $n=6$ ). Where there were not enough matched samples, a Kruskall-Wallis test was conducted for three of the remaining stimuli, which revealed no significant differences ( $\chi^2=2.8$ ,  $df=2$ ,  $p=0.251$ ,  $n_{deer playback}=5$ ;  $n_{tiger playback}=8$ ;  $n_{deer after tiger playback}=7$ ). Other comparisons were not possible due to small sample sizes, figure 43.

### *Vocal behaviour*

McNemar matched-samples tests revealed no significant differences in whether the gibbons gave *hoo responses* to several different stimuli pairs as follows: tiger playback versus deer after tiger playback ( $p=1.000$ ,  $n=9$ ); leopard playback versus deer after leopard playback ( $p=1.000$ ,  $n=5$ ); leopard playback versus deer playback ( $p=1.000$ ,  $n=5$ ), and deer playback versus deer after leopard playback ( $p=1.000$ ,  $n=5$ ).

Similarly, McNemar matched-samples tests showed no significant differences in whether gibbons gave *song responses* to any of the following stimuli pairs: deer playback versus deer after leopard playback ( $p=1.000$ ,  $n=5$ ); tiger playback versus deer after tiger playback ( $p=1.000$ ,  $n=10$ ); leopard playback versus deer after leopard playback ( $p=1.000$ ,  $n=5$ ), and deer playback versus leopard playback where neither stimuli ever elicited singing. Gibbons only engaged in singing as a response to the playback stimuli on two occasions: once in response to a tiger playback and once in response to a barking deer that followed a clouded leopard playback, figure 44.

#### *Proximity change*

A matched-samples Wilcoxon test showed there were no significant differences in proximity change after hearing the tiger playback versus hearing the deer after tiger playback ( $Z=-0.3$ ,  $p=0.786$ ,  $n=7$ ). Other comparisons could not be made due to small sample sizes.

Tables 15 through 26 contain the raw data used for all of the above analyses.

Table 15. The number of defecations in response to the visual predators.

Group	Number of defecations				
	Control	Tiger	Leopard	Snake	Eagle
B	0	?	1	1	0
C	0	0	3	0	0
D	0	?	1	1	1
H	0	1	0	0	0
J	0	0	1	1	0
N	0	0	2	1	
R	0	?	2	0	?
T		1		1	
W	0	0	3	1	0
Median	0.0	0.0	1.5	1.0	0.0
Mean	0.0	0.3	1.6	0.6	0.2
N value	8	6	8	9	6

?=unknown, blank=not tested.

Table 16. The number of branch drops in response to the visual predators.

Group	Number of branch drops				
	Control	Tiger	Leopard	Snake	Eagle
B	0	0	1	0	0
C	0	0	1	0	0
D	0	?	5	0	0
H	0	0	0	0	?
J	0	0	0	0	0
N	0	?	0	0	
R	0	0	0	2	?
T		0		0	
W	0	0	1	0	0
Median	0.0	0.0	0.5	0.0	0.0
Mean	0.0	0.0	0.9	0.2	0.0
N value	8	7	8	9	5

?=unknown, blank=not tested.

Table 17. The distance moved after presentation with visual predators.

Group	Distance moved after presentation (m)				
	Control	Tiger	Leopard	Snake	Eagle
B	?	Lost group	175	0	?
C	40	100	0	50	100
D	?	75	55	15	0
H	0	75	0	0	?
J	0	0	0	30	0
N	?	75	Lost group	25	
R	0	Lost group	100	100	30
T		75		?	
W	0	300	50	100	0
Median	0.0	75.0	50.0	27.5	0.0
Mean	8.0	100.0	54.3	40.0	26.0
N value	5	7	7	8	5

?=unknown, blank=not tested, Lost group=group moved far enough away that we lost them.

Table 18. The closest proximity any gibbon had to the visual predators.

Group	Closest proximity (m)				
	Control	Tiger	Leopard	Snake	Eagle
B	?	?	6	4	5
C	14	?	5	15	2
D	?	?	6	5	?
H	29	?	10	15	?
J	24	?	10	10	?
N	24	?	15	6	
R	14	?	18	2.5	5
T		5		?	
W	11	?	17	18	2.5
Median	19.0	5.0	10.0	8.0	3.8
Mean	19.3	5.0	10.9	9.4	3.6
N value	6	1	8	8	4

?=unknown, blank=not tested.

Table 19. The occurrence of vigilant behaviours in response to visual predators.

Alert/vigilant response					
Group	Control	Tiger	Leopard	Snake	Eagle
B	0	1	1	1	?
C	0	1	1	1	1
D	0	1	1	1	1
H	0	1	1	1	1
J	0	1	1	1	1
N	0	1	1	1	
R	0	1	1	1	?
T		1		1	
W	0	1	1	1	1
Percent	0.0	100.0	100.0	100.0	100.0
N value	8	9	8	9	5

1=yes, 0=no, ?=unknown, blank=not tested.

Table 20. The occurrence of a drop in height response to the visual predators.

Drop in height					
Group	Control	Tiger	Leopard	Snake	Eagle
B	?	1	1	1	?
C	0	0	1	0	1
D	0	1	1	1	1
H	0	1	1	1	1
J	0	1	1	0	1
N	0	1	?	1	
R	0	?	?	1	?
T		1		?	
W	0	0	1	0	1
Percent	0.0	67.0	100.0	63.0	100.0
N value	7	9	6	8	5

1=yes, 0=no, ?=unknown, blank=not tested.

Table 21. The occurrence of a singing response to visual predators.

Song response					
Group	Control	Tiger	Leopard	Snake	Eagle
B	0	1	1	1	0
C	0	1	1	0	0
D	0	1	1	1	0
H	0	1	1	0	0
J	0	1	1	0	0
N	0	1	1	1	
R	0	1	1	1	0
T		1		0	
W	0	1	1	0	0
Percent	0.0	100.0	100.0	44.0	0.0
N value	8	9	8	9	7

1=yes, 0=no, ?=unknown, blank=not tested.

Table 22. The occurrence of a hoo response to visual predators.

Hoo response					
Group	Control	Tiger	Leopard	Snake	Eagle
B	1	0	0	0	1
C	1	0	0	1	No vocals
D	No vocals	0	0	0	1
H	No vocals	0	0	1	1
J	1	0	0	1	1
N	No vocals		0	0	
R	No vocals	0	0	0	1
T		0		1	
W	No vocals	0	0	1	1
Percent	38.0	0.0	0.0	56.0	86.0
N value	8	9	8	9	7

1=yes, 0=no, ?=unknown, blank=not tested.

Table 23. The number of defecations in response to the acoustic predators.

Group	Number of defecations					
	Deer	Tiger	Leopard	Eagle	Deer/Tiger	Deer/Leopard
B	0	?	0	0	?	0
C	0	0	0		0	0
D	0	0	0		0	1
E		0			0	
H		1			0	
J	0		0			0
N		0			0	
R	0	0	?	0	0	?
T		0			0	
W		0			0	
NOS		0		0	0	
Median	0.0	0.0	0.0	0.0	0.0	0.0
Mean	0.0	0.1	0.0	0.0	0.0	0.3
N value	5	9	4	3	9	4

?=unknown, blank=not tested.

Table 24. The occurrence of vigilant responses to the acoustic predators.

Group	Alert/vigilant response					
	Deer	Tiger	Leopard	Eagle	Deer/Tiger	Deer/Leopard
B	1	1	1	0	?	1
C	1	0	1		1	1
D	1	?	1		?	1
E		?			0	
H		1			1	
J	1		1			1
N		0			0	
R	1	1	?	0	0	?
T		1			1	
W		1			1	
NOS	0		0		?	
Percent	100.0	62.5	100.0	0.0	57.0	100.0
N value	5	8	4	3	7	4

1=yes, 0=no, ?=unknown, blank=not tested.

Table 25. The occurrence of singing responses to the acoustic predators.

Song response						
Group	Deer	Tiger	Leopard	Eagle	Deer/Tiger	Deer/Leopard
B	0	0	0	0	0	0
C	0	0	0	0	0	0
D	0	0	0	0	0	1
E	0			0		
H	0			0		
J	0		0			0
N		0		0		
R	0	0	0	0	0	0
T		0		0		
W	1			0		
NOS	0		0	0		
Percent	0.0	10.0	0.0	0.0	0.0	20.0
N value	5	10	5	3	10	5

1=yes, 0=no, ?=unknown, blank=not tested.

Table 26. The occurrence of hoo responses to the acoustic predators.

Hoo response						
Group	Deer	Tiger	Leopard	Eagle	Deer/Tiger	Deer/Leopard
B	1	?	1	No vocals	?	1
C	1	No vocals	1		No vocals	No vocals
D	No vocals	1	1		No vocals	0
E		No vocals			No vocals	
H		1			1	
J	No vocals		No vocals			No vocals
N		No vocals		No vocals		
R	No vocals	1	No vocals	No vocals	No vocals	No vocals
T		No vocals			No vocals	
W		0			1	
NOS		No vocals		No vocals	No vocals	
Percent	40.0	33.0	60.0	0.0	22.0	20.0
N value	5	9	5	3	9	5

1=yes, 0=no, ?=unknown, blank=not tested.

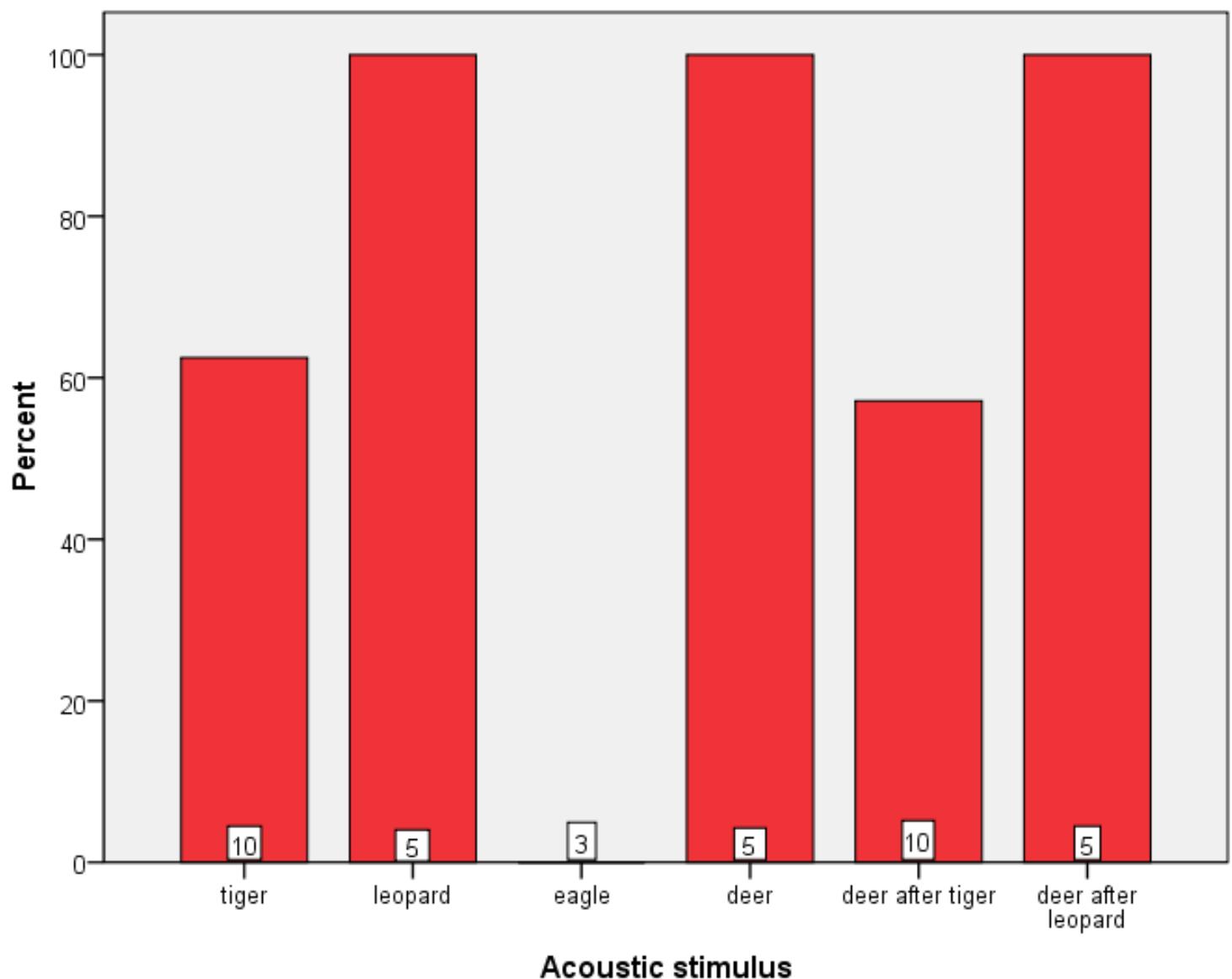


Figure 43. The percentage of trials during which gibbons showed vigilance responses to the different acoustic predator models.

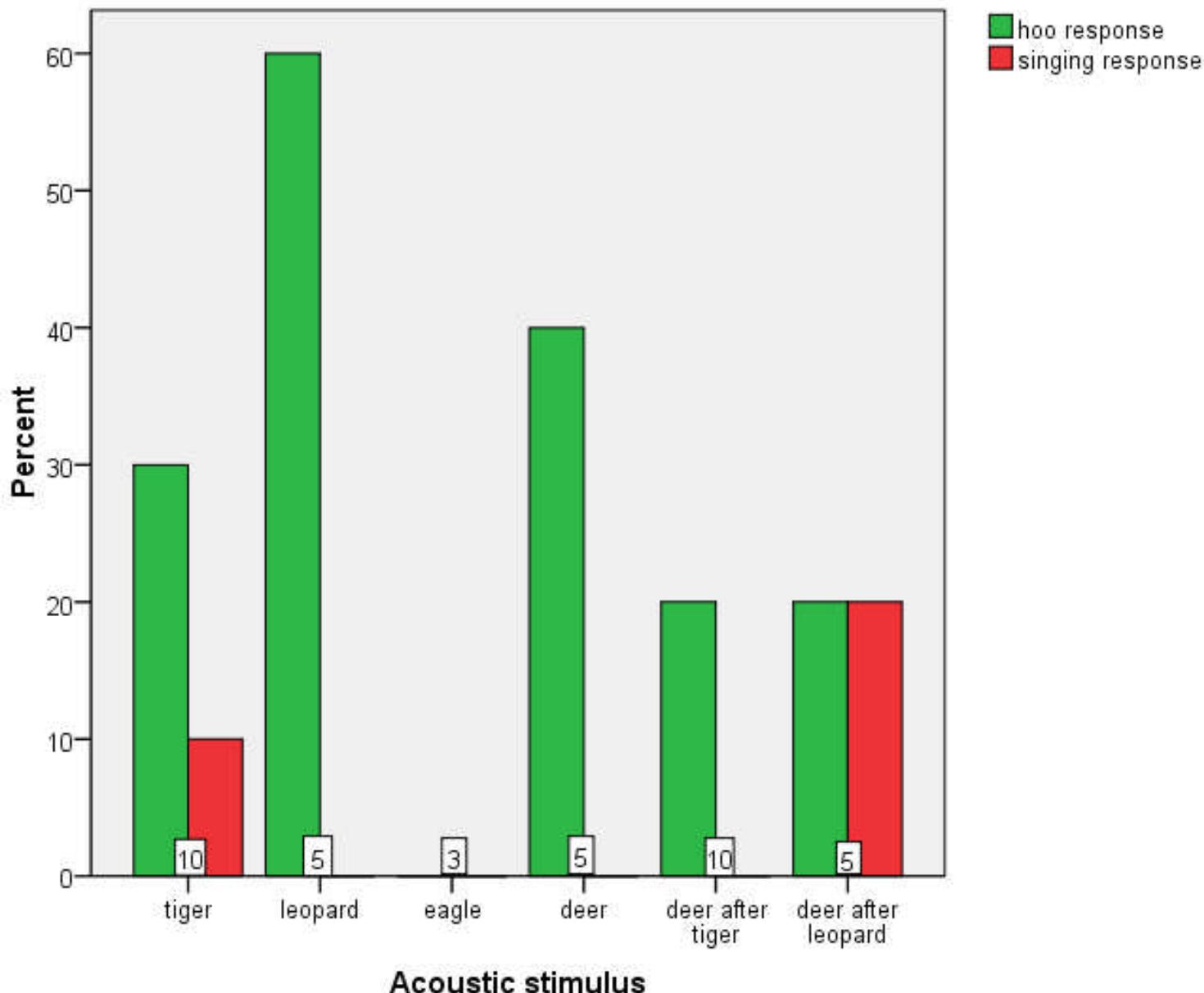


Figure 44. The percentage of trials during which gibbons responded with song and hoo vocalisations to the different acoustic predator models.

### **Comparisons between visual and acoustic stimuli**

#### *Defecations*

Comparisons using Wilcoxon matched-samples tests between the visual and the acoustic predator stimuli revealed no significant differences between the tiger stimuli ( $Z=-1.0$ ,  $p=0.317$ ,  $n=5$ ) or the leopard stimuli ( $Z=-1.9$ ,  $p=0.059$ ,  $n=5$ ).

### *Branch shaking/dropping*

Wilcoxon matched sample tests showed no significant differences in the number of branches dropped in response to either tiger stimulus ( $Z=0.0$ ,  $p = 1.000$ ,  $n=5$ ) or either leopard stimulus ( $Z=-1.6$ ,  $p=0.102$ ,  $n=5$ ).

### *Vocal behaviour*

Where possible, McNemar matched samples tests revealed that gibbons were significantly more likely to sing in response to a visual tiger model than an acoustic tiger model ( $p=0.016$ ,  $n=8$ ); see figure 45. There was no difference in the hoo responses between the two tiger stimuli ( $p=0.250$ ,  $n=7$ ). There was also no difference detected in the song responses between the visual leopard model and the acoustic leopard model ( $p=0.063$ ,  $n=5$ ), despite the fact that gibbons always sang to the visual leopard and never to the acoustic. This is most likely a product of the small matched sample size.

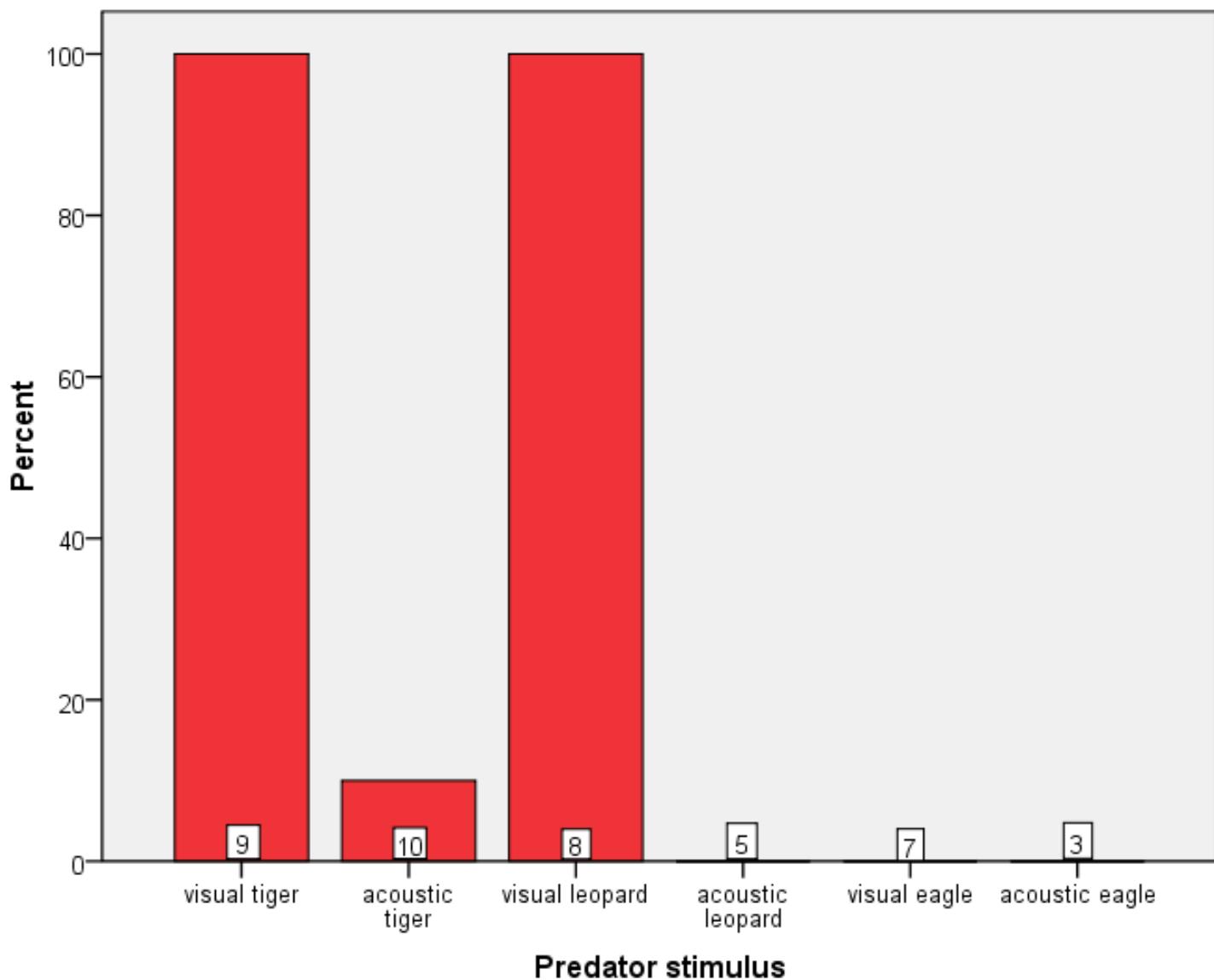


Figure 45. The percentage occurrence of singing in response to visual versus acoustic stimuli.

### **Long-term effects**

#### *Daily activity*

The effects of predator encounters on the gibbons' overall daily activities were also measured. Samples were taken every five minutes one hour before and after detection of a predator model. Then the proportion of times a particular behaviour occurred in the twelve samples taken each before and after exposure was calculated. There were no significant effects. Table 27 summarises the results.

**Table 27.** Average changes in activities after predator model encounters (numbers represent the difference in the average number of samples that occurred out of twelve possible samples for each behaviour before and after model exposure).

Activity	Visual predator model			
	Tiger (n=7)	Leopard (n=3)	Python (n=4)	Control (n=7)
Grooming	-0.09	0.04	0.05	0.02
Moving	-0.01	0.03	0.14	-0.07
Fixing	0.01	0.0	-0.03	0.00
Vocalising	0.06	0.05	0.03	0.08
Resting	0.01	0.0	0.00	0.02
Copulating	0.00	0.0	0.00	0.01
Feeding	-0.09	-0.30	-0.02	-0.05
Scanning	-0.01	0.0	0.00	0.00
Sitting/Hanging	0.07	0.33	0.01	-0.03
Defecating	-0.03	0.0	0.00	0.00
Playing	0.03	0.0	-0.04	0.00
Travelling	-0.01	-0.10	0.06	0.03
Other	-0.01	-0.03	0.00	0.00

#### *Vertical strata use*

Gibbon vertical strata use before and after exposure was measured also. Wilcoxon matched samples tests again revealed no effect of predator exposure (Control: female height:  $Z=-0.3$ ,  $p=0.751$ ,  $n=59$ , male height:  $Z=-0.5$ ,  $p=0.600$ ,  $n=50$ ; Tiger: female height:  $Z=-1.8$ ,  $p=0.070$ ,  $n=49$ , male height:  $Z=-1.6$ ,  $p=0.102$ ,  $n=43$ ; Leopard: female height:  $Z=-0.1$ ,  $p=0.905$ ,  $n=29$ , male height:  $Z=-0.2$ ,  $p=0.842$ ,  $n=15$ ; Snake: female height:  $Z=-0.2$ ,  $p=0.819$ ,  $n=31$ , male height:  $Z=-1.5$ ,  $p=0.125$ ,  $n=20$ ).

### *Group cohesion*

Group cohesion was measured as the inter-individual distance between adult males and females. This distance decreased significantly after seeing the tiger model, but not the other models (Tiger:  $Z=-2.9$ ,  $p=0.004$ ,  $n=25$ ; Leopard:  $Z=-0.3$ ,  $p=0.779$ ,  $n=8$ ; Snake:  $Z=-1.4$ ,  $p=0.173$ ,  $n=7$ ; control:  $Z=-0.2$ ,  $p=0.837$ ,  $n=29$ ; table 28).

Table 28. Average gibbon height and distance (m) between male and female before and after predator stimuli (numbers represent mean male and female height or distance between adult males and females during the two hours before model exposure and the two hours after model exposure).

	Control	Tiger	Leopard	Snake
Female height before stimulus	21.9	28.1	20.7	18.9
Female height after stimulus	20.9	27.6	19.1	19.7
Male height before stimulus	22.1	25.1	19.7	17.8
Male height after stimulus	20.4	24.0	19.6	18.8
Distance between male and female before stimulus	9.3	14.8	6.9	1.7
Distance between male and female after stimulus	8.1	9.0	8.3	3.7

### ***Discussion***

It was of interest to investigating the anti-predatory behaviour of gibbons because observed predation rates among gibbons are remarkably low, despite the fact that they have a low body size and live in small groups: two factors that commonly increase predation risk. The study species are exposed to ten potential predators (Uhde & Sommer 2002). A systematic investigation of the gibbons' reactions to four of them gave the following results.

Gibbons reliably produced anti-predator responses to all visual models of predators, but largely ignored the control model. For example, they defecated significantly more often in response to the clouded leopard (7/8 trials) or the snake (6/9 trials) compared to the control model (0/8 trials). Defecation has been interpreted as a sign of stress (see Boissy, 1995) and it may also function as a predator repellent (Tillmann 2008). In addition, the leopard model elicited more branch dropping (4/8 trials) than any other model (snake=1/9 trials; tiger=0/9 trials; eagle=0/7 trials; control=0/8 trials) although this was not statistically significant. Groups moved significantly further away from the site of presentation after seeing the tiger than after seeing the control or leopard model. They were significantly more likely to drop in canopy height when presented with the leopard or eagle compared to the control model, and finally, they were significantly more likely to increase their vigilance after detecting the tiger, leopard or snake compared to the control model.

In terms of their vocal behaviour, gibbons always gave hoo calls followed by a full song when presented with the tiger or leopard model (17/17 trials), but they were significantly less likely to do so when they saw the control or eagle model, which never elicited singing. Instead, gibbons nearly always produced hoos to the eagle model (6/7 trials) but were less likely to do so to the control model (3/8 trials). The remaining trials (eagle=1/7; control=5/8) elicited no vocal response whatsoever. The snake model received mixed responses (5/9 trials=just hoos, 4/9 trials=singing), possibly as a result of differences in the groups' prior knowledge of this predator (Gursky 2006). The emerging pattern is that aerial and ground predators explain the differences in vocal behaviour. Further studies are needed to determine whether this represents a true predator-specific response. One possibility is that the eagle tested in this study was not a real threat to the gibbons, including their infants. A second possibility is that as sit and wait predators, eagles may be best dealt with a quiet

cryptic response in contrast to ambush ground predators which require loud and conspicuous displays (Sunquist and Sunquist 2002). In addition, it is possible that gibbons tailor their vocal response frequencies dependent on the hearing ranges of their predators, and this could be a worthwhile avenue for further study. Snakes are maximally sensitive to low sounds in the frequency of 75-200Hz (Hartline and Campbell 1969), raptors on the other hand have hearing more like humans but cannot really resolve weak sounds below 1000Hz (like the gibbon raptor hoos) (Ferguson-Lees and Christie 2001). Cats have a much wider hearing range than humans, from 200-6500Hz (Brakefield and Shoemaker 1993). If gibbon anti-predator songs function to harass ambush predators, as suggested by chapters 4 and 5, then high frequency songs would be better suited to cats, and lower frequency loud songs would better target snakes. The quiet hoos produced in response to raptors on the other hand, may be designed to escape their attention altogether. Evidence that gibbons do use song to deter ground predators comes from silvery gibbons that alter their behaviour to human observers based on human reaction and prior exposure. According to Kappeler (1981), when a human observer was encountered for the first time, silvery gibbons harassed the human with disorganized screams. If however, the human did not leave the area (as leopards do when exposed to the same screams), then the gibbons eventually fled silently one by one. After two or three exposures of this kind, on subsequent encounters with humans the gibbons adopted a new strategy: they fled silently, perhaps because their prior experiences had produced a negative feedback to their traditional ground predator response. Having worked out that their attempts to deter the predator had failed, gibbons employed a different escape strategy, one which they incorporated into their repertoire for use specifically against humans.

Uhde and Sommer (2002) described responses to aerial predators as follows: “[they] invariably caused the gibbons to give brief alarm calls and immatures to drop from the tree crown or crouch towards the trunk” (279). Differential responses to raptor models in this study may be due to the gibbons understanding of the model or an ability to assess threat urgency, which may vary considerably between a raptor swooping through the canopy and a predator model mimicking a perched raptor (Boissy 1995). A perched raptor may be still assessing its opportunities and monitoring its behaviour quietly may be the best defensive option.

Another finding was that gibbons produced a weaker overall response to playbacks of predator vocalisations and deer alarm calls compared to visual predator models. For example, they rarely defecated to an acoustic model (2/34 trials), and never dropped any branches (0/34 trials). Vocal responses to acoustic predator models were also weaker; gibbons sang in response to only 2 of 38 playback trials. In 11 of 38 trials hoos were elicited, but there were no significant differences between the different predator stimuli; barking deer alarm calls were no less likely to produce a response than tiger growls. The remaining 23 trials elicited no vocal response at all. However, 22 out of 31 playback trials triggered vigilance behaviours, such as scanning and becoming alert, implying that gibbons treated the stimuli as a possible threat. Acoustic eagle presentations never elicited any vigilance behaviours (0/3 trials), suggesting that they did not readily distinguish these calls from the cacophony of other animal calls present in the forest. Alternatively, eagle calls did not evoke predator response behaviours because they are usually emitted at a time when the eagle is not hunting (Channing 2004), something the gibbons may be aware of. However, more trials are needed before any conclusions can be drawn. On five occasions, gibbons were observed to approach the playback speaker, stopping directly above the equipment. In three of these cases, this was in response to hearing a barking deer alarm call following a leopard or tiger growl. The other two cases were

directly after hearing a tiger or a leopard call. Apart from the striking accuracy with which the gibbons used to locate the position of the hidden playback speaker, these events suggested that the barking deer offered some further clues to predator presence, since gibbons never approached the speaker after hearing a barking deer call alone (0/5 trials).

Further comparisons between visual and acoustic models showed that gibbons were significantly more likely to sing in response to a tiger visual model (9/9 trials) than a tiger acoustic model (1/9 trials). As already mentioned, in general, playback responses were subdued when compared with responses to the same predators using visual cues. Several explanations could account for this difference. First, after hearing a playback, the gibbons sometimes showed efforts to locate the predator but, by default, never managed to do so. This lack of visual predator confirmation could account for the lack of vocal responses.

Second, acoustic cues may be harder to recognise than visual cues because they are species-specific. Visual cues are more widely generalised and shared among different predators, such as all big cats or all eagles (Blumstein et al. 2000). However, a number of studies with primates including Treves (1999) showed that individuals reliably responded to playbacks of predator vocalisations suggesting that acoustic cues can be salient signals.

Thirdly, a recent study with putty-nosed monkeys (Arnold et al. 2007) postulated that acoustic playback signals might be weaker experimental stimuli because they are short-lived and may not give the listener enough evidence upon which to react. Nevertheless, this study showed that putty-nosed monkeys did give similar vocal responses to both acoustic and visual model predators.

Finally, the need for alarm calling may be lessened in response to acoustic predator models because the whole group will be aware of the predator's presence at exactly

the same time and, if calls function primarily to alert kin, there is less urgency to communicate about the presence of a predator to nearby individuals.

The first and third reasons (both stemming from not getting enough information) seem most plausible since other primates do respond reliably to playbacks suggesting they are easily recognisable, and evidence from this and other studies, including chapter 5, suggest that gibbon predator songs have an important function in communicating with the predator, and are not just designed to alert kin. Further experiments with longer playbacks would help discern between these possibilities.

One reason why gibbon behaviours are different from the patterns observed in monkeys could be that they have a more sophisticated understanding of predator behaviour. The idea that apes have superior cognitive skills compared to monkeys is regularly maintained in the literature (Byrne 1995), although good empirical evidence to support this hypothesis is difficult to find. Further studies with other wild apes will be required to test these predictions more thoroughly.

Gibbons' longer-term reactions were mixed, showing only minor evidence of altered behaviour after predator exposure. First, gibbons did not significantly change their normal activities after seeing a predator model. They did not groom or forage less, or become more vigilant in the two hours following a predator sighting compared to the period before detection. Vertical strata use did not alter either. In particular, seeing a ground predator did not cause the gibbons to utilise higher substrates, although there were insufficient data to decide whether seeing an aerial predator had the opposite effect. These observations could be interpreted as the gibbons having a complex understanding of predator behaviour, and a genuine sense of when long-term anti-predatory behaviours are warranted. Alternatively, it may be due to a ceiling effect because the gibbons regularly spend a considerable amount of their time in the highest

canopy, feeding on ripe fruit (Uhde & Sommer 2002). The only effect was that the gibbons significantly increased group cohesion after seeing the tiger model, but not after seeing any of the other models. Tigers are rarely seen in the park (WCS 2001) and this could explain why gibbons initially responded less vigorously (few defecations and zero branch drops), but were then more likely to move further away and show longer-term changes in behaviour because they were unfamiliar with this predator. However, tigers were relatively abundant in the study area two decades ago and some individuals may still be familiar with them. Perhaps then, increasing group cohesion is adaptive specifically during tiger encounters.

Comparisons between visual predator models may be subject to an order effect however, since the tiger trials were usually run before the other predators. In addition, distance between mated pairs was larger for the pre-tiger sampling period than for any other pre-stimuli sample periods, suggesting this result may have been an anomaly, and further research is needed.

In conclusion, gibbons show marked anti-predatory behaviour. They emit hoo vocalisations, which may or may not escalate into a loud song bout, drop in canopy height, defecate and sometimes throw branches. They also show some evidence of modifying their behaviour in the long-term after seeing a predator by increasing group cohesion. These measures coupled with their unrivalled specialisation for the arboreal life may explain their apparent protection from predators in spite of their increased predation risk. In fact, despite their small group size gibbons detect approaching terrestrial predators earlier than, for example, macaques, which live in much larger groups (van Schaik et al. 1983). This may be a result of their preference for the higher canopy, which gives them a better vantage point from which to spot an approaching predator. In addition a reduction in body mass may have further functioned to reduce predation pressure, particularly in concert with the evolution of

high-speed suspensory locomotion that may allow gibbons to escape potential predators more efficiently than quadrupedal and partly terrestrial monkeys. As a consequence, gibbons share with great apes a reduced predation risk, a slow life history, flexible reproductive strategies, and advanced cognitive abilities (Reichard and Barelli 2008).

Further study could help shed light on the motivation behind gibbons' differential responses to acoustic and visual representations of predators. Further playbacks could be combined with visual models. Multi-modal stimulation better replicates natural events and may therefore elicit enhanced responses more in line with those produced by encountering a genuine predator (Partan et al. 2009). Novel stimuli such as music could act as a control, as could playbacks of non-predator-related vocalisations of heterospecific, non-threatening animals, such as bird song. Gibbons would be expected to attend to completely novel stimuli such as music, but not to heterospecific vocalisations that do not encode any relevant cross-species information. Music should not however elicit startle responses, ground scanning or heightened alertness: all behaviours exhibited to playbacks of predator vocalisations in this chapter. This type of further study would help corroborate the theory that gibbons are encoding the playback as evidence of a real predator, but withholding their singing response until further evidence is provided. Furthermore, playbacks should be longer in duration, since this may increase their salience and therefore make them more likely to elicit greater responses. Since raptors evoked responses that were the most subdued of the visual model stimuli, it would be interesting to follow-up with raptor presentations simulating a raptor in flight, swooping through the canopy. This would arguably pose a greater threat and evoke more conspicuous responses, or at least support the observational findings of Uhde and Sommer (2002), which included crouching down towards the tree trunk, and looking upwards.

## **CHAPTER 7. “Hoo” calls and close-range communication**

### ***Abstract***

Long-distance primate vocalisations have been the subject of numerous studies. These calls are often found in species living in dense forest habitat, used presumably to communicate with neighbouring groups or distant group members. Close-range vocal signals serve a different communicative purpose and are presumably directed at immediate family members or other individuals within a short distance of the signaller. Gibbons are well known for their loud and elaborate songs, but their quieter close-range communications have been largely ignored, mainly due to the constraints of their natural environment and difficulty in observing the animals at close quarters.

This study provides a detailed analysis of one such call type, the hoo call, which is frequently utilised by white-handed gibbons. Hoo calls are emitted by both sexes in a variety of different contexts, including feeding, establishing contact, encountering a predator, duet songs, or close encounters with a neighbouring group. Data were collected from fourteen adult males and eleven adult females from thirteen different family groups. Acoustic analyses revealed that a number of spectral parameters separated the hoo calls given in different contexts. These included intensity, duration, inter-call interval, peak frequency, minimum frequency, and frequency modulation. Males’ and females’ hoo calls showed remarkable agreement in these parameter differences between contexts, although a number of consistent gender differences were found as well. This study provides the first evidence that gibbon close-range calls are context-specific. The benefits and possible functions of context-dependent

acoustic communication are discussed in light of the ongoing debate about the origins of referential communication and precursors to human language.

## ***Introduction***

Non-human primate vocalisations have been extensively studied across numerous species, often with the aim of examining the cognitive underpinnings and evolutionary relationship between humans and the rest of the primate order. Language appears to be a uniquely human behaviour, but one that has several precursors, many of which are likely to be present among our extant primate relatives (Hurford 2007). These possible precursors could include context-specific calling behaviour, a prerequisite to referential communication (see chapter 5). The evolutionary benefits of referential communication include the possibility of providing genetic relatives with information pertinent to survival and reproduction, for example during situations of alarm, food procurement or social aggression. The list of primates that utilise referential communication is growing (Gouzoules et al. 1984; Zuberbühler 2000; Di Bitetti 2003; Kirchhof and Hammerschmidt 2006). However, most of the research has come from monkeys, with comparably less focus on our closer relatives, the apes (Crockford and Boesch 2003; Notman and Rendall 2005; Slocombe and Zuberbühler 2005, 2005; Slocombe and Zuberbühler 2006).

The study presented in chapter 5 confirmed that at least one species of ape, the white-handed gibbon, uses song as a part of its' anti-predatory behavioural repertoire to inform nearby listeners about the presence of specific predators. These predator songs are consistently different from duet songs and, judging from conspecifics responses, these differences are meaningful to other gibbons, providing the first evidence of a functionally referential system of communication in this species.

Despite this recent progress, the full level of complexity in the calling behaviour of gibbons is not yet fully understood. Gibbon songs are loud and conspicuous, audible over long distances, which allow inter-group communication through the dense forest habitat. However, close range intra-group communication is also important in this species, although these calls have not yet been well studied. Carpenter (1940) was first to study *Hylobates lar* in the field, and alluded to their close range calls as “low volume sounds” (170), which he found impossible to record with the technology available at the time. Nevertheless, Carpenter managed to describe the lar vocalisations as consisting of nine distinct types which he labelled by number; five of these appeared to be confined to communication within the group. He suggested that these calls had several probable functions, including keeping the group together, having a defensive role, being used in play, begging, and directing group progress. Ellefson (1974) studied the same species in the Malay peninsula and he was more specific about the nature of these close-range calls. He described the hoo call as “broad pitch range soft to medium loud, being emitted singly or in short bursts of two or three per second” (128). The hoo call, he said, was particularly interesting because it was used in a variety of different contexts. Ellefson described four such contexts: short distance separation from group members, responding to a human observer, encountering a preferred food (“glug-hoo”), and when neighbouring groups come into short-range contact with one another (“conflict-hoo”). Raemaekers et al. (1984) described the loud calls of *H. lar*, and made special mention of the hoo call since it often punctuated loud calls.

Acoustically, the hoo calls are related to wa calls because of their similarity in shape. Raemaekers et al. (1984:140) already noted their “short, uninflected and steeply rising” shape, although the hoo is of lower pitch and spans a narrower frequency than

the wa. Analyses presented in chapter 5 confirmed these earlier observations by demonstrating that the hoo was of a consistently lower pitch, a lower amplitude than the wa note, and usually covered a frequency range of less than 150Hz.

To date, no attempts have been made to investigate the acoustic differences within the hoo calls given in different contexts. This chapter describes hoos given in several contexts including feeding, contact, alert, predator encounter, inter-group encounters, and duet calling. Producing acoustically distinct calls in these different contexts can be beneficial to listeners since it may inform them about evolutionarily important events such as food locations, the whereabouts of family members, possible danger, the presence and behaviour of a neighbouring group, as well as allowing partners to coordinate their duet singing each morning.

## **Methods**

### **Study site and subjects**

The study site and general socio-biology of the lar gibbons are described in more detail in chapter 3. Data were collected from thirteen groups with all group members individually known (with the exception of one male from a neighbouring unhabituated group) and long-term social data collected for most of them.

### **Data collection and equipment**

Data were collected between April 2004 and July 2005, and between May and November 2007. Groups were located by means of their morning duet, or if known, their sleeping site from the previous day. Groups were usually followed from the first encounter in the morning until they had located their evening sleeping site, the time of

which varies greatly depending on the season. During these focal follows, all hoo calls were recorded on an all occurrence basis, and their corresponding contexts were noted if possible (table 29). Recording equipment is described in chapter 4.

## Data analyses

All calls were digitised using Cool Edit 2000 and Adobe Audition 3.0 software and measured using PRAAT 5.0.29 phonetics software. PRAAT's standard settings were modified for gibbon hoo calls as follows: *Spectrogram settings*: window length=0.05s; analysis method=Fourier; window shape=Gaussian; Number of time steps=1000; Number of frequency steps=250; Maximum dB/Hz=100.0; Pre-emphasis dB/oct=6.0; Dynamic compression=0.0; *Pitch settings*: range=50-1000Hz (range was set wide to allow for a variety of pitch values); Maximum number of candidates=15; Analysis method=cross correlation; Silence threshold=0.01; Voicing threshold=0.045; Voiced/unvoiced cost=0.014; Octave cost=0.01; Octave-jump cost=0.35; *Intensity settings*: Averaging method=mean energy; subtract mean pressure checked; *Pulse settings*: Maximum period factor=1.3; Maximum amplitude factor=1.6. The viewing window was approximately 0.3s. For each of the eight different contexts, only the very first five hoos of each call bout were selected for measurement. This was based on the assumption that the most relevant contextual information must be transferred early on to mark the beginning of a new event. The following acoustic parameters were selected from PRAAT's default range of parameters: Duration (s); median pitch (Hz); delta pitch (Hz); mean harmonics-to-noise ratio (dB); intensity (dB); fundamental frequency (F0) at the start, middle and end of the call (Hz), peak frequency (Hz), low frequency (Hz), delta frequency (Hz) and inter-call interval (s) (see figures 46 and 47 for illustrations). In some instances, not every hoo of the first five could be measured completely, usually due to poor recording quality or sudden overlap with other sounds. In these cases, the remaining calls available amongst the

first five were included in the analyses. Each context was contributed to by at least five individuals of each sex, and parameters were excluded if this was not the case, see table 30. Data were analysed using SPSS version 14. Where possible, parametric statistical tests such as t-tests and one-way ANOVAs followed by post-hoc Tukey tests were used. When acoustic parameters did not conform to the assumptions of parametric testing, non-parametric Kruskall–Wallis tests, followed by post-hoc Mann–Whitney U statistical tests were used instead. Where necessary a Bonferroni correction was applied to adjust the alpha level, depending on the number of post-hoc tests performed. Following these tests, a Discriminant Function Analysis (DFA) was run to determine whether inter-individual differences could be contributing to any of the significant results found.

Table 29. Behavioural contexts recorded during production of hoo calls.

Context	Definition
Feeding	Focal individuals are engaged in handling or consumption of food
Contact	One or more individual is separated from the rest of the group, often during locomotion
Alert	Focal individual engages in fixing behaviour by staring at a fixed point in space for five seconds or more, often accompanied by alarm calls by other species
Ground predator	As above, but a predator is visible or experimentally presented. Typically hoo call series rapidly escalate into song Predator models were a clouded leopard ( <i>Neofelis nebulosa</i> ), a tiger ( <i>Panthera tigris</i> ) and a snake ( <i>Python reticulatus</i> ) (see chapter 5)
Raptor	Focal individual has perceived a raptor, either real (eagle owl, <i>Bubo bubo</i> ) or elicited experimentally with an eagle model ( <i>Spilornis cheela</i> )
Inter-group encounter	Focal individual makes visual contact with another gibbon group
Duet	Focal individuals produce a duet song

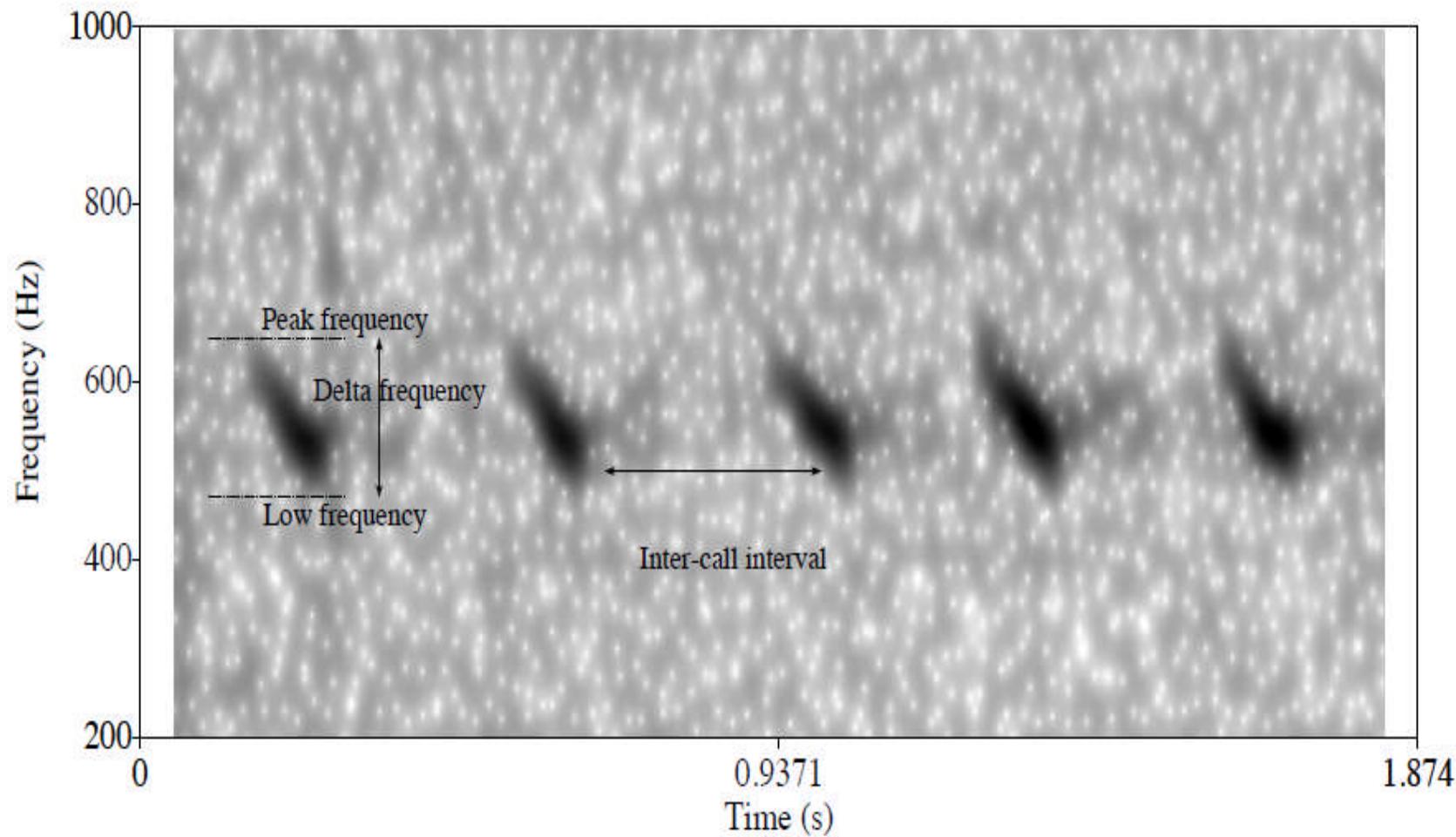


Figure 46. Spectrographic illustration of a series of five hoo calls. Acoustic measurements taken using cursor readings included peak frequency (the highest frequency in a given hoo call as seen on the spectrogram as a dashed line above the first hoo); low frequency (the lowest frequency in a given hoo call as seen on the spectrogram as a dashed line below the first hoo); delta frequency (peak frequency minus low frequency); and inter-call interval (the time span between the end of one hoo call and the start of the next one).

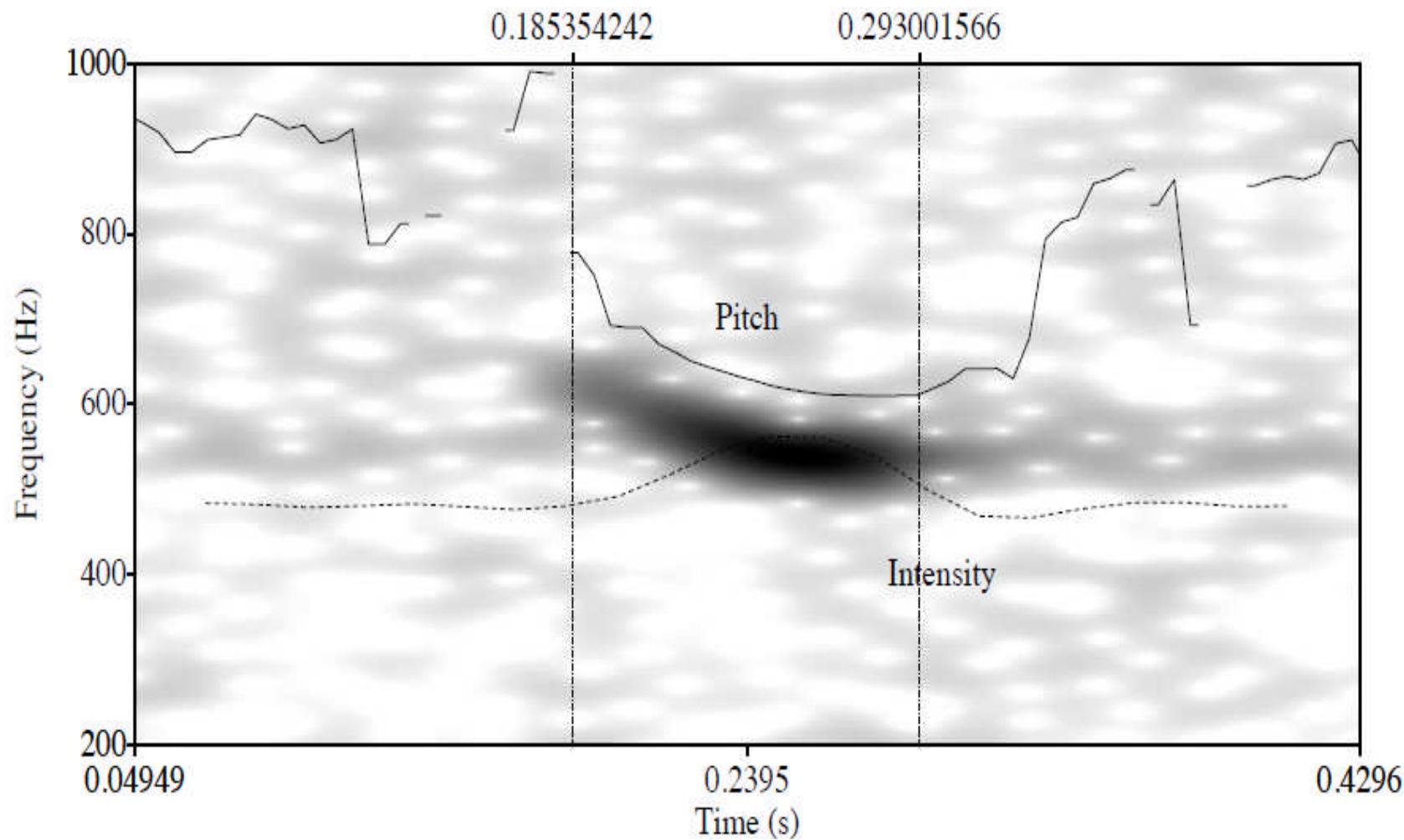


Figure 47. Spectrographic illustration of a single hoo, using PRAAT's automated analysis scripts. Call duration is determined by the distance between the two dashed vertical lines. The pitch contour is visible above the main acoustic energy as a solid line following the shape of the call; the intensity appears below and through the call as a dashed line, peaking in the second half of the call.

Table 30. The number of individuals from each sex in each context that contributed to the final analyses.

Context	Number of individuals (n)
Feeding	M=5; F=5
Inter-group encounter	M=11; F=0
Duet	M=5; F=7
Alert*	M=1; F=2
Contact*	M=3; F=3
Raptor	M=7; F=5
Tiger	M=7; F=7
Leopard	M=8; F=10
Snake*	M=3; F=3

M=Male, F=Female, \*=Contexts that were excluded from the main analyses due to low sample sizes.

## Results

A total of 426 hoos were measured across eight different contexts. Sample sizes for the alert, contact and snake contexts were too small to be included in the analyses (table 30). For the females, the inter-group encounter context was omitted since they did not usually engage in encounters with neighbouring groups, and there were no suggestions that they produced acoustically unique hoo vocalisations during inter-group encounters.

Calls were measured from fourteen males and eleven females. Overall, hoos covered an average frequency range of  $131.3\text{Hz} \pm 61.3\text{SD}$ , ( $n=419$ ) and lasted  $0.08\text{s} \pm 0.02\text{SD}$  ( $n=426$ ). There were not enough recordings for the different individuals in the

different contexts to conduct matched samples analyses, so all individuals of the same sex were analysed together. Certain parameters were easier to extract than others resulting in unequal sample sizes: pitch values, intensities, fundamental frequencies, and harmonics-to-noise ratios yielded smaller sample sizes than call durations, inter-call intervals, peak, low and delta frequencies. As a result, in some cases certain parameters could not be measured for every context. In these cases, only the remaining valid contexts were compared.

## **Males**

There were significant differences in a number of acoustic parameters of hoos recorded from the fourteen adult males in the six different contexts: *Duration*: Kruskall-Wallis test: chi-square=16.0, df=5, p=0.007, n=238; *Peak frequency (Hz)*: one-way ANOVA: F=4.8, df=5, p<0.001, n=212; *Low frequency (Hz)*: One-way ANOVA: F=11.9, df=5, p<0.001, n=211; *Delta frequency (Hz)*: Kruskall-Wallis test: Chi-square =27.9, df=5, p<0.001, n=210, and *Inter-call interval*: Kruskall-Wallis test: Chi-square=17.1, df=5, p=0.004, n=169). For *Intensity (dB)*, duet and feeding contexts were removed due to low sample size: A one-way ANOVA revealed a significant difference between the remaining four contexts (F=12.4, df=3, p<0.001, n=81).

*Delta pitch* could only be compared between the leopard and duet contexts. An independent t test revealed no significant differences ( $t=1.8$ ,  $df=28$ ,  $p=0.076$ ,  $n_{duet}=18$ ,  $n_{leopard}=12$ ). *Mean harmonics-to-noise ratio*, *Median pitch (Hz)* and *Fundamental frequency (F0)* at the start, middle and end of the call only had high enough sample

sizes in the leopard context and so could not be statistically compared with other contexts.

Post-hoc Tukey or Mann-Whitney U tests were performed in all cases where significant differences were observed:

*Peak frequency*: The peak frequency of the raptor hoos was significantly lower than for the duet (Tukey test:  $p=0.001$ ,  $n_{duet}=26$ ,  $n_{raptor}=35$ ) encounter (Tukey test:  $p=0.009$ ,  $n_{encounter}=55$ ,  $n_{raptor}=35$ ) and tiger hoos (Tukey test:  $p=0.002$ ,  $n_{tiger}=35$ ,  $n_{raptor}=35$ ), figure 48.

*Low frequency*: The lowest frequency for the duet hoos was significantly higher than the lowest frequency for feeding hoos (Tukey test:  $p<0.001$ ,  $n_{duet}=26$ ,  $n_{feed}=20$ ), leopard hoos (Tukey test:  $p<0.001$ ,  $n_{duet}=26$ ,  $n_{leopard}=40$ ), raptor hoos (Tukey test:  $p<0.001$ ,  $n_{duet}=26$ ,  $n_{raptor}=35$ ) and tiger hoos (Tukey test:  $p<0.001$ ,  $n_{duet}=26$ ,  $n_{tiger}=34$ ). Also the lowest frequency for the encounter hoos was significantly higher than for the tiger hoos (Tukey test:  $p=0.010$ ,  $n_{tiger}=34$ ,  $n_{encounter}=55$ ), the feeding hoos (Tukey test:  $p<0.001$ ,  $n_{feed}=20$ ,  $n_{encounter}=55$ ), the leopard hoos (Tukey test:  $p=0.006$ ,  $n_{leopard}=40$ ,  $n_{encounter}=55$ ) and the raptor hoos (Tukey test:  $p=0.001$ ,  $n_{raptor}=35$ ,  $n_{encounter}=55$ ), figure 49.

*Delta frequency*: Mann-Whitney U tests were performed with a Bonferroni corrected alpha level=0.013. The delta frequency of the tiger hoos was significantly greater than that of the duet hoos ( $U=245.5$ ,  $p=0.003$ ,  $n_{tiger}=34$ ,  $n_{duet}=26$ ), the raptor hoos ( $U=162.0$ ,  $p<0.001$ ,  $n_{tiger}=34$ ,  $n_{raptor}=35$ ) and the encounter hoos ( $U=497.0$ ,  $p<0.001$ ,

$n_{tiger}=34$ ,  $n_{encounter}=55$ ). The delta frequency of tiger hoos was higher than the leopard hoos ( $U=452.5$ ,  $p=0.014$ ,  $n_{tiger}=34$ ,  $n_{leopard}=40$ ), though this was no longer significant at the corrected alpha level, figure 50.

*Duration:* Mann-Whitney U tests were performed with a Bonferroni corrected alpha level=0.013. The duration of the raptor hoos was significantly shorter than the duet hoos ( $U=225.0$ ,  $p=0.001$ ,  $n_{duet}=26$ ,  $n_{raptor}=35$ ) and the leopard hoos ( $U=438.0$ ,  $p=0.005$ ,  $n_{leopard}=40$ ,  $n_{raptor}=35$ ). The duration of tiger hoos was also greater than the raptor hoos although this was no longer significant at the corrected alpha level ( $U=424.0$ ,  $p=0.027$ ,  $n_{tiger}=34$ ,  $n_{raptor}=35$ ). The duration of feeding hoos was also greater than raptor hoos ( $U=223.0$ ,  $p=0.014$ ,  $n_{feed}=21$ ,  $n_{raptor}=35$ ) though not significantly so at the corrected alpha level, figure 51.

*Intensity:* The raptor hoos were of significantly lower intensity than the leopard hoos (Tukey test:  $p<0.001$ ,  $n_{leopard}=26$ ,  $n_{raptor}=21$ ), the tiger hoos (Tukey test:  $p<0.001$ ,  $n_{tiger}=18$ ,  $n_{raptor}=21$ ) and the encounter hoos (Tukey test:  $p<0.001$ ,  $n_{encounter}=17$ ,  $n_{raptor}=21$ ), figure 52.

*Inter-call interval:* Mann-Whitney U tests were performed with a Bonferroni corrected alpha level=0.013. The inter-call interval for the raptor hoos was significantly larger than that for the duet hoos ( $U=153.0$ ,  $p=0.004$ ,  $n_{raptor}=28$ ,  $n_{duet}=21$ ), the leopard hoos ( $U=201.0$ ,  $p<0.001$ ,  $n_{raptor}=28$ ,  $n_{leopard}=32$ ), the tiger hoos ( $U=207.0$ ,  $p=0.002$ ,  $n_{raptor}=28$ ,  $n_{tiger}=28$ ), and the encounter hoos ( $U=315.0$ ,  $p=0.001$ ,  $n_{raptor}=28$ ,  $n_{encounter}=44$ ), figure 53.

## Females

There were significant differences in a number of acoustic parameters recorded from the eleven adult females in the six different contexts:

*Duration*: chi-square=13.7, df= 4, p=0.008, n=188; *Peak frequency (Hz)*: one-way ANOVA: F=8.4, df=4, p<0.001, n=165; *Low frequency (Hz)*: one-way ANOVA: F=7.8, df=4, p<0.001, n=165; *Delta frequency (Hz)*: chi-square=21.9, df=4, p<0.001, n=166, and *Inter-call interval (s)*: chi-square=18.1, df=4, p=0.001, n=136.

*Median pitch (Hz)*, *Delta pitch (Hz)*, *Mean harmonics to noise ratio (dB)*, and *Fundamental frequency (F0)* at the start, middle and end of the call (Hz) had sample sizes that were too small (parameters were measured from less than five individuals) in all contexts except leopard, and so could not be analysed here. For *Intensity (dB)*, only the leopard and tiger contexts could be compared. An independent samples t-test revealed no significant differences ( $t=1.6$ , df=44, p=0.122,  $n_{\text{leopard}}=27$ ,  $n_{\text{tiger}}=19$ ).

Post-hoc Tukey and Mann-Whitney U tests revealed significant differences in the following parameters:

*Peak frequency*: The peak frequency of the raptor hoos was significantly lower than the duet hoos (Tukey test: p<0.001,  $n_{\text{duet}}=34$ ,  $n_{\text{raptor}}=25$ ), the tiger hoos (Tukey test: p=0.008,  $n_{\text{tiger}}=35$ ,  $n_{\text{raptor}}=25$ ) and the leopard hoos (Tukey test: p<0.001,  $n_{\text{leopard}}=50$ ,  $n_{\text{raptor}}=25$ ), figure 48.

*Low frequency*: The lowest frequency of the duet hoos was significantly higher than the leopard hoos (Tukey test, p=0.003,  $n_{\text{duet}}=34$ ,  $n_{\text{leopard}}=50$ ), the raptor hoos (Tukey test: p<0.001,  $n_{\text{duet}}=34$ ,  $n_{\text{raptor}}=25$ ) and the tiger hoos (Tukey test: p=0.003,  $n_{\text{duet}}=34$ ,

$n_{tiger}=35$ ). The low frequency of the feeding hoos was also significantly higher than the raptor hoos (Tukey test:  $p=0.028$ ,  $n_{feed}=22$ ,  $n_{raptor}=25$ ), figure 49.

*Delta frequency:* Mann-Whitney U tests were performed with a Bonferroni corrected alpha level=0.010. The delta frequency of the leopard hoos was greater than the duet hoos, though this difference was no longer significant at the corrected alpha level ( $U=628.0$ ,  $p=0.043$ ,  $n_{leopard}=50$ ,  $n_{duet}=34$ ). However, the delta frequency of the leopard hoos was significantly greater than that of the feeding hoos ( $U=296.0$ ,  $p=0.002$ ,  $n_{leopard}=50$ ,  $n_{feed}=22$ ) and the raptor hoos ( $U=338.0$ ,  $p=0.001$ ,  $n_{leopard}=50$ ,  $n_{raptor}=25$ ). Similarly, the delta frequency of the tiger hoos was significantly greater than that of the raptor hoos ( $U=203.5$ ,  $p<0.001$ ,  $n_{tiger}=35$ ,  $n_{raptor}=25$ ) and also the feeding hoos ( $U=187.5$ ,  $p=0.001$ ,  $n_{tiger}=35$ ,  $n_{feed}=22$ ), figure 50.

*Duration:* The duration of the raptor hoos was significantly shorter than that of the duet hoos (Tukey test:  $p=0.003$ ,  $n_{duet}=34$ ,  $n_{raptor}=25$ ), the leopard hoos (Tukey test:  $p=0.046$ ,  $n_{leopard}=50$ ,  $n_{raptor}=25$ ), figure 51.

*Inter-call interval:* Mann-Whitney U tests were performed with a Bonferroni corrected alpha level=0.017. The interval between raptor hoos was significantly greater than that between tiger hoos ( $U=135.0$ ,  $p<0.001$ ,  $n_{raptor}=24$ ,  $n_{tiger}=28$ ), and leopard hoos ( $U=263.0$ ,  $p=0.003$ ,  $n_{raptor}=24$ ,  $n_{leopard}=40$ ). Similarly the interval between raptor hoos was greater than that between duet hoos, but this was no longer significant at the corrected alpha level ( $U=214.0$ ,  $p=0.038$ ,  $n_{raptor}=24$ ,  $n_{duet}=27$ ), figure 53.

## **Males versus females**

When males were compared with females across all contexts, Independent sample t-tests revealed the following differences:

Overall, male hoos had a significantly higher median pitch than female hoos ( $t=-4.3$ ,  $df=78$ ,  $p<0.001$ ,  $n_{male}=49$ ,  $n_{female}=31$ ). Male hoos also had a significantly higher F0 at the middle ( $t=-4.5$ ,  $df=82$ ,  $p<0.001$ ,  $n_{male}=50$ ,  $n_{female}=34$ ), and end of the hoo calls ( $t=-3.9$ ,  $df=81$ ,  $p<0.001$ ,  $n_{male}=51$ ,  $n_{female}=32$ ) but not at the start ( $t=-1.6$ ,  $df=72$ ,  $p=0.117$ ,  $n_{male}=46$ ,  $n_{female}=28$ ). Similarly, peak frequencies were significantly higher among male hoos than female hoos ( $t=-9.6$ ,  $df=419$ ,  $p<0.001$ ,  $n_{male}=233$ ,  $n_{female}=188$ ) as were low frequencies ( $t=-13.6$ ,  $df=418$ ,  $p<0.001$ ,  $n_{male}=232$ ,  $n_{female}=188$ ), though delta frequencies were not significantly different between the sexes ( $t=-0.9$ ,  $df=417$ ,  $p=0.386$ ,  $n_{male}=231$ ,  $n_{female}=188$ ).

Conversely, female hoo intensity proved significantly greater than male hoo intensity ( $t=2.8$ ,  $df=185$ ,  $p=0.005$ ,  $n_{male}=116$ ,  $n_{female}=71$ ). There were no significant differences in duration ( $t=-0.7$ ,  $df=420$ ,  $p=0.505$ ,  $n_{male}=234$ ,  $n_{female}=188$ ), mean harmonics-to-noise ratio ( $t=-0.4$ ,  $df=84$ ,  $p=0.710$ ,  $n_{male}=55$ ,  $n_{female}=31$ ) or delta pitch ( $t=1.5$ ,  $df=78$ ,  $p=0.139$ ,  $n_{male}=49$ ,  $n_{female}=31$ ).

## **Discriminant function analysis**

A discriminant function analysis was conducted, entering all twelve acoustic parameters to identify any inter-individual variation between the calls of the different males and females. For both males and females, no discrimination was made between different individuals. Figure 54 shows a scatter plot for the males using discriminant function scores for the first (explaining 69.2% variance, eigenvalue=56.9) and second

(explaining 17.7% variance, eigenvalue=14.5) functions. Figure 55 shows a similar scatter plot for the females where function 1 explains 80.1% of variance; eigenvalue=54.4, and function 2 explains 8.2% variance; eigenvalue=5.6.

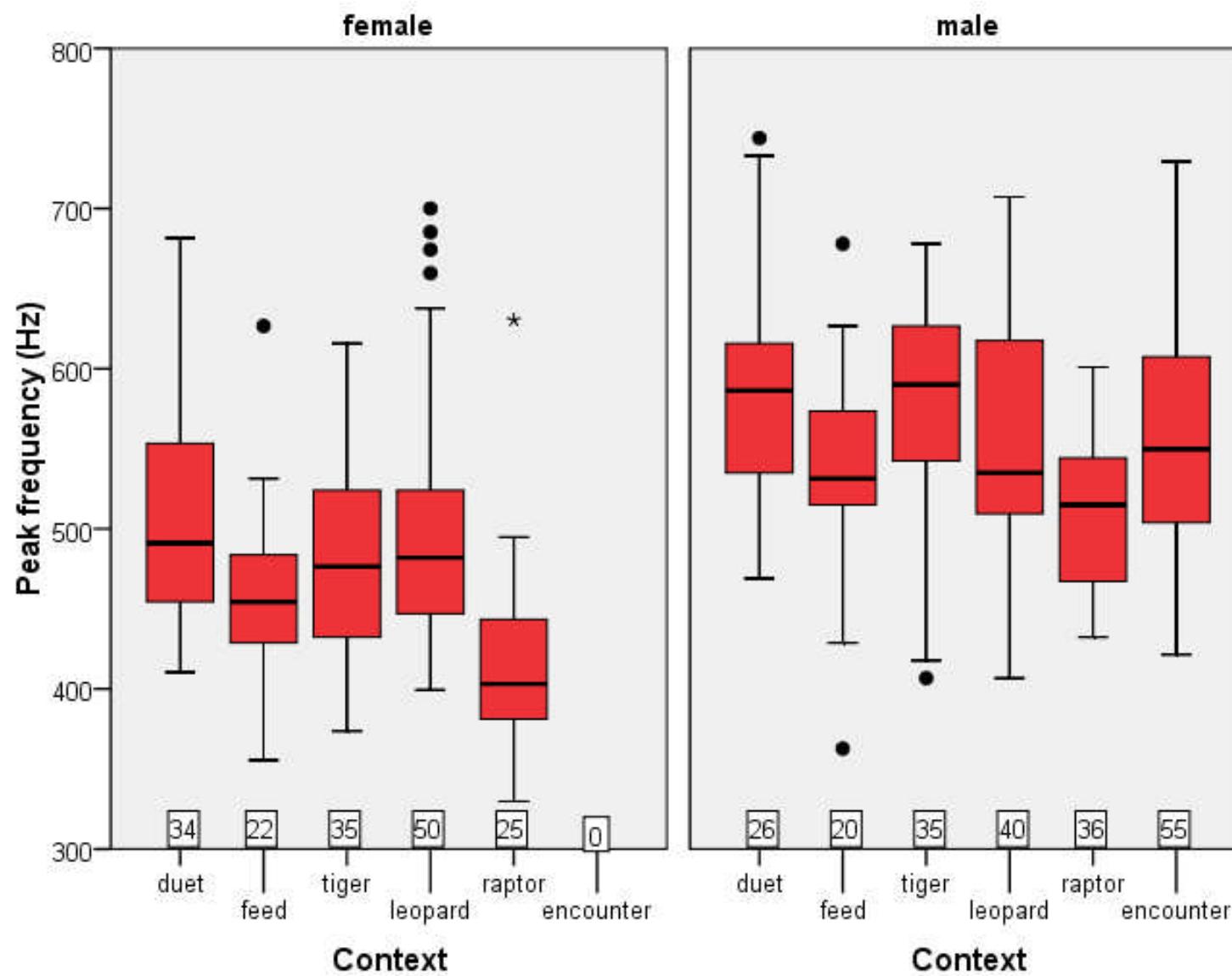


Figure 48. The peak frequencies of the hoos as measured across the different contexts. Females appear on the left-hand graph and males on the right. Box plots represent median lines and inter-quartile ranges. Three extreme values were omitted from the graphs but not the analyses. Numbers in boxes represent n values.

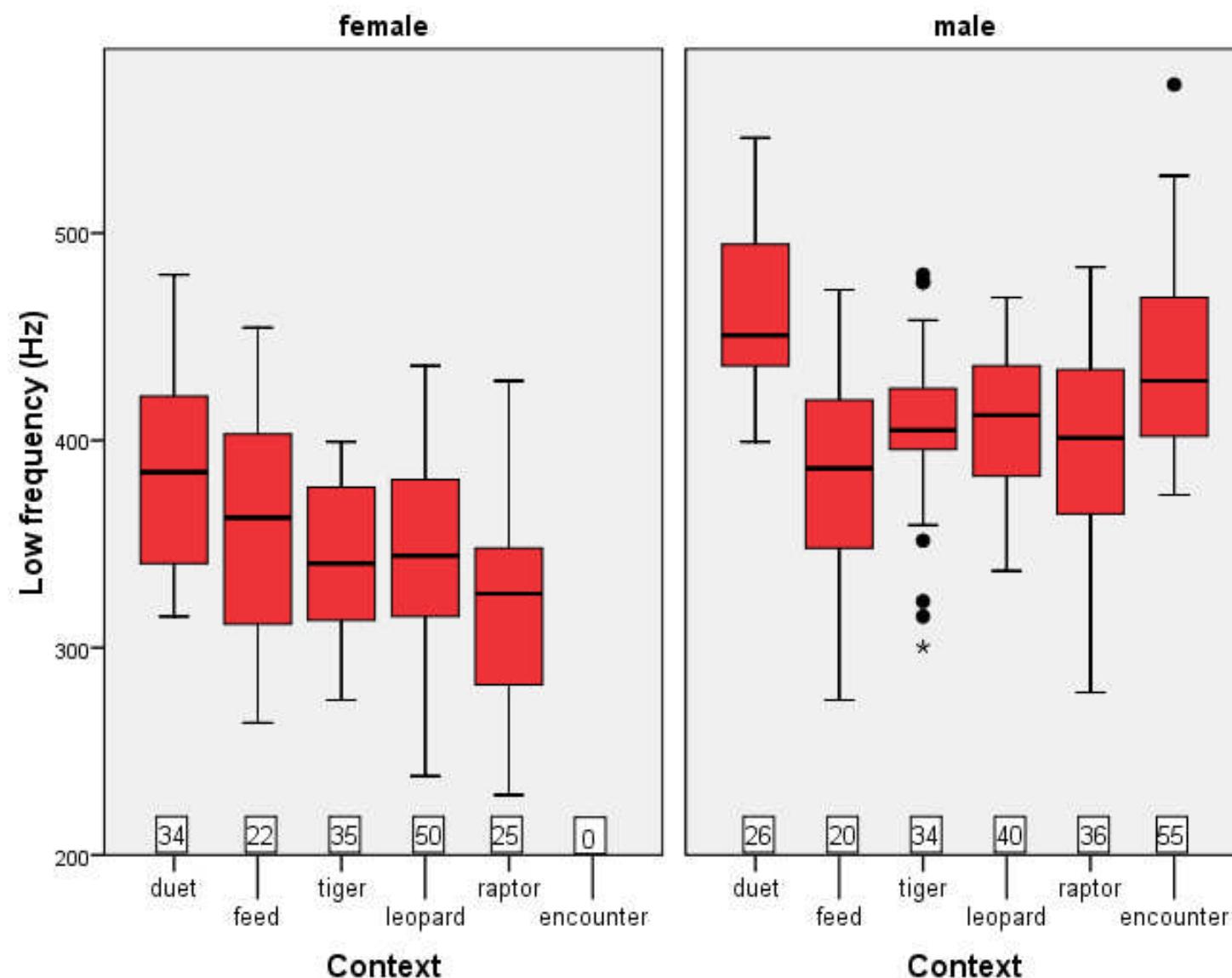


Figure 49. The low frequencies of the hoos as measured across the different contexts. Females appear on the left-hand graph and males on the right. Box plots represent median lines and inter-quartile ranges. Numbers in boxes represent n values.

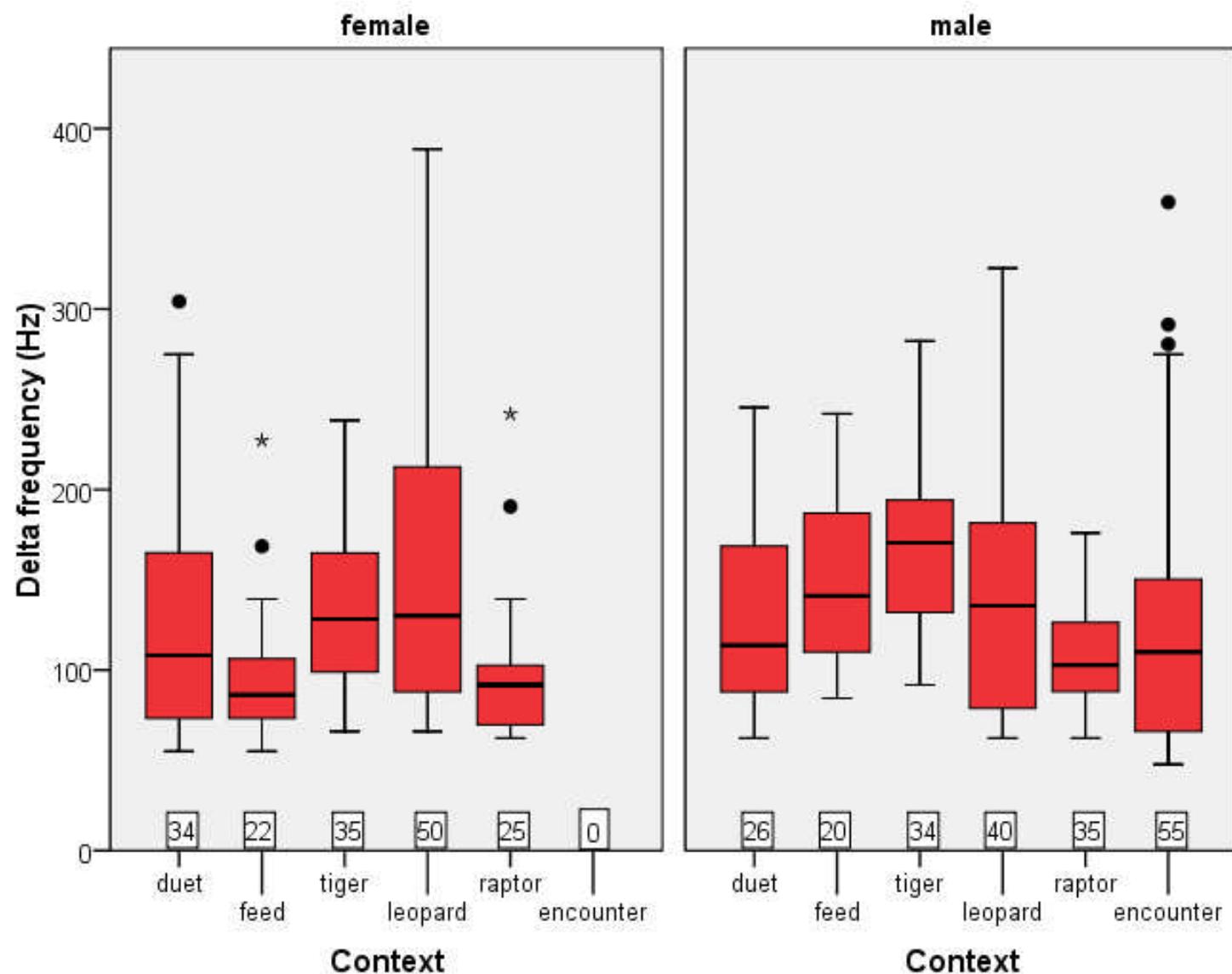


Figure 50. The delta frequencies of the hoos as measured across the different contexts. Females appear on the left-hand graph and males on the right. Box plots represent median lines and inter-quartile ranges. Numbers in boxes represent n values.

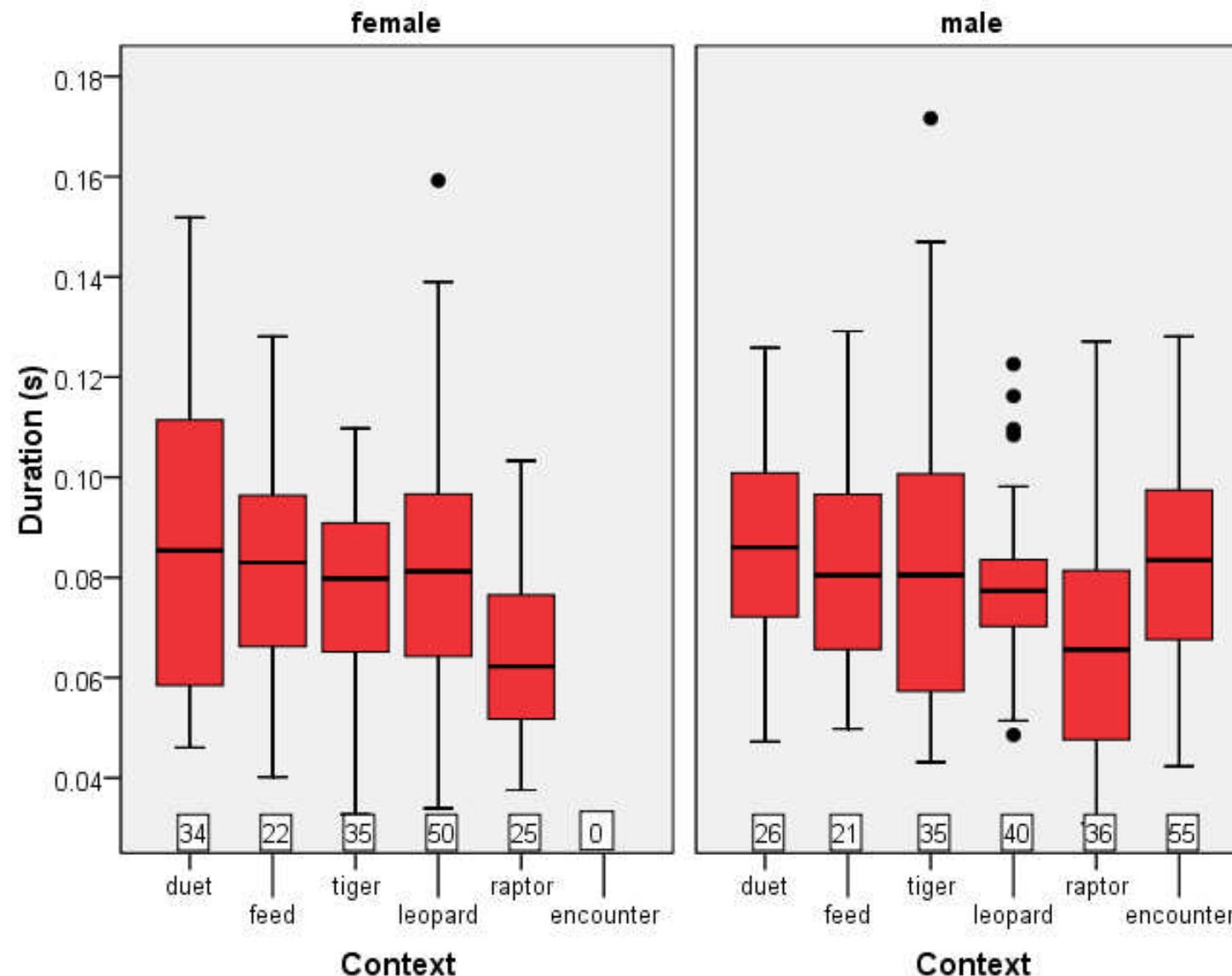


Figure 51. The durations of the hoos across the different contexts. Females appear on the left-hand graph and males on the right. Box plots represent median lines and inter-quartile ranges. Numbers in boxes represent n values.

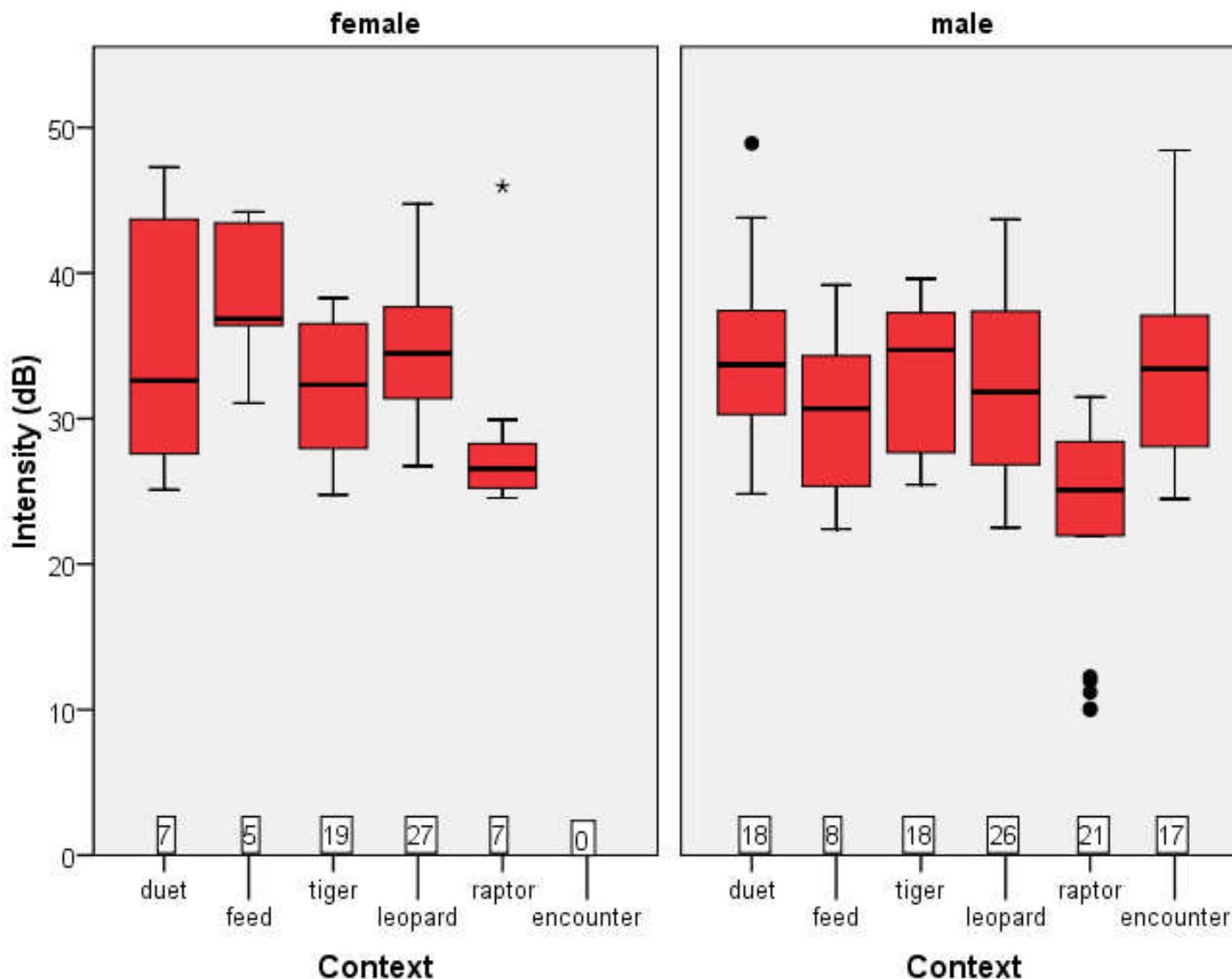


Figure 52. The intensities of the hoos as measured across the different contexts. Females appear on the left-hand graph and males on the right. Box plots represent median lines and inter-quartile ranges. Numbers in boxes represent n values.

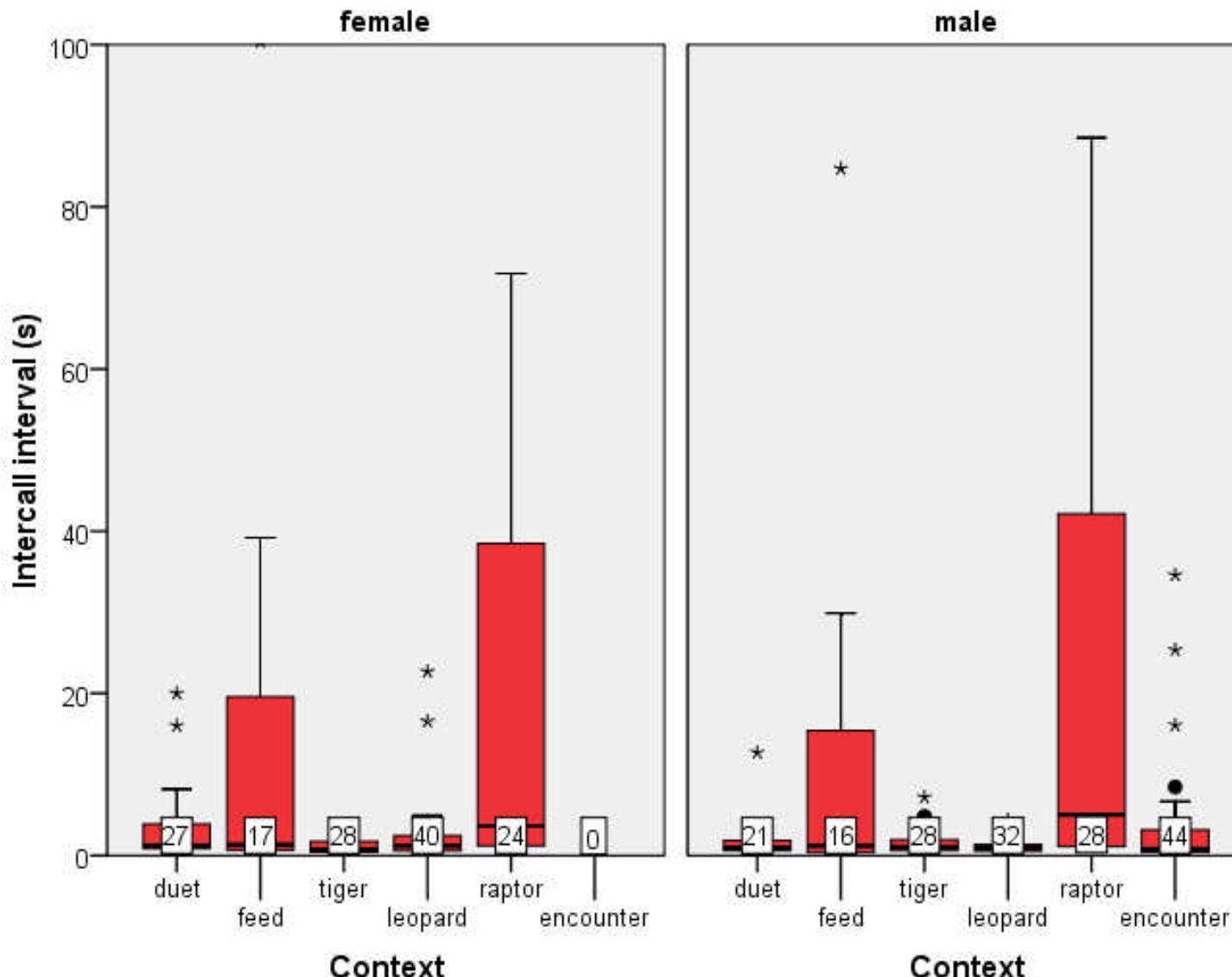


Figure 53. The inter-call intervals of the hoos as measured across the different contexts. Females appear on the left-hand graph and males on the right. Three extreme values were omitted from the graphs but these values are included in the analyses. Box plots represent median lines and inter-quartile ranges. Numbers in boxes represent n values.

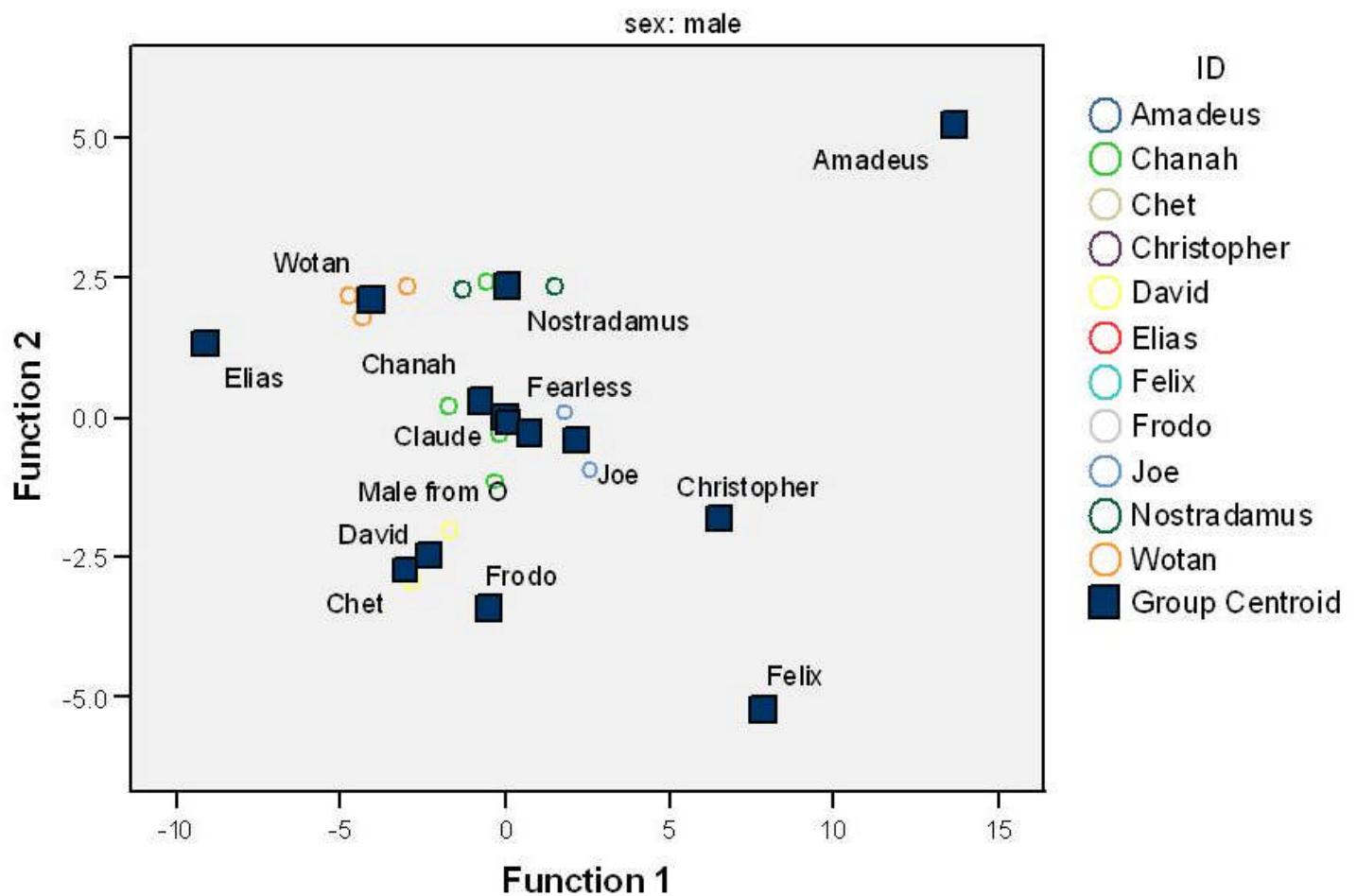


Figure 54. A scatter plot of functions 1 and 2 as they explain the variation between the different males in the study population.

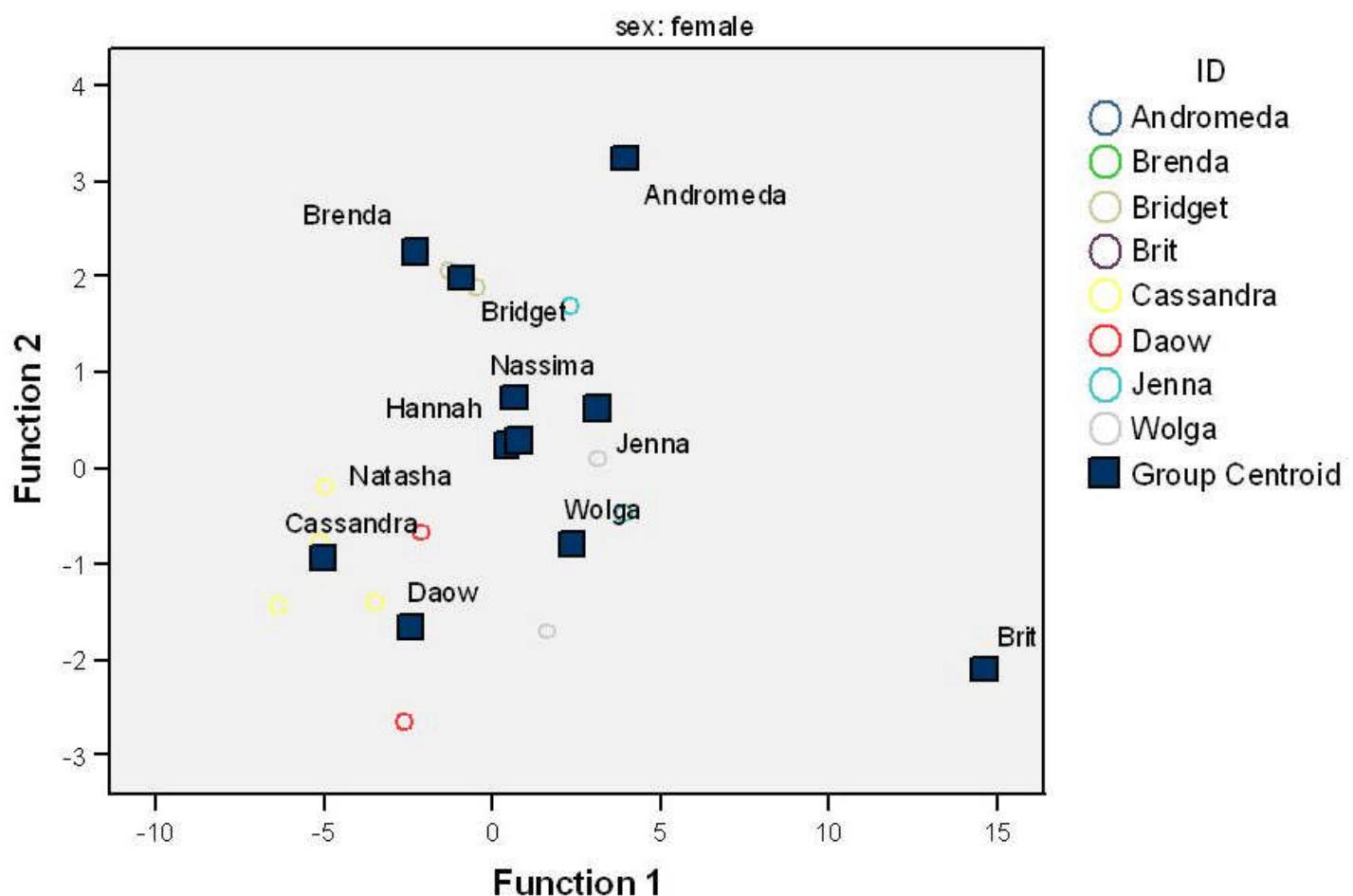


Figure 55. A scatter plot of function 1 and 2 as they explain the variation between the different females in the study population.

## Discussion

The close-range calls of wild gibbons have never received any detailed study despite various studies conducted on these apes' vocal behaviour. This chapter investigated the close-range hoo calls of free-ranging white-handed gibbons in the forests of North-eastern Thailand in order to address this shortfall. Hoos were tape-recorded and compared across several contexts to determine whether there were consistent acoustic differences between these contexts, a crucial prerequisite for conveying referential information.

Results revealed that both adult male and adult female gibbons produce context-specific hoo calls, as follows:

First, males and females showed remarkable agreement in the ways in which they tailored the acoustic structure of their hoo calls to specific contexts. For example, measures of peak and low frequency showed that the hoos given in response to raptors were significantly lower than the hoos given as part of daily duet songs for both males and females. Indeed, the raptor hoos showed significant differences in a number of acoustic parameters compared to many of the other contexts: they were significantly shorter in duration than duet and leopard hoos for both males and females and raptor hoo intensity was significantly lower than for the duet hoos, leopard hoos and feeding hoos for the males. In addition, inter-call intervals separated raptor hoos from hoos given in other contexts, with intervals being significantly longer than for tiger and leopard hoos for the males and females, and for duet and encounter hoos for the males alone.

There were also differences between other contexts, for example, the duet hoos tended to be higher in frequency than the other contexts, significantly so when compared with feeding, leopard, tiger and raptor hoos. The delta frequency of the tiger and leopard hoos tended to be greater than that for the duet and encounter hoos (males), and the feeding and raptor hoos (females). The encounter context was measured solely from the males, since females do not usually engage in territory disputes. These hoos also proved to be different from other male hoos. They showed significantly higher low frequencies than tiger hoos and feeding hoos, and significantly smaller delta frequencies than the tiger hoos. In fact, the only two contexts that did not differ significantly from one another and that similarly differed

from other contexts were the tiger hoo and the leopard hoo. This is presumably because both predators represent similar threats, and therefore warrant similar behavioural responses.

When comparing males against females, the observations of Raemaekers et al. (1984) were upheld in that male calls were pitched significantly higher than female calls. Related to this, the F0 at the middle and end of the calls was higher among male hoos than female hoos. In addition, male hoo peak and low frequencies were significantly higher than the same measurements for female hoos. The delta frequency showed no difference between the sexes however. Interestingly, the intensity of female hoos was significantly higher than that of male hoos. The spectral parameters that differed between sexes, except for the change in intensity, were the same as those that were significantly equivalent within each sex. Without obtaining a larger sample size of excellent quality hoo recordings, it is hard to extrapolate too much from the script-based acoustic analyses available from the PRAAT software. However, the data presented herein show that the differences between males and females are mainly concerned with frequency-related parameters, while the way that both sexes discriminate between the different contexts is otherwise the same. This is good evidence for context-dependent communication within groups and between groups in close range of one-another. Playbacks of these gibbon hoos are now needed to determine whether this call system truly represents a referential system in the way that their long-distance calls appear to (chapter 5).

Why do gibbons and other primates produce context-dependent calls? The hoo calls described here are all quiet, low frequency calls designed presumably to communicate

information at close range between members of the family group. Humans routinely use context-dependent calls, either of a non-linguistic (laughter, screams, crying) or linguistic nature (words) that reliably elicit specific reactions from other humans, and this is just part of what makes human communication so complex and unique.

Gibbons use hoos in a number of contexts that are completely unrelated to each other. Moreover, it makes sense that a duet hoo be distinguishable from a feeding hoo, since the associated behavioural challenges and underlying motivations are completely different: a caller may wish to entice a partner to coordinate themselves at the beginning of a duet song bout, which is different from the caller that wishes to alert a partner to the presence of a delectable food item. In addition, a hoo that informs another about the presence of potential danger, such as an approaching predator, is linked to a very different situation compared to one that informs about the approach of a rival gibbon group. The first situation necessitates that the animals flee to safety, mob or attack the predator to ensure survival, whereas the other requires that they remain alert, protect their mates and defend their territory. Interestingly, a trained human observer can readily distinguish the raptor hoo from the other hoos, including the leopard and tiger hoos. Raptors are smaller and less conspicuous than the big cats, and perhaps depend less on a surprise attack, and can potentially move unnoticed through and above the canopy (see chapter 5 and 6). They are small enough to only really represent a threat to infants, and this may explain the different response tactics used by the gibbons. Raptor hoos are less intense, more widely spread out in terms of inter-call intervals, of shorter duration, lower frequency and smaller frequency modulation than other hoos. Whether this is an adaptation to remain out of sight and escape the attention of the predator is an interesting, but difficult to test, hypothesis.

The gibbons' relatively cryptic responses to raptors contrast strongly with their loud and elaborate display when a leopard or tiger is encountered (chapters 5 and 6). However, this is not unique to gibbon anti-predatory behaviour. Diana monkeys (*Cercopithecus diana*) also adopt differential response tactics dependent on the type of predator. Loud protracted alarm display is usually indicative of the presence of a ground predator, such as a leopard, whereas a quiet and cryptic response may indicate the presence of a chimpanzee troop (Zuberbühler et al. 1999; Zuberbühler 2000). Such responses are suggestive of a sophisticated understanding of predator behaviour. The difference with the gibbon responses is that the close range calls they produce can all be subsumed under the same call type: the hoo, and this is just one of at least seven different call subunits that make up the elaborate vocal repertoire of these animals.

Chapter 5 states how these separate subunits or notes can be combined to create figures and phrases and that these may also be ordered differently depending on the context that elicits a call bout, revealing a simple form of phonological syntax. To see such subtle variation within just one of the seven subunits eludes to a potentially enormous communicative repertoire the likes of which may be compared to human language.

Natural and sexual selection have probably favoured the acoustic diversification of this class of vocalisations, but playbacks are needed to clarify whether receivers are able to discriminate between them and make appropriate responses.

In conclusion, white-handed gibbons use context-dependent vocal signals to communicate about different events, including food procurement, predator detection and avoidance, encountering a neighbouring group and coordinating the start of a duet

song. Differences are not solely between predator and non-predator contexts, but they are also found within these two broad contexts, and based on a complex set of subtle spectral parameters indistinguishable for the most part to the human ear, but relevant enough to be consistent both within and between sexes. Playback experiments will determine whether these calls are functionally referential, an important component of human language. The gibbon vocal repertoire is rich and multifaceted and further study is needed to disclose the full vocal variety of this species. It would be prudent to collect and analyse more snake response hoos, along with those presented above. If raptor and cat hoos are distinct, snake hoos may very well be also. Alert hoos are a separate class of hoo that could not be analysed in this chapter due to small sample size, but these too may represent a distinct unit along with contact hoos. A larger library of recordings is needed to make these analyses possible. Aside from playbacks to gibbons, playbacks aimed at some gibbon predators may help to decide whether the function of their predator response calls is to communicate with the predator, deterring it from attacking, or to hide communication from the predator and avoid it altogether. Are raptor hoos too weak for raptors to hear? Playbacks could answer this question. Are clouded leopards, tigers and snakes deterred by gibbon predator songs? Again, playbacks are needed to answer this question. The acoustic structure of hoos may also help to determine whether gibbons tailor them to each type of predator. For example, snake hoos may be more intense than raptor hoos, but have an equal or lower frequency if they are designed to communicate with the snake who hears better at low frequency (see chapter 6).

## **CHAPTER 8. Conclusion**

The preceding chapters represented a journey through Khao Yai National Park's white-handed gibbons' behavioural repertoire. This final chapter is intended to outline the main points and findings of the research conducted with these remarkable creatures. It also hopes to offer up some speculation about how these behaviours may have developed through evolutionary time, and how they may be related to the ontogeny of human language.

Firstly, to reiterate, there are some unique benefits of studying gibbons: they offer the best avenue for investigating phylogenetic relationships between extant primate species in the hominoidea super-family, to which humans also belong. This may help unearth evolutionary processes that underpin human evolution, including human language. As outlined in chapter 3, the lar gibbons have a well-described vocal repertoire, which is large in comparison with other primates, and especially so when compared with other apes. Similarly, this affords researchers with a rich pool from which to study communication and its changes through evolutionary time. Gibbon vocal units were described in detail, as was their impressive ability to impose temporal modifications on any note type, particularly relevant for adult males who seem to have the more variable of the vocal repertoires.

Chapter 4 then showed that gibbon duets function to communicate with neighbours on all sides without inviting intrusion into their territory. Gibbons ensure this by choosing to broadcast more morning duets from the core of their home range. There

was also evidence for an important communicative function of the female great call since groups paused their own singing, more often than would be predicted by chance, to listen to the great call of a neighbouring female. In addition, oooaa duets proved highly contagious and 90.0% of groups responded in kind when they heard this particular song type. The function of these oooaa calls remains unclear, although they offer good potential for further research.

The gibbons' vocal behaviour in relation to predation was then examined as an excellent way to learn more about their vocalisations, what elicited them, and whether they were used to label distinct events. Long-distance songs were analysed and compared across predatory and non-predatory contexts in chapter 5. There were consistent differences between the two song types illustrating context-specific vocal labelling. In addition, the opening segments of song contained notes that were rearranged in consistently different ways to denote either predator or duet contexts, thus demonstrating a simple form of syntax. Hints of an intermediate song type became apparent when gibbon songs recorded after a predator encounter earlier in the day were compared with those given during a predator encounter, and those given as morning duets. Interestingly, neighbouring groups that heard the study groups' predator song would sometimes respond with their own songs. These response-songs contained elements only found in predator songs, providing the first evidence of a functionally referential call system in this species of ape. In addition, duet songs recorded from groups that were less well habituated to human observers proved consistent exceptions to both the normal duet and the predator song. They did however possess elements more common to predator songs, such as sharp wow notes. These quasi-duets and post-predator songs allowed listeners to glean quite complex

information from signalers in regards to the degree of threat of a potential predator in the area at any given time, and also provided information about a predator that was observed earlier that day. Variations on the normal duet are in fact a remarkable example of vocal plasticity, which is essential for effective and comprehensive use of vocal communication.

With special regards to predation also, gibbon predator songs invariably began with low frequency hoo calls that sometimes escalated into a full song bout dependent on the predator or on the modality in which the predator was encountered. For example, a visual raptor model never elicited song, and an acoustic playback of a predator call rarely did so either. However, a visual model tiger or clouded leopard always elicited full singing, and a visual model snake provoked mixed results. This indicated a differential response pattern was at work based on a variety of factors including, but maybe not limited to: predator identity or mode of attack, and the sensory modality in which the predator was encountered. This chapter suggested that gibbons were able to tailor their predator-response level: firstly they were able to extract information from the stimulus regarding the magnitude of the potential threat it represents, and secondly they could use this information to respond in an appropriate way.

Behaviourally, predator-specific differences were also evident, and detailed in chapter 6. Gibbons reliably responded with anti-predatory behaviours such as defecation, drops in canopy height, and increased vigilance, when presented with a visual predator model, but these behaviours were absent when presented with a visual control model. Also, in some cases gibbons increased group cohesion after seeing a predator model but not after seeing a control model. Acoustic predator stimuli

elicited vigilant behaviour and approach more often than non-predator heterospecific alarm call stimuli, except when the non-predator stimuli followed a predator stimulus. This suggested that gibbons linked the alarm call stimuli to the previous predator stimuli, and showed that in some cases, even when a stimulus was directly indicative of a predator, gibbons could withhold their usual loud display until they had further confirmation of its presence or level of threat. Furthermore, these data implied they had somewhat of an understanding about the nature of predator behaviour - a sophisticated cognitive undertaking that advocates the white-handed gibbon and its sister species receive much more empirical attention in terms of their cognitive capacities, and especially in the light of their troubling current conservation status. In general, the data presented in chapter 6 implied a multifaceted anti-predatory behavioural repertoire, which presumably explains the gibbons' apparent safety from potential predators despite their small stature and the array of big cats, eagles and snakes that share their habitat.

Finally, this thesis presented evidence for context-dependent signals among the gibbons' close-range calls. Chapter 7's examination of one such close-range vocal signal, the hoo call, revealed that despite its myriad contextual uses, the hoo call is reliably distinct in several different contexts across individuals of both the same and opposite sex. With regards to predation, the predator hoo call is distinct from feeding, duet, encounter and other hoo call contexts. Even within the predator context, the raptor hoo call is an acoustically distinct call unit from both the tiger and leopard hoo call units. This means that close family members can probably determine not only the presence of a potential predator, but also its identity as either a ground or aerial predator from these hoos alone.

At the functional level, data from the previous chapters suggest that gibbons communicate about predator identity to other close members of their own group first, with low frequency hoo calls, presumably because of the genetic benefits of protecting immediate relatives. Later they communicate to the predator itself, distant group members, and neighbouring groups with loud elaborate predator songs. The matching neighbour-response songs presented in chapter 5, seemed to also support the kin-selection hypothesis; however, the pursuit-deterrence hypothesis was supported with data from chapters 4 and 6 that revealed gibbons mobbed and harassed potential predators. These two chapters also revealed neighbouring groups did not consistently respond to predator songs, again belying the idea that songs were designed to primarily alert family in neighbouring groups. Communication with neighbouring groups may therefore be a coincidental by-product of loud predator song, but one that has had far-reaching implications. It is obvious that conspecific receivers recognise and utilise the information contained in predator song to help protect themselves against attack as well, but since this was probably not the original function of predator song, its ability to deter a predator should now be tested. To this end, it would be of interest to determine whether a hunting predator could distinguish between predator songs and normal duets as measured by its likelihood to leave the area of song production. If loud predator song discouraged a predator significantly more often than duet song, this would corroborate the pursuit-deterrence hypothesis as a driving force behind gibbons' loud alarm displays. Indeed, other research indicates that leopards on the Ivory Coast abandon their hunting behaviours if presented with high volumes of monkeys' leopard alarm calls (Zuberbühler et al. 1999).

The empirical chapters in this thesis have demonstrated that there is much to be learnt from the gibbons. What is particularly clear is that they possess a complex and rich repertoire of vocal signals, some of which are arranged using combinatorial rules similar to those used in human language and these vocal patterns are meaningful to other individuals. Others are subtly distinct quiet calls that qualify as context-dependent vocal signals, not unlike human words. Gibbons use song as an important means of communication. In terms of song phylogeny, gibbon duet song almost certainly evolved under strong sexual selection since it is an important part of the mated pairs' daily routine, and probably serves to strengthen the pair bond even though its primary function seems to be in communicating about it with other groups. It is possible therefore that gibbon predator songs have secondarily been adapted from duets to communicate about the presence and identity of a predator. Gibbon post-predator songs and other duets elicited by non-predator stimuli have also probably been secondarily adapted to communicate about different objects and events in the environment. At some point then, singing acquired a central role in the gibbons' behavioural repertoire – perhaps paralleling with the appearance of musicality in human evolution. Sexual selection probably shaped our aptitude for music since it has no other obvious genetic benefits (Miller 2000). There is also reason to believe that the evolution of music is related to the evolution of language (Vaneechoutte and Skoyles 1998). Sexual selection could therefore have shaped non-human primate vocal communication in general, driving ever more complicated vocal arrangements and favouring individuals with enhanced memories, organisational skills and learning abilities. In terms of language ontogeny, it plausible that the human aptitude for singing, driven by generations of selection pressures, provided singers with mental representation abilities (linking sounds to behaviours), mental syntax (understanding

the relation between different mental representations) and vocal flexibility (brought about by neural control of respiration). These abilities are all crucial pre-requisites for spoken language; having been already hardwired in the brain, these could have then been expanded for use in linguistic syntax by memetic selection only recently - within the last 100,000 years of human evolution (Vaneechoutte and Skoyles 1998). However, many other primate species use vocalisations as an essential form of communication, and more and more examples of them also using referential communication, context-specific vocal labelling or syntax are appearing in the literature (see chapter 5). These and other studies highlight the non-human primates' already existing ability to make mental representations or use mental syntax. What is missing is the vocal flexibility to produce the variety of sounds that the human vocal tract is capable of; non-human primates simply do not have the physiological adaptations necessary for speech (Lieberman et al. 1969). Singing then may very well have shaped the evolution of the human vocal tract enabling it for its later use in spoken language, but the underlying neural processes and cognitive precursors to language were probably already present. Environmental instability and the daily challenges of avoiding predation, locating food and finding mates were very likely compelling factors in the development of complex cognitive abilities in the hominin lineage (Potts 1996). However, ancestral musical ability and recent memetic selection may have aided in the development and subsequent application of the components specifically necessary for human language. In addition, human speech requires vocal learning, something which has yet to be widely demonstrated in other primates including gibbons (Brockelman and Schilling 1984), but which is regularly found in songbirds (Wilbrecht and Nottebohm 2003). Interestingly, songbirds also have the neural control necessary for vocal flexibility, and in some cases are able to utter

human words. An example is the myna bird, a member of the Sturnidae family. It is likely that birds and humans have independently evolved vocal learning, and its absence among non-human primates either suggests that vocal learning is a relatively recent adaptation in primate evolutionary history, or that studies thus far have failed to extricate its relevance in non-human primate vocal communication.

The gibbons represent a real-life modern-day example of a species other than humans that also utilises complex vocal behaviour; this probably originally evolved under strong sexual selection, but has secondarily been adapted towards a whole suite of contexts, including dealing with predators. Gibbon song, like human language is also highly indicative of neuronal control and complex temporal modulation (see chapter 2). Gibbons therefore offer an exciting potential avenue for further research into how the physiological byproducts of singing relate to the expressive potential of complex vocal communication. What seems clear from this thesis and works with other primates is that the tools for higher cognitive function were already hardwired in the brains of our distant primate ancestors, and that the comparative approach is the most valuable way to examine how these tools have been implemented through evolutionary time.

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