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# Abstract

Gibbons are small, arboreal apes that sing to defend their territory and exclusive access to mates from same sex conspecifics. It is thought that singing is an energetically costly activity and is influenced by the energetic level of the singing animal. It is also thought that the song of the gibbon carries information about the strength of the pair bond; the relationship between the mated pair, to be displayed to other groups as a deterrent to territory invasions. I used focal time sampling to collect behavioural data on two groups of Bornean agile gibbons (*Hylobates albibarbis*) living in the Natural Laboratory of Peat Swamp Forest in the Sabangau Catchment, Central Kalimantan, Indonesia that related to social, feeding, ranging and territoriality. My intention was to use multiple regression and Spearman's rank correlation to find evidence to refute or support the suggestion that differences in energy balance, social behaviours implicative of a strong pair bond and the occurrence of intergroup encounters influenced the level of singing behaviour. Difficulties encountered during the statistical analysis however meant that results were inconclusive with relation to energy balance and intergroup encounters. We did find some evidence however that behaviours associated with pair bond strength are not associated with changes in time spent singing, the time the gibbons began to sing, length of song bouts, number of great calls and group position in the morning chorus of gibbon calls, although a small sample size means these results should be considered with caution. If correct these results could imply that pair bond strength is not an important influence on singing behaviour.

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## List of abbreviations:

- -NLPSF - The National Laboratory of Peat Swamp Forests

- -OuTrop - The Orangutan Tropical Peatland Project

- -CIMTROP - The Center for International Cooperation Management of Tropical Peatland

- -GPNP - Gunung Palung National Park

# Chapter 1: Introduction

## 1.1.1 The Hylobatidae

The gibbons are the small, arboreal apes of the Hylobatidae family. While their precise taxonomy has undergone recent changes and is still disputed it is generally accepted that there are approximately 16 species of gibbon living across South East Asia (Blair, et al., 2011 Geissmann, 2007; www.iucnredlist.org, 2015; Thinh, et al., 2010). Possibly the most notable feature of gibbon behaviour is their propensity to produce loud, distinct songs which have been suggested to fulfil a number of functions, including territory defence, mate defence, mate attraction, intergroup spacing and the maintenance of the bond between mated individuals (Cowlishaw, 1996; Fan, et al., 2009a; Mitani, 1985; O'hagan, 2013).

The influence that energy balance and intake might have on such features of the gibbons' singing behaviour as the number, timing and length of song bouts has been briefly discussed by other authors (Bartlett, 1999; Fan, et al., 2008a). In this study on Bornean agile gibbons (*Hylobates albibarbis*) it was my intention to look at the potential influence of energy balance in further detail, examining such factors as the proportion of figs, leaves and fruit in the gibbon diet, as well as their daily path length and the proportion of time spent travelling. I looked at the potential influence that the relationship between the mated pair (represented by the proportion of social behaviours linked to pair bond strength in the activity budget) and encounters with neighbouring groups might have on singing behaviour. I intended to try and elucidate to what level and in what proportion with regards each other these factors influence gibbon singing behaviour.

Understanding the nature of such relationships may help us to understand how both the physical and social environment influences gibbon singing behaviour. It may also help us to infer social, feeding and ranging behaviours merely from listening to the animals sing. Such a technique would be non-invasive and offer an alternative to many thousands of hours of research time. Furthermore the energy balance and intake of gibbons has been suggested to be a good indicator of environmental health in tropical rainforests, especially when used in conjunction with other indicators (Harrison, et al., 2005). Learning more about the relationship between energy balance and intake as well as singing behaviour may allow future researchers to use measurements of singing behaviour as a further indicator. It is also possible that the health of the gibbons themselves is connected to singing through energy balance and that we may be able to assess the health of individual gibbons and entire populations by quantifying their singing behaviour. Audio survey techniques are frequently used to assess the size of gibbon populations across South East Asia from listening to their singing (Brockelman & Srikosamatara, 1993; Buckley, et al., 2006; Cheyne, 2011; Phoonjampa & Brockelman, 2008). Any increase in our knowledge of what influences singing behaviour and how it does so could improve our use and interpretation of these techniques.

In Central Kalimantan, like much of Indonesia gibbons are threatened by hunting for meat and the illegal pet trade as well as the clearing, conversion and fragmentation of their habitat for the purposes of palm oil agriculture, logging and mining (Campbell, et al., 2008; Cheyne et al., 2008; Geissmann, 2007; Haag, 2007; Nijman, 2006; www.iucnrelist.org, 2015) in addition to habitat loss from forest fires (Cheyne et al., 2008; Cowlishaw, 1992; Haag, 2007). Gibbons also have relatively long interbirth intervals and only reach sexual maturity after many years (Cheyne, 2010; Geissmann, 2007). This slow life history makes them especially vulnerable to threats as they are unable to recover quickly (Buckley, et al., 2006).

Gibbons have been referred to by (McConkey & Chivers, 2007) as "one of the most important frugivores in Asian rainforests" because of the vital role they play in forest ecology as seed dispersers. Of all the species of seeds that gibbons consume 81% of species were capable of germinating after passing through the gibbon gut. This highlights the value of this group of species to the continued health of these vulnerable habitats. When considered alongside the numerous threats they face the importance of studying the biology and ecology of these primates becomes apparent, especially if it leads to improvements in the techniques used to assess and conserve them, or the dwindling habitats in which they live.


## 1.1.2 Taxonomy and Biogeography

The gibbons, along with the great apes, form the Hominoidea superfamily in the Order of Primates. The four genera of gibbons (*Hylobates, Nomascus, Hoolock & Symphalangus*) comprise the 16 officially recognised species (Groves, 2001; www.iucnrelist.org, 2015) that make up the Hylobatidae family. They are almost exclusively arboreal and found in numerous tropical and subtropical forests across a range of East Asia (See **Figure 1.1** for a distribution map), as far north as Myanmar and north-east India and as far south as Java. While gibbon species are typically allopatric (with the notable exception of *Symphalangus syndactylus* with *Hylobates lar* and *agilis*) when multiple species are present on a continuous landmass large rivers and mountain ranges often form the boundaries between them. Where these barriers break down however, for example near the headwaters of such rivers, hybrid zones frequently occur, for example between *Hylobates lar* and *H. pileatus* (Geissmann, 1984), *H. albibarbis* and *H. muelleri* (Mather, 1992), *Nomascus gabriellae* and *N. leucogenys* (Kim, et al., 2011) and *N. leucogenys* with *N. concolor* (Mootnick, 2006) amongst others.
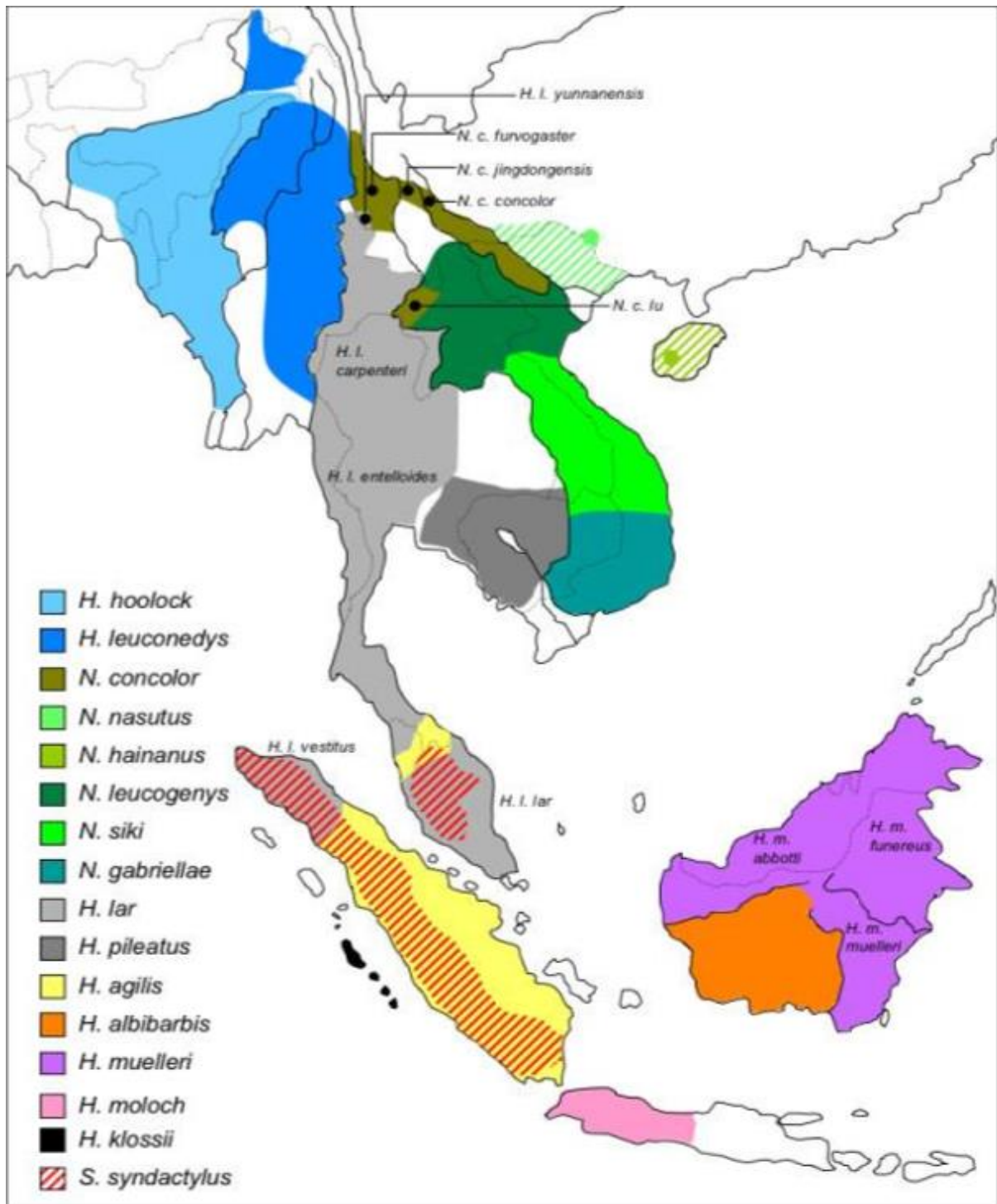
(Figure 1.1. A map showing the global distribution of the 16 gibbon species in the

Hylobatidae family. Image from Thinh, et al., 2010.)

The precise taxonomy of the Hylobatidae has undergone many recent alterations, one of the most important being the revisions of Geissmann, 2007, which suggested uplifting the four taxa of *Hoolock leuconedys*, *Hylobates albibarbis*, *Nomascus siki* and *N. hainanus* from subspecies to species level classification, raising the total number of recognised species to 16 and subspecies to 12, with 28 total individually distinguishable taxa. Gibbon taxonomy remains to this day a contentious and controversial subject and future attempts at revisions using new and old techniques are likely (Kim, et al., 2011); Mootnick, et al., 2010; Thinh, et al., 2010).

The four currently accepted genera are based on differences in chromosome number, although previously all gibbons were classified in the Hylobates genus (Prouty, et al., 1983). Across the family the size, anatomy and behaviour of the gibbons is very similar, meaning that constructing taxonomic trees before the advent of genetic techniques was difficult (Chivers, 1984). Taxonomic confusion has led to difficulties in maintaining and recording captive populations, with many individuals existing in collections (such as zoos and rescue centres) today being incorrectly identified (Mootnick, 2006) or unknowing hybrids, sometimes of species that could never coexist in the wild, such as two individuals born to siamang (*S. syndactylus*) and Mueller's gibbon (*H. muelleri*) parents (Wolkin and Myers, 1980). A survey of European and North American zoos in the 1980s declared that 4% of all captive gibbons were unmistakably hybrids, and that the actual figure was likely much higher (Geissmann, 1995). Should healthy, viable captive populations be required in the future of gibbon conservation then this trend will undoubtedly prove problematic (Mootnick, 2006).

## 1.1.3  Physical Description

The gibbons themselves are smaller and possess a more upright, orthograde posture than their great ape relatives in the genera of *Pan*, *Gorilla* and *Pongo*. The various species range in weight from between 5 to 15kg (Bartlett, 2011). They are highly arboreal and possess proportionally long forearms, with flexible elbow and shoulder joints and powerful, specialised musculature in the shoulders, elbows and wrists (Michilsens, et al., 2008) which aid them in travelling through brachiation, a form of locomotion which involves the use of the forearms to propel the animal forward through the trees in a swinging motion while the body is suspended below the substrate (Cannon & Leighton, 1994). This is the principal form of locomotion for the Hylobatidae (Cheyne, 2010; Cheyne, et al., 2013; Michilsens, et al., 2008). Gibbons also possess ischial callosities, regions of tough, callus-like tissue on their lower pelvis, a trait which is shared with the Cercopithecidae family of Old World monkeys but not the Hominoidea. This feature is thought to serve as a "sitting-pad"; an aid when sitting or sleeping on bare branches, as gibbons do not make nests like the other apes (Rose, 1974). Gibbons show very little sexual dimorphism. Neither sex is substantially larger than the other and both possess large canines which may be used as aids in either feeding or territorial defence (Barelli, et al., 2008; Cheyne et al., 2010).  Pelage colouration is highly variable between species and comes in many shades of black, brown, gold or cream. Some species such as those in the *Nomascus* genus show unusual patterns of sexual dichromatism and colour change from immaturity to adulthood. Sexual dichromatism and immature colouration can be present or absent depending on the species (Mootnick, 2006).

## 1.1.4  Feeding and Ranging

Described gibbons have been described as specialists in ripe, non-fig fruits with diets augmented by figs, flowers and leaves when their preferred foods are not available (Leighton, 1987). An exception to this is *Nomascus concolor* which is said to be more folivorous than other species, possibly due to a lack of fruits, both fig and non-fig, in its atypically cold, montane forest habitat (Fan, et al., 2009b).

The gibbon diet is considered highly seasonal, (although this depends on the habitat) with more preferred foods such as fruits being available in the rainy season and less so in the dry season (Bartlett, 2009; Fan, et al., 2013; Fan, et al., 2008b) which forces the gibbons to fall back on less preferred foods. In *Hoolock leuconedys* and *N. nasutus* this tends to be young leaves and buds (Fan, et al., 2012; Fan, et al., 2013) while for the *H. albibarbis* population living in Gunung Palung National Park (GPNP) figs, unripe fruits and liana products fill this role (Marshall, et al., 2009; Marshall & Leighton, 2006). For *S. syndactylus* living in Sumatra flowers are also an important fallback food (Lappan, 2009). Invertebrates are also consumed in small amounts (Cheyne, 2010; pers. obs.) but in some species and habitats, such as with the *Hylobates lar* in Khao Yai National Park, Thailand, invertebrates are thought to play a more consistent and ecologically important dietary role (Bartlett, 1999). The predation of gibbons on vertebrates such as lizards, the chicks and/or eggs of birds, (unidentified species) and mammals (*Petaurista philippensis)* has been recorded in *N. concolor* although this is an exceptionally rarely documented behaviour (Fan, et al., 2009b).

The influence of food availability on the ranging patterns of gibbons varies between species and is likely to be dependent on environment. Gibbons are thought to have a cognitive map which allows them to remember and locate clumps of preferred foods that are temporally and spatially segregated (Asensio, et al., 2011). In Khao Yai National Park, Thailand the travel time of *H. lar* increases with decreasing fruit availability and this has been described as a trade-off; the animals committing more time and energy to search for more valued fruits that will contribute more calories to their diet (Bartlett, 1999; Bartlett, 2009). *Hoolock hoolock* and *N. concolor* however decrease travel time and spend more time resting when fruit was low, (Fan, et al., 2013; Fan and Jiang, 2008). This was interpreted as cutting their losses and not wasting energy on searching for increasingly rare fruits. Here fallback foods such as leaves and flowers are abundant and uniformly distributed, which may explain the decreased travel time as the gibbons focus on these easy to reach, lower quality foods (Fan, et al., 2008b). The interaction of feeding and ranging may be a result of just how temporally and spatially rare preferred foods are in comparison to fallback foods  So far studies have not shown any change in travelling time in *H. albibarbis* with changing fruit scarcity (Marshall, et al., 2009; Vogel, et al., 2009).


When travelling gibbons vary between climbing, clambering, jumping, bipedal walking and brachiating (Cheyne, et al., 2013), brachiating being the dominant form of travel, followed by jumping (Cheyne, 2010; Cheyne, et al., 2013). They are found to prefer moving through the emergent canopy in *H. albibarbis* (Cannon & Leighton, 1994) and are capable of crossing large gaps in the canopy of up to 12m, although this is subject to influence by forest disturbance (Cheyne, et al., 2013). The daily path length is approximately 2433m in *H. albibarbis* and 1254m in *H. lar* gibbons (Bartlett, 1999; Cheyne, 2010). Groups with ventral

infants also travel less, probably to avoid risking injury to the baby which might arise should it fall while it's mother is moving quickly (Cheyne, 2010).

## 1.1.5 Social structure

Typically, gibbon groups are formed of a male, female and their immature offspring. The mated pair form a long term bond and defend an exclusive territory from other gibbons (Cowlishaw, 1992). For much of the history of Hylobatidae research the taxa at large has been considered sexually monogamous, with individuals mating with only a single partner for their entire life (Bartlett, 2011). Another longstanding tradition of gibbon research describes how they show surprisingly little intragroup social behaviour (Leighton, 1987). Both of these view have been eroded over the last few decades as more and more evidence has shown that gibbon sociality is not so simple (Fuentes, 2000). Gibbons are not strictly monogamous. Both mates in a dyad may attempt to take part in extra-pair copulations with non-group individuals (Palombit, 1994a  Reichard, 1995; Reichard & Sommer, 1997), may desert their partner or be forcefully replaced by an invading individual of the same sex, who will also inherit their territory (Brockelman, et al., 1998; Koda, et al., 2012; Palombit, 1994b). While social monogamy is indeed the most frequent form of social organisation in most instances, stable polygynous groups (in *N. concolor*, (Fan, et al., 2009a) *H. pileatus* (Srikosamatara & Brockelman, 1987) and polyandrous groups (in *H. lar* (Borries, et al., 2011) *S. syndactylus* (Lappan, 2008) do occur, although they are not the norm in any species. It is unclear why gibbons should display social monogamy in the majority of instance when there would be an obvious benefit to their fecundity in alternative strategies. Males in polygynous groups father more offspring, and in polyandrous siamang groups males are thought to indirectly contribute

to greater reproduction rates in females by providing additional care to the offspring (Lappan, 2008).

It is possible that infanticide, historical or present may explain the existence of gibbon social monogamy. The act of males devoting the majority of their time to guarding a single mate is considered an effective counter to infanticide in other species of mammals (Opie, et al., 2013; Van Schaik & Dunbar, 1990). Evidence of the presence of infanticide in gibbons has not been forthcoming however. In fact in *H. lar* in instances where the resident group male has been replaced, invading males have been shown to display great tolerance for existing offspring (Brockelman, et al., 1998; Reichard & Sommer, 1997). However, an isolated incident reported in (Borries, et al., 2011) described how when a new male joined a monogamous group of *H. lar* to form a polyandry, the infant, which was between 3-21 months old disappeared shortly afterwards and was presumed to have died. This incident was considered by the author to be the first and only (albeit circumstantial) evidence for infanticide in gibbons.

Gibbons are also being shown to display more intragroup social behaviour than previously thought (Bartlett, 2003). The processes of emigration, mate desertion and replacements form non-nuclear family groups, where offspring are not necessarily related to the present adults. This may entail the existence of more complex social lives (Brockelman, et al., 1998). In fact it has been shown that the replacement of individuals from pre-existing groups is the most common strategy for dispersing gibbons to form groups, rather than inheriting their natal territory or occupying a previously empty territory space with another recently dispersed mate (Guan, et al., 2013). In *H. lar* extra-group emigrants and offspring that have passed the age of dispersal may be tolerated in a group because they contribute to territory defence, and because they participate in grooming and playing with the immature group members, which may benefit them in their development (Brockelman, et al., 1998; Guan, et al., 2013;

Reichard & Sommer, 1997). In situations where environments are saturated with existing gibbon territories it could be beneficial for young gibbons to stay in their natal group until they are large enough to displace the adults of other existing groups (Brockelman, et al., 1998). Grooming, which is thought to ease tension and helps maintain social bonds in many species of primates (Dunbar, 1991; Schino, 2001) could be the way in which these gibbons achieve the tolerance of other, senior group members. In *N. concolor* both new immigrants and offspring past the age of dispersal spent more time grooming than older residents, and targeted older residents for grooming more frequently (Guan, et al., 2013).

The relationship between mated individuals is referred to as the pair bond. Mated gibbons are thought to vary in the strength of their relationship and individuals with stronger pair bonds should theoretically invest more energy into territory or mate defence and are less likely to desert (Palombit, 1996). Higher levels of mutual grooming, behavioural synchronization and the maintaining of a short distance between the mated pair are thought to be indicative of a stronger pair bond (Cowlishaw, 1992; Palombit, 1996). It is also possible that other social behaviours such as playing and cofeeding represent the strength of a relationship between mated pairs as these behaviours also require the animals to retain close proximity and tolerate each other around food. Although playing is rather uncommon in adults. There is little sexual dimorphism between males or females in either tooth or body size (Barelli, et al., 2008), which has encouraged the view of these animals as codominant (Smuts, 1987).

Gibbon groups are highly territorial, and defend an exclusive range from neighbouring groups. The defence of this territory is speculated to be the principal function of gibbon singing (Cowlishaw, 1996; Haimoff, 1984; Mitani, 1985). When a group or individual gibbon breaches the boundaries of a neighbouring territory then the territory holders may act aggressively towards them, alarm calling, displaying, shaking branches and even chasing, grappling and biting them (Bartlett, 2003; Cheyne et al., 2010). Typically the male plays the

largest role in aggressive intergroup encounters (Bartlett, 1999; Reichard & Sommer, 1997) although females have been seen acting aggressively, alarm calling, mobbing and sometimes physically attacking extra-group individuals (Cheyne et al., 2010; Haag, 2007). It is thought that having a dependent infant limits the aggressive role females can play in encounters for risk of harming the infant (Mitani, 1987).

It is believed by Cowlishaw, 1992 & Reichard & Sommer, 1997 that when female gibbons sing and behave aggressively towards neighbouring groups it is to defend their territory and the food that it contains, while when males behave in this way it is to defend their exclusive access to their mate/s. This model of territoriality might exist because the fruit that gibbon primarily feed on are found in small patches scattered geographically and temporally and are capable of being monopolised by a single group. It is true that in *H. lar* nearly half of all encounters were within 25m of a feeding tree (Bartlett, 1999). Encounters between groups are not always hostile however. In *H. lar* they can be affiliative, with the adult gibbons from both groups resting and travelling in close proximity while the infants play (Bartlett, 1999; Bartlett, 2003). Extra pair copulations are also known to occur in these situations (Bartlett, 2003; Reichard & Sommer, 1997).  Around a quarter of all encounters between *H. lar* groups in this study were non-hostile (Bartlett, 1999).

## 1.1.6 Conservation

Gibbons across the world are at risk of numerous threats including hunting for food and traditional medicine, the illegal trade in young gibbons as pets, the loss, fragmentation and conversion of their habitat in the name of such industries as palm oil, lumber, paper, coffee, rubber and food crops. Forests are also at risk of encroaching human settlements and destruction in forest fires which are facilitated by irresponsible agricultural practices

(Campbell, et al., 2008; Cheyne et al., 2008; Geissmann, 2007; Haag, 2007; Nijman, 2006; www.iucnrelist.org, 2015). Some populations are at such low numbers that they have become more vulnerable to inbreeding and genetic drift and the further complications that these cause (Blair, et al., 2011; Duckworth, 2008; Geissmann, 2007). In 2015 every species of gibbon is considered Endangered or Critically Endangered by the IUCN Redlist (www.iucnrelist.org, 2015). One species, the Hainan black crested gibbon (*Nomascus hainanus*) is the rarest of all primates, consisting of approximately 25 individuals in one population on the island of Hainan, China (www.iucnrelist.org, 2015). The Yunnan lar gibbon (*H. lar yunnanensis*), a subspecies of the lar gibbon may already be extinct, with no confirmed recordings since 1992 (Phoonjampa & Brockelman, 2008).

## 1.2 Study Species

The subject of this study is the Bornean agile gibbon (*Hylobates albibarbis*), also known as the southern Bornean gibbon or the white-bearded gibbon. Until recently it was considered a subspecies of the agile gibbon (*H. agilis albibarbis*) but has since been given full species classification (Geissmann, 2007; Groves, 2001). There is in fact little genetic distance between *H. agilis* and *albibarbis* but (Hirai, et al., 2005) consider differences in DNA structure and morphology to be significant enough to support the division. The Sumatran agile gibbon most notably possess a chromosomal arm translocation between chromosomes 8 and 9 which is not present in their Bornean counterparts.

The pelage of this gibbon may be many variants of brown. It possesses a dark brown cap, hands and feet while the rest of its body may vary from dark brown to tawny depending on the individual. The brow is a distinct pair of white lines. The cheeks and chin may also be white, especially in juveniles and adult males, although it is darker and comparable with the

rest of the pelage in adult females (Mootnick, 2006). Measurements on a small sample of specimens put the weight of adult males at 6.1-6.9kg and females at 5.5-6.4kg (Cheyne, 2007). They are found in a variety of tropical forest subtypes across Indonesian Borneo, including primary and secondary evergreen forests, and various lowland peat swamp forest types, both intact and disturbed (www.iucnrelist.org, 2015). Its global range is bordered by the Kapuas River to the west, the Barito River to the east, the Busang River to the north and the Schwanner Mountains to the south and east (Cheyne, 2007) (See **Figure 1.2.** for the global range of *H. albibarbis*).  The Kapuas and Barito rivers separate its range from that of *H. muelleri* although the two species are known to hybridise where this barrier is incomplete, such as at the headwaters of the Barito River (Geissmann, 1995; Mather, 1992).

(**Fig 1.2.** Showing the island of Borneo, divided between the nations of Indoensia, Malaysia and Brunei. The global range of the Bornean agile gibbon (*H. albibarbis*) is depicted in yellow. Image from www.iucnrelist.org, 2015)

The species predominantly feed on fruits, especially in the wet season. In the dry season their diet expands to include more leaves and flowers. Invertebrates are also eaten in small amounts (Cheybe & Shinta, 2006; Marshall, et al., 2009; pers. obs.). There are 77 species of confirmed food plants, all of them trees, lianas, figs or epiphytes (Cheyne, 2010). Many of these provide fruit irregularly in a non-seasonal pattern and are important for supporting gibbon populations all year round. In the Sabangau at least figs are not considered to occupy

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the role of fallback foods that they do in other areas, including the GPNP (Cheyne, 2010; Marshall, et al., 2009) where figs are thought to have a substantial impact on gibbon populations. Foods that are high in tannins or with a tough outer casing are generally avoided (Cheyne, 2010).

The group defends a territory of approximately 390-520m$^2$, this is thought to overlap about 15% with that of neighbouring groups but intergroup encounters are thought to be infrequent (Cheyne, 2010; Cheyne et al., 2008). The daily path length is approximately 2433m (with a range of 1030-5310m) which decreases in the wet season and increases in the dry (Cheyne, 2010; Cheyne et al., 2008). Mating occurs year round, gestation lasts about 7 months and births occur between November and May. The interbirth interval is about 2.4 years (Cheyne, 2010). One notable feature of the Bornean agile gibbon is that they enter their sleeping tree and end their feeding and ranging activities approximately 260minutes before sunset, much earlier than other gibbon species. This might be to avoid feeding competition with sympatric orangutans (*Pongo pygmaeus*) and monkey species which stay up later (Cheyne, 2010). The gibbons share 69% of their diet with the orang-utans and are known to be chased from feeding trees by them.

The mixed swamp forest of the Sabangau was estimated to contain roughly 10.7 individuals per km$^2$ in 2010 (Hamard, et al., 2010). Densities of 8.7 individuals/km$^2$ were estimated in the predominantly heath forest of Tanjung Puting National Park (Mather 1992), and 14.9 individuals/km$^2$ in the largely montane forest of the GPNP (Mitani, 1990). An estimated total of over 25'000 gibbons are thought to live in the entire Sabangau catchment as of 2008 (Cheyne et al., 2008), which would make it one of the largest contiguous populations of the ape left in the world. There has not been a total population analysis on the species as a whole due to the lack of studies in unprotected and smaller forest areas (Cheyne, 2011)

The Bornean agile gibbon is considered Endangered on the IUCN Redlist (www.iucnrelist.org, 2015) due to an estimated drop in population of 50% over the past 30 years and the next 15, approximately 3 generations for this species. Its principle threats are hunting for food and the pet trade and habitat destruction by forest fires and for logging and mining, both legal and illegal (Campbell, et al., 2008; Geissmann, 2007). Should rates of habitat destruction increase in future then the species may soon qualify for a Critically Endangered classification (www.iucnrelist.org, 2015).

# 1.3 Singing in Gibbons

All gibbons sing. These songs tend to be elaborate and unique to the species of gibbon and to the sex of the singer (Geissmann, 2002). Studies on hybrid gibbon in captivity (Geissmann, 1984) have confirmed that singing is at least partially genetically determined while the existence of females capable of singing the songs of their male counterparts (Cheyne, et al., 2007; Geissmann, 1983) suggests that there is also a significant learned component. Immatures learn to sing by copying their same-sex parent (Cheyne, 2010). In females the basic structure of the great-call is learned by the age of 6. Daughters co-sing less with their mothers as their song becomes a better copy of the original call (Koda, et al., 2013).

## 1.3.1 How Gibbons sing

Gibbons typically sing before or just after dawn (Marshall and Marshall, 1976; Mitani, 1985) usually from high in the canopy (Fan, et al., 2009a). The male and female sing different components which are combined into a duet in most species (Marshall and Marshall, 1976). Males typically, but not always begin a singing bout. In *Nomascus* species 95.3% are begun by the male (Coudrat, 2015). The male sings short phrases which build from simple to

complex (Geissmann, 2002). The female may also contribute simple short phrases but the duet is eventually dominated by her loud and distinct great call, which is believed to be the primary carrier of information in the song (Cowlishaw, 1992). The male will usually fall silent during the great call but will add a short, rapid coda to the interval afterwards (Cheyne, 2010). While gibbons do not sing on every morning it is still common for large numbers of groups to sing at the same time in what is referred to as a chorus. In (Cheyne, 2010) it was noted how no group consistently began the chorus and no connection could be found to explain a groups positioning in the order of singing on any given day.

Not all gibbon species follow this typical model of singing. Two species, *H. klossii* and *H. moloch* do not duet (Dooley, et al., 2013; Geissmann & Nijman, 2006; Tenaza, 1976). Instead the two sexes sing temporally segregated solo bouts (Geissmann, 2002). As the males and females of these species do not sing at the same time the males do not produce codas. Females of the *Nomascus* genera also do not produce anything other than the great call section (Geissmann, 2002).

The ancestral state of gibbon singing is disputed although (Geissmann, 2002) believes that the ancestor duetted. The "Song Splitting Hypotheses", created by (Wickler and Seibt, 1982) tries to explain the origin of duetting by suggesting that in the ancestral form both sexes sang the same components and that this was since divided between sexes in all species. This would explain the ability of some female gibbons to sing the male repertoire (Cheyne, et al., 2007; Geissmann, 1983). They would then have become temporally split at a later stage, resulting in the singing patterns seen in *H. klossii* & *moloch*.

## 1.3.2 The Purpose of Singing

While it has been noted that some gibbons also sing duets and great calls in response to predator sightings in a manner similar to an alarm call (Clarke, et al., 2006) it is accepted that their primary purpose is in intragroup communication. The duet can be heard by humans from approximately 1.1km away in dense woodland and can be long and highly redundant, features that make it ideal for the transmission of information (Mitani, 1985). In addition high levels of variation in the songs of individuals has been noted (Cheyne, et al., 2007; Haimoff & Gittins, 1985; Oyakawa, et al., 2007; Wanelik, et al., 2013) which suggests that a gibbon may be able to identify other individuals from their songs alone.

It is a common strategy in many vertebrates to use long range calling as a form of territorial defence. It is more common to see this in males rather than females (Delgado, 2006; Thorpe, 1961) and the vocalisation is typically a costly signal. As both male and female gibbons sing it seems that both are involved in territory defence. Playback experiments in *H. muelleri* were used to replicate territorial invasions. Female calls and duets played in the territory core triggered duets and group approaches, typically led by the female. When a male call was played then the group male did not sing but instead approached towards the singer silently (Mitani, 1984). Another study recorded aggressive brachiation displays by both sexes towards the speaker (Mitani, 1985). These studies provide evidence that singing is involved with the intergroup spacing of groups into exclusive territories. It was found by (O'hagan, 2013) that not all components of gibbon song transmit as far as others. A significant loss of signal content was noted by as little as 350m, implying that singing may be used both in inter and intragroup communication.

It was suggested by Cowlishaw, 1996 that females sing to defend territory and food while males sing to defend access to the female and possibly also to defend their offspring from the

risk of infanticide (Reichard & Sommer, 1997). Males may also sing to attract mates and as such it is a signal of male quality (Cowlishaw, 1992). Singing is also thought to be linked to pair bond maintenance (Geissmann & Orgeldinger, 2000).  Duets may advertise the existence of a pair bond between the animals and the occupancy of a territory and reduce the likelihood of invasions (Cowlishaw, 1992).

### 1.3.3 Influences on Singing

Singing is connected to food availability. In *Nomascus concolor jingdongensis* singing decreased as less fruit and more of the less preferred leaves were eaten (Fan, et al., 2008b). Similarly *H. lar* sang more when food was abundant (Cheyne, 2011). The implication being that singing is energetically costly, similar to in many territorial species (Clutton-Brock & Albon, 1979; Eberhardt, 1994; Oberweger, & Goller, 2001; Thomas, 2002; Thomas, et al., 2003)

It is also possible that the social situation of a gibbon influences singing behaviour. The playback experiment of (Mitani, 1985) also noted that over the course of the experiment which replicated invasions in *H. muelleri* that gibbons began to duet for longer on that day and in the immediate future. Similarly (Fan, et al., 2006) recorded an incident where a polygynous *N. concolor* group was faced with a persistent invading female over 4 days. During this period the female great called 2-3 times as frequently per day.  There is also evidence that duetting strengthens pair bond in Siamangs (Geissmann, 1999).

A meteorological influence has also been documented numerous times on the singing of gibbons. Wind strength was found to reduce the number of singing days in *H. pileatus* by Brockelman & Srikosamatara, 1993 and in *Nomascus* species song bout length was also negatively influenced by wind (Coudrat, 2015) although this has not been found to be the

case in *H*. *albibarbis*. Rain was found to reduce the number of singing days in *H*. *albibarbis* (Cheyne, 2008) and *Nomascus* species (Coudrat, 2015). The given thinking being that the rain causes the animals to become cold, necessitating them to begin feeding earlier to regain lost energy rather than singing. In *H*. *klossii* however male gibbons sang more frequently on cold days, but would not sing on mornings when it rained, although rain on the previous night would not influence them (Dooley, et al., 2013). The proposed explanation for this is that the rain interferes with sound transmission and any time and energy invested in singing would be wasted. This explanation may also hold true for the influence of wind strength.

In the Sabangau peat swamp forest fires are frequent, especially during El Niño years. It was found that *H*. *albibarbis* sing less and with shorter bouts during years with frequent fires (Cheyne, 2008; Harrison, et al., 2007). It is suggested that the excess smoke found in the forest during these years has a negative influence on the health of the gibbons, similar to the way it does on the humans living in nearby settlements and that this interferes with the gibbons' singing.

## 1.4 Objectives and hypotheses

Gibbon singing behaviour is highly variable in the short term with such variables as average bout length, total time singing, number of great calls and whether the gibbons sings or abstains in a given day changing on a day to day basis. As described in the above chapter singing behaviour is believed to be influenced by such factors as energy balance and social environment.

In this study I will address three statements:

1. That singing is energetically costly, and the energy balance of an animal will influence their singing behaviour. Gibbons with a higher energy balance should devote more time and energy into singing behaviour.

2. That singing is influenced by the strength of the relationship between the mated pair. Gibbons that display signs of a strong pair-bond will devote more time and energy into singing.

3. That intergroup encounters are challenges to the exclusive rights of a gibbon to territory or mate. Gibbons that experience intergroup encounters will afterwards devote more time and energy into singing behaviour to reaffirm this exclusivity.

It is the objective of this study to provide evidence to support or refute these statements. To do this I will test the following hypotheses:

Hypothesis for Statement 1:That gibbons that feed more on non-fig fruits, less on leaves and figs, spend less time travelling and more time resting will be unlikely to abstain from singing, spend more time singing, start singing earlier in the morning, will have an earlier position in the chorus and produce more great calls per day (if female).

Hypothesis for Statement 2: That gibbons that take part in more grooming, playing and cofeeding with other group members will be unlikely to abstain from singing, spend more time singing, start singing earlier in the morning, will have an earlier position in the chorus and produce more great calls per day (if female).

Hypothesis for Statement 3: That gibbons that have undergone recent intergroup encounters will be unlikely to abstain from singing, spend more time singing, start singing earlier in the morning, will have an earlier position in the chorus and produce more great calls per day (if female).

# Chapter 2: Methods

## 2.1 Study Area

The study took place at the Natural Laboratory of Peat-swamp Forest (NLPSF), formerly known as the Setia Alam logging concession, in Central Kalimantan, Indonesia, approximately 20km south-west of the provincial capital of Palangka Raya (Coordinates: 2° 31' S and 113° 90' E). The site covers 500km$^2$ of the north-eastern Sabangau catchment, which is a partially forested 9,200km$^2$ area between the Katingan and Sabangau rivers ( Of this area approximately 6,300km$^2$ remains covered in peat swamp forest, making it the largest area of lowland forest left in Borneo. The site rests at about 10m above sea level. The temperature ranges from between 18-38° with an average of 26° and 232mm average rainfall per day (Husson, et al., 2008). **Figure 2.1** shows the location of the NLPSF in Borneo.
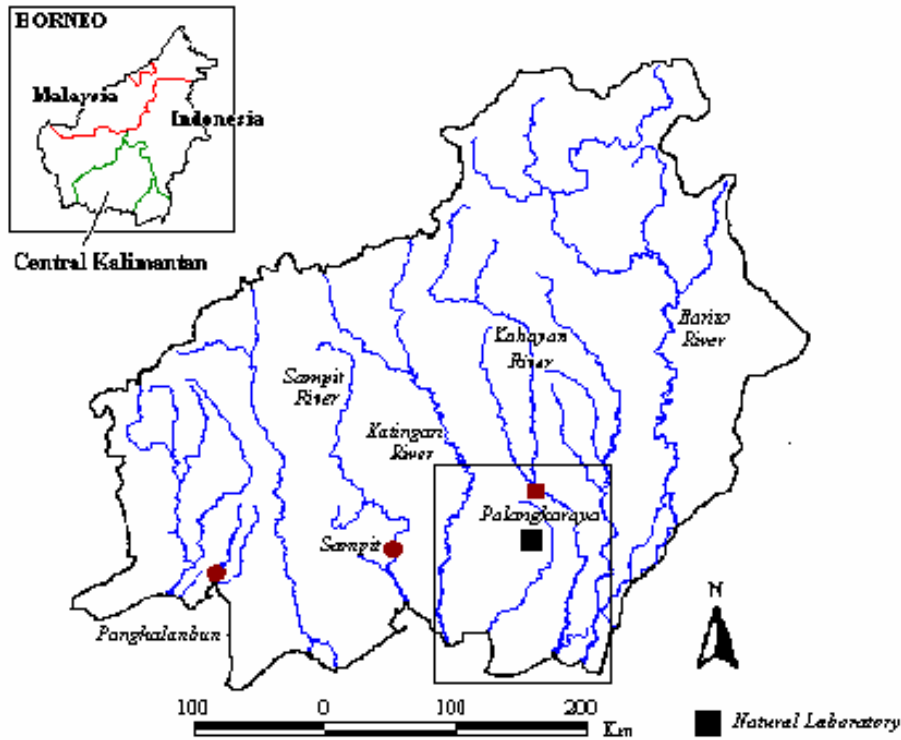
(**Figure 2.1**. showing the island of Borneo. The black square represents the location of the

NLPSF while the red square represents the location of the nearby city of Palangka Raya.)

The Sabangau contains a progression of four different forest types from the river to the top of

the peat dome; mixed swamp forest, a mixed swamp forest-low pole forest transition area,

low pole forest and tall interior forest (Page, et al., 1999). It is recognised as a low

productivity habitat (Morrogh-Bernard, et al., 2003). The forest floods annually between

October and June. It contains the largest populations of orangutans (Morrogh-Bernard, et al.,

2003) left in the world and one of the largest populations of the Bornean agile gibbon

(www.iucnrelist.org, 2015) as well as many more species uniquely adapted to its unusual

habitat (Haag, 2007).

The NLPSF forest was selectively logged for 30 years, and was illegally logged for several years after the official closure of the concession. In 1996 the Mega Rice Project was created, which aimed to transform 1'000'000 hectares of peat swamp forest in Central Kalimantan into agricultural land. It was later discovered that the soil pH of the targeted area was too low to efficiently grow rice and the project was abandoned, but not before significant damage had already been done to the Sabangau forest (Aldhous, 2004). Drainage canals in excess of 4,600km were cut into the forest, effecting the hydrology of the area and drying out the highly flammable peat which makes up a large proportion of the catchment. Ever since then fires have been a major threat to the forest, especially during the droughts brought by El Niño years. While further areas of forest are destroyed (Cheyne, 2008; Harrison, et al., 2007) the smoke released has been implicated in causing health complications in both humans and animals (Cheyne, 2008). The release of large volumes of carbon dioxide trapped in the peat is also thought to be a large contributor to climate change (Haag, 2007). The smoke from these fires has been shown to reduce the amounts of singing seen in the resident gibbons (Harrison, et al., 2007). During the length of this study no forest fires occurred. An area of 5,300km2 of the Sabangau forest was officially declared a National Park in 2005.

The NLPSF is operated and maintained by the Center for International Cooperation Management of Tropical Peatland (CIMTROP), based out of the University of Palangka Raya. The Orangutan Tropical Peatland Project (OuTrop) works in partnership with CIMTROP to research and conserve the forest and the animals that live within. OuTrop has been operating in this area since 1999 and behavioural research on the resident gibbons has been ongoing since 2005.

The study took place within 6km$^2$ area of the NLPSF. It contains many intersecting transects cut into the forest, organised and labelled into a grid system which allows quick and easy

navigation of the forest (**Figure 2.2**. shows a map of these transects). This area can be described as recovering mixed swamp forest.
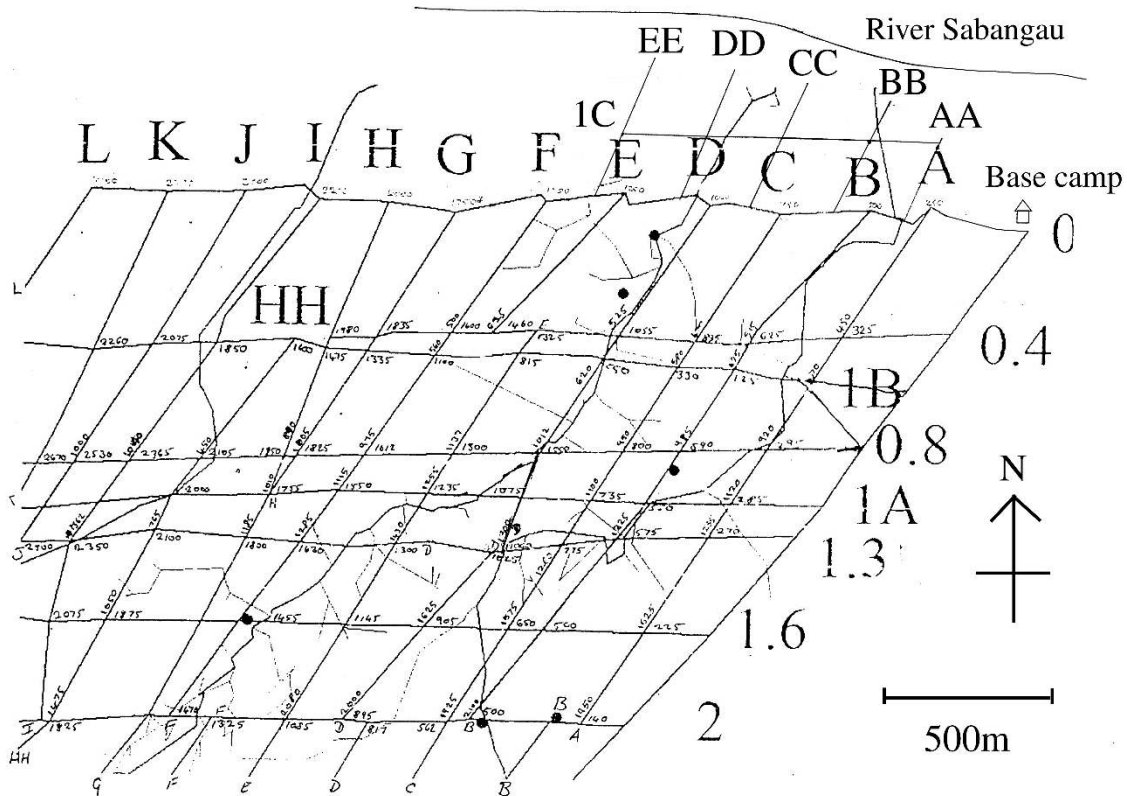


(**Figure 2.2.** showing the transect lines cut into the mixed swamp forest of the NLPSF. The basecamp is visible in the upper right hand corner and north of that the Sabangau River.)

## 2.2 Study groups

Four focal animals split between two groups were followed during this study. All four were well habituated and the territories of the two groups were well known. They individuals are as follows:

- -Coklat is the adult mated female in group C. She does not have a dependent infant. She is Chilli's mother and the partner of Captain.

- -Captain is the adult mated male in group C. He is Chilli's presumed father and the partner of Coklat.

- -Chun is the adult mated female in group Karate. At the time of the study she had a dependant infant, Elen. She is also the mother of Brandi and Jet and the partner of Bruce.

- -Bruce is the adult male in group Karate. He is Brandi Jet and Elen's presumed father and partner of Chun.

Also present in group C is Chilli, Coklat and Captain's daughter, an adolescent (5-7 years of age) gibbon nearing adulthood.

Also present in group Karate are Brandi and Jet, Bruce and Chun's adolescent daughters as well as Elen, their infant daughter. **Figure 2.3.** shows the territory map for these groups
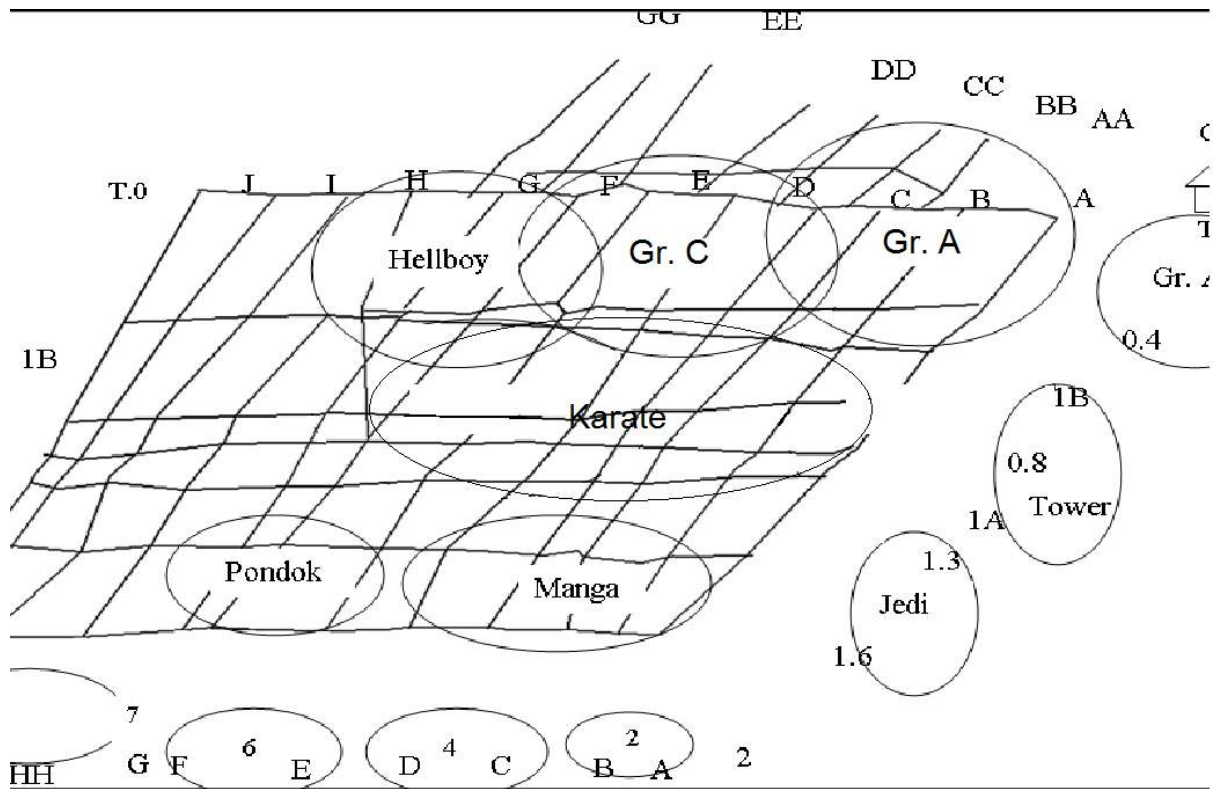
(**Figure 2.3.** shows the territory map for the gibbon groups in the NLPSF. The focal animals were from group C and Karate.)

While immature gibbons do join in with their parent's singing I chose to focus my studies on the two mated pairs as it is thought adults play the largest role in territory defence (Koda, et al., 2013), while immatures are still learning how to sing correctly.

## 2.3 Data collection

### 2.3.1 Locating and following the focal animals

In order to locate the gibbons in the morning two researchers would wait at a listening post at 4:30 am in the centre of the focal animal's territory. As mentioned a gibbon's song can be heard by humans in excess of a kilometre away (Mitani, 1985) and the territory of *H. albibarbis* is approximately $0.47km^2$ in size (Cheyne, 2010). A researcher in the centre of the group's territory can therefore hear them sing from anywhere within their territory range. Should the focal group sing the researchers shall move towards them until they have located the group. Should the gibbons not sing then after the chorus (the remaining groups of neighbouring gibbons that are singing) has finished the researchers shall split up and travel up and down the transects within the territory range of the focal group, waiting at transect junctions for ten minute periods, searching for the group visually and by listening for the sound of them moving though the canopy. Should the group be found the researchers shall reunite and follow the focal animal until it enters a sleeping tree. The sleeping tree shall be marked with a trail of coloured cotton string leading to the nearest transect so that tomorrow's researchers are able to easily locate the focal group. This is preferable to waiting at a listening post for the animals to sing as gibbons do not necessarily sing every day and data can be collected from as soon as the animals awaken in the morning.

Once the focal animal was located the researchers followed it at a distance of just over 20m to avoid disturbing it, attempting to keep the animal within their field of vision at all times. Once the gibbon entered a sleeping tree (at approximately 2pm) the researchers waited for a period of 20-30 minutes to ensure that the animal had finished activities for the day, and was indeed going to sleep. If the focal animal remained inactive in the tree for this length of time then the follow would end.

Although this was the ideal sequence of events it was sometimes the case that the researchers lost the gibbon before it entered the sleeping tree. Gibbons, especially adult males are capable of reaching exceptional speeds when moving through the canopy and were noted to increase their rate of travel in the hour before they finished their daily activity, sometimes making it impossible for researchers to keep up with them (pers. obs.). At the same time the animals can be hard to locate when they are high in the canopy and holding still. In this situation when the focal animal is lost shortly before the usual time that it would enter a sleeping tree, the location is marked on the map for tomorrow's researchers as it was likely that the gibbon had entered a nearby sleeping tree unnoticed.

## 2.3.2 Collecting Singing Data

Singing occurs in the morning, usually before and just after sunrise. In order to collect singing data the researchers would aim to arrive at the listening post or beneath the singing tree by 4:30am. Once there whether the group sang at all would be recorded, as well as the time the gibbons first began to sing, the time the female first great called, the number of great calls, the total time spent singing and the groups position in that morning's chorus. Further data such as the proportion of time spent singing, the average bout length and the number of great calls per bout would be calculated back at camp. Gibbons can sing multiple bouts in a

day. It was the policy at OuTrop to consider a bout to have ended if the gibbons retained 30 minutes of silence. Any singing recorded after that was regarded as a separate bout.

Sometimes it was necessary to move through the forest when the gibbons were still singing, such as when the researchers were at a listening post and the gibbons began to sing from a large distance away, or on the rare occasion when the gibbons began to sing before 4:30am. This was not ideal because the sound of humans moving through the undergrowth could obscure the sound of gibbons singing. On these occasions the researchers collected data at the same time as moving to the best of their abilities.

### 2.3.3 Collecting feeding data

While following the focal animal's data was collected every time they fed. This data included the length of the feeding bout, the species of plant they fed on and what part of the plant they were feeding on (such as leaf, flower, shoot, fruit, etc). To identify species and part eaten researchers were provided with an identification sheet. and some of the Bornean researchers had many years of experience in identifying plant species. When the species or part was uncertain a sample would be collected for the senior researchers to identify later that day. Once data had been collected the total time spent feeding could be calculated as well as the total time spent feeding on fruit, leaves, flowers and figs, the total proportion of time spent feeding, and proportion of fruits, leaves and figs in that days diet.

### 2.3.4 Collecting Behavioural & Ranging Data

We used focal time sampling to record the activities of the focal animal every five minutes. Researchers were familiar with an ethogram covering the full range of the animals' behaviour

(please see **Appendix 1** for a copy of this ethogram). From this we calculated many categories of behavioural data, including the proportion of the gibbons' activity budget spent grooming, feeding, playing, cofeeding, resting, traveling and singing by dividing the number of recordings of these behaviours by the total recordings for that day. As we theoretically followed the animals from when they awoke to when they went to sleep this represents the frequency of these behaviours as a proportion of the activity period for the entire day.

During the period of the study play did not occur between mated individuals but only between adults and offspring. We kept this value in the final analysis however as it could still be interpreted as the focal animal displaying an investment or strong relationship with the individuals in its group.

Originally the proportion of time spent mating was to be recorded but the gibbons were not recorded to mate during my time at the research station and so the variable was dropped for the final analysis. The pair association (or distance between the mated pairs, which has been shown to be a good representative of pair bond strength was also recorded every five minutes but it was particularly difficult to keep track of both adult gibbons at the same time and the majority of readings were recorded as 'unknown'. For this reason pair association was not used in the final analysis.

Interactions between groups were recorded as they occurred. Due to the chaotic nature of such encounters, often with numerous individuals chasing each other at high speeds through dense canopy it was not possible to quantitatively measure these events.

In order to collect ranging data we used a GPS (Make: Garmin; Model: 60CSX) to record the location of the researcher every 5 minute. As we were rarely far from the focal animal this functions as an adequate proxy for the location of the gibbon. We did not take a recording if

the accuracy error was greater than 15m. Using Garmin "Basecamp" software we were able to calculate the daily path length and average speed of the animal.

## 2.4 Data Analysis

## 2.4.1 Sample Size

During the course of my time at the NLPSF 57 follows were attempted from the 18th of May to the 7th of July. Of those 48 successfully collected singing data and 43 successfully collected behavioural data. Behavioural data could not be collected in such as when the gibbons could not be located, were lost shortly after beginning the follow or when heavy rain obscured singing. Singing data, as it occurs in a discrete portion of the morning could sometimes still be collected even when behavioural data could not.

In order to not bias my sampling regime towards an individual or sex I tried to have approximately the same number of follows for each individual. This was not possible however as certain gibbons were harder to locate and follow than others. Of the 14 follows that were unsuccessful the majority were on Bruce, the adult male of group Karate, a particularly fast and unpredictable gibbon. The number of follow days was bolstered by the addition of 20 further follows from the 13th of May to the 5th of April which raised the total available data to 68 follows.

For many of the studies it was often the case that the gibbon was temporarily out of sight, or obscured when high in the canopy. It was also not unusual for the gibbon to be temporarily lost by the researchers for any length of time between a few minutes and several hours. When this occurred it was not possible to record behavioural data for the period when the focal animal could not be seen. As behavioural data from these days was not representative of the

gibbon's activity for that day a compromise was made to remove the days which had the least cumulative follow hours from the analysis. The total observed hours were calculated for each follow and an interquartile range worked out. The 25% of follows below the lower quartile for total observed hours (approx. 4.5 hours) were not used in the final analysis. 16 follows were removed. The final sample size was 68 days of singing data and 52 days of behavioural data. This sample size varies between certain variables for miscellaneous reasons, such as damage to datasheets. In additions males do not produce great calls so tests examining great calls only take into account behavioural data on female gibbons.

## 2.4.2 Data analysis

Gibbon song is represented by 8 variables describing their singing behaviour on the day in question. These are:

- -Abstinence from singing,
- -Proportion of time spent singing,
- -Total time spent singing (min),
- Time of first sing (the time of day that the gibbon group began to sing for the first time that day),
- -Time of first great call (the time of day that the gibbon began to great call for the first time that day),
- -Position of song in the order of the morning chorus,
- -Total number of great calls,
- -Average number of great calls,

- -Average length of song bouts (min).

It should be noted here that for ease of analysis 'time of first sing' and 'time of first great call' were transformed into decimal proportions of 1, so that an event occurring at 24:00 hours would be 1; one occurring at 12:00 hours would be 0.5; one at 06:00 would be 0.25, and so on.

We used multiple regression analysis to construct models explaining variation in these singing variables using 12 explanatory variables representing feeding, ranging and social behaviour. These are:

- -Total time spent feeding (min),

- -Time spent feeding on fruit (min),

- -Time spent feeding on leaves/flowers (min),

- -Time spent feeding on figs (min),

- -Proportion of time spent resting,

- -Proportion of time spent travelling,

- -Daily path length (km),

- -Average speed (km/h$^2$),

- -Proportion of time spent grooming,

- -Proportion of time spent playing,

- -Proportion of time cofeeding,

- -Intergroup encounter (did an encounter occur).

Transformations were used on explanatory data when they did not possess linear residuals and breached the assumptions of the test. When functional models could not be found for the response variables Spearman's rank order correlation tests were performed to find the correlation between the response and the 12 explanatory variables. All tests were performed with IBM SPSS Statistics 22 software.

# Chapter 3: Results

## 3.1. Multiple Regression Analysis

Models were created using multiple regression to see which of the explanatory variables (total time spent feeding, time spent feeding on fruit, time spent feeding on leaves/flowers time spent feeding on figs, proportion resting, proportion travelling, daily path length, average speed, proportion grooming, proportion playing, proportion cofeeding, and the presence of an intergroup encounter) best explained variation in the response variables (abstinence from singing, proportion singing, total time singing, time of first singing, time of first great call, and average song bout length). Three models were significant while fulfilling all of the assumptions of the multiple regression analysis (a lack of collinearity and standardised residuals). These models explained variation in the proportion of time spent singing, total time spent singing and time of first great call and response variables and they are presented in **Tables 3.1**, **3.2** and **3.3** respectively. Scatterplots were also made to visually display the relationship between individual response and explanatory variables (**Figures 3.1. – 3.8.** ). It was not possible to create significant models for the other response variables, including abstinence from singing, the time of first sing, the order in the chorus, the total

number of great calls per day, the average number of great calls per bout and the average length of a song bout.

## 3.1.1 Proportion of Time Spent Singing

The best model to explain variation in the proportion of time spent singing used the feeding length on fruit, proportion resting, proportion traveling, proportion grooming and proportion playing explanatory variables.

The p-value of the Anova test for the model was < 0.001.

The $R^2$ value for the model was 0.336.

The Kolmogorov-Smirnov value was 0.078.

(**Table 3.1**. Displaying the test statistics and p-values for the best model explaining variation in the proportion of time spent singing.)

| Variable | B-value | P-value |
|---|---|---|
| Feeding Length Fruit (Square Root) | -0.05 | 0.030 |
| Proportion Rest (Square Root) | 0.159 | 0.005 |
| Proportion Play (Square Root) | 0.227 | 0.011 |

Adding any additional explanatory variable to the model, including total time feeding,

feeding length leaves/flowers, feeding length figs, proportion travel, daily path length,

average speed, proportion groom, or the presence of interactions, whether transformed or not

caused either the Anova p-value to become non-significant or the Kolmogorov-Smirnov

value to become significant, (rendering the assumptions of the test invalid), or both.
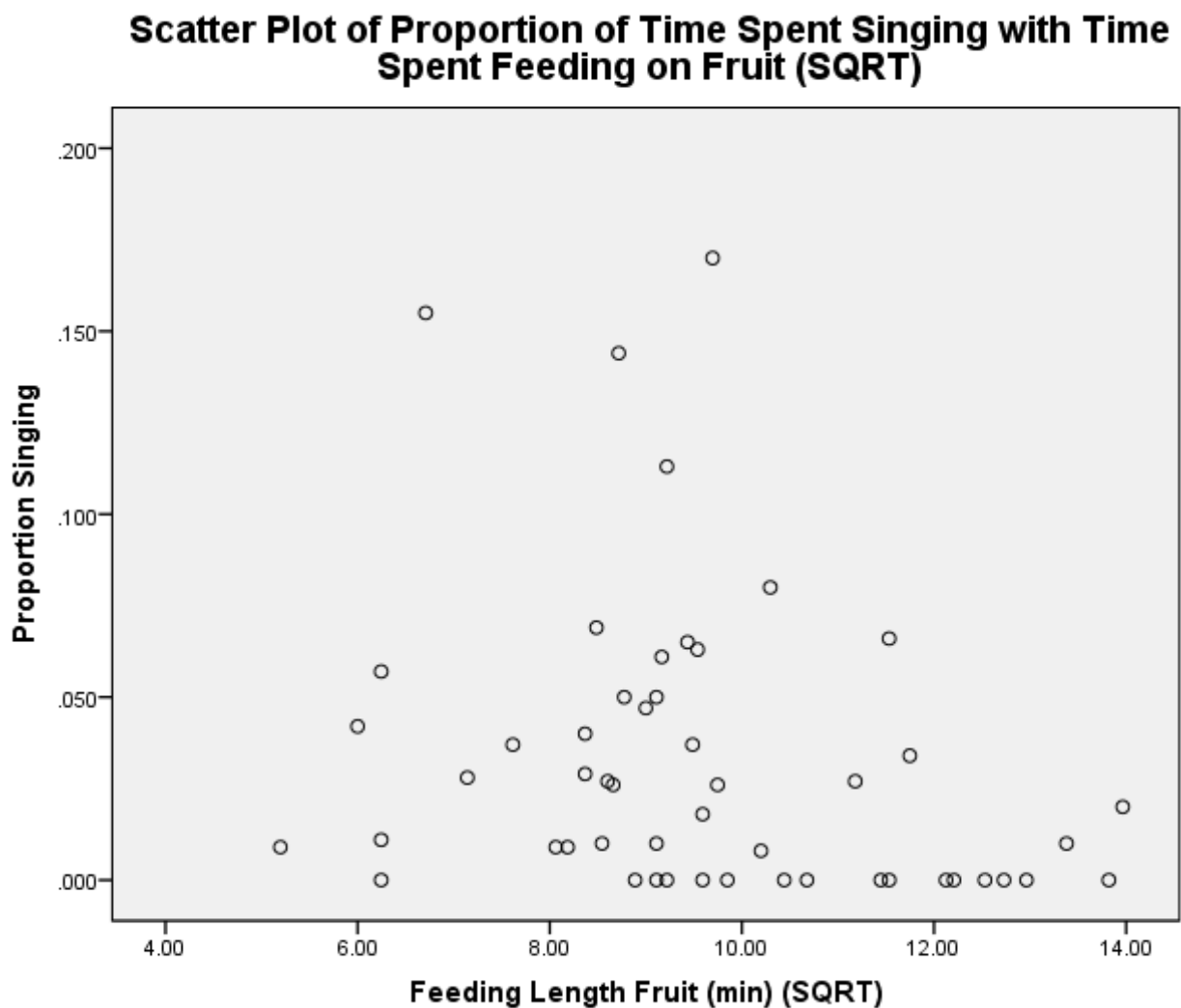


(**Figure 3.1.** Scatterplot showing the relationship between the proportion of time spent

singing and the time spent feeding on fruit (transformed with square root) n.=51).

**Scatterplot of Proportion Time Spent Singing with Proportion Time Spent Resting (SQRT)**
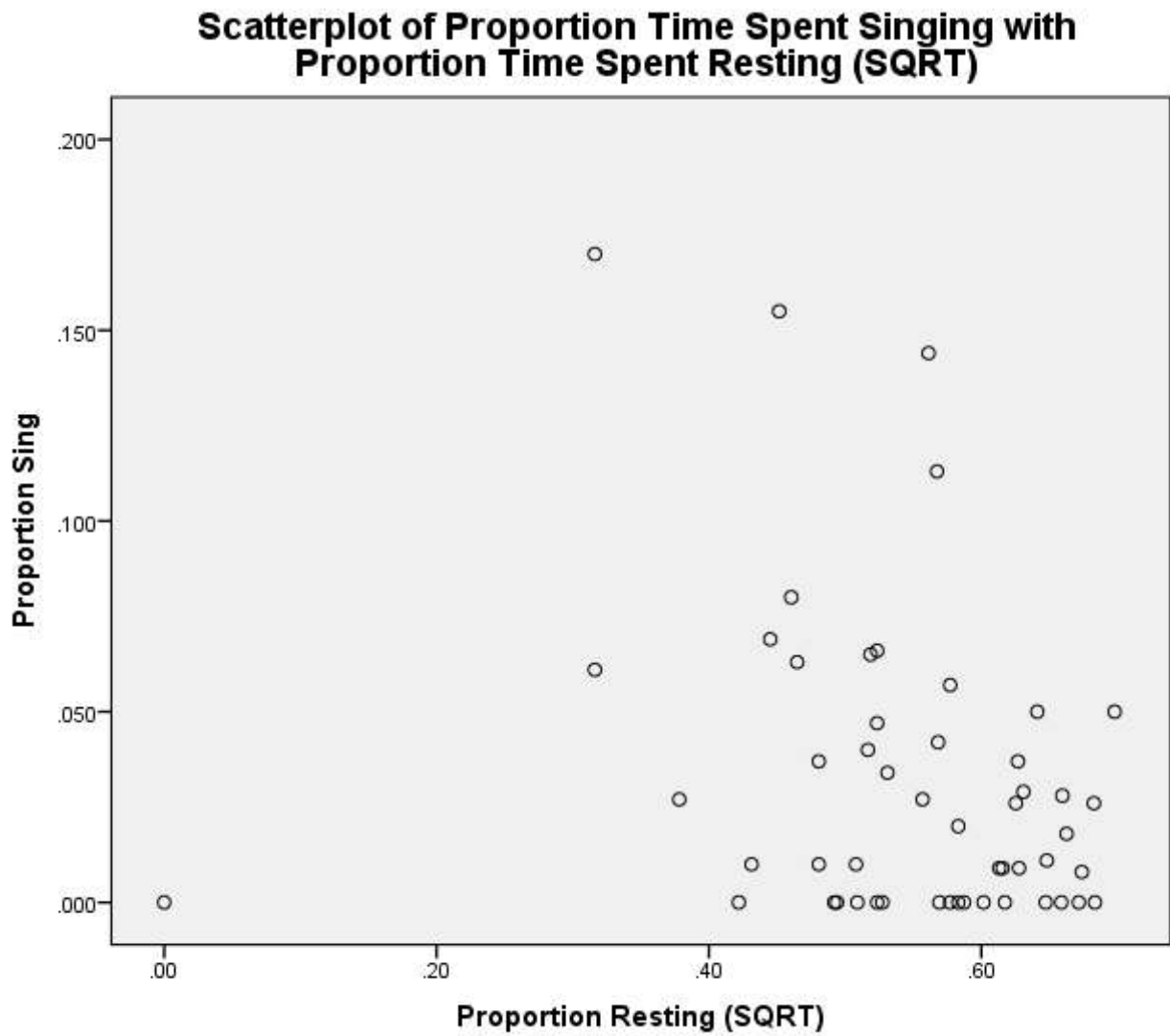
(**Figure 3.2.** Scatterplot showing the relationship between the proportion of time spent

singing and the proportion of time spent resting (transformed with square root) n. =51).

**Scatterplot of Proportion Time Spent Singing with Proportion Time Spent Playing (SQRT)**
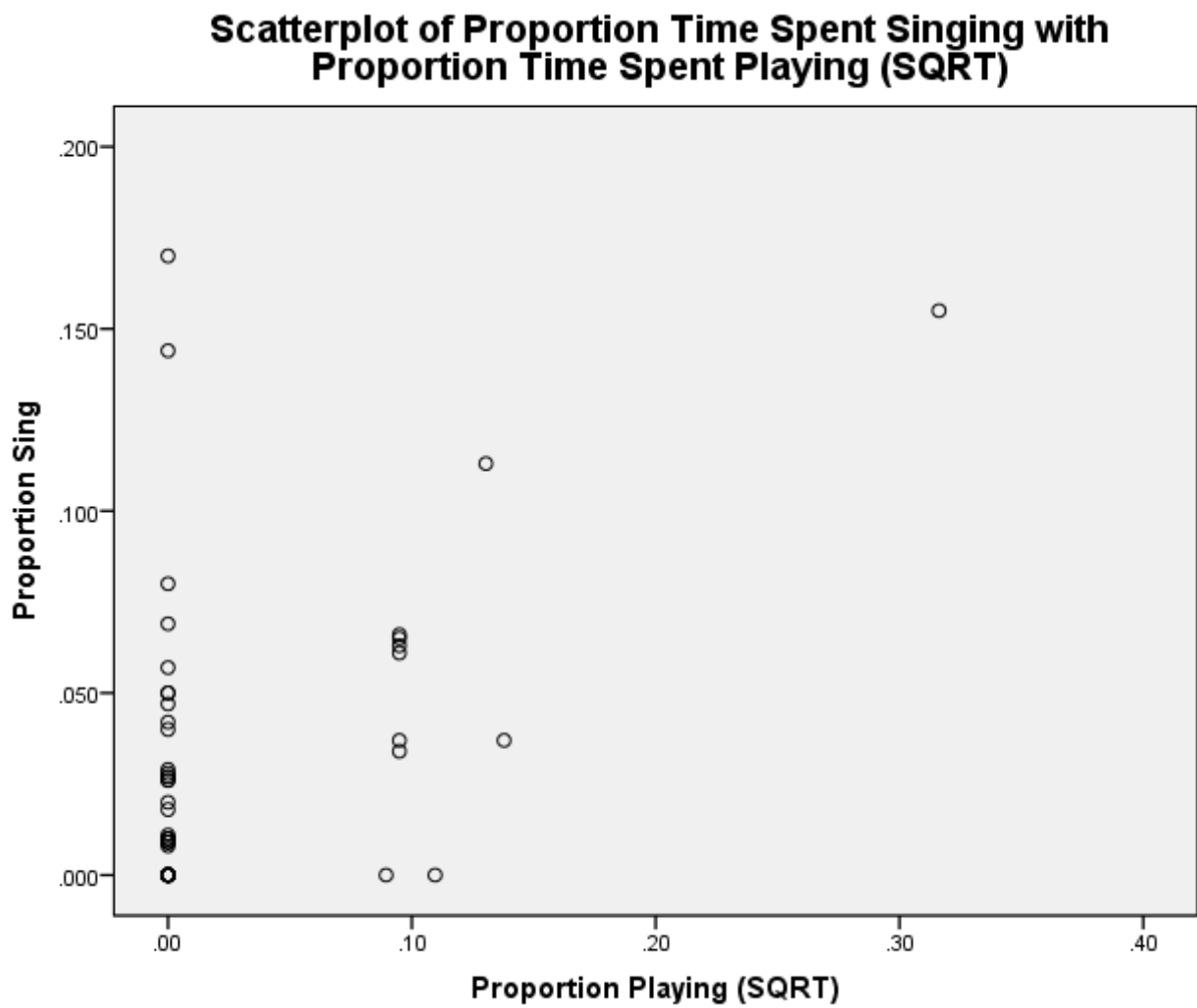
(**Figure 3.3.** Scatterplot showing the relationship between the proportion of time spent singing and the proportion of time spent playing (transformed with square root) n. =52).

## 3.1.2 Total time spent singing

The best model to explain variation in the total time spent singing used the total time feeding, feeding length leaves/flowers, proportion resting, average speed and proportion grooming, explanatory variables.

The p-value of the Anova test for the model was 0.034

The $R^2$ value for the model was 0.311

The Kolmogorov-Smirnov value was 0.2.

(**Table 3.2.** Displaying the test statistics and p-values for the best model explaining variation in the total time spent singing.)

| Variable | B-value | P-value |
|---|---|---|
| Total Time Feeding | -0.263 | 0.036 |
| Feeding Length Leaves/Flowers | 29.216 | 0.294 |
| Proportion Rest | -128.314 | <0.001 |
| Average Speed | -353.941 | 0.015 |
| Proportion Groom | -30.732 | 0.923 |

Adding any additional explanatory variable to the model, including feeding length fruit, and feeding length figs, proportion travel, daily path length, proportion play, proportion cofeed and the presence of interactions, whether transformed or not caused either the Anova p-value

to become non-significant or the Kolmogorov-Smirnov value to become significant

(rendering the assumptions of the test invalid) or both.
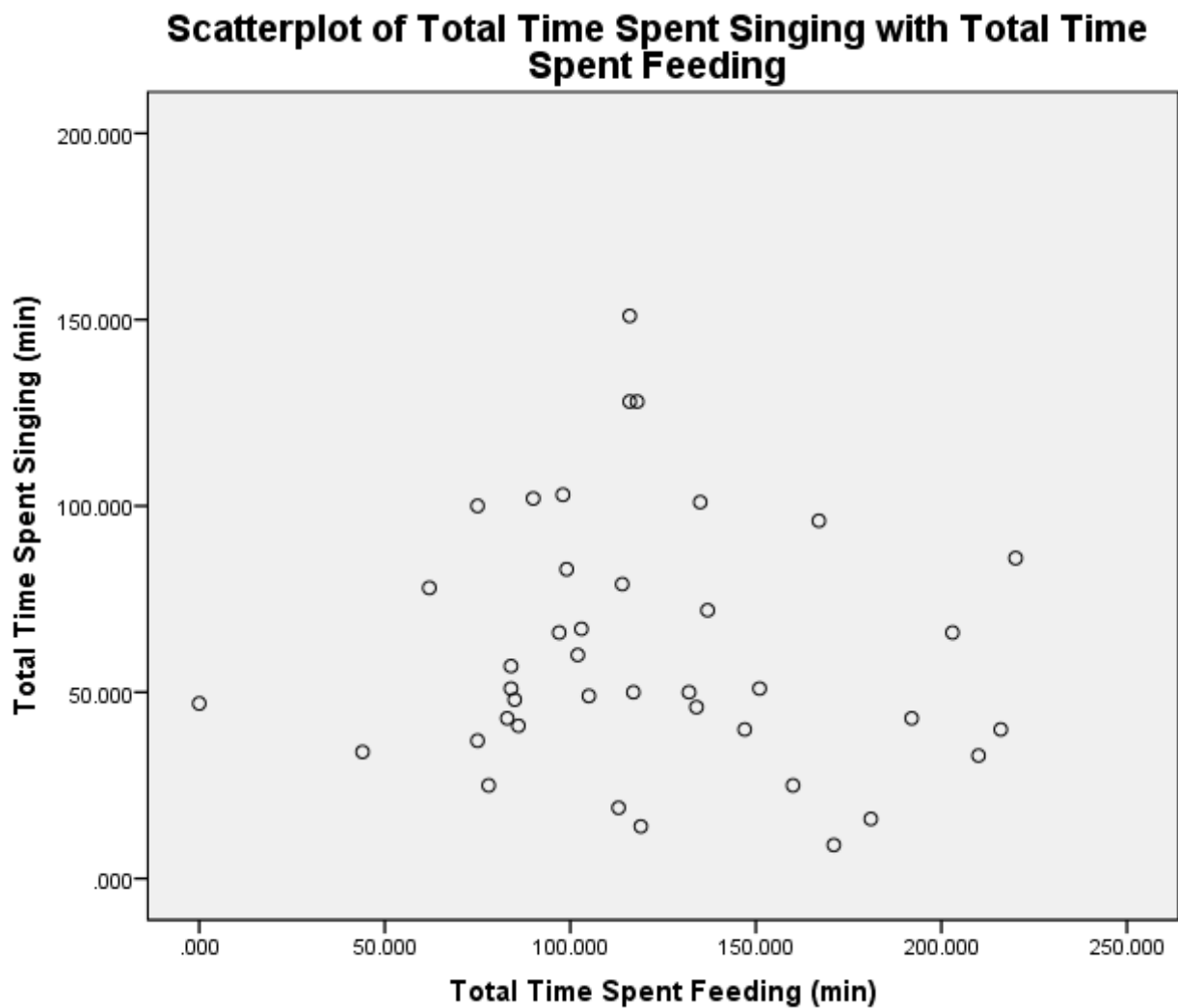


(**Figure 3.4.** Scatterplot showing the relationship between the total time spent singing (min)

singing and the total time spent feeding (min) n. =40).
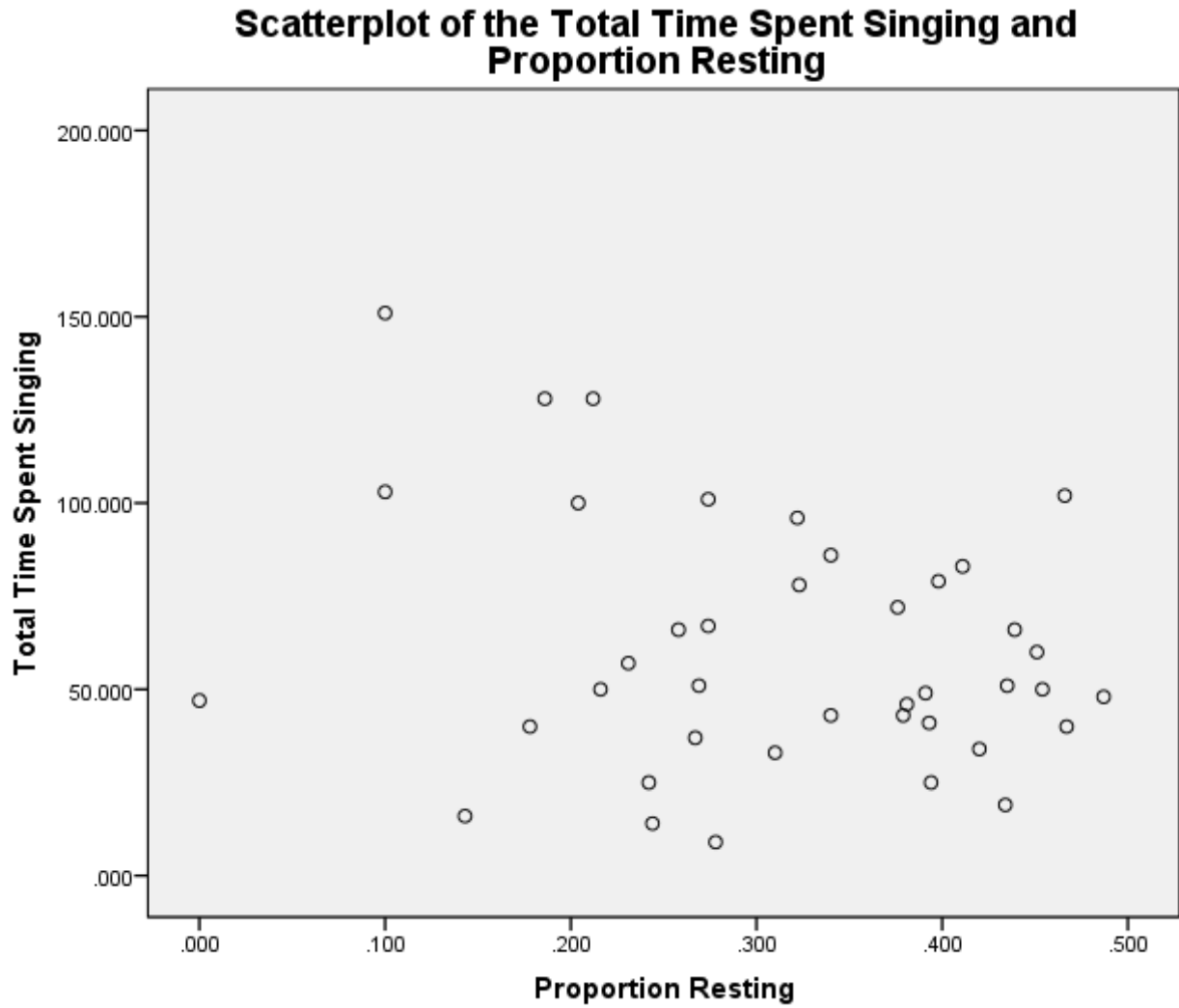
(**Figure 3.5.** Scatterplot showing the relationship between the total time spent singing (min) singing and the proportion of time spent resting. n. =40)
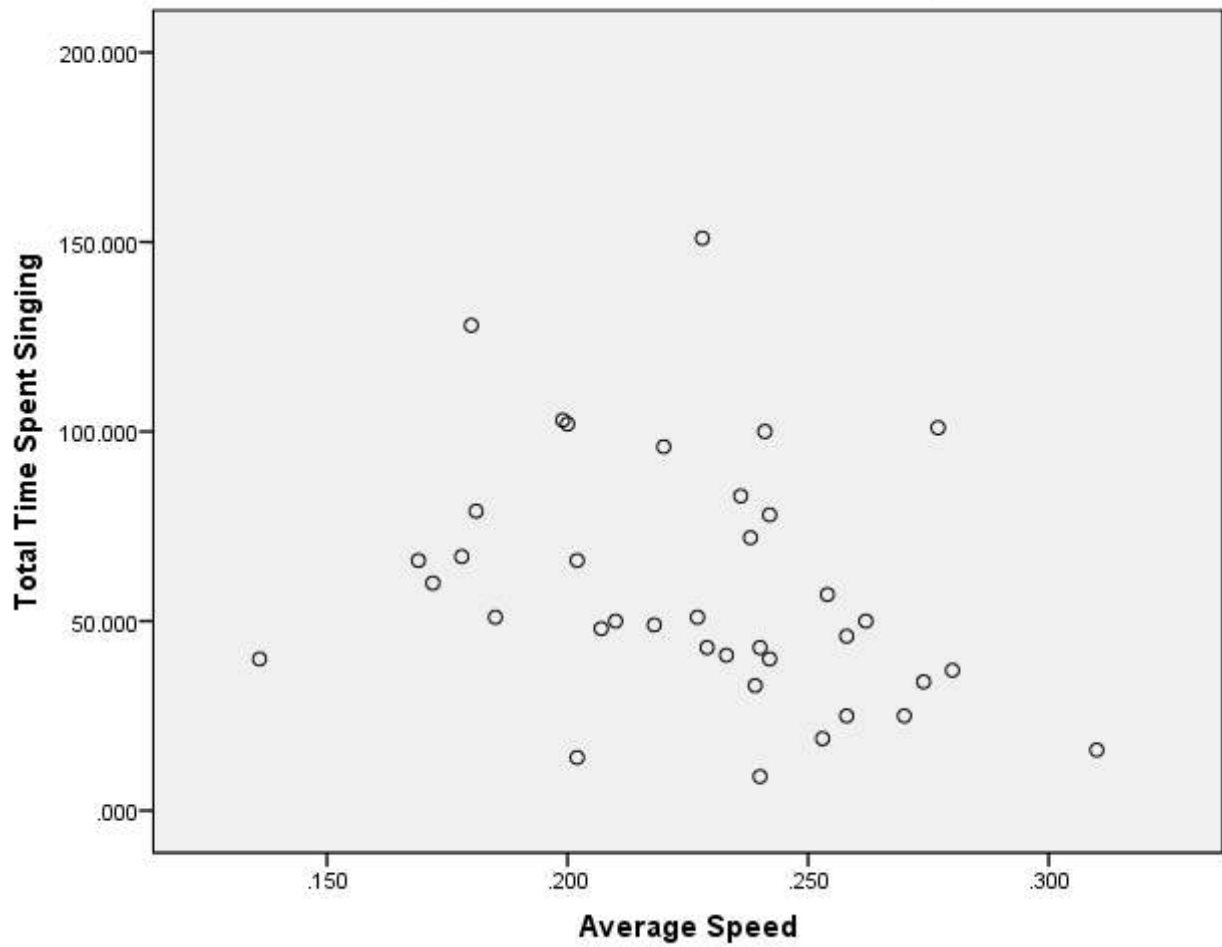
(**Figure 3.6.** Scatterplot showing the relationship between the total time spent singing (min) singing and the average speed (km/h) n. =37).

### 3.1.3 Time of first great call

The best model to explain variation in the time of first great call used the total time feeding, feeding length figs proportion resting, daily path length and proportion playing, explanatory variables.

The p-value of the Anova test for the model was 0.042

The $R^2$ value for the model was 0.566

The Kolmogorov-Smirnov value was 0.136.

(**Table 3.3.** Displaying the test statistics and p-values for the best model explaining variation in the time of first great call.)

| Variable | B-value | P-value |
|---|---|---|
| Total Time Feeding (Square Root) | -0.002 | 0.634 |
| Feeding Length Fig | 0.0002 | 0.044 |
| Daily Path Length (Square Root) | -0.058 | 0.449 |
| Proportion Play | 4.451 | 0.008 |

Adding any additional explanatory variable to the model, including feeding length fruit, feeding length leaves/flowers, proportion rest, proportion travel, average speed, proportion

groom, proportion cofeed or the presence of interactions whether transformed or not caused

either the Anova p-value to become non-significant or the Kolmogorov-Smirnov value to

become significant, (rendering the assumptions of the test invalid), or both.

**Scatterplot of Time of First Great Call and Time Spent Feeding on Figs (min)**
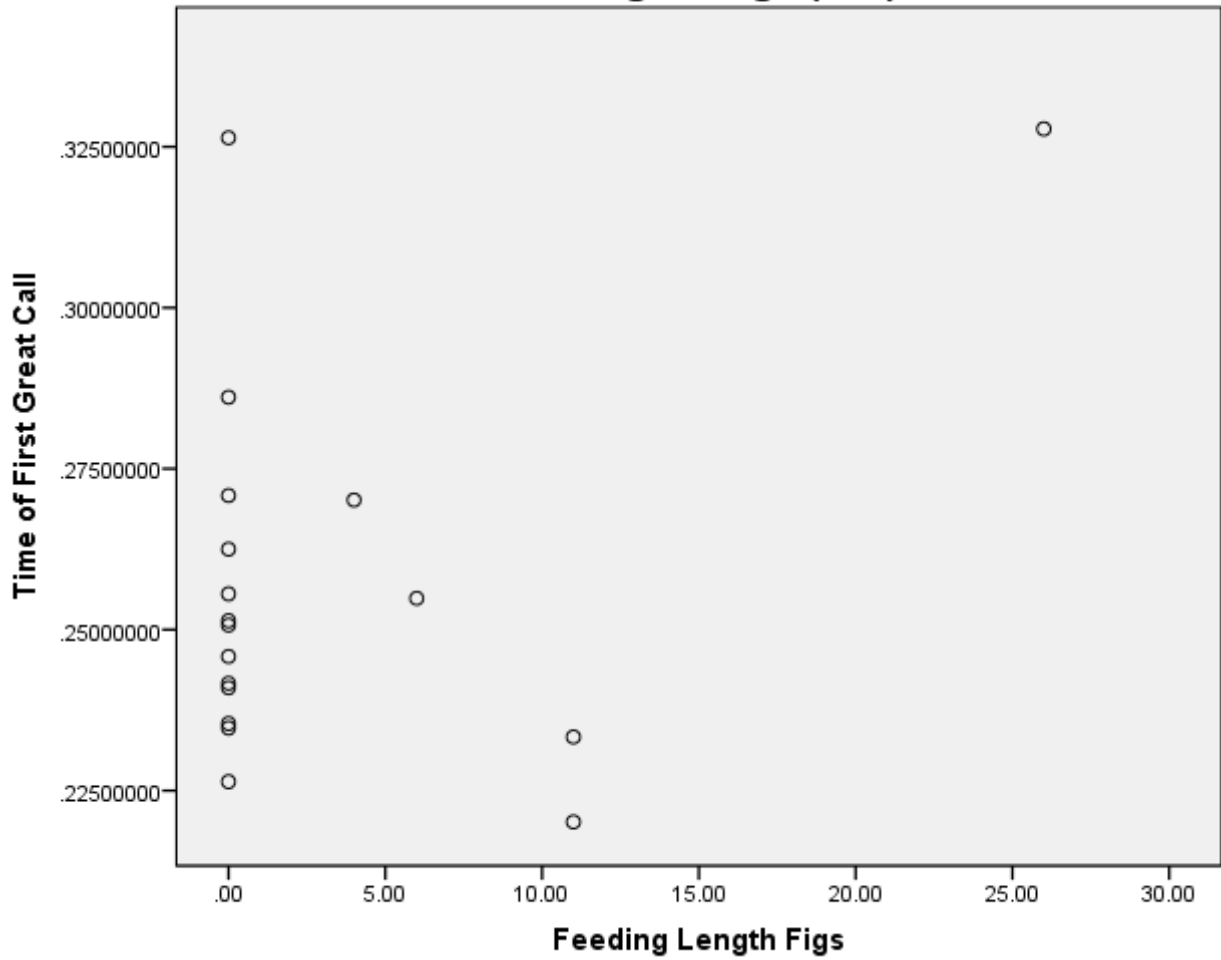
(**Figure 3.7.** Scatterplot showing the relationship between the time of first great call (shown here in decimal form as a proportion of a whole day) singing and the time spent feeding on figs. n.=18)

**Scatterplot of Time of First Great Call and Proportion Playing**
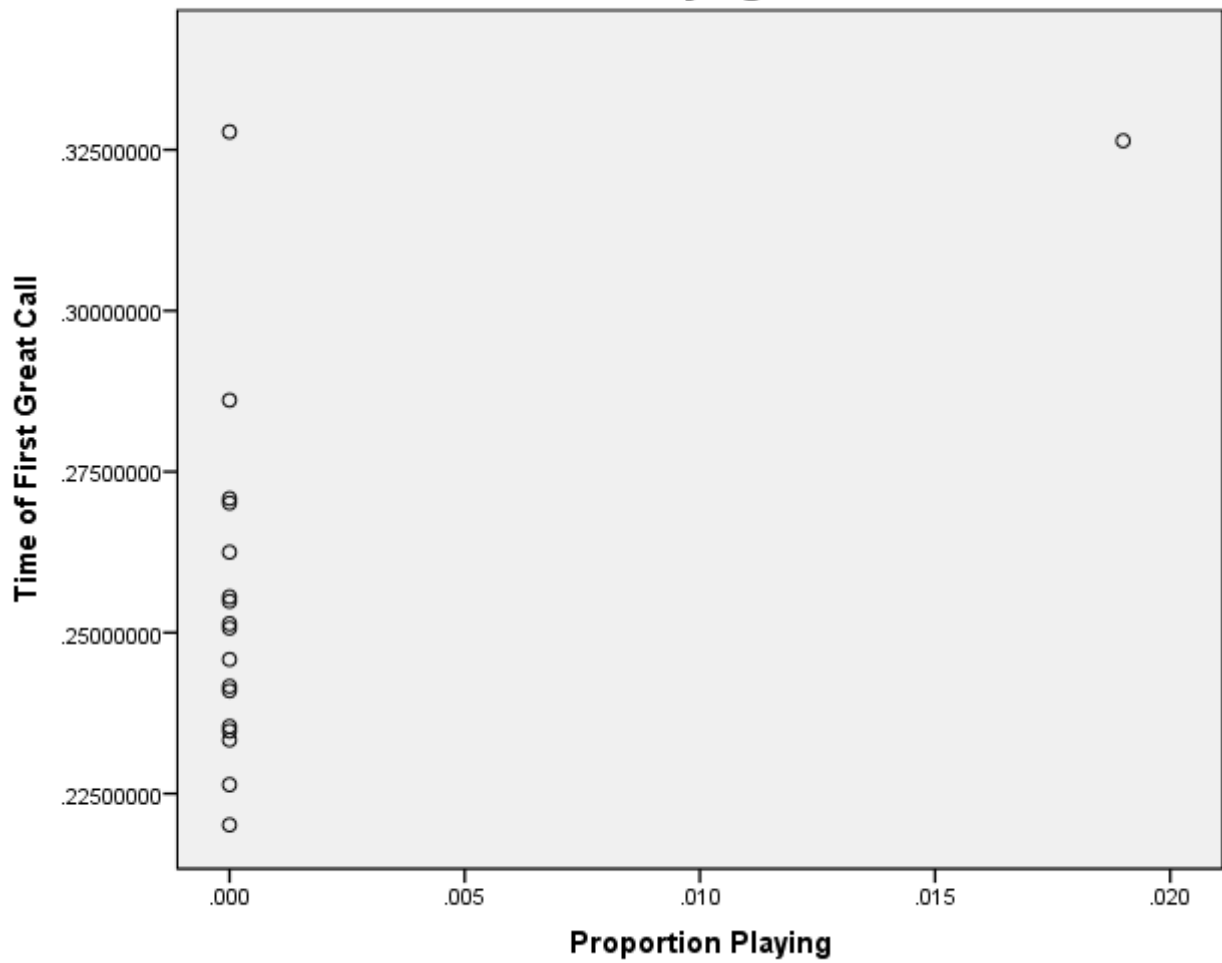
(**Figure 3.8.** Scatterplot showing the relationship between the time of first great call (shown here in decimal form as a proportion of a whole day) singing and the proportion of time spent playing. n. =18)

## 3.2 Spearman's Rank Correlations

Models made using multiple regression to explain abstinence from singing, the time of first sing, the order in the chorus, the total number of great calls per day, the average number of great calls per bout and the average length of a song bout were either non-significant (Anova > 0.05) or did not possess linear residuals (Kolmogorov-Smirnov <0.05) and defied the assumptions of the multiple regression test.

For these failed models I used Spearman's rank-order correlation to show the correlations between the response and explanatory variables. As a total of 12 explanatory variables were used in this test the threshold of significance is multiplied by 12. The new significance threshold is 0.0042.

(**Table 3.4.** Showing the Spearman's rank correlation results for abstinence from singing with all 12 explanatory variables)

| Variable | $r_s$ (Correlation coefficient) | P-Value | Sample Size |
|---|---|---|---|
| Total Time Feeding | 0.075 | 0.612 | 48 |
| Feeding Length Fruit | 0.096 | 0.519 | 47 |
| Feeding Length Leaves/Flowers | 0.089 | 0.550 | 47 |
| Feeding Length Figs | -0.052 | 0.724 | 48 |
| Proportion Rest | 0.068 | 0.642 | 49 |
| Proportion Travel | 0.342 | 0.016 | 49 |
| Daily Path Length | 0.010 | 0.948 | 45 |
| Average Speed | -0.096 | 0.532 | 45 |
| Proportion Groom | 0.68 | 0.646 | 48 |

| | | | |
|---|---|---|---|
| Proportion Play | 0.051 | 0.729 | 48 |
| Proportion Cofeed | -0.193 | 0.194 | 47 |
| Intergroup Encounter | -0.007 | 0.957 | 61 |

(**Table 3.5.** Showing the Spearman's rank correlation results for time of first sing with all 12

explanatory variables)

| Variable | $r_s$ (Correlation coefficient) | P-Value | Sample Size |
|---|---|---|---|
| Total Time Feeding | 0.128 | 0.419 | 42 |
| Feeding Length Fruit | 0.075 | 0.641 | 41 |
| Feeding Length Leaves/Flowers | 0.030 | 0.854 | 41 |
| Feeding Length Figs | -0.044 | 0.784 | 42 |
| Proportion Rest | 0.074 | 0.640 | 42 |
| Proportion Travel | -0.017 | 0.917 | 42 |
| Daily Path Length | 0.005 | 0.975 | 39 |
| Average Speed | 0.109 | 0.508 | 39 |
| Proportion Groom | -0.162 | 0.306 | 42 |
| Proportion Play | -0.004 | 0.981 | 42 |
| Proportion Cofeed | 0.191 | 0.231 | 41 |
| Intergroup Encounter | 0.042 | 0.766 | 53 |

(**Table 3.6.** Showing the Spearman's rank correlation results for the order in the chorus with

all 12 explanatory variables)

| Variable | $r_s$ (Correlation coefficient) | P-Value | Sample Size |
|---|---|---|---|

| | | | |
|---|---|---|---|
| Total Time Feeding | 0.067 | 0.682 | 40 |
| Feeding Length Fruit | 0.020 | 0.902 | 39 |
| Feeding Length Leaves/Flowers | -0.228 | 0.163 | 39 |
| Feeding Length Figs- | 0.125 | 0.441 | 40 |
| Proportion Rest | 0.326 | 0.040 | 40 |
| Proportion Travel | 0.028 | 0.863 | 40 |
| Daily Path Length | 0.151 | 0.373 | 37 |
| Average Speed | 0.191 | 0.258 | 37 |
| Proportion Groom | -0.186 | 0.249 | 40 |
| Proportion Play | 0.156 | 0.337 | 40 |
| Proportion Cofeed | -0.114 | 0.491 | 39 |
| Intergroup Encounter | 0.170 | 0.239 | 50 |

(**Table 3.7.** Showing the Spearman's rank correlation results for total number of great calls

with all 12 explanatory variables)

| Variable | $r_s$ (Correlation coefficient) | P-Value | Sample Size |
|---|---|---|---|
| Total Time Feeding | -0.150 | 0.445 | 28 |
| Feeding Length Fruit | -0.259 | 0.183 | 28 |
| Feeding Length Leaves/Flowers | 0.180 | 0.361 | 28 |
| Feeding Length Figs | 0.178 | 0.365 | 28 |
| Proportion Rest | 0.065 | 0.737 | 29 |
| Proportion Travel | 0.255 | 0.182 | 29 |
| Daily Path Length | -0.093 | 0.650 | 26 |
| Average Speed | -0/075 | 0.715 | 26 |

| | | | |
|---|---|---|---|
| Proportion Groom | 0.160 | 0.415 | 28 |
| Proportion Play | -0.086 | 0.665 | 28 |
| Proportion Cofeed | 0.009 | 0.962 | 28 |
| Intergroup Encounter | 0.162 | 0.392 | 30 |

(**Table 3.8.** Showing the Spearman's rank correlation results for average number of great

calls with all 12 explanatory variables)

| Variable | $r_s$ (Correlation coefficient) | P-Value | Sample Size |
|---|---|---|---|
| Total Time Feeding | -0.045 | 0.818 | 28 |
| Feeding Length Fruit | -0.182 | 0.353 | 28 |
| Feeding Length Leaves/Flowers | 0.208 | 0.288 | 28 |
| Feeding Length Figs | 0.182 | 0.354 | 28 |
| Proportion Rest | 0.050 | 0.798 | 29 |
| Proportion Travel | 0.252 | 0.187 | 29 |
| Daily Path Length | -0.080 | 0.698 | 26 |

| | | | |
|---|---|---|---|
| Average Speed | -0.090 | 0.662 | 26 |
| Proportion Groom | 0.114 | 0.565 | 28 |
| Proportion Play | -0.073 | 0.711 | 28 |
| Proportion Cofeed | 0.037 | 0.853 | 28 |
| Intergroup Encounter | 0.145 | 0.446 | 30 |

(**Table 3.9.** Showing the Spearman's rank correlation results for average Bout length with all 12 explanatory variables)

| Variable | $r_s$ (Correlation coefficient) | P-Value | Sample Size |
|---|---|---|---|
| Total Time Feeding | 0.057 | 0.728 | 40 |
| Feeding Length Fruit | 0.086 | 0.604 | 39 |
| Feeding Length Leaves/Flowers | 0.039 | 0.815 | 39 |
| Feeding Length Figs | -0.038 | 0.816 | 40 |
| Proportion Rest | -0.108 | 0.506 | 40 |
| Proportion Travel | -0.167 | 0.303 | 40 |
| Daily Path Length | -0.163 | 0.336 | 37 |
| Average Speed | -0.293 | 0.079 | 37 |
| Proportion Groom | -0.071 | 0.662 | 40 |
| Proportion Play | 0.115 | 0.479 | 40 |
| Proportion Cofeed | 0.029 | 0.859 | 39 |
| Intergroup Encounter | -0.224 | 0.118 | 50 |

# Chapter 4: Discussion

## 4.1 Statistical Difficulties

It should be noted before discussing the results that the multiple regression analysis was not entirely appropriate in the form used here and caused an issue of causality. Comparing explanatory and response variables from the same day, as was done here is not sufficient to tell us about the influence of the explanatory on the response as the response (singing behaviour) has already occurred by the time the explanatory variables are measured. In variables meant to look at social behaviour this is less of a problem as pair bond strength is unlikely to fluctuate on a day to day basis, although the energy balance of a gibbon might change very rapidly. This limits the ability of these tests to fulfil my objectives for some of my variables, although some inferences about the nature of energetics can still be made. Using alternative statistical tests such as cross correlation and time series analysis would perhaps have solved these issues and allowed me to look at the relationships between explanatory and response variables over time. Comparing response data with behaviour from the day before in multiple regression would also achieve that to a smaller extent, although only over one day. These were not done however as by the stage the mistake had been recognised time constraints had become too severe.

## 4.2 The Influence of Energy Balance and Intake on Singing Behaviour

Only small influences were found between feeding or ranging variables and singing variables. Total time spent feeding was found to have a minor negative influence on total

time spent singing. It was not however found to influence or correlate with abstinence from singing, proportion singing, time of first singing, time of first great call, and average song bout length. Similarly time spent feeding on fruit was shown to have a minor negative influence on proportion of time spent singing but to have no influence or correlation on abstinence from singing, total time singing, time of first singing, time of first great call, and average song bout length. This, admittedly very slight, negative influence of high energy foods on the amount of time that gibbons sang for is surprising as other studies have shown the consumption of high energy foods to be associated with increased singing time (Fan, et al., 2008b; Tenaza, 1976). It is probably best explained by flaws in statistical method which influenced the causality of this study. An alternative interpretation could be that gibbons that sang less were more likely to spend more time feeding, in general and on fruits. Both the decreased singing and the increased consumption could be a result of having a lower energy balance on that day. Gibbons may sing less because of lower energy balance and feed more to regain energy.

Time spent feeding on leaves/flowers, was not shown to have an influence or correlation on any singing variable which is also unusual considering that we would expect more leaves in the diet to be associated with a reduction in time singing (Fan, et al., 2008b).

Time spent feeding on figs, another typically less preferred food was found to have a minor positive relationship with time of first great call, meaning that gibbons with later great calls (perhaps with less energy) ate more figs.

This would collide with the previous suggestion that gibbons with other indicators of a lower energy balance ate more preferred fruit. As figs are typically less preferred foods gibbons would be expected to eat less of them when better quality alternatives are available. However this could be influenced by the availability of preferred fruit. A gibbon that has a low energy

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balance would feed on less preferred foods if it does not have alternatives. Remember however that the shown relationship here is also quite weak. When considering this it should be noted that the mixed swamp forest of the Sabangau is considered to be low productivity and that fig and non-fig fruit availability has not been shown to vary significantly with seasons (Morrogh-Bernard, et al., 2003). There was no found influence or correlation of time spent feeding on figs on any other singing variables.

The proportion of time spent resting was found to have a minor negative influence on the total time spent singing and a minor positive influence on the proportion of time spent singing. This is unusual as both singing variables are representative of the same feature of singing behaviour, making these results contradictory. It is possible that the detected influences are so weak that they could be changed by the numerical differences between presenting singing time in minutes or as a proportion of activity budget. Or that the total activity budget is appropriately smaller on days when singing bouts are shorter so as to compensate for the loss of singing time, however I find this latter explanation to make little logical sense. From an energetics point of view resting would have been expected to be higher on days with more singing to conserve energy. No influence or correlation was found with any other singing variables.

The proportion of time spent travelling, daily path length and average speed were intercorrelated and could not be used in the same multiple regression test. Of the three average speed best explained variation in total time spent singing by showing a slight negative relationship. This meant that gibbons that sang more in the morning travelled less that day and that gibbons that sang less travelled more. This could be explained by the use of energy in singing causing gibbons to conserve energy by not travelling at higher speeds in the ensuing day where gibbons that did not sing were able to travel more with the energy they had saved. This however would contradict the explanation for increased feeding when

singing levels were low as a result of a lower energy balance. In this scenario gibbons that sang more fed less because they possessed greater energy and fed more when they sang less to recover energy. These two explanations are incompatible, but I am not certain which, if either best describes reality. Time spent travelling, daily path length and average speed had no other influence or correlation with other singing variables.

In summary the tests connecting energetics with singing behaviour are contradictory, implying the influence of energetics in multiple directions. That these suggested influences and relationships are all so weak also does not provide convincing evidence that energetics has a strong influence on singing behaviour. Flaws in statistical analysis however preclude me from dismissing altogether that such relationships exist. Should methodology be improved these relationships may become apparent. I consider the first objective, to support or refute the assertion that energy balance influences singing behaviour to not have been met

## 4.3 The Influence of Social behaviour on Singing Behaviour

The proportion of time spent grooming, playing and cofeeding were not found to correlate or have a relation with any singing variables, meaning variation in singing behaviour was not followed by consistent variations in social behaviours and suggesting that pair bond strength as represented by these social behaviours is not related to singing behaviour. This is possibly not as influenced by statistical problems of causality as much as feeding and energetic data as it is possible that social behaviour does not vary as much over short periods of time. The social bond between gibbons would be expected to remain the same from one day to the next as well as behaviours associated with it. This result indicates that the strength of a pair bond may not be important in terms of influencing gibbon song.

The occurrence of intergroup encounters was not found to be related or correlated to singing behaviour. This result is not valid however as all it tells us is that variation in singing does not cause and is not associated with an encounter with a neighbouring group later that day and therefore does not provide evidence to prove or disprove the hypotheses that intergroup encounters influences singing behaviour.

To summarise social behaviour, I believe that I have provided evidence that the pair bond between gibbons does not influence singing behaviour in the capacities that I have studied, although the sample size of two pairs is very small. This was unexpected as gibbons that exhibited these behaviours were expected to have stronger pair bonds and to put more time and energy into singing. It is possible that social behaviour is not related to pair bond strength as much as expected or that pair bond strength does not influence singing behaviour as much as was expected. The small sample size of this study however should be considered when taking this result into account. In this way I believe I have fulfilled my objective to provide evidence to support or refute the statement that pair bond strength influence singing behaviour. The test to show a relationship between interactions and singing behaviour was inappropriate however and as such I have not fulfilled my objective to support or refute the statement that intergroup interactions influence singing behaviour.

## 4.4 Methodological flaws

Alongside flaws in the statistical planning of the multiple regression tests there were other minor difficulties during data collection which may have reduced the accuracy of the data collected. They are as follows:

- Accurately recording singing behaviour could be difficult as the sound of the gibbons singing could be obscured by the sounds of wind and rain and even the movements of

the observer against the undergrowth. This was especially true when the gibbon was in the distance, such as when waiting for the gibbon to sing at a listening post. Even the singing of other gibbon groups could interfere with data collection if it was especially loud.

- When gibbons sing they also begin at lower volumes and get louder. Therefore when a group was far away it was hard to accurately judge a start time.

- When recording the order in the chorus from a listening post it is likely to differ from what the gibbons can hear at their own position and may not accurately reflect the progression of the chorus as they can hear it.

- Some gibbons were harder to follow than others, resulting in more losses during the follow. This meant it was not possible to get an optimum proportion of follows between sexes and groups to avoid bias.

- Before sunrise it was usually too dark to accurately record behavioural data.

- My study only analysed data from two gibbon groups. This is obviously a very small sample size and calls into question the validity of these results for the remaining global population of *H. albibarbis*.

- This study involved following incredibly athletic and acrobatic animals through dense swamp forest. Even for experienced researchers this could be very physically demanding, especially considering a typical day involved 10 or more hours of work. The concern here is that tired researchers will experience researcher fatigue; that the quality of their data collection will reduce with their level of physical exhaustion.

# Chapter 5: Concluding Statement

In this study I used focal time sampling, multiple regression analysis and Spearman's rank correlation to search for evidence to support or refute a potential influence of feeding, ranging and social behaviour as well as the occurrence of intergroup encounters on the singing behaviour of *Hylobates albibarbis*. Due to errors in the statistical method I was unsuccessful in finding evidence to support or refute the hypothesis that a greater energy intake, as represented by increased feeding on non-fig fruits, decreased feeding on leafs/flowers and figs and more time spent travelling influences singing behaviour, or that the occurrence of intergroup encounters does the same. I did however find that variables such as proportion of time spent grooming, playing and cofeeding have no influence on singing behaviour, suggesting that the strength of the relationship between a mated pair of gibbons is not indicative of their singing behaviour. This is an unusual response to receive as it was anticipated that signs of a strong pair bond would be associated with increased levels of singing. The study however only took into account data from two gibbon groups, a very small sample size which may not be representative of the population as a whole.

The use of more appropriate statistical tests such as cross correlation and time series analysis as well as further modifications to the methodology used for multiple regression analysis may provide results that better represent the actual relationship between these factors and are more helpful to the understanding of gibbon biology. Increasing the sample size to more gibbon families would also lend more credibility to results. This study also does not take into account the influence of meteorology and seasonality. Measuring the influence of weather and seasonal conditions as well as gibbon energetics and sociality would be an interesting avenue

of research and would make this study more holistic and better able to interpret gibbon behaviour.

Some further modifications to methodology could improve this study. The distance between a mated pair of animals has also been shown to be a good indicator of pair bond strength (Geissmann & Orgeldinger, 2000) and I would be interested to add this variable to the test. While my technique for collecting data on this factor was unsuccessful it is possible that following both gibbons in a dyad simultaneously and recording GPS data for both could be a highly accurate way to assess this. The long hours in this study may have caused a decrease in data collection accuracy because of researcher fatigue. I recommend in future studies swapping researchers half way through the day, although of course this will require more personnel to achieve. More data could have been collected on intergroup encounters, despite the difficulties in recording such events. Information such as the level of aggression or affiliation could have been recorded, as well as whose territory the encounter took place in. Future studies could look in more detail at this.

While this study was not hugely successful in achieving the set objectives it did provide information about the relationship between gibbon social behaviour and singing. With further amendments to methodology its potential to explain the phenomenon of gibbon singing can be improved.

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# Appendix 1: Behavioural Ethogram

## GIBBON ACTIVITIES 2015
### GENERAL ACTIVITIES

| 1. FEEDING | F |
|---|---|
| CO-FEEDING | CF |
| FOOD SEARCH | FS |
| *Fruit:* | |
| Fruit ripe | FR |
| Fruit unripe | FUM |
| Pulp | / P |
| Seeds | / S |
| Skin | / SK |
| whole fruit | / WH |
| Unknown part | / U |
| *Flowers and Leaves:* | |
| Flowers | FL |
| Flower bud | FLB |
| Mature leaves | L |
| Leaf shoots | LS |
| Epiphytes (orchids, ferns etc.) | E |
| Rattan stem | R |
| Pandan | PP |
| Liana stem | LI |
| Pith | PI |
| *Other Food Items:* | |
| Bark (cambium) | B |
| Roots | RT |
| Invertebrates (termites, ants, caterpillars etc.) | IV |
| Honey | H |
| Fungi | FG |
| Meat (vertebrates) | V |
| Soil | SL |
| Rotten wood (no termites) | RW |
| Sap | SAP |
| Water | W |
| Milk | SUSU |
| Unknown Food (Take sample) | UF |
| Other (Specify) | OF |

| 2. PLAYING | P |
|---|---|
| Independent play, e.g. swinging, twirling | IPS |
| Independent play with object | IPO |
| Play with other individual | PL |
| With mother | / M |
| With offspring | / O |
| With other gibbon (specify who) | / OG |
| With other species (details) | / OS |

| 3. SOCIAL | SO |
|---|---|
| Mating | M |
| Aggressive chase | ACH |
| Aggressive contact | ACT |
| Non-aggressive chase | NACH |
| Threatening behaviour | TH |
| Submissive | SB |
| Allogroom | AL |
| Autogroom | GS |
| Groomed by other individual | GB |
| Groom other individual | GO |

| 4. TRAVELLING | T |
|---|---|
| Jumping | J |
| Clambering | CLA |
| Climbing | CLI |
| Brachiating | BR |
| Bipedal walking | BW |
| Flee | F |
| Swing | SW |
| Treesway | TT |

| 5. ACTIVITIES TOWARDS OBSERVER | ATO |
|---|---|
| ACTIVITIES TOWARD OTHER PERSON | AOP |
| Observes researcher or other person | OOP |
| Vocalisation towards researcher or other person | VTO |
| Threatening researcher or other person | TO |

| 6. CALLING | C |
|---|---|
| Great Call (Female only) | GC |
| Coda (Male only) | CO |
| Alarm call | AC |
| Duet | D |
| Hoot | HO |
| Mating squeeks | RU |
| Playing call | PC |
| Female solo call | SC |
| Other call (Describe/record) | OC |

| 7. RESTING | R |
|---|---|
| Sitting | SI |
| Hanging | HA |
| Standing | ST |
| Lying down | LD |
| Tree | / TR |
| Sleeping tree | / SLT |
| Liana | / LI |
| Ground | / G |
| Mother | / M |

| Unknown | U |
|---|---|
| Lost | L |
| Other | O |

| TREE/GIBBON HEIGHT CATEGORIES |
|---|
| 0m (i.e. on the ground) |
| 1-5m |
| 6-10m |
| 11-15m |
| 16-20m |
| 21-25m |
| 26-30m |
| 31-35m |
| 36m+ |