POPULATION DENSITIES OF AGILE GIBBON (*HYLOBATES AGILIS*) AND THEIR RELATIONSHIP WITH HABITAT CHARACTERISTICS AND HISTORY OF DISTURBANCE IN THE ULU MUDA FOREST RESERVE, MALAYSIA

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by

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LIST OF ABBREVIATIONS

a.k.a.	also known as
asl	above sea level
DBH	Diameter at breast height
GIS	Geographic information system
IUCN	International Union for Conservation of Nature
LP	Listening post
LA	Listening area
MADA	Muda Agricultural Development Authority
VP	Vegetation “speed plot”
mya	million years ago
UMFR	Ulu Muda Forest Reserve

LIST OF APPENDICES

KEPADATAN POPULASI UNGKA TANGAN HITAM (*HYLOBATES AGILIS*) DAN PERKAITANNYA DENGAN CIRI-CIRI HABITAT DAN SEJARAH GANGGUAN DI HUTAN SIMPAN ULU MUDA.

ABSTRAK

Populasi spesies mawas kecil di Semenanjung Malaysia telah lama tidak dikaji semenjak awal tahun 1980-an, sedangkan semakin banyak kawasan habitat mereka telah ditukar untuk kegunaan tanah lain. Tujuan kajian ini adalah untuk menganggar bilangan kumpulan ungka tangan hitam (*Hylobates agilis*) di bawah 450 m atas paras laut (apl) di kawasan Hutan Simpan Ulu Muda (HSUM), Kedah. Perbezaan kepadatan kumpulan di kawasan HSUM yang mempunyai tahap gangguan yang berbeza telah dibandingkan. Tinjauan bioakustika telah dijalankan di sembilan kawasan kajian untuk menganggar kepadatan kumpulan, serta "plot gerakan" dan imej satelit untuk mengenalpasti ciri-ciri habitat. kepadatan kumpulan bagi julat kawasan HSUM ialah dari 3.89 kepada 4.17 kumpulan per kilometer segi (95% C.I.), dan ianya tidak menunjukkan perbezaan signifikasi antara jenis-jenis hutan ($p = 0.27$). Peramal ekologi yang terbaik untuk menentukan kepadatan kumpulan ialah "lintupan kanopi hutan" dan "pengkadaran kawasan penebangan hutan". Jumlah anggaran bilangan kumpulan *H. agilis* pada julat kawasan $\leqslant$450 m apl di HSUM ialah dari 2,825 kepada 3,028 kumpulan (95% C.I.). HSUM merupaka satu-satunya kawasan yang luas serta habitatnya masih tidak diganggu oleh penerokaan, dan berkemungkinan dihuni oleh populasi *H. agilis* yang terbesar di

tanah besar Asia. Dengan kepadatan kumpulan yang agak tinggi di kawasan pendalaman dan juga hutan yang ternyahgred di sekelilingnya, HSUM merupakan habitat yang amat penting untuk *H. agilis*. Justeru, kawasan ini wajib dilindungi dengan sepenuhnya (i.e. taman negeri). Lanjutan penyelidakan terhadap bilangan dan juga kepadatan populasi dibahagian lain di Malaysia, ekologi terhadap tingkah laku, interaksi inter-spesifik, taburan serta dinamik populasi sesama sepanjang kecerunan aras ketinggian, serta tindak balas ungka terhadap pengurangan jenis-jenis hutan dan fragmentasi diperlukan untuk merancang langkah-langkah pemuliharaan serta perlaksanaan yang lebih baik.

POPULATION DENSITIES OF AGILE GIBBON (*HYLOBATES AGILIS*) AND THEIR RELATIONSHIP WITH HABITAT CHARACTERISTICS AND HISTORY OF DISTURBANCE IN THE ULU MUDA FOREST RESERVE.

ABSTRACT

The population of small ape species in Peninsular Malaysia has not been studied since the early 1980s, while many of their habitats are increasingly being converted for other land use types. This study aims to estimate the total number of agile gibbons (*Hylobates agilis*) groups in areas below 450 m above sea level within Ulu Muda Forest Reserve (UMFR), Kedah. The group densities in different parts of UMFR with different degrees of disturbance were compared. Bioacoustic surveys were conducted in nine study sites to estimate group density, while vegetation "speed plots" and satellite imagery were used to qualify habitat characteristics. The group density in UMFR ranged from 3.89 to 4.17 groups per km^2 (95% C.I.), and did not show any significant difference among forest types ($p = 0.27$). The best ecological predictors for group density were "canopy cover" and "proportion of area deforested". The total estimated number of *H. agilis* groups in areas ≤450m asl in UMFR ranged from 2,825 to 3,028 groups (95% C.I.). UMFR is likely the largest relatively undisturbed habitat site for H. agilis mainland Asia. With group densities remaining high in all forest types, UMFR and the degraded forests surrounding it are important gibbon habitats and must be totally protected (i.e., gazetted as state or national park). Further studies on population abundance and density in other parts of

Malaysia, behavioural ecology, inter-specific interactions, current distribution and population dynamics along elevational gradients, as well as gibbons' responses to different types of forest degradation and fragmentation are needed for better conservation action planning and implementation.

CHAPTER 1

INTRODUCTION

In 2000, 62% of Malaysia's land area was covered by natural forest; however, 26% of this forest cover, or 7.73 million hectares, had been lost as of 2018 (Global Forest Watch, 2018). The main driver of deforestation (and subsequent habitat fragmentation and degradation) in Malaysia is conversion of forest for development (i.e. industries, housing, etc.), as well as monoculture plantation (i.e. oil palm and rubber). Forest loss and degradation, however, put the viability of small apes (family Hylobatidae) populations in Malaysia at risk. Small apes are vulnerable to deforestation, habitat degradation and fragmentation, as they are 1) true brachiators that live on the upper canopy (Gittins, 1983), 2) reliant on continuous and dense canopy cover for locomotion (Cheyne, Thompson, & Chivers, 2013), 3) unable to persist in monoculture plantations (Choudhury, 2006; Zhang, et al., 2010), and 4) usually unwilling to cross roads as they rarely descend to ground level (Lim, 2017).

With many of the small ape habitats throughout Malaysia becoming modified by anthropogenic activities (Lappan & Ruppert, 2019), detailed knowledge about their abundance, occurrence and ability to persist in disturbed environments becomes critical for the development of effective small apes' conservation plans. Protection of forested areas, including those are logged at regular intervals, is needed to protect viable populations of small apes, and consequently, small ape conservation efforts will also

benefit many other species inhabiting the same forests, thus making small apes umbrella species (Chan et. al, 2014).

1.1 Problem statement

The population status of most small ape populations in Peninsular Malaysia is currently unknown, as the most recent studies were carried out between 1970s and 1980s (e.g. Southwick & Cadigan, 1972; Chivers, 1980; Mitani, 1987). By overlapping the species' distribution (IUCN, 2020) and maps of current forest cover (Hansen et. al., 2013), it is apparent that most *H. agilis* habitat in Peninsular Malaysia has been converted for other land uses, and that the remaining forests are fragmented (Figure 1.1).

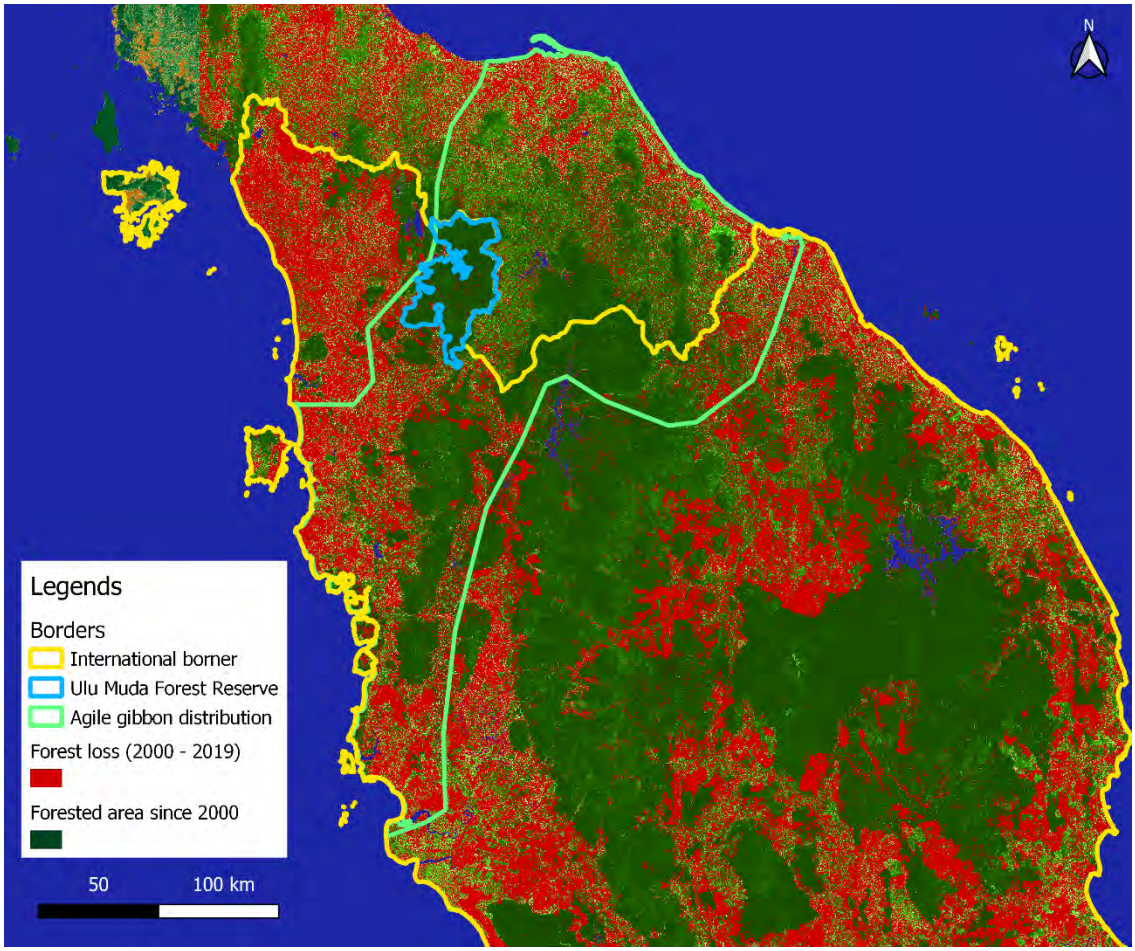

Figure 1.1 Distribution of *Hylobates agilis* in Malay Peninsula (IUCN 2020) and forest cover in 2019 (Hansen et. al. 2013).

Based on the current forest cover data by Hansen et. al. (2013), Ulu Muda Forest Reserve (hereinafter, UMFR) is a large, unfragmented wildlife habitat with virtually no human settlement within (Suksuwan, 2008). It is located entirely within the historical range of *H. agilis* (Figure 1.1) and without the presence of other allopatric and sympatric small ape species (Gittins 1978; Marshall 1981). With its habitat elsewhere, including in Thailand, being highly degraded and fragmented, UMFR is likely to the largest mainland Asia's population of *H. agilis* in mainland Asia. While other small ape species in

neighbouring countries are shown to be able to adapt in degraded forest, the response to anthropogenic activities and ecological predictors of the *H. agilis* group density in Malaysia were not examined for the past four decades. There is a knowledge gap in the population occurrence (current distribution), density and abundance of small apes (including *H. agilis*) in Malaysia, hindering any conservation action planning for protecting them. Hence, this study aims to quantify the overall *H. agilis* population abundance, evaluate their group density in forests with different degrees of human disturbance, and identify ecological predictors of *H. agilis* abundance in areas of lower elevation (≤ 450 m asl, where the species is known to thrive in other studies and logistically achievable) within UMFR. This study hopes to elevate the conservation value of UMFR to a higher position (with gibbons as umbrella species) and eventually advocating for the forest to receive a higher protection status, as to trigger a nation-wide comprehensive population survey to give rise an updated population status in order to develop an action plan for protecting small apes as well as their priority habitats in Malaysia.

1.2 Objectives and hypothesis

1.2.1 Estimation of gibbon group density in Ulu Muda Forest Reserve (UMFR)

The first study aim was to estimate the group densities of *H. agilis* at nine sampling areas in UMFR.

1.2.2 Comparing group density at different habitat types

The second objective was to determine the relationship between group density and difference degrees of habitat disturbance. The null hypothesis for the second objective

was that the group density of *H. agilis* at UMFR is not significantly different across different habitat types with different disturbance history. The alternative hypothesis was that the group density is higher in unlogged forest than previously (1960s – 1990s) and recently logged forest (2015 - 2017).

1.2.3 Determining the best ecological predictors of group density.

The third objective was to determine which variables (i.e. canopy cover, tree height, forest cover in 2000, and others) best predict group densities of *H. agilis* at UMFR using General Linear Model selection. The null hypothesis for this objective was none of the variables predicts the group density of *H. agilis*. The alternative hypothesis was some of the variables predicts the group density of *H. agilis*.

1.2.4 Estimation of total number of groups in UMFR.

The fourth objective was to extrapolate the total number of gibbon groups in forested areas of UMFR below 450m asl (i.e. the range of elevations surveyed in this study) by using the estimated group densities from objective 1.

CHAPTER 2

LITERATURE REVIEW

2.1 Introduction

Research on small apes, ranging from taxonomy, biology to behavioural ecology was first established in Southeast Asia in the 1930s (e.g. Miller, 1933; Carpenter, 1940). However, as the region has been undergoing rapid development, small apes are losing habitats, thus raising conservation concern.

Studies of small apes in Malaysia, though they have provided useful baseline data (i.e. behavior, distribution range), are outdated as most were done predominantly in the 1970s and 1980s. With rapid developments from industries, agriculture, and urban expansion since then, many suitable habitats have been degraded, if not destroyed, rendering the current conservation status of Malaysian small apes unknown and in dire need of updating.

A rapid literature review was performed using the Scopus website (Table 2.1). There were only 16 peer-reviewed articles on Peninsular Malaysia's small apes. Of the 16 articles, 12 articles were published between 1964 to 1997.

While the last studies took place in Malaysia some 40 years ago, many extensive studies on small apes have been conducted in Thailand, Indonesia, Vietnam, China, and other countries in recent years. Despite the lack of updated baseline data in Malaysia, these studies provide useful knowledge about research methods, small ape biology and conservation issues, therefore informing researchers in Malaysia conducting studies on small apes.

Table 2.1 Flowchart of rapid literature review on Scopus.

Scopus search term on title, abstract and keywords	"gibbon"
Result	4765

↓

Limit title, abstract and keywords search to	"Malaysia"
Result	31

↓

Exclude term from title, abstract and keywords	"Sabah" & "Sarawak
Result	19

↓

Title read to exclude unrelated studies	"Malaysia"
Result	16

↓

Exclude reports on behavior from captivity	
Result	15

More studies on population dynamics, survey methods, and the use of new technologies were carried out to contribute additional baseline information for small ape conservation. This literature review about small apes is subdivided into the following sections: 1) Taxonomy, 2) Small ape studies in Peninsular Malaysia, 3) Biogeography, 4) Ecology, 5) Behaviour, 6) Conservation issues, 7) Population assessment, and 8) Ecological predictor.

2.2 Small ape taxonomy

Gibbons, also known as small apes, belong to the primate family Hylobatidae, the sister lineage to the great ape family (Hominidae) which includes the orangutans (*Pongo spp*.), gorillas (*Gorilla spp*.), chimpanzees and bonobos (*Pan spp*.) and humans (Reichard, Barelli, Hirai, & Nowak, 2016) (Figure 2.1). Hylobatidae and Hominidae together constitute the superfamily Hominoidea. The small ape genome is estimated to share 96% of its sequence with the human genome (Dunham, 2014). The lineage that led to hominoids diverged from that leading to the Old World monkeys (subfamily Cercopithecoidea) around 29 million years ago (mya), and subsequently from the great apes during the early Miocene (16-22 mya), and experienced a relatively rapid radiation around 5 mya (Carbone, et al., 2014; Reichard, Barelli, Hirai, & Nowak, 2016). Previously divided into two genera (*Hylobates* and *Symphalangus*), further studies on their diploid chromosomal number and other genetic features suggest that there are four genera of small apes: *Hoolock*: 2n = 38; *Hylobates*: 2n = 44; *Symphalangus*: 2n = 50; *Nomascus*: 2n = 52 (Stanyon, 2013). With the recent description of the species *Hoolock tianxing* by Fan et. al.

in 2017, the small ape family comprises 20 extant species (Rawson, et. al., 2011; Fleagle, 2013; IUCN, 2020).

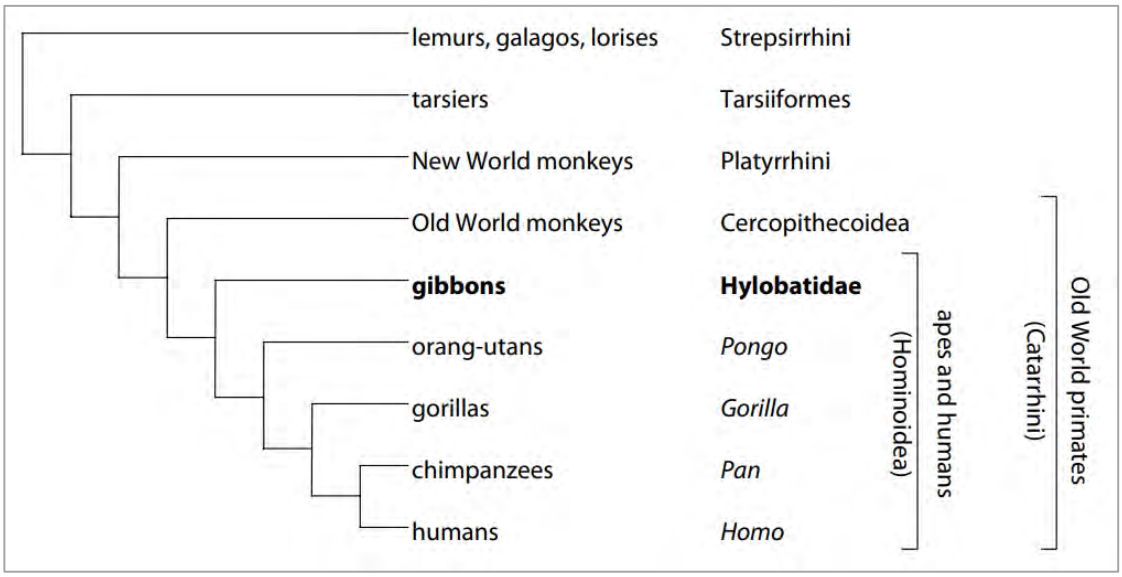

Figure 2.1 Phylogentic position of gibbon (family Hylobatidae) within the order Primates (Rawson et. al., 2011, Figure 9).

2.3 Biogeography

Small apes are distributed throughout Southeast Asia and in parts of South Asia and southern China (Figure 2.2). The genus *Nomascus*, also known as the crested gibbons, is comprised of seven species, and is mainly restricted to the western part of Indochina (Laos and Vietnam and bordering areas in China), as well as Hainan Island in China (Geissmann, 2005; Rawson et al., 2011). Consisting of three species, the genus *Hoolock* ranges from Yunnan Province in China in the east (Fan et. al., 2017) to northeast India and eastern Bangladesh (Choudhury, 2006; Zhang et. al., 2014). The most species-rich genus in the family, *Hylobates*, has nine species in the genus, and is distributed from the central part of Indochina (Brockelman et. al., 2005; Geissmann, 2007; Bartlett et. al., 2016), through the Malay Peninsula (Gittins, 1978; Gittins, 1982), to the islands of Borneo (Cheyne et. al., 2016), Sumatra including the Mentawai Islands (Consiglio, 2015), and Java (Setiawan, 2012).

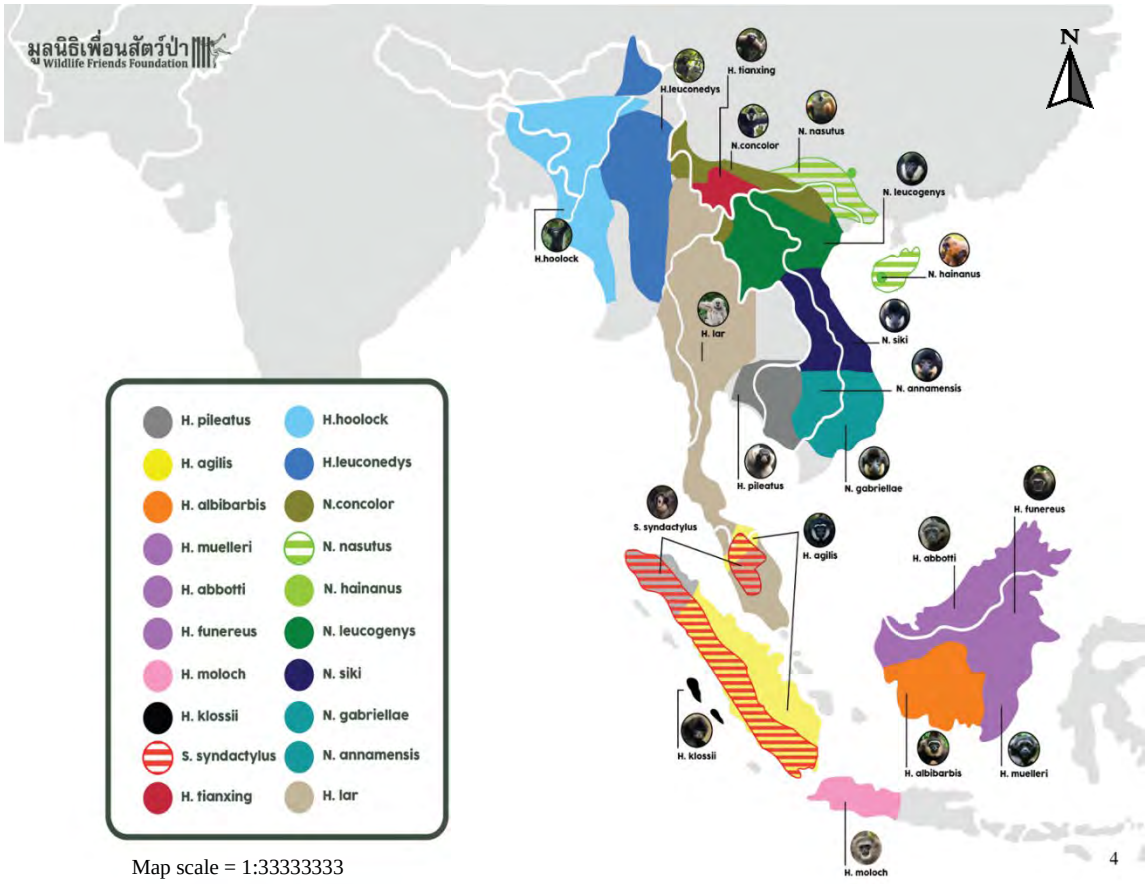

Figure 2.2 Distribution of family Hylobatidae in Southeast Asia by genus (Wildlife Friends Foundation, 2020).

Within Peninsular Malaysia, there are three species of small apes, namely the siamang (*S. syndactylus*), lar gibbon (*H. lar*) and agile gibbon (*H. agilis*) (Figure 2.3), whereas northern Bornean gray gibbon (*H. funereus*) and Abbott's gray gibbon (*H. abbotti*) are present in Malaysian Borneo (Figure 2.4). Ulu Muda Forest Reserve, the study site for this research, is located entirely within the distribution range of *H. agilis* (Figure 2.3).

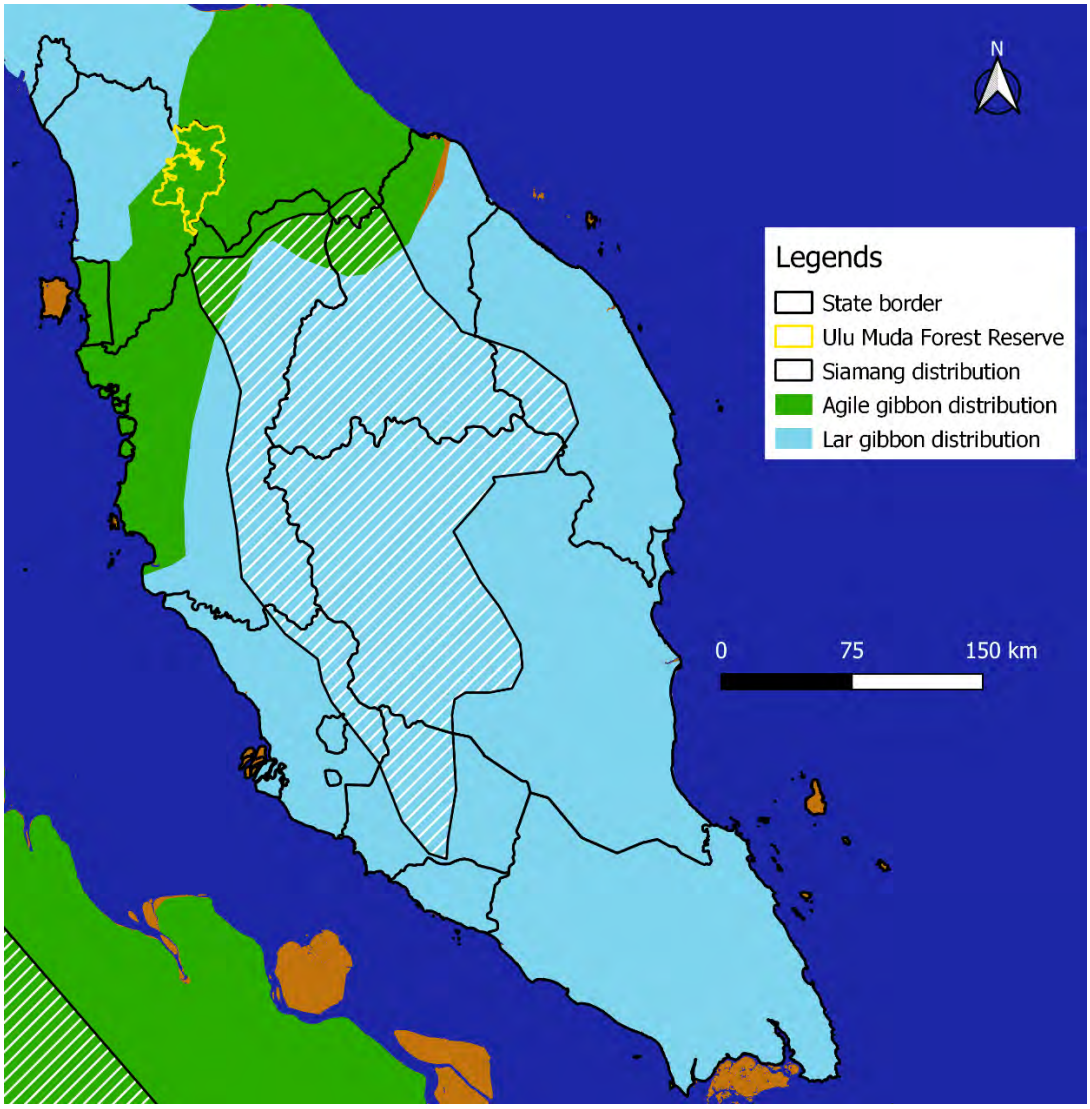

Figure 2.3 Distribution of small apes in Peninsular Malaysia (IUCN 2020).

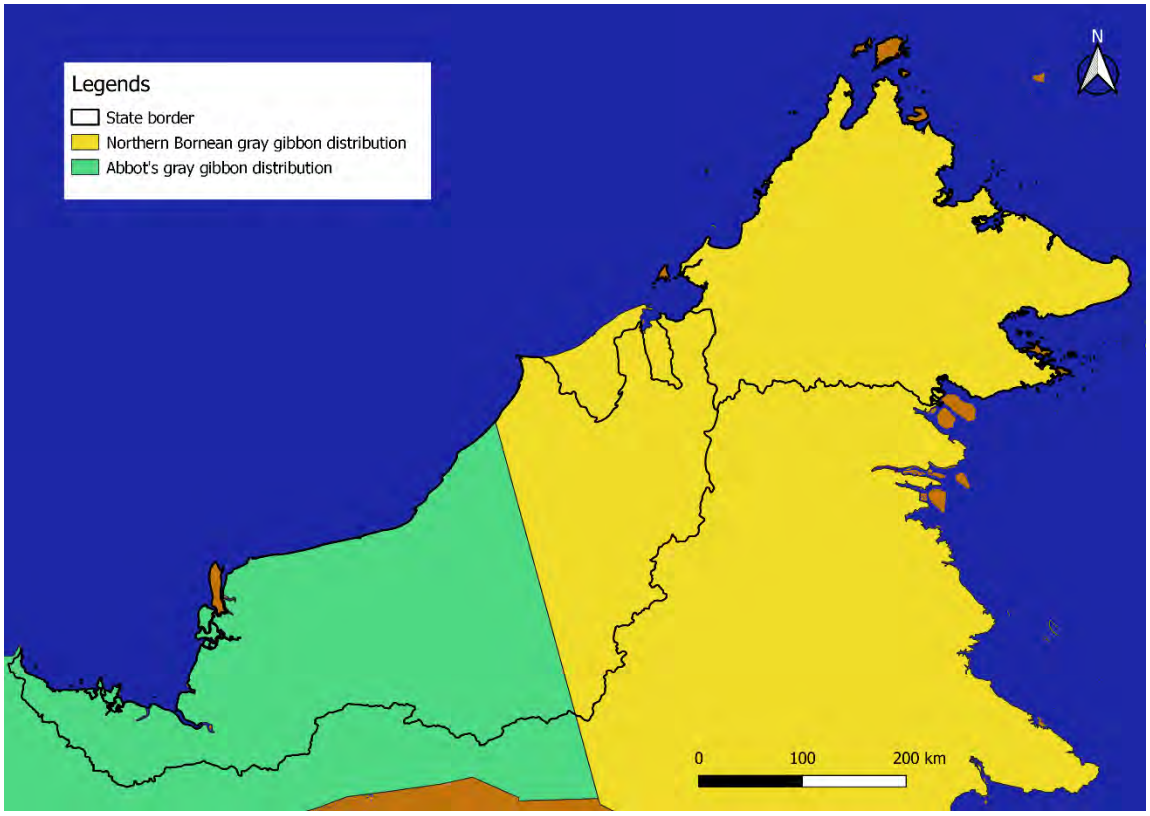

Figure 2.4 Distribution of small apes in Malaysian Borneo (IUCN 2020).

There are five subspecies of *H. lar*: *H. l. lar*, *H. l. carpenter*, *H. l. entelloides*, *H. l. vestitus* (Marshall & Sugardjito, 1986) and *H. l. yunnanensis* (Ma & Wang, 1986). Only two subspecies can be found within Peninsular Malaysia: *H. l. lar* is found from central to southern part of Peninsular Malaysia, while *H. l. entelloides* is found from central to southern Thailand, southern Myammar, to northwestern Kedah (north of Muda River) (Geissmann, 1995; Mootnick, 2006) (Figure 2.5). Lar gibbon can be distinguished from agile gibbon by recognising the complete white ring on the face, as the white fur at the back of its hands and feet (Mootnick, 2006; Figure 2.6 & Figure 2.7).

Hylobates agilis is distributed in two discrete areas: mainland Asia and Sumatra. The mainland population is distributed from southernmost Thailand in the north, to

northeast Kelantan in the east, and Kedah and Perak to the southwest (Gittins, 1978; Marshall, 1981). *Hylobates agilis* also occurs in the southern part of Sumatra (Yanuar, 2001; Groves, 2016). *Hylobates agilis* was originally comprised of three subspecies: *H. a. agilis*, *H. a. unko* and *H. a. albibarbis* (Marshall & Sugardjito, 1986), until Groves (2001) listed *H. a. albibarbis* as a full species. *Hylobates agilis agilis* is found in highlands of northern Malay Peninsula and western Sumatra (south of Lake Toba, in the Bukit Barisan range), while *H. a. unko* is found in lowlands of northern Malay Peninsula and eastern Sumatra (south of Lake Toba) (Mootnick, 2006). Peninsular Malaysia is thus within the range of both subspecies, found between Muda and Perak Rivers (Mootnick, 2006). For the purpose of this study, both subspecies were treated as one species.

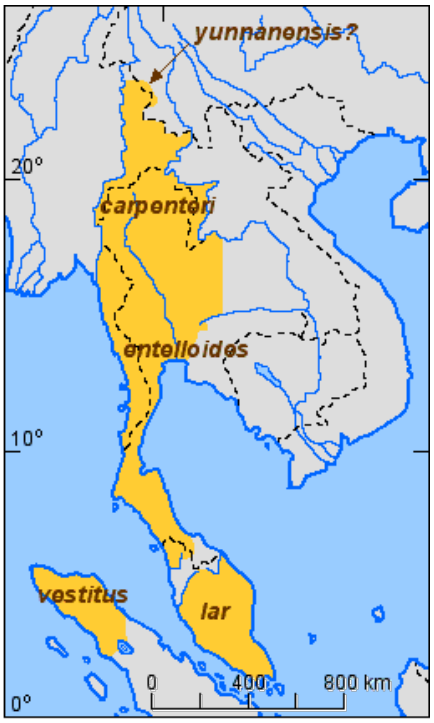

Figure 2.5 Approximate distribution of the subspecies of the white-handed gibbon (*Hylobates lar*) (Geissmann, 1995).

Figure 2.6 Agile gibbon (*Hylobates agilis*). Photo courtesy: Lee Zan Hui

Figure 2.7 Lar gibbon (*Hylobates lar*).

The siamang (*Symphalangus syndactylus*), the only extant species in the genus *Symphalangus*¸ is mainly distributed in the central part of Peninsular Malaysia (Kawabe, 1970; Southwick & Cadigan, 1972) and Sumatra (Brandon-Jones et. al., 2004; Lappan, 2007) (Figure 2.3). At the places where the distribution of more than one species overlaps, a small degree of sympatry can occur. For example, *Nomascus concolor* and *Hylobates lar* ranges overlap in southwest Yunnan Province (Ma & Wang, 1986; Zhang, Quan, Zhao, & Southwick, 1992; Rawson et. al., 2011). *Nomascus concolor* is also known to live sympatrically with *N. leucogenys* in Vietnam (Rawson et. al., 2011). *Symphalangus syndactylus* is distributed entirely within the range of *H. lar* and *H. agilis* in Peninsular Malaysia and Sumatra, and is extensively sympatric with both species (Southwick & Cadigan, 1972; Caldecott, 1980; Raemaekers, 1980; O'Brien, Kinnaird, Nurcahyo, Iqbal, & Rusmanto, 2004). There are some cases of hybridization in the contact zones. For instance, *H. lar* and *H. pileatus* hybridise in Khao Yai National Park, Thailand (Brockelman & Gittins, 1984; Matsudaira, Reichard, Malaivijitnond, & Ishida, 2013) as do *H. muelleri* with *H. albibarbis* in central Kalimantan (Mather, 1992; Cheyne, et al., 2016). Gittins (1978) discovered a *H. lar* male has formed a group with a *H. agilis* female, and *H. agilis* male formed a group with *H. lar* female at the forest adjacent to the main body of Muda Lake (GPS coordinates: 6.133293, 100.883152), both of which seem to interbreed and produce offspring, as stressed the contact zone between both species is narrow.

2.4 Ecology

2.4.1 Habitat

Small apes inhabit evergreen and semi-deciduous tropical and subtropical rainforest of South and Southeast Asia. Despite being broadly distributed, the habitat requirements of small apes remain fairly uniform and specific (Lappan & Whittaker, 2009; Fleagle, 2013). Small apes are exclusively arboreal, moving and feeding in the middle and upper canopy layers of the rainforest (Gittins, 1983; Brockelman & Ali, 1987; Whittaker, 2009) and rarely descend to ground level (Lim, 2019). Due to their locomotor niche, small apes prefer forest with continuous, dense canopy cover and high trees (Cannon & Leighton, 1994; Hamard, 2008; Hamard, Cheyne, & Nijman, 2010; Phoonjampa et. al., 2011; Cheyne et. al., 2013; Cheyne et. al., 2016). Dipterocarp trees are shown to be important platforms for resting and vocalization (Yusof & Faridah-Hanum, 2008). *Symphalangus syndactylus* was found to occur at higher altitudes than *H. lar* in the hilly parts of Peninsular Malaysia, suggesting that gibbon ranges are restricted by altitude, which might be due to changes in availability of preferred foods and more difficult terrain at higher elevations (Caldecott, 1980).

2.4.2 Locomotion

Although many members of the apes (superfamily Hominoidea) have anatomical adaptations in their upper torso and arms that reflect the ability to brachiate, only small apes have perfected the suspensory bimanual brachiation, that is to primarily use forelimbs in an upright suspensory fashion for locomotion, supporting more than 50 % of the body

weight with elbow joint extended, and the brachium (upper arms) fully abducted (Carpenter, 1940; Fleagle, 1976; Cannon & Leighton, 1994). Small apes locomote in several ways, including: 1) brachiation, and 2) climbing, 3) bipedal walking (Figure 2.6) and 4) leaping (Figure 2.7) (Chivers, 1974; Fleagle, 1976; Reichard, Hirai, & Barelli, 2016).

Brachiation also refers to the bimanual (performed with both hands) suspensory progression, which the small apes swing between branches through a series of pendular movement below alternating handholds while rotating the branch up to 180◦ in each swing (Fleagle, 1976). The rapid, ricochetal brachiation where the small apes throw itself midair from one branch to another (sometimes over the gap of 10m or more) is less common in *S. syndactylus* than other smaller gibbon species (Carpenter, 1940; Chivers, 1972), although such locomation is more frequent in juvenile *S. syndactylus* (Chivers, 1974).

Climbing is when the animal uses three or more limbs to progress, which is highly irregular in small apes as its gait and limb use vary with substrate characteristic (i.e. branch size, orientation, continuity, etc), and involves frequent flexing of forelimbs and hindlimbs than extending (Fleagle, 1976). At least for *S. syndactylus*, the animal occasionally assumes quadrumanous climbing gait for long, continuous trunk (Fleagle, 1976).

Bipedalism occurs when the small ape needs to walk on branches or ground, which involves leaning the body (trunk) slightly forward, abducted forelimbs with flexed elbows for balancing, partially flexing the hip and knee, and raising the hindlimbs (abducting at hip) at each step forward, with considerable amount of pelvic rotation (Fleagle, 1976).

Leaping usually occurs at terminal branches, where the animal aquires momentum by “pumping in place” on a branch, before taking off by pulling forelimbs forward while giving a little thrust with the hindlimbs (Fleagle, 1976). The animal then extends its limbs in order to better grasp any support in contact (Fleagle, 1976). Small-bodied gibbons perform better leaping than *S. syndactylus*, the latter which usually leaps from higher tree to lower tree (Fleagle, 1976).

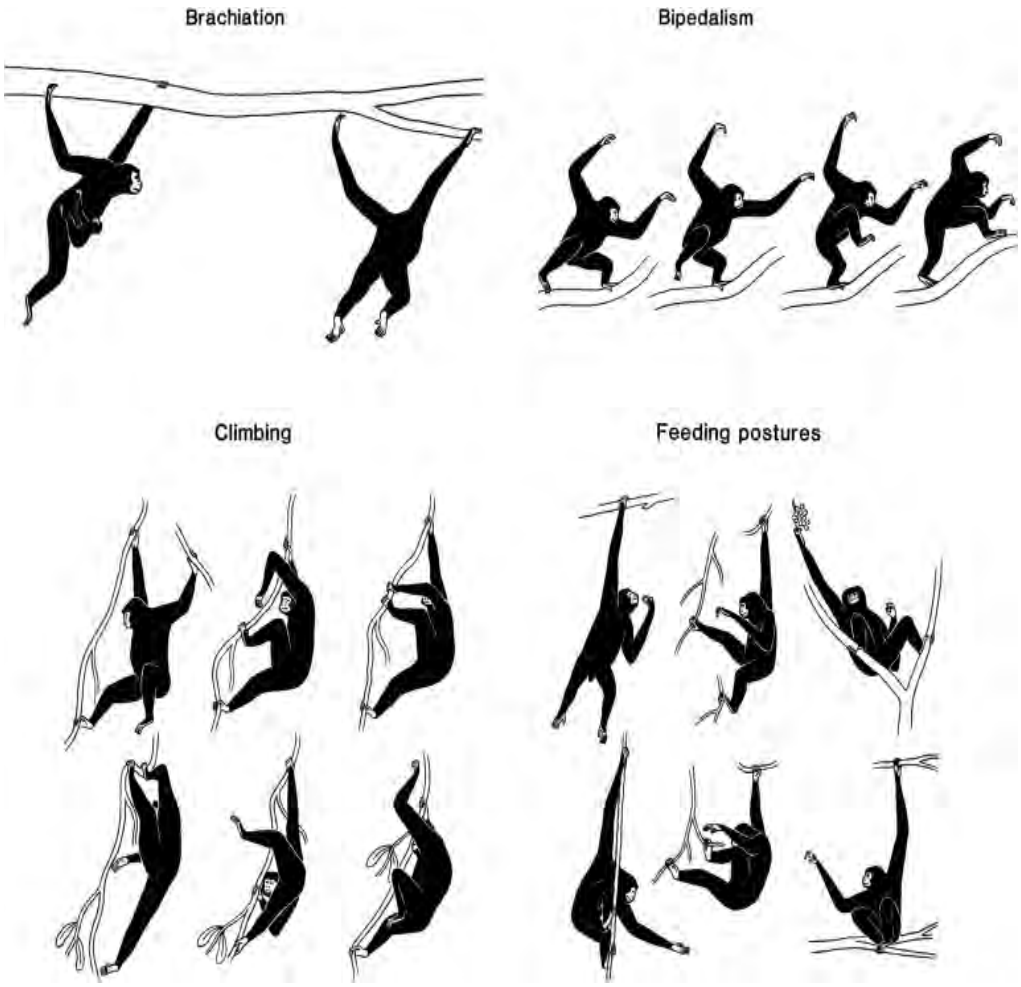

Figure 2.8 Locomotion of siamang (*Symphalangus syndactylus*) (Fleagle, 1976, Figures 1, 2, 5, 7).

Figure 2.9 Siamang (*Symphalangus syndactylus*) leaping (Fleagle, 1976, Figures 8).

2.4.3 Diet

The small apes have a highly frugivorous diet that they supplement with leaves, flower buds, invertebrates and occasionally vertebrates (Gittins & Raemaekers 1980; Gittins, 1982; Palombit, 1997; Cheyne, 2008 & 2010; Fan et. al.,2009). Trees from the families Moraceae (which include the genus *Ficus*) and Annonaceae are integral food sources for small apes as their asynchronous fruiting cycles makes them produce fruits at different times throughout the year, therefore ensuring small apes' food supply during low fruiting seasons (Cheyne, 2010). In a meta-analysis on 21 studies across 15 sites, gibbon

diet is shown to be comprised of 22% ripe figs, 47% ripe fruits of other species, 20% leaves/shoots, 10% flowers and 1% insects (Elder, 2009). Also, the diet of *Symphalagus syndactylus* at Kuala Lompat, Malaysia, is similar, with figs making up to 39% of their diet (49% fruit, 38% leaves, 3% flowers, 10% insects; Chivers, 1974).

2.4.4 Ecological role

Small apes play a crucial ecological role in dispersing seeds (Brockelman et. al, 2005). Gibbons usually swallow seeds whole and defecate them intact (McConkey, 2000; McConkey & Chivers, 2007). Seeds of the Pacific walnut (*Dracontomelon dao*) defecated by *N. gabriellae* have a higher germination rate than those handled by long-tailed macaques (*Macaca fascicularis*), and more than 90% of the seeds dispersed by *N. gabriellae* were dropped >20 m away from the parent's crown (Hai et. al., 2018). Likewise, *H. muelleri* and *H. albibarbis* disperse most seeds (> 90%) at least 100 m away from the parent tree (McConkey & Chivers, 2007). McConkey (2000) estimates that a gibbon group at Barito Ulu in Kalimantan, Indonesia dispersed approximately 13 seedlings per hectare in a year. As small apes are integral seed dispersers, understanding their population dynamics and developing effective plans to protect them is important for maintaining the ecosystem services that they provide, especially for forest regeneration in disturbed forests.

2.5 Behaviour

2.5.1 Social structure

Small apes are gregarious animals with groups that usually consist of a paired adult male and female and between zero and four, and occasionally more, immature individuals (Kawabe, 1970; Lee et. al., 2015). For example, *Symphalangus syndactylus* groups in Fraser's Hill were described as monogamous, with families consisting one pair of adult individuals and one or more subadults (Kawabe, 1970). Monogamy is a norm among gibbons (Kawabe, 1970; Mitani, 1987 & 1990; Palombit, 1994 & 1996, although extra-pair copulation and variant group structures have been documented across different species and populations. For instance, Reichard (1995) and Barelli, et. al. (2013) have described groups with one adult female and up to three male *H. lar* at Mo Singto in Thailand. While one male is generally dominant, extra-pair paternity has been confirmed in this population (Barelli et. al., 2013). Extra-pair copulation (Palombit, 1994) and multi-male grouping (Lappan, 2007) have also been reported in *S. syndactylus.* Polygyny was reported to coexist with monogamy in *N. concolor* in China (Jiang et. al., 2016).

Monogamy in small apes is associated with their territoriality. Females and males do not contribute equally to pair movements or to answering songs; in the event of inter-group encounters, males lead most approaches, while females initiate all duets (Mitani, 1987). In both *H. muelleri* and *H. agilis*, the mated pair approached and duetted in response to sound playbacks of duets that simulated territorial intrusion by neighboring groups and solitary females, but the pair-bonded male led approaches towards the speaker

for playbacks of solitary male songs (Mitani, 1984 & 1987). Pair-bonded monogamy is usually regulated by intrasexual aggression (Mitani, 1984).

2.5.2 Ranging behaviour

Gibbon home ranges are ca. 30 ha (range = 5 to >100 ha), and gibbons usually defend all or part of them as territories (Chivers, 1977; Palombit, 1993), although home ranges can be partially shared by neighbouring groups (Cheyne et. al., 2019). A territory (or core area) refers to the area that it is actively defended (Burr, 1943), and it is where sleeping trees and trees which they duet from are usually found (Cheyne et. al., 2019). However, gibbons may intrude into the territory of neighbouring group to feed (Gittins, 1980). On the opposite extreme, one habituated group of *H. leuconedys* in Gaoligongshan, Yunnan, China, was recorded a home range size of 93 hectares during the study duration (one year), as it shifted its home range according to the seasonal availability of food species (Zhang et. al., 2014). In the tropical mixed peat swamp forest of central Kalimantan, *H. albibarbis* home range sizes are reported to be between 16.5 to 43 hectares, 75% of which are defended as territory (Thompson, 2016), while a more recent study at a similar area revealed it to be between 20.7–51.31 hectares (Cheyne et. al., 2019). Southwick and Cadigan (1972) conducted a preliminary systematic study on seven species of primates in five different types of forest and concluded the group density of gibbons (*H. lar*) and siamangs (*S. syndactylus*) are 2.85 groups/km^2.

2.5.3 Duet

Small apes produce loud calling bouts that are audible from >1 kilometer away. These calls, or "songs" consist of phrases and occasional single notes (Geissmann, 2002), and are made to repel conspecific intruders, advertise pair bonds, and attract mates (Ellefson, 1968; Clarke et. al., 2006; Thinh et. al., 2010).

Paired adult males and females perform the duet in a coordinated song bout, but they do not contribute the same song notes. Both male and/or female make "interlude sequences" (notes and phrases interspersed between "great call sequences") before the onset of the female's stereotypical "great call" that swells in volume after soft opening notes, achieving a climax in pitch, intensity (or rapidity) before it subsides, during which the male falls silent (Figure 2.8) (Marshall & Marshall, 1976; Haimoff & Gittins, 1985, Geissmann, 2002). The characteristic short phrases from the male follow the end of the female's great call is the coda (Figure 2.8) (Geissmann, 2002). Hence, the combination of the female's great-call and the corresponding coda is called a "great-call sequence", and the cycle repeats (Geissmann, 2002). Great calls are usually a few minutes apart (Marshall & Marshall, 1976; Gittins, 1980; Geissmann, 1999; Phillips & Hill, 2006). Duets usually occur from before dawn until noon (Gittins 1980; Geissmann 1996; Inoue, Sinun, & Okanoya, 2016). Exceptions are *H. klossii* and *H. moloch*, in which the males chorus before dawn, while the females chorus after dawn (Geissmann & Nijman, 2006; Whittaker, 2009).