SLEEPING IN SAVANNAH TREES: SLEEPING TREE REUSE, INDIVIDUAL VARIATION, AND THE INFLUENCE OF FOREST TYPE ON SLEEPING TREE SELECTION BY WHITE-HANDED GIBBONS (*HYLOBATES LAR*) IN A SAVANNAH HABITAT

by

Kristen Stout

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Approved by:

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Dr. Lydia Light

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Dr. Jonathan Marks

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Dr. Susan Lappan

ABSTRACT

KRISTEN STOUT. Sleeping in Savannah Trees: Sleeping Tree Reuse, Individual Variation, and the Influence of Forest Type on Sleeping Tree Selection by White-Handed Gibbons in a Savannah Environment (Under the direction of DR. LYDIA LIGHT)

Gibbons are small, diurnal, arboreal apes and are most vulnerable to predators at night while they sleep. Previous research has shown that gibbons across a range of species exhibit cryptic pre-sleep behaviors, select sleeping trees with characteristics that may protect them from predators, and exhibit infrequent and irregular reuse of these sites. This study focuses on a group of white-handed gibbons (*Hylobates lar*) living in a savannah habitat with an intact predator community. I looked at antipredation strategies, intragroup variation in sleeping tree characteristics, and the influence of forest type on sleeping tree selection. As predicted, these gibbons likewise exhibited cryptic pre-sleep behaviors and selected sleeping trees similar to those observed in prior studies. Rates of sleeping tree reuse, however, were unusually high. Since sleeping tree reuse in this study followed a pattern of temporal clustering, higher rates of observed reuse may be influenced by a more continuous sampling of sleeping trees. Additionally, I argue that higher rates of sleeping tree reuse may be attributed to higher levels of predation pressure in combination with a suboptimal forest structure. Differences in sleeping tree canopy preferences between the adult individuals and the subadult were notable and may relate to size differences and therefore distinct predation pressures between age classes, especially from predatory birds. The subadult's preference for denser foliage in sleeping trees could also be driven by a biological need for better sleep quality, as wind has been identified as a key factor affecting sleep among captive gibbons. Though forest type has been shown to exert an influence on habitat use in this same population, I observed no significant effects on sleeping tree location in this dataset.

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LIST OF ABBREVIATIONS

AF: Adult female

AM: Adult male

DD: Dry dipterocarp

EE: Evergreen

HR: Home range

HKK: Huai Kha Khaeng Wildlife Sanctuary

KNR: Khao Nang Rum Research Station

MCP: Minimum convex polygon

MD: Mixed deciduous

REM: Rapid eye movement

SAF: Subadult female

CHAPTER 1: INTRODUCTION

Gibbons are perhaps most vulnerable to predation when asleep and it is thought that sleeping tree choice is primarily driven by predator avoidance (Tenaza & Tilson 1985, Reichard 1998, Fan & Jiang 2008, Cheyne et al. 2013, Fei et al. 2012, Fei et al. 2017, Fei et al. 2019, Harrison et al. 2021). Studies of sleep behaviors and sleeping site characteristics can provide valuable insights into a species' ecology, inform efforts in husbandry, and aid in the formulation of conservation strategies, particularly for endangered species (Anderson 1998, Reichard 1998). This research will serve as the first comparative study on white-handed gibbon (*Hylobates lar*) sleeping behavior. Sleeping behaviors of gibbons at Huai Kha Khaeng Wildlife Sanctuary in Thailand (**HKK**) may be particularly interesting, given that they cope with both suboptimal habitat conditions and a high density of predators. I will ask three primary questions: 1. Does sleeping tree selection by white-handed gibbons in HKK mirror previous sleeping tree selection by this species (Reichard 1998), further lending support to predator avoidance as a primary pressure in sleeping tree selection? 2. Do gibbons exhibit distinct preferences in sleeping trees regarding age or sex? And 3. Does forest type have a significant effect on sleeping tree location?

CHAPTER 2: LITERATURE REVIEW

2.1 *Gibbon social ecology*

The gibbons and siamang, or *Hylobatidae*, are the most speciose of the apes, totaling 20 different species (Fan et al. 2016, Fan & Bartlett 2017). This abundance of extant species across diverse habitats provides great potential for comparative studies, making gibbons of particular interest to primatologists. The white-handed gibbon, or *Hylobates lar*, was the first gibbon species studied in the wild (Carpenter 1940) and today remains the most well-studied of the hylobatid species (Brockelman 2009, Malone 2021).

Due to the Endangered status of most hylobatids and a host of worsening ecological concerns (Fan & Bartlett 2017, Pang et al. 2022), there is pressure to collect wild data while still possible and to provide information that may assist in conservation efforts (Estrada & Garber 2022). Gibbons and siamang (hereafter gibbons) receive relatively little attention when compared to their larger cousins, the “great” apes (Whittaker & Lappan 2009, Fan & Bartlett 2017). This inequality is unwarranted as gibbons play crucial roles in the ecosystems in which they are found. The role gibbons play in seed dispersal makes them a keystone species in southeast Asian forests (McConkey 2000, McConkey & Chivers 2007, Corlett et al. 2017, Phiphatsuwannachai et al. 2018, Ong et al. 2022).

Gibbons are smaller than other apes yet find their place in the *Hominoidea*, or ape, superfamily due to derived morphologies such as a Y5 molar dentition, a postcranial structure which supports erect posture, and the absence of a tail (Cheyne 2011, Bartlett 2015). Hylobatids, like other apes, share a basic cognitive capacity for “solving nonsocial problems with social solutions” (Reichard 2009 p. 371). Hylobatid life histories also closely resemble those of larger apes, meaning they reach maturity slower than monkeys and have longer intervals between reproduction (Reichard & Barelli 2008). Gibbons can be found throughout the remaining forests of southeast Asia (Fan & Bartlett 2017). Gibbons are not sexually dimorphic and adult individuals typically weigh 5-7 kg, though the larger siamang can weigh over 10 kg (Carpenter 1940, Zihlman et al. 2011). Long arms and fingers as well as small size makes gibbons specialized for life in the canopy and terminal branch feeding as opposed to terrestrial foraging (Brockelman 2009 p. 211). Gibbons are strictly arboreal and navigate the canopy by a locomotor adaptation known as brachiation (Cheyne 2011). This adaptation allows them to travel at great speeds of up to 55 km/h which is especially impressive considering they travel through dense forest - and can do so silently. They are most active from dawn until noon and retire to their sleeping trees several hours before dusk (Reichard 1998, Fei 2017). Gibbons typically live in small groups composed of one mating pair and offspring; however, group composition does not always follow this rule and gibbons exhibit social flexibility (Reichard 2003, Reichard & Barelli 2008, Savini et al. 2009, Malone 2021). Though hylobatids are typically described as frugivorous, monogamous, and territorial, many primatologists have warned against using these "blanket terms" as they conceal subtle ecological and behavioral distinctions among gibbon species and understate their behavioral flexibility (Bartlett 2003, Brockelman 2009, Bartlett 2016, Malone 2021, Light et al. 2021).

2.2 *The Importance of Sleep Studies*

The study of sleeping behaviors in primatology allows for crucial insights into the intricate balance between rest and survival strategies. All apes show selectivity in sleeping site choice and may spend roughly half of their lives at these locations (Anderson 1998). Therefore, an understanding of the range of adaptations that apes exhibit in their environment requires acquiring knowledge about behavior relating to sleeping behaviors and sleeping sites. Studying sleep-related behavior provides valuable insights into a species' ecology, aiding in the formulation of conservation strategies (Anderson 1998, Reichard 1998). The implications of sleep studies extend beyond the wild, offering valuable applications for captive primates. In essence, the exploration of primate sleeping behaviors is a key avenue for the study of adaptive behaviors and can inform efforts in both husbandry and conservation (Anderson 1998, Fei et al. 2017, Fruth et al. 2018, Anderson et al. 2019).

Depending on the behavioral criteria for defining sleep, it can be recognized as a nearly universally conserved trait across all animals with a nervous system. Sleep accompanied by a rapid eye movement (REM) stage evolved more recently and is only observable in mammals, birds, and reptiles (Rihel 2020). Sleep is marked by behavioral inactivity or quiescence, an increase in sleep periods after sleep deprivation, and a reversible elevated arousal threshold to stimuli (Rihel 2020). “Scientists have provided evidence for physiological functions of sleep such as energy saving, tissue repairing, thermoregulation, metabolic regulation, immunological enhancement, and memory formation” (Fruth et al. 2018 p. 499). Even flatworms sleep, and it is during this stage that flatworms exhibit their remarkable regeneration capacities (Omond et al. 2023). Sleep is nearly universally conserved across the animal kingdom and therefore proves itself crucial to animal well-being and worthy of study.

Many papers emphasize that reduced responsiveness during sleep poses risks. This state of decreased arousal inhibits an animal’s vigilance against life-threatening factors such as predators. Diurnal animals are also at a disadvantage when responding to nocturnal attacks since they often have poorer night vision than nocturnal or crepuscular predators (Bidner et al. 2018). Inactivity during periods of sleep not only jeopardizes an animal’s ability to respond promptly to threats but also leads to missed opportunities for vital activities like feeding, caring for the young, and socializing, thereby compromising individual fitness (Fruth et al., 2018).

Anderson (1998) emphasizes that knowledge of behavior around sleeping sites and analysis of factors influencing their use are integral to comprehending the range of primate adaptations. Primates employ various strategies to cope with specific environmental challenges and sleeping adaptations are no less diverse (Anderson 1998). Most papers investigate primate sleeping site selection in relation to several mutually nonexclusive factors: predator avoidance, proximity to food sources, competition with conspecifics, parasite avoidance, physical comfort, and thermoregulation (Reichard 1998, Stewart 2011, Fei et al. 2012, Fruth et al. 2018). Reviews of sleep behavior studies across the primate order reveal that the primary factor influencing sleep-related behaviors and sleeping site selection in primates is safety from predators (Anderson 1998, Anderson 2000).

2.3 *Predation Pressure*

Gibbons have evolved alongside four main predator types: felines, pythons, eagles, and humans (Clarke et al. 2012). They are not part of the primary diet of any large carnivore and may rather be considered opportunistic prey (Uhde & Sommer 2002). Predation likely plays a critical role in the structuring of gibbon morphology, social units, behavior, and cognitive abilities (Clarke et al. 2012, p. 85). Though predation events are rare, their occurrence would be especially harmful to apes with long life histories and extensive investment in offspring (Anderson et al. 2019). Furthermore, Boesch (1991) argues potential risks of encountering a predator are more important than mortality rates. Low mortality rates may rather be seen as an outcome of effective antipredation measures.

Predation risk and feeding competition strongly influence group size and composition across the primate order (Van Schaik & Van Hooff 1983). Individuals engaging in group living can benefit from alarm calls and defensive behaviors such as mobbing. However, gibbon group units remain small, suggesting efficient antipredator strategies despite the obvious threat of predation. Gibbons have shown the cognitive ability to differentiate between predator threats (Clarke et al. 2012) and to use spatial cognition to navigate to proper sleeping trees (Fei et al. 2022). In this way, behavioral ecology and cognition have been shaped to a degree by predation.

Though events of predation on white-handed gibbons have rarely been observed, predatory pressure can be supported through investigation of remains, predatory events on similar species, and gibbon reactions towards predators. To provide background I will first review potential gibbon predators before describing gibbon sleeping behavior and the reasons for classifying these behaviors as antipredator adaptations. In the methods section, I will cover predator abundance at HKK to demonstrate the relevance of predation to gibbons in this study.

Potential feline predatory threats to gibbons include the leopard cat (*Prionailurus bengalensis*) 3-5 kg, jungle cat (*Felis chaus*) 4-6 kg, Asian golden cat (*Felis temminckii*) 12-15 kg, clouded leopard (*Neofelis nebulosa*) 16-23 kg, Asiatic leopard (*Panthera pardus*) 45-75 kg, and Asiatic tiger (*Panthera tigris*) 180-250 kg (Rabinowitz & Walker 1991, Uhde & Sommer 2002). These predatory cats primarily hunt in the evenings and at night (Karanth & Sunquist 2000). While observed predation events are uncommon, Luca Morino (2011) published his observations of the capture of a juvenile siamang by a clouded leopard. Since the young siamang weighed 3.7 kg, roughly the weight of a small, adult *Hylobates lar* (Zihlman et al. 2011), it is reasonable to infer that clouded leopards would also prey on adult white-handed gibbons. Expanding on this size-based argument, there are also documented observations of clouded leopard predation on an infant and juvenile proboscis monkey where the juvenile weighed 2.55 kg (Matsuda et al. 2008). Clouded leopards were also the chief suspects in an attack on reintroduced orangutans who are obviously much larger than any gibbon (Sunderland-Groves et al. 2021). Given these observations, it seems unlikely that clouded leopards would discriminate against hunting white-handed gibbons of any age. Leopards and tigers tend to hunt on the ground and gibbons might be most susceptible to attack from these larger felines during daytime activities in the lower canopy and during rare occasions when they venture to the forest floor (Sommer & Uhde 2002). Gibbon remains have been found in the scat of both leopards and tigers (Rabinowitz & Walker 1991, Simcharoen et al. 2018), and in Huai Kha Khaeng Wildlife Sanctuary, a gibbon carcass was found at a tiger feeding site (Lydia Light, personal communication). Furthermore, in response to feline presence, gibbons have been observed to engage in especially loud and long vocalizations (Ellefson 1967, Uhde & Sommer 2002). A group of gibbons that encountered a tiger also increased group cohesion, displaying another antipredator adaptation provoked by big cats (Uhde & Sommer 2002).

In addition to feline predators, gibbons may also fall prey to the reticulated python (*Python reticulatus*). The reticulated python is the longest and second heaviest snake in the world (Shine et al. 1998). It is an ambush predator which primarily hunts at night (Fredriksson 2005). Once it has a hold, the python will asphyxiate their prey through constriction before swallowing them whole. Investigations of fecal matter revealed that adult individuals often consumed large mammals such as macaques, leaf monkeys, and wild boar (Shine et al. 1998). There is at least one confirmed case of predation on hylobatids, as researchers discovered a siamang in the stomach of a python during dissection (Schneider 1906 cited in Uhde & Sommer 2002). In a study on radio-collared sun bears in Indonesia, the prolonged stillness of one adult bear gave researchers cause to investigate. The 23 kg bear was found with its collar pinging from inside of a reticulated python (Fredriksson 2005). Pythons are gape limited, meaning an individual can eat any animal which will fit into its mouth (Shine et al. 1998). A python of sufficient size would be able to eat even the largest adult gibbon. Mobbing of pythons by white-handed gibbons is further evidence of the threat these giant snakes pose (Nettelbeck 1998).

Along with big cats and pythons, birds of prey are also considered potential gibbon predators (Ellefson 1967, Uhde & Sommer 2002, Clarke et al. 2012). Uhde and Sommer (2002) identified four bird species that pose a threat to gibbons: the changeable hawk eagle (*Spizaetus cirrhatus*), mountain hawk eagle (*Spizaetus nipalensis*), black eagle (*Ictinaetus malayensis*) and crested serpent eagle (*Spilornis cheela*). Most of these birds primarily feed on lizards and to a lesser degree on small mammals. While these birds are not large enough to carry off an adult gibbon, they frequently prey on small mammals of comparable size to infants and juvenile gibbons (Uhde & Sommer 2002). Supporting this, gibbons exhibit mobbing behavior directed towards raptors and vocalize in their presence, even when no young are part of the group (Ellefson 1967, Uhde & Sommer 2002).

Humans have also been known to hunt gibbons for food or for spiritual reasons (Tenaza & Tilson 1985, Estrada & Garber 2022). Predatory pressure from humans may remain relevant although gibbons within most studies have become habituated to human presence. In unprotected areas, habituation raises ethical concerns and sometimes habituation and research must be halted (Fei et al. 2017). Additionally, in the current Anthropocene, gibbon infants are often sold in the illegal wildlife trade (Malone et al. 2002). The wildlife trade may be much older given the discovery of an extinct gibbon species in the grave of a Chinese royal dating back to the

Holocene (Turvey et al. 2018). Since parents are poached in order to capture infants, this practice hurts not only future generations but currently reproducing generations as well.

Gibbons appear cognitively aware of distinctions between dangerous and non-dangerous species and between the types of dangers they pose. Gibbons emitted “hoos” in the presence of a potentially dangerous binturong but not in the presence of less dangerous competitors such as macaques and toucans (Nettelbeck 1998). They remain cautious of other potentially dangerous species such as vipers at whom they have also been known to “hoo” (Nettelbeck 1998). Further supporting gibbon cognition of danger, *Hylobates lar* at Khao Yai National Park in Thailand displayed predator-specific behaviors to the simulated presence of four distinct species: the clouded leopard, the tiger, the reticulated python, and the crested serpent eagle (Clarke et al. 2012). The simulated models caused gibbons to defecate (a sign of distress), increase vigilance, drop in canopy height, and emit short “hoos” that often escalated into predator-specific songs (a behavior which might benefit nearby related groups). Gibbons engaged in distinct behaviors when presented with aerial or ground predators. This research confirms their concern for predators and reveals their ability to discern and react to distinct threats (Clarke et al. 2012).

Because the most dangerous predators, felines and pythons, are active at night (Weins & Zitzmann 1999, Karanth & Sunquist 2000), this heightens the gibbons’ state of vulnerability as they sleep. Though a variety of ecological pressures, such as meteorological concerns, distance to food resources, and territory monitoring may influence sleep behavior and sleeping tree selection, there is a consensus across gibbon species and habitat types that predation is the primary pressure (Tenaza & Tilson 1985, Reichard 1998, Fan & Jing 2008, Phoonjampa et al. 2010, Clarke et al. 2012, Cheyne et al. 2013, Fan & Jiang 2008, Fei et al. 2017, Fei et al. 2019, Harrison et al. 2021). Since predation can have a definite and permanent effect on the fitness of an individual, selecting a suitable sleeping tree is a very important task for gibbons.

2.4 *Anti-predation Sleeping Behaviors*

Gibbon pre-sleep behavior can best be described as cryptic, lowering their risk of detection by predators such as felines which are typically active at dusk. Gibbons enter their trees quickly and quietly several hours before sunset and remain still once situated (Reichard 1998, Fei et al. 2012). They have been shown to move faster to their sleeping trees when compared to average travel speeds (Fei et al 2012, Fei et al. 2022). Siamangs have been known to share sleeping trees (Lappan 2007, Lappan 2008, Harrison et al. 2021). Gibbons, however, share sleeping trees infrequently, tending to sleep separately from one another (Reichard 1998, Fan & Jiang 2008, Cheyne 2013, Bartlett 2015, Fei et al. 2017). Females usually sleep with infants or juveniles in their laps, but otherwise when gibbons do share trees, they tend to sleep on separate branches. Dispersed sleeping patterns might mitigate predation risks, as sleeping separately can diminish the concentration of gibbon-specific odors, thereby reducing detection (Reichard, 1998). In northern, montane regions, however, gibbons have been observed huddling (Fan & Jiang 2008, Fei et al. 2012). Huddling as a sleeping behavior is more common when temperatures are lower (Fei et al. 2019). A lack of suitable sleeping trees may also influence gibbons to sleep together (Tenaza & Tilson 1985).

The safest spot for gibbons is high up in the trees on branches inaccessible to heavier predators. Gibbons and siamang typically choose to sleep in emergent trees with greater than average trunk diameter, a well-connected canopy and the lowest branches high off the ground (Reichard 1998, Fan & Jing 2008, Phoonjampa et al. 2010, Fei et al. 2012, Fei et al. 2017, Cheyne et al. 2013, Harrison et al. 2021, Fei 2022). They typically sleep on thin branches, far from the trunk (Fei et al. 2012). The trees they choose are usually free of liana (Fan & Jiang 2008, Fei et al. 2012), a potential hiding place for snakes (Phoonjampa et al. 2010). Presence of climbable lianas on the trunk may also influence sleeping tree suitability. These may be used by human hunters or pythons to gain access to gibbons (Tenaza & Tilson 1985, Cheyne et al. 2013).

Studies of sleeping site selection show that gibbons alternate between sleeping sites, rarely using the same tree consecutively (Fan & Jing 2008, Phoonjampa et al. 2010, Fei et al. 2012, Fei et al. 2017, Cheyne et al. 2013). Reichard (1998) observed few trees reused by white-handed gibbons, but the number of reused trees increased over time, suggesting a pattern of long-term use. Other studies have likewise shown that gibbons reuse trees over time, hinting at their memory of these spots (Fan & Jing 2008, Fei et al. 2017, Cheyne et al. 2013, Fei et al. 2022). Some authors suggest that reuse events are irregular and infrequent and that gibbons typically reuse a sleeping tree only after periods of 60+ days (Reichard 1998, Fan & Jiang 2008, Fei et al. 2012). Two notable exceptions to this pattern exist. Harrison et al. (2021) observed more frequent sleeping tree reuse in their study of siamang. Because siamang occupy smaller home ranges than gibbons, the authors argue that higher frequencies of sleeping tree reuse may be attributed to a lower availability of choices. Tenaza & Tilson (1985) studied 11 groups of gibbons, obtaining nearly 1,000 nights of observation. The gibbons in their study used less than 5 sleeping trees per group and thus reused these trees heavily. The authors suggested that this pattern of reuse is likely due to human hunting practices. Gibbons slept in tall trees lacking climbable lianas and there were few of these to choose from.

Reproductive and morphological asymmetries between individuals can elicit distinct behaviors. For example, orangutans generally sleep in the vicinity of their last food source

(Prasetyo et al. 2009), however, mother-infant dyads and juveniles who are more vulnerable to predation, tended to sleep farther away from their last food source than adult males or solo females (Anderson 2000). Adult female gibbons lead group travel movement more frequently than conspecifics and therefore may increase their chances of encountering potential mates from other groups and benefit from a priority of access to resources (Barelli et al. 2007). Though gibbons are not sexually dimorphic, differences in size across age groups make younger individuals susceptible to different predators.

Female gibbons are on average, the first to retreat to their sleeping trees (Reichard 1998, Fan & Jiang 2008). Reichard (1998) noted variations in sleeping tree height and sleeping spot elevation based on sex, specifically among adult females still sleeping with offspring. Reichard posited that females accompanied by infants and juveniles might face challenges in evading predators, prompting them to seek safer sleeping spots positioned higher in the canopy. However, Fan and Jiang (2008) had two adult females with infants in their study group and found that they did not sleep significantly higher than other members. The subadult male in that group was found to sleep the highest. Another study on a single group including one adult male and one adult female with an infant found no significant difference in sleeping height (Phoonjampa et al. 2010). Phoonjampa et al. (2010) likewise found no significant differences in canopy structure of sleeping trees between adult male and adult female individuals.

Sleeping site location matters and may be affected by many different factors including, predation pressures, food availability, meteorological variables, and territoriality. The selection of a sleeping site location and sleeping tree are considered two different tasks for chimpanzees (*Pan troglodytes*). Site location appears to be the first variable in consideration of where to sleep, while sleeping tree selection within that area becomes a second consideration (Hernandez-

Aguilar & Reitan 2020). For primates who do not manipulate sleeping sites and require trees or topography with certain characteristics these factors likely work in conjunction.

Research which simultaneously examined baboon and leopard ranging patterns discovered that most attacks occur at or near to sleeping sites, suggesting that leopards seek baboons out when sleeping (Bidner et al. 2018). As previously mentioned, unpredictable sleeping site reuse may be an efficient strategy to evade detection. Safe sleeping sites, however, are not always abundant. Ramakrishnan & Coss (2001) observed sleeping behaviors across troops of macaques (*Macaca radiata*). While other groups in the study tended to alternate between several sleeping sites, one group selected the same sleeping site each night during the entire study. After assessing the troop's home range, these researchers concluded that there were no alternatives which matched the desired criteria of height, proximity to water sources, and closeness to human settlements within their territory. Proximity to human settlements has been shown to have a negative relationship with frequency of leopard attacks (Isabell & Young 1993).

Research on the movements of wild gibbons offers evidence of spatial memory of sleeping sites and food resources and planned route navigation to these locations (Asensio et al. 2011, Fei et al. 2022). To maximize foraging efficiency, primates may strategically choose sleeping site locations near feeding locations. For example, Cancellor et al. (2011) found that when food was scarce, chimps (*Pan troglodytes schweinfurthii*) nested closer to the forest border where they engaged in crop raiding. Patterns of sleeping site reuse may also relate to resource availability. Western lowland gorillas (*Gorilla g. gorilla*) in Moukalaba-Doudou National Park in Gabon reused more nests in the fruiting season than non-fruiting season (Iwata & Ando 2007). Sleeping close to a feeding tree, however, may put primates at greater risk of being disturbed by nocturnal frugivores and the predators which hunt them (Prasetyo et al. 2009).

Reichard (1998) found no correlation between the locations of white-handed gibbon sleeping trees and food resources. Fan and Jiang (2008) found that sleeping trees correlated positively with feeding tree locations and were usually located nearer the last feeding trees of the day than the first feeding tree of the next. Other researchers have also found that sleeping trees are located closer to the last feeding tree of the day than the first feeding tree of the next (Phoonjampa et al. 2010, Harrison et al. 2021) but have not argued that food influences site selection. Fei et al. (2012) rejected the idea that sleeping site locations were dependent on food access. Food resources were located on average 146 m from the last feeding tree and 118 m from the first feeding tree of the next day and the authors argue that these distances are too large relative to daily path length (Fei et al. 2012). Gibbons have been recorded sleeping in feeding trees, however not at times when edible parts were available in the tree (Cheyne et al. 2013).

Meteorological variables and territoriality may also be factors which influence sleeping site location. In regions with colder temperatures, temperature may have an effect the distance gibbons choose to sleep from their food resources. In China where temperatures were recorded as low as -3.0 °C, gibbons slept closer to both morning and evening food resources during colder seasons (Fei et al. 2019). Wind may also be a factor influencing sleeping site selection as it has been recognized as a strong driver in sleep–wake regulation of captive gibbons (Reyes et al. 2021). Territoriality and border patrol may also influence the location of sleeping sites. Sleeping in areas of home range overlap may be potentially dangerous. Sleeping trees of both gibbons and siamangs may occur in areas of home range overlap, but this is the case less frequently than would be assumed by random models (Phoonjampa et al. 2010, Harrison et al. 2021).

2.5 *Forest Type and Ranging behavior*

As frugivores, gibbons must adjust their diets with different phenological states of resources, and this variability has a definite effect on their social ecology (Lappan & Whittaker 2009). While gibbons exhibit a degree of flexibility in their diets, they remain highly dependent on energy-rich fruits. Resource availability impacts home range size, group composition, energy budgets, and many aspects of behavior. Gibbons in poor habitats must occupy larger home ranges to maintain access to sufficient amounts of food (Kim et al. 2011, Light et al. 2021). *Nomascus* and *Hoolock* gibbons also appear to adjust the size of their home ranges to seasonal fluctuations, occupying larger home ranges in the dry season when fruit is scarce (Zhang et al. 2014, Hai et al. 2020).

In addition to food availability, forest structure influences primate movement decisions (McLean et al. 2016). Habitat type has been shown to influence sleeping site location in spider monkeys (Pozo 2005). The home range of the chosen study group at Khao Nang Rum (KNR) in Huai Kha Khaeng Wildlife Sanctuary (HKK) has been described as a savannah habitat, with two primary forest structures, dry dipterocarp (DD) and mixed deciduous (MD). There is reason to believe that differences between these two forest structures would be accompanied by distinctions in the availabilities of sleeping trees with preferred characteristics. Gibbons in adjacent savannah habitats showed an apparent preference for MD forest, although they still frequently visited and fed in DD (Light 2016). Fan & Jiang (2008) did not directly investigate the effects of forest type on sleeping tree location, however, a map provided in the results showed that gibbons never slept in secondary forest.

2.6 *Research Objective and Hypotheses*

This research explores sleeping site characteristics, reuse, and location in a group of free-ranging white-handed gibbons living in a savannah habitat. I investigate these variables both in relation to the group and individually. The chosen research site, marked by both harsh environmental conditions and a high density of predators, serves as an excellent setting for testing the following hypotheses:

Hypothesis 1: Sleeping tree selection and sleep-related behaviors of white-handed gibbons in a predator rich, savannah environment will reflect prior findings in support of predator avoidance theory.

<u>Prediction 1.1</u>: Gibbons will rapidly retreat to their sleeping trees on average 3 hours before sunset and remain relatively still and silent once in tree.

<u>Prediction 1.2</u>: Sleeping trees will have thicker trunks than surrounding trees.

<u>Prediction 1.3</u>: Sleeping trees will be taller than surrounding trees.

<u>Prediction 1.</u>4: Sleeping tree reuse will be a rare event.

Hypothesis 2: Adult females will sleep in taller trees than group members but exhibit no further distinct preferences in canopy structure.

<u>Prediction 2.1</u>: The adult female, sleeping with a juvenile, will choose significantly taller trees than others in the group and will sleep at higher heights in these trees.

<u>Prediction 2</u>.2: There will be no individual variation in sleeping tree canopy structure.

Hypothesis 3: Gibbons will be more reliant on MD forest for sleeping trees than DD.

<u>Prediction 3.1</u>: Sleeping trees will be located in MD forest significantly more so than in DD when compared to predictions based on home range forest type percentages.

CHAPTER 3: METHODS

3.1 *Study Site*

I carried out my study in Huai Kha Khaeng Wildlife Sanctuary (HKK), a 278,000-hectare reserve surrounded by 17 other wildlife sanctuaries and national parks (Bunyavejchewin *et al.* 2004). The sanctuary is in Northwestern Thailand (see Figure 1) and forms part of the largest continuous protected forest in mainland Southeast Asia - Thailand's Western Forest Complex (WEFCOM) (Bunyavejchewin *et al.* 2004). Today, HKK is recognized as a UNESCO World Heritage Site. It is one of Thailand's least accessible and least disturbed forest areas, in part due to strong restrictions on visitor access.

I conducted my research at the Khao Nang Rum Wildlife Research Station (KNR) (15º25′-15°31'N, 99º15′-99°20'E) in HKK. The vegetation in HKK is less dense than in surrounding areas and it is considered a dry tropical forest mosaic (Bunyavejchewin *et al.* 2004). The forest surrounding KNR can be categorized into dry dipterocarp (DD), seasonal dry evergreen (EG), and mixed deciduous (MD) forest areas (Light *et al.* 2021). Habitats around the research station have been classified as either (1) savannah, characterized by a mosaic of DD and MD forest with small patches of evergreen, a relatively open canopy, and tall grasses or (2) evergreen, predominately evergreen forest characterized by a closed canopy and year-round streams (Walker & Rabinowitz 1992, Light et al. 2021).

Annual rainfall in HKK averages 1447 mm (Simcharoen & Duangchantrasiri 2008). There are three distinct seasons: the 6-month wet season (May–October), the cool-dry season (November–January), and the hot-dry season (February–April). Rainfall peaks twice during the year typically in May and again September–October. Mean annual high and low temperatures are 30.4 and 17.7 C (Bunyavejchewin et al. 2004).

3.2 *Predator Community and Potentially Dangerous Animals*

HKK supports the largest population of tigers and leopards in Southeast Asia (Saisamorn et al. 2019). Across protected forests in Thailand where tigers (*Panthera tigris*) are present, population density average is 1 tiger per 100 km^2 (Rabinowitz 1993). Average observed tiger density in HKK is 4 tigers per 100 km^2 (Simcharoen et al. 2007). Leopard (*Panthera pardus delacouri*) populations in HKK are thought to be even higher than tiger populations (Saisamorn et al. 2019). Simcharoen & Duangchantrasiri (2008) made a conservative density estimate of 7 adult female leopards per 100 km^2 based on radiotelemetry data. In addition to leopards and tigers, clouded leopards (*Neofelis nubulosa*), Asian golden cats (*Felis temminicki*), jungle cats (*Felis chaus*), and leopard cats (*Felis bengalensis*) have been confirmed in HKK by camera traps (Rabinowtiz & Walker 1991, Bunyavejchewin et al. 2004). HKK falls within the geographic range of extant reticulated pythons (Stuart 2018). Though to my knowledge no articles exist to confirm their presence, they are commonly seen around KNR (Shomphot Duangchantrasiri, personal communication). Additionally, there are other potentially dangerous non-predator animals in HKK, including Asian elephants (*Elephas maximas*) (Rabinowtiz & Walker 1991).

3.3 *Study Group*

My study focuses on a single group of gibbons. Group L was comprised of 4 members - one adult female (AF), one young adult male (AM), one young sub-adult female (SAF), and one juvenile. I assigned an age class to each gibbon, following age classes outlined by (Brockelman et al. 1998). I identified individuals by age, size, fur color, and other salient features. Using data on gestation length from Barelli et al. (2007), I estimate that the adult female was 2 months pregnant at the start of the study and gave birth sometime between Oct. 10th and Nov. 1 (Madeja

Rheddick, personal communication). Group L was first habituated in 2012 and has been the subject of several published and unpublished studies since (Phiphatsuwannachai et al. 2018, Dai et al. 2018, Light et al. 2021). While there is one evergreen patch in group L's home range, it has been characterized as a savannah habitat with a mosaic forest structure, very few evergreen trees, and an overall lower abundance of fruit (Light et al. 2021).

3.4 *Behavioral and Geospatial Data Collection*

To reacclimatize the members of group L to human presence, I followed them for 6 days, taking only geospatial data (June 7 - 13, 2023). This was also a period in which I familiarized myself with gibbon behavior, learned to distinguish between individuals, and adjusted to the demands of field research.

I conducted behavioral observations over a 60-day period from June 14, 2024 - August 8, 2024. I followed the AF in group L up to 5 days a week for a total of 30 follows. Station safety regulations prevented us from beginning data collection before 7:00 am, so I was unable to reach the gibbons before they left their night trees. The search for group L began each day at 7:00 am and they were generally located by following the sound of vocalizations. On occasion the group would show up before 7:00 am to feed at a tree next to my cabin and I could begin observations earlier (4 days). Since there is a female bias in group movement decisions and access to resources (Barelli *et al.* 2008), and since female white-handed gibbons generally are the first to retreat to sleeping trees (Reichard 1998), the AF was chosen as the focal individual in the group for the entire length of the study. I began observations once the AF was identified and ended observations once all individuals had been stationary in their sleeping trees for more than 30 minutes (Fan & Jiang 2008, Fei et al. 2012, Fei et al. 2023).

I recorded locations of the focal individual at five-minute intervals with a Garmin eTrex Summit® handheld GPS unit (<10 m 95% accuracy). I used an instantaneous focal animal sampling method (Altmann 1974) to collect behavioral data of the AF every 5 minutes. The recorded behavior was the first sustained for at least 5 seconds. I indexed behaviors of the focal individual by making small adaptations to an ethogram developed by Bartlett (2015 p. 37) and recorded these using the CyberTracker app on a smartphone (see table 1). For social behaviors, I recorded directionality and social partner. For foraging behaviors, resource type was noted as one of the following: non-fig fruit, fig fruit, mature leaves, young leaves, vine shoots, flowers, insects, or animal matter. Time of entry into the sleeping tree was recorded for the AF. Behavioral observations on the AF continued for 30 minutes after entry into a sleeping tree and I noted any in-tree movement if the AF was observed changing branches.

3.5 *Sleeping Trees*

I defined night trees as any tree in which the gibbons enter before dusk and remained stationary in for more than 30 minutes (Fei et al. 2023, Fan & Jiang 2008). I marked each sleeping tree with flagging tape to verify future identification of reused trees and recorded each sleeping tree location with the GPS unit. The juvenile always slept with the AF. From here on, for simplicity's sake, I will refer only to the female when discussing sleeping behavior, with the understanding that the juvenile was always with her, typically nestled in her lap. Since the group split into three units at the end of the day, I would follow the AF to her sleeping tree and my field assistant, Ann, would follow either the AM or the SAF. We did not have a third person available, so we had to choose between following the AM or the SAF. Often, we were able to locate all three individuals in their sleeping trees.

To explore tree characteristics related to predator avoidance, I recorded the following data for each sleeping event: trunk diameter at breast height (DBH), tree height, sleeping spot height, resting branch estimated thickness, and proximity to tree trunk. I measured sleeping tree DBH at 1.4 m from ground height. Tree heights were visually estimated and verified with a rangefinder when possible. Individual heights in the canopy were measured with an optical rangefinder from directly below the individual when possible. Otherwise, I positioned myself where both the individual and the tree trunk were visible, allowing me to measure the distance to both. I then used the Pythagorean theorem to calculate the individual's height ($a^2 + b^2 = c^2$). The thickness of the branches on which individuals were resting were noted as: 1) thicker than an adult gibbon’s leg 2) about as thick as leg 3) less thick than leg (Fan & Jiang 2008). I scored proximity of individuals to tree trunks under one of four criteria: 1) in contact 2) within arm’s length 3) within 3 m distance 4) beyond 3 m distance (Fan & Jiang 2008). Sleeping tree species were identified by my field assistant and identifications were verified with a Thailand-specific field guidebook and by a second field assistant.

To investigate intragroup differences in sleeping tree canopy structure, I made visual estimations of canopy thickness of branches and leaves, including liana, and sored these as: 0 (thin, less than 24% canopy density), 1 (medium thin 25-50%), 2 (medium thick 50-75%), and thick (>75% canopy density). Liana estimations were generated via an inductive/deductive process of scoring and note taking. I scored liana in the tree canopy as one of the following: 0 (no liana at all), 1 (liana makes up less than 25% of canopy density near sleeping spot, or liana present but more than 2 m away), 2 (liana makes up more than 25% of canopy density within 2 m of sleeping spot), 3 (liana makes up more than 50% of canopy density within 2 m of sleeping spot, liana may obscure individual).

We were very successful in locating sleeping trees after a follow (93%), locating at least one sleeping tree on all but 2 behavioral follow days. I was able to collect additional data on days off by walking to known sleeping trees within the camp at the end of the day to check for sleeping gibbons. I counted these days in several, but not all analyses (6 days; 4 AF, 4 AM, 0 SAF).

Whereas most sleeping studies on gibbons prioritize representativeness by rotating between groups each week and therefore only gather sleeping tree reuse data on average 5 days a month (Reichard 1998, Fan & Jiang 2008, Phoonjampa et al. 2010, Cheyne et al. 2013) my data is relatively continuous. Despite our success in locating gibbons after a follow, certain variables precluded a complete dataset. Finding the gibbons proved to be challenging on days they did not vocalize (6 days). Furthermore, the nature of the research required some potential follow days to be dedicated to other data collection and still my field assistant and I required days of rest. In total, we located at least one individual in a sleeping tree 57% of all days during the total 60-day span of the study (AF 32 days = 53%; AM 27 days = 45%; SAF 20 days = 33%).

3.6 *Geospatial Processing*

I calculated a minimum convex polygon (MCP) home range (HR) estimate in ArcGIS Pro 10.6 by using all observed waypoints of the focal subject and group sleeping tree locations. Waypoints from the 6 days of purely geospatial data collection were included in my home range estimations and when building a cumulative home range area asymptote. Since there were many areas of broken canopy within the home range, my field assistant and I made informed, conservative visual estimations of breaks in the canopy. I recorded these by walking the perimeter of broken canopy areas and taking a GPS point every 5 m. We were able to record most areas with broken or inaccessible canopy.

HR forest type percentages as well as sleeping event types were derived using an existing map (Light 2016, Light et al. 2021). Forest-type categories were previously assigned to a Landsat image through leaf area index density and using an image taken in 2012 at the peak of the leaf-off period (Light et al. 2021). I overlayed this categorical raster data on group L's home range and calculated percentages of each forest type (EG, MD, DD) in ArcGIS Pro 10.6 for both the full MCP HR and the MCP HR after removing areas of known broken canopy. I only analyzed locations of AF sleeping events in relation to forest type as results of sleeping tree forest type might be skewed through inclusion of the AM and SAF since they were not always found. For example, it might be easier to spot individuals when sleeping in DD forest versus MD due to canopy coverage. To minimize this effect, I analyzed just the AF's sleeping tree locations regarding forest type, and I only included data from days I observed her entering her sleeping tree as part of a follow.

Further geospatial analysis of sleeping trees investigated the effects of proximity to last-known feeding tree, HR border, and group cohesion. I used ArcGIS to measure all distances. I calculated the distance between the AF's sleeping tree and the location of her last 2 consecutive feeding scans for each day. I measured distances between sleeping trees and the MCP HR border for the AF and AM on days the gibbons were located after a follow. To quantify group cohesion, I measured the distances between all observed individuals for each date.

3.7 *Data Analyses*

I retrospectively calculated time of sunset at KNR for each date using the free online program SunCalc (Hoffman 2015). I ran calculations in Excel to find the average time of entry, differences between time of entry and time of sunset, and average difference between entry time and sunset. I compared DBH and tree height of all observed sleeping trees to transect forest data collected in 2013 (Lydia Light, 2016) in savannah habitats adjacent to group L's home range. To do this, I used the Mann-Whitney U test. I also used the Mann-Whitney U test to compare individual difference in DBH, sleeping tree height, and sleeping spot height. I used chi-squared tests to analyze individual variation in branch thickness, proximity to tree trunk, canopy thickness, and liana presence.

I calculated sleeping tree reuse percentages based on all events as a group and per individual. I also calculated reuse as an average of how many distinct trees are reused. To explore the effect of continuous versus discontinuous data collection on sleeping tree reuse, I split my data into 4 data sets – each derived by combining 2 single weeks, which were separated by one month (June 14-20 and July 14-20; June 21-27 and July 21-27; June 28-July 4 and July 28-August 3; July 5-11 and August 4-10). These 4 data sets were analyzed separately and then averaged (see Table 4). To quantify forest type as a variable in sleeping tree location, I ran a chi-square test to compare observed sleeping event forest types to what would be expected based on HR forest type percentages (Pozo 2005). I ran the chi-square tests using the full MCP HR.

CHAPTER 4: RESULTS

4.1 *Behavior*

During the study, temperature highs and lows averaged 28.8°C and 22.8°C. The maximum temperature was 34°C and the minimum temperature was 20°C. The forest received 205.7 mm of rainfall during this time.

The AF entered a sleeping tree on average 3 hours before sunset (mean 15:56; median 15:53; range 14:01 - 17:08; n = 25). Once the AF had entered a sleeping tree, she generally stayed very still. Behavioral scans taken within sleeping trees were limited to grooming of the juvenile and resting. The female was only observed changing branches within a sleeping tree once. This occurred on a night when the male and female shared a tree (July 11, 2024). The AF entered the sleeping tree first at 15:38 and originally took a spot opposite in the canopy from where the AM chose to rest. At 15:53, the AF, followed by the juvenile, moved close to the AM so that all three were resting on the same branch. At 16:14, the AM moved to take the opposite side of the canopy about 4 meters away from the AF and juvenile. I ended observations 45 minutes later during which time they had remained still.

The second time I observed the AF, juvenile, and AM sharing a sleeping tree was August 2, 2024. The group had their last feeding bout in a fruit tree 63 meters away (B713). The AF left the feeding tree first and headed towards a sleeping tree which the AM had already used 6 times during the study - This tree was used by the AM 10 times and was the most reused tree during the study period (M07). The AF rested in the male's preferred spot in the crook of a tree limb far from the trunk. The AM entered the tree after the female and moved towards her. The AF and juvenile did not move at which point the AM settled for a different branch lower in the canopy and all three slept in the same tree. The very next evening, both individuals approached the same sleeping tree again (M07) after feeding again in the same tree 63 m away (B713). This time, the AM made it to the sleeping tree first. The AF approached the male in his preferred sleeping spot and he did not move for her. Instead of choosing another branch in the same tree, the AF chose to sleep in a separate tree approximately 28 m away.

4.2 *Sleeping Tree Characteristics and Individual Variation*

When considering sleeping tree DBH per event, the average DBH is 49 cm (n = 75; range 23.3 cm - 92.1 cm; SD 13.4). DBH is slightly higher, 51cm, if analyzing per tree without accounting for reuse (n = 35). Sleeping trees had significantly greater DBH when compared to DBHs of transect trees in the adjacent savannah habitat (Transect average = 25.6 cm, n = 4,157; Z = 11.49953; $\boldsymbol{p} = \mathbf{0.0001}$) (see Figure 3). There were no significant differences in sleeping tree DBH values between individuals (p = 0.7579). Sleeping trees were on average 23.6 m tall per event (n = 72; SD 5.3, range 16 - 40) and 24.8 m per distinct tree (n = 34). Observed sleeping trees were significantly taller than transect trees (ST average = 24.8 m; transect trees average = 13 m, n = 4,157; Z = 12.33680; $\boldsymbol{p} = \mathbf{0.0001}$) (see Figure 4). The estimated heights of sleeping trees differed significantly between the three individuals (Z = 14.9396; $\boldsymbol{p} = \mathbf{0.0006}$). The AM chose significantly shorter sleeping trees than the AF (AM average = 21 m; AF average = 26 m; Z = -3.64026; $\boldsymbol{p} = \mathbf{0.0003}$) and the SAF (SAF average = 23 m; Z = 2.18994; $\boldsymbol{p} = \mathbf{0.0285}$). The AF chose taller sleeping trees on average than the SAF but did not differ significantly (Z = -1.85119; p = 0.641).

Group average sleeping spot height was 19.4m (min 12 m, max 26 m; n = 72; SD = 3.0). The AF slept significantly higher than the AM (AF average = 21 m; AM average = 19 m; Z = -3.12119; $\boldsymbol{p} = \mathbf{0.0018}$) and the SAF (SAF average = 18 m; Z = 13.7586, $\boldsymbol{p} = \mathbf{.0010}$) (see Figure 5).

There was no significant difference in the sleeping heights of the AM and SAF (Z = -0.44169; *p* = 0.6496). The AF and AM generally slept far from the trunk on terminal branches (AF = 81%, *n* = 32; AM = 93%, *n* = 27; SAF = 50%, *n* = 16). The SAF was the only individual who ever slept leaning against the trunk of a tree (31%).

The gibbons slept in trees nearly exclusively but with one exception when the SAF settled into bamboo (*Thyrsostachys siamensis*) for the night 17 m high. Of the observed 40 distinct sleeping trees, we were able to identify 38 to the species level (see Table 3). These fell into 17 different species, including the bamboo. The most common species of sleeping tree was *Shorea siamensis*. This species accounted for 36.8% of identified sleeping trees (14/38) and 40.8% of sleeping events (31/76). It should also be noted that on one night, the SAF chose to sleep in a long-dead *Shorea siamensis* tree.

As a group, these gibbons most frequently slept in trees with thin canopies but showed no obvious preference for canopy density: 35.1% thin, 24.3% medium thin, 20.3% medium thick, 20.3% thick. Individual differences in canopy density, however, were stark. The AF spent 58% of nights in trees with a thin canopy, 16% in medium thin, 16% in medium thick, and 10% in thick. The SAF slept in trees with a thin canopy 24%, medium thin 12%, medium thick 12%, and thick canopy 53%. For the male these percentages were 18%, 50%, 36%, and 13%. Differences in canopy density were significant between the AF and AM (***p* = 0.0237**) and most pronounced between the AF and SAF (***p* = 0.0007**). There was no significant difference in canopy density between the sleeping trees of the AM and SAF (*p* = 0.1035).

As a group, these gibbons commonly slept in trees without any liana in the canopy (45%; *n* = 79). Individual differences in liana preference were substantial (see Figure 6). The AF slept almost exclusively in trees without any liana (41%), or with thin or bare liana solely in the lower canopy (53%; combined total 94%; *n* = 32). It is notable that the thin liana in the AF's sleeping trees were a known food source. Only on two occasions did the AF sleep in a tree which was scored as a medium amount of liana (6%). She never slept in a tree with liana that was scored as thick. It is also notable that the two occasions the AF slept in a tree with a medium amount of liana were the only two days in which my field notes indicated a heavy rain at the end of the day. In contrast to the AF, the SAF most frequently slept in trees with thick liana and would usually sleep within the liana itself (30% no liana, 5% thin liana; 0% medium liana; 65% thick liana; *n* = 20). The AM most frequently slept in trees without liana (63% no liana, 4% thin liana; 0% medium liana; 33% thick liana; *n* = 27).

4.3 *Sleeping Tree Reuse*

My field assistant and I together observed 79 individual sleeping events in 40 different sleeping trees (total observed sleeping events per individual: AF = 32, AM = 27, SAF = 20). Tree reuse over the course of the study varied between individuals and was highest for the AF; 78.1% of the nights observed, the AF slept in a tree that was used more than once within the two-month span (32 sleeping events; 25 in a tree that was reused). For the AM, observed tree reuse was 70.4% (27 sleeping events; 19 in a tree that was reused) and for the SAF it was 45.0% (20 sleeping events; 9 in a tree that was reused).

At the start of the study, the AF slept in the same tree four nights in a row. Towards the end of the study, from 7/12 to 8/12, the AM consistently revisited the same tree three times a week over a five-week span. Of the AF's 32 observed sleeping events, 22% of nights she slept in a tree that was reused consecutively (consecutive reuse *n* = 7) and on 53% of the nights, she slept in a tree that was reused within a 7-day span (reuse within 7 days *n* = 17). Of the AM's 27 observed sleeping events, 19% were consecutive (consecutive reuse *n* = 5) and 52% occurred within a 7-day span (reuse within 7 days *n* = 14). The SAF only slept in the same tree consecutively once (10%; consecutive reuse *n* = 2). With no further reuse occurring within a 7-day span, her within-week reuse is also 10%. ST's reused by the AF greater average DBH (reused = 55 cm; used once = 50 cm) and average height (reused = 33 m; used once = 27 m) than trees used only once, but these did not differ significantly (*p* = 0.4094; *p* = 0.1039).

One tree commonly used by the AF (F01; used 8 times) was bare at first. I did not notice it had a liana growing in it since the vines were very thin and bare of leaves. As the leaves started to come in on the liana, the female used the tree less and less (6 times in June and twice in July). The last observed day she slept in the tree was 7/19. The next day, 7/20, she fed on the liana in that tree for 10 minutes and later on 4 more occasions - 7/28, 7/31, 8/2, and 8/3 (shortest feeding bout 5 min, longest feeding bout 30 min). This sleeping/feeding tree was also located next to a frequently visited fruit tree (*Schleichera oleosa*) which I first observed her feeding in on 7/14.

4.4 *Home Range and Forest Type*

To see if the MCP home range was representative of the actual HR, I graphed the cumulative HR area for each day (see Figure 7). I used visual estimation to confirm that the total HR area had reached an asymptote by the end of the study. Group L's estimated HR was 42.27 hectares. The 42.27 ha estimate was comprised of 71% DD, 29% MD, and 0.3% EG forest types. When I subtracted 5.54 ha of fragmented canopy, the new estimated HR was 36.73 hectares, and the forest type percentages became 69% DD 30% MD and 0.3% EG.

Much of group L's HR overlapped with the research station so that they primarily ranged north and east of camp, but occasionally would access regions to the northeast and southwest so that their HR formed a semi-circle around camp (see Figure 2). They frequently traveled through camp in areas with sufficient canopy coverage. They fed within campgrounds and towards the end of the study favored a group of sleeping trees which were on the edge of camp and less than 20 m from an occupied cabin. On days I observed the AF entering a tree after a follow, she slept in DD 81% of times, 22/27 (12 distinct trees), and in MD 19% of times, 5/27 (4 distinct trees) (see Figure 8). Compared to what I would expect based on HR forest type percentages, the AF slept in DD forest more frequently than in MD. The difference was not significant ($p = 0.2061$).

The AF slept, on average, 109 m away from the location of her last 2 consecutive feeding scans of the day (SD = 13.9; median = 106 m; min = 20 m, max = 329 m; $n = 25$). The AF slept on average 131 m from the estimated MCP HR border (SD = 75.1; median = 123 m; min = 9 m, max = 248 m; n = 25). 63% of the 8 occasions that the AF slept within 100m of the HR border, the AM slept closer to the border. On two occasions, as mentioned above, the AF and AM shared a sleeping tree. On average the AF and AM slept on average 57 m away from each other (range = 1m – 277 m; median = 34; $n = 23$). The AF and SAF slept 43 m away from each other (range = 11m – 140 m; median = 31.4 m; $n = 21$). The SAF and AM slept 73m away from each other on average (range = 6 m – 277 m, median = 39 m; $n = 15$).

CHAPTER 5: DISCUSSION

5.1 *Sleep-related Behaviors*

In several ways, the white-handed gibbons in this study exhibited cryptic sleep-related behaviors, consistent with those documented by earlier researchers (Reichard 1998, Phoonjampa et al. 2010, Fei et al. 2012, Harrison et al. 2021). All gibbons entered a sleeping tree several hours before sunset, quickly settled in their tree, and remained relatively motionless. This behavioral adaption allows them to retire inconspicuously before dusk when predatory felines are typically active. The fact that gibbons are active at dawn, another period of feline activity, does not contradict this suggested behavioral adaptation, since excellent mobility in the canopies allows for quick escapes during periods of wakefulness.

Like Reichard (1998), I found that aside from adult females and with infants or juveniles, white-handed gibbons rarely share sleeping trees. When they do so, sleeping spots are not shared simultaneously. Intragroup competition between individuals for sleeping spots were mediated by who arrived first, as suggested by Reichard (1989). Within-tree movement was observed only once.

5.2 *Sleeping Tree Characteristics and Individual Variation*

The physical sizes of sleeping trees in this study match prior research – sleeping trees were significantly thicker and taller than other trees in the forest (Reichard 1998, Phoonjampa et al. 2010, Fei et al. 2017, Harrison et al. 2021). All individuals chose sleeping trees with similar DBH, suggesting that tree stability matters regardless of age class or sex. Trees with larger DBH will sway less, causing fewer disruptions during the night (Cheyne et al. 2009). Thicker trees may also offer more protection from larger animals capable of uprooting them such as elephants

(Mehlman & Doran 2023). Sleeping in taller trees offers protection from felines who are primarily terrestrial hunters (Anderson 1998).

Though all individuals chose trees significantly taller than average trees in the savannah habitat, there were significant differences in sleeping tree heights between individuals. The AF chose significantly taller trees than the AM. While the SAF did not choose trees that differed significantly in height from the AF, the AF tended to sleep higher in the canopy than both the AM and SAF. Reichard (1998) observed sex-based differences in sleeping tree height and sleeping spot height but only for adult females still sleeping with offspring. Females with infants and juveniles may be at a disadvantage when escaping from predators and therefore may seek safer sleeping locations higher in the canopy (Reichard 1998).

Earlier research has proposed that sleeping far from the trunk of a tree, on thin, terminal branches, may provide further protection from predators (Fan & Jiang 2008, Fei et al. 2012). This is because thin branches are less accessible to heavier predators and the vibrations of the branches may alert the gibbon to the presence of a predator, providing an opportunity to escape (Fei et al. 2017). Choosing sleeping trees with thin canopies can enhance vigilance (Phoonjampa et al. 2010). Primates may also avoid liana tangles as pythons may hide within them (Anderson 1984). Finally, lianas may also be used by pythons or human hunters to scale sleeping trees (Tenaza & Tilson 1985).

Reichard (1998), who studied a mix of adult and subadult individuals found no pattern in canopy structure preference as a group. Other research, which investigated individual variations in canopy structure and looked at only adult individuals, found that gibbons prefer to sleep on terminal branches, far from the trunk, in thin canopies, with little liana (Phoonjampa et al. 2010). These researchers found no differences in adult male and adult female preferences for liana

(Phoonjampa et al. 2010). As a group, the gibbons in this study showed no significant preference for sleeping spot or canopy characteristics and showed a tendency to avoid liana-laden trees as predicted (Reichard 1998, Phoonjampa et al. 2012, Harrison et al. 2021). Individual differences, however, were most obvious between the two adult individuals and the SAF. While the AF and AM slept almost exclusively on terminal branches, in thin canopies, with little to no liana coverage. The SAF showed more variation in her choice of sleeping spot.

AM and AF liana avoidance mirrored past research. And like Phoonjampa et al. (2012), I found no significant differences in canopy liana loads between the AM and AF. Observations of the SAF differed from common descriptions of gibbon sleeping tree canopy preference. Instead, she tended to sleep in trees with thick canopies, lots of liana, and showed no preference for sleeping far from the trunk on thin, terminal branches, frequently sleeping leaned against the trunk of the tree. Size-based arguments put young subadults within the prey weight range for predatory birds (Uhde & Sommer 2002). It may be that the SAF chooses trees which obscure her from arial attacks. Since two of the SAF's sleeping trees were trees in which we had previously observed the group resting, it may also be that she chooses liana dense trees as these are trees she remembers from previous daytime resting episodes when liana may provide shade from heat stress. Subadult animals generally require more REM sleep than their adult counterparts (Danker-Hopfe et al. 2015, Burger et al. 2020). For chimpanzees, hypotheses of nest function include: antipredation, antipathogen, thermoregulation, and comfort in relation to increased REM sleep (Stewart 2011). Though gibbons do not build nests, and typically sleep on bare branches, sleeping within lianas may offer protection from wind which has been recognized as a driving predictor of sleep quality in captive gibbons (Reyes et al. 2021). Though there are no existing reports to my knowledge of differences between canopy preference in subadult and adult individuals, my results suggest this may be an area to investigate in the future.

Furthermore, it may be interesting to investigate liana density in sleeping trees in relation to precipitation. On only two occasions, the AF slept in trees with a medium amount of liana. On both days, there was heavy rain at the time of sleeping tree entry. Similarly, Harrison et al. (2021) found that siamang rarely changed STs in the night but did so on two distinct nights of heavy rain. Fei et al. (2012) likewise found a gibbon in a different sleeping trees the morning after a storm.

Adult male and female gibbons slept in live trees without exception. The subadult also diverted from this behavior in that she was observed both sleeping in a dead *Shorea siamensis* as well as in a bamboo patch (*Thyrsostachys siamensis*). *Shorea siamensis* accounted for over a third of all distinct sleeping trees. Previous data from adjacent forest transects revealed that savannah habitat was comprised of 5.5% *shorea siamensis (*229/4157) (Lydia Light, unpublished data). This suggests that gibbons are selectively seeking out this species as a good sleeping location.

5.3 *Sleeping Tree Reuse*

Most studies have thus far classified gibbon sleeping tree reuse as irregular and only occurring between long intervals (Reichard 1998, Fan & Jiang 2008, Fei et al 2017, but see Tenaza & Tilson 1985). Contrary to this pattern, the gibbons in my study displayed consistent sleeping tree reuse, often sticking to the same trees for several weeks before transitioning to a new heavily reused sleeping tree (see Figure 9). Choosing to sleep in frequently used sleeping trees is not strictly at odds with the predator avoidance hypothesis. Opting for well-known sleeping trees might offer an advantage, as it allows animals to become familiar with escape routes (Harrison et al. 2021).

My study suggests that the frequency of sleeping tree reuse by gibbons may have been underestimated in previous research. While it is possible that the behavior of the gibbons observed in this study represents an outlier, my findings raise the possibility that infrequent observation of sleeping tree reuse could be an artifact of methodology. Previous studies have opted for representativeness across populations rather than data continuity in gibbon sleeping studies. While the data I present cannot argue that Group L's sleeping habits are representative, it does provide a clearer picture of a single group's sleeping habits over the course of two months. My data suggest that individuals in Group L are reusing sleeping trees during specific time periods, with distinct preferences observed between the first and second months of the study. Rather than a continuous pattern of tree reuse, I observed clustering in timing, where favored sleeping trees changed over time. This temporal clustering of tree reuse may explain why previous researchers found fewer patterns of reuse. Rotating between study groups each week may prevent researchers from noticing these short-term sleeping tree preferences.

I was able to locate at least one gibbon in a sleeping tree on 58% of the nights over the 60-day period. In contrast, similar studies, while providing much larger data sets, have drawn conclusions about trees reuse from data collected on average 5 days each month, 16% of nights each month (Reichard 1998, Fan & Jiang 2008, Phoonjampa et al. 2010, Cheyne et al. 2013). Certain researchers have suggested that ST reuse typically occurs only after a period of more than 60 days (Reichard 1998, Fan & Jiang 2008, Fei et al. 2012). Reichard (1998) found that by the end of the study almost half of the chosen sleeping trees were previously used and found patterns of long-term reuse. However, with such large breaks in the data, the assumption that short-term reuse is not happening in these populations is perhaps unjustifiable.

When I segment my data to simulate month-long intervals between observation weeks, the rates of sleeping tree reuse markedly decreases (see Table 4). In this simulated dataset, the AF reused sleeping trees on only 33% of nights, with just 14% of all distinct sleeping trees being reused – much lower than the actual observed rate of 78.1% of nights sleeping in a tree that was reused. Since I found a gibbon night tree 16 days the first month and 19 days the second month, I am missing data for 42% of the nights. If I were able to collect the other 42% of sleeping trees, it is possible that my reuse estimations would be even greater than they currently are. Reuse rates are also affected when researchers look at reuse as it relates to all observed events (Reichard 1998) or reuse as it relates to each distinct tree observed (Fan & Jiang 2008, Phoonjampa et al. 2010, Fei et al. 2012, Fei et al. 2017). When looking at the AF's frequency of sleeping tree reuse as it relates to all her distinct sleeping trees, I find that 53.3% of the AF's sleeping trees were revisited by her or another individual (15 distinct trees; 8 trees reused by AF or another group member; 6 reused by AF).

While methodological limitations and analytical decisions may negatively skew the rates of sleeping tree reuse in prior studies, alternatives need to be considered to explain the apparent spike in sleeping tree reuse observed by Tenaza & Tilson (1985). These researchers observed 11 kloss gibbon groups over a span of two years, totaling nearly 1,000 nights of observation. Despite this extensive sampling, they found that these groups predominantly utilized only three distinct sleeping trees each. This pattern was attributed to the gibbons' need to evade human hunters who used climbable lianas to gain a vantage point to shoot them from. Limited availability of trees lacking climbable lianas may have driven these kloss gibbons to repeatedly utilize the same sleeping sites, resulting in a notably high frequency of sleeping tree reuse. This suggests a potential correlation between increased sleeping tree reuse and habitat limitations. Studies across species have found that frequently reused sleeping locations offer greater protection from predators or meteorological elements than sleeping locations which are infrequently used (Schnell 1969, Markham et al. 2016). An examination of the home range of a troop of macaques that consistently reused a single sleeping site revealed the absence of other suitable sleeping trees within their territory (Ramakrishnan & Coss 2001).

Similarly, Harrison et al. (2012) reported high rates of sleeping tree reuse among siamang living in a habitat with an active clouded leopard community. These authors pointed out that siamang home ranges are smaller than gibbon home ranges and would therefore have fewer sleeping trees within them. I also suggest that owing to the tendency of siamang to sleep as a cohesive unit, they require multiple suitable sleeping spots within a single tree. This amplifies the requirements for sleeping tree suitability and thus may further reduce the overall availability of sleeping trees. The idea that these siamang are reusing sleeping trees more frequently due to a lower availability of suitable sleeping trees in a predator habitat remains consistent with observations of a solo female in the same study who reused sleeping trees significantly less often than the family group (Harrison et al. 2021). More felines are found at HKK than anywhere else in the region (Simcharoen et al. 2007, Saisamorn et al. 2019). Meanwhile, the savannah habitat is suboptimal (Light et al. 2021) and likely offers less suitable sleeping trees than are generally available to gibbons. The increased predation pressure exerted on the gibbons in this study combined with lower availability of protective sleeping trees may prompt an increase in the frequency of sleeping tree reuse.

Consecutive sleeping tree reuse at this site was likewise higher than previously reported, even in reports which control for consecutive observations (Phoonjampa et al. 2010). The AF and AM frequently reused trees twice in the same week and on several occasions the same tree was used on consecutive nights. An increase in consecutive sleeping tree reuse by the gibbons in this study might be explained by a poor habitat, with fewer suitable sleeping trees, and furthermore, a lower abundance of fruit. Fruit at this savannah site is observed in lower abundance than in evergreen habitat (Light et al. 2021). Fruit is both spatially scattered and ephemeral and gibbons tend to adjust their foraging habits in response to its abundance. Temporal clustering of sleeping tree reuse may perhaps be linked to feeding tree ephemerality. The AF slept on average 100 m from her last feeding tree of the day. Prior research on gibbons has concluded that sleeping tree structure rather than proximity to food is the primary influence on sleeping tree location (Reichard 1998, Fei et al. 2012, Harrison 2019). However, in a savannah habitat, where home ranges are larger and fruit trees are more scarce (Light et al. 2021), and where suitable sleeping trees are likely less common, the occurrence of these within manageable proximity to one another is perhaps quite low.

In the future, it would be interesting to investigate the biological mechanism behind temporal clustering of sleeping tree reuse by gibbons in a savannah habitat. Since phenology was not within the scope of this study, and morning feeding trees were unobservable due to station safety restrictions, I cannot investigate this question. However, I suggest that it would be quite interesting to investigate the spatial relationship between feeding resources and commonly reused sleeping trees in this habitat with active predators, fewer potentially suitable sleeping trees, and fewer, more scattered feeding resources across a larger HR. I hypothesize that sleeping trees which have high frequencies of temporally clustered reuse, will spatially correlate with the locations of calorically valuable feeding resources.

5.4 *Geospatial Elements*

The estimated HR for these savannah gibbons was 42.16 hectares, and 36.3 hectares when fragmented canopy was subtracted. Both estimations are much larger than is commonly seen for white-handed gibbons (Savini et al. 2008, Bartlett et al. 2016). Gibbons in an adjacent home range in this same habitat have been shown spend more of their activity periods in MD forest than in DD forest (Light et al. 2021). The gibbons in this study slept more often in DD forest than MD forest, but not significantly more frequently than expected values based on home range forest type percentages. Many sleeping sites were located close to or within the research station camp, which happened to be DD forest. Sleeping close to the research station may offer protection from predator since human presences has been shown to reduce rates of predation (Isabell & Young 1993). Furthermore, DD forest has a more open canopy structure than MD forest (Light et al. 2021), potentially allowing for greater vigilance.

These gibbons slept on average 131 m form the estimated MCP HR border. The gibbons in this study only had one observed intergroup encounter and it was during the first week when I was only collecting geospatial data and not behavioral data. Intergroup encounters are known to be very rare for this group of gibbons (Light, unpublished data). Poor habitat quality may require gibbons to travel farther distances to obtain food and devote less energy to border patrol (Light et al. 2021). The influences of border patrol and safety from neighboring groups are likely minimal in this group.

CHAPTER 6: CONCLUSION

The general aim of this study was to produce the first comparative study of white-handed gibbon sleeping behavior. The first and only other paper on white-handed gibbon sleeping behavior was published in 1998 and focused on a group living in an evergreen forest with few natural predators (Reichard 1998). This study aimed not only to generate a first comparative study, but to analyze intragroup differences in sleeping tree selection and to investigate the effects of ecological variables on sleeping tree location in a savannah habitat.

My first hypothesis was supported in that gibbons in this study engaged in cryptic sleep-related behaviors and chose sleeping trees which align with the predator avoidance hypothesis. My first three predictions were met. Gibbons rapidly retreated to their sleeping trees several hours before sunset and remained still and silent once in their tree. The trees they chose had a greater DBH and were taller than other trees in the habitat. Only prediction 1.4 was not supported. Sleeping tree reuse was a common event for the duration of the study. I assert that previous research may have underestimated sleeping tree reuse due to methodological limitations or analytical choices. Using two studies which reported higher rates of sleeping tree reuse as support for my argument, I suggest that stronger pressures of predation, combined with a suboptimal habitat with potentially less suitable sleeping trees may have contributed to the high frequency of sleeping tree reuse observed in this study. An interesting facet of the sleeping tree reuse observed in this study is that reuse was temporally clustered. The biological mechanisms behind this observation may be a unique area of interest in the future.

For Hypothesis 2 on individual variation in sleeping tree characteristics, one prediction was supported and the other was not. Reichard (1998) observed that adult females sleeping with infants or juveniles sleep higher in the canopy than other group members. This study likewise found that the AF, who slept with a juvenile, chose significantly taller sleeping trees than the AM and slept at higher locations than both the AM and SAF, supporting our first prediction. Based on previous research that looked at canopy structure as a group average (Reichard 1998), and other research which investigated differences in adult male and adult female preferences for liana (Phoonjampa et al. 2010), I predicted that there would be no individual variation in canopy structure. As a group average, these gibbons exhibited no preferences in canopy structure. Likewise, there were no significant differences in sleeping spot or canopy characteristics between adult individuals. Results from the subadult, however, differed significantly. Future studies should opt to analyze subadult and adult individuals separately to investigate these findings.

Finally, my hypothesis on the impact of forest type on sleeping tree selection was not supported. Gibbons did not sleep in MD forest more often than would be predicted based on home range forest type percentages. They slept more often in DD forest but not significantly more often than would be predicted based on chance. While previous research on this same study group has revealed an avoidance of DD forest in daytime activities, this avoidance is not observed in sleeping tree selection. Trees in DD forest are generally thinner and shorter than trees in MD forest. However, the thinner canopy in DD, allowing for enhanced vigilance, may be a key feature to explain the higher frequency of sleeping trees in DD forest. My data set only consisted of the AF's sleeping trees on days I saw her enter her tree. Though my results show no significant preference for sleeping in DD forest, I suggest that this same analysis should be run again in the future with a larger number of observations and that sleeping site proximity to camp may be an interesting variable to investigate.

Most of my results reflect prior gibbon sleeping behaviors papers and support the predator avoidance theory. Of the three individuals in my study, only the SAF showed a significant difference in canopy preference. Individual variation in sleeping tree preferences between age classes may be interesting to explore in future studies, especially regarding the effects body size and age have on predation pressures and biological needs. I found much higher rates of sleeping tree reuse than has previously been documented by most gibbon researchers. Sleeping tree reuse in gibbons may be underestimated due to long breaks in observations when researchers choose to rotate between groups. I suggest temporal gaps in the behavioral research should be noted within one's methods and regarded as information just as imperative to analyses as total days logged. Intensive observation may uncover nuanced patterns in animal behavior that might be missed when representativeness of data is prioritized over continuity. Though methodological differences may account for some increase in reuse frequency, I argue that these savannah gibbons necessarily reuse sleeping trees as a strategy to cope with three different elements 1) increased pressure from predators to choose safer locations 2) a lower abundance of safe sleeping trees in a savannah habitat and 3) a lower abundance of safe sleeping trees within relative proximity to feeding resources. Finally, I found no significant effect of forest type on sleeping tree location, although I suggest this should be explored again with a larger dataset.

CHAPTER 7: ETHICS

Obligations to study subjects

This research was observation-based, involved no direct handling of the subjects, and likely had minimal effect on their behavior. Approval from UNC Charlotte's IACUC was not required due to the observational nature of this research. IACUC was informed of the aims and methods of this research and provided a letter of exemption. The intended purpose of this research was to provide further information on white-handed gibbon sleeping behaviors, which may be applied to improve captive gibbon habitats, and to inform conservation efforts to protect wild populations of *Hylobatidae* species. It is my hope that this research may also be relevant to better understanding the dynamics between predator-prey relations, habitat, and characteristics of sleeping sites, their frequency of use and location across other primate species and animal kingdom orders.

Positionality statement

As a U.S.-born citizen, I recognize that I have obligations to the people of Thailand and to the land in which I intend to conduct my research. As a language enthusiast, I dedicated myself to learning and embracing the Thai language. While in Thailand, I strove to communicate to the best of my abilities in the local language. A portion of the funding for this project will be allocated to translating my results so that they may be accessible in Thai. In this way, I hope to promote a shared scientific responsibility and enhance inclusivity. While in the forest, I abided by the principles of "leave no trace" and consider the consequences of my actions beyond the wilderness border (Simon & Alagona 2009). Finally, in conversations and through my work, I aim to promote an understanding that conservation efforts must not infringe on human rights.

Reconciliation of human rights with conservation not only benefits human communities in habitat countries but can lead to longer-lasting and more effective solutions to problems posed by human-wildlife interactions. This reconciliation can be achieved through acknowledgment of shared responsibility, equitable allocation of costs and benefits, respect for diverse views and values, and the empowerment and inclusion of all implicated parties (Harris et al. 2023).

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APPENDIX A: TABLES

Table 1: Ethogram developed by Bartlett (2015 p. 37) with minor adaptations.

Behavior	Description
Auto-grooming	Grooming oneself, usually during rest.
Drinking	Pulling water out of a tree hole or basin with a hand and catching run-off in their mouth or licking water from fur
Feeding	Pulling a food item off a tree, chewing, or brief pauses during a feeding bout. Briefly holding a leaf to one's mouth, dropping the leaf, and chewing was considered feeding on insects.
Grooming	Using fingers or mouth to slowly comb through the fur of another individual.
Intergroup encounter	Any behavior, except vocalization, directed toward or performed with a member of another social group.
Interspecies encounter	Any behavior, except vocalization, directed towards an individual of another species.
Play	Active but nonaggressive interactions such as wrestling, chasing, or pulling and slapping, between two individuals
Rest	Any period of inactivity lasting at least 5 seconds
Social contact	Two or more individuals sitting adjacent to one another with body contact.
Travel	Movement between trees or within a single tree which involves traveling more than three arm spans in distance.
Vocalization	Any vocalization including solo calls, duetting, alarm calls, or contact calls.

Table 2: Meteorological data obtained from KNR staff during the period of this study June 14, 2023- August 12, 2023. Weekly averages of minimum and maximum temperatures and weekly total rainfall are displayed. Average daily minimum and maximum temperatures are included at the bottom with average daily rainfall. Total rainfall for the 2-month study period is also calculated. Temperatures are given in °C, rainfall is measured in mm.

WEEK	AVERAGE TEMP (MIN)	AVERAGE TEMP (MAX)	WEEKLY RAINFALL (mm.)
JUNE 14- JUNE 20	24	30	17.7
JUNE 21- JUNE 27	23.4	30.9	0
JUNE 28- JULY 4	21.3	27.4	40
JULY 5- JULY 11	21.6	31.4	65
JULY 12- JULY 18	22.7	30.1	0
JULY 19- JULY 25	22.3	27.3	75
JULY 26- AUGUST 1	23.7	27.9	0
AUGUST 2- AUGUST 8	23.1	26.7	8
AUGUST 9- AUGUST 12	23.5	27	0
DAILY AVERAGE	22.8	28.8	3.7
TOTAL RAINFALL			205.7

Table 3: A list of all observed sleeping tree species. N indicated the number of times each species was observed as being used as a sleeping tree.

Species	**N**
Shorea siamensis	31
Dalbergia oliveri	10
Terminalia tiptera	10
Terminalia mucronata	4
Dipterocarpus alatus	2
Lagerstroemia cochinchinsis	2
Lagerstroemia venusta	2
Melia azedarach	2
Pterocarpus macrocarpus	2
Shorea obtusa	2
Terminalia corticosa	2
Terminalia nigrovenulosa	2
Angiogeissus acuminata	1
Thyrsostachys siamensis	1
Dillenia parviflora	1
Hibiscus tiliaceus	1
Lagerstroemia villosa	1

Table 4: Simulation of discontinuous data set. The data on sleeping tree reuse was broken by week. The four week-long periods of data from the first month were then combined with the four week-long periods of the following month to generate 4 data sets. These four data sets simulate reuse observations as if taken for one week each month. The frequencies of reuse from the four data sets were then averaged together.

Dates	Nights Observed	Distinct Sleeping Trees	% Nights in a Reused Tree	% of Trees Reused
6/14-6/20 and 7/14-7/20	9	5	0.56	0.20
6/21-6/27 and 7/21-7/27	6	6	0.00	0.00
6/28-7/4 and 7/28-8/3	7	6	0.29	0.17
7/5-7/11 and 8/4-8/10	7	5	0.43	0.20
Averages			0.32	0.14

APPENDIX B: FIGURES

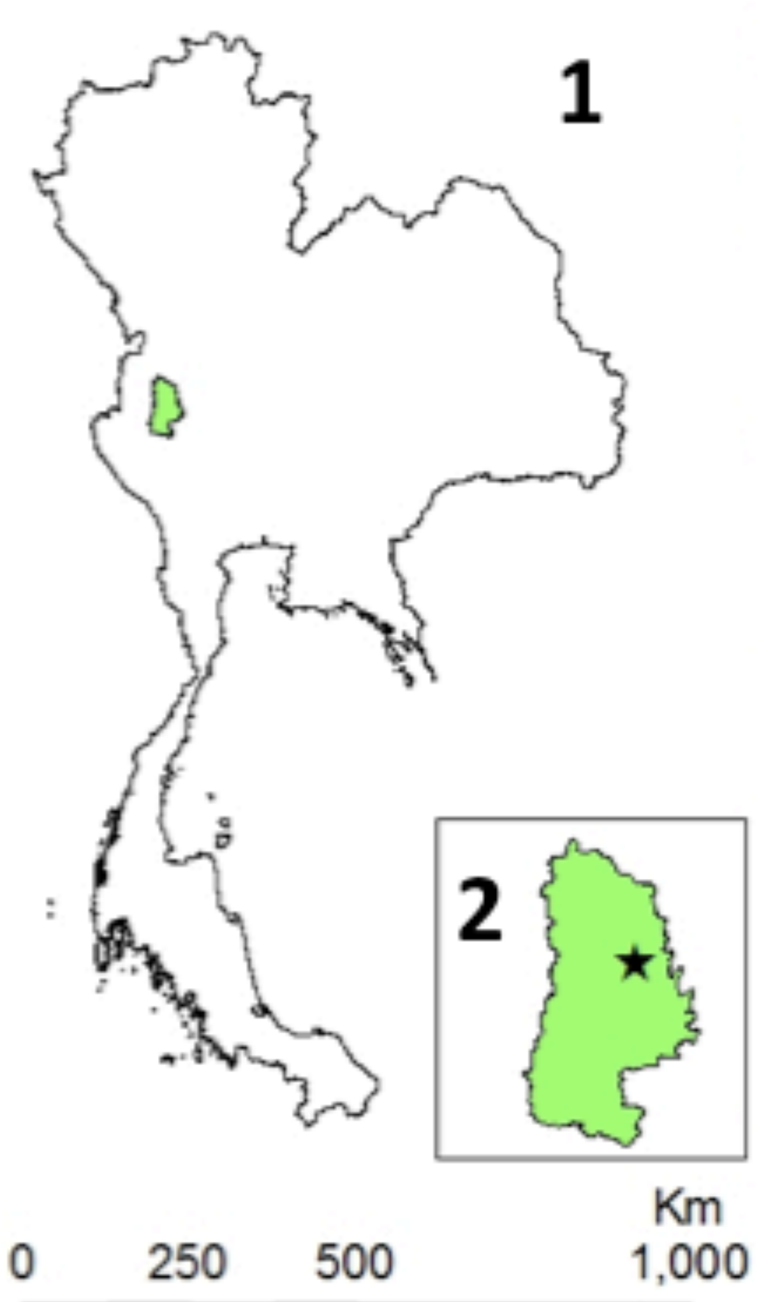


Figure 1. Map of Thailand with HKK highlighted in green. KNR is marked with a star. Map provided by Lydia Light.

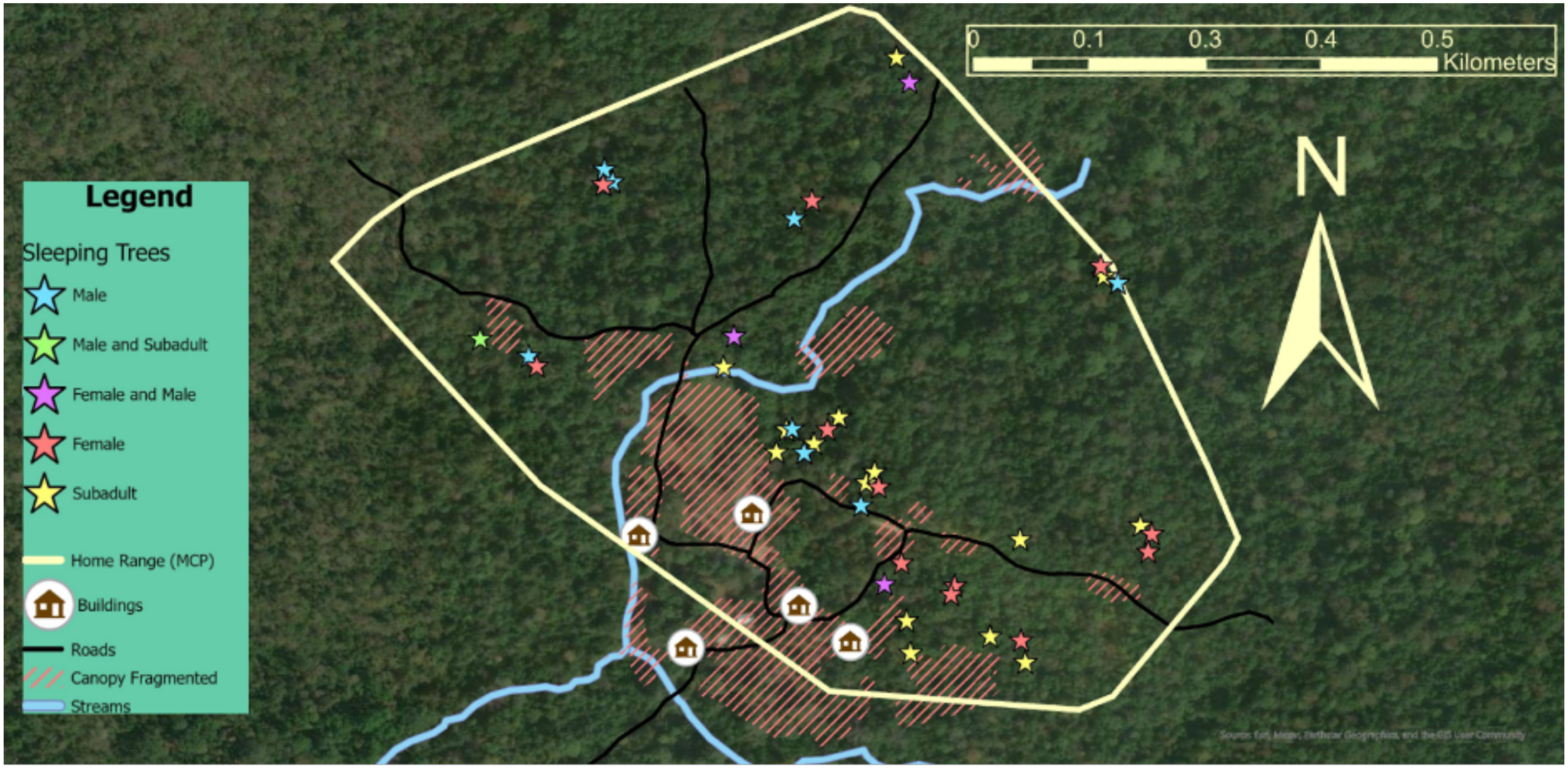


Figure 2: Map of estimated HR for group L derived from MCP analysis of all observed locations is provided as a yellow outline. Locations of sleeping trees are marked with stars and color coded per individual while trees used by two different individuals are given a distinct color. The camp library and kitchen along with 3 cabins are indicated by the building icons. Many more cabins were not included in this map. Black lines indicate unpaved roads accessible to camp vehicles and blue lines indicate streams. Red hatched lines show areas of fragmented canopy, presumably inaccessible to gibbons.

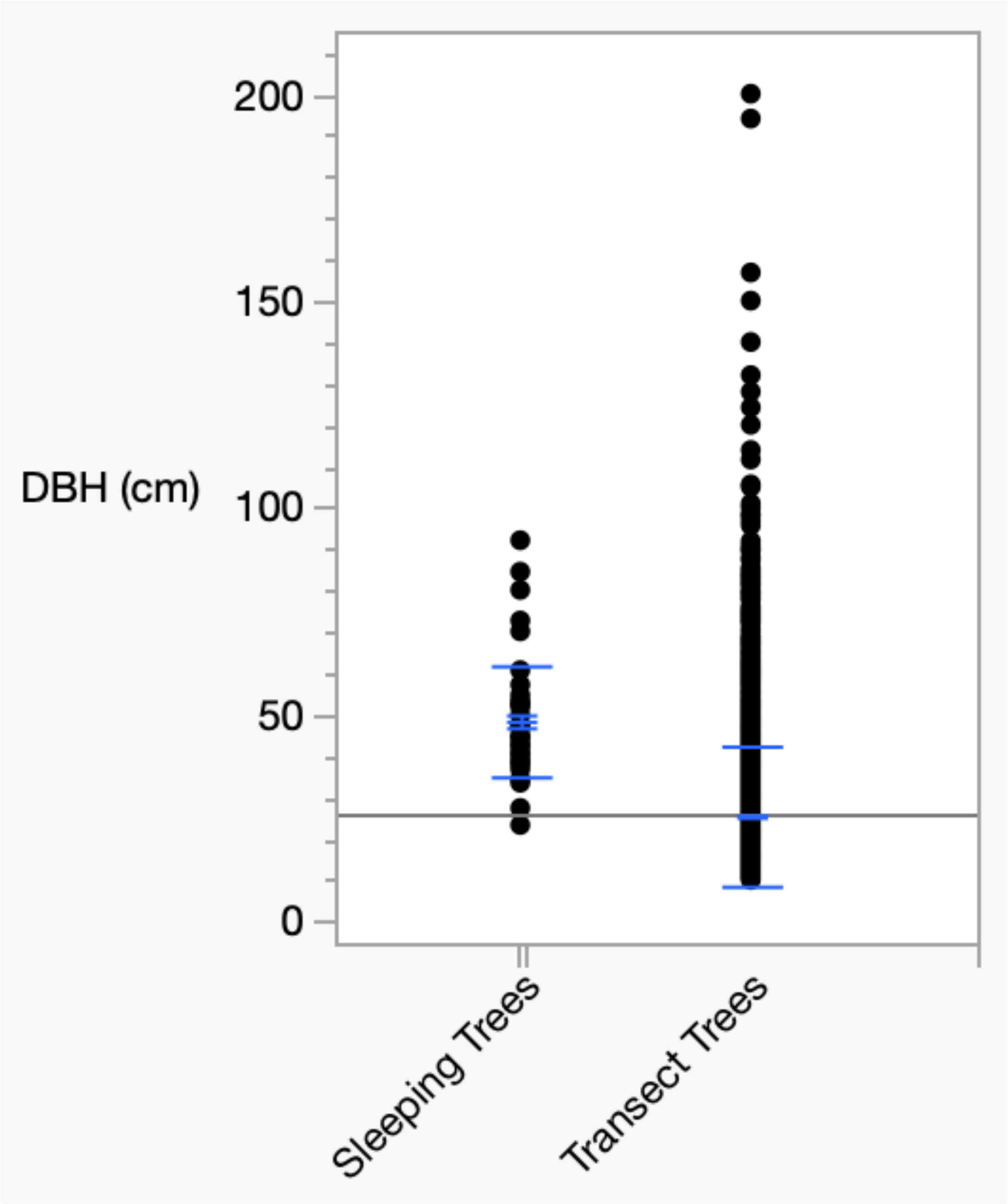


Figure 3: A comparison DBH between sleeping tree and trees in adjacent savannah habitat transects. Sleeping trees had significantly larger DBHs than transect trees (***p*** = 0.0001).

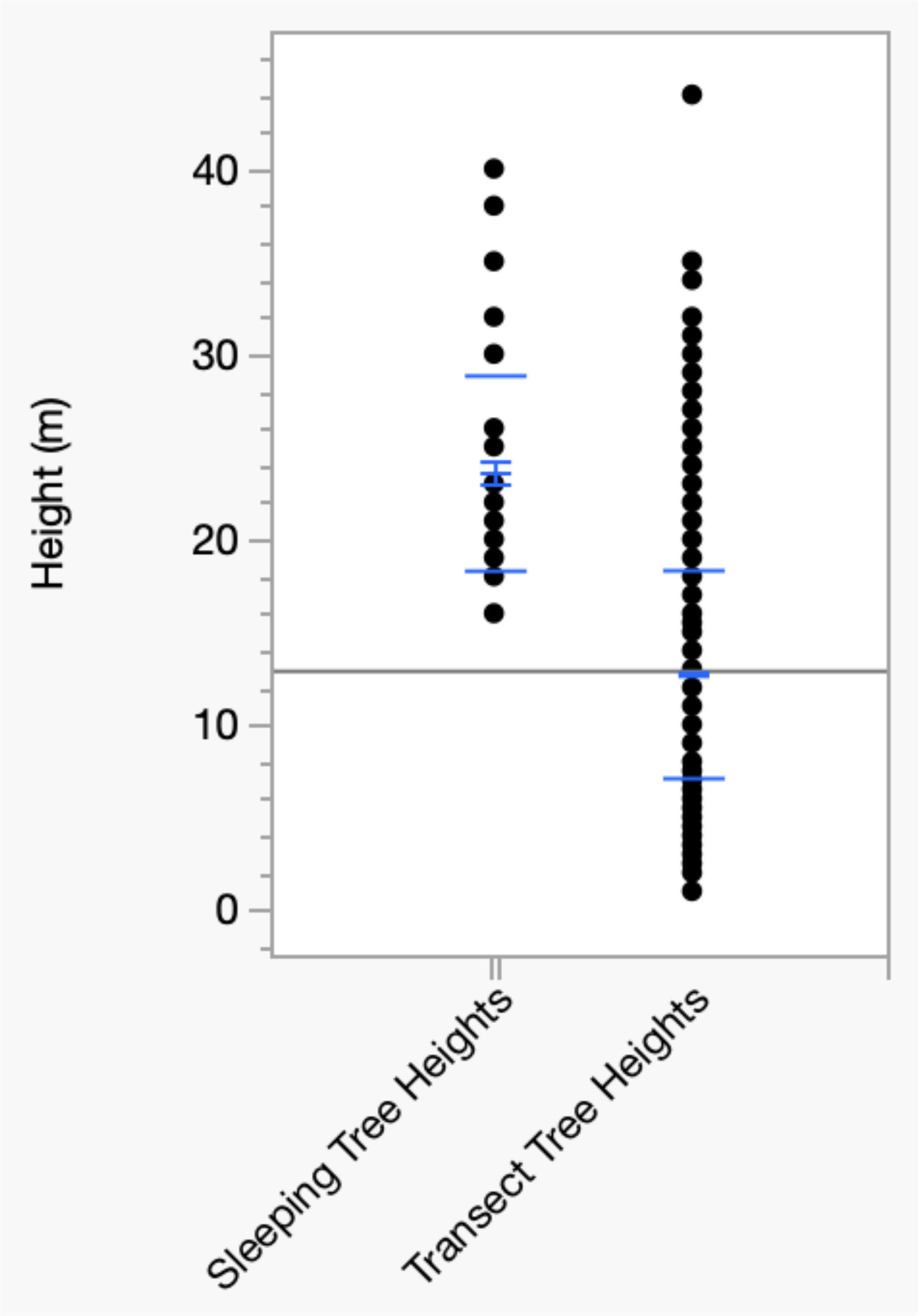


Figure 4: A comparison of sleeping tree heights with heights of trees in adjacent savannah habitat transects. Sleeping trees were significantly taller than transect trees (***p*** = 0.0001).

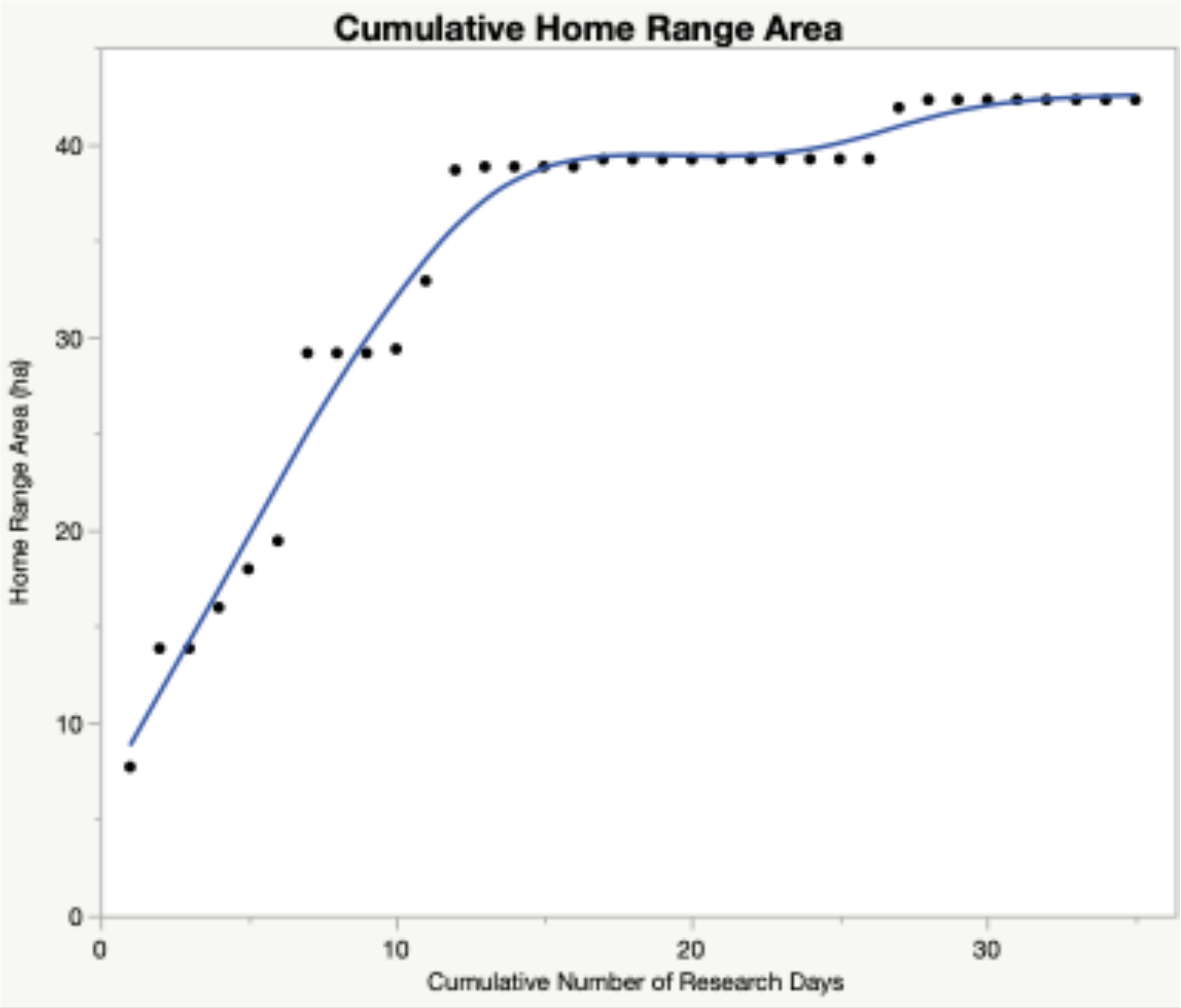


Figure 5: Number of days of observation in relation to cumulative MCP HR area in hectares.

LIANA DESNITY

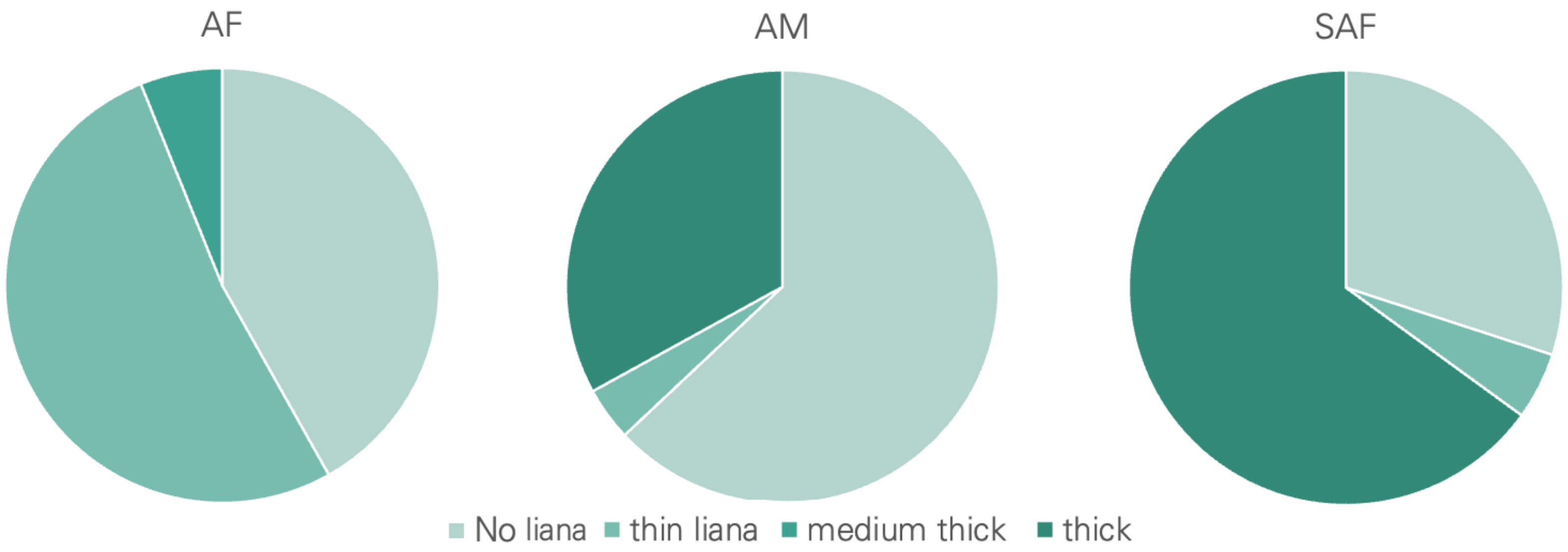


Figure 6: Pie charts of frequency of liana density in sleeping trees per individual. The AF frequently slept in trees without any liana (41%), or trees with thin or bare liana solely in the lower canopy (53%; combined total 94%). She never slept in trees with thick liana (6% medium thick liana; 0% thick; *n* = 32). The AM most frequently slept in trees without liana (63% no liana, 4% thin liana; 0% medium thick liana; 33% thick liana; *n* = 27). The SAF most frequently slept in trees with thick liana (30% no liana, 5% thin liana; 0% medium thick liana; 65% thick liana; *n* = 20).

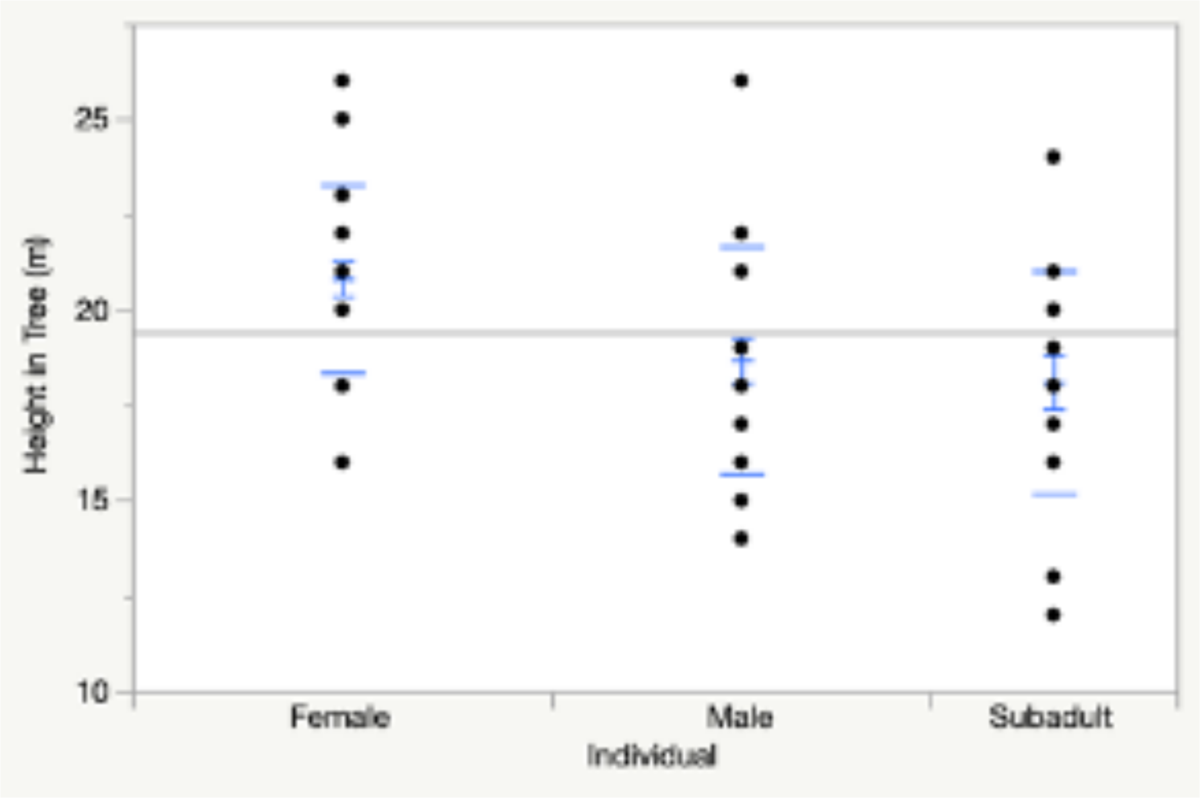
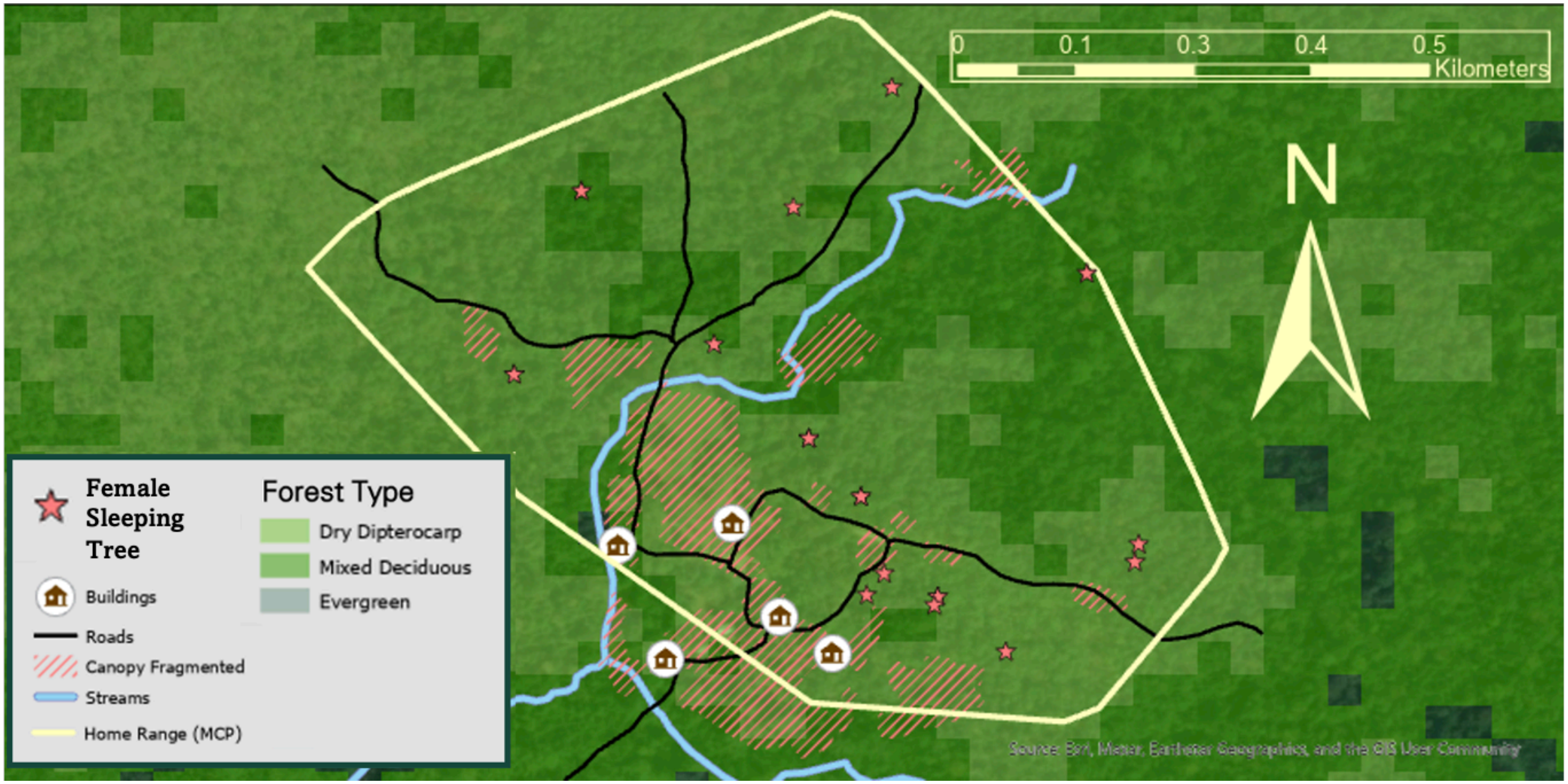


Figure 7: Differences in sleeping spot height between AF with juvenile, AM, and SAF. The AF slept significantly higher than both the AM (***p*** = 0.0018) and SAF (***p*** = 0.0019).



Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community

Figure 8: Map of forest type classifications and locations of AF sleeping trees. The 42.27 ha estimate was comprised of 71% DD, 29% MD, and 0.3% EG forest types. When I subtracted 5.54 ha of fragmented canopy, the new estimated HR was 36.73 hectares, and the forest type percentages became 69% DD 30% MD and 0.3% EG. On days I observed the AF entering a tree after a follow, she slept in DD 81% of times 22/27 (12 distinct trees) and she slept in MD 19% of the times 5/27 (4 distinct trees). Compared to what I would expect based on HR forest type percentages, the AF slept in DD forest more frequently than in MD. The difference was not significant (*p* = 0.2061).

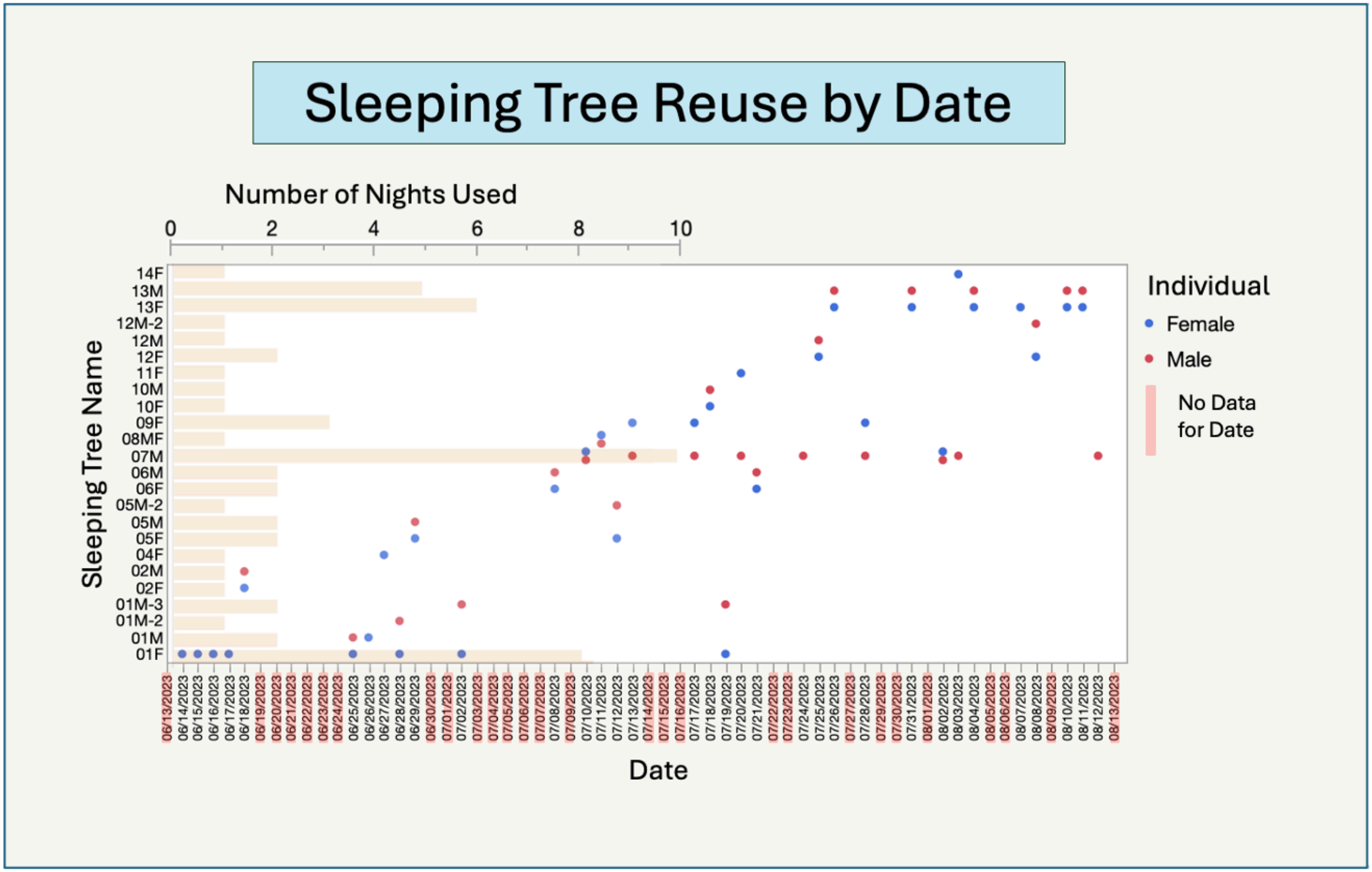


Figure 9: Adult male (red) and female (blue) sleeping tree use by date. Dates highlighted in red have no data for either individual. Larger dots indicate more frequent use of tree. Trees are listed in ascending order from the time it was used.