

Maintaining Hornbills in the Working Landscape of the Southern Tenasserim Western
Forest Complex Corridor in Thailand

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Jiraporn Teampanpong

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Dr. Robert B. Blair

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CHAPTER 1 - INTRODUCTION

Tropical forests in Southeast Asia are limited in extent and among the most vulnerable to conversion for other land uses as a consequence of human population pressure, poverty, weak institutions and poor policies (Laurance 1999, Sodhi et al. 2004, Wright and Muller-Landau 2006). Forest conversion unavoidably results in habitat loss, forest fragmentation, and degradation that could bring about severe droughts, wildfires, and even accelerated climate change on a global scale, and diminished ecological stability of watersheds, soils, biodiversity, global climate, pollination, seed dispersal, and local fisheries on a regional scale (Sodhi and Smith 2007, Laurance 1999). If this continues, by 2100 Southeast Asia could lose three quarters of its original forests along with 42% of its biodiversity (Sodhi et al. 2004). Because the process and effects of rampant anthropogenic intrusion in tropical forests are poorly understood (Laurance 1999), these have become the major conservation threats in the tropics (Raman and Mudappa 2003) especially for birds (Cordeiro and Howe 2003, Sodhi and Smith 2007), that become locally extinct in fragmented landscapes (Wilcove et al. 1986).

Protected area systems are therefore essential for reducing human pressure on biodiversity. Unfortunately, only 12% of Earth's land lies within protected area systems and less than half of this is too small, too isolated, too static, and not long-lasting enough to protect biodiversity and prevent over exploitation (Brooks et al. 2004, Rodrigues et al. 2004, Chape et al. 2005) especially in the changing global climate (Hannah et al. 2007). Consequently, benefits of conservation of secondary forest outside protected areas are beginning to be recognized because they harbor significant levels of biodiversity and

should be targeted for long-term conservation (Raman and Mudappa 2003, Daily 2001, Daily et al. 2001, Polasky et al. 2005).

However, as conversion of native lands to human-modified uses accelerates, more supplemental approaches are required for protecting wild lands adjoining protected areas for wildlife, increasing landscape connectivity, and restoring degraded lands (Laurance and Bierregarrd 1997). Accordingly, ecological restoration of degraded habitats is now regarded as an effective response to reverse and reduce the negative impacts of habitat loss, fragmentation, and degradation of native plants and animals (Lamb et al. 1997, Pejchar et al. 2008, Gomes et al. 2008, Lamb 2010).

The role of frugivores in dispersing viable seeds from primary forests to degraded lands is one key component of this restoration. Lack of seed dispersal to facilitate seed collection and germination can be a major challenge limiting tropical forest recovery on abandoned land (Holl 1998, Blakesley et al. 2002). Hornbills are known as keystone species of the tropical forest, where they may be referred to as ‘farmers’ of the forest (Kinnaird and O’Brien 2007 and Poonswad et al 2013). Their presence has a disproportionate effect on ecological processes through seed dispersal. Consequently, they are perfect agents for maintaining forests and restoring forests by carrying genetic materials from one habitat to another that is suitable for forest regeneration (Sekercioglu 2006).

Large-seeded native fruiting trees may depend on hornbills as the remaining disperser of their seeds. Consequently, with the additional loss of hornbills, they may no longer regenerate in the landscape and other animals that highly depend on these plant species will be negatively impacted. The loss of these diverse plants and animals may, in

turn, reduce gene flow among forest remnants and threaten the stability of the ecosystem over the long term.

The Tenasserim Western Forest Complex Corridor (TWFC) is one of the nine high-priority Greater Mekong Subregion biodiversity conservation landscapes (GMS-BCI) and the first biodiversity corridor of Thailand (GMS-BCI 2005). It has experienced a long history of natural resource harvesting and its location in the Greater Mekong Subregion economic corridor, the area has been being threatened by development, with more than 50% of the area classified as degraded forest and human-dominated zones (WCS-TP 2009b). Discontinuity of ecological connectivity and integrity may increase because of development activities in the area, causing fragmentation throughout the landscape.

Regrettably, its capacity to support a unique assemblage of large populations of globally threatened species and provide a high level of biodiversity and natural resources in the Indo-Pacific region have been gradually reduced by a long history of natural resource harvesting including mining, logging, collecting of non-timber forest products, hunting. The area is becoming increasingly popular with tourists and this is leading to unplanned tourism development.

To remedy the effects of human activities on the ecosystem of the TWFC, WCS-TP (2009a) suggested conserving a corridor area to facilitate the movement of large animals (tiger, leopard, elephant, serow, gaur, sambar deer, barking deer, and great hornbill) in the landscape. The report advises that the primary forest should be maintained, that degraded forest should be restored naturally and by humans, and that sustainable management zone should be implemented. Conservation of those large, landscape-level species eventually could relieve the discontinuity of ecological

connectivity and integrity of the ecosystem that has resulted from development activities in the area, causing fragmentation throughout the Tenasserim both in Myanmar and in Thailand.

As one part of implementing this corridor management plan, I have studied hornbills as potential agents for increasing ecological resilience by maintaining healthy forests and restoring biodiversity in the degraded forests of the southern TWFC. Hornbills are the only landscape-level species that can fly over this fragmented landscape and they are known for their long-distance movements. The research presented in this dissertation initiated the first intensive study of hornbills in the southern TWFC. The overall goal of this research was not only to reveal the first records of population dynamics and human effects on hornbills in the southern Tenasserim, but also to facilitate the implementation of conservation activities to maintain these populations of hornbills and their habitats. This research addresses the importance of conservation of the forest outside of the protected areas with a special focus on hornbills and involvement of the local people in the hornbill's conservation. The major objectives of this work are 1) to describe nest characteristics and the nest environment of the four sympatric hornbill s in the southern TWFC, 2) to study movement patterns and foraging range of immature Oriental-pied, Wreathed, and Great Hornbills, 3) to estimate accuracy of radio telemetry used for hornbill study in this landscape, 4) to understand resource selection by immature Oriental-pied hornbills, and 5) to estimate occupancy of the four sympatric hornbills.

1) The Study Areas and Significance

The Tenasserim Western Forest Complex Corridor (TWFC: Figure 1.1) is named after the Tenasserim Mountain Range, which forms the backbone of mainland Southeast Asia's largest tract of intact natural forest. TWFC is located at the juncture of four biogeographical realms, between two forest complexes in Thailand and large forest tracts in Myanmar that are vulnerable to logging and clearance for agriculture. The upper forest complex is called the Western Forest Complex (WEFCOM), the largest forest complex in southeast Asia of which the core is a Natural World Heritage Site. The lower forest complex is Kaeng Krachan Forest Complex (KKFC), an Asian Heritage Site (Association of Southeast Asian Nations 2003). The combination renders the TWFC one of the world's most outstanding tropical and subtropical moist broadleaf forests, and it is one of the nine high-priority Greater Mekong Subregion biodiversity conservation landscapes (GMS-BCI) as well as the first designated biodiversity corridor in Thailand (GMS-BCI 2005). This combination of factors has earned it designation as a major Indo-Burma Biodiversity hotspot (Myers et al. 2000). Its importance was elevated by the Asian Development Bank (ADB) when it decided to prioritize the protection of biodiversity from development projects that it funded and it became a crucial link in the Tenasserim landscape (GMS-BCI 2006).

TWFC supports a unique assemblage of large populations of globally threatened species and provides a high level of biodiversity and natural resources in the Indo-Pacific region. Based on these features, TWFC is classified as an Important Bird Area (IBA) that contains many globally threatened bird species (BCST 2004) and as a Tiger Conservation Landscape Class I based on the global priority for the persistence for tiger populations

(Sanderson et al. 2006). Additionally, the corridor is potentially a trans-boundary natural resource conservation and management zone between Thailand and Myanmar that aims not only to preserve biodiversity but also to bring peace and co-operation to the region (Qunli and Nitta 2003).

My research focused mainly on the southern TWFC (Figure 1.2) emphasizing on three major types of land use. I called it as a working landscape because it has humans as a major component of which their activities should allow the natural ecosystem to be sustained to provide ecosystem services to humanity and the planet. It included 1) Maenam Pachee Wildlife Sanctuary (MPWS), part of KKFC representing forest inside protected area, 2) the Natural History Park initiated by Princess Maha Chakri Sirindhorn (NHP) representing forest outside protected area, and 3) forest edges and remnants in human-dominated areas near MPWS and NHP.

The climate in the southern TWFC is tropical with mild weather. The daytime temperature recorded from Meuang District of Ratchaburi Province from 2010 to 2012 ranged from an average of 24.3°C in December and January to 30.7°C in April and with 1028.3 mm annual precipitation (Thai Meteorological Department, 2013). The rainfall is seasonal and numerous temporary streams run dry from December to April Figure 1.3.

Figure 1.1 The Tenasserim Western Forest Complex Corridor (TWFC). TWFC is comprised of three protected areas, Sai Yok National Park in the north, and Maenam Pachee Wildlife Sanctuary and Chalerm Prakiet Thai Prachan National Park in the south. The corridor includes three areas under the management of the Royal Thai Government:

Wang Yai Maenamnoi Reserved Forest, the area under the Royal Thai Army, and the Royal Princess Project initiated by Royal Princess of Thailand (WCS-TP 2009a).

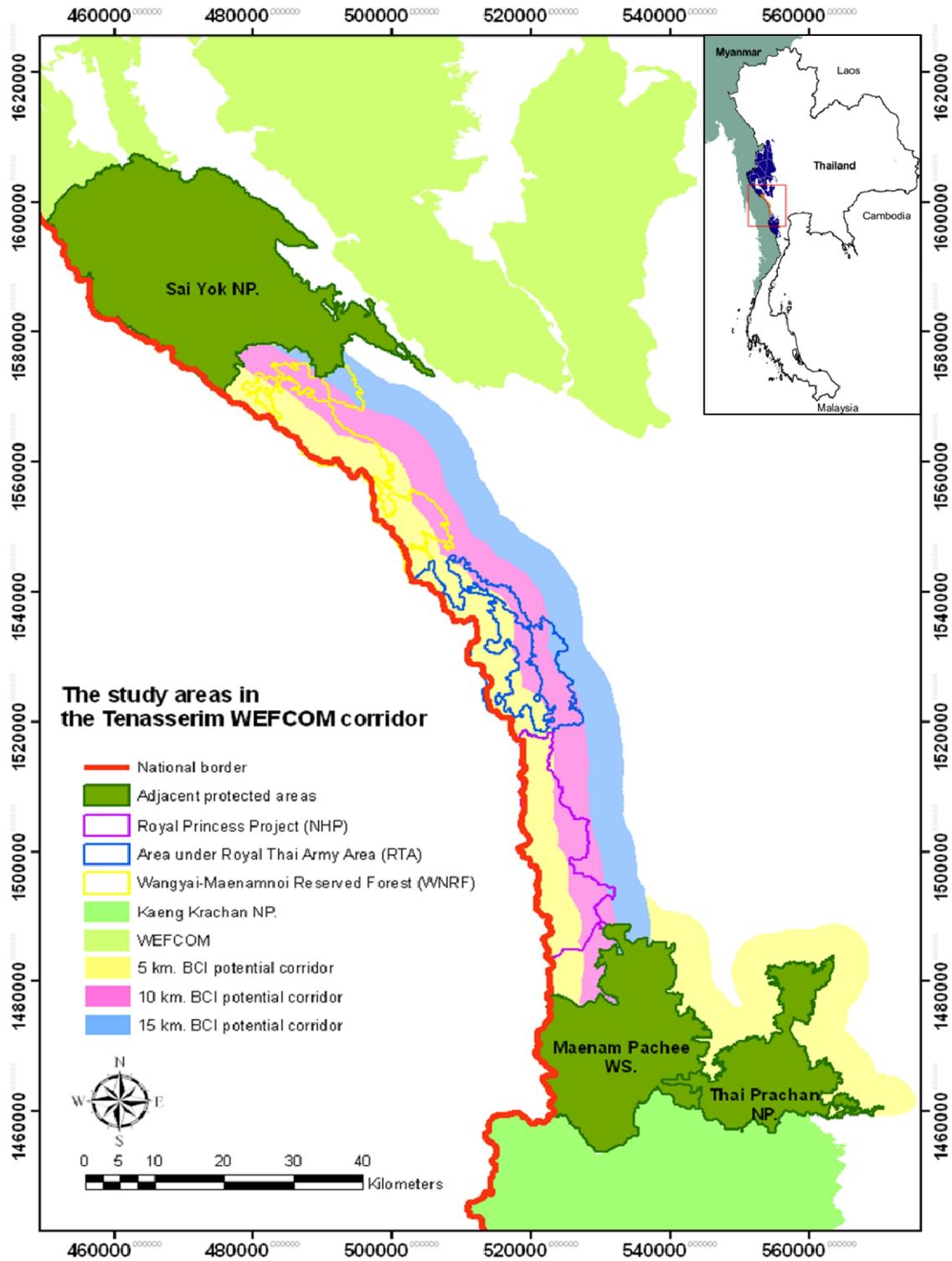


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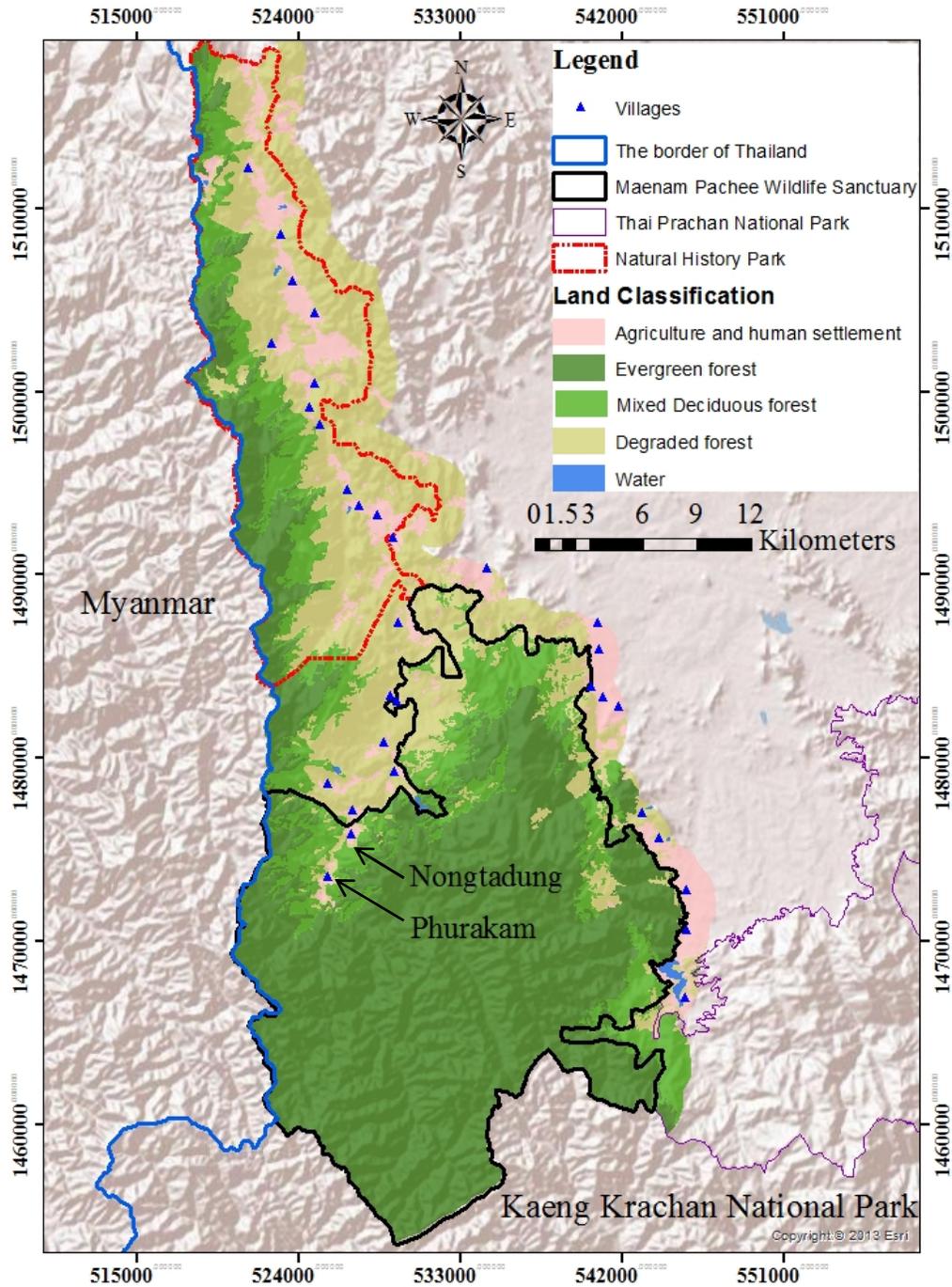
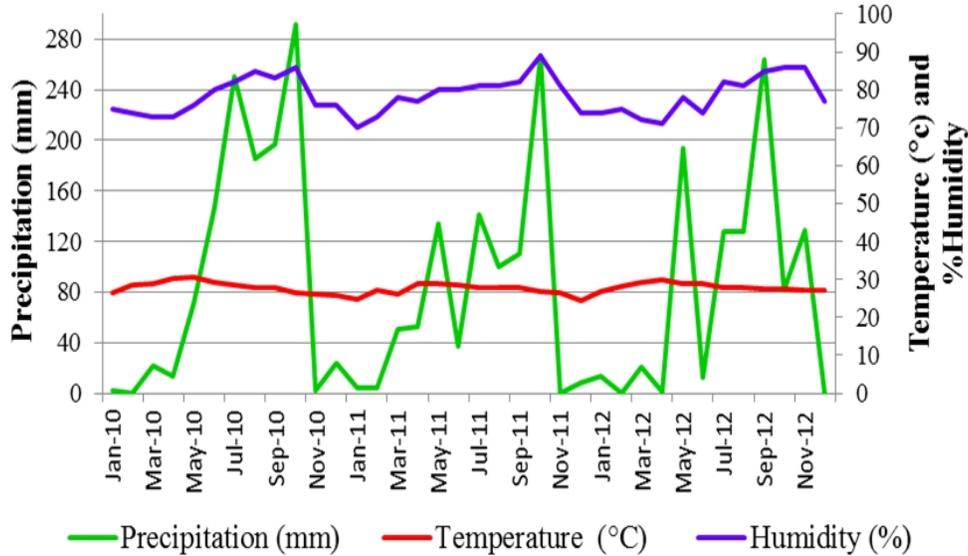


Figure 1.3 Monthly average temperature, precipitation, and relative moisture in the southern TWFC based on Ratchaburi Meteorological station



1.1) Maenam Pachee Wildlife Sanctuary (MPWS: 13° 29'-38' N and 99° 12'-25' E) is designated as an Important Bird Area in Thailand (BCST 2004). It is located in the uppermost part of KKFC and covers an area of roughly 489.31 km² (WCS-TP 2009a) of the total 4,822.26 km² of KKFC. MPWS was designated by the Council of Ministers of Thailand on August 1st 1978 in Royal Thai Government Gazette and protected under the Thai Wildlife Protection and Preservation Act, 1992. There are two villages located inside the sanctuary: Phurakam and Nongtadung.

MPWS is located in the upper part of KKFC lying in Ratchaburi province, western Thailand. MPWS is also contiguous to Tanintharyi National Park in Myanmar (GMS-CEP 2008). The sanctuary is located in hilly terrain (altitude 300- 980 m.a.s.l.) and contains five main land-use types. The vast majority is evergreen forest (50.2%), degraded forest (36.7%) and mixed deciduous forest (11.5%) while human-dominated

zones (1.6%) are minimal (WCS-TP 2009b). The forest cover close to Kaeng Krachan National Park is in good condition while the areas contiguous to human-dominated zones are susceptible to the impact of different land-use patterns such as human settlement and the cultivation of several vegetable crops.

Based on the survey by WCS-TP (2009a), MPWS is the home of leopard, gaur, serow, sambar deer, barking deer, wildboar, otter, porcupine, banteng, bear (black and sun), tapir, white-handed gibbon, dusky langur, small felids, civets, and Oriental-pied, Tickell's Brown, Great, and Wreathed Hornbills. The abundance of wildlife is lower than 0.1 individual/km except barking deer (0.15), bear (0.26), wildboar (0.33), tapir (0.12), and Tickell's Brown Hornbill (0.19).

1.2) The Natural History Park initiated by Her Royal Highness Maha Chakri Sirindhorn (NHP: 13° 25'-44' N and 99° 10'-27' E) is located to the north of MPWS and covers an area of roughly 210 km² (Office of Her Royal Highness Princess Maha Chakri Sirindhorn's Project 2006). The area had experienced logging and mining but this was banned in 1989. The area is also known as the Suan Phung Natural Education Park or the Royal Princess Project and was formally declared the Royal Princess Project in January 2003. The management objective of the park is to conserve wildlife and wild lands for sustaining the livelihood of local communities using environmental education and a community-based learning center. NHP is located in Ratchaburi province, which is under the supervision of the Royal Thai Army and the Treasury Department of Thailand (TRD).

NHP is located in mountainous terrain (altitude 148 - 1150 m.a.s.l.). The remaining forest in NHP is composed of a narrow strip of undisturbed forest with evergreen (15.5%) and mixed deciduous (13.0%) trees as the dominant species, while the

major land type is degraded forest(67.9%) with scattered areas of agricultural use and human settlement (3.5%: WCS-TP 2009b). The survey by WCS-TP (2009a) found NHP contains habitat for serow, barking deer, sambar deer, bear (black and sun), wild dog, wildboar, small felids, mouse deer, otter, porcupine, and civet. All of these species had very low abundance with less than 0.10 individuals/km except wildboar (0.10), barking deer (0.20), and serow (0.21). The Great Hornbill was reported once during the survey, but outside the transect boundary.

Because the Treasury Department of Thailand (TRD) has managed the lands within and surrounding NHP with the intent of renting land for development purposes, local people are allowed to harvest non-timber forest products (NTFPs) in NHP but hunting, logging, and encroachment are prohibited. Owing to its attractive landscape, the area in NHP has become one of the most popular domestic tourist destinations in Thailand. Tourism is increasingly affecting through land encroachment in developing tourist infrastructure and the collection of non-timber forest products, particularly orchids, bamboo shoots, and honey (Kanna 2013). In addition to uncontrolled tourism development, the expansion of agriculture and human settlement are the principle challenges to nature conservation in this landscape. Multiple agencies with multiple objectives in managing the land create conflicting ideas over appropriate land use and between economic development and conservation.

1.3) Threats to the Southern Tenasserim Landscape

The southern Tenasserim Landscape has faced several threats due to human activity. This landscape has long history of tin mining (from 1913 to 1991: Leua-lamai

2005), timber concession (1968 to 1989; Pragtong 2000), lumber logging for household use and charcoal production (Sutchaya and Phumsiri 1998).

The main threats to wildlife in the protected area (MPWS) are hunting (WCS-TP 2009a) and the collection of non-timber forest products (NTFPs). Elephant smuggling from Myanmar to Thailand is the most obvious example of notorious hunting at this site occurring in 2012. Karen, an ethnic group living in the protected area, still depends highly on the forest resources for their livelihood. The major NTFPs that Karen people collect for both personal and commercial use include wild honey, bamboo shoots, termites mushrooms (*Termitomyces* sp.), *Parkia* sp., and *Gnetum gnemon* Linn. Meanwhile, the threats to wildlife in the forest outside protected area are more diverse and include disturbance from livestock, illegal logging, tree cutting, and the collection of NTFPs. The major NTFPs collected outside of the protected area for personal use and sale include termite mushrooms, bamboo shoots, bamboo stems, Emblic myrablan (*Phyllanthus emblica* L.), Beleric myrobalan (*Terminalia bellirica* (Gaertn.) Roxb), and timber.

Currently, this landscape has been threatened by unplanned tourism development. Tourists are attracted to this landscape because of the similar beauty of nature to northern Thailand, which is in proximity to Bangkok, the capital city of Thailand. Additionally, the Regional Treasury Office has policies to rent land for development for tourism and agriculture. These policies have brought about increasing land-use change with the development of resorts and the associated changes in the quality of life, environment, and available natural resources without regard to developing policies to promote good governance and environmental management (Kanna 2013).

2) Hornbill Ecology

The geographical topography of Thailand results in diverse habitats that can support 13 species of hornbills in the Family Bucerotidae, which is almost half of the 32 hornbill species in Asia, and accounts for roughly one-fourth of the 57 hornbill species worldwide (Kemp 1995, Poonswad et al.2013).

From this number, four species have lived in southern Tenasserim Western Forest Complex Corridor (WCS-TP 2009a). These include the Oriental-pied (*Anthracoceros albirostris* Shaw & Nodder, 1807), Tickell's Brown (*Ptilolaemus tickelli* Blyth, 1855), Wreathed (*Rhyticeros undulatus* Shaw, 1811), and Great (*Buceros bicornis* Linnaeus, 1758) Hornbills.

Asian Hornbills are diurnal, arboreal, and forest dwellers (Poonswad et al. 2013). They usually inhabit moist and dry evergreen; mixed deciduous; and degraded forests and use the mid-canopy and canopy levels of these forests (Kemp 1995). The distribution of these Asian hornbills ranges of from the Himalayas and southern India through China, the Philippines in the north, and Myanmar, Thailand, Laos PDR, Cambodia, Vietnam, to Malaysia and Indonesia south-east Asia (Kemp 1995, Poonswad et al. 2013).

Most of the Asian hornbills are considered outstanding landscape species; species that use large areas, play significant role in ecosystems, and have social-cultural values for the local communities. These species also are vulnerable to human activity (Sanderson et al. 2002).

2.1) Breeding Ecology of Hornbills

Hornbills are monogamous, seasonal breeders. They have a peculiar breeding behavior that has become a ritual story of ethnic groups living in the same landscape with

them (Thongmak and Hulse 1993). Female Asian hornbills imprison themselves inside the nest cavity, usually for three to four months to lay eggs and raise chicks (Kemp 1995, Poonswad et al. 2013). They depend on their male partner to supply them, and their chicks, with food for this entire period. They are secondary hole-nesters, meaning that they cannot excavate their own nest cavity but, rather, rely on using cavities that have been excavated by other animals or that form in other ways, such as when a large limb falls off the tree (Kemp 1995, Kinnaird and O' Brien 2007, Poonswad et al 2013).

The species of trees in which hornbills nest vary based on availability of nest cavities in geographical ranges. In Thailand, hornbills usually nest in the trees of the genera *Dipterocarpus* and *Eugenia* (Poonswad 1995) while hornbills in northeast India tend to nest in *Tetrameles nudiflora* (Datta and Rawat 2004). The Oriental-pied Hornbills have been known to nest in a range of atypical cavities including those in dead trees, a household jar, and an empty Stupa (Poonswad et al. 2013).

The female hornbills use mud, feces, wood debris, and fruit pulp as materials for nest sealing (James and Kannan 2007, Poonswad et al. 2013,) and retain only a narrow open slit for the male hornbills to transfer food to them. Meanwhile, the male hornbills play a crucial role in searching for food and feeding the female and chick(s). The female molts during the incubation period and she stays inside the nest cavity until the chick(s) is/are ready for emergence. However, in some species such as the Great Hornbill, the female emerges a month before the chick(s) emerge to help the male feed chicks (Poonswad et al. 2013). Usually, hornbills are territorial in breeding season (Kinnaird and O' Brien 2007, Poonswad et al. 2013) but larger-sized hornbills become non-territorial in the non-breeding season (Kinnaird and O' Brien 2007).

The breeding season of hornbills varies based on geographical ranges. In Thailand, breeding season of hornbills generally starts in dry season around January and February and ends at the end of dry season or beginning of wet season around May and June (Kinnaird and O' Brien 2007 and Poonswad et al. 2013).

2.2) Feeding Ecology of Hornbills

Hornbills are primarily frugivores of tropical forests where they occupy the top of the trophic level (Kemp 1995, Poonswad et al 2013)., In theory, they depend highly on fruits and figs and feed on more than 748 plant species in 252 genera of 79 families (Kitamura 2011, Poonswad et al. 2013). In Thailand, they feed primarily on fruits in the Annonaceae, Lauraceae, Miliaceae, Moraceae, and Myristicaceae families (Poonswad et al. 2013).

In fact, hornbills are actually omnivorous and have been observed feeding on more than 70 small animals in Thailand (Poonswad et al. 2013). Consequently, they also play a role in controlling populations of small animals (Poonswad et al. 2013). Asian hornbills tend to defend their territory, and this is particularly pronounced in the smaller-sized hornbills (Kinnaird and O' Brien 2007). The Hornbill species that specialize in fruits such as the Wreathed Hornbill tend to be less territorial (Kinnaird and O' Brien 2007).

2.3) Ecological Roles of Hornbills

Hornbills are the keystone species of many tropical forests in Asia and Africa (Kemp 1995, Kinnaird and O'Brien 2007, Poonswad et al. 2013) because of their disproportionate role in long-distance dispersal of many dominant plants that have large-sized seeds (Kemp 1995, Corlett 2002, Kinnaird and O'Brien. 2007). They are

particularly important dispersers of seeds that are greater than 15 mm in size (Kitamura et al. 2004), a major component of the tropical forest community that cannot be dispersed by small frugivores (Hardwick et al. 2004). As a result, hornbills are responsible for the establishment of plant populations across tropical habitats (Poonswad 1993a, Kemp 1995, Kinnaird and O'Brien 2007, McConkey et al 2012) and are one element in maintaining high-quality tropical forest ecosystems (Kemp 1995, Kinnaird et al. 1998, Kinnaird and O'Brien 2007).

In short, hornbills perform two uniquely crucial functions: 1) they provide an ecosystem service by maintaining a healthy ecosystem and restoring degraded areas by carrying genetic materials from one habitat to another that is suitable for forest regeneration (Sekercioglu 2006) and 2) they serve as useful indicators of the quality of forest conditions and the extent of human-induced disturbances (Poonswad 1993a, Kinnaird and O'Brien 2007).

Finally, hornbills are conspicuous and spectacular inhabitants of the forest, and can serve as flagship species for the conservation of their environments (Kemp 1993, Kemp 1995). For these reasons, hornbills have been designated as a landscape species for conservation in the Tenasserim Western Forest Complex Corridor (TWFC) and due to their low abundance (WCS-TP 2009a).

2.4) Threats to Hornbills

Worldwide, hornbill populations are vulnerable to extinction because of great reductions in their suitable habitat from human activities. These include habitat loss, fragmentation, forest clearance, and degradation (Poonswad 1993, Sokhavicheboth 1998, Kinnaird and O'Brien 2007, Poonswad et al 2013). This vulnerability is

compounded in highly fragmented and small forest patches because they are also typically associated with other human-induced threats to natural systems, including logging, forest burning, and the hunting of other key vertebrate seed dispersers within these forest remnants (Tabarelli et al. 2004),

Another major factor that affects the viability of hornbill populations is the low quality and lack of natural cavities with suitable characteristics for nest building (Kemp 1993, Poonswad 1995). For this reason, hornbills tend to avoid highly disturbed areas such as burned forests, small forest patches, logged habitats, and areas with low numbers of fruiting trees (Pattanavibool and Dearden 1999, Anggraini et al. 2000, Raman and Mudappa 2003).

Yet another major factor that affects the viability of hornbill populations is the splendid characteristics of hornbills. Their large beaks are ornamented with casques, which are made into souvenirs (Kinnaird and O' Brien 2007). Their large-body size makes them a target for commercial hunting for live birds (Kemp 1995, Stone 2007, Gale and Thongaree 2006, Poonswad et al. 2012, Poonswad et al 2013), subsistence hunting for food (Poonswad 1993a, Kemp 1995), and international trade (Trail 2007).

Habitat fragmentation and removal can alter hornbill population viability by decreasing habitat availability and increasing the isolation of each remaining habitat patch (Joly et al. 2004). This reduces population size and creates barriers to immigration from other populations (Linderman et al. 2005, Olsen et al. 2007). Finally, hornbills may become locally extinct (Corlett 2002, Kinnaird and O'Brien 2007). Consequently, almost all hornbills in Thailand and Southeast Asia are designated as vulnerable or endangered (ONEP 2007, IUCN 2014).

3) Identification and Ecology of the Four Sympatric Hornbills

In this study, I classified the Oriental-pied and Tickell's Brown Hornbills as smaller-sized hornbills because their body size is smaller than 100 cm. Meanwhile, the Great and Wreathed Hornbills are considered having the larger body size than 100 cm. The identification of these four sympatric hornbill species is described based on Kemp (1995) and Poonswad et al. (2013).

3.1) Oriental-pied Hornbill spreads from Himalayan foothill to Assam India through Nepal, Bhutan, Myanmar, south Guangxi China, Thailand, and northeastern Malaysia. It is the smallest Asian hornbill with a body size of 70 to 89 cm. It has black and white plumage similar to other *Anthracoceros* but its outer tail feather is black with a board white tip of undertail feathers. The male Oriental-pied Hornbill is distinguished from the female by larger body size, larger casque, and a black pattern on the tip of its casque (Lekagul and Round 1991, Poonswad 1993c, Poonswad et al 2013).

The Oriental-pied Hornbill is a generalist, able to feed on both fruits (33-35% figs and 45-47% non-figs: Kemp 1995, Poonswad et al. 2013) and animals. It is also able to inhabit the forest edge, cultivated areas, forests spanning the range of succession from degraded to secondary growth, mixed deciduous forests, and evergreen forests ranging from inland plain to mountainous areas up to 700 m.a.s.l. In Thailand, its breeding season starts in late February and runs through June. The nesting period takes approximately 70-107 days. The immature Oriental-pied flocks in the non-breeding season.

Currently, its national and international conservation status in Thailand is of least concern (ONEP 2007, IUCN 2014). It is listed in Appendix II in Convention on

International Trade in Endangered Species of Wild Fauna and Flora (CITES). The CITES Appendix II states that the species is not currently threatened to extinction but may become so unless strict regulations are imposed to avoid overutilization by hunters and to limit trade (CITES 2014).

3.2) Tickell's Brown Hornbill is a medium-sized hornbill with size of 60-75 cm (Kemp 1995, Poonswad 1998d, Kinnaird and O' Brien 2007, Poonswad et al 2013). It is distributed along the Tenasserim between southern Myanmar and south-west Thailand. It usually dwells in evergreen and mixed deciduous forests from the plain to 1,500 m. It is slightly sex dimorphic. The female has brown plumage and white tips on the flight feathers and tail, a patch of blue naked skin around eyes, a darker cheek and darker black bill and casque. The male has a pale yellow bill and lower casque ridge (Kemp 1995, Poonswad 1993c, Poonswad et al 2013). The Tickell's Brown Hornbill starts its breeding season in February and chicks fledge from May to June and generally take 98 ± 22 days. It shows co-operative breeding behaviors with one to five helpers and remains with this small group of five to seven birds throughout the year (Poonswad et al. 2013).

The Tickell's Brown Hornbill is nationally vulnerable (ONEP 2007), globally near threatened (IUCN 2014), and listed in CITES Appendix II.

3.3) Wreathed Hornbill is distributed from southern Phutan, Assam (India), to Myanmar, Thailand, Vietnam, Malaysia, and Indonesia. It usually occurs in evergreen forest and mixed deciduous forest from the plain to 1,800 m.a.s.l.).

The Wreathed Hornbill is a large hornbill with an average body size of 114 cm. It has a white bill ivory and a low and wreathed casque with a number of ridges that indicate years of growth and can be used as a surrogate of age. The male and both sexes

of the immature Wreathed Hornbills have yellow pouches but females have blue pouches. The mature Wreathed Hornbill has black bar on both sides of the pouch but the immature has a very pale bar on both sides (Lekagul and Round 1991, Poonswad 1993d, Poonswad et al 2013).

The breeding season of the Wreathed Hornbill varies between geographical regions. Its breeding season in Sumatra may start in January and last until November but in India starts in March and last until August (Kinnaird and O' Brien 2007). In Thailand, its breeding season may start anytime from January and last until June. The bird generally flocks in a very large group in the non-breeding season and moves far from nest sites (Poonswad et al 1986). It is likely to reach maturity at 4-5 years old.

The Wreathed Hornbill is principally a frugivore relying on both fig and non-fig species for food depending upon availability in an area and may supplement the diet with less than 5% of animal-based food, which is less supplementation than the other three hornbill species (Poonswad et al. 2013). Currently, its conservation status in Thailand is vulnerable (ONEP 2007) but its global conservation status is of least concern (IUCN 2014).

3.4) Great Hornbill occurs in south-west India, south Himalayas, south China, to Myanmar, Thailand, Malaysia, and Sumatra. It occupies primary in evergreen and dense deciduous forests from 600 – 1000 m.a.s.l. The Great Hornbill starts its breeding season in January or February and it ends between June and August. The entire nesting cycle ranges from 102-144 days (Kinnaird and O' Brien 2007, Poonswad et al. 2013).

The Great Hornbill is the largest hornbill in Southeast Asia with a body size up to 150 cm. This species has black flight feather with a white trailing edge and a white stripe

on the wing that is intentionally stained yellow by the hornbill. It also has a black band across the white tail. The Great Hornbill is sexually dimorphic. The male can be distinguished from female by having larger body size, black-rimmed red eyes, and a flat casque that is forked at the front with a black edge. The female has white eyes with red rims and smaller casque without a black stripe (Poonswad et al. 2013).

The breeding season of the Great Hornbill runs from January to August (Kinnaird and O'Brien 2007, Poonswad et al. 2013). The nest period is between 102 and 144 days.

The Great Hornbill shares similar fruit food with the Wreathed Hornbill. In the breeding season, it relies on figs (57%) more than non-figs (29%), and 14% of its diet is derived from animal food (Poonswad et al 2013). Currently, its conservation status in Thailand is vulnerable (ONEP 2007) but its global conservation status is least concern (IUCN 2014).

4) Research Objectives and Summary

To address the critical consequences of forest loss, fragmentation, and degradation via natural restoration, and to maintain the hornbill population in the southern Tenasserim landscape, understanding the natural history and ecology of hornbills as key seed dispersers is most urgent. I initiated my research to document the breeding, foraging patterns, and occupancy of hornbills that live in the southern Tenasserim Corridor in Thailand. In order to do this, I established the following research objectives.

1. Describe nest site characteristics of four sympatric hornbills in the southern Tenasserim Corridor of Thailand
2. Study movement patterns and foraging range of immature Oriental-pied, Wreathed, and Great Hornbills
3. Estimate accuracy of radio telemetry used for hornbill study
4. Understand resource selection by immature Oriental-pied and Wreathed Hornbills
5. Estimate occupancy of the four sympatric hornbills

This dissertation is composed of six chapters. Chapters 2, 3, 5, and 6 are about nest site ecology of hornbills, foraging ranges, resource selection, and site occupancy by hornbills. The fourth chapter is associated with the accuracy of radio telemetry that I used to track hornbills in the rugged terrain of Maenam Pachee Wildlife Sanctuary.

It has been acknowledged that protection of nest sites and maintaining their characteristics are essential for conserving a viable population of hornbills over the long term (Poonswad 1995, Marsden and Jones 1997, Mudappa and Kannan 1997, Datta and Rawat 2004, James and Kannan 2009). In chapter 2, I investigated the nest site characteristics of four sympatric hornbills in Maenam Pachee Wildlife Sanctuary: the Great, Wreathed, Oriental Pied, and Tickell's Brown Hornbills. My primary goal was to examine factors that affect the use of nest site of the four sympatric hornbill species in the southern Tenasserim. I hypothesized that the physical characteristics of nest locations of four hornbill species do not differ. In addition, I also examined density of trees, potential nest trees, and species known to be used as food by hornbills between forest areas that

hornbills use and do not use as breeding sites. My hypothesis was that nest sites do not differ between where hornbill nests are found and not found.

I found that 25 out of 42 nests of all sympatric hornbills were active throughout the study period. Although other hornbill studies found Dipterocarpaceae and Myrtaceae to be the principle nest tree species in Thailand (Chimchome et al. 1998, Thailand Hornbill Project 2003, Thiensongrusamee et al. 2005), I found hornbills in MPWS used the nests in the tree trunks of 11 species of living trees and 76% were found in only three species: *Tetrameles nudiflora* in Datisceae family, *Manikara* sp. in Sapotaceae family, and *Terminalia bellerica* in Combretaceae family. I found the four sympatric hornbills selected nest locations at different slopes, tree sizes, distances to streams, and cavity formations. In general, smaller-sized hornbills selected nests closer to streams, at lower altitudes and less steep areas, and used smaller size nests than the bigger hornbills.

Not only do hornbills require breeding sites, but they also require good forests with fruit available year-round to encourage hornbills to stay at the site and disperse seeds to neighboring forests. Overall, the quality of forest inside the protected area (MPWS), in terms of providing food and breeding sites for hornbills, is comparable to other high quality habitat for hornbills in Thailand such as Huai Kha Khaeng Wildlife Sanctuary and Budo-Sankai National Park. In contrast, hornbills were found in forest areas outside the protected area (NHP) - where the density of known fruit trees are low and the hornbills do not have breeding sites - as temporary feeding sites in the non-breeding season.

In chapter 3, I focus on the movement of six immature hornbills and one mature female Oriental-pied Hornbill in the southern Tenasserim landscape. My primary goal

was to determine the distance moved from natal nests of all individuals, examine overall foraging sizes, quantify the range of overlap and interaction of individual hornbills, and to determine if breeding and non-breeding seasons and wet and dry seasons pose any effects on the size and overlap of foraging ranges. I also determined the differences between foraging ranges and range overlap of the smaller-sized hornbills (Oriental-pied and Tickell's Brown Hornbills) and the larger-sized hornbills (Great and Wreathed Hornbills), and between breeding and non-breeding, and wet and dry seasons.

I assumed that distance moved from the natal nest of each hornbill did not differ. Moreover, I hypothesized that the ranges of the all hornbills between breeding and non-breeding, and wet and dry seasons were not different but the foraging size of the smaller and larger-sized hornbills did differ. In addition, I theorized that different hornbill species overall were neither attracted to nor avoided each other.

Even though other research has found that Oriental-pied and Wreathed Hornbills are capable of using degraded forest (Tsuji et al. 1987), my study did not detect either species in degraded forest and they did not use the forest edges near human-dominated areas. It is clear that the immature Wreathed Hornbill, a larger-sized hornbill, used larger foraging ranges and moved farther from natal nests than the smaller Oriental-pied Hornbill chicks. This result was similar to other research (Poonswad and Tsuji 1994). However, I did not detect size differences of foraging ranges between breeding and non-breeding seasons or between wet and dry seasons. All individual hornbills tended to have a moderate interspecific overlap. The Wreathed and Oriental-pied Hornbills captured in the same year had moderate intraspecific overlaps but the one Oriental-pied Hornbill captured in the first year tended to avoid the range of the other Oriental-pied birds

captured in the second year. These results confirm MPWS as an existing breeding and foraging site for hornbills.

In chapter 4, the research goal was not directly about hornbills; rather it was related to the accuracy of VHF radio telemetry, which may have a significant impact on the accuracy of the research findings in chapter 5 on resource selection by hornbills. I hypothesized that data from VHF radio telemetry had high accuracy and landscape variables did not influence the accuracy of locations produced with this technique.

Due to landscape challenges, percent of successfully locating the transmitters was moderate (58.75%). In most cases, failure in successfully locating the transmitter was due to loss of signal and uncrossed locations. The findings showed an association between angular errors and linear distance from tracking stations to the true location of the transmitters. The crucial landscape variables that introduced deviation to linear distances were elevation, location on lower hillsides, slope, and distance from both tracking stations.

As a method to test errors of radio telemetry on movement studies of hornbills, this is not time-consuming or effort-intensive, but needs to be tested broadly in a greater variety of land characteristics. Thus, I recommended that study on wildlife movement should take into account the repercussions of location errors that may mislead resource selection models (Withey et al. 2001, Montgomery et al. 2010, Frair et al. 2010) and researchers should be aware of landscape characteristics when collecting field data.

In the fifth chapter, I narrowed my research question to factors that may influence habitat use and habitat selection by the Oriental-pied and Wreathed chicks in the southern Tenasserim landscape. I hypothesized that the landscape variables that the Oriental-pied

and Wreathed Hornbill chicks used and did not use were not different and the birds did not prefer one habitat to another in the southern Tenasserim. The assumption is based on an absence of limitations for hornbills' use of multifunctional landscapes in the southern TWFC. As I was concerned about the accuracy of radio telemetry and the potential for location errors, I conducted the resource selection model based on four correction methods and used two statistical approaches, logistic regression and generalized linear mixed model to compare results. Consequently, this is a sensitivity analysis on results from the best-fit resource selection model.

The results from the four correction methods showed a consistency of landscape variables that influence landscape use and selection by the two immature hornbill species. Evergreen forest played a significant role for both the immature Oriental-pied and Wreathed chicks. While the Oriental-pied Hornbill is known to adapt well to degraded forests (Tsuji et al. 1987, Kemp 1995) and the Wreathed Hornbill, the nomadic species, can occupy a large range and use multiple habitats including degraded forest (Kemp 1995), both of these species are less likely to visit degraded forest. The Oriental-pied Hornbill chicks also preferred habitat at lower elevations and with steeper terrain in large forest patches.

My final chapter focuses on the site occupancy and probability of detection of the four sympatric hornbills in the southern Tenasserim landscape in relation to landscape variables, available resources, and habitat quality. I assumed no limitations for hornbills' use of multifunctional landscapes in the southern Tenasserim Western Forest Complex Corridor. I hypothesized that the four sympatric hornbills responded to landscape characteristics, resource availability, and habitat quality equally.

Generally, all hornbill species responded negatively to human disturbance. We also identified the positive influences of numbers of potential fruiting trees that were not fig trees (hereafter known as non-fig trees), and numbers of potential nest trees on occupancy and detection probabilities of the hornbills.

Moreover, my results confirmed that while the larger-sized hornbills (the Great and Wreathed Hornbills) tended to be less affected by fragmentation than the smaller ones (the Tickell's Brown and Oriental-pied Hornbills) because they are able to fly over the canopy level and search for foods scattered in fragmented forest patches, the presence of mature evergreen forest with dense canopy cover is important for maintaining their population in a working landscape. In contrast, the smaller-sized hornbills, capable of moving in the mid-layer of the forest, struggled to move across large fragmented landscapes. It appears that they can persist in human-dominated landscapes if the habitats have denser canopy cover with less disturbance by humans while maintaining available fruits both fig and non-fig species.

While concerns about conservation outside protected area in the Tenasserim landscape have been urgently expressed, there is an apparent lack of policies to protect this forest that has been exhausted for decades. In addition, rapid development for tourism in the region, and limited funds for conservation and management in underrepresented areas make it difficult to restore biodiversity in the southern Tenasserim.

This dissertation, which considers the interaction between hornbills and landscape conditions, contributes to knowledge on the current state of the hornbill population and the factors that influence it, especially human impacts that may interrupt ecological

efforts to maintain and restore forest in the southern Tenasserim. Meanwhile, it also provides an example of a method important for reducing errors and bias in research so that conservationists can gather information that is more accurate in order to devise effective conservation and management plans.

**CHAPTER 2 - CHARACTERISTICS OF THE NEST AND NEST
ENVIRONMENT OF FOUR SYMPATRIC HORNBILL IN THE SOUTHERN
TENASSERIM WESTERN FOREST COMPLEX CORRIDOR IN THAILAND**

Summary

This study compares the nest site characteristics and environment of four sympatric hornbills in Maenam Pachee Wildlife Sanctuary (MPWS): the Great, Wreathed, Oriental Pied, and Tickell's Brown Hornbills. Forty-two nests of all sympatric hornbills were recorded but only 25 were active throughout the study period. All hornbills nested in the tree trunks of 11 species of living trees located in the interior forest, but 76% were found in only three species: *Tetrameles nudiflora* (29%), *Manikara littoralis* (29%), and *Terminalia bellerica* (19%). The availability of both potential nest trees and known fruit trees that provide food for hornbills in the MPWS was in sufficient supply for hornbills to use as breeding and feeding sites and was comparable to other good hornbill habitats in Thailand. However, the adjacent unprotected forest area could serve only as a temporary feeding site because of its very low density of known fruit trees. The statistically significant influences on selection of different nest sites by the four hornbills were altitude, slope, tree diameter at breast height (DBH), distance to stream, and cavity formation. The Oriental-pied Hornbill used nests that were excavated by woodpeckers at lower altitudes than other hornbills. It also nested in flatter areas than the Wreathed and closer to streams than the Wreathed and Great Hornbills. The Wreathed Hornbill used larger nest trees at higher slopes, and farther from streams compared to the Tickell's Brown. It also nested farther from streams than the Great Hornbill. The

Tickell's Brown also nested in smaller trees than the Oriental-pied and Great Hornbills. These specific nest site attributes may indicate less nest site competition between hornbill species in MPWS. However, human disturbance appears to cause the low density of active nests in the MPWS.

Introduction

Most Asian hornbills are forest dwellers requiring large suitable mature trees for nesting. They are secondary cavity nest dwellers with high nest site fidelity (Poonswad et al. 1987, Poonswad and Tsuji 1995, Poonswad et al. 2013). Their inability to excavate their own nests makes the availability of suitable natural cavities critical to their ability to reproduce and becomes a limiting factor on their population dynamics (Poonswad 1995, Chuailua et al. 1998, Poonswad et al. 2013).

Most research on nesting of Asian hornbills demonstrates site-specific nest site characteristics and nesting environment based on availability of tree cavities at a site (e.g. Poonswad et al. 1987, Mudappa and Kanna 1997, Klop 2000, Datta and Rawat 2004). Consequently, the management of nest sites and their characteristics is essential to conserve viable hornbill population over the long term effectively (Poonswad 1995 Marsden and Jones 1997, Mudappa and Kannan 1997, Datta and Rawat 2004, James and Kannan 2009).

The southern Tenasserim Western Forest Complex Corridor (TWFC) is a new hornbill study site in Thailand. It is home to four sympatric hornbill species (Bucerotidae): the Great Hornbill (*Buceros bicornis*), Tickell's Brown Hornbill (*Anorrhinus tickelli*); Wreathed Hornbill (*Aceros undulatus*); and Oriental-pied Hornbill

(*Anthracoceros albirostris*) (WCS-TP 2009a). Lack of information on the nesting ecology of hornbills in this landscape results in deficient good suggestions and practices to facilitate hornbills to disperse large-sized seeds of tropical plants.

This study investigates 1) the characteristics of the nest sites of the four sympatric hornbills in the southern Tenasserim Western Forest Complex Corridor (TWFC), 2) availability of nest trees in the landscape, and 3) availability of known fruit trees used for feeding by hornbills in the landscape. This is essential information that can be quantified and used for managing hornbills for conservation in TWFC.

Methods

1) Selection of Field Site

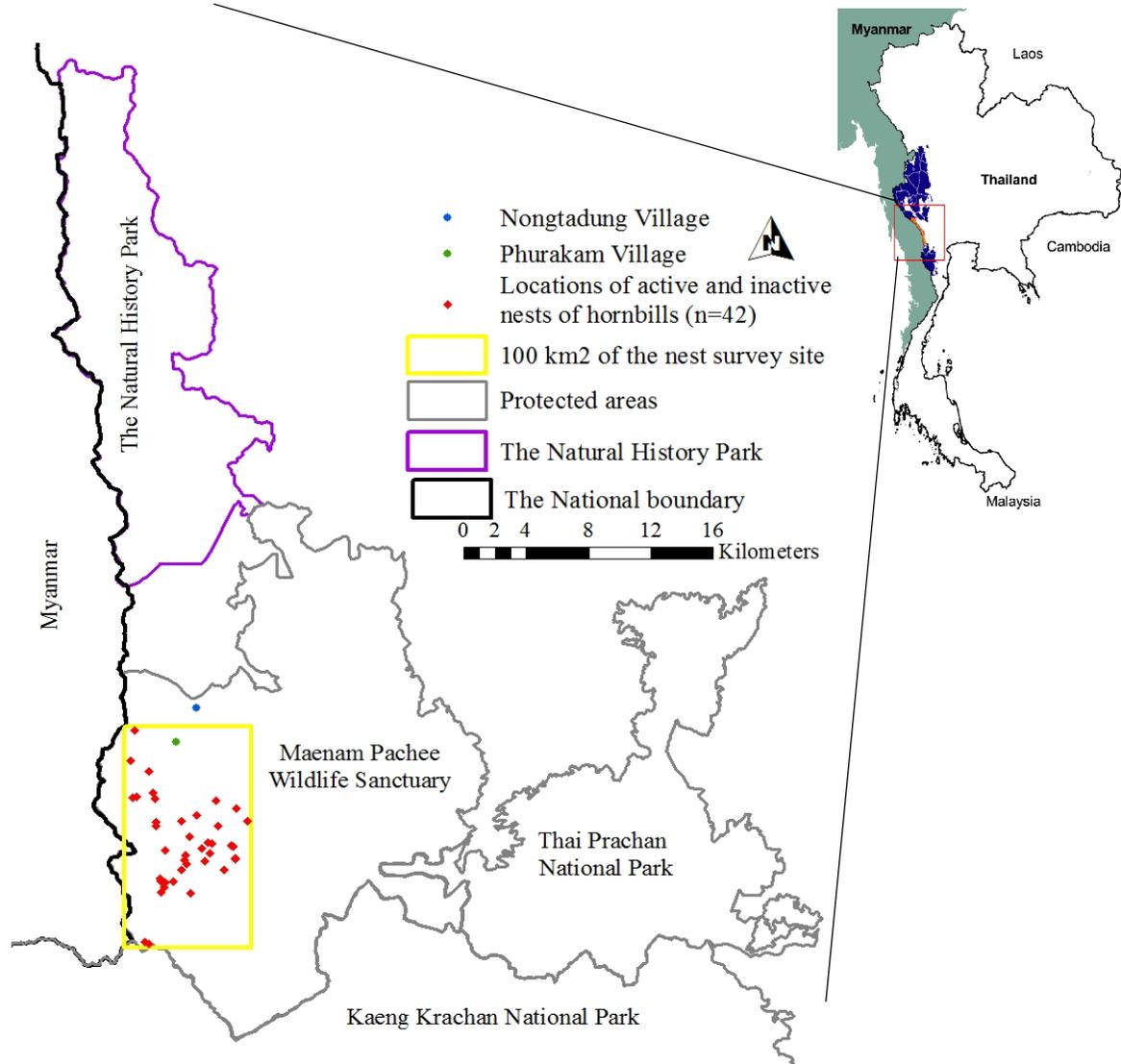
Because of hornbills' secretive behaviors – they are canopy dwellers and the female imprisons herself during the breeding season inside a tree cavity where she lays eggs and raises chicks – successful scouting of hornbill nest sites required the assistance of the villagers.

I offered monetary reward for local people and forest rangers who were able to clue nest sites of all hornbill species in the forest areas throughout the southern Tenasserim Western Forest Complex Corridor (TWFC: see Figure 2.1). This included both inside the protected area (Maenam Pachee Wildlife Sanctuary: MPWS) and outside the protected area (the Natural History Park initiated by Royal Princess Sirindhorn: NHP).

Within two years of the study (February 2010 to May 2012), even though I cooperated with local people and forest rangers to search for nest sites of hornbills

throughout the southern TWFC (see more description of this study in chapter 1), only local people from Phurakam village provided clear evidence of both active and inactive nest sites of hornbills within MPWS. As a result, I limited my study and intensive nest searching in the area of 100 km² near Phurakam village (see Figure 2.1).

Figure 2.1 Location of nest sites of four hornbill species in the sampled area (100 km²) found from February 2010 to May 2012 in the southern Tenasserim Western Forest Complex Corridor



This 100 km² (13°12'-19' N and 99° 11'-15' E) is located in the western portion of the sanctuary in the upper part of Kaeng Krachan Forest Complex, an Asian Natural Heritage Site (Association of Southeast Asian Nations 2003) and is adjacent to vast contiguous forests in Myanmar (WCS-TP 2009a). It ranged from 268- 980 m.a.s.l. It is composed of 90.44% of dry evergreen forests interspersed with small patches of 7.61% of mixed deciduous forests, 1.26 % of degraded forest, and 0.71% of agriculture (WCS-TP 2009b).

2) Scouting Hornbill Nests and Nest Status

Local people usually detected nest locations of hornbills when they explored non-timber forest products (NTFPs) that mostly occurred during the breeding season of hornbills, roughly from December through June depending on the species (Poonswad 1993a, Kinnaird and O'Brien 2002).

My team conducted the initial nest survey between February and May 2010. Both active and inactive nests were marked in the Global Positioning System (GPS) so they could be scouted in the following breeding seasons: December 2010 to May 2011 and December 2011 to May 2012. By training with researchers from the Thailand Hornbill Project, the two field crews were able to use suggestions from Poonswad (1993) to search for nest sites of the hornbills and to repair and maintain the suitable conditions of the hornbill nests.

I considered nests active if the male hornbills came back to feed females and chicks. I additionally checked deposits of fresh dropping feces and/or an accumulation of nest debris and seed regurgitation (Poonswad 1995) such as *Polyalthia* spp., *Canarium* spp., *Horsefieldia* sp., *Knema* sp. , *Algaia* sp. (Poonswad 1993a), to confirm that the nests

were active. I explained nest status, nest density per 100 km², breeding onset, and nest competition between con- and hetero-specific hornbills based on field observation.

3) Nest Tree Species and Characteristics of Nest Locations

For all nest locations, I identified trees to genus and species, if possible. I measured the tree diameter at breast height (DBH) using a metric diameter tape. The total height and cavity height of the nest trees were measured using a rangefinder and clinometers. I classified positions of the nest holes into three forest strata according to Poonswad (1995): the top or emergent layer (>25m), the middle layer (>15-25m), and the lowest layer (4-15m). I recorded the altitude and slope at the nest-tree locations in a hand-held GPS and a clinometer. In addition, the team recorded the orientation of the nest holes using a hand-held compass.

I used the Proximity Analysis Tool in ArcMap 10.1 (Environmental System Research Institute, Inc., Redlands, CA) to estimate the distance from the nest locations to the nearest stream and nest spacing between the intraspecific and heterospecific hornbill species. I calculated the distance to human settlements only from active nests to explain the potential for human disturbance. I classified the cavity formation into two categories: nests excavated by woodpeckers (round shape: Poonswad 2001) and nests excavated by other causes such as bears or broken branches. I also observed nest success and defined it as when at least one chick fledged at the end of the breeding season without clues of nest failure due to predation or nest abandonment (Mudappa and Kannan 1997).

I used these data to understand characteristics of nest locations and to estimate availabilities of potential nest trees and known fruit species fed upon by hornbills in the landscape. I compared all nest characteristics among the four hornbill species using a

non-parametric test, Kruskal-Wallis Test and each pair of hornbills using Mann-Whitney U Test in R 2.15.3. I applied a Bonferroni correction for multiple comparisons (Moore, and McCabe 2006). I included repeated data of two nest trees that were alternatively used by the Great and Wreathed in a subsequent year for analysis (Poonswad 1995).

4) Quality of Forest Habitats in Breeding and Non-breeding Sites for Hornbills

I randomly set up the equal numbers of 36 temporary plots in the forest areas with sizes of $20 \times 50 \text{m}^2$ (1000m^2) covering 0.02% of the forest area in the southern TWFC in two habitat conditions where nest locations of hornbills were found (MPWS) and not found (NHP). I counted, measured, and identified the genus and species (if identifiable) of all reproductive-sized trees (i.e. trees capable of producing fruit) with a $\text{DBH} \geq 10 \text{cm}$ (Kalayakool 2010). I calculated the density, of reproductive-sized trees and compared them between MPWS and NHP using a matched-pairs t-test.

4.1) Potential Nest Trees for Hornbills

Based on information from forest inventory, I considered only the trees with a $\text{DBH} \geq 40 \text{cm}$ as potential nest trees because this is the minimum size used by nesting hornbills (Poonswad et al 1987). I calculated the density of potential nest trees and compared them between MPWS and NHP using matched-pairs t test.

4.2) Known Fruit Tree Species Fed Upon by Hornbills

In addition to reproductive trees and potential nest trees, I listed all known fruit tree species used by hornbills for feeding (Chimchome et al. 1998, Poonswad et al. 1998a, Kitamura et al. 2002, Savini 2007, Kalayakool 2010, Kitamura et al. 2011, Chaisuriyanan et al. 2011) with $\text{DBH} \geq 10 \text{cm}$. I calculated the density of known fruit tree

species fed upon by hornbills and compared it between MPWS and NHP using a match-pairs t-test.

Results

Based on 25 active of 42 nests of hornbills found in the 100 km² area of MPWS, I am able to quantify the characteristics of hornbill nest sites and the availability of potential nest trees and known fruit tree species fed upon by hornbills.

1) Nest Discovery and their Status

All 42 nest cavities were in tree trunks of living trees. Most nest trees were located in dry evergreen forest except for two inactive nest trees that local people said were previously occupied by Wreathed Hornbills. These were in mixed deciduous forest. The forest type was based on the land-use and forest type classification produced by WCS (2009b).

In 2011, hornbills started entering their nests by mid-February and emerged from their nests by mid June 2011. In 2012, hornbills gradually entered their nests by mid-January and emerged by mid May 2012. Although the exact dates that the hornbills entered their nests were not determined in both years, I found the Tickell's Brown Hornbill emerged from the nests the earliest followed by the Great, Oriental-pied, and Wreathed Hornbills, respectively.

I found 25 active nests between 2010 and 2012 within the area of 100 km² (Table 2.1). This resulted in an overall nest density of 0.25 nests/km² and the densities of the active nests of the Great, Wreathed, Oriental-pied, and Tickell's Brown Hornbills were 0.05, 0.08, 0.05, and 0.07 nest/km², respectively. Because all but three active nests used

by two Wreathed Hornbills and one Great Hornbill were clumped together in the area of 50 km², the total density of active nests was almost double at 0.4 nest/km² in this localized area. The nest densities of the Great, Wreathed, Oriental-pied, and Tickell's Brown Hornbills in this localized area were 0.08, 0.12, 0.10, and 0.14 nests per km², respectively.

Nest trees were reused by the same hornbill species in the following year (n=16). I did see evidence of one instance of nest competition. In 2012, a nest used by the Wreathed Hornbill in 2011 was used by the Great Hornbill. Although local people anecdotally reported nest competition between Tickell's Brown and Oriental-pied Hornbills, I did not see any evidence of this.

I did observe four possible reasons for a nest becoming inactive, disturbance by humans, nest competition, unsuitable conditions, and unknown. One Wreathed Hornbill abandoned the nest because the birds were hunted for food by a villager in Phurakam village and the nest remained inactive throughout the study period. Another Wreathed Hornbill nest was inactive with unknown cause. Two active Tickell's Brown Hornbill nests became inactive because of competition by ants and unidentified causes. I also found four nests with unsuitable conditions since they had large entrances with sunken floors that were almost a meter below the entrance, which makes them unusable for breeding (Kemp 1995, Poonswad 1998a).

Table 2.1. Summary of the results of nest scouting from 2010 to 2012

Hornbill Species	2010		2011		2012		Total nest		Total						
	Active		Inactive		Active		Inactive			Active*	Inactive**				
	O	N	O	N	O	N	O	N							
Great	-	-	-	3	-	2	2	2	1	2	6	2	5	7	11
Wreathed	-	1	-	3	1	4	4	2	3	1	8	3	8	6	15
Oriental- pied	-	2	-	1	2	2	1	-	4	1	1	-	5	1	6
Tickell's Brown	-	-	-	-	-	4	-	1	1	3	5	1	7	3	10
TOTAL	-	3	-	7	3	12	7	5	9	7	20	6	25	17	42

Active = active nest, Inactive = inactive nest, O = the nests found in the previous year, N = the new nests found during the year, * = all nests found to be active at least once during 2010 -2012. ** = all nests were used by hornbills in other years reported by local people but were not active during the study period.

I explored two nest failures during 2011. One nest of the Wreathed Hornbill failed due to unknown causes. I observed an opened nest entrance with the presence of relatively fresh feces, fallen feathers and seeds of known fruit eaten by hornbills such as *Polyalthia* spp., *Horsefieldia* sp., *Knema* sp., *Algaia* sp. under the nest, but no female hornbill remained inside the nest and no male hornbill returned to feed his mate and chick. A Tickell's Brown Hornbill nest failed as evidenced by an open entrance and fallen feathers in front of the empty nest. There was no nest failure in 2012. From these observations, I infer that there was a high percentage of nesting success both in 2011 (88.89% n=18) and 2012 (100% n=20).

2) Nest Tree Species

Of 42 known nest trees examined, the three most common species used were *Tetrameles nudiflora* R.Br. and *Manilkara* sp. (28.57% each) with *Terminalia bellerica* Roxb. (19.05%: Table2.2).

Table2.2 Number and percent of nest trees used by four hornbill species from 2010-2012

Tree Species	Families	GH	WH	OPH	TBH	Total
<i>Ailanthus integrifolia</i> Lam	Simaroubaceae	1	-	-	-	1 (2.38%)
<i>Antiaris toxicaria</i> Lesch	Moraceae	1	2	-	-	3 (7.14%)
<i>Choerospondias axillaris</i> (Roxb.) B.L. Burtt. & Hill	Anacardiaceae	-	-	1	1	2 (4.76%)
<i>Manilkara</i> sp.	Sapotaceae	2	5	2	1	10(23.81%)
<i>Pterospermum cinnamomeum</i> Kurz	Sterculiaceae	-	-	-	2	2 (4.76%)
<i>Terminalia bellerica</i> Roxb.	Combretaceae	1	3	-	4	8 (19.05%)
<i>Tetrameles nudiflora</i> R.Br.	Datisceae	5	5	2	-	12 (28.57%)
<i>Toona ciliate</i> M. Roem	Meliaceae	-	-	-	1	1 (2.38%)
Unknown 1	-	-	-	-	1	1 (2.38%)
Unknown 2	-	-	-	1	-	1 (2.38%)
Unknown 3	-	1	-	-	-	1 (2.38%)
Total		11	15	6	10	42 (100%)

GH = Great hornbill, WH = Wreathed hornbill, OPH = Oriental-pied hornbill and TBH = Tickell's Brown hornbill

3) Characteristics of Nest Locations

The four hornbill species had similar nest characteristics (Table 2.3). Four parameters differed significantly among the species including slope ($H=9.45$, $P=0.024$), tree DBH ($H=9.88$, $P=0.020$), distance to a stream ($H=25.66$, $P<0.001$) and cavity formation ($H=9.07$, $P=0.03$). Specifically, the Wreathed Hornbill used nests on steeper slopes compared to the Oriental-pied Hornbill ($U=9.5$, $n_1=15$, $n_2=6$, $P=0.006$), and nest trees with larger DBH than Tickell's Brown Hornbill ($U=22$, $n_1=15$, $n_2=10$, $P=0.004$).

Different species also tended to use nest sites at different distances to streams. The Wreathed Hornbill nested in trees that were farther from streams compared to the Great ($U=34.5$, $n_1=15$, $n_2=11$, $P=0.004$), the Tickell's Brown ($U=7$, $n_1=15$, $n_2=10$, $P<0.001$), and the Oriental-pied ($U=0$, $n_1=15$, $n_2=6$, $P=0.005$) Hornbills. In addition, Oriental-pied Hornbills nests were located nearer streams compared to Great Hornbill nests ($U=65$, $n_1=10$, $n_2=6$, $P=0.004$).

Moreover, I found 54.76% of the nests were located from >20 to 30 m above ground. More than half (59.5%) of all nest trees were at lower than 500 m.a.s.l. on steep terrain (>25° of slope). The Great (547 ± 118 m.a.s.l.), Wreathed (524 ± 122 m.a.s.l.), and Tickell's Brown (564 ± 106 m.a.s.l.) Hornbills tended to nest at similar altitudes. Meanwhile the Oriental-pied Hornbill used nests at lower altitudes (413 ± 60 m. a.s.l.). None of the nest locations of individual hornbill species was located in significantly different altitudes (see Table 2.3).

All Hornbills nest trees had a diameter at breast height (DBH) larger than 40 cm and 90% ($n=38$) of all nest trees had DBH larger than 80 cm, three of them were

occupied by the Tickell's Brown Hornbill (DBH = 48.7, 52.8, and 54.2 cm) and one nest tree of the Great Hornbill had DBH = 80 cm. The mean DBH of nest trees used by the Great, Wreathed, Oriental-pied, and Tickell's Brown Hornbills were 144 ± 64 , 123 ± 44.64 , 1121 ± 26 , and 82 ± 27 cm, respectively. The larger hornbills tended to require larger trees for nesting.

I found all four sympatric hornbills chose nest trees overlapping in total height with most (76 %, n=32) in high trees from 30 to 45 m. In addition, the preponderance (57 %) of nest cavities was in the mid layer of the forest (15 – 25m), and 24 % and 19 % of the nest cavities were in the upper (>25 m) and lowest layer (10-15 m) respectively.

Although there was no significant difference between species on distance to human settlement from a nest, the mean distance to human settlement of the Wreathed Hornbills was shorter than the other hornbill species. This may imply that Wreathed Hornbill better tolerate human disturbance than the Oriental-pied, Tickell's Brown, and Great Hornbills.

Nest spacing between both intraspecific and heterospecific hornbill nests did not significantly differ among the four hornbill species. However, the mean nest spacing between heterospecific nests was shorter than the intraspecific hornbills.

Table 2.3 Summary of nest tree characteristics of four hornbill species in Maenam Pachee Wildlife Sanctuary

Nest Tree Parameters	GH	WH	OPH	TBH	Kruskal-Wallis Test		Mann-Whitney U Test		
					H	P (df = 3)	Sig. diff. pair	U	P
Mean body mass(g)¹	3007	2540	735	869					
N	11	15	6	10					
Altitude (m a.s.l)					7.49	0.058	WH &OPH	20	0.040
Range	362 – 812	361 – 812	305 – 503	416 – 705			TBH&OPH	7	0.011
Mean	547.0	524.5	413.7	564.1			OPH&GH	60	0.028
S.D.	118.5	122.4	60.6	106.2					
Slope (°)					9.98	0.019	WH&OPH ²	9.5	0.005
Range	5-47	22.5 – 45	0 – 37	0-49			WH &TBH	38	0.028
Mean	28.14	38.07	16.83	20.8					
S.D.	15.12	6.63	14.62	18					
Diameter at breast height: DBH (m.)					9.88	0.020	WH&TBH ²	22	0.004
Range	73.02 – 236	81.8 – 271	84.8 – 164	48.7 - 146.6			TBH&OPH	2.01	0.045
Mean	143.9	123.5	112.0	81.6			TBH&GH	2.51	0.012
S.D.	64.0	44.6	26.0	27.2					
Nest tree height (m)					4.79	0.188			
Range	30 -50	32 – 50	28 – 42	18-53					

Nest Tree Parameters	GH	WH	OPH	TBH	Kruskal-Wallis Test		Mann-Whitney U Test		
					H	P (df = 3)	Sig. diff. pair	U	P
Mean	41	40	34	34					
S.D.	6	5	5	11					
Cavity height (m)					1.67	0.64			
Range	15 – 38	17 – 28	15 – 30	7 – 40					
Mean	23	23	24	16.95					
S.D.	7	3	6	10					
No. of cavities located in each forest layer (%)					1.40	0.705			
Low:10-15 m	1 (2%)	0 (0%)	1 (2%)	6 (14%)					
Mid:>15-25 m	6 (14%)	12 (29%)	2 (5%)	2 (5%)					
Top: >25 m	4 (10%)	3 (7%)	3 (7%)	2 (5%)					
Distance to the closest stream (km)					25.66	<0.001	GH&OPH ²	65	0.004
Range	0.201 -0.68	0.23-2.03	0.06 – 0.13	0.08-0.44			WH&OPH ²	0	<0.005
Mean	0.29	0.90	0.05	0.15			WH&GH ²	34.5	0.005
S.D.	0.18	0.57	0.05	0.13			WH&TBH ²	7	<0.001
Distance to the closest human settlement (km)					5.036	0.169			
Range	6.95 -12.00	2.30-12.00	3.15-7.66	4.54 -8.49					
	(n = 5)	(n = 9)	(n = 5)	(n = 8)					
Mean	8.80	5.98	6.13	6.01					

Nest Tree Parameters	GH	WH	OPH	TBH	Kruskal-Wallis Test		Mann-Whitney U Test		
					H	P (df = 3)	Sig. diff. pair	U	P
S.D.	1.92	3.45	1.65	1.40					
Distance to the nearest active nest to intraspecific neighbor (km)					5.77	0.123			
Mean	2.99 (n = 5)	1.40 (n = 9)	1.83 (n = 5)	1.97 (n = 8)			WH &GH	2.41	0.016
Range	2.02-4.23	1.37– 2.45	0.94-3.35	0.87– 2.64					
S.D.	0.89	0.60	0.99	0.90					
Distance to the nearest active nest of heterospecific neighbor (km)					1.54	0.672			
Mean	0.62 (n = 5)	1.37 (n = 9)	0.94 (n = 5)	0.90 (n = 8)					
Range	0.08 – 0.14	0.24 – 4.40	0.60-1.68	0.075 – 2.45					
S.D.	0.49	1.31	0.39	0.80					
Cavity Orientation (°)					1.77	0.623			
Range	5 -332	5 – 340	40-332	5 – 294					
Mean	222	192	202	169					
S.D.	90	99	97	97					
Nest tree species	11	15	6	10	3.39	0.335			
<i>Ailanthus integrifolia.</i>	1(2.4%)								
<i>Antiaris toxicaria</i>	1(2.4%)	2 (4.8%)							
<i>Choerospondias axillaris</i>			1(2.4%)	1 (2.4%)					

Nest Tree Parameters	GH	WH	OPH	TBH	Kruskal-Wallis Test		Mann-Whitney U Test		
					H	P (df = 3)	Sig. diff. pair	U	P
<i>Manilkara</i> sp.	2 (4.8%)	5 (11.8%)	2 (4.8%)	1 (2.4%)					
<i>Pterospermum</i> <i>cinnamomeum</i>				2 (4.8%)					
<i>Terminalia bellerica</i>	1 (2.4%)	3 (7.1%)		4 (9.5%)					
<i>Tetrameles nudiflora</i>	5 (11.8%)	5 (11.8%)	2 (4.8%)						
<i>Toona ciliate</i>				1 (2.4%)					
Unknown1	1 (2.4%)								
Unknown2			1 (2.4%)						
Unknown3				1 (2.4%)					
Cavity formation					9.07	0.028	WH & OPH	2.26	0.024
Woodpecker (%)	0	1 (2%)	3 (7%)	0			TBH&OPH	2.32	0.020
Other formation (%) ³	11 (26%)	14 (33%)	3 (7%)	10 (24%)			OPH & GH	2.54	0.011

¹ Kemp (1993), GH = Great Hornbill, WH = Wreathed Hornbill, OPH = Oriental-pied Hornbill, TBH = Tickell's Brown Hornbill, ²A pair of hornbills that preferred statistically significant characteristics at nest sites with Bonferroni correction., ³ Other formation may include broken branches, bear excavation (%)

4) Tree Density in Breeding and Non-breeding Sites for Hornbills

I compared the density of potential nest trees for hornbills, and known fruit trees fed by hornbills between two sites. MPWS represented forest that the hornbills used as breeding sites and NHP represented forest that hornbills did not use as breeding sites. This section also compared my results on density of productive trees, potential nest trees, and known fruit species fed by hornbills to Kalayakool (2010) who studied in HKK and Budo-Su-Ngai Padi National Park (BUDO: Table 2.4). HKK and BUDO are all important habitats for hornbill conservation in Thailand (Poonswad 1993b, Poonswad et al. 2012).

I found the tree species, the total number of trees, and the density of the reproductive trees in MPWS were higher than NHP (see Table 2.4). The reproductive-sized trees did not have a significantly different mean number of trees ($t = -0.64$, $DF = 485$, $P = 0.260$) nor total density ($t = 0.88$, $DF = 484$, $P = 0.190$) between MPWS and NHP.

Table 2.4 Comparison of the density of reproductive trees, potential nest trees for hornbills, and known fruit trees for hornbills in various hornbill habitats

Density (trees $\times 10^3/\text{km}^2$)	HKK ¹	BUDO ¹	MPWS	NHP
Trees with DBH ≥ 10 cm	48	57	54	46
Potential nest trees with DBH ≥ 40 cm	9	8	6	6
Known fruit trees with DBH ≥ 10 cm	16	17	15	4

¹Results from Kalyakool (2010), HKK= Huai Kha Khaeng Wildlife Sanctuary, BUDO = Budo- Sungai Padi National Park, MPWS = Maenam Pachee Wildlife Sanctuary, NHP = The Natural History Park initiated by Royal Princess of Thailand

4.1) Potential Nest Trees for Hornbills

In MPWS, I found 1939 reproductive-sized trees in 319 species of trees in 205 genera of 69 families. Of these, I found only 14 intraspecific reproductive trees used for nesting in MPWS (0.7%) in six species or 389 trees per km². Of these 14 reproductive trees, only eight trees (0.4%) in three species were as large as potential nest trees or 222 trees per km² (see Table 2.5).

In NHP, I found 1658 reproductive-sized trees in 293 species in 207 genera of 63 families. From this number, I found only five reproductive-sized trees (0.3%) in three species that were intraspecific with nest tree species found in MPWS but only one of them (0.06%) was as large as the potential nest tree of hornbills (see Table 2.5). In other words, the density of reproductive trees and potential nest trees that were intraspecific with the hornbill nest trees in NHP were only 139 and 28 trees per km², respectively.

Not surprisingly, potential nest trees were significantly fewer in mean numbers ($t = -3.46$, $DF = 194$, $P < 0.001$) and total density ($t = -1.74$, $DF = 194$, $P = 0.042$) in NHP compared to MPWS.

Table 2.5 A comparison on numbers and density (trees/km²) of intraspecific reproductive trees (DBH ≥ 10cm) and potential nest trees (DBH ≥ 40 cm) to nest tree species for hornbills found in MPWS between the habitats where the hornbills' nests were found and not found

Tree Species (mean ± s.d.)	Tree Family	Number of Trees (Density: trees×10 ³ /km ²)			
		DBH ≥ 10cm		DBH ≥ 40 cm	
		MPWS	NHP	MPWS	NHP
<i>Manilkara</i> sp.	Sapotaceae	1 (28)	-	-	-
<i>Terminalia bellerica</i> Roxb.	Combretaceae	3 (8)	1 (28)	3 (83)	-
<i>Tetrameles nudiflora</i> R.Br.	Datisceae	3 (8)	2 (56)	3 (83)	1 (28)
<i>Toona ciliate</i> M. Roem	Meliaceae	5 (139)	-	2 (56)	-
<i>Ailanthus integrifolia</i> Lam	Simaroubaceae	1 (28)	-	-	-
<i>Antiaris toxicaria</i> Lesch.	Moraceae	1 (28)	2 (56)	-	-
Total		14 (389)	5 (139)	8 (222)	1 (28)

MPWS = Maenam Pachee Wildlife Sanctuary, NHP = Natural History Park

initiated by Her Royal Highness Princess Maha Chakri Sirindhorn

4.2) Known Fruit Trees for Hornbills

There were 61 species of fruit trees known to be a source of food for hornbills with DBH ≥ 10 cm in 42 genera of 27 families in MPWS. The total number of known fruit trees in MPWS was 529 trees (27 %) out of 1,939 trees or approximately 14,690 trees per km². In contrast, there were significantly fewer known fruit trees -- 145 (9%) out of 1,658 trees in 49 species of 35 genera and 22 families or approximately 4,030 trees per km² in NHP (t = 2.45, DF = 77, P = 0.008).

The density of known fruit trees that feed the hornbills in NHP was considerably lower than MPWS, BUDO, and HKK (Table 2.4). NHP had significantly lower mean numbers ($t = 2.62$, $DF = 77$, $P = 0.005$) and a lower density ($t = 2.35$, $DF = 77$, $P = 0.010$) of known fruit trees that feed hornbills than MPWS.

Discussion

My results clearly demonstrate that sympatric hornbills in MPWS use nests with different nest site characteristics. They also emphasize the importance of protected areas as breeding sites and food sources for secure hornbill populations in the working landscape of southern Tenasserim Corridor of Thailand. They also provide the first empirical record on the natural history of hornbills in this region, which is of great interest for hornbill conservation.

1) Nest Discovery and their Status

I found hornbill nest cavities only in the trunks of living trees in MPWS. This is similar to what other researchers have discovered, including Poonswad et al. (1987) and Poonswad (1995) who worked in Khao Yai National Park (KYNP) in Thailand; Kemp (1995) in Southeast Asia and Africa; Klop et al. (2000) in Panay, Philippines; Cahill (2003) in Sulawesi, Indonesia; and Stauffer and Smith (2004) in south-central Cameroon. In contrast, I found none of the nests in dead trees while those studies found 1.2% (Poonswad 1995), 12.5% (Klop 2000), 4 and 7.7% (Stauffer and Smith 2004) of nesting cavities in dead trees. I also found more nests, the longer I looked with an increasing number of active and inactive nests located from 2010 to 2012. This is consistent with Poonswad et al. (1983) and Poonswad et al. (1987) who found consistently more nests the

longer they worked in an area. This may be attributed to two things: 1) due to secretive breeding behaviors of hornbills, the longer that you search in an area, the more likely you are to find more nests, and 2) breeding pairs may build new nests from year to year if any competition, disturbance, or unsuitable nest conditions occur, leaving a trail of inactive ones.

The density of all active nests for sympatric hornbills in the area of 50 km² in MPWS (2.27km² per nest), is four times lower than KYNP (0.55 km² per nest Poonswad et al. 1987) and two times lower than Arunachal Pradesh in India (0.93 km² per nest: Datta and Kannan 2004). Kemp (1995) found that nest density of the Great, Wreathed, and Oriental-pied Hornbills in KYNP were 2.3, 2.6, and 1.67 km²/nest which are approximately 3-6 times higher than the densities that I found in my study area.

Although the data in the current study demonstrate that nest density in the MPWS was lower than in KYNP and Arunachal Pradesh, the density of potential nest trees in MPWS (6,250 trees/ km²) is slightly higher than in Arunachal Pradesh, India (5,900 trees/ km²: Datta and Kannan 2004). Moreover, following the criteria suggested by Poonswad et al. (1986), the habitat in MPWS is not nest-site limited because it still maintains the density of large nest-sized trees with DBH \geq 60 cm more than 2,500 trees per km². This discrepancy is difficult to explain because of different locations in biogeographical subregions (Huggett 1998) that may result in different available resources for nesting and food (Cahill 2003), and different adaptations to the environment. Potentially, the condition of suitable cavities (Poonswad et al. 1987, Chuailua et al. 1998, Cahill 2003, Datta and Rawat 2004) might be the key to explaining this discrepancy because suitable nest-site habitats for hornbills should have at least 600 natural cavities per km²

(Poonswad et al. 1986). Another explanation for the lower hornbill densities at my site may be the condition of the interiors of the cavities in MPWS. I found, roughly, that four out of five inactive nests had sunken floors, an empirically unsuitable condition for nesting (Poonswad et al. 1987, Chuailua et al. 1998).

Nest failure and abandonment due to human disturbance occurred at the site. My finding was consistent with Poonswad et al. (1983), Poonswad et al. (1987), Chuailua et al. (1998), Datta and Rawat (2004) that human disturbance is a major cause of nest failure and abandonment. I found that the one Wreathed Hornbill nest remained inactive throughout the study period after it was hunted by a local villager for food in 2009. Moreover, activities -- such as collecting honey and *Perkia* spp. at tall trees near active nest trees; hunting of other animals; forest camping and travelling of Karen villagers between Phurakam and Pong Luek villages located in Kaeng Krachan National Park; and fighting between Karen rebels and Myanmar troops – could potentially result in the low population density and low number of active nests in MPWS. Consequently, I suggest more research on the direct effects of human disturbance on hornbill nesting activity.

2) Breeding Onset

Breeding onset of hornbills in the study area was similar to KYNP and Myanmar (Poonswad et al. 1983, Poonswad et al 1987, Poonswad et al. 1999, Kinnaird and O’ Brien 2007). The breeding season started in January and February and lasted until April (Kinnaird and O’ Brien 2007). Hornbill chicks in my site also emerged from the nest about the same time as in KYNP and Myanmar. Nest emergence happened over the span of three months from May to July (Poonswad et al. 1983, Poonswad et al. 1987, Poonswad et al. 1999, Kinnaird and O’Brien 2007). The breeding onset and nest

emergence of the four sympatric hornbill species found in the southern Tenasserim landscape differ from sites nearer the equator such as in Malaysia and Indonesia and from sites at higher latitudes such as China and India (Kinnaird and O'Brien 2007).

3) Nest Competition

Although Poonswad et al. (1987), Poonswad (1995), and Kemp (1995) explored several cases of intra- and inter-specific nest competition among hornbill species and other animals such as wild marten (*Martes* spp.), leopard (*Panthera pardus* (Linnaeus, 1758)), and mongoose (*Hytespes* spp.), I recorded only two clear incidences of nest competition: 1) between the Great and Wreathed Hornbills and 2) between ants and the Tickell's Brown Hornbill.

However, I did not design this study to measure nest competition and consequently, I did not devote a substantial amount of time observing nest cavities before they were occupied. I theorize that none of the interspecific nest competition in my site occurred because smaller-sized hornbills selected nests that differed from nests selected by larger-sized hornbills in altitude, slope, tree DBH, distance to a stream, and cavity formation to avoid nest competition with larger-sized Hornbills (Cahill 2003).

I believe that nest reuse may be associated with nest competition. While Poonswad et al. (1983, 1987) and Kemp (1995) discovered variation in nest reuse by the same hornbill species in KYNP year after year, I found a high rate (approximately 80%) of nest reuse by the same species in the subsequent year even though there was no clear proof whether the same pairs or different pairs used the nest year after year. I agree with Poonswad et al. (1987) that conditions of the interior of the nest and nest entrance, surrounding environment at nest sites, current competition by other hornbills and other

animals, as well as human disturbance could drive different rates of nest reuse year by year. I speculate that the high reuse rate during the two-year period at my site occurred because the conditions of internal nest and nest entrance were in good shape and surrounding environment was suitable with low interference by other competitors and humans.

4) Nest Characteristics

Hornbill researchers have identified a wide array of nest characteristics that govern the choice of nest locations for each hornbill species. In most cases, larger hornbills such as the Great Hornbill and Red-knobbed Hornbill chose larger and taller trees in mature forests (Poonswad et al. 1987, Cahill 2003, Stauffer and Smith 2004, Datta and Rawat 2004, James and Kannan 2009). Although my study did not provide robust statistical evidence on a larger tree requirement by larger hornbills, the mean heights of nest trees used by the Wreathed and Great Hornbills were larger than of the Oriental-pied and Tickell's Brown Hornbill. The DBH of nest trees used by the Great and Wreathed Hornbills was statistically significantly larger than the Tickell's Brown Hornbill. Additionally, the DBH of nest trees used by the Great and Wreathed Hornbills tended to be larger than those of the Oriental-pied Hornbill, however, this was not a statistical difference.

Most nests of the four hornbill species in MPWS were within the interior dry evergreen forest, which is similar to hornbill habitats described elsewhere (Poonswad et al. 1983, Poonswad et al. 1987, Poonswad (1993b, Datta and Rawat 2004, James and Kannan 2009). Although I found no statistically significant effect of distance to human settlement on nest locations of the four hornbill species in MPWS, my observations

suggest that the Wreathed Hornbill can better tolerate human disturbance compared to the other hornbills, and the Great Hornbill is the most sensitive species to human disturbance. Even the Oriental-pied Hornbill, the species that is said to be well adapted to forest edges and disturbed forests (Poonswad et al. 1987, Poonswad 1993b) selected nest locations in the dry evergreen forest of MPWS farther from human settlement than the Wreathed Hornbill. Since local people in Phurakam and Nongtadung villages located in MPWS still intensively harvest resources from this forest more than other parts of MPWS and there was some evidence of poaching at the study site (WCS-TP 2009a, Teampanpong per obs.), the local people may be disturbing and preventing Oriental-pied Hornbills and other hornbill species from nesting close to human settlements.

Distance from the nest sites to human settlement is another important factor of nest site selection. The effect of human disturbance found in this study is similar to Datta and Rawat (2004) and James and Kannan (2009). They found that the Great Hornbill avoided human disturbance and degraded forests and the Wreathed Hornbill can better tolerate moderate disturbance compared to the Great Hornbills, though they still avoid human disturbance (Datta and Rawat 2004). This consistency across biogeography emphasizes my strong concerns about the impact of human disturbance on the survival and distribution of hornbills.

Many studies have discerned the nest location relationship of each hornbill species and their distance to streams. Although hornbills do not drink water directly from water bodies, they consume water through the fruit they feed on (Kemp 1995). Interestingly, this study identified a substantial statistical difference in the preference of the Oriental-pied Hornbill to nest closer to streams than the Wreathed, Tickell's Brown,

and the Great Hornbills. The result is consistent with the findings by Datta and Rawat (2004) that the Oriental-pied Hornbill tends to nest closer to rivers than the Great and Wreathed Hornbills. Potentially, the Oriental-pied Hornbill mainly use mud and soil for nest sealing, so they can find it easily from stream bank. Meanwhile the Great Hornbill seals nest entrance with droppings, chewed pieces of woods, and nest debris and the Wreathed Hornbill can seal nest with mud and dry leaves (Kemp 1995).

Water does influence the distribution of some hornbill species. Tefong (2007) found that the distance to a stream was the most statistically significant factor correlated to the distribution and presence of Rufous-necked Hornbills in Huai Kha Khaeng Wildlife Sanctuary (HKK) in Thailand. Keartumsom (2011) used a Maximum Entropy Model to predict the distribution of the Great and Wreathed Hornbill in KYNP, the finding showed that the closer to water, the greater the probability of finding the Great and Wreathed Hornbills.

One possible reason that water is a key influence on nest site selection and the distribution of some hornbills is that they can easily search for and have access to crabs, mollusks, small fish, and frogs for their chicks and use the mud beside the body of water to seal the nest entrance (Tickell 1864, Kemp 1995). Hornbills sometimes even use streams as a landmark to search for animals for food, and rest close to or along the stream especially on very hot days (Tickell 1864, Kemp 1995).

The altitude of where a nest tree grows seems crucial to nest site selection by hornbills. Poonswad et al. (1987) found that four sympatric hornbills in KYNP selected their nest sites at different altitudes. The Brown Hornbill tended to restrict its nest to higher altitudes than other sympatric hornbills, and the altitude of Wreathed Hornbills'

nest locations was random. My study, however, found altitude convergence of nest locations among the Tickell's Brown, the Great and Wreathed Hornbills in MPWS. However, I found that the Oriental-pied Hornbill selected nest sites at lower altitudes than the Wreathed, Great, and Tickell's Brown Hornbills. Likewise, Poonswad et al. (1987), and Poonswad (1995) found nest competition among four sympatric hornbills in KYNP from 700 to 800 m.a.s.l. and the Tickell's Brown Hornbill occupied nests at higher altitudes than the Oriental-pied Hornbills.

Altitude also influences the distribution and perhaps their nest locations of some hornbills. Keartumsom (2011) more frequently detected the Great and Wreathed Hornbills in KYNP at 700 - 800 m.a.s.l. The Rufous-necked Hornbill is highly attached to habitat above 900 m (Tefong 2007, Jinamoy et al. 2014).

Other characteristics that many hornbill researchers have focused on are the heights of nest trees and of cavities above the ground. My study shows that the Tickell's Brown Hornbill was capable of using nest trees and nest cavities in lower forest layers. The finding is similar to that of Poonswad (1995) who reported that that the Brown Hornbills in KYNP tended to select cavities in lower main canopy more than the other hornbill species. However, some of my findings are inconsistent with Poonswad (1995). For instance, in KYNP, the Wreathed Hornbill selected the highest nest trees and highest cavities while I found that the Great Hornbill tended to select both the highest nest trees and cavities.

Both this research and Poonswad (1995) found that the Oriental-pied Hornbill exhibited great variation in the cavity height and tree height of their nests. However, Datta and Rawat (2004) reported that Oriental-pied Hornbill chose nest cavities and nest

trees at lower canopy. The apparent discrepancies may be due to differences in the biophysical environments of each site. Poonswad (1995) suggested that these might correlate to everyday activities and feeding behaviors. However, the observations in this study did not allow for the same conclusion.

Slope is a physical characteristic that most hornbill studies ignore. Surprisingly, I found that the four sympatric hornbills selected nest locations at statistically different slopes, particularly the Wreathed Hornbill that was prone to locate the nests on steeper slopes than the Oriental-pied and Tickell's Brown Hornbills. My study area is located in rugged terrain with locations at higher elevation that usually have steeper slope. However, steeper slope may indicate other things that occur in the landscape. For example, steeper slope may have less human disturbance or different vegetation. However, I could find no publication addressing this vegetation change on evergreen forests in this region of Thailand.

I did not find any differences in nest spacing of active nests between intraspecific and heterospecific nests. In addition, all spaces between the nests of the heterospecific pairs were shorter than the space between the nests of intraspecific hornbill pairs. This may imply that, during the breeding season, heterospecific hornbills may nest closer together (Poonswad et al. 1987). The male hornbills use overlapping territories and may not protect their territory against the incursion of other hornbill species. As shown in this study, the nearest space from the active nests of the Great to the Tickell's Brown and Wreathed was only 75 and 237 m, respectively.

The intraspecific hornbills, however, tended to avoid each other. This study found that the shortest distance between intraspecific Tickell's Brown Hornbills was 868 m and

the greatest distance between the intraspecific Great Hornbill was 2997 m. This result is consistent with Poonswad et al. (1987) indicating that the Tickell's Brown and the Great Hornbills had the shortest (565 m) and longest (1001 m) spaces between their nests and intraspecific neighbors, respectively.

Very few hornbill studies have focused on the cavity orientation as a preferred characteristic for nests. There were inconsistencies on the distribution of nest orientation in two studies. Stauffer and Smith (2004) found the nest orientation was random for the Black-casqued and White-thighed Hornbills in Cameroon but uniformly distributed for Visayan Tarictic Hornbill in the Philippines (Klop et al. 2000). My study found that the nest orientations of the majority of nests for all four hornbill species faced southwest (180 - 269°). The hornbill species did not differ in any specific orientation of the nest hole, corresponding to findings of the four hornbill species in Thailand (Poonswad et al. 1987, Poonswad 1995, Kemp 1995), the Visayan Tarictic Hornbill in the Philippines (Klop et al. 2000), and the Black-casqued and White-thighed Hornbills in Cameroon (Stauffer and Smith 2004). Only Mudappa and Kannan (1997) discovered a significant orientation to the northeast for Malabar Gray Hornbills in Indonesia.

The last factor that I examined was the shape of the cavity chosen by hornbills (Poonswad 1998a). Because it was impossible to reach all nest cavities to check the shape, especially the ones that opened upward, I assumed that cavities excavated by woodpeckers had a round shape for the nest entrance (Poonswad 2001), and nest cavities formed by other natural causes could have either an oval or an elongated shape.

I found statistically significant differences in cavity formation between the four sympatric hornbills. Most hornbills preferred cavities that had been excavated by natural

causes other than woodpeckers. Only three Oriental-pied Hornbills and one Wreathed Hornbill used cavities excavated by woodpeckers. This is similar to other studies. The Great Hornbill did not use the nest excavated by woodpeckers (Poonswad 2001) potentially because it preferred an elongated shape (Poonswad 1995, Poonswad 1998a, Datta and Rawat 2004), whereas the Tickell's Brown, Wreathed, and Oriental-pied Hornbill could use either round, oval, or elongated entrances (Poonswad 1995, Poonswad 1998a). However, Datta and Rawat (2004) found that Wreathed Hornbills are likely to use a more oval entrance and Oriental-pied Hornbills tend to choose more round entrances.

5) Nest Tree Species and Density

I found that the four sympatric hornbills in MPWS can use at least 11 tree species in 11 genera for nesting and that three species -- *Tetrameles nudiflora* and *Manilkara* sp. and *Terminalia bellarica* – accounted for 77% of all nests and should be considered as crucial for nesting in the region. In KYNP of Thailand, *Eugenia* and *Dipterocarpus* were chosen over 13 other tree genera for nesting by four hornbill species (Poonswad et al. 1983, Poonswad 1995). In HKK, Rufous-necked Hornbill also preferred *Eugenia* sp. as nest trees while the Plain-pouched Hornbill more frequently nested in *Tetrameles nudiflora* (Chimchome et al. 1998). Other hornbill studies have found more diverse use of tree species but hornbills frequently selected only two to four tree species for most of their nesting at most sites (Cahill 2003, Datta and Rawat 2004, Stauffer and Smith 2009, James and Kannan 2009). However, it should be noted that in some areas, such as Panay in the Philippines, Visayan Tarictic Hornbills nest in various tree species randomly (Klop et al 2000).

Tetrameles nudiflora is listed as an important nest tree at other sites for several hornbill species. These include the Great, Wreathed, and Oriental-pied Hornbills in KYNP (Poonswad et al. 1983, Poonswad 1995) and in Arunachal Pradesh (Datta and Rawat 2004), the Plain-pouched Hornbill in HKK (Chimchome et al. 1998), the Red-knobbed and Sulawesi Dwarf Hornbills in north Sulawesi (Cahill 2003), the Sumba Hornbill in Sumba, Indonesia (Marsden and Jones 1997), and the Great Hornbill in Anaimalai hills, India (James and Kannan 2009). *Tetrameles nudiflora* is a common large tree species found across south and Southeast Asia, and this species often contains large hollows inside the trees (Hyland et al. 2010). In addition, *Tetrameles nudiflora* is large softwood (Datta and Rawat 2004), so woodpeckers can excavate holes in it, and later hornbills can make use of these excavated holes for nests (Poonswad 2001).

James and Kannan (2009) reported the use of *Terminalia bellarica* for nesting by the Great Hornbill in the Anaimalai hills of India. However, there are other species in the genus *Terminalia* that were used for nesting by hornbills such as *T. myriocarpa* in Arunachal Pradesh (Datta and Rawat 2004) and *T. superba* in south-central Cameroon (Stauffer and Smith 2004). Although *Terminalia* sp. is a large hardwood tree (Datta and Rawat 2004), it may attract hornbills because of its long survival rate, which may provide a higher frequency of holes than other trees (Poonswad 1995).

Although there are no records elsewhere that hornbills use *Manilkara* sp. for nesting, other species of trees in the same family (Sapotaceae) have been used. These species include *Palaquium amboinens* (Cahill 2003, Kinnaird and O' Brien 1999), *Palaquium ellipticum* and *Chrysophyllum* sp. (James and Kannan 2009), and *Mimusops elengi* (Mudappa 1998). This suggests that hornbills use diverse species of tall and large

trees that provide suitable holes for nesting based on the availability of trees in each forest area.

6) Habitat Quality in Breeding and Non-breeding Sites for Hornbills

Appropriate sizes of potential nest trees seemed to vary for the different hornbill species and different sites. This study found the DBH of the smallest tree used for nesting was 48.7 cm, by the Tickell's Brown Hornbill. Poonswad et al. (1983) reported the minimum DBH size of trees for nesting was 40 cm but their later study at the same site detected the smallest DBH size of nest tree used by Oriental-pied Hornbill was 46 cm (Poonswad 1995). James and Kannan (2009) suggested that the Great Hornbill used the smallest tree with a width of DBH of 50cm for nesting but the smallest-sized tree used by the Great Hornbill in the MPWS was 73 cm. Cahill (2003) found the smallest-sized nest tree for the Red-knobbed Hornbill was 48 cm. The average DBH of nest trees used by the Malabar Gray Hornbill and the endemic Sumba Hornbill was 133 (Mudappa and Kannan 1997) and 49 cm (Marsden and Jones 1997), respectively. In contrast, Klop et al. (2000) reported the smallest-sized tree for the Visayan Tarictic Hornbill was only 17 cm. These differences suggest that hornbills may select their nest locations based on their body size (Poonswad 1995, Cahill 2003, Datta and Rawat 2004). However, this may not always be true, as shown in this study. I found that the mean DBH of nest trees that the Oriental-pied Hornbill, the smallest hornbill species in Thailand (Poonswad et al 1993a), was larger than the Tickell's Brown. The Oriental-pied Hornbill also used trees comparable in size to the Great and Wreathed Hornbills This result agreed with Poonswad et al. (1983) that the Austin's Brown Hornbill used smaller trees for nesting than the Oriental-pied Hornbill.

7) Comparison on Forest Quality at Other Hornbill Habitats

Although, the data suggest that the density of reproductive-sized trees and large trees with DBH \geq 40 cm in NHP is comparable to HKK, BUDO, and MPWS (see Table 2.4), it may not imply that their quality is comparable.

The findings from plant community surveys where nest sites of hornbills were found (MPWS) and not found (NHP) indicated that the southern TWFC can provide nest trees for hornbills because the density of nest tree species is higher than the density of all active nests. In addition, when comparing the density of potential nest trees and known fruit trees that fed hornbills in this study to Kalayakool (2010) in HKK and BUDO, the habitats in MPWS are comparable to HKK and BUDO in providing good forest conditions with abundant large trees, and available known fruit species for hornbills to nest and survive. Unfortunately, my study indicates that habitats in NHP can serve as temporary foraging habitats but they are unlikely to be suitable for nesting because of the low fruit availability. This could pose a risk to nest success (Stauffer and Smith 2004) especially because male hornbills must fly far from the nest to search for adequate food, particularly in years when that fruit trees do not produce enough fruit (Corlett 2009).

Interestingly, the results of my study lead me to speculate on the causes of a very low nest density and low abundance of the four sympatric hornbills in MPWS (WCS-TP 2009a) even though essential resources are apparently available in sufficient amounts. It is possible that existing potential nest trees do not fit with the particular characteristics that each hornbill requires such as availability of suitable nest holes (Kannan 1994), appropriate tree heights and cavities, commonality of the trees (Datta and Rawat 2004), and unsuitable conditions of the tree cavities (Poonswad et al. 1987, Chuailua et al. 1998,

Cahill 2003). In other words, the limiting factors for these populations may not be things that I measured.

In conclusion, the four sympatric hornbill species in MPWS tended to use different nest characteristics suggesting low competition among smaller- and larger-sized hornbills that resulted in high nest reuse. In most cases, smaller-sized hornbills used nesting sites closer to stream, at lower altitude in less steep areas, and in smaller DBH. Forest conditions in the southern Tenasserim both outside and inside protected areas are capable of providing food sources for hornbills year-round but only the forest inside the protected area appears to be suitable for breeding. This result supports the importance of forest conservation and restoration outside the protected area to provide foods for hornbills in the years that fruit sources are rare with irregular distribution.

I recommend further study to examine internal conditions of nest cavities and to quantify natural potential nest holes to estimate rarity of nest sites for hornbills in southern Tenasserim landscape. I also suggest conservationists increase the opportunity for hornbills to find nest sites by repairing of old hornbill nests that have unsuitable conditions for nesting. This activity may include modifying cavities for hornbills at potential nest trees that may have deficient conditions for suitable nesting such as lack of perch, too wide or too narrow nest entrance, too deep floor. With these actions, community-based conservation for hornbills, as shown in Poonswad et al. (2012) and Poonswad et al. (2005), is highly recommended because it will not only reduce the chance of human threats and increase opportunity to increase breeding success and hornbill population at this site, but also support local livelihood and indirectly inculcate local people about conservation.

CHAPTER 3 - MOVEMENT OF IMMATURE HORNBILLS IN THE WORKING LANDSCAPE OF THE SOUTHERN TENASSERIM WESTERN FOREST COMPLEX CORRIDOR IN THAILAND

Summary

Little is known about how immature hornbills use the landscape in the marginal forests of protected areas that are adjacent to large and continuous tropical forest. I studied the foraging range of the immature Oriental-pied, Wreathed, and Great Hornbills using VHF radio telemetry in the Maenam Pachee Wildlife Sanctuary, a protected area in the Southern Tenasserim Western Forest Complex Corridor (TWFC) in Thailand. I conducted the study for 17 months between June 2011 and March 2013 to understand movement and foraging ranges of individual juvenile hornbills year-round, differences in this movement and foraging range between the breeding and non-breeding seasons, and between the wet and dry seasons. In addition, I also compared behaviors of the small (the Oriental-pied) and larger-sized (the Wreathed and Great) hornbills.

I found that the distance moved from the natal nest tended to increase with tracking time. The Wreathed Hornbill chicks (3.27 ± 0.74 km) dispersed farther from natal nests than the Oriental-pied (1.75 ± 0.78 km) hornbill chicks and neither species used human-dominated areas, though the Wreathed Hornbills tended to approach degraded forests near human settlement. The two larger hornbill species (the Wreathed and Great) used significantly larger ranges than the smaller (Oriental-pied) one. Foraging range size in both the breeding and non-breeding seasons of the juvenile Oriental-pied Hornbill and the juvenile Wreathed Hornbill did not differ significantly. Additionally, foraging range

of the Oriental-pied Hornbill chicks in the dry season tended to be larger than during the wet season. Overall, I found moderate interspecific range overlap between the Oriental-pied and the Wreathed and Great Hornbill chicks and moderate intraspecific overlap between the two Wreathed chicks, which neither avoided nor preferred each other. The Oriental-pied chicks captured in different year avoided each other but those that were captured in the same year had moderate overlapping ranges and were slightly cohesive with one another.

This study confirms that Maenam Pachee Wildlife Sanctuary remains good habitat for the Oriental-pied, Wreathed, and Great Hornbills. I suggest that the sanctuary cooperate with border patrol police, infantry, and local people in the two villages living within the sanctuary to reduce and control human disturbance, especially poaching wildlife, so that the forest will help maintain viable populations of these hornbill species at local, regional, and global scales. This may facilitate hornbills dispersing seeds to degraded forest in the Southern TWFC.

Introduction

Hornbills are vital agents of restoration and regeneration of degraded forests (Kinnaird and O' Brien 1996, Corlett 2009b). Much evidence has confirmed the long-distance movement of hornbills (Kemp 1995, Holbrook et al. 2002, Keartumsom 2011) and, consequently, the potential for seed regurgitation and deposition far from trees where the hornbills forage (Kitamura et al 2011). However, hornbills may not occupy forests smaller than 1 km² (Pattanavibool and Dearden 2002) especially if ripe figs are not present (Sitompul et al. 2004). A lack of hornbills in small fragmented forests may

result in changes of the ecological composition and structure of a forest. The main concern is loss of many keystone plant species with large seeds that are known to be fed upon and dispersed by hornbills (Holbrook and Smith 2000, Kitamura et al. 2004, Kemp 1995, Kinnaird and O' Brien 2007, Kitamura et al 2011). Therefore, deforestation, with its accompanying fragmentation, can not only lead to the local extinction of hornbills but also seriously limit the dispersal of plants with large-sized seeds to degraded areas from forest fragments (Hardwick et al. 2004).

Thus far, the study of hornbills in Thailand has been conducted exclusively in large protected areas, even though hornbills occasionally occupy disturbed and degraded forests in unprotected areas (Anggraini et al. 2000, Holbrook et al. 2002, Sethi and Howe 2009, WCS-TP 2009a). Most of these movement studies of hornbills have focused on adults (Poonswad and Tsuji. 1994, Tefong 2007, Kalayakool 2010, Keartumsom 2011) rather than dispersing immature hornbills. Consequently, this study fills a gap of knowledge on movement of immature hornbills, helping to understand the requirements of optimal habitats for maintaining viable populations of hornbills, which could facilitate the regeneration of degraded forest habitats by maintaining hornbill populations over the long term.

In this paper, I estimate distance moved from the natal nest, foraging range, and overlap of landscape use of three species of immature hornbills: the Oriental-pied, Great, and Wreathed Hornbills in the Southern TWFC. I pay special attention to the Oriental-pied Hornbill because it is well-adapted to forest edges and disturbed forest (Tsuji et al. 1987, Poonswad 1993b), and the Wreathed Hornbill because it is a nomadic and wide-ranging species (Poonswad et al. 1986, Kemp 1995). Understanding the dispersion of and

use of marginal forest by these two hornbill species will allow us to assess their potential role in restoring degraded habitats and in sustaining healthy habitats in working landscapes.

The specific objectives of this study are to 1) quantify and compare distances moved from the natal nests of juvenile Great, Oriental-pied, and Wreathed Hornbills, 2) determine the size of the annual foraging area of these species and evaluate if it differs between the breeding season and non-breeding season as well as between the wet and dry seasons, and 3) quantify the overlap in foraging range between individual hornbills to see if it differs in intra- and inter-specific comparisons.

Methods

1) Study Site

I captured hornbills at nest sites in Maenam Pachee Wildlife Sanctuary within an area of 100 km² (MPWS: 13°12'-19' N and 99° 11'-15' E: Figure 3.1). This area is located in the western portion of the sanctuary, in the upper part of Kaeng Krachan Forest Complex, an Asian Natural Heritage Site (Association of Southeast Asian Nations 2003) and is adjacent to vast contiguous forests in Myanmar (WCS-TP 2009a).

2) Capturing and Tagging Hornbills

I examined every active nest found during February 2010 – May 2012 and assessed the potential to capture hornbills at these nests. I made an attempt to capture chicks at the more easily accessed nests before dawn by erecting two layers of pulley-mounted mist nets 12 m long and 4 m high with 270 mm mesh size in the canopy near the nest entrances. I captured the chicks in the late breeding season (May to June),

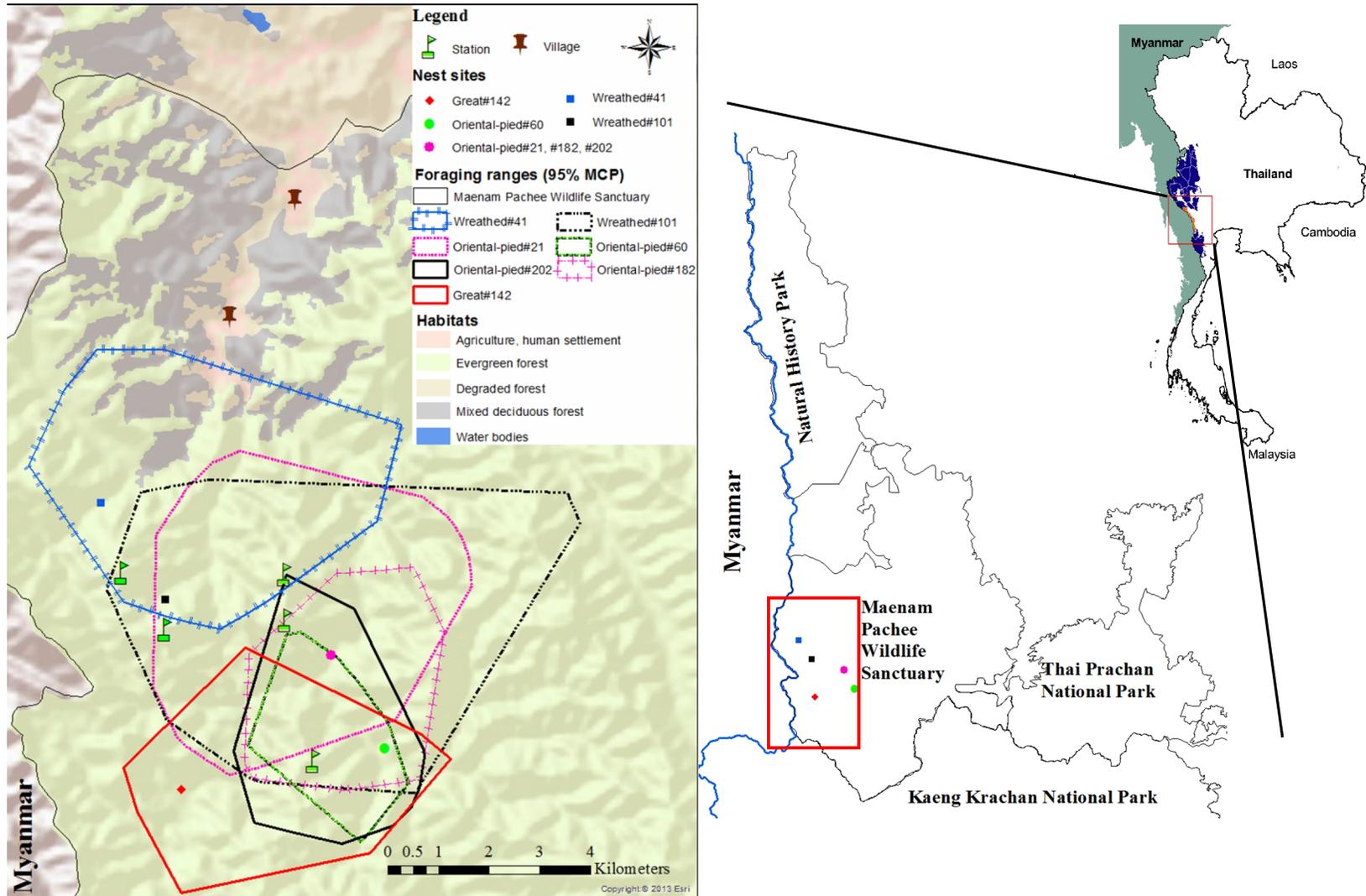
approximately a week before they were expected to emerge from the nesting cavity, which is the most appropriate time to reduce nest abandonment and promote survival (Tsuji 1993). Once captured, each individual chick was removed from the net, hooded to calm the bird, weighed for body weight, and measured for bill and tarsus lengths (Tsuji 1993). Then I attached transmitters (57 g., A1530B backpack model, ATS Telemetry, MN, USA) with harnesses to the hornbills' backs. The transmitters can emit a signal that is detectable up to a 10 km radius.

In 2011, I captured the chicks of one Oriental-pied (transmitter frequency 137.21 for brevity henceforth abbreviated to 11OPH#21 where 11 represents the year captured and #21 represents the frequency) and two Wreathed Hornbills (transmitter frequency #137.41 (11WH#41) and 137.101(11WH#101)). In 2012, I captured, two chicks of the Oriental-pied (# 137.60 (12OPH#60) and 137.202 (12OPH#202)), one chick of the Great (137.142 (12GH142)), and one adult female of the Oriental-pied (137.182 (12OPH182)) Hornbills. I show nest locations of tagged hornbills and their ranges in Figure 3.1.

3) Tracking Hornbills

Two observers tracked hornbills in June 2011, August 2011 to July 2012 and November 2012 to March 2013. The two observers spent four to five consecutive days a month in tracking the birds from 0500h to 1100h and 1500h to 1900h. These efforts resulted in 17 replicate months of the birds captured in 2011 and seven replicate months for the birds captured in 2012 (Table 3 in appendix).

Figure 3.1 Nest locations of the tagged hornbills and their 95% minimum convex polygon foraging range in Maenam Pachee Wildlife Sanctuary along the western border of the Sanctuary and of Thailand.



The two observers used three-element Yagi antennas and receivers (Wildlife Materials, IL, USA) to triangulate locations of the birds from two of five stations, two of which were on tree platforms (~20 m above the ground) located at points on a mountain ridge that were neither obstructed by cliffs nor large trees. They attempted to determine locations at 30-minute intervals to reduce autocorrelation (Lane 1997) and used two-way radios to report each individual's locations to ensure simultaneous bearings. I then projected the hornbill locations from bearing positions to the UTM coordinate system (WGS 1984 UTM Zone 47N).

4) Data Analysis

The sizes of the Wreathed (1,850±50 g. with a total length 81±2 cm) and Great Hornbill (2,350 g with a total length 96 cm) chicks were 2.5 and 3.3 times larger than the Oriental-pied chicks (717±85g. with a total length 56±31 cm), respectively. As a result, I defined the Oriental-pied Hornbill as a smaller-sized hornbill and the Wreathed and Great hornbills as larger-sized hornbills after Poonswad et al. (1998b) and analyzed data from these classifications (as opposed to species) to insure adequate sample sizes for comparison.

4.1) Distance from Natal Nests

While distances moved from fledging sites to breeding sites during natal dispersal is essential to understanding the demography, population dynamics, dispersion, distribution, colonization, and gene flow of wild animals (Sutherland et al. 2000), it has not been studied at either the individual or population levels of hornbills..

In this study, I used the term “distances from natal nest” rather than “natal dispersal” because the immature hornbills did not reach maturity and settle in their

breeding sites (Whitfield et al. 2009) during the study. Age of maturity of the Oriental-pied, Great, and Wreathed Hornbills are 2, 4-5, and 3 years, respectively (Kemp 1995). I calculated the average distance from a natal nest to the locations of individual hornbills using the Data Management Tool (Feature: XY to Line) in ArcMap 10 (ESRI, Redlands, CA). I also compared the mean distances between smaller- and larger-sized hornbills using Mann U Whitney test R 3.02 (R Core Team 2013). I then used the Spearman correlation to test if the distance from natal nest was related to the time since fledging.

4.2) Foraging Ranges

I used the minimum convex polygon method (MCP) to determine range size because it has been consistently used in previous home-range studies of hornbills (Tefong 2007, Poonswad and Tsuji 1994, Holbrook and Smith 2000, Kalyakool 2010, Keartumsom 2011). I employed both the 95% and 50% contours to illustrate annual total and core foraging ranges of hornbills, respectively. I estimated both annual foraging ranges and compared foraging ranges using the Wilcoxon and Mann U Whitney tests in R 3.02 (R Core Team 2013) in three ways: 1) on a year-round basis, 2) between the breeding and non-breeding and 3) the wet and dry seasons.

The breeding season of hornbills at this site started in January and ran through May or early June. The non-breeding season extended from the middle of June to December. The wet season was from May to October and the dry season was from November to April (Thai Meteorological Department 2013). Consequently, the dry and the breeding season overlap, as do the wet season and the non-breeding season. However, I make these different comparisons because I assumed that wet and dry seasons may have

clearer influence on the range size of immature hornbills than the breeding and non-breeding seasons.

4.3) Range Overlap

In order to quantify range overlap of each hornbill (HB_{ij}), I applied the formula provided by Kernohan et al. (2001):

$$HB_i = \frac{O}{i} \times 100 = \% \text{ of foraging range of species } i \text{ by species } j$$

$$HB_j = \frac{O}{j} \times 100 = \% \text{ of foraging range of species } j \text{ by species } i$$

where i and j are the foraging sizes of hornbill i and j and O is the overlapped foraging range size (km^2) between the hornbills i and j . The calculation of range overlap ranges between 0 and 100%, 100% representing that the foraging range of hornbill i completely overlapped with that of hornbill j and 0 representing that the foraging ranges of the two hornbills did not overlap.

I then modified the Jacob's preference index (D) to define the range overlap by intraspecific hornbills using this formula: $D = (r - p)/(r + p - 2rp)$ (Jacobs 1974, Brown et al. 2000, Green et al. 2013). I defined "r" as the HB_{ij} or HB_{ji} derived from the above calculations on range overlap between two individuals (Kernohan et al. 2001).

Meanwhile, "p" is a ratio of foraging range of hornbill i or j to the sum of foraging range of the hornbill i and j . The Jacob's index ranges from -1 (completely not overlapped or avoidance) to +1 (entirely overlapped) and 0 refers to the proportional use of resource to its availability (Brown et al. 2000, Green et al. 2014).

Results

I captured seven hornbills and tracked the birds captured in 2011 ($n = 3$) for 17 months and tracked those caught in 2012 ($n = 4$) for seven months. Four chicks were not within telemetry range for three months after tagging. Consequently, I had a low success rate in locating the individuals in successive attempts (11WH#41, 12OPH#60, and 12GH#142 Hornbills).

However, one chick – 11WH#101 – was detectable in January–February and April–June 2012 though it was undetectable from October to December 2011. This resulted in a successful tracking rate of 24.29% meaning that the individual was found 24.29% of the times that I attempted to locate it. In contrast, three individuals had higher successful tracking rates – 11OPH#021 (56.87%), 12OPH#182 (49.39%), and 12OPH#202 (44.39%) – and lived within telemetry range throughout the study period.

Overall, the four Oriental-pied Hornbills were tracked for a mean of 6.80 ± 2.23 (mean \pm s.d.) months while the larger hornbills (Wreathed and Great) were tracked for a mean of 3.5 ± 2.23 months. The total successful locations for three Oriental-pied chicks, all four Oriental-pied Hornbills, two Wreathed chicks, and three large hornbill chicks were 1154, 1480, 264, and 342 locations, respectively (Table 3.1).

The mean distance error of the VHF radio telemetry in my study was 250.82 ± 221.146 m (20.29 to 1221.80 m: Teampanpong et al. (2014b)). This error is comparable to other studies (Zimmerman and Powell, 1995: 279m, Palomares et al., 2000: 207m, Kauhala and Tiilikainen 2000: 281m). The mean polygon error was only 0.23 km^2 , ranging from $0.02 - 1.49 \text{ km}^2$.

1) Distances from Natal Nests

The mean distance and maximum distance from natal nests of individual hornbills and the group of four Oriental-pied Hornbills, three Oriental-pied chicks, the two Wreathed chicks, and three large hornbills varied (Table 3.1). The distances from the natal nest of all four Oriental-pied Hornbills (Spearman correlation (ρ) = 0.52, P = 0.0021, n =34) and three Oriental-pied Hornbill chicks (ρ = 0.60, P < 0.001, n =27) increased over the study period (Figure 3.2).

Figure 3.2 Correlations between the distance from natal nests and study period of all four Oriental-pied Hornbills and the three Oriental-pied Hornbill chicks

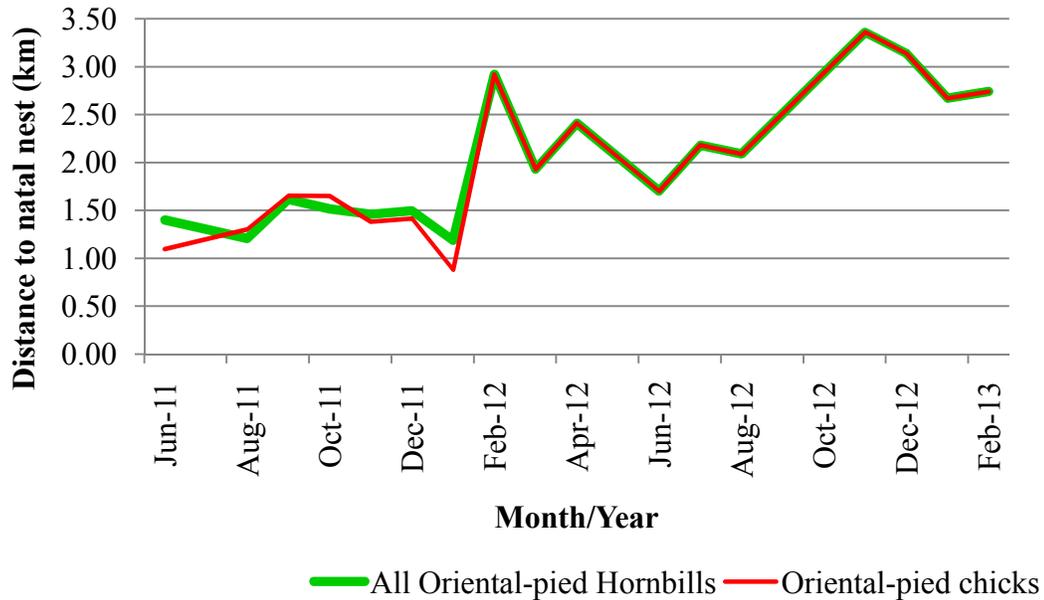


Table 3.1 Tracking effort, successful locations, and average and maximum distance from natal nests of seven tagged hornbills. The average was calculated and bolded for the Oriental-pied chicks, all Oriental-pied Hornbills, two Wreathed Hornbill chicks, and the three large-sized hornbills

Hornbill	Age	Month	No. (successful locations: %)	Distance (mean \pm s.d.: km)	Maximum distance (km)
11OPH#21	Chick	17	836 (56.87%)	2.01 \pm 0.22	3.36
12OPH#60	Chick	3	116 (17.58%)	1.57 \pm 0.11	2.08
12OPH#182	Female	7	354 (53.64%)	1.63 \pm 0.24	2.31
12OPH#202	Chick	7	291 (44.39%)	1.59 \pm 0.37	2.24
11WH#41	Chick	3	57 (7.04%)	2.90 \pm 0.41	3.87
11WH#101	Chick	8	210 (14.29%)	3.38 \pm 0.33	5.17
12GH#142	Chick	3	78 (11.82%)	2.30 \pm 0.30	3.33
Mean OPH chick	Chick	-	384.67 (41.36%)	1.75\pm0.78	-
Mean all OPH	-	-	370 (42.29%)	1.72\pm0.72	-
Mean WH chick	Chick	-	113.5 (11.71%)	3.27\pm0.74	-
Mean large hornbills	Chick	-	115 (11.74%)	3.07\pm1.04	-

Similarly, the distances from the natal nest of the larger-sized hornbill chicks ($\rho = 0.49$, $P = 0.07$, $n = 14$) and the two Wreathed chicks ($\rho = 0.59$, $P = 0.06$, $n = 11$) tended to be greater over study period but not statistically. It is clear that the larger hornbills had significantly larger monthly distances from their nests than the smaller-sized ones ($n_{\text{small}} = 34$, $n_{\text{large}} = 14$, $U = 3.83$, $P < 0.001$).

2) Annual Foraging Ranges

The mean annual 95% and 50% foraging range for the Oriental-pied Hornbill chicks (n = 3) were 12.76 ± 3.44 (mean \pm s.d.) and $2.93 \pm 0.71 \text{ km}^2$, respectively. The mean annual 95% and 50% foraging ranges increased slightly when it included the female Oriental-pied Hornbill#182. The mean annual 95% and 50% foraging range for the Wreathed Hornbill chicks (n=2) were approximately double of the range of Oriental-pied Hornbill chicks (n=3) and similar to the mean annual 95% and 50% foraging range for the large hornbill chicks (n=3). I summarize estimated foraging range of individual hornbills and the mean of Oriental-pied Hornbill chicks, all Oriental-pied Hornbills, Wreathed Hornbill chicks, and larger-sized Hornbills in Table 3.2.

Table 3.2 Annual estimated foraging range (km^2) throughout the study period, and the first- and the second years of study using the minimum convex polygon method

Hornbill	50% MCP			95% MCP		
	1 st Year	2 nd Year	Total	1 st Year	2 nd Year	Total
11OPH#21	3.55	1.78	7.21	16.89	13.35	29.87
12OPH#60	-	2.91	-	-	7.34	-
12OPH#182	-	3.12	-	-	13.85	-
12OPH#202	-	3.47	-	-	13.47	-
Oriental-pied chicks (mean \pm s.d.)	2.93 ± 0.71			12.76 ± 3.44		
all Oriental-pied (mean \pm s.d.)	2.97 ± 0.64			12.98 ± 3.11		
Wreathed#41	2.46	-	-	27.33	-	-
Wreathed#101	8.23	7.71	10.47	32.11	15.15	42.17
Wreathed chicks (mean \pm s.d.)	6.13 ± 2.61			28.66 ± 7.14		
Great#142	-	6.66	-	-	18.96	-

Hornbill	50% MCP			95% MCP		
	1 st Year	2 nd Year	Total	1 st Year	2 nd Year	Total
Larger-sized hornbills (mean ± s.d)	6.27±2.27			25.43±6.69		

The 1st year of study period ran from June 2011 – May 2012

The 2nd year study period ran from June 2012 – February 2013

The Oriental-pied#21 shifted and expanded its range from month to month. Its two-year's range (29.87km²) was larger than its annual range in 2011-2012 (16.89 km²) and in 2012-2013 (13.35 km²). Similarly, its 50% two-year range (7.21km²) was larger than its annual range in 2011-2012 (3.55km²) and in 2012-2013 (1.78km²). In June 2012, it moved closer to the forest edge and human settlement but stayed within the dry evergreen forest.

Oriental-pied#60 moved northwest as well, not far from its natal nest but then stayed beyond telemetry range in November 2012. Oriental-pied#182 moved northward, not far from the nest. She stayed in one area in January 2012 and I assumed she was attempting to enter a cavity to nest in February 2012 because her range narrowed to 0.19 km². Her chick, Oriental-pied#202, stayed in the same area as the mother but moved beyond that range from November 2012 to March 2013, though not far from its natal nest.

The mean annual foraging range of the two Wreathed Hornbill chicks (n =2) was 24.86±7.14, and 6.13±2.61 km², respectively. The large-sized hornbills (n=3) made the 95% range slightly smaller (23.39±6.69 km²) but the 50% range was slightly larger (6.25±2.27 km²) than the two Wreathed Hornbill chicks.

Similar to the Oriental-pied#21, the 95% two-year range of the Wreathed#101 was 1.31 and 2.78 times larger than its one-year range for 2011-2012 (32.11 km²) and 2012-2013 (15.15 km²). Its 50% two-year range was approximately 1 and 2 times larger than its one-year ranges for 2011-2012 (8.95 km²) and 2012-2013 (4.32 km²).

3) Annual Foraging Range in Breeding and Non-Breeding Seasons

The Oriental-pied Hornbill chicks (n=3) and all Oriental-pied Hornbills (n=4) tended to have larger mean annual foraging ranges in the non-breeding season than in the breeding season for both the 95% and 50% mcps (Table 3.3). However, there was no statistically significant difference in annual ranges of all Oriental-pied hornbills between non-breeding and breeding seasons for both the 95% and 50% mcps foraging range (n_{nb} =6 n_b =5, 95%: U = 11, P = 0.54 and 50%: U = 16, P = 0.93). Sample size was not enough to compare the foraging ranges between non-breeding and breeding seasons of the three Oriental-pied Hornbill chicks (n_{nb}=5 n_b=4).

Table 3.3 Estimated 95% and 50% annual foraging ranges (km²) of individual hornbills and the mean ± s.d. of foraging range of Oriental-pied chicks (n=3), all Oriental-pied hornbills (n=4), Wreathed chicks (n=2) and larger-sized hornbills (n=3) in comparing breeding and non-breeding seasons

Hornbill	Non-Breeding Season						Breeding Season					
	50% MCP			95% MCP			50% MCP			95% MCP		
	1 st	2 nd	Total	1 st	2 nd	Total	1 st	2 nd	Total	1 st	2 nd	Total
11OPH#21	2.40	2.45	5.40	9.78	14.30	25.30	4.79	1.28	8.79	17.58	5.59	26.10
12OPH#60	-	2.91	-	-	7.34	-	-	-	-	-	-	-
12OPH#182	-	4.53	-	-	15.00	-	-	0.11	-	-	0.54	-

Hornbill	Non-Breeding Season						Breeding Season					
	50% MCP			95% MCP			50% MCP			95% MCP		
	1 st	2 nd	Total	1 st	2 nd	Total	1 st	2 nd	Total	1 st	2 nd	Total
12OPH#202	-	2.40	-	-	11.90	-	-	1.73	-	-	5.38	-
OPH chicks	2.54±0.21			10.83±2.57			2.6±1.56			9.52±5.70		
All OPH	2.94±0.82			11.66±2.84			1.98±1.73			7.27±6.28		
11WH#41	2.46	-	-	27.33	-	-	-	-	-	-	-	-
11WH#101	2.56	7.71	8.52	17.06	15.20	30.80	6.64	-	-	25.63	-	-
WH chicks	4.24±2.45			19.86±5.33			-			-		
12GH#142	-	-	6.66	-	19.00	-	-	-	-	-	-	-
Larger-hornbill chicks	4.85±2.37			19.65±4.63			-			-		

Breeding season = January/February - May and non-breeding season = June -December

4) Annual Foraging Ranges in Wet and Dry Seasons

The mean annual foraging ranges in the dry season tended to be larger than in the wet seasons (Table 3.4). The same trend happened for individual hornbills except Oriental-pied Hornbill#182 because she attempted to nest during the dry season. However, both 95% and 50% foraging ranges between wet and dry seasons did not differ significantly in size for Oriental-pied chicks ($n_{\text{wet}} = 5$, $n_{\text{dry}} = 4$, 50%: $U = 16$, $P = 0.19$, 95%: $U = 18$, $P = 0.06$) nor for all Oriental-pied Hornbills ($n_{\text{wet}} = 6$, $n_{\text{dry}} = 5$, 50%: $U = 19$, $P = 0.54$, 95%: $U = 22$, $P = 0.25$). I did not have enough data to make a comparison for the Wreathed Hornbill chicks ($n_{\text{wet}} = 4$, $n_{\text{dry}} = 1$) and the larger-sized hornbills ($n_{\text{wet}} = 5$, $n_{\text{dry}} = 1$).

Table 3.4 Annual estimated 95% and 50% foraging ranges (km²) of hornbills in comparing between wet and dry seasons (wet season = May - October and dry season = November – April)

Hornbill	Wet Season						Dry Season					
	50% MCP			95% MCP			50% MCP			95% MCP		
	1 st	2 nd	All	1 st	2 nd	All	1 st	2 nd	All	1 st	2 nd	All
11OPH#21	1.84	0.97	3.36	7.87	6.18	13.79	4.41	1.76	8.47	16.53	13.88	29.95
12OPH#60	-	2.91	-	-	7.34	-	-	-	-	-	-	-
12OPH#182	-	5.78	-	-	14.66	-	-	1.63	-	6.94	-	-
12OPH#202	-	1.04	-	-	5.40	-	-	3.05	-	7.35	-	-
OPH chicks	1.68±0.80			6.68±0.95			12.59±3.86			3.07±1.08		
All OPH	2.50±1.79			8.28±3.30			11.18±4.14			2.71±1.13		
11WH#41	2.46	-	-	27.33	-	-	-	-	-	-	-	-
11WH#101	2.56	16.96	8.52	16.96	15.15	30.75	6.23	-	-	27.24	-	-
WH chicks	4.24±2.45			19.81±5.37			-			-		
12GH#142	-	6.66	-	-	18.96	-	-	-	-	-	-	-
Larger-hornbill chicks	4.85±2.37			19.60±4.66			-			-		

5) Range Overlap

I examined the range overlap of the individual hornbills based on 95% MCP in five ways: annual range, breeding and non-breeding seasons, and wet and dry seasons.

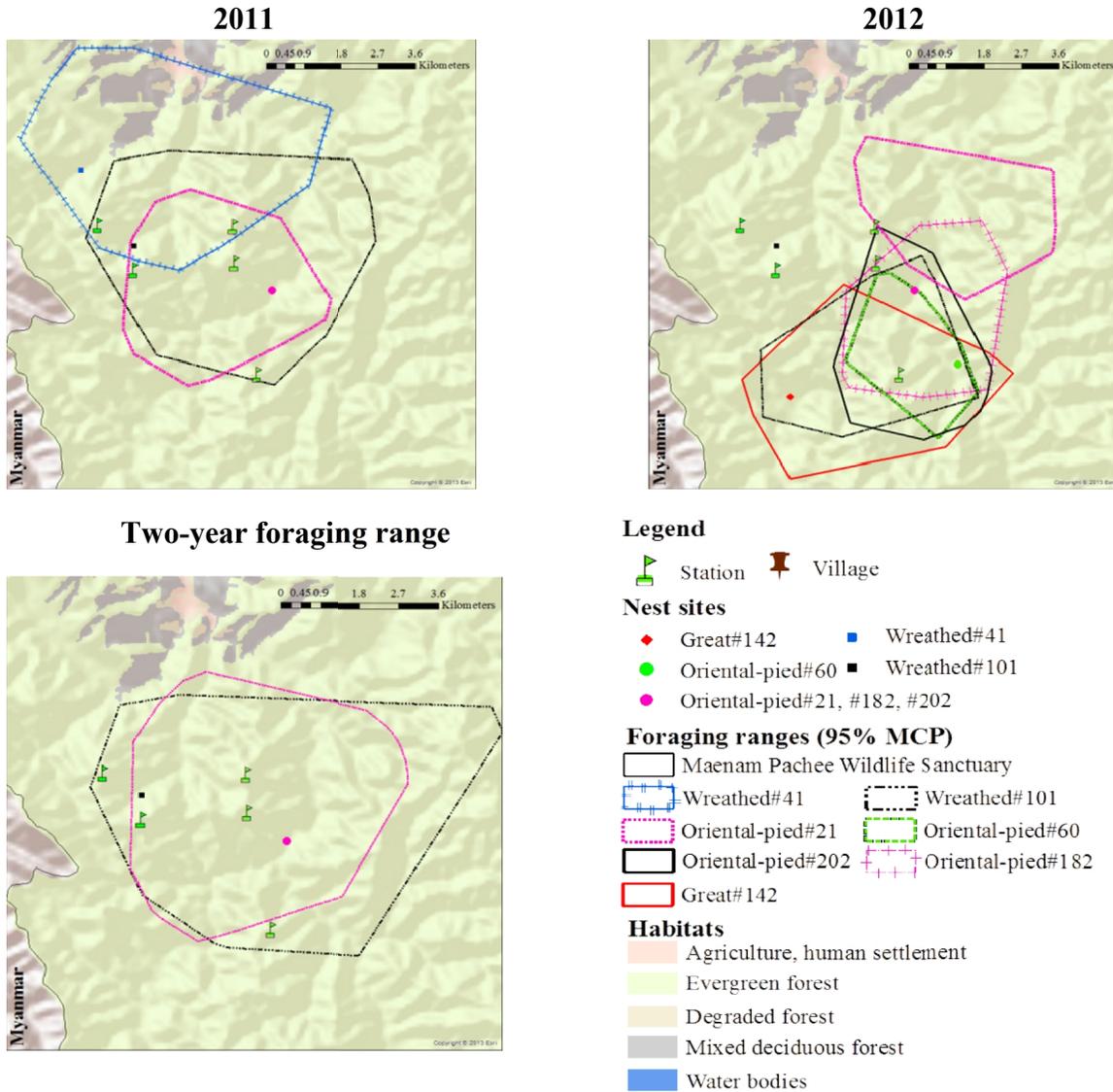
The percent overlap if ranges for individuals and intra- and inter-specific comparisons of hornbills appear in Tables 4 to 6 and the Jacob's index in Tables 7 to 9 in the Appendix. I found that the overlap and Jacob's indices for annual, non-breeding, and

wet seasons were similar but those of breeding and dry seasons were less so. Moreover, I found moderate interspecific overlap and slightly less intraspecific overlap among the seven hornbills.

The annual interspecies overlap between the Oriental-pied chicks and Wreathed chicks ($37.08 \pm 36.28\%$: 0-90%) and between the Oriental-pied chicks and the Great chick ($39.67 \pm 32.63\%$: 0-84%) were moderate. However, the Jacob's index suggests the Oriental-pied chicks had no distinct attraction to be near or not near the Wreathed chicks (-0.129 ± 0.697) nor the Great Hornbill chick (-0.241 ± 0.738).

The annual range overlap of the Oriental-pied chick#21 captured in the first year had minimal overlap with the other Oriental-pied chicks captured in the second year ($2.75 \pm 2.77\%$: 0-6%). The foraging range of Oriental-pied#21 was almost completely separate from the chicks captured in the second year (Jacob's index -0.79 ± 0.22 : - 1.00 to - 0.47). The Oriental-pied#21 also had less intraspecific overlap and tended to avoid the Oriental-pied#182 (25.5% of overlap ranges with Jacob's index of -0.49 ± 0.024) and #202 (5.5% of overlap ranges with Jacob's index -0.890 ± 0.011) despite of emerging from the same nest in the previous year.

Figure 3.3 Range overlap between individual hornbills in the first, second, and combined two-year ranges.



In contrast, the immature and female Oriental-pied Hornbills captured in the same year tended to overlap greatly ($68 \pm 14.23\%$: 45-84%) and the Jacob's index indicated that their annual ranges were slightly cohesive (0.32 ± 0.45 : -0.40 to 0.81). The range of the female Oriental-pied Hornbill was very small in the breeding season owing to a breeding attempt within an area of 0.19 km^2 . Therefore, her range did not overlap with her chick

(Oriental-pied#202) during the breeding season (Jacob's index = -1) but they shared a great proportion of their ranges annually (71.5%), in non-breeding season (75.5%), and wet (87%), and dry seasons (46.5%). The Jacob's indices suggests that they were slightly cohesive to each other for their annual forage range (0.43 ± 0.03) and the range in wet season (0.51 ± 0.49) but did not show distinct preference or avoidance to each other in non-breeding season (-0.10 ± 0.33) and dry season (-0.07 ± 0.06).

As for the two Wreathed chicks, their overlap averaged $37.5 \pm 1.5\%$ and varied from 36 to 39%. Therefore, neither refrained from nor associated with each other as shown by the Jacob's index of -0.25 ± 0.11 .

Discussion

My study provides a fundamental understanding of dispersal from natal nest, foraging range, and overlapping of ranges of immature hornbills in the Southern TWFC. This knowledge is vital for estimating the minimum forest size necessary for conserving viable population of hornbills (Poonswad and Tsuji 1994) in Southern TWFC.

Because I tracked all hornbills during the same time period on a monthly basis, I had equally sampling effort. However, the number of successful readings per day varied upon several factors including weather, manpower, transmitting power, search effort (FAO 2007), animal locations (Tsuji et al 1987) and ability to detect signals from two tracking stations simultaneously. However, these factors are typical in field work and do not appear to affect the total variance in the home range size (Borger et al 2006).

1) Distance from Natal Nest

Natal dispersal is essential in moderating behaviors, spatial dynamics, geographic ranges, abundance, demographics, and gene flow in wild populations (Brown et al. 2000, Sutherland et al, 2000, Nesbitt et al, 2002, Lester et al. 2007, Liu and Zhang 2008,). Although it is essential for species conservation, natal dispersal is one of the least understood phenomena for many species (Sutherland et al 2000).

Although I could not quantify true natal dispersal as even the smallest-sized hornbill, the Oriental-pied Hornbill, takes at least 2 to 3 years to reach maturity and the larger-sized hornbills take at least 4 to 5 years to reach reproductive age (Kemp 1995, Poonswad et al. 2013), this study adds to the body of research on hornbills and the distances they move from natal nest.

My study is the first record of distance traveled from the natal nest of immature Oriental-pied Hornbills. However, the distance moved from natal nest was similar to the male Oriental-pied Hornbill in Khao Yai National Park (KYNP), Thailand that moved only 3-4 km from its natal nest (Poonswad et al. 1986). The distanced move by the Wreathed and Great Hornbill chicks was also similar to Poonswad et al. (1986) and Tsuji et al. (1987). They reported that the Great Hornbill chick stayed within 2 km of its natal nest for several months while the Wreathed Hornbill chicks moved at least 10 km from the natal nest including dispersing more than 5 km just after two weeks of fledging.

Keartumsom (2011) calculated monthly distance moved from the center of foraging range by a Great Hornbill chick using GPS telemetry in KYNP. He found that it moved less than 3 km after fledging but the distance increased over the study period. In some months, it would move a long distance – up to 12 km – from its core range.

The distance moved from natal nests of both smaller- and larger-sized hornbills may increase over a study period for several reasons. The chicks may potentially move far from their natal nest to avoid inbreeding pressure, density-dependent conditions, intrasexual and kin competition for mates and foods, space and searched for available of breeding sites and mates to a wider extent, and individual exploratory behaviors (Daniels and Walter 2000, Sutherland 2000, Dingemanse et al. 2003, Liu and Zhang 2008). Moreover, parental care can be another driving force of offspring dispersal via post-fledging care and phenotypic genes (Dingemanse et al. 2003). For example, Dingemanse et al. (2003) found that the offspring of fast-exploring parents and fast-moving females tended to disperse furthest and had a greater proportion of the variation in natal dispersal distances. They also found that the immigrated birds are able to explore site faster than resident birds.

2) Overall Foraging Ranges

Many studies have found that movement patterns, home range sizes and landscape use by hornbills varies depending upon a hornbill's species diet, feeding behavior, breeding period, breeding strategy, age, territorial behavior, and habitat conditions (Poonswad 1993a, Poonswad and Tsuji 1994, Kemp 1995, Holbrook and Smith 2000, Holbrook et al. 2002, Kinnaird and O' Brien 2007, Kalayakool 2010, Keartumsom 2011).

Despite the inappropriateness of comparing results under different sampling conditions using different sampling and estimation methods (Fieberg and Borger 2012), I wish to highlight some aspects of hornbill movement that differed from other locations in Thailand.

The Wreathed Hornbills travel farthest from their natal nests and have the largest foraging ranges, followed by the Great, and Oriental-pied Hornbills (Poonswad et al. 1986, Tsuji et al. 1987, Poonswad and Tsuji 1994, Keartumsom 2011). My estimate of the home range of Wreathed and Great Hornbills was not substantially different from any of the other studies on the same species (Tsuji et al. 1987, Poonswad and Tsuji 1994, Kalayakool 2010) even though these studies varied from mine in the age of birds, number of tracking days, detectable locations, tracking duration, and forest conditions.

Table 3.5 Comparison on annual foraging range (km²) of the Wreathed and Great Hornbills from various studies on hornbill movement

Studies	Tracking technique	Age	Great Hornbill	Wreathed Hornbill
This study	VHF telemetry	chick	19.00 (n=1)	28.66±7.14 (n=2)
Kalayakool (2010)	VHF telemetry	Male	15.621	-
Keartumsom (2011)	Satellite telemetry	male	184.83 (n=1)	594.52±288.80 (n=2)
		chick	619.20 (n=1)	-
		Chicks	1.514±0.4675 (n=2)	-

Compared to other studies that tagged Oriental-pied Hornbills (Tsuji et al 1987, Chaiyarat et al 2012), my study revealed a much larger foraging range. Tsuji et al (1987) visually observed and found the Oriental-pied hornbill used about 15 km², about the same size of my study but their estimate based on VHF telemetry was much less – 0.9 -5.6 km². I believe that the longer tracking duration and larger numbers of sample sizes of my study lead to the difference in estimates based on the same method. Chaiyarat et al (2012), in contrast, used satellite telemetry and found a relatively small range for

reintroduced adults (male $0.13 \pm 0.11 \text{ km}^2$ and female 0.26 km^2). I speculate that the reintroduced adult Oriental-pied Hornbills were wary of unexpected changes in the new environment, hence they selected not to move far from their original habitats. In addition, this may be due to the careful selection of the reintroduction site itself, which already had diverse fruit and animal food sources at the edge of forest adjacent to a wildlife sanctuary, the more preferable habitat for the Oriental-pied Hornbills (Tsuji et al 1987, Kemp 1995, Poonswad 1993b, Kinnaird and O'Brien 2007). In addition, juvenile hornbills tend to wander over larger areas than adults do in the first two years after fledging as they are trying to assess potential home range and nest sites (Kemp 1995).

3) Range Overlap

Range overlap indicates some extent of resource partitioning among the intra- and inter-species comparisons (Fieberg and Kochanny 2005). I examined foraging range overlap both within (intra-) and between (inter-) species during different periods of the year. I found moderate annual and seasonal interspecific overlap among the Wreathed, Great, and Oriental-pied Hornbill chicks. In addition, I found moderate intraspecific overlapped ranges between the two Wreathed chicks and a low to moderate intraspecific overlap both annually and seasonally among Oriental-pied Hornbills.

These results support Poonswad and Tsuji (1994), Kalayakool (2010), and Keartumsom (2011). Although hornbills shared some foraging ranges, they tended not to show a distinct preference or avoidance of one another, except Oriental-pied #21 that avoided the Oriental-pied Hornbills captured in a different year.

The fact that these hornbills neither avoid nor intentionally encounter one another, is potentially because, *Buceros* and *Aceros* are non-territorial species throughout the year

and *Anthracoceros* is only territorial in breeding season for breeding site and food sources but changes to non-territorial behavior during the non-breeding season. In non-breeding season, hornbills (*Buceros*, *Aceros*, *Anthracoceros*) also roost and feed communally (Kinnaird and O'Brien 2007). Because Poonswad et al. (2013) also reports that the Great and Wreathed Hornbills in KYNP consume similar fruit species, consequently, the immature hornbills in this site may be sharing space temporally in searching for fruits with others of the same or different hornbill species without regard to the presence of others.

I also found that the female Oriental-pied and her chick had a medium to great overlap in range when sharing the landscape for the few months after fledging. This result is consistent with Tsuji et al. (1987) and Keartumsom (2011). They found that, after fledging, hornbill chicks usually follow their parents for four to seven months before leaving to join a juvenile flock (Tsuji et al. 1987).

Even though it is very difficult to explain range overlap – or lack of range overlap -- under natural conditions without knowledge about resource availability within the foraging range, the Oriental-pied, Great, and Wreathed Hornbills could be avoiding competition by using food types in different proportions (Poonswad et al. 1998a). They could potentially search for food to the same extent and, consequently, have overlapping ranges because 1) fruit availability in the landscape is limited (Poonswad 1993), 2) it is varied within and between the years (Corlett 2009), and 3) the distribution of fruit species in tropical forest is clumped (Corlett 2009). Territoriality, as implied by non-overlapping ranges, requires a defensible resource in short supply. The nature of these fruiting resources may preclude territoriality.

The Oriental-pied Hornbill, as a smaller-sized hornbill, tended to share a greater proportion of overlapping ranges with the Wreathed Hornbill as the larger-sized one because they have a higher feeding rate and specialize on figs compared to the smaller-sized hornbills (Poonswad et al. 1998a). Consequently, they have to search for figs and fruits in a wider range than the smaller hornbills. This lack of defensibility of the fruiting resource is supported by the observation that some hornbill species tend to avoid only intraspecific competition in locating nests but share fruit resources with different species because of the low fruit densities and consequent inability to defend them as a resource (Kinnaird and O'Brien 2007).

Conservation Implications

While Thailand has numerous studies on the natural history and ecology of Hornbills that offer abundant information on the conservation and management of hornbills in general, the need remains for site-specific research that addresses local challenges that affect their long-term population management and conservation. This study provides the first record on ranges, distance from natal nests, and overlap of immature Oriental-pied and Wreathed hornbills in the Southern TWFC using VHF radio telemetry. It offers essential natural history information for planning for the conservation, specifically, of breeding sites for hornbills in the Southern TWFC region.

My findings are consistent with previous studies that the Wreathed Hornbills and larger-sized hornbills travel farther and use larger ranges than the smaller-sized, Oriental-pied Hornbills. Additionally, dispersal of immature hornbills was not yet influenced by the requirement of breeding, and consequently I saw no difference in their use of the

landscape between these two seasons. However, I did see differences between the wet and dry seasons. Hornbills forage in larger ranges in the dry season, presumably because of the scarcity of food. In addition, the individuals of the same species tend to forage in different areas and share more overlap of their foraging ranges with individuals of other species of hornbills.

I had several indications that hornbills in my study site near Phurakam village tended to avoid human settlement. Only one Wreathed Hornbill chick ranged over this human-dominated zone, and this despite previous research demonstrating that Oriental-pied Hornbills select degraded forest over primary forest (Tsuji et al. 1987, Datta 1998, Anggraini et al. 2000). The Wreathed Hornbills in this study did not use the degraded forest near the village but maintained their ranges in dry evergreen forest. Teampanpong (2014c) also found that Oriental-pied Hornbills appeared in degraded forest and the edge of forest around MPWS except near Phurakam village (Teampanpong 2014d).

I strongly suggest that MPWS should cooperate with the border patrol police and infantry to establish a substation at the edge of forest near Phurakam village to reduce threats to wildlife due to local people. This village is located inside MPWS and local people still utilize resources from the forest year-round and travel through this forest to Karen village located in Kaeng Krachan National Park. There are some researchers in Thailand who have found that wildlife distribution/presence tended to increase near ranger stations because human disturbance can be examined such as Vinitpornsawan (2003) studying elephant distribution of elephants at Phu Khieo Wildlife Sanctuary and Keartumsom (2011) studying the Wreathed and Great Hornbills in Khao Yai National Park. The best location should be at the site used most frequently for forest entry by the

local people. Additionally, MPWS should invest and support the implementation of a more intensive SMART Patrol, the adaptive management cycle that encourages more effective law enforcement by implementing a suite of strategic planning, training and staffing, and equipment (Stokes 2010) to reduce wildlife poaching. The consequence of using SMART Patrol could reduce poaching and other human disturbance that indirectly affects the dispersal of hornbills to degraded forest near Phurakam village.

However, using law enforcement alone may not be effective in a landscape where local people still depend on the forest resources provided in that landscape. I also recommend starting a community-based conservation initiative, similar to Poonswad et al. (2012) and Poonswad et al. (2005), in the area.

Because my study was the first intensive study on hornbills in the Southern TWFC, I encountered several items that require further research. In particular, I suggest that future research examine how the Wreathed Hornbill selects habitat within the larger extent of the whole landscape of the Southern TWFC as well as in the adjoining forest area in Myanmar. GPS telemetry tracking technology would provide more insightful information on crucial information about hornbill dispersal, inbreeding avoidance, and gene flow across this political boundary. Finally, because I found that found Oriental-pied Hornbill used degraded forests, along the edge of forest and human-dominated areas at the other sites of MPWS, I suggest that future research examine factors that influence natal dispersal and breeding site establishment of immature Oriental-pied Hornbills throughout the MPWS.

CHAPTER 4 – ACCURACY OF VHF RADIO TELEMETRY IN A RUGGED LANDSCAPE: IMPLICATIONS FOR STUDYING HORNBILL MOVEMENTS IN MAENAM PACHEE WILDLIFE SANCTUARY IN THAILAND

Summary

This study assesses the accuracy of VHF radio telemetry for tracking hornbill movements in the mountainous area of Maenam Pachee Wildlife Sanctuary, Ratchaburi Province, Thailand. I identify landscape factors that affect location errors in this rugged landscape. Two forest rangers, who were not involved in triangulation, carried VHF transmitters to 80 different locations with diverse landscape characteristics in the forest. These locations were marked with GPS and then compared to the locations that two observers determined by simultaneously biangulating the transmitters from two fixed stations. I found 58.75% of total attempts successfully located the transmitters, while 20.00% and 21.25% of total attempts failed to determine the locations due to loss of signal and uncrossed triangulated lines from the two stations. The mean distance error of successfully determined locations was 250.82 ± 221.15 m. Meanwhile, the mean angular error measured by observer#1 and #2 were $6.44 \pm 5.58^\circ$ and $5.85 \pm 9.79^\circ$, respectively. Distance errors were positively correlated with angular errors measured by both observer#1 and #2. Distance errors occurred when transmitter locations were lower on a hillside, lower in elevation, with a steeper slope, and/or at a greater distance from the fixed station #2. These results reinforce the idea that it is important to report radio telemetry errors based on triangulation techniques in any study on animal movement.

Introduction

Conventional VHF radio telemetry has been widely employed to estimate locations of animals in the wild (Kenward 2001, Rodgers 2001). This technique has heightened the ability to investigate more insightfully an animal's home range, movement, their biophysical use of landscape, and behaviors that are valuable to wildlife management and conservation (Powell 2000). However, field data obtained from this technique may be biased due to sampling errors in representing the actual locations of animals in the landscape (Withey et al. 2001, Powell 200). As a result, using VHF radio telemetry to determine animal movement telemetry also requires calculating an estimate of location error (Zimmerman and Powell 1995, Bartolommei et al. 2013).

These habitat-biased locations may bring about misleading conclusions regarding conservation and management especially when modeling resource selection and habitat use (Withey et al 2001, Montgomery et al. 2010, Frair et al. 2010). While many researchers have suggested that estimation of location errors (Withey et al. 2001, Montgomery et al. 2010, Bartolommei et al. 2012) is necessary for all telemetry studies, almost no studies have reported location errors inherent to radio-transmitters in a mountainous, tropical landscape.

The research objective of this study was to assess the accuracy of estimated locations using conventional VHF radio telemetry based on linear distance and angular errors in the mountainous area of Maenam Pachee Wildlife Sanctuary, Ratchaburi Province, Thailand. I also evaluate the influence of landscape covariates on the accuracy of this technique.

Methods

1) Study Site

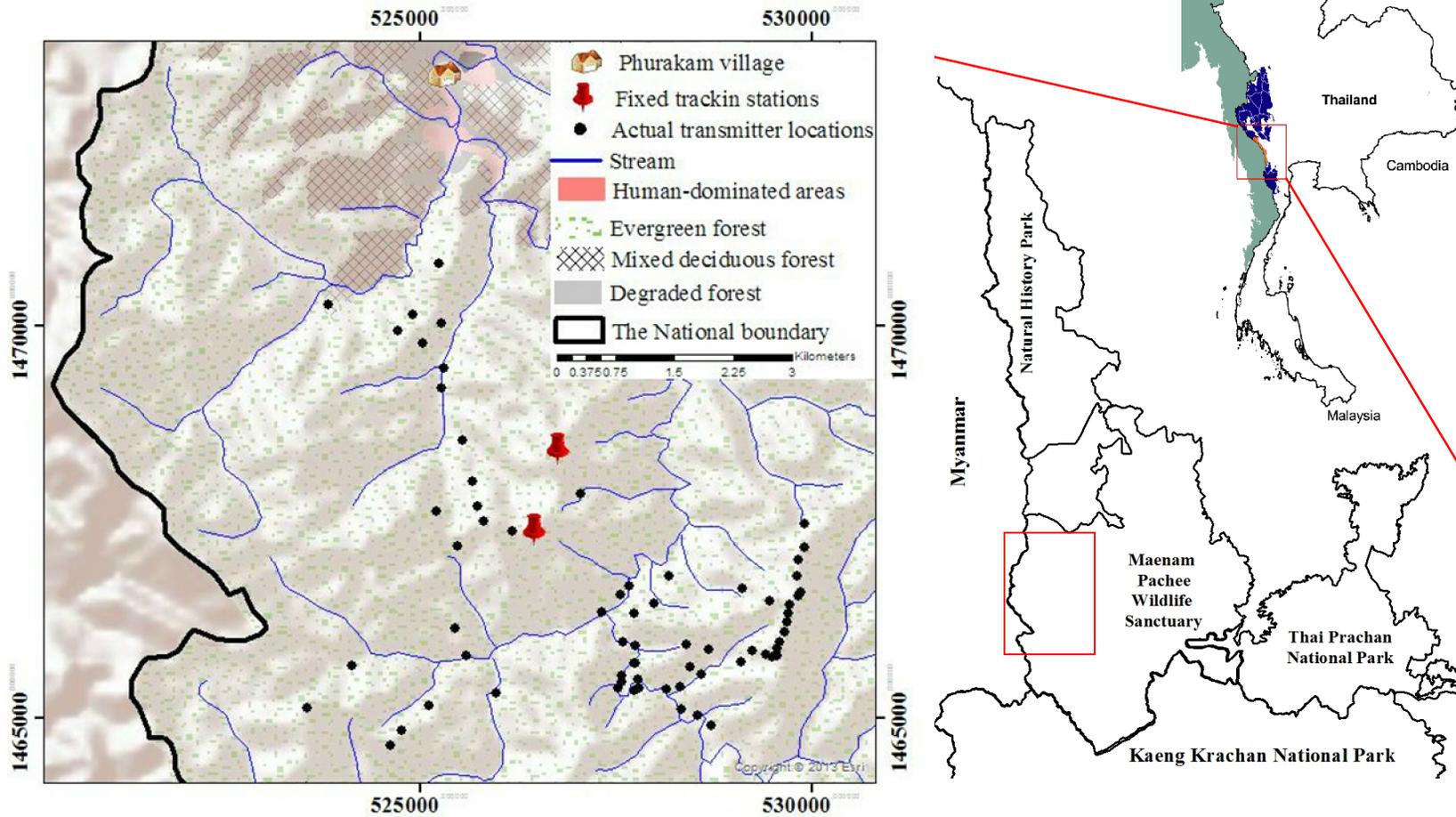
I conducted this study in Maenam Pachee Wildlife Sanctuary (MPWS: 13° 29'-38' N and 99° 18'-29' E), the core area of the southern Tenasserim Western Forest Complex Corridor (Figure 4.1) where the study on foraging range of immature hornbills by Teampanpong (2014b) was conducted. The key vegetation types in the sanctuary include dry evergreen forests interspersed with small patches of mixed deciduous forests, degraded forest, and agriculture (WCS-TP 2009b). The sanctuary is located in hilly terrain (altitude 300- 980 m.a.s.l.) in the upper part of the Kaeng Krachan Forest Complex, an Asian Natural Heritage Site (Association of Southeast Asian Nations 2003). It is adjacent to the vast contiguous forests of Myanmar (WCS-TP 2009a).

2) Accuracy of VHF Radio Telemetry Test

Between April 22 and 30, 2011, forest rangers, who were not involved in triangulation, carried and randomly placed three transmitters (57 g., A1530B backpack model, ATS Telemetry, MN, USA) at shoulder-level at 80 locations in the sanctuary and marked them in the GPS 60 CSX every 30 minutes. The mean accuracy of the GPS was 7.69 ± 3.15 m, which ranged from 2.8 to 19 m.

At an appointed time, two observers used three-element Yagi antennas (ATS and Wildlife Materials) and receivers (Wildlife Materials) to triangulate locations of the transmitters from two fixed stations. The fixed locations were located on a high mountain with few large trees and no cliffs that could cause signal bounce or interfere with signals.

Figure 4.1 Location of Maenam Pachee Wildlife Sanctuary where the accuracy test was conducted and the Southern Tenasserim Western Forest Complex Corridor of Thailand.



I calculated the deviation of distance and azimuth from the actual and the triangulated locations (Bartolommei et al. 2013) using the Proximity tool in ArcMap 10.1 (ESRI, Redlands, CA). Then, I tested the effects of biophysical covariates on location errors including slope, elevation, terrain type (valley, mountain ridge, foothill, and hillside), tracking day, time of day, transmitter, distance from fixed station #1 and #2 to actual locations of transmitters, and errors of azimuth measurement.

I transformed data, if needed, to meet assumptions of normality; standardized; and tested for collinearity. With a pair of covariates with high correlation (Spearman correlation (ρ) ≥ 0.60 with $P \leq 0.05$), I retained only one covariate in the model. I then used Analysis of Covariance (ANCOVA) to determine covariates that significantly affected location errors. All statistical analysis was performed in R 3.0.2 (R Core Team 2013).

Results

1) Accuracy of VHF Radio Telemetry

Only 47 of the 80 locations were successfully detected (58.75%). The average deviation from actual locations was 250.82 ± 221.15 m (mean \pm s.d.) varying from 20.33 to 1221.80 m with a median of 208.02 m. The average angular error measured by observer#1 was $6.44 \pm 5.58^\circ$ (median 5.28°) varying from 0.32° to 24.19° and by observer#2 was $5.85 \pm 9.79^\circ$ (median 2.31° ranging from 0.21 - 44.09°).

Distance errors also positively correlated with angular errors measured by observer#1 ($r = 0.88$, $P < 0.001$, $n = 47$) and observer#2 ($r = 0.86$, $P < 0.001$, $n = 47$). Sixteen out of 80 (20.00%) were undetected due to lack of signal reaching one station or

both. I detected 17 locations (21.25%) from both locations but the triangulated lines did not cross.

2) Covariates Affecting Location Errors

That covariates that influenced linear distance errors in my landscape were elevation, location lower on a hillside, slope, and distance from tracking station#2 (Table 4.1). Linear distance errors were larger at locations at lower elevations, lower on specific hillsides at increasing slope (residual SE = 0.796, adjusted $R^2 = 0.366$, $F=7.641$, $DF=42$, $P<0.001$).

Locations lower on a hillside played the largest role in causing error as the coefficient was highest, followed by distance from station#2 to transmitters, slope, and elevation. The time of day, day of tracking, which of the three transmitters was used, and other locations in the landscape (in the valley, at the mountain top, in the middle of hillside) did not show any effects on location errors.

Table 4.1 Coefficients for the standardized ANCOVA of influencing covariates to location errors

Covariates	Estimate of coefficient	Std. Error	t- value	p-value	Interpretation
Intercept	-0.154	0.126	-1.219	0.230	
Elevation	-0.267	0.120	-2.227	0.031	The probability of errors increase when elevations decrease
Slope	0.308	0.118	2.611	0.013	The probability of errors increase when slopes increase
Location at lower hillside	1.032	0.330	3.125	0.003	The probability of error increase at lower mountainside

Covariates	Estimate of coefficient	Std. Error	t- value	p-value	Interpretation
Distance to station#2	0.398	0.120	3.325	0.002	The probability of errors increase when distances to tracking station#2 increase

Discussion

This study assessed the accuracy of VHF radio telemetry in the mountainous landscape of Maenam Pachee Wildlife Sanctuary in order to supplement a study on the foraging ranges of hornbills at this site (Teampanpong 2014b). It calls attention to the landscape features that can affect VHF radio telemetry in any animal study in a mountainous area.

1) Accuracy of VHF Radio Telemetry

I found a mean positional error of 250.82 ± 221.15 m. in this terrain. This level of error is similar to many other studies that assessed location errors. For examples, Zimmerman and Powell (1995) found the mean location error on black bear research in North Carolina was 279m. Palomares et al. (2000): found the mean error of 207m on the study on Iberian lynx in southwestern Spain and Kauhala and Tiilikainen (2000) found the mean error of 281 m on hare in southern Finland. It highlights that estimated locations from conventional VHF radio telemetry typically contain errors that need to be reported. This is particularly important when researchers are determining home ranges, animal movements, habitat use, and resource selection models based on these data. The error may bring about misclassification of habitats and lead to misleading results (Withey et al 2001, Kauhala and Tiilikainen 2002, Bartolommei 2013).

There are several reasons that create errors from two-bearing triangulation. This includes signal bounce, interference from canopy cover, electromagnetic interference, movement of the animal while triangulating, locations of the animals with respect to landscape features, observer experience, topographical characteristics, location of a fixed station with respect to animals, and distance from the receivers to the animals (Tsuji et al 1993, Parker et al 1996, Withey et al 2001, Kauhala and Tiilikainen, Gantz et al 2006, Bartolommei et al 2013).

I attempted to reduce these errors by establishing fixed stations on high mountain tops to increase my chances of having direct lines of sight to the transmitters so that their locations could be detected and read more accurately (Tsuji et al 1987, Kenward 2001). However, I confirmed that it is likely impossible to avoid location errors in rugged landscapes (Tsuji et al 1993, Kenward 2001, Whitney et al. 2001) and errors still appeared. I was unable to take three bearings in determining the transmitter locations because of a shortage of equipment, manpower and budget, all of which are typical of field studies in the tropics.

Angular errors in my study were slightly less than Tsuji et al (1987). However, this did not include angular errors due to signal bounce that resulted in 17 non-successful locations (21.25%). Suggestions for obtaining more accurate location data from VHF telemetry are using at least three bearing stations, increasing the number of elements of directional antenna system, employing experienced field operators, using a null-peak system, and setting tracking stations in high and open areas (Tsuji 1993, Kenward 2001, Withey et al 2001, Bartolommei et al 2013).

2) Effects of Landscape Covariates on Location Errors

It is imperative to take location errors of VHF telemetry into account when reporting home range and resource selection models of any species (Whitney et al 2001, Bartolommei et al 2013). My findings confirmed the study by Gantz et al (2006), who stated that high distance errors occurred in canyon and hillsides as a result of high reflection. They suggested that this problem could be solved by using an aerial tracking system (Gantz et al 2006). Similar to Tsuji et al (1987), transmitters hidden in a deep valley or behind a hill were difficult to track in spite of being located close to tracking stations. My results also agree with Zimmerman and Powell (1995), Whitney et al. (2001) and Bartolommei et al (2013) who all found that the greater distance between stations and animals also brought about larger location errors.

Angular errors were not substantial in my study despite inexperienced operators. This result is in line with some studies (Whitney et al. 2001, Bartolommei et al 2013), though some researchers caution that operators with different tracking experiences can have different levels of error and these differences should be tested before using the locations in modeling (Kauhala and Tiilikainen, Bartolommei et al. 2013). Although I did not explore errors associated with the different operators, the correlation between distance errors and angular errors measured from station#2 suggest that errors may be due to an inexperienced operator. Additionally, the high percentage (21.25%) of locations that were tracked but did not cross in my study could indirectly imply inexperienced operators. Therefore, I concur that experienced operators could reduce location errors from signal bounce by modifying their bearings (Lindsey and Arendt 1991).

Although selection of appropriate fixed stations above the landscape with respect to the movement of the animals could potentially improve accuracy (Tsuji et al 1993, Bartolommei et al 2013), I found that accuracy might not improve despite tracking from higher locations when animals stayed at lower elevations in this rugged landscape. Potentially, locations for fixed stations at lower elevations in rugged areas may be needed near valleys where signal bounce can occur.

White and Garrott (1990) and Frair et al. (2010) suggested that steep terrain and closed canopies induced habitat-biased locations when using GPS telemetry. This observation is in line with my study where I found that transmitter locations on steeper slopes resulted in larger linear distance errors.

Other covariates that may affect location errors in my study were not taken into account. Positions of transmitters above ground might affect location errors (Tsuji et al 1987, Townsend et al 2007). Townsend et al (2007) found location errors of transmitters located 15 – 46 cm above ground were greater than at 92 cm above ground. This suggests that my linear location errors should be lower since forest rangers carried transmitters at a shoulder-level or about 120 cm above ground. In the hornbill study, the estimated errors should be less since the Wreathed and Great Hornbills use the canopy level of the forest and the Oriental-pied Hornbill uses the mid-canopy (Kemp 1995, Poonswad 1993a).

In conclusion, estimated locations acquired from conventional VHF radio telemetry are acceptable in studying wildlife that live within telemetry range and are substantially less expensive to obtain than locations derived from GPS telemetry. However, when studying animals that use large areas of the landscape, such as the Wreathed and Great Hornbills that were recently reported to use home ranges over 100

km² in size (Keartumsom 2011), GPS-transmitters would be the best solution for obtaining results that are more reliable and to understand ecological use of landscape at a larger scale.

Even though location errors inherent in this technique are unavoidable, they can be accommodated through well-planned research design (Frair et al. 2010). Once location errors are taken into account starting with the study design phase, error propagation can be minimized to acceptable levels in specific conditions. In addition to a well-designed study, positional errors are manageable by using several methods to correct location errors (Johnson and Gillingham, 2008, Frair et al. 2010, Montgomery et al. 2010). Nevertheless, screening out locations that are suspected of having unacceptable errors may be a more satisfactory solution (Kenward 2001, Frair et al. 2010).

**CHAPTER 5 – MODELING RESOURCE SELECTION FOR IMMATURE
ORIENTAL-PIED AND WREATHED HORNBILL IN THE WORKING
LANDSCAPE OF THE SOUTHERN TENASSERIM WESTERN FOREST
COMPLEX CORRIDOR OF THAILAND**

Summary

While Oriental-pied and Wreathed Hornbills are not globally endangered, understanding their habitat use and resource selection in working landscapes is necessary to understand their ability to disperse large seeds from mature forests into adjacent degraded areas. I used VHF radio telemetry to track habitat and resource use by immature Oriental-pied and Wreathed Hornbill chicks in a working landscape in Thailand over a 17 month period from 2011-2013. I assessed habitat use and habitat selection by using four correction methods that adjust for location errors and compared the results in a sensitivity analysis on habitat use and habitat selection. The results from the different correction methods were statistically similar, based on analyses by both a logistic regression model and a generalized linear mixed effects model. I found the Oriental-pied chicks selected dry evergreen forest habitat closer to the forest edge than to the reserve core but would not go beyond the edge of the forest. They also selected habitat at lower elevations. Similarly, Wreathed Hornbill chicks selected dry evergreen forest near the forest edge that was adjacent to degraded forests and human settlement. My intent was to assess whether Oriental-pied Hornbill, a hornbill species known to use degraded forests, and Wreathed Hornbills, a nomadic species that uses very large home ranges, could potentially disperse large seeds from mature forests into adjacent degraded areas of

forest. My findings show that this is not likely under the current conditions in the Southern Tenasserim Western Forest Complex in Thailand. However, as both Oriental-pied and Wreathed Hornbill chicks were likely to disperse to the edge of dry evergreen forest adjacent to human settlement, I do suggest further research on the effects of human activities on hornbills in these forest edges to understand better the limits to permeability across these edges by Oriental-pied and Wreathed Hornbills.

Introduction

Hornbills are effective seed dispersers throughout tropical forests (Kemp 1995, Holbrook et al. 2002, Kinnaird and O' Brien 2007, Kitamura 2011), particularly of large-sized seeds (Kitamura et al. 2004a, Kitamura 2011). In addition, hornbills may occasionally occupy disturbed forests and degraded forest in unprotected areas (Anggraini et al. 2000, Holbrook et al. 2002, Sethi and Howe 2009, WCS-TP 2009a, Kalayakool 2010). Therefore, they could potentially be vital agents in the restoration and regeneration of degraded forests (Kinnaird and O' Brien 1996, Holbrook et al. 2002, Corlett, 2009).

Unfortunately, loss of conterminous forest, creation of very small fragmented forest patches with low densities of ripe figs, and frequent hunting threaten hornbill populations throughout their ranges (Poonswad 1993a, Pattanavibool and Dearden 2002, Raman and Mudappa 2003, Sitompul et al. 2004, Kinnaird and O'Brien 2007, Wilson and Hockey 2013, Trisurat et al 2013). Additionally, local extinction of hornbills substantially decreases large-sized seed dispersal from mature forests to degraded lands (Hardwick et al. 2004, Kinnaird and O'Brien 2007).

In this study, I aim to understand habitat use and resource selection by immature Oriental-pied and Wreathed Hornbills in an old growth forest adjacent to the human-dominated areas of the southern Tenasserim, Thailand. The study focuses on the immature Oriental-pied Hornbill because it is known to inhabit forest edges and disturbed forests (Poonswad et al. 1987, Poonswad 1993b) and the Wreathed Hornbill because it is nomadic and requires a very large range (Poonswad et al. 1986, Kemp 1995, Kinnaird and O'Brien 2007, Margareta and Nugroho 2013). Specifically, I want to define the landscape factors that affect the distribution of immature hornbills in order to evaluate the potential role of hornbills to regenerate nearby degraded habitats and to sustain healthy habitats.

Methods

1) Hornbill Data

I built the resource selection models from a VHF radio telemetry database gathered between June 2011 and March 2013 (Teampanpong, 2014b) in Maenam Pachee Wildlife Sanctuary (MPWS) where I studied the foraging range and range overlap of the hornbills (Figure 5.1). Because of low sample sizes, I modeled resource selection for 1) individual hornbills, 2) for all samples of the Oriental-pied Hornbill chicks combined and 3) for all samples of the Wreathed Hornbill chicks combined.

To create a comparison data set, I generated random locations within 95% minimum convex polygon home ranges for each individual hornbill with replacement to hornbill locations (Erickson et al. 2001), therefore, creating “available locations” that were unique to each individual (Gilles et al. 2006).

These random locations represent points that may or may not be used by the hornbills but are located within their foraging ranges. Since I was concerned about different samples sizes because of the different number of hornbill locations collected due to the different time frames used for monitoring each individual, I generated random locations (availability) for each by continuing to increase the number of random locations until the logistic regression coefficient of covariates stabilized or converged. These sets of random points for particular individuals were then used across models so that biases inherent to generating random points would be removed. The total numbers of hornbill and random locations generated are shown in Table 5.1.

2) Positional Correction

Positional errors are common when performing VHF radio telemetry. Many researchers recommend that location errors should be reported when estimating home range, resource use, and resource selection (Gantz et al. 2006) because they may be a source of habitat misclassification and misleading results (Withey et al. 2001, Kauhala and Tiilikainen 2002, Bartolommei 2013).

Figure 5.1 Nest locations of tagged hornbills and their foraging range in the Southern Tenasserim Western Forest Complex Corridor of Thailand.

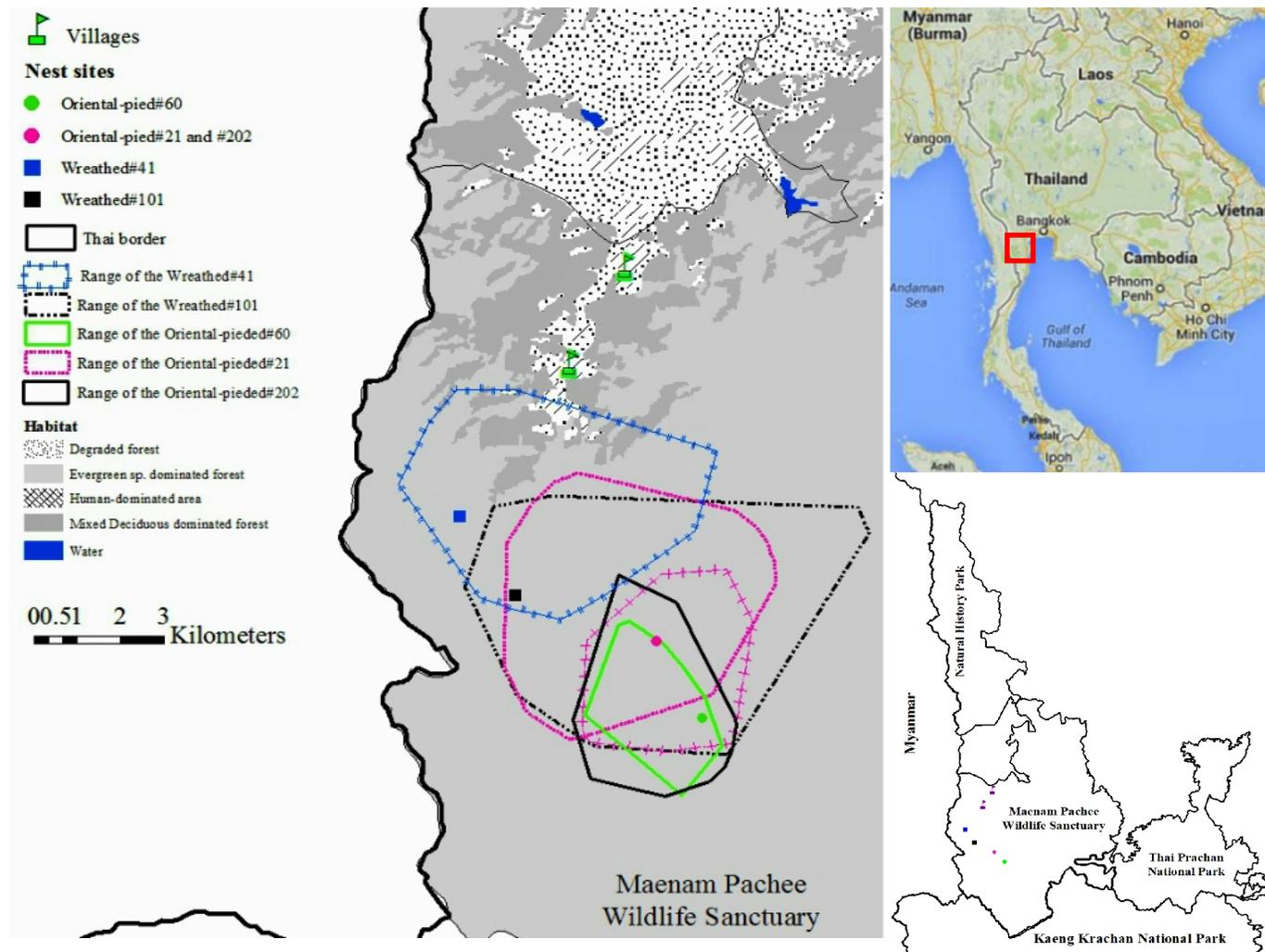


Table 5.1 Summary of sampling effort and number of hornbill locations used in creating the resource selection models for each individual. Total effort = number of times that I attempted to locate an individual. Number of locations denotes 1) where a hornbill was located successfully (Hornbill) and 2) the number of random locations that were generated within the established home range of each individual (Random)

Hornbills	Months	Total effort	No. of Locations	
			Hornbill	Random
Oriental-pied#21	17	1,470	836	936
Oriental-pied #60	3	660	97	397
Oriental-pied#202	7	660	209	609
Wreathedl#41	3	1,470	49	499
Wreathed#101	8	1,470	193	393
Oriental-pied chicks	17	2,790	1142	1942
Wreathed chicks	8	2,940	242	892

Due to the location errors inherent to the VHF radio telemetry in my study (mean \pm s.d. = 250.82 \pm 221.15 m ranging from 20.33 to 1221.80 m: Teampanpong, 2014b), I used three correction methods suggested by Montgomery et al (2010) -- ignorance, rescaling, and zonal means. I also used a lognormal method to amend errors. The ignorance technique assumes the actual locations from VHF telemetry are the best (i.e. one ignores the question of error). The rescaling technique adjusts the resolution of raster covariates using the telemetry errors (Telesco and Van Manen 2006). The zonal means technique treats mean errors around telemetry locations as polygon errors by averaging

values of covariates in pixels within the error polygons (Dickson and Beier 2002).

Additionally, I modified the log-normal decay technique (Montgomery et al. 2010) which randomly generates new locations from distance and angular errors obtained from a VHF accuracy test (Teampanpong et al., 2014b) based on log-normal distribution.

3) Landscape Covariates

I examined five continuous landscape covariates (digital elevation model, slope, proximity to stream, proximity to human activities, and proximity to edge of evergreen forest) and two categorical covariates which I converted to dummy variables (habitat classification [evergreen, mixed deciduous, and degraded forests] and patch size [large: $>300 \text{ km}^2$, slightly large: $>200\text{-}300 \text{ km}^2$, medium: $>100\text{-}200 \text{ km}^2$, and small: $< 100 \text{ km}^2$]).

I derived the values of these covariates from a geographic information system (GIS). Stream within study site was manually digitized based on Topographic map (WGS 1984 UTM Zone 47). I obtained contour line and digital elevation (DEM) of the study site from the Biodiversity Corridor Initiative Project (BCI: WCS-TP 2009a) and used them to generate slope of the study site using Spatial Analyst Tool in ArcMap10.1. I also obtained digital habitat classifications from the BCI (WCS-TP 2009b). Habitat classifications were grouped into evergreen forest, mixed deciduous forest, degraded forest, and human-dominated zone (road, agricultural areas, plantation, orchard, and human settlement).

To assign landscape data to each point in the ignorance, rescaling, and log-normal correction methods, I used the Extraction Tool in Spatial Analyst of ArcMap 10.1 (ESRI, Redlands, CA). With the zonal mean technique, I assigned the mean of the covariate data within the buffered areas by using the Proximity Tool in ArcMap 10.1 to buffer 250.5 m

errors (Teampanpong et al. 2014b) around each point. I then assigned covariate data to each buffered polygon using the “isectoplyrst” command in Geospatial Model Environment (Beyer 2012).

4) Habitat Use

I explained habitat use by calculating a habitat use ratio. I estimated this by dividing the percentage of hornbill locations by random locations within a habitat type (Johnson and Gillingham 2008) for each correction method. I used Kruskal-Wallis Test and Mann-U Whitney Test with Bonferroni correction to test difference on habitat use by comparing data from individual hornbill species, using all of the correction method scenarios.

5) Resource Selection Model and Sensitivity Analysis

I identified a higher likelihood of habitat selected within home ranges using single locations a.k.a. the third-order resource selection mode (Johnson 1980). I employed a “use” and “availability” approach to overcome the assumption that some areas were never used by hornbills (Boyce et al 2002, Pearce and Boyce 2006). This approach also assumes that actual observations are a subset of available sites that explain habitat preference (Manly et al, 2002).

To select candidate covariates for the model, I calculated the mean difference of landscape covariates between hornbill locations and random locations for individuals using a Mann U Whitney test. Only covariates with significant differences ($p < 0.05$) were kept in the model (Erickson et al, 2001, Klar et al, 2008). I then explored collinearity between covariates using Spearman’s correlation (ρ) and contingency coefficient among covariates to find out the best meaningful ecological covariates. Only

one of the pair with a very strong correlation ($\rho \geq 0.6$, $p < 0.05$) was kept (Fielding and Haworth 1995, Erickson et al. 2001, Klar et al. 2008).

I performed forward stepwise logistic regression (LR) to build resource selection for 1) individual hornbills, 2) the three Oriental-pied Hornbill chicks together, and 3) the two Wreathed Hornbill chicks together. I selected as the best model with the smallest AIC criteria and lowest residual deviance. To deal with uncertainty in the model (Ascough II et al. 2005) and to evaluate input improvement for imperfect models (Johnson and Gillingham 2008), I compared the best fit model among the four error correction methods fitted with both LR and generalized linear mixed effect model (GLMM: Johnson and Gillingham 2008) as a sensitivity analysis to explore the optimal covariates and to validate the influential covariates on the resource selection models. For GLMM, I treated individual hornbills as a random effect to avoid pseudo-replication (Salek and Lovy 2012) and selected the best model with the smallest AIC criteria and deviance. I then tested the difference of results performed by all four correction methods for individual Oriental-pied and Wreathed Hornbill chicks using a Kruskal Wallis Test.

I performed statistical analysis in R 3.0.2 (R Development Core Team, 2013). I fitted LR and GLMM with the “aod” and “lme4” packages, respectively.

Results

I used 17 months of tracking data for the Oriental-pied#21, the Wreathed#41, and Wreathed#101 hornbills and seven months of tracking data for the Oriental-pied#60 and #202 individuals (Teampanpong 2014b) for an analysis of habitat use and habitat selection by immature Oriental-pied and Wreathed Hornbill chicks in the core area of

southern Tenasserim. The analysis was based on the four positional correction methods described previously.

Overall, the Oriental-pied and Wreathed Hornbill chicks maintained their range in the largest patch of evergreen forest (385.25 km²) that cover 47.96% of the southern TWFC landscape while the average patch size of evergreen forest in this landscape is 20.12±64.44 km² ranged in size 0.01- 385.25 km².

1) Habitat Use by Oriental-pied Hornbill Chicks

The foraging ranges of individual Oriental-pied chicks were predominantly within the largest patch of evergreen forest inside MPWS (selection ratio 1 – 1.01). This can be explained by the high percentages of hornbill and available locations (99.76 -100% and 99.36-100%, respectively: see Table 5.2). I also found that they disproportionately used evergreen forest compared to other forest types (Kruskal Wallis Test: $H=30.3716$, $df = 2$, $P < 0.001$, Mann-U Whitney: evergreen forest vs. degraded forest; $W = 0$, $P < 0.001$, evergreen forest vs. mixed deciduous forest; $W=144$, $P < 0.001$, mixed deciduous forest vs. degraded forest; $W = 72$, $P = 1$) regardless of the correction method.

2) Habitat Use by Wreathed Hornbill Chicks

I found that the two Wreathed Hornbill chicks tended to use evergreen forest as well. The Wreathed Hornbill#41 primarily used evergreen forest, as demonstrated by a high selection ratio (0.91 – 1.12) with a high percentage of hornbill locations (81.63 - 100%) and available random locations (84.17 - 89.78%). However, its habitat use partially included mixed deciduous forest near Phurakam village (selection ratio = 0 - 2.35) with slightly lower percent of hornbill locations (0 - 16.33%) and available random locations (5.21 - 10.42%) and degraded forest adjacent to the village (selection ratio = 0 –

1.70) with a very low percent of hornbill locations (0 - 2.04%) and available random locations (0 - 10.26%). In contrast, the Wreathed#101 mainly used the evergreen forest with a perfect selection ratio (1) with a very high percent of hornbill (99.48-100%) and available locations (100%).

In contrast to the Oriental-pied chicks (see Table 5.2), the foraging ranges of the two Wreathed chicks combined covered a large portion of the largest evergreen forest patch in MPWS (selection ratio = 1.00) with a high percent of hornbill locations and available random locations (99.82 - 100% and 99.69 - 99.79%, respectively). They were less likely to use the mixed deciduous (selection ratio = 0 - 0.36) with a very low percent of hornbill and available random locations (0.09% and 0.26%, respectively) and the degraded forest (selection ratio = 0) with a very low percent of hornbill and available random locations (0 - 0.09% and 0 - 0.26%, respectively). Additionally, it is clear that the Wreathed Hornbill chicks did use evergreen forest more than mixed deciduous and degraded forests proportionally (Kruskal Wallis Test: $H=18.036$, $df=2$, $P < 0.001$, Mann-U Whitney: evergreen forest vs. degraded forest; $W = 0$, $P < 0.001$, evergreen forest vs. mixed deciduous forest; $W=64$, $P \leq 0.001$, mixed deciduous forest vs. degraded forest; $W = 18.5$, $P = 0.097$).

Table 5.2 Numbers and percent of hornbill and available random locations and habitat use ratio of individual hornbill chicks and all Oriental-pied chicks (n=3) and all Wreathed chicks (n=2)

Hornbills	Methods	Evergreen forest			Mixed deciduous forest			Degraded forest		
		Hornbill	Available	Selection ratio	Hornbill	Available	Selection ratio	Hornbill	Available	Selection ratio
Oriental-pied#21	Ignorance	836 (100%)	932 (99.57%)	1.00 (100/99.57)	0 (0%)	4 (0.23%)	0.00 (0/0.23)	0 (0%)	0 (0%)	-
	Rescale	836 (100%)	931(99.47%)	1.00 (100/99.47)	0 (0%)	5 (0.53%)	0.00 (0/0.53)	0 (0%)	0 (0%)	-
	Zonal mean	836 (100%)	930 (99.36%)	1.01 (100/99.36)	0 (0%)	1 (0.11%)	0.00 (0/0.11)	0 (0%)	5 (0.53%)	0.00 (0/0.53)
	Log normal	834(99.76%)	932 (99.57%)	1.01 (100/99.57)	1 (0.12%)	4 (0.43%)	0.00 (0/0.43)	1 (0.12%)	0 (0%)	-
Oriental-pied#60	Ignorance	97 (100%)	397(100%)	1.00 (100/100)	0 (0%)	0 (0%)	-	0 (0%)	0 (0%)	-
	Rescale	97 (100%)	397(100%)	1.00 (100/100)	0 (0%)	0 (0%)	-	0 (0%)	0 (0%)	-
	Zonal	97 (100%)	397(100%)	1.00	0 (0%)	0 (0%)	-	0 (0%)	0 (0%)	-

Hornbills	Methods	Evergreen forest			Mixed deciduous forest			Degraded forest		
		Hornbill	Available	Selection ratio	Hornbill	Available	Selection ratio	Hornbill	Available	Selection ratio
	mean			(100/100)						
	Log normal	97 (100%)	397(100%)	1.00 (100/100)	0 (0%)	0 (0%)	-	0 (0%)	0 (0%)	-
	Ignorance	209 (100%)	609 (100%)	1.00 (100/100)	0 (0%)	0 (0%)	-	0 (0%)	0 (0%)	-
	Rescale	209 (100%)	609 (100%)	1.00 (100/100)	0 (0%)	0 (0%)	-	0 (0%)	0 (0%)	-
Oriental- ped#202	Zonal mean	209 (100%)	609 (100%)	1.00 (100/100)	0 (0%)	0 (0%)	-	0 (0%)	0 (0%)	-
	Log normal	209 (100%)	609 (100%)	1.00 (100/100)	0 (0%)	0 (0%)	-	0 (0%)	0 (0%)	-
All Oriental- ped chicks	Ignorance	1142 (100%)	1938 (99.79%)	1.00 (100/99.8)	0 (0%)	4 (0.21%)	0 (0/0.21)	0 (0%)	0 (0%)	-
	Rescale	1142 (100%)	1937 (99.74%)	1.00 (100/99.8)	0 (0%)	5 (0.26%)	0 (0/0.26)	0 (0%)	0 (0%)	-

Hornbills	Methods	Evergreen forest			Mixed deciduous forest			Degraded forest		
		Hornbill	Available	Selection ratio	Hornbill	Available	Selection ratio	Hornbill	Available	Selection ratio
	Zonal mean	1142(100%)	1936 (99.69%)	1.00 (100/99.7)	0 (0%)	1 (0.05%)	0 (0/0.05)	0 (0%)	5 (0.26%)	0 (0/0.26)
	Log normal	1140(99.82 %)	1938 (99.79%)	1.00(99.8/99.8)	1 (0.09%)	4 (0.21%)	0.43 (0.09/0.21)	1 (0.09%)	0 (0%)	N/A (0.09/0)
	Ignorance	49 (100%)	442 (88.58%)	1.12 (100/88.6)	0 (0%)	46 (9.22%)	0 (0/9.22)	0 (0.00%)	11 (2.04%)	0 (0/2.20)
	Rescale	40 (81.63%)	448 (89.78%)	0.91 (81.6/89.8)	8 (16.33%)	45 (9.02%)	1.81 (16.3/9.02)	1 (2.04%)	6 (1.20%)	1.70 (2.04/1.20)
41	Zonal mean	43 (87.76%)	420 (84.17%)	1.04 (87.8/84.2)	6 (12.25%)	26 (5.21%)	2.35 (12.2/5.2)	0 (0%)	53 (10.62%)	0.96 (10.2/10.6)
	Log normal	45 (91.84%)	447 (89.58%)	1.03 (91.8/88.5)	4 (8.16%)	52 (10.42%)	0.78 (8.2/10.4)	0 (0%)	0 (0%)	0 (0/1.20)
Wreathed#	Ignorance	193 (100%)	393 (100%)	1.00 (100/100)	0 (0%)	0 (0%)	-	0 (0%)	0 (0%)	-
101	Rescale	193 (100%)	393	1.00	0 (0%)	0 (0%)	-	0 (0%)	0 (0%)	-

Hornbills	Methods	Evergreen forest			Mixed deciduous forest			Degraded forest		
		Hornbill	Available	Selection ratio	Hornbill	Available	Selection ratio	Hornbill	Available	Selection ratio
			(100%)	(100/100)						
	Zonal mean	193 (100%)	393 (100%)	1.00 (100/100)	0 (0%)	0 (0%)	-	0 (0%)	0 (0%)	-
	Log normal	192 (99.48%)	393 (100%)	1.00 (99.48/100)	1 (0.52%)	0 (0%)	-	0 (0%)	0 (0%)	-
	Ignorance	1142 (100%)	1938 (99.79%)	1.00 (100/99.79)	0 (0%)	4 (0.21%)	0 (0/0.21)	0 (0%)	0 (0%)	-
All Wreathed chicks	Rescale	1142 (100%)	1937 (99.74%)	1.00 (100/99.74)	0 (0%)	5 (0.26%)	0 (0/0.26)	0 (0%)	0 (0%)	-
	Zonal mean	1142 (100%)	1936 (99.69%)	1.00 (100/99.69)	0 (0%)	1 (0.05%)	0 (0/0.05)	0 (0%)	5 (0.26%)	0 (0/0.26)
	Log normal	1140 (99.82%)	1938 (99.79%)	1.00 (99.8/99.8)	1 (0.09%)	4 (0.21%)	0.355 (2.07/5.83)	1 (0.09%)	0 (0%)	-

3) Resource Selection Model

To select the candidate covariates, I considered only the ones with significant mean differences between “use” and “availability” (Tables 10-14 in Appendix) which also did not have strong correlations with other covariates that were retained in the model.

3.1) Resource Selection Model for Individual Hornbill Chicks

Resource selection by individual Oriental-pied and Wreathed Hornbill chicks depended on distance to edge of evergreen forest, distance to human-dominated areas, distance to stream, elevation, patch size, and slope.

Because distance to human-dominated areas and distance to edge of evergreen forest are positively correlated for all individual hornbills and all correction methods ($\rho \geq 0.94$, $P < 0.001$), I kept only distance to edge of evergreen forest in the model because it is a more meaningful interpretation than distance to human-dominated area.

The probability of selection by Oriental-pied#21, #60, and #202 increased nearer the edge of evergreen forest. The Oriental-pied#21 and #202 also selected habitats at lower elevation. Additionally, the Oriental-pied#21 and #60 selected habitats that were closer to streams for all positional correction methods. Additionally the Oriental-pied#21 potentially selected steeper area based on zonal mean correction technique.

Individual Wreathed chicks more likely selected evergreen forest near the edge of the evergreen forest as well. I also found the Wreathed#41 selected relatively non-steep habitats based on the rescaling correction method ($z = -2.843$, $P = 0.005$).

I depicted results from LR analysis for each Oriental-pied Hornbill and Wreathed chicks in Table 5.3.

Table 5.3 Covariates that affected resource selection by individual Oriental-pied and Wreathed chicks

Methods	Landscape covariates of the best fit model															
	Edge of evergreen forest*				Elevation				Stream				Slope			
	Est.	SE	Z	P	Est.	SE	Z	P	Est.	SE	Z	P	Est.	SE	Z	P
Oriental-pied Hornbill#21																
Ignore	-0.277	0.052	-5.331	<0.001	-0.286	0.056	-5.152	<0.001	-0.169	0.056	-3.012	0.003	-	-	-	-
Rescale	-0.263	0.052	-5.083	<0.001	-0.255	0.055	-4.821	<0.001	-0.150	0.055	-2.703	0.007	-	-	-	-
Zonal mean	-0.294	0.053	-5.605	<0.001	-0.282	0.057	-4.986	<0.001	-0.164	0.057	-2.879	0.004	0.114	0.050	2.291	0.022
Log normal	-0.257	0.052	-4.963	<0.001	-0.259	0.056	-4.663	<0.001	-0.182	0.056	-0.182	0.001	-	-	-	-
Oriental-pied Hornbill#60																
Ignore	-0.245	0.115	-2.128	0.033	-	-	-	-	-0.298	0.127	-2.342	0.019	-	-	-	-
Rescale	-0.293	0.117	-2.495	0.013	-	-	-	-	-0.340	0.123	-2.773	0.006	-	-	-	-
Zonal mean	-0.194	0.117	-1.660	0.050	-	-	-	-	-0.433	0.139	-3.124	0.002	-	-	-	-
Log normal	-0.250	0.117	-2.14	0.032	-	-	-	-	-0.312	0.126	-2.47	0.014	-	-	-	-
Oriental-pied Hornbill#202																
Ignore	-1.232	0.118	-10.422	<0.001	-0.291	0.102	-2.851	0.004	-	-	-	-	-	-	-	-
Rescale	-1.396	0.126	-11.115	<0.001	-0.338	0.106	-3.192	0.001	-	-	-	-	-	-	-	-
Zonal mean	-1.383	0.125	-11.077	<0.001	-0.293	0.109	-2.692	0.007	-	-	-	-	-	-	-	-
Log normal	-1.103	0.112	-9.824	<0.001	-0.344	0.103	-3.351	<0.008	-	-	-	-	-	-	-	-
Ignore	-0.554	0.181	-3.061	0.002	-	-	-	-	-	-	-	-	-	-	-	-

Landscape covariates of the best fit model																
Methods	Edge of evergreen forest*				Elevation				Stream				Slope			
	Est.	SE	Z	P	Est.	SE	Z	P	Est.	SE	Z	P	Est.	SE	Z	P
Rescale	-0.485	0.179	-2.711	0.007									-0.482	0.170	-2.843	0.005
Zonal mean	-0.547	0.182	-3.006	0.003									-	-	-	-
Log normal	-	-	-	-									-	-	-	-
Wreathed Hornbill#101																
Ignore	-0.227	0.089	-2.538	0.011	-	-	-	-	-	-	-	-	-	-	-	-
Rescale	-0.289	0.090	-3.209	0.001	-	-	-	-	-	-	-	-	-	-	-	-
Zonal mean	-0.260	0.090	-2.893	0.004	-	-	-	-	-	-	-	-	-	-	-	-
Log normal	-0.316	0.091	-3.492	<0.001	-	-	-	-	-	-	-	-	-	-	-	-

3.2 Resource Selection Model for the Three Oriental-pied Chicks

Resource selection by the three Oriental-pied Hornbill chicks depended on four covariates as indicated by a significant mean difference between ‘use’ and ‘availability’ for that covariate: distance to edge of evergreen forest, elevation, patch size, and slope based on covariates (Table 14 in Appendix). I did not count four covariates in the model due to significant correlations under all of the correction methods. These included the distance to human-dominated areas because it was highly positively correlated to distance to edge of evergreen forest ($\rho = 0.913$ to 0.998 , $P < 0.001$). I also excluded evergreen forest ($\rho = 0.82$ to 1 , $P < 0.001$) that was positively correlated with patch size and mixed deciduous forest that was negatively correlated with patch size ($\rho = -0.82$ to -1 , $P < 0.001$).

I found the probability of resource selection by the Oriental-pied Hornbill chicks ($n=3$) greater when closer to the edge of evergreen forest (see Table 5.4). While the Oriental-pied chicks might select resources in larger patch sizes based on the log-normal correction method ($z = 8.569$, $P = 0.003$ for LR, $z=2.432$, $P=0.015$ for GLMM) and at steeper area based on ignore method ($z = 2.185$, $P = 0.029$ for GLMM) and zonal mean method ($z = 3.023$, $P=0.003$ for LR, $z = 3.925$, $P < 0.001$ for GLMM), these results did not agree with the other three correction methods and were not comprehensively significant covariates. Results from all correction methods for Oriental-pied Hornbill chicks were accurate and reliable because they were statistically similar ($H = .099$, $df = 3$, $P = 0.992$).

Table 5.4 Summary of the best-fit resource selection model for the Oriental-pied Hornbill chicks (n=3) using logistic regression (LR) and a generalized linear mixed model (GLMM) comparing different location correction methods

Methods	Statistics	Coefficient	Evergreen		Patch size	Slope	Residual Deviance	AIC
			forest edge	Elevation				
Ignore	LR	Estimate	-0.719	-0.182	-	-	3720	3726
		SE	0.044	0.04	-	-		
		Z	-16.46	-3.46	-	-		
		P	<0.001	<0.001	-	-		
	GLMM	Estimate	-0.574	-0.224	-	0.09	3693.2	3703
		SE	0.052	0.041	-	0.04		
		Z	-10.99	-5.46	-	2.19		
		P	<0.001	<0.001	-	0.03		
Rescale	LR	Estimate	-0.736	-0.176	-	-	37047.4	3713.4
		SE	0.044	0.040	-	-		
		Z	-16.73	-4.73	-	-		
		P	<0.001	<0.001	-	-		
	GLMM	Estimate	-0.608	-0.219	-	-	3688.9	3696.9
		SE	0.054	0.041	-	-		
		Z	-11.34	-5.308	-	-		
		P	<0.001	<0.001	-	-		
Zonal mean	LR	Estimate	-0.736	-0.157	-	0.124	3692.3	3700.3
		SE	0.044	0.040	-	0.041		
		Z	-16.70	-3.876	-	3.023		
		P	<0.001	<0.001	-	0.003		
	GLMM	Estimate	-0.592	-0.222	-	0.164	3665.1	3675.1

Methods	Statistics	Coefficient	Evergreen		Patch size	Slope	Residual Deviance	AIC
			forest edge	Elevation				
		SE	0.053	0.042	-	0.042		
		Z	-11.166	-5.332	-	3.925		
		P	<0.001	<0.001	-	<0.001		
		Estimate	-0.708	-0.159	0.114	-		
	LR	SE	0.043	0.040	0.045	-	3729.3	3737.3
		Z	-16.273	-3.991	2.552	-		
		P	<0.001	<0.001	0.012	-		
Log normal		Estimate	-0.563	-0.208	0.110	-		
	GLMM	SE	0.053	0.041	0.045	-	3705.6	3715.6
		Z	-10.707	-5.050	2.432	-		
		P	<0.001	<0.001	0.015	-		

3.3 Resource Selection Model for the Wreathed Hornbill Chicks

Resource selection by the Wreathed Hornbill chicks was influenced by distance to edge of evergreen forest, patch size, degraded forest, and slope (Table 14 in Appendix). I excluded distance to human-dominated area due to its positive correlation with distance to edge of evergreen forest under all correction methods ($\rho = 0.971$ to 0.979 , $P < 0.001$). Meanwhile, I excluded evergreen forest ($\rho = 0.816$ to 1.000 , $P < 0.001$) because of its positive correlation with forest patch size under all correction methods, and negative correlation with mixed deciduous forest ($\rho = -0.523$ to -0.943 , $P < 0.001$).

It is evident that only distance to edge of evergreen forest had an outstanding influence on resource selection by the Wreathed Hornbill chicks (Table 5.5). However, the direction of the effect was inconsistent between models fitted by LR and GLMM.

This is because GLMM estimated the mean for particular individuals rather than averaged over individuals as LR does.

As a result, this suggests the need for a larger sample size to predict habitat use and habitat selection by the Wreathed Hornbill chicks using these covariates for individual Wreathed Hornbills and all samples of the Wreathed Hornbill chicks.

Table 5.5 Summary of the best-fit resource selection model for the two Wreathed Hornbill chicks (n=2) using logistic regression (LR) and generalized linear mixed model (GLMM) using four different location correction methods

Correction Methods	Statistics	Coefficient of Evergreen forest edge				Residual	AIC
		Estimate	SE	Z	P	Deviance	
Ignore	LR	0.251	0.071	3.518	<0.001	1163.5	1167.5
	GLMM	-0.317	0.094	-3.365	<0.001	1071.0	1077.0
Rescale	LR	0.224	0.072	3.135	0.002	1166.0	1170.0
	GLMM	-0.389	0.097	-4.019	<0.001	1066.00	1072.0
Zonal mean	LR	0.248	0.071	3.479	<0.001	1163.8	1167.8
	GLMM	-0.355	0.097	-3.681	<0.001	1068.7	1074.7
Log-normal	LR	0.273	0.108	2.528	<0.001	1160.7	1164.7
	GLMM	-0.267	0.094	-2.850	0.004	1074.4	1080.4

Discussion

This study focused on habitat use and habitat selection by Oriental-pied and Wreathed Hornbill chicks in the southern TWFC. Specifically, I wanted to know if hornbills use multiple forest types, including degraded ones. My findings indicate that Oriental-pied and Wreathed Hornbill chicks rarely venture from mature forests and,

consequently, are not likely to serve as dispersers of large tree seeds from mature forests to degraded ones. However, my work does highlight the importance of preserve areas in maintaining hornbill populations and of the habitat factors likely to predict the presence of hornbills in those preserves.

My findings emphasize the necessity of maintaining protected areas for hornbill survival in Thailand where their suitable habitat has sharply decreased over the last 20 years (Trisurat et al. 2013). My work identifies key habitat factors for hornbills by producing a habitat selection model based on the response of Oriental-pied and Wreathed chicks to the landscape. This provides the fundamental knowledge for site- and species-based conservation (MacKenzie 2006) and landscape conservation planning (Sanderson et al. 2002).

1) Habitat Use and Resource Selection by Oriental-pied Hornbill Chicks

Little research on habitat selection by Oriental-pied Hornbills adults exists and none for chicks. I found that Oriental-pied hornbill chicks selected habitat ranging between 400 and 800 m.a.s.l. but they preferred habitats at lower elevations between 400-500 m.a.s.l. This result is consistent with Datta (1998) who was working in Arunachal Pradesh, India. According to most studies, the Oriental-pied Hornbills are generalists of the landscape (Kemp 1995, Datta 2003, Kinnaird and O' Brien 2007) that can range from evergreen to mix deciduous to degraded forests, to plantations (Tsuji et al. 1987, Datta 1998, Anggraini et al. 2000). They consume many types of small-sized berries including those from lianas (Datta 2003), and fallen fruits (Kitamura et al. 2009). However, I found that they live only within the evergreen forest near its edge with mixed deciduous forest

that is adjacent to Phurakam village located inside MPWS and favor it greatly compared to other available habitats.

Oriental-pied Hornbill chicks in my study were likely to be found near the edge of evergreen forests, of which its average proximity to human-dominated areas is 2.5 km. They may select evergreen forests in this region for several reasons. First, the Oriental-pied Hornbill chicks tend to range near their natal nesting sites in the first year before gradually moving outward to other habitats. One of my chicks -- Oriental-pied#21 -- moved outward to marginal forest in the second year of the study (Teampanpong et al. 2014b).

Second, the Oriental-pied chicks in my study may have stayed within the evergreen forest potentially to avoid threats due to local people living inside the sanctuary. This was confirmed by the relatively far distance of their nest locations to forest edges (mean 6.13 km, range 3.15-7.66 km: Teampanpong et al. 2014a). The local people in Phurakam village also confirmed that Oriental-pied Hornbills did not appear near the forest edge (local people in Phurakam Village, personal communication.) but were frequently found in former old clearing area in which tree are now regenerating near a soldier frontier camp deep within the sanctuary (pers. obs. and local people in Phurakam village, personal communication). Although Oriental-pied Hornbills avoided the forest edge adjacent to Phurakam village, they appeared at other forest edges near ranger stations (Teampanpong et al. 2014e). This may imply that the Oriental-pied Hornbills also use degraded and marginal forests near human activities, except when human disturbance exceeds a certain level and then drives them away from degraded habitats.

Third, the low densities of nest trees (Teampanpong et al. 2014a) and low abundance of hornbills (THP 2009) at my site may suggest that there are still abundant available resources for the Oriental-pied Hornbills to select within the preferred evergreen forest.

Fourth, Oriental-pied Hornbill chicks may avoid degraded forests because of the lower density of fruit trees known to be used by hornbills in degraded forests and in the forests outside MPWS (Teampanpong et al. in 2014a). Typically, disturbed forests have and low levels of fruiting crop (Anggraini et al. 2000). These low levels of food may also have made the degraded forests less attractive to the Oriental-pied chicks at the start of their dispersal even though they can consume the smaller-sized fruits typical of degraded forests (Datta 2003).

My findings were consistent with Trisurat et al. (2013) that proximity to human settlement significantly reduces the numbers of the Oriental-pied Hornbill in Thailand. While Trisurat et al. (2013) proposed to change the conservation status of the Oriental-pied Hornbill from least concerned to near threatened, they procrastinated the proposal based on high numbers of nest sites of the Oriental-pied Hornbill in the southern portion of the Western Forest Complex in Thailand. Nonetheless, I am aware that its local population is small. The marginal fragmented protected areas of the southern TWFC may pose a risk of inbreeding and local extinction as a result of low nest density (Teampanpong et al. 2014a), low occupancy rate (Teampanpong et al. 2014d) and their inability to migrate across large fragmented landscape compared to the larger hornbills like the Wreathed and the Great Hornbills.

2) Habitat Use and Resource Selection by Wreathed Hornbill Chicks

My findings are consistent with Keartumsom (2011) who found a greater probability of finding the Wreathed Hornbill in evergreen forests compared to other forest types. Anggraini et al. (2000) and John (1987) confirmed that the Wreathed Hornbills prefer closed-canopy forests and tend to avoid highly disturbed open habitats. In addition, diminished fruit availability in degraded, open-canopy and smaller fruit crop were less likely attractive to the Wreathed hornbills in Bukit Barisan Selatan National Park, Sumatra (Anggraini et al. 2000).

I found that Wreathed chicks occasionally used mixed deciduous and degraded forests. This may be because the Wreathed Hornbills are nomadic (John 1987, Kemp 1995, Datta 1998, Datta and Rawat 2003), rely more on fruits (Poonswad et al. 1998a, Datta and Rawat 2003) that are ephemeral in their abundance, and are present in many types of habitats (Anggraini et al. 2000). Therefore, they wander widely in search of fruit patches (Kemp 1995, Datta 1998). Local people in Phurakam village confirmed the occasional presence of the Wreathed Hornbills at fruit trees located at the forest edge (personal communication) near the village.

My results also agreed with Trisurat et al. (2013) that distance to human settlement significantly reduced the presence of the Wreathed Hornbill in Thailand. Even though the LR and GLMM gave different directions of the effect on the distance to edge of evergreen forest to habitat selection by the Wreathed Hornbill, I speculated that the Wreathed Hornbill chicks would prefer habitat far from human settlement. The findings from Teampanpong (2014d) may confirm this speculation because I did not detect the Wreathed Hornbill along forest edges nor in human-dominated areas in that study. In

addition, the occupancy rate of the Wreathed Hornbill inside the protected area (in MPWS) was greater than in forests outside the protected area.

I believe the Wreathed Hornbill chicks moved toward the human-dominated area of Phurakam village in order to disperse to a forest area in Myanmar. Local people in Phurakam village also confirmed detecting Wreathed Hornbills flying across the village and heading west (personal communication). Teampanpong (2014b) confirmed the dispersal of these two Wreathed chicks out of the telemetry range three months after fledging but Wreathed#101 came back to the original range from January to July 2012 while the Wreathed#41 approached degraded and mixed deciduous forest near Phurakam village.

While my results do not offer a clear understanding of the influence of slope on habitat selection by the Oriental-pied and Wreathed Hornbill chicks, I speculate that using habitats at steeper areas could be one way to avoid disturbance by humans. It appears that Oriental-pied Hornbills may select their foraging habitat differently from their nest site locations because their nest locations tend to be located on gradual slopes (Teampanpong 2014a). In contrast, the Wreathed Hornbill tends to select both their foraging habitat and their nest locations in very steep terrain (Teampanpong 2014a).

In addition to slope, my results provide evidence that larger forest patch size may significantly positively influence habitat selection by the Oriental-pied Hornbill chicks. This is consistent with the result from Trisurat et al. (2013) that forest patch size has the most significant effect on hornbill distribution in Thailand, especially the Oriental-pied, Great, and Wreathed Hornbills.

While my findings were conclusive that the Oriental-pied and Wreathed Hornbill chicks do prefer evergreen forest to other habitats but move toward degraded forest and human settlement, they also suggest interesting paths of future research. These include examining large-scale landscape dispersal of immature hornbills, their range overlap within and between species, effects of human disturbance on natal dispersal, age effects on habitat selection, food choice and food availability for hornbills, and the possibility of inbreeding in hornbill populations in the Southern TWFC. I presume that the adult Oriental-pied and Wreathed Hornbills may select habitat differently and could be a further research topic in the study area.

3) Model Discrepancy in using Different Correctional Methods and Statistics

I believe that all discrepancies in the models occurred due to low sample sizes. A larger sample size is needed to detect variability in resource selection of the Oriental-pied and Wreathed Hornbill chicks in different demographic groups and in different parts of the working landscape of the southern TWFC. Especially for the Wreathed Hornbill chicks, the low number of the sample size may have caused the inconsistent direction of influence of the distance to edge of evergreen forest between the LR and GLMM models. This can happen because LR model estimates probability to detect hornbills using averaged single values of covariates across all samples while GLMM estimates the probability based on individual hornbills as a random effect.

Conservation Implications

Many studies suggest that natural restoration of degraded forests is the first step in ameliorating the negative effects of habitat loss, fragmentation, and degradation (Lamb et al. 1997, Pejchar et al. 2008, Gomes et al. 2008, Lamb 2010).

My findings, combined with other hornbill studies in Thailand and Asia, suggest that both maintaining evergreen forest and large trees as nesting sites for hornbills are essential management interventions for increasing the seed dispersal from neighboring primary tropical forest to degraded forests by hornbills (Poonswad 1995, Marsden and Jones 1997, Mudappa and Kannan 1997, Holl 1998, Blakesley et al. 2002, Datta and Rawat 2004, James and Kannan 2009).

Even though the Oriental-pied and Wreathed Hornbills are not of conservation concern at the national or global scales (ONEP 2007, IUCN 2014, Trisurat et al. 2013), the population decline of these species in the southern TWFC may affect forest quality. I perceive hornbill conservation as essential to maintaining healthy ecosystems. Loss of hornbills as effective agents for dispersing seeds in the landscape with low abundance of other key wildlife that can do this ecosystem service, paired with a high rate of wildlife poaching (WCS-TP 2009a), may pose significant risk to forest community dynamics (Seth and Howe 2008). In addition, seed dispersal by other frugivores may not compensate for the loss of hornbills in this landscape (Seth and Howe 2008, Savini et al. 2009).

To conserve effectively the Oriental-pied and Wreathed Hornbills and the other two hornbill species in this landscape, I suggest adaptive management by enhancing the value of this sanctuary for hornbill conservation in order to draw indirect benefits to local

communities. The folklore of the local Karen communities place offensive behaviors to hornbills as equal a sin as offensive behavior to holy men (local people in Phurakam village, personal communication, Thongmak and Hulse 1993). Consequently, this can encourage local people to refrain from activities that may disturb hornbills. As local people played a vital role in identifying both active and inactive nests of hornbills for this study (Teampanpong 2014a), I recommend a collaboration between the sanctuary rangers and the local people in maintaining key habitats and nest sites for hornbills.

One way to do this is to implement the prototype developed by the Thailand Hornbill Project (Poonswad et al. 2005, Poonswad et al. 2012). It engages local people in hornbill research and conservation in order to reduce human disturbance and diminish poaching.

CHAPTER 6 - FACTORS AFFECTING HABITAT OCCUPANCY OF FOUR SYMPATRIC HORNBILL SPECIES IN THE WORKING LANDSCAPE OF THE SOUTHERN TENASSERIM WESTERN FOREST COMPLEX CORRIDOR IN THAILAND

Summary

As development continues to encroach on the natural landscape of the southern Tenasserim Corridor, conservationists struggle to protect its biodiversity to sustain ecological services. While protection of existing forest areas is the highest priority, knowing the occupancy of hornbills, the key seed dispersers in the forest ecosystem, is the first step in promoting the natural restoration and maintaining the stability of these forest ecosystems. I conducted point transect surveys from February 2011 to February 2012 to assay forest composition in order to estimate the occupancy and detection probabilities of four sympatric hornbills- the Tickell's Brown, Oriental-pied, Wreathed, and Great Hornbills – in the region. I generated occupancy models based on landscape characteristics, habitat quality, and resource availability in three land uses; the forest inside the protected area, the forest outside the protected area, and the edge of forests both inside and outside protected area and remnants in human-dominated zones. The encounter rate and occupancy probabilities of all hornbills in the forest inside the protected area was higher than in the forest outside the protected area and only the Oriental-pied Hornbill used the forest edge in human-dominated area. My models suggest that occupancy by all four sympatric hornbills decreases with human disturbance. Moreover, occupancy and detection probability increase with the number of non-fig trees,

numbers of potential nest trees, and abundance of ripe fig fruits. The results also suggest that, in order to attract Oriental-pied Hornbills to degraded forest and forest edges near human-dominated areas, mixed deciduous forests with dense canopy cover and available figs should be maintained and disturbance by humans should be minimized. To promote hornbills as agents for seed dispersal in degraded habitats, I recommend that conservationists preserve existing forest area, available fig and non-fig species, and any large trees that have the potential of being used for nesting. I also recommend collaborating with local people to minimize the human disturbance of hornbills.

Introduction

Human modification of the landscape in the southern Tenasserim has altered the composition of its terrestrial forest communities. These modifications affect species interactions, food chains, and ecological function (Soulé et al. 2005). To maintain ecosystem function in this landscape, it is necessary to conserve keystone species in the form of viable seed dispersal that maintains forest regeneration and recovery (Nepstad et al. 1991, Holl 1998, Holl 1999).

Hornbills are keystone species in tropical forests (Poonswad and Kemp 1993, Kemp 1995, Kinnaird and O' Brien 2007). Their presence has a disproportionate effect on ecological processes through seed dispersal. Because hornbills are able to disperse long distances over a fragmented landscape, they are better suited to carry seeds to degraded habitats than other frugivores that occur in this same landscape including barking deer, sambar deer, gibbons, and macaques (WCS-TP 2009a). Unfortunately, most hornbills are threatened by development. If hornbills are eradicated, there may be a

range of rapid changes in the ecosystem, putting the long-term future of the forest at risk (Soulé et al. 2005). Even though hornbills are able to survive in disturbed and fragmented landscapes (Datta 1998, Raman and Muddapa 2003, Sitompul et al. 2004), factors affecting the occupancy of each species are rarely reported (Hadiprakarsa 2008).

With this research, I investigate site occupancy and detection probabilities of four sympatric hornbills in the southern Tenasserim landscape. I also examine the influences of landscape variables, resource availability, and habitat quality on persistence of hornbills in this modified landscape. Determining this information is an essential first step in conserving hornbills and promoting their seed dispersal role in the modified landscape of the Southern Tenasserim.

Methods

1) Study Areas

I collected data in three major types of land use found in the southern Tenasserim landscape of Thailand (Figure 6.1). These included forest areas inside protected area system in Thailand (Maenam Pachee Wildlife Sanctuary: MPWS), forest areas outside protected area system (Natural History Park initiated by was initiated by Princess Maha Chakri Sirindhorn: NHP), and forest edges and remnants in human-dominated areas near MPWS and NHP. Details of the study area are shown in Chapter 1.

2) Bird Survey

I focused my study on the four hornbill species sympatric to the region: Tickell's Brown (*Anorrhinus tickelli* Blyth, 1855), Oriental-pied (*Anthracoceros albirostris*

Shaw & Nodder, 1807), Wreathed (*Rhyticeros undulatus* Shaw, 1811), and Great (*Buceros bicornis* Linnaeus, 1758) Hornbills.

I used distance sampling combined with point counts aligned on transects to sample hornbills (Kinnaird & O'Brien 1996; Marsden 1999; Anggraini et al. 2000; Buckland et al. 2001; Gale & Thongaree 2006) in the three land-use types. Transects varied in length depending on landscape configuration. I placed each transect at least 1,000 m apart from neighboring transects to minimize double counting of individuals during simultaneous surveys. I established 100 m radius Variable Circular Plots (VCP) placed at 200 m intervals along each transect (Jornburom 2009, THP 2009).

In the forest, both inside and outside the protected areas, I first established transect lines where local people and forest rangers frequently detected hornbills and added other areas that hornbill presence was lesser reported. I also established transects along forest edge and remnants adjacent to forest areas both inside and outside the protected area including on forest edges, in plantations, and near human settlements. I walked the total of 59.8 km of 19 transects to survey hornbills at 318 point locations for 10 replicates. The point transect lines were located inside MPWS for 29.6 km (154 points), in forest outside the protected area (NHP) for 18 km (93 points), and 11.8 km in forest edge adjacent to human-dominated lands (71 points). I show total lengths of each transect line, number of points, and number of point in each habitat types in Table 6.1 and locations of point transect lines in Figure 6.1. At each point count, observers conducted the survey at least a month apart from February 2011 - February 2012. Bird surveys started one hour after sunrise and ended at least one hour before sunset (Marsden 1999; Barraclough 2000; Gregory et al. 2004) and no surveying was carried out in heavy

rain, heavy mist, or strong wind. Observers spent 10 minutes at each point, excluding time for identification and noting of data (Marsden 1999). Observers identified hornbill species sight or heard, sex (if possible), numbers of individuals, detection cue (visual/vocal), behavior, estimated distance from the center point to focal species, angle between an observer and birds relative to the transect, and compass direction to estimate position.

Figure 6.1 Locations of point transect lines in the Southern Tenasserim Western Forest Complex Corridor

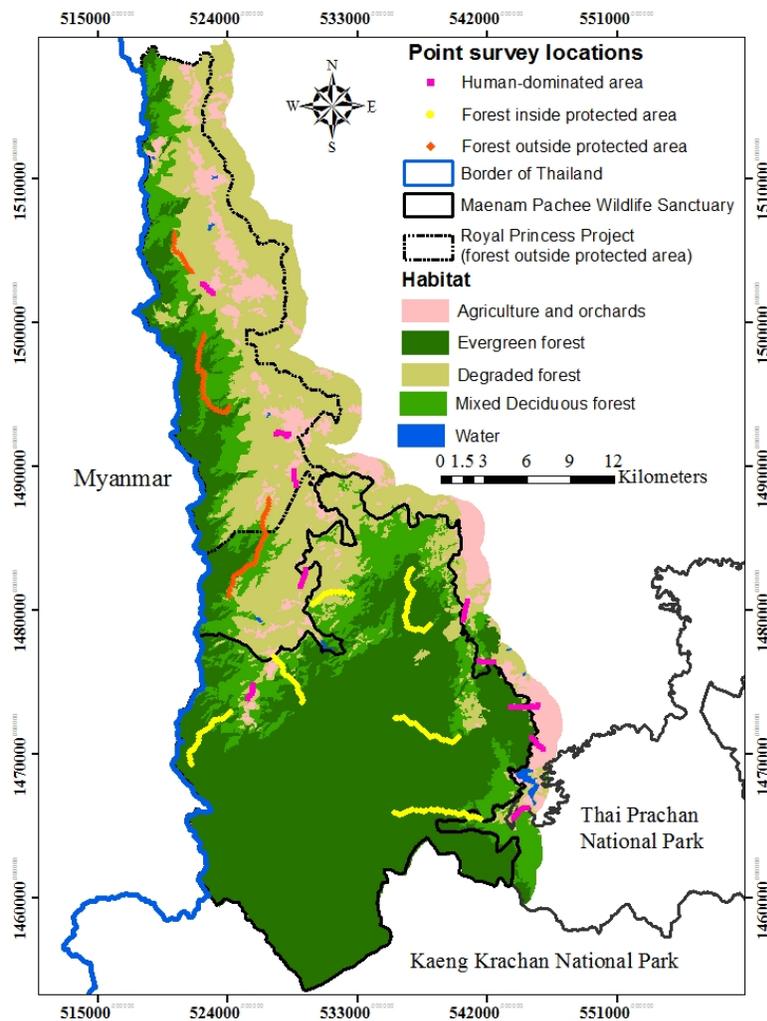


Table 6.1 Description of transect locations and point locations in each habitat type.

Habitat types	Survey Route	Distance (km)	Total points	Points in evergreen forest	Points in mixed deciduous	Points in degraded forest	Points along forest edge of human- dominated areas
Forest inside the protected area system	Nongtadung	4.2	22	12	7	3	1
	Nongyao	3.0	16	0	5	11	0
	Phurakam	5.2	27	23	3	1	0
	Phunamron	6.0	31	25	6	0	0
	Angkala	5.2	27	26	1	0	0
	Lumbuathong	6.0	31	31	0	0	0
	Total	29.6	154	117	22	15	1
Forest outside the protected area system	Huainamsai	3.0	16	0	5	11	0
	Khaokrajom	7.0	36	23	13	0	0
	Huaikokmoo	8.0	41	15	13	12	1
	Total	18	93	38	31	23	1
Forest edge and remnants in human-	Huainamsai	1.0	6	0	0	4	2
	Ban-Huaisuanphu	1.2	7	0	0	4	3
	Ban Phunamron	1.4	8	0	0	6	2

Habitat types	Survey Route	Distance (km)	Total points	Points in evergreen forest	Points in mixed deciduous	Points in degraded forest	Points along forest edge of human- dominated areas
dominated	Ban Phurakam	1.2	7	0	4	2	1
landscape	Ewog	1.0	6	0	0	3	3
	Demonstration farm	1.0	6	0	0	3	3
	Head quarter	2.0	11	0	0	6	5
	Ban Huaiphak	1.0	6	0	0	5	1
	Kaengsommeaw	1.2	7	0	0	7	0
	Subtae	1.2	7	0	0	6	1
	Total		12.2	68	0	4	46
Total		59.8	318	155	57	84	24

3) Site and Survey Covariates

I quantified physical and biological environmental variables using various techniques at each point transect location marked on GPS.

3.1) Forest Composition and Structure

I used two methods to quantify forest composition and structure. A plant taxonomist at the herbarium of the Department of National Park, Plants, and Wildlife Conservation of Thailand identified all plant specimen using plant nomenclature in Thai Plant Names (Smithinan 2001).

3.1.1) Survey Covariates on Abundance of Ripe Fruits for Hornbills

Along transects for the bird surveys, I mapped, tagged, identified, and measured fruit tree species of both figs and non-fig species with diameter at breast height (DBH) \geq 10 cm within 20 m of each side of the transect line. I initially measured the DBH to the nearest millimeter and tree height. At the initial visit and after each bird-surveying visit, I noted fruit crop size to document fruiting phenology. I categorized fruit coverage of individual trees in five intervals as suggested by Savini (2007); 76-100%, 51-75%, 26-50%, 1-25%, and 0%. I counted only ripe fruits as judged by color changes (Anggraini et al. 2000). I then multiplied percent fruit coverage in a given month by the basal area of the tree to provide a measure of fruit abundance. This calculation is modified from Anderson et al. (2002) who study the relationship between social group of chimpanzees and abundance and distribution of food in the Tai National Park, Cote d' Ivoire because I focused on the abundance of all ripe fruits in association with a particular point count, rather than the density of the species and percentage of the fruit species in this analysis. I

summed and assigned abundance of either figs or non-fig fruits from a single tree to the point count if the tree was within a 100 m radius of the bird survey point.

I took into account only the fig and non-fig fruits known to be fed upon by hornbills (for brevity henceforth referred to as “figs” and “non-figs”, respectively). The categorization of known figs and non-fig species are based on Poonswad (1993), Chimchome et al. (1998), Poonswad et al. (1998a, 1998b), Kitamura et al. (2002), Savini (2007), Boonkhao (2009, 2010), Kalayakool (2010), Kitamura et al. (2011), Chaisuriyanan et al. (2011). For fig species, I included all figs species found in the study except *Ficus hispida* L.f., *Ficus racemosa* L., *Ficus variegata* Blume, *Ficus callosa* Willd., *Ficus fistulosa* Reinw. Ex Blume, and *Ficus schwarzii* Koord because hornbills do not use them (Kinnaird et al. 1996, Poonswad et al. 1998a, P. Poonswad Mahidol University, personal communication).

3.1.2) One-time Survey on Resource Availability and Forest Quality

I used the point-centered quarter method (PCQ: Mitchell, K. 2007) to quantify the forest composition at the point counts from the bird surveys located at 200 m intervals. I collected data from two sampling points, one point was located at the point count location and the second was located 50 m ahead along the transect. I identified reproductive-sized tree species ($DBH \geq 10$ cm) in each quarter, measured the distance from the center to that tree, height of the lowest branch of each tree, and percentage of canopy cover at the point. I estimated canopy cover using a densiometer. As the height of the lowest branch of trees showing morphological inversion of trees, it is the most distinctive feature of forest age (Alexandre 1982). More disturbed forests tend to have lower heights of the lowest branch than the mature forests (for brevity henceforth referred to as “mature

forest”). I considered the trees with $DBH \geq 40.0$ cm as a potential nest trees as suggested by Poonswad et al. (1987) and Hadiprakarsa (2008), though Teampanpong (2014a) found that the minimum size of nest trees in MPWS was 48.7 cm.

I determined the density (D) for non-figs and figs, and potential nest trees at each VCP using this formula; density (D) = $\frac{1}{\text{Mean point-to-plant distance}^2}$ (trees/m²: Mitchell 2007). I then calculated dominance (D_o) of those categories of trees by multiplying average basal areas of those trees at the VCP by the density (D) (Mitchell 2007).

3.2) Landscape Covariates

At each point count, I determined distance to paved roads, unpaved roads, stream, evergreen forest, mixed deciduous forest, degraded forest, and human-induced areas based on map classifications by WCS-TP (2009b). Human-dominated areas included human settlement, agricultural area, orchard, plantation, old clearing, and human-made tourist site. To obtain the distance to these landscape features, I used Spatial Analyst Tool in ArcGIS 10.1(ESRI, Redlands, CA) to extract values to each location.

3.3) Human Disturbance

I recorded any evidence of human disturbance found during the bird survey. These included evidence of hunting (cartridges, carcasses, human encounter with guns, temporary camps with hunting equipment), tree cutting (cutting marks, tree stumps), tree clearing, fire, collection of non-timber forest products (NTFPs: residuals from NTFPs collecting), and disturbance due to domestic animals (Wieland 2008, WCS-TP 2009a). I classified forest paths, sounds, garbage, direct encounters with humans, and temporary campfires as threats of undetermined purpose.

I weighted the signs of disturbance according to the level of threat to wildlife. I considered hunting, fire, and human settlement as the most severe and gave it a level of (3). This was followed by tree cutting, forest clearing, and tourism with a level of (2) and collecting NTFPs and other threats of undetermined purposes with a level of (1).

4) Occupancy Models

I developed occupancy models for the three levels of land use – forest edge adjacent to human-dominated area, the forest outside protected areas (NHP), the forest inside protected areas (MPWS) – and combined data from those three levels of land use to represent the entire landscape for each hornbill species as well as the larger-sized hornbills combined (the Great and Wreathed Hornbills).

To estimate occupancy rate (ψ) and detection probability (p), I used a single-site species occupancy model using the “unmarked” package in R version 3.0.2 (R Core Team 2013). This method has three assumptions: 1) the closure occurrence of species throughout the course of the study, 2) no false positive identification, and 3) independent detection at all sites. I standardized continuous covariates before running the model. I then tested the multicollinearity of all site covariates using Spearman correlation and Variance Inflation Factor (VIF). VIF measures the increased variance of an estimated coefficient due to collinearity. Its value greater than 5 indicates a high multicollinearity. I also used the automated model selection process to select the covariates for building parsimonious models.

I used Akaike’s Information Criterion (AIC) to rank the models and I considered only the models with $\Delta\text{AIC} \leq 2$ to have strong support (Burnham and Anderson 2002). I did model averaging when a number of top ranked models had similar AIC weights to

estimate occupancy from multiple models of each species (Burnham and Anderson 2002). I then assessed the best-fit model based on 2000 parametric bootstraps of the candidate set for each species (Mackenzie and Bailey 2004).

I constructed models with the most basic null model with no spatial dependence [$\psi(\cdot), p(\cdot)$]. In other words, the model occupancy and detection probabilities were constant across sampling period and habitat covariates. I then incorporated covariates that may affect occupancy rate and detection probability of each hornbill species by modeling the parameters as a logit function of landscape characteristics, resource availability, and habitat quality. Description of the covariates used in occupancy estimation is shown in Table 6.2.

I considered all landscape variables, forest composition and structure, and numbers of fruit species and individual fruit trees as site-specific covariates because they were based on one-time survey. In contrast, I considered abundance of ripe fig and non-fig species, and threat severity during the bird survey as sampling-occasion covariates in my occupancy model.

Table 6.2 Description of covariates used in occupancy models

Covariates	Code	Values
Landscape Characteristics		
Slope	slope	0-42 degree
Digital elevation	dem	164.67 – 1,057 m.
Patch size	area	0.051 – 385.10 km ²
Distance to stream	stream	0 - 966.08 m
Distance to evergreen forest	green	0 - 4,588.43 m

Covariates	Code	Values
Distance to mixed deciduous forest	mixed	0 - 3,695 m
Distance to degraded forest	degraded	0 - 5,949.16 m
Distance to human settlement/agriculture	human	0 - 7,561.55 m
Distance to paved road	paved	0 – 11,873.70 m
Distance to unpaved road	unpaved	0 – 5,608.15 m
Resource availability		
Number of fig species	figsp	0 - 8
Number of non-figs species	hbsp	0 - 8
Numbers of fig trees	fig	0 - 8
Numbers of non-fig trees species	hb	0 - 8
Number of potential nest trees	potent	0 - 5
Monthly abundance of ripe fig fruits	mofig	0 - 71.28%
Monthly abundance of ripe non-fig fruits	mohb	0 - 51.95
Habitat Quality		
Threats due to human	threat	0 = none, 1 = low, 2 = medium, 3 = high
Density of trees (trees/m ²)	den	0.002 - 0.262
Density of non-figs species (trees/m ²)	hbden	0 - 0.718
Density of fig species (trees/m ²)	figden	0 - 1
Density of potential nest tree (trees/m ²)	potden	0 - 0.592
Dominance of non-fig species	hbdo	0 - 2.177
Dominance of fig species	figdo	0 - 50.691
Dominance of trees	do	0.003 - 5.359
Dominance of potential nest trees	potdo	0 - 128.328
%Crown Cover	crown	0 - 100%
Height of the first branch of tree	fh	1.21 – 17 m

Results

I found only four hornbill species including the Oriental-pied, Tickell's Brown, Wreathed, and Great Hornbills out of five species thought to be endemic to the southern Tenasserim Corridor according to a survey by Thailand Hornbill Project (Vithedhamr et al. 1995).

I did not find the Great, Wreathed, and the Tickell's Brown Hornbill in the forest edge in human-dominated areas. However, I found two detections of the Brown Hornbill approximately 200 m from the edge of evergreen forest and approximately 800 m from the edge of degraded forest adjacent human settlement near a forest ranger station. The Oriental-pied Hornbill was the only hornbill species that made use of the sharp edge of forest adjacent to human-influenced areas near forest ranger stations.

1) Number of Detections

The total numbers of detection was 308 (9.686%) out of 3,180 efforts in the entire landscape, with relative abundance of four hornbill species of 0.515 individuals/km. The Wreathed Hornbill had the highest number of detections (101 or 3.176%) and highest relative abundance (0.169 individuals/km), followed by the Great (94 detections or 3.000%, and 0.157 individuals/km), Oriental-pied (75 detections or 2.359% and 0.125 individuals/km), and Tickell's Brown (38 detections or 1.195% and 0.064/km) Hornbills.

The total number of detections and relative abundance in forest inside the protected area was highest for the Wreathed Hornbill (90 detections or 5.844%, 0.304 individuals/km), followed by the Great (86 detections or 5.584%, 0.324/km), the Oriental-pied (56 detections or 3.636%, 0.189 individuals/km), and the Tickell's Brown (31 detections or 2.013%, 0.105 individuals/km) Hornbills.

In forest outside the protected area, the total number of detections and abundance of the Wreathed Hornbill was greatest (11 detections or 1.183%, 0.061 individuals/km), followed by the Great Hornbill (8 detections or 0.860%, 0.044/km), the Tickell's Brown Hornbill (5 detections or 0.538%, 0.028/km), and Oriental-pied Hornbill (1 detection or 0.108%, 0.006/km). Lastly, I found the Oriental-pied Hornbill in the forest edge along human dominated areas with 18 detections (2.535%) and an abundance of 0.148 individual/km. In addition, The Tickell's Brown Hornbill was able to use degraded forest within 200 m of the edge of evergreen forest and 800 m from the edge of degraded forest to human settlement, though these were still within the boundary of MPWS.

2) Occupancy Rate and Detection Probability of Hornbills

I estimated site occupancy and detection probability of the individual hornbill species and the larger-sized hornbills based on three set of covariates including landscape characteristics, habitat quality, and resource availability.

2.1) Entire Landscape

The detection probability of the Wreathed Hornbill was highest followed by the Great, Oriental-pied, and Tickell's Brown Hornbills for all set of covariates (see Table 6.3). However, the site occupancy of the smaller-sized hornbills (Oriental-pied and Tickell's Brown Hornbills) was likely to be higher than the Wreathed, Great Hornbills (see Table 6.4). Generally, all four sympatric hornbills tended to negatively respond to any form of human disturbance including distance from human settlement, roads, and threats due to human activity. They were likely to be found in habitats providing higher numbers of potential nest trees and numbers of non-fig trees. While the smaller-sized hornbills were likely to be encountered in habitats with a higher density of non-fig trees,

the larger-sized hornbills tended to use the more mature forest with denser canopy cover and less severity of threat.

The Tickell's Brown Hornbill was likely to occupy habitats farther from unpaved roads (estimate \pm se: 1.68 ± 0.52 , $z = 3.21$, $P = 0.001$) providing higher numbers of non-fig species (1.79 ± 0.69 , $z = 2.57$, $P = 0.010$). Meanwhile, its detection probability increased in habitats farther from unpaved road (0.834 ± 0.155 , $z = 5.4$, $P < 0.001$) having higher density of non-fig trees (0.528 ± 0.198 , $z = 2.67$, $P = 0.008$) with decreased threat severity (-0.481 ± 0.243 , $z = -1.98$, $P = 0.048$).

The Oriental-pied Hornbill tended to inhabit larger forest patches (1.68 ± 0.78 , $z = 2.16$, $P = 0.030$) at lower elevation (-4.90 ± 1.79 , $z = 2.74$, $P = 0.006$) ranging from 219-965 m.a.s.l. It tended to be detected farther from human settlements (0.54 ± 0.10 , $z = 5.18$, $P < 0.001$). A higher density of non-fig species (0.163 ± 0.067 , $z = 2.41$, $P = 0.016$), numbers of fig species (0.186 ± 0.094 , $z = 1.99$, $P = 0.047$) and numbers of potential nest trees (0.255 ± 0.124 , $z = 20.5$, $P = 0.040$) in more mature forest (0.334 ± 0.127 , $z = 2.64$, $P = 0.008$) also increased its detection probability.

The Wreathed Hornbill tended to occupy the more mature forest (0.442 ± 0.225 , $z = 1.96$, $P = 0.050$) containing higher numbers of non-fig trees (2.6 ± 1.17 , $z = 2.22$, $P = 0.026$) but farther from human settlement (2.93 ± 0.709 , $z = 4.13$, $P < 0.001$). The detection probability of the Wreathed Hornbill tended to increase near evergreen forest (-4.43 ± 2.03 , $z = -2.18$, $P = 0.029$) with lower threat severity (-1.11 ± 0.30 , $z = -3.68$, $P < 0.001$).

The Great Hornbill was likely to occupy habitats with thicker canopy cover (1.079 ± 0.464 , $z = 2.327$, $P = 0.020$) containing higher numbers of potential nest trees (0.877 ± 0.417 , $z = 2.102$, $P = 0.036$) and increased non-fig trees (1.954 ± 0.520 , $z = 3.756$,

P = <0.001) farther from human settlement (3.80±1.18, z = 3.22, P = 0.001). Its detection probability also increased in larger (0.624±0.209, z = 2.98, P = 0.003), more mature (0.283±0.132, z = 2.14, P = 0.032) evergreen forest patches (-5.93±2.63, z = -2.26, P = 0.020) that were located farther from human settlement (0.669±0.207, z = 3.24, P = 0.001) with less threat severity (-1.548±0.633, z = -2.45, P = 0.014).

Table 6.3 Summary of detection probability (mean ± se and its 95% CI) estimated from the top and naïve models of the four sympatric hornbills in three different land-use types and the entire landscape of the southern Tenasserim. “Entire” refers to the entire landscape. “Inside” refers to forests within protected areas. “Outside” refers to forests outside of protected areas. “Forest edge” refers to forests intermixed with other land-use types.

Hornbill	Entire	Inside	Outside	Forest edge
Landscape variables				
Tickell's	0.024±0.014	0.034±0.009	0.005±0.003	-
Brown	(0.014 - 0.041)	(0.021 - 0.057)	(0.002 - 0.019)	-
Oriental-pied	0.041±0.007	0.059±0.013	N/A	0.027±0.011
	(0.030 - 0.057)	(0.038 - 0.09)		(0.015 - 0.049)
Wreathed	0.078±0.014	0.083±0.014	0.021±0.021	-
	(0.055 - 0.109)	(0.059 - 0.116)	(0.003 - 0.133)	-
Great	0.046±0.031	0.003±0.004	0.009±0.035	-
	(0.027 - 0.083)	(0.004 - 0.023)	(0.058 - 0.097)	-
Larger-sized	0.074±0.010	0.124±0.017	0.029±0.017	-
hornbills	(0.057 - 0.097)	(0.095 - 0.162)	(0.009 - 0.090)	-
Resource availability				

Hornbill	Entire	Inside	Outside	Forest edge
Tickell's	0.025±0.010	0.021±0.005	0.049±0.024	N/A
Brown	(0.014 -0.047)	(0.013 – 0.035)	(0.009 – 0.116)	
Oriental-pied	0.041±0.013 (0.024 – 0.070)	(naïve)	N/A	0.027±0.009 (0.014 – 0.054)
Wreathed	0.071±0.010 (0.053 – 0.094)	0.086±0.017 (0.058 – 0.125)	(naïve)	N/A
Great	0.069±0.010 (0.052 - 0.092)	0.088±0.013 (0.065-0.127)	(naïve)	N/A
Larger-sized hornbills	0.101±0.013 (0.078 – 0.128)	0.128±0.022 (0.100 – 0.162)	(naïve)	N/A
Tickell's	0.021±0.013	0.021±0.008	0.005±0.003	N/A
Brown	(0.008 – 0.051)	(0.012 – 0.039)	(0.002 – 0.017)	
Oriental-pied	0.041±0.011 (0.025 – 0.069)	0.055±0.015 (0.032 – 0.092) naïve	N/A	0.039±0.027(0.017 – 0.073)
Wreathed	0.066±0.011(0.047 – 0.094)	0.085±0.020 (0.059 – 0.121)	(naïve)	N/A
Great	0.055±0.012 (0.036 - 0.089)	0.092±0.014 (0.069 – 0.122)	0.009±0.004 (0.004 – 0.022)	N/A
Larger-sized hornbills	0.092±0.011 (0.073 – 0.118)	0.129±0.016 (0.101 – 0.163)	(naïve)	N/A
Habitat				
quality				
Tickell's	0.018±0.010	0.023±0.013	0.005±0.003	-
Brown	(0.006 – 0.055)	(0.008 – 0.067)	(0.002 – 0.014)	
Oriental-pied	0.043±0.011 (0.026 – 0.072)	0.055±0.015 (0.032 – 0.092)	-	0.027±0.006 (0.017 – 0.042)
Wreathed	0.085±0.014	0.094±0.015	0.021±0.021	N/A

Hornbill	Entire	Inside	Outside	Forest edge
	(0.062 – 0.116)	(0.068 – 0.129)	(0.003 – 0.133)	
Great	0.078±0.014	0.087±0.015	0.009±0.003	N/A
	(0.055 – 0.109)	(0.062 – 0.122)	(0.004 – 0.017)	
Larger-sized	0.121±0.012	0.134±0.014	0.039±0.021	N/A
hornbills	(0.099 – 0.147)	(0.109 – 0.163)	(0.013 – 0.110)	

Table 6.4 Summary of occupancy rates estimated from the top model or model averaging and its 95% CI of the four sympatric hornbills in three different land uses and the entire landscape of the southern Tenasserim. “Entire” refers to the entire landscape. “Inside” refers to forests within protected areas. “Outside” refers to forests outside of protected areas. “Forest edge” refers to forests intermixed with other land use types.

Hornbill	Entire	Inside	Outside	Forest edge
Landscape variables				
Tickell’s	0.644± 0.344	0.611±0.144	-	N/A
Brown	(0.078 – 0.742)	(0.212 – 0.827)		
Oriental-pied	0.627±0.588	0.594±0.105	N/A	0.999±0.013
	(0.388 – 0.743)	(0.156 – 0.796)		(3.12×10 ⁻²⁴ -1)
Wreathed	0.389±0.067	0.624±0.080	(naïve)	N/A
	(0.256 – 0.519)	(0.412 – 0.767)		
Great	0.316±0.080	0.807±0.238	-	N/A
	(0.222 – 0.561)	(0.150 – 0.853)		
Larger-sized	0.542±0.065	0.728±0.059	0.698±0.352	N/A
hornbills	(0.411 - 0.673)	(0.547 – 0.829)	(0.081 – 0.984)	
Resource availability				
Tickell’s	0.511 ±0.238	-	0.147±0.069	N/A

Hornbill	Entire	Inside	Outside	Forest edge
Brown	(0.109 – 0.694)		(0.038 – 0.395)	
Oriental-pied	0.576±0.139 (0.309 – 0.805)	(naïve)	N/A	-
Wreathed	0.418±0.062 (0.283 – 0.533)	0.667±0.093 (0.468 – 0.820)	(naïve)	N/A
Great	0.427±0.076 (0.251 - 0.560)	0.626±0.112 (0.339 -0.798)	-	N/A
Larger-sized hornbills	0.529±0.061 (0.384 - 0.636)	0.784±0.124 (0.562 – 0.885)	(naïve)	N/A
Habitat				
quality				
Tickell's	0.653±0.324	0.993±0.127	-	N/A
Brown	(0.132 – 0.904)	(1.47×10 ⁻¹³ -1)		
Oriental-pied	0.580±0.013 (0.314 – 0.795)	(naïve)	N/A	0.893±0.099 (0.522 – 0.985)
Wreathed	0.466±0.082 (0.311 – 0.621)	0.670±0.130 (0.440 – 0.835)	(naïve)	N/A
Great	0.461±0.096 (0.279 – 0.651)	0.595±0.108 (0.342 – 0.777)	-	N/A
Larger-sized hornbills	0.544±0.077 (0.393 – 0.691)	0.769±0.076 (0.583 – 0.884)	(naïve)	N/A
Naïve model				
Tickell's	0.649±0.351	-	-	N/A
Brown	(0.083 - 0.974)			
Oriental-pied	0.547±0.132 (0.298 – 0.774)	0.649±0.157 (0.324 – 0.877)	N/A	-
Wreathed	0.375±0.056	0.608±0.086	0.552	N/A

Hornbill	Entire	Inside	Outside	Forest edge
	(0.273 - 0.488)	(0.433 - 0.760)	(0.028 - 0.986)	
Great	0.379±0.061	0.628±0.095	-	N/A
	(0.269 - 0.502)	(0.433 - 0.788)		
Larger-sized	0.46±0.044	0.752±0.064	0.526±0.268	N/A
hornbills	(0.376 - 0.547)	(0.608 - 0.856)	(0.119 - 0.901)	

Lastly, the larger-sized hornbills (the Great and Wreathed Hornbills combined) tended to occupy habitats with denser canopy cover (0.835 ± 0.351 , $z = 2.378$, $P = 0.017$) at farther distance from paved roads (2.784 ± 0.595 , $z = 4.68$, $P < 0.001$) that still provided higher numbers of non-fig trees (1.98 ± 0.536 , $z = 3.69$, $P < 0.001$). Meanwhile, their detection probability increased with remote distance from unpaved road (0.78 ± 0.113 , $z = 6.91$, $P < 0.001$) in habitats with higher numbers of potential nest trees (0.202 ± 0.76 , $z = 2.65$, $P = 0.008$) and having lower severity threats (-1.15 ± 0.295 , $z = -3.9$, $P < 0.001$).

I depicted the occupancy rate and detection probability of each hornbill species based on three sets of covariates in the entire landscape based on different set of covariates in Tables 15-17 in the appendix.

2.2) Forest Inside Protected Area

Forest inside protected areas plays a significant role in conserving the four sympatric hornbills in the southern Tenasserim landscape. The occupancy probabilities of Tickell's Brown and Oriental-pied Hornbills were comparable to those of the entire landscape. However, the occupancy probabilities of the Wreathed and Great Hornbills and the larger-sized hornbills combined in the forest inside protected area were higher than those in the entire landscape. In addition, the detection probabilities of the larger-

sized hornbills tended to be greater than those of the smaller-size hornbills (see Table 6.3 and 6.4).

Similar to the entire landscape, all four sympatric hornbills were likely to occupy habitats farther from any forms of human disturbance but near or within evergreen forest. The Tickell's Brown Hornbill was likely to occupy habitats farther from degraded forest (1.877 ± 0.935 , $z = 2.008$, $P = 0.045$) which is positively significantly correlated to distance to unpaved road ($\rho = 0.807$, $P < 0.001$, $VIF = 13.734$). Moreover, its detection probability was likely to increase in habitats farther from unpaved road (0.479 ± 0.190 , $z = 2.52$, $P = 0.012$) with lower severity of threat (-0.231 ± 0.110 , $z = 2.1$, $P = 0.035$) that still retained higher numbers of non-fig species (0.338 ± 0.153 , $z = 2.21$, $P = 0.027$) and a higher density of non-figs (0.594 ± 0.276 , $z = 2.15$, $P = 0.031$).

Besides occupying habitat farther from human settlement (1.591 ± 0.637 , $z = 2.498$, $P = 0.013$), the Oriental-pied Hornbill tended to select habitats at lower elevations (3.848 ± 1.591 , $z = -2.15$, $P = 0.032$) ranging from 229 - 965 m.a.s.l. Its detection probability was higher at distances farther from human settlement too (0.341 ± 0.163 , $z = 2.1$, $P = 0.036$).

In addition to avoiding paved road (2.56 ± 0.816 , $z = 3.13$, $P = 0.002$), the Wreathed Hornbill was likely to occupy more mature forest (3.470 ± 1.478 , $z = 2.35$, $P = 0.019$). Its detection probability increased farther from mixed deciduous forest (0.385 ± 0.103 , $z = 3.73$, $P < 0.001$) and in the more mature forest (0.313 ± 0.096 , $z = 3.25$, $P = 0.001$) with increased numbers of potential nest trees (0.319 ± 0.146 , $z = 2.18$, $P = 0.029$).

Similar to the Wreathed Hornbill, the Great Hornbill was prone to use habitats farther from human settlement (2.777 ± 0.675 , $z = 4.112$, $P < 0.001$). It also inhabited forests with increased numbers of potential nest trees (4.529 ± 2.292 , $z = 1.975$, $P = 0.050$) and higher numbers of non-fig trees (1.302 ± 0.563 , $z = 2.312$, $P = 0.021$). Additionally, it was likely to occupy mature forests (0.976 ± 0.497 , $z = 1.97$, $P = 0.050$) with denser canopy cover (2.076 ± 0.738 , $z = 2.81$, $P = 0.005$).

Lastly, I found the larger-sized hornbills used evergreen forest (-8.391 ± 3.93 , $z = -2.14$, $P = 0.033$) with denser canopy cover (10.4 ± 0.433 , $z = 2.41$, $P = 0.016$) that was farther from paved road (3.173 ± 0.136 , $z = -14.73$, $P < 0.001$). They were also likely to occupy habitats with higher numbers of potential nest trees (1.40 ± 0.62 , $z = 2.26$, $P = 0.024$) and higher numbers of non-fig trees (2.29 ± 1.02 , $z = 2.24$, $P = 0.025$). Their detection probability increased in the more mature forest (0.264 ± 0.077 , $z = 3.43$, $P < 0.001$) at farther distances from paved roads (0.368 ± 0.130 , $z = 2.83$, $P < 0.001$) in habitats having higher numbers of non-fig trees (0.24 ± 0.10 , $z = 2.4$, $P = 0.017$) and higher numbers of potential nest trees (0.222 ± 0.083 , $z = 2.66$, $P = 0.008$).

I described the occupancy rate and detection probability of each hornbill species in forest inside protected areas based on different set of covariates shown in Table 18 -20 in the appendix.

2.3) Forest outside Protected Area

Due to one detection of the Oriental-pied Hornbill in the forest outside protected area, I was able to model only the Tickell's Brown, Wreathed, and Great Hornbills.

The detection probability of the Tickell's Brown Hornbill was lowest in the forest outside protected areas (number of detections = 5). All detections occurred in one

approximately 3 km² area during three contiguous replicates in a breeding season. Local people reported its nest location in the same area but I could not find it. I found the Tickell's Brown Hornbill occupied habitats providing higher numbers of non-fig trees (2.24 ± 1.09 , $z = 2.06$, $P = 0.040$). Its detection probability increased at farther from unpaved road (1.19 ± 0.59 , $z = 2.01$, $P = 0.045$) in the habitats providing higher abundance of ripe fig fruits (2.84 ± 1.44 , $z = 1.97$, $P = 0.049$) and higher dominance of non-fig trees (0.363 ± 0.134 , $z = 2.72$, $P = 0.007$).

I was unable to detect any covariates on landscape variables, resource availability, and habitat quality on the occupancy and detection probability of the Wreathed Hornbill. As for the Great Hornbill, its detection probability increased in habitats farther from degraded forests (1.10 ± 0.385 , $z = 2.85$, $P = 0.004$). More interestingly, I also found the higher detection probability of the Great Hornbill in habitats with a greater severity of threat (0.336 ± 0.158 , $z = 2.13$, $P = 0.033$). However, none of covariates on resource availability had an effect on its occupancy and detection probabilities. As for the larger-sized hornbills, their detection probability increased at habitats farther from human settlement (0.76 ± 0.349 , $z = 2.18$, $P = 0.029$). I present the occupancy rate and detection probability of each hornbill species in different set of covariates in the forest outside protected area in Table 21- 23 in appendix.

2.4) Forest Edge and Remnants in Human-dominated Areas

Though I detected the Oriental-pied Hornbill in forests outside the protected area only once ($n = 1$), it is the only hornbill species that made use of the edge of the forest inside the protected area adjacent to ranger stations.

The Oriental-pied Hornbill was detected in the forest edge farther from human settlement (0.447 ± 0.199 , $z = 2.25$, $P = 0.025$) but closer to mixed deciduous forest (-0.628 ± 0.294 , $z = -2.14$, $P = 0.033$). Its detection probability was higher in the forest edge with denser canopy cover (0.545 ± 0.224 , $z = 2.44$, $P = 0.015$) containing higher abundance of ripe fig fruits (21.758 ± 6.496 , $z = 6.496$, $P < 0.001$); higher dominances (0.612 ± 0.164 , $z = 3.73$, $P < 0.001$) and numbers (0.557 ± 0.176 , $z = 3.16$, $P = 0.002$) of fig trees; higher dominance (0.970 ± 0.316 , $z = 3.07$, $P = 0.002$) and numbers of potential nest trees (0.970 ± 0.316 , $z = 3.07$, $P = 0.002$); but less threat severity (-0.841 ± 0.291 , $z = -2.89$, $P = 0.004$). The occupancy rate and detection probability of the Oriental-pied Hornbill in forest edges based on different set of covariates is in Table 24 in appendix.

Discussion

This study estimated site occupancy and detection probability of four sympatric hornbills in the southern Tenasserim landscape. I compared the results in three different land-use types -- forest inside protected areas, forest outside protected areas, and in human-dominated areas – as well as in the entire landscape of the southern Tenasserim. Specifically, I was curious if occupancy and detection rates of hornbills may be influenced by landscape characteristics, resource availability, and habitat quality.

My findings highlight the importance of mature evergreen forest farther from human disturbance in maintaining the existing hornbill population. In addition, it highlights the need to preserve available non-fig fruiting trees, and fig trees in the landscape because they play a significant role in attracting hornbills from the source

populations within protected area out to the marginal habitats of the landscape.

Undoubtedly, human activities are also a significant risk to hornbills.

1) Effects of Landscape Characteristics on Hornbills

My results emphasize the importance of evergreen forest in maintaining hornbill population in the southern Tenasserim landscape. This is consistent with many hornbill studies (Datta 1998, Tefong 2007, Kalyakool 2010, Keartumsom 2011, Jinamoy et al. 2014). Moreover, my findings agree with Hadprakarsa (2008) that forest patch size influences the distribution of the Great Hornbill. Contrarily, I found forest patch size did not influence the distribution of the Wreathed Hornbill. While I agreed with Hadprakarsa (2008), Trisurat et al. (2013) remarked about the significance of patch size on the distribution of Wreathed, Brown, and Great Hornbills.

Moreover, my results support both Datta (1998), who worked in Arunachal Pradesh, India, and my earlier work (Teampanpong 2014b), studying resource selection models for immature Oriental-pied Hornbill in working landscape of the southern Tenasserim corridor in Thailand. The Oriental-pied Hornbill tended to occupy habitats in lower elevation.

2) Effects of Human Activities on Hornbills

Although hornbills are capable of long-distance dispersal (Kemp 1995, Poonswad 1998a, Holbrook et al. 2002, Kinnaird and O'Brien 2007), I show that human disturbance may affect their distribution, abundance, and survival. This supports other work in Thailand (Vidhidharm et al. 1995, Poonswad 1998a, Pattanavibool et al. 2004, Trisurat et al. 2013) and in other countries (Kemp 1995, Datta 1998, Kinnaird and O'Brien 2007, Stone 2007, Trail 2007, Martin and Blackburn 2010).

My study underlined that human settlement and associated activities pose significant vulnerability in this landscape by reducing abundance, numbers of detections, and occupancy rates of all four sympatric hornbills in the forest outside the protected area. This result was similar to Sethi and Howe (2009) that the abundances of the Great, Wreathed, and Oriental-pied Hornbills in disturbed forests were lower than in protected areas. Hadprakarsa (2008) also found that the patch occupancy of the Great Hornbill was greater in forest patches with lower human disturbance. In contrast, while Hadprakarsa (2008) found that habitat disturbance did not affect the occupancy of the Wreathed Hornbill, detection probability of the Wreathed Hornbill in my study was reduced when threat severity increased. I speculate that this inconsistent result is because Hadprakarsa (2008) classified only two levels of threats-high (1) and low (0).

Impact of human activities seems to affect particularly the occupancy of the Oriental-pied Hornbill. This can be clearly seen by the single detection of an Oriental-pied Hornbill in the forest outside the protected area with 18 detections occurring in the forest edge near ranger stations of MPWS where the patrolling system is more intensive and/or local people depend less on natural resources from forests. This may imply that activities in villages both located inside and outside the protected area effectively fragment the forest by breaking linkages between the forests inside and outside the protected area. This may impede dispersal of the Oriental-pied Hornbill and supports the idea that fragmentation tends to negatively affect smaller-sized hornbills than the larger ones (Hadprakarsa 2008).

The deleterious effects of human disturbance were confirmed by Teampanpong (2014d). In that study, I reported that immature Oriental-pied Hornbills emerging from

the nest not far from the village in MPWS tended to approach the edge of evergreen forest but did not go beyond it to reach degraded forests. This occurred despite Oriental-pied being classified as generalists (Kemp 1995, Datta 2003, Kinnaird and O' Brien 2007), which can inhabit a wide range of forests including evergreen, mixed deciduous, degraded, and plantation forests (Tsuji et al. 1987, Datta 1998, Anggraini et al. 2000) and can consume several small-sized berries including lianas (Datta 2003) and fallen fruits (Kitamura et al. 2009) that are more typical of degraded forests.

In summary, although land development in the southern Tenasserim landscape has not fragmented the forest into many small patches as viewed from the human perspective; sparse human use of these forests may have resulted in *de facto* fragmentation from the perspective of the hornbills. Despite the remaining forest being adjacent to large contiguous forest tracts in Myanmar and Kaeng Krachan National Park (KKNP), I found that land conversion and less regulated use of natural resources and human disturbance in the forest has negatively influenced hornbill dispersal between those forest areas, MPWS and NHP.

3) Effects of Available Resources on Hornbills

Available known non-figs species is one of the most influential factors in determining occupancy and detection probabilities of all hornbill species according to this study. Additionally, the monthly abundance of ripe fig species was also important in determining detection probability of the Tickell's Brown in both the forest outside the protected areas and of the Oriental-pied Hornbill in the forest edge.

Some of my findings are similar to Datta and Rawat (2003) who worked in Arunachal Pradesh, India. They found that in the non-breeding season, the Wreathed

Hornbill depended more on non-fig species than figs and the Oriental-pied Hornbill ate both figs and non-figs equally. Hadiprakarsa and Kinnaird (2004) similarly reported that the Wreathed Hornbill preferred non-figs and oily drupes.

My results support Anggraini et al. (2000) who found that the numbers of Sumatran hornbills increased when available ripe fruits increased. Additionally, Raman and Muddapa (2003) found that abundance of the Great Hornbills positively correlated to richness of food tree species. I (Teampanpong 2014a) found that the density of non-figs species in the forest inside the protected areas was significantly higher than outside the protected area. This supports further the idea that lower occupancy rate of hornbills in the forest outside protected area was due to food availability. Additionally, Anggraini et al. (2000) found that highly disturbed forest had significantly lower numbers of all families of non-fig species compared to the primary forest.

Contrarily, Datta (1998) discovered that the abundance of hornbills in Arunachal Pradesh, India correlated with density of trees but did not correlate to the densities of fig trees, potential fruit species of hornbills, nor the potential nest trees.

Figs are a year-round keystone food for tropical frugivores including hornbills (Kinnaird et al. 1996, Poonswad et al. 1998b, Kannan and James 1999, Savini 2007, Sanitjan and Chen 2009). Poonswad et al. (1998a) found that the larger-sized hornbills preferred figs more than the smaller-sized hornbills did. Additionally, many studies in India and Thailand have reported reliance of the Great Hornbill on fig species (Poonswad et al. 1988, Kannan and James 1998, Kannan and James 1999, Ouithavon 2000, Data and Rawat 2003). Contrarily, I found abundance of ripe fig fruits played a pivotal role in

determining the occupancy of the smaller-sized hornbills (Tickell's Brown and Oriental-pied Hornbills) in less healthy forest outside protected area and at the forest edge.

I speculate that figs species in my site may likely produce fruits smaller than 3 cm so the Great Hornbills are less likely to eat them (Ouithavon 2000). Boonkhao et al. (2010) confirmed that the Tickell's Brown and Oriental-pied Hornbills were likely to consume medium-sized fig fruits (1.1-1.5 cm) at my site but were likely to use a very large-sized fig fruits (>2.1 cm) at Kaeng Krachan National Park, south of MPWS (Boonkhao et al. 2010). Potentially, the smaller-sized hornbills in less healthy forests relied more on the abundance of ripe fig fruits because of low density of non-fig trees (Teampanpong 2014a) although the smaller hornbills are known to consume fruits at a lower rate than the larger hornbills (Poonswad et al. 1998a). In addition, I found none of non-fig species in the forest edge along human-dominated areas.

In addition to the importance of fig and non-fig fruits, I found that the larger-size hornbills, including the Wreathed and Great Hornbills, relied on the availability of potential nest trees. This is similar to the study by Hadiprakarsa (2008) in Southern Sumatra, Indonesia who found that the density of potential nest trees was one the most important covariates for determining occupancy for the Great Hornbill.

4) Effects of Forest Quality on Hornbills

Older-growth forest and closed canopy cover are important features of a forest for the larger-sized hornbills. My findings underscored the necessity of older-growth forest as foraging and breeding sites for the Great and Wreathed Hornbills. This result is consistent with many other hornbill studies (John et al. 1987, Kannan and James 1998, Datta 1998, James and Kannan 2009, Martin and Blackburn 2010, and Margareta and Nugroho 2013).

Furthermore, threats due to humans such as hunting, collecting NTFPs, cutting of trees, clearing forests, and other activities associated with the presence of humans in the forest area played a significant role in manipulating site occupancy of all hornbill species in the entire landscape of the southern Tenasserim. Nevertheless, I found that the Great Hornbill in the forest outside protected areas tended to be detected in habitats that had higher levels of human disturbance. This most likely is because prime forest at the site has become trekking trail for tourists, sources of non-timber forest products, and is situated near routes that Karen troops use to travel to town in Thailand.

I speculate that lax management over the long term in the forest outside the protected area, pressure from development, and the uncontrolled harvest of natural resources all combine to increase the severity of threats to hornbills. This has led to the gradual eradication of hornbills outside the protected areas in the region, consequently resulting in my low detection of all four hornbill species, particularly the Oriental-pied Hornbill.

These results highlight the importance of protected areas for the conservation of hornbills in this landscape. Sethi and Howe (2009) support this idea by emphasizing the importance of a protected area system for hornbill conservation in Indian Eastern Himalaya. They, too, found the lower abundance of the Great, Wreathed, and Oriental-pied Hornbills and more severe depression in recruitment of seedlings in hunted and logged forest than in protected forests.

Conservation Implications

Knowing about a species that inhabits both degraded and mature forest landscapes and the extent of its presence in both of these types of forest can lead to a more accurate measure of the value of modified landscapes and ability to conserve regional forest biodiversity. This paper provides information on one group of such species – the hornbills – in the southern Tenasserim corridor in Thailand. My research provides useful guidelines for promoting natural restoration of the area by hornbills.

I found a high dependence of all four sympatric hornbills on mature evergreen forests that were far from human-dominated areas, which had ripe figs and other large non-fig fruits available. This suggests that in order to maintain hornbills in this landscape, it will be necessary to maintain existing mature evergreen forests and available fig and non-fig trees, as well as reducing human disturbances to hornbills.

However, to promote natural restoration by hornbills in this landscape, the protection of existing protected areas is not enough. I recommend promoting local communities around the forest areas both inside and outside the protected area to maintain native fig trees in their farms as temporary food sources for hornbills.

In addition to landscape protection, the low occupancy rate and detection of hornbills in the forest outside protected area and the resistance of hornbills to use human-dominated areas, suggests that conservation action and outreach are essential. I recommend two paradigms for sustainable development of this landscape: 1) the prototype of hornbill conservation outreach in southern Thailand (Poonswad et. al. 2005, Poonswad et al. 2012) which engages local people in hornbill conservation and 2) the

“new theory agriculture” (NTA) based on sufficiency economy theory proposed by His Majesty King Bhumibol Adulyadej (Sathirathi and Piboolsravut 2004).

NTA is an integrated self-reliance agricultural system that yields benefits for humans while living harmoniously with nature. Its practice supports crop diversification that rely on ecological control and combines it with comprehensive afforestation for providing nutrient cycling and the conservation of soil and water by growing non-crop plants to provide “lumber, edible products, and commercial timber” (Sathirathi and Piboolsravut 2004). The “Khiriwong model”, the entity of mixed orchards near natural forest, in southern Thailand, is an example of NTA. It maintains 75% of the bird species found in the forested areas in the working portions of the landscape; however, dominant species are smaller frugivorous and nectarivorous birds and generalists (Round et al. 2006).

I believed these paradigms can diversify biodiversity in the human-dominated areas of this landscape and can be demonstrated at local schools, with local youth groups, in collaboration with the Queen Sirikit’s Model Farm and Food Bank Project in the Queen Sirikit Forest Park.

In addition to conservation outreach and eco-friendly agriculture, I also recommend pursuing two further areas of research. First, I encourage the study on population and distribution of smaller-sized frugivorous birds in the landscape to understand their role in dispersing seeds from primary forest to degraded forest in the region. The second study is to explore dispersal routes for facilitating movement of the two smaller-sized hornbills—the Tickell’s Brown and Oriental-pied Hornbills – between the forest inside and outside protected area. This will also potentially slow down their

local extinction from the forest outside the protected area. These territorial hornbills (Kinnaird and O' Brien 2007, Hadprakarsa 2008), using the mid-canopy (Kemp 1995, Poonswad 1993a), are more likely to suffer from fragmentation than the larger-sized hornbills (Hadprakarsa 2008).

I suggest two locations to study dispersal routes of the Oriental-pied Hornbill. The first location is at the Queen Sirikit Forest Park (QSF), a forest plantation and tourist site adjacent to Nongyao ranger station of MPWS, which its gap between the forests inside and outside protected area with a two-lane road and sparse human settlement. I found a pair of breeding Oriental-pied Hornbill occasionally visited QSF when ripe fig fruits were available. The second location is at Nongtadung ranger station of MPWS, where I found a pair of breeding Oriental-pied Hornbill. It is adjacent to a recently established National Park and is approximately 3 km to the location that the Oriental-pied Hornbill was detected in the forest outside the protected area.

If these connections are identified, not only the Oriental-pied Hornbill can use it, but a breeding flock of Tickell's Brown Hornbill detected outside the protected area may use it as a corridor to move to forest inside the protected area. However, this seems difficult because its average year-round home range was only $32.41 \pm 15.88 \text{ km}^2$ with a mean daily movement of $8.99 \pm 1.41 \text{ km}$ (Kanishthajata 2013). While the flock of Tickell's Brown Hornbill in the forest outside protected area may move only 2 km toward the forest in Myanmar, it will face a high risk of being hunted by Karen and Myanmar's troops. This condition may result in lower fitness on survival rate of this species and finally may lead to inbreeding pressure and the local extinction of the population outside the protected area.

While I do not have a good solution for this trouble, I supported Trisurat et al. (2013) who proposed to change a conservation status of the Tickell's Brown Hornbill from vulnerable to endangered. This is because my study depicted a low occupancy and detection rate of Tickell's Brown Hornbill even in the protected area, and also many hornbill studies have found a very low abundance or disappearance of this species in key protected areas of Thailand (Jornburom 2009, THP 2009).

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APPENDIX

Table 1 Summary of nest characteristics of four hornbill species in 100 km² survey area within the Maenam Pachee Wildlife Sanctuary, Thailand.

Nest No.	Nest Status (Year)			Nest Tree Species	Tree height	Cavity height	Alt	DBH (cm)	Basal (m ²)	Cavity creation	Slope	Hole direction	No. of hole/ trunk
	2012	2011	2010										
WH01	AC	AC	-	<i>Manilkara</i> sp.	32	18.5	743	81.8	0.53	NC	45	270	1
WH02	IN	IN	AC	<i>Tetrameles nudiflora</i> R.Br.	32	22	599	110.6	0.96	NC	45	240	1
WH03	AC	AC	AC	<i>Tetrameles nudiflora</i> R.Br.	38.5	18	432	127.3	1.27	WC	33	150	1
WH04	IN	IN	IN	<i>Manilkara</i> sp.	40	24.5	465	121.5	1.16	NC	40	270	1
WH05	IN	IN	AC	<i>Tetrameles nudiflora</i> R.Br.	38	23	476	110.6	0.96	NC	31	340	1
WH06	IN	IN	IN	<i>Tetrameles nudiflora</i> R.Br.	40	28	483	150	1.77	NC	45	45	1
WH07	IN	IN	AC	<i>Manilkara</i> sp.	37	25	438	90.9	0.65	NC	43	332	1
WH08	IN	IN	IN	<i>Manilkara</i> sp.	42	21	422	155.8	1.91	NC	22.5	195	1
WH09	AC	AC	AC	<i>Antiaris toxicaria</i> Lesch.	40	22	582	134.8	1.43	NC	43	266	1
WH10	AC	AC	-	<i>Manilkara</i> sp.	37.5	22	419	103.2	0.84	NC	45	332	1
WH11	AC	AC	-	<i>Terminalia bellerica</i> Roxb.	37	26.5	361	94.6	0.70	NC	35	169	1
WH12	IN	IN	IN	<i>Terminalia bellerica</i> Roxb.	35	19	466	90.2	0.64	NC	37	300	1
WH13	IN	IN	IN	<i>Tetrameles nudiflora</i> R.Br.	48	28	546	271	5.77	NC	29	332	1

Nest No.	Nest Status (Year)			Nest Tree Species	Tree height	Cavity height	Alt	DBH (cm)	Basal (m ²)	Cavity creation	Slope	Hole direction	No. of hole/ trunk
	2012	2011	2010										
WH14	AC	AC	AC	<i>Antiaris toxicaria</i> Lesch. **	33	24	812	239	4.49	NC	42	320	2
WH15	IN	IN	IN	<i>Terminalia bellerica</i> Roxb.	50	22	623	99	0.77	NC	40	198	2
GH01	INc	IN	IN	<i>Tetrameles nudiflora</i> R.Br.	50	38	362	236	4.37	NC	18	294	1
GH04	IN	IN	IN	<i>Tetrameles nudiflora</i> R.Br.	30	20	646	220	3.80	NC	45	260	3
GH03	IN	IN	IN	<i>Tetrameles nudiflora</i> R.Br.	45	22	469	229.50	4.14	NC	10	240	1
GH02	IN	IN	IN	<i>Tetrameles nudiflora</i> R.Br.	40	18	453	220	3.80	NC	25	80	2
GH05	AC	AC	-	<i>Terminalia bellerica</i> Roxb.	45	26	654	80	0.50	NC	43	170	1
GH06	AC	-	-	<i>Ailanthus integrifolia</i> Lam.	39.6	30	488	93.5	0.69	NC	5	156	1
GH07	AC	AC	-	<i>Manilkara</i> sp.	48	28	677	111.7	0.98	NC	47	140	1
GH08	AC	AC	AC	<i>Manilkara</i> sp.	45	17	751	111.1	0.97	NC	37.5	5	1
GH09	IN	-	-	<i>Manilkara</i> sp.	32	15	423	84.7	0.56	NC	44	30	1
GH10	IN	IN	-	<i>Tetrameles nudiflora</i> R.Br.	45	22	469	73.02	0.42	NC	10	240	1
GH11	IN	IN	AC	Unknown 1	34.5	17	653	123.5	1.20	NC	25	230	1
OPH01	AC	AC	-	<i>Tetrameles nudiflora</i> R.Br.	30	18	447	89	0.62	WC	3	300	3
OPH02	IN	IN	IN	<i>Choerospondias axillaris</i> (Roxb.) B.L. Burtt. & Hill	28	15	404	117.73	1.09	WC	20	40	4

Nest No.	Nest Status (Year)			Nest Tree Species	Tree height	Cavity height	Alt	DBH (cm)	Basal (m ²)	Cavity creation	Slope	Hole direction	No. of hole/ trunk
	2012	2011	2010										
OPH03	AC	AC	AC	<i>Tetrameles nudiflora</i> R.Br.	38	27	305	164	2.11	WC	7	160	2
OPH04	AC	AC	AC	<i>Manilkara</i> sp.	35	25	389	105	0.87	NC	37	120	1
OPH05	AC	AC	-	<i>Manilkara</i> sp.	32	28	434	111.5	0.98	NC	0	15	1
OPH06	AC	-	-	Unknown 2	42	30	503	84.8	0.56	NC	34	260	1
TBH01	IN	AC	-	<i>Choerospondias axillaris</i> (Roxb.) B.L. Burtt. & Hill	25	14	685	48.7	0.19	NC	30	320	1
TBH02	AC	AC	-	<i>Terminalia bellerica</i> Roxb.	32	12	416	95.0	0.71	NC	0	260	2
TBH03	IN	IN	-	<i>Pterospermum cinnamomeum</i> Kurz.	38	9.5	466	95.1	0.71	NC	0	310	1
TBH04	AC	AC	-	Unknown 3	18	7	491	54.2	0.23	NC	24	180	1
TBH05	AC	-	-	<i>Terminalia bellerica</i> Roxb.	40.5	22	481	90.4	0.64	NC	49	216	1
TBH06	IN	IN	-	<i>P.cinnamomeum</i> Kurz.	41	21	558	72.7	0.42	NC	12	216	1
TBH07	IN	AC	-	<i>Toona ciliate</i> M. Roem	19	8	684	52.8	0.22	NC	0	117	1
TBH08	AC	-	-	<i>Manilkara</i> sp.	53	40	478	146.6	1.69	NC	40	168	1
TBH09	IN	AC	AC	<i>Terminalia bellerica</i> Roxb.	27	10	705	80.3	0.50	NC	10	90	1
TBH10	AC	-	-	<i>Terminalia bellerica</i> Roxb.	45	26	677	80	0.50	NC	43	170	1

Hornbill Species: GH = Great hornbill, OPH = Oriental-pied hornbill, WH = Wreathed hornbill, TBH = Tickell's Brown hornbill, Nest status: AC = Active nest, IN = Inactive nest, Acronyms: a =Nest failure by humans, b = Nest failure by natural predators, c = Fixed nests, Nest locations: * = the cavity was used by WH in 2011, ** the cavity was used by GH in 2012, Cavity creation: NC = a cavity excavated by natural phenomenon such as a broken branches or excavated by bear, WC = a cavity excavated by woodpeckers and then used by hornbills. This creation can be identified from the rounded shape of the nest entrance and its location on the tree trunk.

Table 2 Comparison of forest community in two reserves in the southern TWFC/.

Maenam Pachee Wildlife Sanctuary (MPWS) represents the forest area that hornbills use as a breeding site and the Natural History Park initiated by Royal Princess of Thailand NHP represents the forest area that hornbills do not use as a breeding. site DBH = diameter at breast height (cm)

Forest Characteristics	MPWS	NHP
All trees with DBH \geq 10 cm		
Total number of trees	1939	1658
Total number of species	319	293
Total number of genera	205	207
Total number of families	69	63
Density (trees $\times 10^3$ / km ²)	53.86	46.06
<hr/>		
Total number of trees in the genera used for nesting in MPWS	48	37
Total genera of trees used for nesting in MPWS	7	4
Density of all trees in the same genera used for nesting in MPWS (trees $\times 10^3$ / km ²)	1.33	1.03
<hr/>		
Total number of tree species used for nesting in the MPWS	14	5
Total species of trees used for nesting in the MPWS	6	3
Density of all tree species used for nesting in the MPWS (trees $\times 10^3$ / km ²)	0.39	0.13
<hr/>		
Potential nest trees for Hornbills (all tree with DBH \geq 40 cm)		
Total number of trees	225	197
Total number of species	126	88
Total number of genera	99	63
Total number. of families	44	38
Density (trees $\times 10^3$ / km ²)	6.25	5.47
<hr/>		
Total number of potential nest trees in the same genera used for nesting in	9	5

Forest Characteristics	MPWS	NHP
MPWS		
Total genera of potential nest trees used for nesting in the MPWS	4	2
Density of potential nest trees in the same genera used for nesting in the MPWS (trees×10 ³ / km ²)	0.25	0.13
Total number of intraspecific potential nest trees used for nesting in the MPWS	8	1
Total species of intraspecific potential nest trees used for nesting in the MPWS	3	1
Density of intraspecific potential nest trees used for nesting in the MPWS (trees×10 ³ / km ²)	0.22	0.028

Table 3 Size of monthly foraging range for each individual hornbill in km²

Hornbills	Month/Year	Breeding Status	Wet-Dry	50%MCP	95%MCP
OPH#021	June 2011	NB	wet	0.530	3.900
OPH#021	August 2011	NB	wet	0.750	2.880
OPH#021	September 2011	NB	wet	0.370	4.630
OPH#021	October 2011	NB	dry	0.800	4.820
OPH#021	November 2011	NB	dry	0.430	3.740
OPH#021	December2011	NB	dry	0.650	3.640
OPH#021	January 2012	B	dry	0.760	3.210
OPH#021	February 2012	B	dry	1.890	4.110
OPH#021	March 2012	B	dry	1.280	3.780
OPH#021	April 2012	B	dry	2.310	4.300
OPH#021	June 2012	NB	wet	0.280	2.000
OPH#021	July 2012	NB	wet	1.580	4.970
OPH#021	August 2012	NB	wet	0.210	1.510

Hornbills	Month/Year	Breeding Status	Wet-Dry	50%MCP	95%MCP
OPH#021	November 2012	NB	dry	0.840	3.970
OPH#021	December 2012	NB	dry	0.970	3.810
OPH#021	January 2013	B	dry	1.720	10.960
OPH#021	February 2013	B	dry	0.980	3.270
All				0.962±0.585	4.088±1.930
Non-Breeding				0.674±0.369	3.625±0.369
Mean ± s.d.	Breeding			1.490±0.536	4.938±2.722
	Wet			0.620±0.464	3.315±1.290
	Dry			1.148±0.559	4.510±2.084
OPH#60	June 2012	NB	wet	1.180	3.760
OPH#60	July 2012	NB	wet	1.080	3.370
OPH#60	August 2012	NB	wet	1.210	6.150
Mean ± s.d.	All			1.180±0.056	3.760±1.229
OPH#182	June 2012	NB	wet	0.460	4.620
OPH#182	July 2012	NB	wet	1.260	4.760
OPH#182	August 2012	NB	wet	0.350	2.930
OPH#182	November 2012	NB	dry	0.710	4.040
OPH#182	December 2012	NB	dry	0.720	2.340
OPH#182	January 2013	B	dry	0.090	0.400
OPH#182	February 2013	B	dry	0.050	0.190
All				0.520±0.390	2.754±1.752
Non-Breeding				0.700±0.314	3.738±0.951
Mean ± s.d.	Breeding			0.070±0.020	0.295±0.105
	Wet			0.690±0.406	4.103±0.832
	Dry			0.287±0.307	1.743±1.569
OPH#202	June 2012	NB	wet	2.140	4.810

Hornbills	Month/Year	Breeding Status	Wet-Dry	50%MCP	95%MCP
OPH#202	July 2012	NB	wet	0.210	1.270
OPH#202	August 2012	NB	wet	0.460	2.410
OPH#202	November 2012	NB	dry	0.480	4.000
OPH#202	December 2012	NB	dry	1.070	5.290
OPH#202	January 2013	B	dry	1.280	3.290
OPH#202	February 2013	B	dry	0.330	1.830
All				0.853±0.640	3.271±1.404
Non-Breeding				0.872±0.499	3.556±1.517
Mean ± s.d.	Breeding			0.805±0.020	2.560±0.105
	Wet			0.937±0.857	2.830±0.832
	Dry			0.790±0.323	3.603±1.569
WH#41	June 2011	NB	wet	1.080	4.700
WH#41	August 2011	NB	wet	1.650	3.470
WH#41	September 2011	NB	wet	2.280	23.990
Mean ± s.d.	Monthly median			1.670±0.490	10.720±9.937
WH#101	June 2011	NB	wet	2.810	4.580
WH#101	August 2011	NB	wet	1.380	4.930
WH#101	September 2011	NB	wet	3.420	14.280
WH#101	January 2012	B	dry	2.160	7.950
WH#101	February 2012	B	dry	5.620	10.400
WH#101	April 2012	B	dry	3.140	10.700
WH#101	June 2012	NB	wet	2.370	8.320
WH#101	July 2012	NB	wet	0.700	3.160
All				2.700±1.387	8.040±3.484
Mean ± s.d.	Non-Breeding			2.136±0.979	7.054±3.990
	Breeding			3.640±1.456	9.683±1.232

Hornbills	Month/Year	Breeding Status	Wet-Dry	50%MCP	95%MCP
	Wet			2.136±0.979	7.054±3.990
	Dry			3.640±1.456	9.683±1.232
GH#142	June 2012	NB	wet	2.990	7.150
GH#142	July 2012	NB	wet	0.550	2.130
GH#142	August 2012	NB	wet	2.070	7.420
Mean ± s.d.				1.870±1.006	5.567±2.433

Table 4 Percent of foraging range overlap (HR: km²) between each pair of tagged hornbills. HB_i represents the individual hornbill shown in the column and HB_j represents the individual hornbill shown in the row of table. HR_{ij} refers to the percent of foraging range of hornbill *i* that overlapping with the foraging range of the hornbill *j* and HR_{ji} refers to the percent of foraging range of hornbill *j* overlapping with the foraging range of the hornbill *i*.

HB _j \ HB _i	Seasons	OPH60		OPH182		OPH202		WH41		WH101		GH142	
		HR _{ij}	HR _{ji}										
OPH21	1 st Annual	N/A		N/A		N/A		23%	14%	93%	49%	N/A	
	2 nd Annual	No overlap		26%	25%	6%	5%	N/A		1%	1%	No overlap	
	Biannual	No overlap		N/A		N/A		N/A		95%	68%	N/A	
	1 st Breeding	N/A		N/A		N/A		No overlap		55%	38%	N/A	
	2 nd Breeding	No overlap		9%	98%	01%	1%	N/A		N/A		N/A	
	1 st Non-breeding	N/A		N/A		N/A		8%	3%	73%	26%	N/A	
	2 nd Non-breeding	No overlap		19%	18%	2%	3%	N/A		0.4%	0.4%	No overlap	
	1 st Wet	N/A		N/A		N/A		0.04%	0.01%	67%	31%	N/A	
	1 st Dry	N/A		N/A		N/A		N/A		59%	38%	N/A	
	2 nd Wet	No overlap		38%	16%	1.3%	1.4%	N/A		1%	0.4%	No overlap	

HB _j		OPH60		OPH182		OPH202		WH41		WH101		GH142	
HB _i	Seasons	HR _{ij}	HR _{ji}										
	2 nd Dry	N/A	14%	27%	No overlap		N/A						
	All wet	N/A	N/A		N/A		N/A	64%	31%	N/A		N/A	N/A
	2 nd Annual	[Shaded]		83.81%	44.46%	99.89%	54.46%	N/A	N/A		84%	33%	
OPH60	2 nd Non-breeding			99.47%	40.97%	76.25%	34.54%	N/A	92%	45%	84%	33%	
	2 nd Wet			93%	47%	48%	66%	N/A	92%	45%	84%	33%	
	2 nd Annual			[Shaded]		70.37%	72.33%	N/A	58%	53%	46%	34%	
	2 nd Breeding	No overlap				N/A	N/A		N/A				
OPH182	2 nd Non-breeding	67%	84%			N/A	64%	63%	54%	42%			
	2 nd Wet	74%	100%			N/A	72%	70%	59%	46%			
	2 nd Dry	[Shaded]		48%	45%	N/A	N/A		N/A				
	2 nd Annual			N/A	73%	65%	70%	50%					
	2 nd Breeding			N/A	N/A		N/A						
OPH202	2 nd Non-breeding			N/A	84%	66%	74%	47%					
	2 nd Wet	[Shaded]		96%	34%	70%	50%						

HB _j		OPH60		OPH182		OPH202		WH41		WH101		GH142	
HB _i	Seasons	HR _{ij}	HR _{ji}										
	2 nd Dry									N/A		N/A	
	1 st Annual									39.31%	35.70%	N/A	
WH41	1 st Non-breeding									32%	51.00%	N/A	
	1 st Wet									31%	50%	N/A	
	2 nd Non-breeding											84%	67%
WH101	2 nd Wet											84%	67%

Table 5 The intraspecies overlap indices (0-100%: mean ± s.d.) for hornbills. Sample sizes, and minimum and maximum index are shown in parenthesis. Overlap ranges have three conditions. Overall overlap range refers to range overlap of all intraspecies hornbills. HB_i refers to the range of hornbill *i* overlapping to the range of hornbill *j* and HB_j refers to range of hornbill *j* overlapping to the range of hornbill *i*.

Pair Comparison	Overlap range	Annual	Breeding season	Non-breeding season	Wet season	Dry season
All Oriental-pied Hornbill	overall	18.5±22.57% (n=6:0-55%)	3.33±4.7% (n = 6: 0-1%)	19.33±28.20% (n = 6:0-76%)	19.45±27.06% (n =6:0 – 66%)	0% (n=6: 0)

Pair Comparison	Overlap range	Annual	Breeding season	Non-breeding season	Wet season	Dry season
Oriental-pied#21 (HB _i) and other	overall	10.33±10.96% (n=6:0-26%)	18.17±35.84% (n=6:0-98%)	7±8.21% (n=6:0-19%)	9.45±13.95% (n=6:0.38%)	6.83±10.37% (n=6:0-27%)
	HB _i	10.67±11.11 (n=3: 0-26%)	3.33±4.03% (n=3: 0-9%)	7±8.52% (n=3: 0-19%)	13.10±17.62% (n=3: 0-38%)	4.67±6.60% (n=3: 0-14%)
Hornbills (HB _j)	HB _j	10±10.8% (n=3: 0-25%)	33±46% (n=3:0-98%)	7±7.9% (n=3: 0-18%)	5.8±7.2% (n=3: 0-16%)	9±12.7% (n=3: 0-27%)
	overall	2.75±2.77% (n=4: 0-6%)	0.5±0.5% (n=4: 0-1%)	1.25±1.30% (n=4: 0- 1.4%)	0.68±0.68% (n=4: 0-1.4%)	0% (n=4: 0%)
Oriental-pied#21 (HB _i) & other Oriental-pied chicks (HB _j)	HB _i	3±3% (n=2: 0- 6%)	0.5±0.5% (n=2: 0-1%)	1±1% (n=2: 0-3%)	0.7±0.7% (n=2: 0-1.4%)	0% (n=2: 0%)
	HB _j	2.5±2.5% (n=2:0-5%)	0.5±0.5% (n=2: 0-1%)	1.5±1.5% (n=2: 0-3%)	0.7±0.7% (n=2:0-1.4%)	0% (n=2: 0%)
Female (HB _i) & all immature (HB _j) Oriental- pied Hornbills	overall	53.83±23.16% (n=6: 25-84%)	17.83±36.00% (n=6: 0-98%)	54.67±31.04% (n=6: 18-99%)	61.33±30.18% (n=6: 16-100%)	22.33±19.41% (n=6: 0-48%)
	HB _i	47.0±18.8% (n=3:25-71%)	32.67±46.20% (n=3: 0-98%)	42±20.02% (n=3:18-67%)	45.67±23.70% (n=3: 16-74%)	25±19.65% (n=3: 0-48%)

Pair Comparison	Overlap range	Annual	Breeding season	Non-breeding season	Wet season	Dry season
	HB _j	60.67±25.0% (n=3:26-84%)	3±4.24% (n=3: 0-9%)	67.33±34.72% (n=3: 19-99%)	77.00±27.72% (n=3:38-100%)	19.67±18.80% (n=3: 0-45%)
Female (HB _i) & immature (HB _j)	overall	68±14.23% (n=4: 45-84%)	0±0% (n=4: 0%)	72.75±21.55% (n=4: 41-99%)	78.50±20.52% (n=4: 47 -100%)	23.25±23.27% (n=4: 0-48%)
Oriental-pied Hornbills	HB _i	58±13% (n=2: 45-71%)	0±0% (n=2: 0%)	54±13% (n=2:41 - 67%)	60.50±13.50% (n=2: 47 -74%)	24±24% (n=2: 0-48%)
captured in the 2nd year	HB _j	78±6% (n=2: 72-84%)	0±0% (n=2: 0%)	91.5±7.5% (n=2: 84-99%)	96.50±3.50% (n=2: 93-100%)	22.50±0% (n=2:0-45%)
Wreathed 41(HB _i)&101 (HB _j)	overall	37.50±1.50% (n=2: 36-39%)	-	41.50±9.50% (n=2: 32-51%)	40.50±9.50% (n=2: 31-50%)	-
	HB _i	39% (n=1)	-	32.00% (n=1)	31% (n=1)	-
	HB _j	36%(n=1)	-	51%(n=1)	50% (n=1)	-

Table 6 The interspecies overlap indices (0-100%: mean \pm s.d.) for hornbills. Sample sizes, and minimum and maximum index are shown in parenthesis. HB_i refers to range of hornbill *i* overlapping with hornbill *j* and HB_j refers to range of hornbill *j* overlapping with hornbill *i*. HR_{ij} refers to the percent of foraging range of hornbill *i* that was overlapped with the foraging range of the hornbill *j* and HR_{ji} refers to the percent of foraging range of hornbill *j* that was overlapped with the foraging range of the hornbill *i*.

HB _i \ HB _j	Seasons	Wreathed chicks		Great Hornbill	
		HR _{ij}	HR _{ji}	HR _{ij}	HR _{ji}
Oriental-pied chicks	Annual	37.08 \pm 36.28% (n=8:0-95%)	24.63 \pm 28.71% (n=8: 0-68%)	52.67 \pm 37.46% (n=3: 0-84%)	26.67 \pm 19.70% (n=3: 0-47%)
	breeding	9.30 \pm 18.98% (n=8: 0-55%)	4.75 \pm 12.57% (n=8: 0-38%)	0% (n=3)	0% (n=3)
	non-breeding	30.60 \pm 34.87% (n=8:0-92%)	17.55 \pm 23.98% (n=8: 0-66%)	52.67 \pm 37.46% (n=3: 0-84%)	26.67 \pm 19.70% (n=3: 0-47%)
	wet	32.96 \pm 33.97% (n=8: 0-96%)	17.68 \pm 18.04% (n=8: 0-45%)	52.67 \pm 37.46% (n=3: 0-84%)	26.67 \pm 19.70 (n=3: 0-47%)
	dry	10.78 \pm 20.76% (n=8: 0-59%)	4.75 \pm 12.57% (n=8: 0-38%)	0% (n=3)	0% (n=3)

HB _i \ HB _j	Seasons	Wreathed chicks		Great Hornbill	
		HR _{ij}	HR _{ji}	HR _{ij}	HR _{ji}
Female Oriental-pied Hornbill	Annual	29±29% (n=2:0-58%)	26.50±26.50 (n=2:0-53%)	46% (n=1)	35% (n=1)
	breeding	0% (n=2)	0% (n=2)	0% (n=1)	0% (n=1)
	non-breeding	32±32% (n=2: 0-64%)	31.5±31.5% (n=2: 0-63%)	54% (n=1)	42% (n=1)
	wet	36±36% (n=2: 0-72%)	35±35% (n=2: 0-70%)	59% (n=1)	46% (n=1)
	dry	0% (n=2)	0% (n=2)	0% (n=1)	0% (n=1)
Wreathed chicks	Annual			42±42% (n=2:0-84%)	33.50±33.50% (n=2: 0-67%)
	breeding			0% (n=2)	0% (n=2)
	non-breeding			42±42% (n=2:0-84%)	33.50±33.50% (n=2: 0-67%)
	wet			42±42%	33.50±33.50%

HB _i \ HB _j		Seasons	Wreathed chicks		Great Hornbill	
			HR _{ij}	HR _{ji}	HR _{ij}	HR _{ji}
					(n=2:0-84%)	(n=2: 0-67%)
		dry			0% (n=2)	0% (n=2)

Table 7 Jacob's index (D) between the pair of individual hornbills annually, between breeding and non-breeding seasons, and between wet and dry seasons.

HB _i \ HB _j		OPH60		OPH182		OPH202		WH41		WH101		GH142	
		HR _{ij}	HR _{ji}										
OPH21	1 st Annual	N/A	N/A	N/A	N/A	N/A	N/A	-0.35	-0.82	0.92	-0.33	N/A	N/A
	2 nd Annual	-1.00	-1.00	-0.47	-0.51	-0.8	-0.90	-	-	-0.983	-0.98	-1.00	-1.00
	2years biannual			N/A	N/A	N/A	N/A	-	-	0.93	0.20	-	-
	1 st Breeding	N/A	N/A	N/A	N/A	N/A	N/A	-	-	0.28	-0.41	N/A	N/A
	2 nd Breeding			-0.98	1.00	-0.98	-0.98	-	-	-	-	-	-
	1 st Non-breeding	N/A	N/A	N/A	N/A	N/A	N/A	-0.61	-0.98	0.65	-0.67	N/A	N/A
	2 nd Non-breeding	-1.00	-1.00	-0.61	-0.65	-0.97	-0.93	-	-	-0.99	-0.99	-1.00	-1.00

HB _j		OPH60		OPH182		OPH202		WH41		WH101		GH142	
HB _i	State	HR _{ij}	HR _{ji}										
	1 st Wet	N/A	N/A	N/A	N/A	N/A	N/A	-1.00	-1.00	0.63	-0.66	N/A	N/A
	1 st Dry	N/A	N/A	N/A	N/A	N/A	N/A	-	-	0.41	-0.46	N/A	N/A
	2 nd Wet			0.19	-0.85	-0.98	-0.97	-	-	-0.95	-1.00	-1.00	-1.00
	2 nd Dry	N/A	N/A	-0.85	-0.15	-1.00	-1.00	-	-	-	-	-	-
	All wet	-	-	-	-	-	-	-	-	0.60	-0.67	-	-
	2 nd Annual	-	-	0.81	-0.40	1.00	-0.21	-	-	0.92	-0.43	0.86	-0.68
OPH60	2 nd Non-breeding	-	-	0.99	-0.49	0.68	-0.51	-	-	0.92	-0.43	0.86	-0.68
	2 nd Wet	-	-	0.93	-0.39	-0.19	0.45	-	-	0.92	-0.43	0.86	-0.68
	2 nd Annual	-	-	-	-	0.40	0.46	-	-	0.20	0.02	0.08	0.38
	2 nd Breeding	-	-	-	-	-1.00	-1.00	-	-	-	-	-	-
OPH182	2 nd Non-breeding	-	-	-	-	0.23	-0.43	-	-	0.29	0.25	0.20	-0.31
	2 nd Wet	-	-	-	-	0.02	1.00	-	-	0.45	0.39	0.30	-0.21
	2 nd Dry	-	-	-	-	-0.01	-0.13	-	-	-	-	-	-
	2 nd Annual	-	-	-	-	-	-	-	-	0.51	0.25	0.60	-0.23
OPH202	2 nd Breeding	-	-	-	-	-	-	-	-	-	-	-	-

HB _j		OPH60		OPH182		OPH202		WH41		WH101		GH142	
HB _i	State	HR _{ij}	HR _{ji}										
	2 nd Non-breeding	-	-	-	-	-	-	-	-	0.74	0.21	0.64	-0.65
	2 nd Wet	-	-	-	-	-	-	-	-	0.97	-0.69	0.82	-0.60
	2 nd Dry	-	-	-	-	-	-	-	-	-	-	-	-
	1 st Annual	-	-	-	-	-	-	-	-	-0.14	-0.35	N/A	N/A
WH41	1 st Non-breeding	-	-	-	-	-	-	-	-	-0.55	0.25	N/A	N/A
	1 st Wet	-	-	-	-	-	-	-	-	-0.56	0.23	N/A	N/A
	2 nd Non-breeding	-	-	-	-	-	-	-	-	-	-	0.74	0.24
WH101	2 nd Wet	-	-	-	-	-	-	-	-	-	-	0.74	0.24

Table 8 Jacob's index (D) for comparison within hornbill species (mean \pm s.d.) shown for different seasons. Sample sizes, and minimum and maximum index are shown in parentheses.

Pair Comparison	Overlap range	Annual season	Breeding season	Non-breeding season	Wet season	Dry season
Oriental-pied#21 (HBi) and other Oriental-pied Hornbills (HBj)	overall	-0.793 \pm 0.220 (n=6: -1.00 to -0.466)	-0.486 \pm 0.856 (n=4: -0.981 to -0.996)	-0.859 \pm 0.165 (n=6: -1.00 to -0.605)	-0.769 \pm 0.429 (n=6: -1.00 to 0.185)	-0.750 \pm 0.352 (n=4: -1 to -0.150)
	HB _i	-0.782 \pm 0.229 (n=3: -1 to -0.466)	-0.981 \pm 0.002 (n=2: -0.981 to -0.981)	-0.857 \pm 0.179 (n=3: -1 to -0.605)	-0.597 \pm 0.553 (n=3: -1 to 0.185)	-0.925 \pm 0.075 (n=2: -1 to -0.850)
	HB _j	-0.805 \pm 0.210 (n=3: -1 to -0.514)	0.008 \pm 0.988 (n=2: -0.979 to -0.996)	-0.861 \pm 0.149 (n=3: -1 to -0.654)	-0.940 \pm 0.064 (n=3: -1 to -0.851)	-0.575 \pm 0.425 (n=2: -1 to -0.150)
Oriental-pied#21 (HBi) & other Oriental-pied chicks	overall	-0.811 \pm 0.205 (n=4: -1 to -0.466)	-0.980 \pm 0.001 (n=2: -0.981 to -0.979)	-0.974 \pm 0.030 (n=4: -1 to -0.928)	-0.986 \pm 0.015 (n=4: -1 to -0.968)	-1.00 \pm 0.00 (n=2: -1 to -1)
	HB _i	-0.939 \pm 0.061	-0.981 (n=1)	-0.983 \pm 0.017	-0.987 \pm 0.011	-1 (n=1)

Pair Comparison	Overlap range	Annual season	Breeding season	Non-breeding season	Wet season	Dry season
		(n=2: -1 to -0.879)		(n=2: -1 to -0.967)	(n=2: -1 to -0.977)	
	HB _j	-0.950±0.050	-0.979 (n=1)	-0.964±0.036	-0.984±0.016	-1 (n=1)
		(n=:2 -1 to -0.901)		(n=2: -1 to -0.928)	(n=2: -1 to -0.968)	
Female (HBi) & all immature (HBj) Oriental-pied Hornbills	overall	0.047±0.526 (n=6: -0.514 to 0.814)	-0.496±0.862 (n=4: -1 to 0.996)	-0.159±0.594 (n=6: -0.654 to 0.995)	0.150±0.662 (n=6: -0.851 to 1)	-0.285±0.33 (n=4: -0.850 to -0.011)
	HB _i	-0.174±0.405 (n=3: -0.514 to 0.396)	-0.002±0.998 (n=2: -1 to 0.996)	-0.304±0.386 (n=3: -0.654 to 0.234)	-0.404±0.357 (n=3: -0.851 to 0.024)	-0.08±0.069 (n=3: -0.15 to -0.011)
	HB _j	0.269±0.539 (n=3: -0.466 to 0.814)	-0.991±0.01 (n=3: -1 to -0.981)	-0.14±0.833 (n=3: -0.981 to 0.995)	0.704±0.368 (n=3: 0.185 to 1)	-0.489±0.361 (n=3: -0.849 to -0.128)
Female (HBi) & immature (HBj) Oriental-pied Hornbills captured in the 2nd year	overall	0.316±0.445 (n=4: -0.404 to 0.814)	-1.00±0.00 (n=2: -1 to -1)	0.076±0.603 (n=4: -0.493 to 0.234)	0.392±0.591 (n=4: -0.385 to 1)	-0.070±0.059 (n=2: -0.128 to -0.011)
	HB _i	-0.004±0.400 (n=2: -0.404 to 0.396)	-1.00 (n=1)	-0.130±0.363 (n=2: -0.493 to 0.234)	-0.181±0.204 (n=2: -0.385 to 0.024)	-0.011 (n=1)
	HB _j	0.636±0.178 (n=2: 0.458 to 0.814)	-1.00 (n=1)	0.281±0.714 (n=2: -0.433 to 0.995)	0.964±0.036 (n=2: 0.927 to 1)	-0.128 (n=1)

Pair Comparison	Overlap range	Annual season	Breeding season	Non-breeding season	Wet season	Dry season
Wreathed (HBi)41&101 (HBj)	overall	-0.247±0.105 (n=2: -0.352 to -0.142)	-	-0.148±0.398 (n=2: -0.546 to 0.250)	-0.165±0.399 (n=2: -0.564 to 0.234)	-
	HB _i	-0.142 (n=1)	-	-0.546 (n=1)	-0.564 (n=1)	-
	HB _j	-0.353 (n=1)	-	0.250 (n=1)	0.234 (n=1)	-

Table 9 Jacob's index (D) of interspecific hornbills (mean ± s.d.). Sample sizes, and minimum and maximum index are shown in parenthesis. The result compared between the Wreathed, Oriental-pied, and Great Hornbill chicks.

HB _j HB _i	Seasons	Wreathed chicks		Great Hornbill chick	
		HB _{ij}	HB _{ji}	HB _{ij}	HB _{ji}
		-0.129±0.697 (n=8: -0.982 to 0.924)		-0.241±0.738 (n=6: -1 to 0.863)	
Oriental-pied chicks	Annual	0.5±0.518 (n=4: -0.348 to 0.938)	-0.267±0.3655 (n=4: -0.817 to 0.246)	0.154±0.823 (n=3: -1.00 to 0.863)	-0.636±0.317 (n=3: -1.00 to -0.227)
	Non-breeding	-0.215±0.729 (n=10: -0.993 to 0.919)		-0.305±0.762 (n=6: -1 to 0.863)	
		0.142±0.784	-0.573±0.442	0.167±0.831	-0.777±0.158

HB _j HB _i	Seasons	Wreathed chicks		Great Hornbill chick	
		HB _{ij}	HB _{ji}	HB _{ij}	HB _{ji}
		(n=5: -1.00 to 0.919)	(n=5: -0.993 to 0.206)	(n=3: -1.00 to 0.863)	(n=3: -1.00 to -0.652)
		-0.320±0.783 (n=10: -1.00 to 0.971)		-0.266±0.800 (n=6: -1 to 0.863)	
	Wet	0.114±0.896	-0.754±0.227	0.227±0.868	-0.759±0.174
		(n=5: -0.997 to 0.977)	(n=5: -0.997 to -0.432)	(n=3: -1.00 to 0.863)	(n=3: -1.00 to -0.597)
		0.109±0.094 (n=2: 0.015 to 0.203)		-0.188±0.265 (n=2: -0.453 to 0.077)	
	Anuual	0.203±0.00 (n=1)	0.015±0.00 (n=1)	0.077±0.00 (n=1)	-0.453±0.00 (n=1)
	non-	.270±0.016 (n=2: 0.254 to 0.286)		-0.06±0.253 (n=2: -0.310 to 0.196)	
Female Oriental-pied Hornbill	breeding	0.286±0.00 (n=1)	0.254±0.00 (n=1)	0.196±0.00 (n=1)	-0.310±0.00 (n=1)
	wet	0.420±0.034 (n=2: 0.386 to 0.453)		0.048±0.253 (n=2: -0.206 to 0.301)	
		0.453±0.00 (n=1)	0.386±0.00 (n=1)	0.301±0.00 (n=1)	-0.206±0.00 (n=1)

Table 10 Summary of covariates for Oriental-pied#21 measured at hornbill locations and random locations (mean \pm s.d. for continuous covariates and contingency analysis for categorical covariates) and their mean difference test using Mann-Whitney U test.

Covariate description	Correction Methods	Locations		U	P
		Hornbill	Random		
Distance to stream (km, mean \pm s.d.)	Ignore	0.26 \pm 0.22	0.24 \pm 0.19	2218.5	0.307
	Rescale	0.22 \pm 0.22	0.21 \pm 0.19	402773.5	0.263
	Zonal mean	0.26 \pm 0.20	0.24 \pm 0.17	397253.5	0.577
	Log normal	0.26 \pm 0.22	0.23 \pm 0.19	405014.5	0.200
Distance to agricultural areas (km, mean \pm s.d.)	Ignore	6.16 \pm 1.10	6.73 \pm 2.060	310371.5	< 0.001
	Rescale	6.27 \pm 1.12	6.82 \pm 2.056	313741	< 0.001
	Zonal mean	6.16 \pm 1.10	6.77 \pm 2.07	305680	< 0.001
	Log normal	6.18 \pm 1.25	6.75 \pm 2.05	311232	< 0.001
Distance to edge of evergreen forest (km, mean \pm s.d.)	Ignore	3.65 \pm 1.03	4.19 \pm 2.00	313868.5	< 0.001
	Rescale	3.83 \pm 1.02	4.33 \pm 1.98	317386.5	< 0.001
	Zonal mean	3.65 \pm 1.03	4.22 \pm 2.00	309069	< 0.001
	Log normal	3.67 \pm 1.17	4.21 \pm 1.98	313779	< 0.001
Patch size (km ² , mean \pm s.d.)	Ignore	385.10 \pm 0.00	385.10 \pm 0.00	389576	0.059
	Rescale	385.10 \pm 0.00	385.10 \pm 0.00	393338	0.034
	Zonal mean	385.10 \pm 0.00	385.10 \pm 0.00	395010	0.005
	Log normal	385.10 \pm 0.00	385.10 \pm 0.00	391988	0.494
Slope ($^{\circ}$, mean \pm s.d.)	Ignore	13.47 \pm 11.01	12.43 \pm 10.82	412061	0.050
	Rescale	12.85 \pm 11.06	12.63 \pm 10.56	396242.5	0.637
	Zonal mean	13.31 \pm 5.80	12.54 \pm 6.26	417874	0.013
	Log normal	13.25 \pm 11.08	12.47 \pm 10.72	408675	0.100
Elevation (m a.s.l., mean \pm s.d.)	Ignore	551.48 \pm 104.07	577.10 \pm 107.03	337357.5	< 0.001
	Rescale	552.49 \pm 104.64	577.21 \pm 107.13	338331.5	< 0.001

Covariate description	Correction Methods	Locations		U	P
		Hornbill	Random		
	Zonal mean	552.76±100.11	577.75±103.21	336305	< 0.001
	Log normal	553.18±104.76	576.73±108.04	341649.5	< 0.001
Evergreen forest	Ignore	47.17%	52.60%	389576	0.059
	Rescale	47.17%	52.54%	389158	0.034
	Zonal mean	47.18%	52.48%	388740	0.021
	Log normal	47.18%	52.60%	390512	0.500
Mixed deciduous forest	Ignore	0.00%	0.23%	392920	0.059
	Rescale	0.00%	0.28%	393338	0.034
	Zonal mean	0.00%	0.06%	391666	0.345
	Log normal	0.00%	0.23%	392452	0.223
Degraded forest	Ignore	-	-	-	-
	Rescale	-	-	-	-
	Zonal mean	0.00%	0.28%	393338	0.034
	Log normal	-	-	390780	0.291

Table 11 Summary of covariates for Oriental-pied #60 measured at hornbill locations and random locations (mean ± s.d. for continuous covariates and contingency analysis for categorical covariates) and their mean difference tests using Mann-Whitney U test.

Covariate description	Correction Methods	Locations		U	P
		Hornbill	Random		
Distance to stream (km, mean ± s.d.)	Ignore	0.14±0.11	0.18±0.14	21646	0.058
	Rescale	0.11±0.12	0.16±0.15	16329	0.012
	Zonal mean	0.14±0.09	0.19±0.12	15501	0.003
	Log normal	0.15±0.11	0.18±0.15	17090.5	0.09
Distance to	Ignore	8.31±0.99	8.63±1.13	22152	0.022

Covariate description	Correction Methods	Locations		U	P
		Hornbill	Random		
agricultural areas (km, mean \pm s.d.)	Rescale	8.44 \pm 0.99	8.80 \pm 1.06	15859.5	0.007
	Zonal mean	8.33 \pm 0.99	8.55 \pm 1.04	17347	0.130
	Log normal	8.39 \pm 1.05	8.67 \pm 1.08	16564	0.033
	Ignore	5.90 \pm 0.99	6.17 \pm 1.14	21648	0.058
Distance to edge of evergreen forest (km, mean \pm s.d.)	Rescale	6.09 \pm 0.99	6.38 \pm 1.11	16757.5	0.048
	Zonal mean	5.90 \pm 0.99	6.09 \pm 1.06	16946	0.067
	Log normal	5.96 \pm 1.06	6.21 \pm 1.10	-	-
	Ignore	385.10 \pm 0.00	385.10 \pm 0.00	19254.5	-
Patch size (km ² , mean \pm s.d.)	Rescale	385.10 \pm 0.00	385.10 \pm 0.00	19254.5	-
	Zonal mean	385.10 \pm 0.00	385.10 \pm 0.00	19254.5	-
	Log normal	385.10 \pm 0.00	385.10 \pm 0.00	19254.5	-
	Ignore	15.56 \pm 10.09	14.87 \pm 10.91	18948.5	0.807
Slope ($^{\circ}$, mean \pm s.d.)	Rescale	15.70 \pm 9.53	14.40 \pm 10.83	20871.5	0.196
	Zonal mean	15.26 \pm 6.33	14.23 \pm 7.00	20818.5	0.215
	Log normal	14.10 \pm 10.58	14.81 \pm 10.87	18511	0.553
Elevation (m a.s.l, mean \pm s.d.)	Ignore	520.85 \pm 94.36	531.20 \pm 96.28	20397	0.364
	Rescale	517.14 \pm 93.09	521.64 \pm 96.69	18796.5	0.716
	Zonal mean	523.394 \pm 89.17	530.18 \pm 91.38	18523.5	0.562
	Log normal	521.196 \pm 95.84	528.08 \pm 97.62	18605.5	0.606
Evergreen forest	Ignore	19.64%	80.36%	19254.5	N/A
	Rescale	19.64%	80.36%	19254.5	-N/A
	Zonal mean	19.64%	80.36%	19254.5	N/A
	Log normal	19.64%	80.36%	19254.5	N/A

Table 12 Summary of covariates for Oriental-pied chick#202 measured at hornbill and random locations (mean \pm s.d. for continuous covariates and contingency analysis for categorical covariates) and their mean difference tests using Mann-Whitney U test.

Covariate description	Correction Methods	Location		U	P
		Hornbill	Random		
Distance to stream (km, mean \pm s.d.)	Ignore	0.19 \pm 0.15	0.26 \pm 0.20	51709.5	< 0.001
	Rescale	0.16 \pm 0.15	0.24 \pm 0.21	50939.5	< 0.001
	Zonal mean	0.18 \pm 0.13	0.26 \pm 0.19	49965	< 0.001
	Log normal	0.19 \pm 0.16	0.26 \pm 0.20	50316	< 0.001
Distance to agricultural areas (km, mean \pm s.d.)	Ignore	7.53 \pm 1.06	9.07 \pm 1.50	26765.5	< 0.001
	Rescale	7.64 \pm 1.07	9.38 \pm 1.48	23007	< 0.001
	Zonal mean	7.53 \pm 1.06	9.19 \pm 1.44	23487	< 0.001
	Log normal	7.69 \pm 1.32	9.18 \pm 1.45	28320	< 0.001
Distance to edge of evergreen forest (km, mean \pm s.d.)	Ignore	5.08 \pm 1.30	6.58 \pm 1.48	26973	< 0.001
	Rescale	5.27 \pm 1.02	6.92 \pm 1.46	23553.5	< 0.001
	Zonal mean	5.08 \pm 1.03	6.69 \pm 1.42	23614	< 0.001
	Log normal	5.23 \pm 1.30	6.69 \pm 1.43	28098	< 0.001
Patch size (km ² , mean \pm s.d.)	Ignore	385.10 \pm 0.00	385.10 \pm 0.00	63640.5	N/A
	Rescale	385.10 \pm 0.00	385.10 \pm 0.00	63640.5	N/A
	Zonal mean	385.10 \pm 0.00	385.10 \pm 0.00	63640.5	N/A
	Log normal	385.10 \pm 0.00	385.10 \pm 0.00	63640.5	N/A
Slope ($^{\circ}$, Mean \pm s.d.)	Ignore	14.26 \pm 10.96	12.36 \pm 10.55	70100.5	0.026
	Rescale	14.58 \pm 11.02	12.62 \pm 11.12	71096	0.010
	Zonal mean	15.23 \pm 6.10	12.27 \pm 6.89	80004	< 0.001
	Log normal	14.21 \pm 10.89	12.35 \pm 10.49	69477.5	0.045
Elevation (m)	Ignore	516.13 \pm 90.43	568.14 \pm 104.63	45207	< 0.001

Covariate description	Correction Methods	Location		U	P
		Hornbill	Random		
a.s.l, mean ±	Rescale	516.73±92.27	576.93±106.66	42633.5	< 0.001
s.d.)	Zonal mean	516.11±83.79	571.98±102.33	43182	< 0.001
	Log normal	514.01±87.26	571.96±106.37	43036.5	< 0.001
	Ignore	25.55%	74.45%	63640.5	N/A
Evergreen	Rescale	25.55%	74.45%	63640.5	N/A
forest	Zonal mean	25.55%	74.45%	63640.5	N/A
	Log normal	25.55%	74.45%	63640.5	N/A
Mixed	Ignore	-	-	-	-
deciduous	Rescale	-	-	-	-
forest	Zonal mean	-	-	-	-
	Log normal	-	-	-	-
	Ignore	-	-	-	-
Degraded	Rescale	-	-	-	-
forest	Zonal mean	-	-	-	-
	Log normal	-	-	-	-

Table 13 Summary of landscape covariates for individual Wreathed Hornbill chicks measured at hornbill locations (Hornbill) and random locations (Random) (mean \pm s.d. for continuous covariates and contingency analysis for categorical covariates) and their mean difference test using Mann-Whitney U test.

Covariate description	Correction Methods	Wreathed Hornbill#41				Wreathed Hornbill#101			
		Location		U	P	Location		U	P
		Hornbill	Random			Hornbill	Random		
Distance to stream (km, mean \pm s.d.)	Ignore	0.34 \pm 0.22	0.31.591 \pm 0.23	13191.5	0.361	0.268 \pm 0.22	0.261 \pm 0.21	37842.5	0.966
	Rescale	0.31 \pm 0.23	0.26 \pm 0.23	13728.5	0.144	0.240 \pm 0.30	0.229 \pm 0.22	39386.5	0.431
	Zonal mean	0.33 \pm 0.21	0.29 \pm 0.20	13965	0.100	0.270 \pm 0.21	0.258 \pm 0.20	39071	0.552
	Log normal	0.28 \pm 0.20	0.31 \pm 0.23	11929.5	0.780	0.292 \pm 0.24	0.260 \pm 0.20	39870	0.313
Distance to agricultural areas (km, mean \pm s.d.)	Ignore	3.23 \pm 1.36	3.96 \pm 1.34	8362	<0.001	6.081 \pm 1.51	6.547 \pm 1.80	32086.5	0.002
	Rescale	3.38 \pm 1.37	4.11 \pm 1.35	8375	<0.001	6.19 \pm 1.51	6.782 \pm 1.80	30467	0.001
	Zonal mean	3.23 \pm 1.36	3.97 \pm 1.28	8134	<0.001	6.082 \pm 1.51	6.584 \pm 1.73	31076	<0.001
	Log normal	3.87 \pm 1.61	3.94 \pm 1.31	11671.5	0.601	5.96 \pm 1.48	6.516 \pm 1.74	30488	<0.001
Distance to edge of evergreen forest (km,	Ignore	0.85 \pm 1.04	1.390 \pm 1.14	8941.5	0.002	3.562 \pm 1.52	3.950 \pm 1.83	33235	0.015
	Rescale	0.99 \pm 1.07	1.556 \pm 1.20	8877	0.002	3.741 \pm 1.51	4.232 \pm 1.81	31913.5	0.002
	Zonal mean	0.85 \pm 1.04	1.374 \pm 1.13	8760.5	0.001	3.562 \pm 1.52	3.951 \pm 10.72	32386	0.004
	Log normal	1.46 \pm 1.49	1.332 \pm 1.12	12476.5	0.813	3.419 \pm 1.50	3.944 \pm 1.76	31004.5	<0.001

Covariate description	Correction Methods	Wreathed Hornbill#41				Wreathed Hornbill#101			
		Location		U	P	Location		U	P
		Hornbill	Random			Hornbill	Random		
mean ± s.d.)									
Patch size (km ² , mean ± s.d.)	Ignore	338.46±126.16	341.34±121.98	7340	< 0.001	385.10±0.00	385.10±0.00	37924.5	N/A
	Rescale	314.96±149.41	346.01±115.99	11277	0.098	385.10±0.00	385.10±0.00	37924.5	N/A
	Zonal mean	328.99±111.21	349.14±92.10	10443	0.021	384.903±2.72	385.10±0.00	37728	0.155
	Log normal	353.82±106.02	340.59±122.86	12678.5	0.436	383.113±27.59	385.10±0.00	37728	0.155
Slope (°, mean ± s.d.)	Ignore	9.94±10.68	13.08±10.79	10683.5	0.139	14.23±9.855	13.49±10.82	39577	0.387
	Rescale	7.63±9.96	12.82±10.55	8784.5	0.001	13.29±9.898	13.50±10.52	38343	0.826
	Zonal mean	10.94±5.42	13.12±6.87	9807.5	0.022	13.44±5.470	13.22±5.89	38433	0.792
	Log normal	12.78±11.85	12.98±10.72	11991.5	0.823	15.20±10.661	13.32±10.80	41735.5	0.046
Elevation (m a.s.l, mean ± s.d.)	Ignore	536.67±131.25	553.02±121.80	11013	0.251	575.94±106.212	591.75±108.00	34822	0.107
	Rescale	534.51±131.78	543.88±124.84	11447	0.461	574.89±104.081	590.32±106.36	34585	0.083
	Zonal mean	535.83±127.86	545.42±115.58	11343	0.404	577.12±102.515	586.54±106.24	36152	0.358
	Log normal	518.65±122.86	552.76±120.71	10024.5	0.0373	582.48±112.200	592.40±111.75	36158.5	0.359
Evergreen forest	Ignore	7.85%	80.66%	12326	0.8641	32.94%	67.06%	37924.5	N/A
	Rescale	7.30%	81.75%	13221.5	0.0818	32.94%	67.06%	37924.5	N/A

Covariate description	Correction Methods	Wreathed Hornbill#41				Wreathed Hornbill#101			
		Location		U	P	Location		U	P
		Hornbill	Random			Hornbill	Random		
	Zonal mean	6.93%	76.64%	13034.5	0.2336	32.94%	67.06%	37924.5	N/A
	Log normal	8.21%	80.47%	11802.5	0.4666	32.76%	67.06%	38121	0.155
Mixed deciduous forest	Ignore	1.09%	8.39%	11855.5	0.4913	-	-	-	-
	Rescale	1.46%	8.21%	11332	0.0991	-	-	-	-
	Zonal mean	1.10%	4.74%	11365.5	0.04541	-	-	-	-
	Log normal	0.73%	9.49%	12501.5	0.6195	0.17%	0.00%	37728	0.155
Degraded forest	Ignore	0.00%	2.01%	12495	0.2951	-	-	-	-
	Rescale	0.18%	1.10%	12123	0.62	-	-	-	-
	Zonal mean	0.91%	9.68%	12276.5	0.9286	-	-	-	-
	Log normal	0.00%	1.09%	12372.5	0.4422	-	-	-	-

Table 14 Summary of landscape covariates for three Oriental-pied Hornbill chicks (n=3) and the two Wreathed Hornbill chicks (n=2) measured at hornbill locations and random locations (mean \pm s.d. and contingency analysis) and their mean difference test using Mann-Whitney U test.

Covariate description	Correction Methods	Three Oriental-pied Hornbill Chicks				Two Wreathed hornbill chick			
		Locations		U	P	Locations		U	P
		Hornbill	Random			Hornbill	Random		
Distance to stream (km, mean \pm s.d.)	Ignore	0.23 \pm 0.20	0.23 \pm 0.19	1094452	0.534	0.28 \pm 0.22	0.289 \pm 0.22	105345.5	0.567
	Rescale	0.20 \pm 0.21	0.21 \pm 0.19	1082853	0.253	0.26 \pm 0.23	0.244 \pm 0.22	111115	0.467
	Zonal mean	0.23 \pm 0.19	0.23 \pm 0.17	1073965	0.144	0.28 \pm 0.21	0.275 \pm 0.20	10148.5	0.624
	Log normal	0.23 \pm 0.20	0.23 \pm 0.19	1089870	0.440	0.29 \pm 0.23	0.286 \pm 0.22	108138.0	0.964
Distance to agricultural areas (km, mean \pm s.d.)	Ignore	6.59 \pm 0.13	7.85 \pm 2.05	630518	< 0.001	5.51 \pm 1.87	5.102 \pm 2.02	123796	< 0.001
	Rescale	6.71 \pm 1.32	8.03 \pm 2.08	619244	< 0.001	5.61 \pm 1.87	5.289 \pm 2.05	121416	0.003
	Zonal mean	6.59 \pm 1.31	7.89 \pm 2.04	613115	< 0.001	5.51 \pm 1.87	5.123 \pm 1.97	122966	< 0.001
	Log normal	6.64 \pm 1.47	7.90 \pm 2.05	639123.5	< 0.001	5.54 \pm 1.72	5.073 \pm 1.98	126287	< 0.001
Distance to edge of evergreen	Ignore	4.10 \pm 1.29	5.35 \pm 2.03	633442.5	< 0.001	3.01 \pm 1.80	2.518 \pm 1.95	127491	< 0.001
	Rescale	4.28 \pm 0.13	5.56 \pm 2.06	624154.5	< 0.001	3.17 \pm 1.81	2.735 \pm 2.001	125721.5	< 0.001
	Zonal mean	4.10 \pm 1.29	5.38 \pm 2.02	615845.5	< 0.001	3.02 \pm 1.80	2.529 \pm 1.94	126636.5	< 0.001

Covariate description	Correction Methods	Three Oriental-pied Hornbill Chicks				Two Wreathed hornbill chick			
		Locations		U	P	Locations		U	P
		Hornbill	Random			Hornbill	Random		
forest (km, mean \pm s.d.)	Log normal	4.150 \pm 1.44	5.40 \pm 2.03	638129.5	< 0.001	3.02 \pm 1.69	2.483 \pm 1.94	129727.5	< 0.001
Patch size (km ² , mean \pm s.d.)	Ignore	385.10 \pm 0.00	384.31 \pm 17.41	1111568	0.125	375.66 \pm 59.23	360.619 \pm 93.70	62549	< 0.001
	Rescale	385.10 \pm 0.00	384.11 \pm 19.45	1111737	0.086	369.41 \pm 75.75	363.230 \pm 88.81	110136.5	0.209
	Zonal mean	385.10 \pm 0.00	384.50 \pm 11.25	1114021	0.021	373.58 \pm 54.44	364.980 \pm 71.09	112424.5	0.068
	Log normal	384.71 \pm 11.50	384.308 \pm 17.41	1108658	0.849	377.18 \pm 54.51	360.199 \pm 94.42	112757.5	0.007
Slope ($^{\circ}$, mean \pm s.d.)	Ignore	13.80 \pm 10.93	12.90 \pm 10.79	1157138	0.042	13.36 \pm 10.13	13.26 \pm 10.75	109923.5	0.655
	Rescale	13.41 \pm 10.96	12.99 \pm 10.81	1139860	0.188	12.10 \pm 10.07	13.12 \pm 10.53	103694.5	0.342
	Zonal mean	13.83 \pm 5.95	12.80 \pm 6.64	1208405	< 0.001	12.94 \pm 5.53	13.16 \pm 6.45	104783	0.486
	Log normal	13.50 \pm 10.99	12.90 \pm 10.71	1143023	0.141	14.71 \pm 10.91	13.13 \pm 10.74	116928.0	0.044
Elevation (m a.s.l, mean \pm s.d.)	Ignore	542.30 \pm 101.91	564.98 \pm 105.52	970884.5	< 0.001	567.99 \pm 112.32	570.08 \pm 117.38	107324.5	0.893
	Rescale	542.94 \pm 102.64	565.76 \pm 107.21	969418	< 0.001	567.21 \pm 111.01	564.34 \pm 119.18	109698	0.696
	Zonal mean	543.56 \pm 97.52	566.22 \pm 102.22	964752	< 0.001	568.76 \pm 108.88	563.54 \pm 113.29	111480.5	0.432
	Log normal	543.29 \pm 102.24	565.33 \pm 107.09	974723.5	< 0.001	569.55 \pm 116.79	570.22 \pm 118.37	108389.5	0.919
Evergreen	Ignore	37.06%	62.81%	1106996	0.125	21.34%	73.63%	103711	0.019

Covariate description	Correction Methods	Three Oriental-pied Hornbill Chicks				Two Wreathed hornbill chick			
		Locations		U	P	Locations		U	P
		Hornbill	Random			Hornbill	Random		
forest	Rescale	37.03%	62.81%	1106027	0.086	20.55%	74.16%	105775	0.218
	Zonal mean	37.03%	62.78%	1105456	0.060	20.37%	71.69%	103279	0.028
	Log normal	36.98%	62.83%	1107968	0.851	20.90%	73.54%	103144	0.008
Mixed deciduous forest	Ignore	0%	0.13%	1111568	0.125	0%	4.06%	110822	0.078
	Rescale	0%	0.16%	1111737	0.086	0.71%	3.97%	109809	0.256
	Zonal mean	0%	0.03%	1109453	0.444	0.53%	2.29%	108402	0.717
	Log normal	0.03%	0.13%	1109625	0.430	0.44%	4.59%	111994	0.018
Degraded forest	Ignore	-	-	-	-	0%	0.97%	109263	0.083
	Rescale	-	-	-	-	0.09%	0.53%	108212	0.648
	Zonal mean	0%	0.16%	1111737	0.8625	0.44%	4.67%	112115	0.015
	Log normal	0.03%	0%	1107341	0.193	0%	0.53%	108658	0.201

Table 15 The top candidate models and naïve model to estimate occupancy of the four sympatric hornbills in the entire landscape based on landscape variables.

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
Tickell's Brown Hornbill							
ψ(unpaved)p(.)	3	0.773	0.55	0.00	387.21	0.347±0.099 (0.143 – 0.527)	0.035±0.010 (0.020 – 0.060)
ψ(.)p(unpaved)	3	0.853	0.45	0.36	387.57	0.999±0.023 (3.53×10 ⁻¹⁹ -1)	0.012±0.003 (0.008 – 0.019)
ψ(.)p(.)	2	0.502	4×10 ⁻⁷	28.25	415.46	0.649±0.351 (0.083-0.974)	0.018±0.010 (0.006 – 0.055)
Oriental-pied Hornbill							
ψ(dem+area)p(human)	5	0.455	0.98	0.00	648.15	0.627±0.588 (0.388 – 0.743)	0.041±0.007 (0.030 – 0.057)
ψ(.)p(.)	2	0.931	4.7×10 ⁻¹⁴	61.32	709.47	0.547±0.132 (0.298 -0.774)	0.043±0.011 (0.026 – 0.072)
Wreathed Hornbill							
ψ(human)p(green)	4	0.878	0.29	1.80	696.65	0.327±0.047 (0.235-0.433)	0.060±0.011 (0.044 – 0.100)
ψ(.)p(.)	2	0.959	2.4×10 ⁻²⁹	131.12	825.97	0.375±0.056 (0.273 – 0.488)	0.085±0.014 (0.062 – 0.116)
Great Hornbill							
ψ(human)p(human)	4	0.6	0.61	0.00	690.30	0.316±0.080 (0.222 – 0.561)	0.046±0.013 (0.027 – 0.083)
ψ(human)p(area)	4	0.905	0.21	2.19	692.49	0.342±0.048 (0.245 – 0.445)	0.070±0.013 (0.049 – 0.102)
ψ(human)p(green)	4	0.827	0.13	3.10	693.40	0.333±0.048 (0.239 – 0.443)	0.058±0.010 (0.043 – 0.094)

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
ψ(human+green)p(.)	4	0.916	0.06	4.83	695.13	0.299±0.039 (0.219 – 0.392)	0.099±0.122 (0.078 – 0.125)
ψ(.)p(.)	2	0.948	2.1×10 ⁻³⁰	135.67	825.97	0.379±0.061 (0.269 – 0.502)	0.078±0.014 (0.055 – 0.109)
Larger-sized Hornbills							
ψ(paved)p(unpaved)	4	0.805	1.00	0.00	1120.78	0.542±0.065 (0.411 -0.673)	0.074±0.010 (0.057-0.097)
ψ(.)p(.)	2	0.461	4.2×10 ⁻⁴³	195.16	1315.94	0.46±0.044 (0.376 – 0.547)	0.121±0.014 (0.099 – 0.147)

¹number of parameters in the model (including parameters for intercept)

²Goodness of fit

³AIC weight- relative strength of mode support

⁴ΔAIC- the difference in AIC value between model and the strongest model

⁵the estimate of overall occupancy probability, its standard error and 95% confidence interval

⁶the estimate of overall detection probability, its standard error and 95% confidence interval

Table 16 The top candidate models and naïve model to estimate occupancy of the four sympatric hornbills in the entire landscape based on resource availability.

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
Tickell's Brown Hornbill							
ψ(hb)p(.)	3	0.865	0.84	0.00	395.80	0.432±0.125 (0.130 – 0.635)	0.028±0.008 (0.016 – 0.050)
ψ.)p(hb)	4	0.953	0.16	3.27	399.07	0.917±0.417 (0.000 – 1)	0.013±0.007 (0.005 – 0.035)

Models	nPars¹	GOF²	AICwt³	ΔAIC⁴	AIC	ψ±SE (95%CI)⁵	P±SE (95%CI)⁶
ψ(.)p(.)	2	0.522	4.5×10 ⁻⁵	19.66	415.46	0.649±0.351 (0.083 – 0.974)	0.018±0.010 (0.006 – 0.055)
Oriental-pied Hornbill							
ψ(.)p(potent)	3	0.884	0.49	0.00	707.26	0.558 ±0.131 (0.308-0.781)	0.043±0.012 (0.024 – 0.074)
ψ(.)p(fig)	3	0.623	0.34	0.71	707.97	0.627±0.165 (0.297 – 0.870)	0.037±0.011 (0.021 – 0.066)
ψ(.) p(.)	2	0.937	0.16	2.21	709.47	0.547±0.132 (0.298 – 0.774)	0.043±0.011 (0.026 – 0.072)
Wreathed Hornbill							
ψ(hb)p(.)	3	0.141	0.99	0.00	783.64	0.418±0.062 (0.283 – 0.533)	0.071±0.010 (0.053 – 0.094)
ψ(potent)p(hb)	4	0.973	0.006	10.18	793.82	0.523±0.101 (0.303 – 0.696)	0.053±0.011 (0.036 – 0.079)
ψ(.)p(hb+potent)	4	0.997	0.0003	16.56	800.20	0.600±0.096 (0.408 – 0.766)	0.049±0.011 (0.031 – 0.076)
ψ(.)p(.)	2	0.937	6.4×10 ⁻¹⁰	42.33	825.97	0.379±k0.061 (0.269 – 0.502)	0.078±0.014 (0.055 – 0.109)
Great Hornbill							
ψ(potent+hb)p(.)	4	0.149	1.00	0.00	776.92	0.427±0.076 (0.251 – 0.560)	0.069±0.010 (0.052 – 0.092)
ψ(.)p(.)	2	0.942	6.5×10 ⁻¹¹	46.71	825.97	0.379±0.061 (0.269 – 0.502)	0.078±0.014 (0.055 – 0.109)
Larger-sized hornbills							
ψ(hb)p(potent)	4	0.942	1.00	0.00	1267.42	0.529±0.061 (0.384 -0.636)	0.101±0.013 (0.078 – 0.128)
ψ(.)p(.)	2	0.461	2.9×10 ⁻¹¹	48.52	1315.94	0.46±0.044 (0.376 -0.547)	0.121±0.012 (0.099 – 0.147)

¹number of parameters in the model (including parameters for intercept)

²Goodness of fit

³AIC weight- relative strength of mode support

⁴ Δ AIC- the difference in AIC value between model and the strongest model

⁵the estimate of overall occupancy probability, its standard error and 95% confidence interval

⁶the estimate of overall detection probability, its standard error and 95% confidence interval

Table 17 The top candidate models and naïve model to estimate occupancy of the four sympatric in the entire landscape based on habitat quality.

Models	nPars ¹	GOF ²	AICwt ³	Δ AIC ⁴	AIC	$\psi \pm \text{SE (95\%CI)}$ ⁵	$P \pm \text{SE (95\%CI)}$ ⁶
Tickell's Brown Hornbill							
$\psi(\cdot)p(\text{threat})$	3	0.823	0.47	0.00	412.35	0.767 \pm 0.418 (0.033 – 0.997)	0.016 \pm 0.009 (0.005 – 0.048)
$\psi(\cdot)p(\text{hbden})$	3	0.806	0.43	0.22	412.57	0.527 \pm 0.150 (0.255 – 0.783)	0.027 \pm 0.011 (0.011 – 0.053)
$\psi(\cdot)p(\cdot)$	2	0.528	0.10	3.11	415.46	0.649 \pm 0.351 (0.083 – 0.974)	0.018 \pm 0.010 (0.006 – 0.055)
Oriental-pied Hornbill							
$\psi(\text{hbden})p(\text{fh})$	4	0.536	0.998	0.00	696.59	0.580 \pm 0.013 (0.314-0.795)	0.041 \pm 0.011 (0.025 – 0.069)
$\psi(\cdot)p(\cdot)$	2	0.94	0.002	12.87	709.47	0.547 \pm 0.132 (0.298 – 0.774)	0.043 \pm 0.011 (0.026 – 0.072)
Wreathed Hornbill							
$\psi(\text{fh})p(\text{threat})$	4	0.857	0.97	0.00	839.54	0.466 \pm 0.082 (0.311 – 0.621)	0.066 \pm 0.011 (0.047 – 0.094)

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
ψ(crown)p(fh)	4	0.949	0.02	7.73	847.27	0.461±0.102 (0.257 – 0.643)	0.066±0.015 (0.043 – 0.102)
ψ(crown) p(potent)	4	0.969	0.011	8.93	848.48	0.426±0.085 (0.264 -0.590)	0.072±0.015 (0.047-0.107)
ψ(fh)p(crown)	4	0.986	0.002	12.25	851.80	0.429±0.075 (0.289 – 0.573)	0.073±0.014 (0.050 – 0.104)
ψ(.)p(.)	2	0.949	3.2×10 ⁻⁷	29.85	869.40	0.376±0.056 (0.273 – 0.488)	0.085±0.014 (0.062 – 0.116)
Great Hornbill							
ψ(crown)p(fh+threat)	5	0.663	0.79	0.00	774.18	0.461±0.096 (0.279 – 0.651)	0.055±0.012 (0.036 – 0.089)
ψ(crown)p(threat)	4	0.542	0.17	3.13	777.31	0.436±0.091 (0.260 – 0.617)	0.058±0.011 (0.040 – 0.090)
ψ(fh)p(threat+crown)	5	0.705	0.03	6.46	780.64	0.530±0.103 (0.326 – 0.715)	0.052±0.011 (0.035 – 0.080)
ψ(fh)p(threat)	4	0.697	0.009	9.02	783.20	0.475±0.087 (0.307-0.639)	0.059±0.010 (0.042 – 0.086)
ψ(.)p(.)	2	0.942	4.5×10 ⁻¹²	51.79	825.97	0.379±0.061 (0.269 – 0.502)	0.078±0.014 (0.055 – 0.109)
Larger-sized hornbills							
ψ(crown)p(threat)	4	0.93	0.88	0.00	1257.27	0.544±0.077 (0.393 – 0.691)	0.092±0.011 (0.073 – 0.118)
ψ(fh)p(threat)	4	0.936	0.12	3.96	1261.23	0.580±0.067 (0.443-0.702)	0.092±0.010 (0.075-0.116)
ψ(.)p(.)	2	0.461	21.6×10 ⁻¹¹	58.68	1315.94	0.46±0.044 (0.376 -0.547)	0.121±0.012 (0.099 – 0.147)

¹ number of parameters in the model (including parameters for intercept)

² Goodness of fit

³ AIC weight- relative strength of mode support

⁴ ΔAIC- the difference in AIC value between model and the strongest model

⁵the estimate of overall occupancy probability, its standard error and 95% confidence interval

⁶the estimate of overall detection probability, its standard error and 95% confidence interval

Table 18 The top candidate models and naïve model to estimate occupancy of the four sympatric hornbills inside protected area of the Southern Tenasserim based on landscape variables.

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
Tickell's Brown Hornbill							
ψ(degraded)p(.)	3	0.312	0.964	0.00	317.54	0.611±0.144 (0.212 – 0.827)	0.034±0.009 (0.021 – 0.057)
ψ(.)p(unpaved)	3	0.176	0.371	0.95	319.45	0.999±0.021 (5.38×10 ⁻³⁰ – 1)	0.021±0.005 (0.013-0.034)
ψ(.)p(.)	2	0.964	0.036	6.57	324.21	0.879±0.464 (0.002 -1)	0.023±0.013 (0.008 – 0.067)
Oriental-pied Hornbill							
ψ(human+dem)p(human)	5	0.477	0.35	0.00	447.95	0.594±0.105(0.156 – 0.769)	0.059±0.013 (0.038 – 0.09)
ψ(stream)p(human)	4	0.514	9.8×10 ⁻⁷	26.88	474.83	0.691±0.176 (0.242 – 0.963)	0.050±0.015 (0.028 – 0.087)
ψ(.)p(.)	1	0.197	3.7×10 ⁻⁹	36.76	484.70	0.649±0.157 (0.324 – 0.877)	0.055±0.015 (0.032 – 0.092)
Wreathed Hornbill							
ψ(paved)p(mixed)	4	0.674	0.79	0.00	629.64	0.624±0.080 (0.412 – 0.767)	0.083±0.014 (0.059 – 0.116)
ψ(.)p(.)	2	0.399	9×10 ⁻¹¹	44.83	682.22	0.612±0.087 (0.435 – 0.764)	0.094±0.015 (0.068 – 0.129)
Great Hornbill							

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
ψ(.)p(human)	3	0.980	0.61	0.00	607.10	1.00±0.007 (3.58×10 ⁻¹³ -1)	0.055±0.008 (0.042 – 0.072)
ψ(human)p(.)	3	0.819	0.39	0.86	607.97	0.511±0.059 (0.380 – 0.626)	0.107±0.013 (0.084 – 0.136)
ψ(.)p(.)	2	0.591	4.8×10 ⁻¹³	55.74	662.84	0.628±0.095(0.433 – 0.788)	0.087±0.015(0.062 – 0.122)
Larger-sized hornbills							
ψ(paved+green)p(paved)	5	0.47	1.00	0.00	943.93	0.728±0.059 (0.547 – 0.829)	0.124±0.017 (0.095 – 0.162)
ψ(.)p(.)	2	0.929	7.6×10 ⁻¹⁷	74.23	1018.16	0.752±0.064 (0.608 – 0.856)	0.134±0.014 (0.109 – 0.163)

¹number of parameters in the model (including parameters for intercept)

²Goodness of fit

³AIC weight- relative strength of mode support

⁴ΔAIC- the difference in AIC value between model and the strongest model

⁵the estimate of overall occupancy probability, its standard error and 95% confidence interval

⁶the estimate of overall detection probability, its standard error and 95% confidence interval

Table 19 The top candidate models and naïve model to estimate occupancy of the four sympatric hornbills inside protected area of the southern Tenasserim landscape based on resource availability.

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
Tickell's Brown Hornbill							
ψ(.)p(hb)	3	0.748	0.49	0.00	321.724	0.996±0.004 (5.99×10 ⁻¹⁸ – 1)	0.021±0.005 (0.013 – 0.035)

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
ψ(.)p(.)	2	0.029	0.22	2.49	324.21	0.873±0.430 (6.93×10 ⁻¹³ – 1)	0.022±0.010 (0.009 – 0.054)
Oriental-pied Hornbill							
ψ(.)p(.)	2	0.195	-	-	484.70	0.649±0.157 (0.324 – 0.877)	0.055±0.015 (0.032 – 0.092)
Wreathed Hornbill							
ψ(.)p(potent)	3	0.876	0.928	0.00	678.07	0.667±0.093 (0.468 – 0.820)	0.086±0.017 (0.058 – 0.125)
ψ(.)p(.)	2	0.407	0.0072	5.12	683.19	0.608±0.086 (0.433 – 0.760)	0.094±0.015 (0.068 – 0.129)
Great Hornbill							
ψ(hb+potent)p(.)	4	0.201	0.994	0.00	648.03	0.626±0.112 (0.339 -0.798)	0.088±0.013 (0.065 – 0.127)
ψ(.)p(.)	2	0.571	0.0006	14.81	662.84	0.628±0.095 (0.433 – 0.788)	0.087±0.015 (0.062 – 0.122)
Larger-sized hornbills							
ψ(potent)p(potent)	5	0.967	0.572	0.00	1004.63	0.761±0.071 (0.557 – 0.867)	0.132±0.017 (0.103 – 0.168)
ψ(potent)p(hb)	4	0.855	0.428	0.58	1005.21	0.815±0.068 (0.568 – 0.910)	0.122±0.014 (0.097 – 0.153)
ψ(.)p(.)	2	0.929	0.0007	13.53	1018.16	0.752±0.064 (0.608 – 0.856)	0.134±0.014 (0.109 – 0.163)

¹number of parameters in the model (including parameters for intercept)

²Goodness of fit

³AIC weight- relative strength of mode support

⁴ΔAIC- the difference in AIC value between model and the strongest model

⁵the estimate of overall occupancy probability, its standard error and 95% confidence interval

⁶the estimate of overall detection probability, its standard error and 95% confidence interval

Table 20 The top candidate models and naïve model to estimate occupancy of the four sympatric hornbills inside protected area of the southern Tenasserim landscape based on habitat quality.

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
Tickell's Brown Hornbill							
ψ(.)p(threat)	3	0.167	0.42	0.00	322.86	0.999±0.046 (8.65×10 ⁻³³ -1)	0.021±0.005 (0.014 – 0.033)
ψ(.)p(hbden+hbden^2)	4	0.194	0.37	0.25	323.11	0.999±0.043 (1.57×10 ⁻²¹ – 1)	0.021±0.007 (0.013-0.038)
ψ(.)p(.)	2	0.029	0.21	1.36	324.21	0.873±0.430 (6.93×10 ⁻¹³ – 1)	0.022±0.010 (0.009 – 0.054)
Oriental-pied Hornbill							
ψ(.)p(.)	2	-	-	-	484.70	0.649±0.157 (0.324 – 0.877)	0.055±0.015 (0.032 – 0.092)
Wreathed Hornbill							
ψ(.)p(fh)	3	0.963	0.651	0.00	675.88	0.701±0.108 (0.461 – 0.866)	0.081±0.016 (0.055 – 0.117)
ψ(fh)p(.)	3	0.952	0.292	1.60	677.48	0.604±0.098 (0.394 -0.768)	0.096±0.015 (0.070 – 0.129)
ψ(.)p(hbden)	3	0.803	0.040	5.57	681.45	0.617±0.085 (0.444 – 0.766)	0.094±0.018 (0.064 – 0.136)
ψ(.)p(.)	2	0.342	0.017	7.31	683.19	0.608±0.086 (0.433 – 0.760)	0.094±0.015 (0.068 – 0.129)
Great Hornbill							
ψ(crown+fh+fh^2)p(.)	5	0.607	0.84	0.00	642.08	0.595±0.108 (0.342 – 0.777)	0.092±0.014 (0.069 – 0.122)
ψ(.)p(.)	2	0.563	2.6×10 ⁻⁵	23.51	662.84	0.628±0.095 (0.433 – 0.788)	0.087±0.015 (0.062 – 0.122)

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
Larger-sized hornbills							
ψ(crown)p(fh)	4	0.976	0.999	0.00	1001.27	0.769±0.076 (0.583 – 0.884)	0.129±0.016 (0.101 – 0.163)
ψ(.)p(.)	2	0.929	0.0002	16.89	1018.16	0.752±0.064 (0.608 – 0.856)	0.134±0.014 (0.109 – 0.163)

¹number of parameters in the model (including parameters for intercept)

²Goodness of fit

³AIC weight- relative strength of mode support

⁴ΔAIC- the difference in AIC value between model and the strongest model

⁵the estimate of overall occupancy probability, its standard error and 95% confidence interval

⁶the estimate of overall detection probability, its standard error and 95% confidence interval

Table21 The top candidate models and naïve model to estimate occupancy of the four sympatric hornbills outside protected area of the Southern Tenasserim based on landscape variables

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
Tickell's Brown Hornbill							
ψ(.)p(unpaved)	3	0.116	0.80	0.00	63.42	0.999±0.023 (5.91×10 ⁻⁶⁷ -1)	0.005±0.003 (0.002 – 0.019)
ψ(.)p(.)	2	0.895	0.20	2.81	66.23	0.996±0.177 (2.34×10 ⁻³⁶ -1)	0.005±0.003 (0.002 – 0.014)
Wreathed Hornbill							
ψ(.)p(.)	2	0.998	1.00	0.00	123.17	0.552±0.512 (0.028 – 0.986)	0.021±0.021 (0.003 – 0.133)

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
Great Hornbill							
ψ(.)p(degraded)	3	0.769	0.984	0.00	87.81	0.999±0.045 (2.79×10 ⁻³¹ -1)	0.009±0.004 (0.004 – 0.023)
ψ(.)p(.)	2	0.838	0.016	8.21	96.02	0.999±0.057 (1.07×10 ⁻⁴² -1)	0.009±0.003 (0.004 – 0.017)
Larger-sized hornbills							
ψ(.)p(human)	3	0.090	0.88	0.00	184.28	0.698±0.352 (0.081 – 0.984)	0.029±0.017 (0.009 – 0.090)
ψ(.)p(.)	2	0.736	0.12	3.96	188.24	0.526±0.268 (0.119 – 0.901)	0.039±0.021 (0.013 – 0.110)

¹number of parameters in the model (including parameters for intercept)

²Goodness of fit

³AIC weight- relative strength of mode support

⁴ΔAIC- the difference in AIC value between model and the strongest model

⁵the estimate of overall occupancy probability, its standard error and 95% confidence interval

⁶the estimate of overall detection probability, its standard error and 95% confidence interval

Table 22 The top candidate models and naïve model to estimate occupancy of the sympatric hornbills in the forest outside protected area of the southern Tenasserim landscape based on resource availability.

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
Tickell's Brown Hornbill							
ψ(hb)p(mofig)	4	0.067	0.737	0.00	57.98	0.147±0.069 (0.038 – 0.395)	0.049±0.024 (0.009 -0.116)

Models	nPars ¹	GOF ²	AICwt ³	Δ AIC ⁴	AIC	$\psi \pm \text{SE}$ (95%CI) ⁵	$P \pm \text{SE}$ (95%CI) ⁶
$\psi(\text{hb})p(\cdot)$	3	0.139	0.235	2.28	60.27	0.195 \pm 0.116 (0.027 – 0.584)	0.028 \pm 0.018 (0.008 – 0.097)
$\psi(\cdot)p(\text{mofig})$	3	0.316	0.016	7.72	65.70	0.170 \pm 0.102 (0.047 – 0.459)	0.042 \pm 0.024 (0.006 – 0.129)
$\psi(\cdot)p(\cdot)$	2	0.887	0.012	8.25	66.23	0.996 \pm 0.177 (2.34×10^{-36} – 1)	0.005 \pm 0.003 (0.002 – 0.014)
Wreathed Hornbill							
$\psi(\cdot)p(\cdot)$	2	0.999	-	-	123.17	0.552 \pm 0.512 (0.028 – 0.986)	0.021 \pm 0.021 (0.003 – 0.133)
Great Hornbill							
$\psi(\cdot)p(\cdot)$	2	0.845	-	-	96.02	0.999 \pm 0.057 (1.07×10^{-42})	0.009 \pm 0.003 (0.004 – 0.017)
Larger-sized hornbills							
$\psi(\cdot)p(\cdot)$	2	0.736	0.12	3.96	188.24	0.526 \pm 0.268 (0.119 – 0.901)	0.039 \pm 0.021 (0.013 – 0.110)

¹number of parameters in the model (including parameters for intercept)

²Goodness of fit

³AIC weight- relative strength of mode support

⁴ Δ AIC- the difference in AIC value between model and the strongest model

⁵the estimate of overall occupancy probability, its standard error and 95% confidence interval

⁶the estimate of overall detection probability, its standard error and 95% confidence interval

Table 23 The top candidate models and naïve model to estimate occupancy of the sympatric hornbills outside protected area of the southern Tenasserim landscape based on habitat quality.

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
Tickell's Brown Hornbill							
ψ(.)p(hbdo)	3	0.424	0.75	0.00	64.06	0.999±0.019 (1.41×10 ⁻⁴¹ - 1)	0.005±0.003 (0.002 – 0.017)
ψ(.)p(.)	2	0.222	0.25	2.17	66.23	1±0.007 (0 – 1)	0.005±0.003 (0.002 – 0.103)
Wreathed Hornbill							
ψ(.)p(.)	2	0.999	-	-	123.17	0.552±0.512 (0.021 – 0.986)	0.021±0.021 (0.003 – 0.133)
Great Hornbill							
ψ(.)p(threat)	3	0.138	0.61	0.00	95.13	0.999±0.069 (2.54 ×10 ⁻⁴¹ -1)	0.009±0.004 (0.004 – 0.022)
ψ(.)p(.)	2	0.828	0.39	0.90	96.02	0.999±0.057 (1.072×10 ⁻⁴² -1)	0.009±0.003 (0.004 – 0.017)
Larger-sized hornbills							
ψ(.)p(.)	2	0.736	0.12	3.96	188.24	0.526±0.268 (0.119 – 0.901)	0.039±0.021 (0.013 – 0.110)

¹number of parameters in the model (including parameters for intercept)

² Goodness of fit

³AIC weight- relative strength of mode support

⁴ ΔAIC- the difference in AIC value between model and the strongest model

⁵the estimate of overall occupancy probability, its standard error and 95% confidence interval

⁶the estimate of overall detection probability, its standard error and 95% confidence interval

Table 24 The top candidate models and naïve model to estimate occupancy of the Oriental-pied Hornbill in forest edge of human-dominated areas of the Southern Tenasserim.

Models	nPars ¹	GOF ²	AICwt ³	ΔAIC ⁴	AIC	ψ±SE (95%CI) ⁵	P±SE (95%CI) ⁶
Landscape variables							
ψ(.)p(mixed)	3	0.830	0.551	0.00	166.80	1.00±0.013 (7.38×10 ⁻³¹ - 1)	0.027±0.008 (0.015 - 0.050)
ψ(.)p(human)	3	0.925	0.352	0.90	167.70	1.00±0.010 (9.11×10 ⁻⁴⁰ - 1)	0.026±0.008 (0.014 -0.049)
ψ(.)p(.)	2	0.829	0.098	3.46	170.26	1±0.007 (5.16×10 ⁻¹⁵ - 1)	0.027±0.006 (0.017 - 0.042)
Resource availability							
ψ(.) p(mofig+ mofig^2)	4	0.618	0.902	0.00	158.82	0.999±0.005 (1.89×10 ⁻⁴⁰ - 1)	0.027±0.009 (0.014 - 0.054)
ψ(.)p(potent)	3	0.677	0.082	4.81	163.63	0.999±0.010 (1.289 ×10 ⁻²⁵ - 1)	0.027±0.008 (0.014 - 0.049)
ψ(.)p(fig)	3	0.685	0.013	8.43	167.25	0.999±0.020 (1.791×10 ⁻²⁴ -1)	0.027±0.008 (0.015 -0.048)
ψ(.)p(.)	2	0.282	0.003	11.44	170.26	1±0.0007 (0- 1)	0.027±0.006 (0.017 - 0.042)
Habitat quality							
ψ(.)p(threat+fighbdo)	4	0.857	0.424	0.00	159.69	0.888±0.103 (0.511 - 0.984)	0.037±0.014 (0.016 - 0.072)
ψ(.)p(podo+crown)	4	0.749	0.379	0.26	159.95	0.899±0.095 (0.535-0.986)	0.042±0.012 (0.017-0.074)
ψ(.)p(crown)	3	0.829	0.131	2.35	162.30	0.999±0.014 (1.35×10 ⁻²³ -1)	0.027±0.008 (0.014 - 0.049)
ψ(crown)p(.)	3	0.282	0.070	3.61	163.30	0.545±0.124 (0.160 - 0.781)	0.049±0.014 (0.028 - 0.083)

Models	nPars¹	GOF²	AICwt³	ΔAIC⁴	AIC	ψ±SE (95%CI)⁵	P±SE (95%CI)⁶
ψ(.)p(.)	2	0.829	0.002	10.57	170.26	1±0.007 (5.16×10 ⁻¹⁵ - 1)	0.027±0.006 (0.017 – 0.042)

¹number of parameters in the model (including parameters for intercept)

² Goodness of fit

³AIC weight- relative strength of mode support

⁴ ΔAIC- the difference in AIC value between model and the strongest model

⁵the estimate of overall occupancy probability, its standard error and 95% confidence interval

⁶the estimate of overall detection probability, its standard error and 95% confidence interval