

Estimating the availability of potential hornbill nest trees in a secondary forest patch in Kinabatangan, Sabah

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Eight species of hornbill occur in the Lower Kinabatangan Wildlife Sanctuary, Sabah. Hornbills are secondary cavity-nesting birds and one of the limiting factors to sustain their numbers is the availability of naturally-formed tree cavities. Past timber extraction has left behind highly degraded forest patches without large emergent trees that usually provide suitable cavities for nesting hornbill pairs. Therefore, we conducted a study to assess how widespread this key resource is and to estimate the proportion of a forest patch currently occupied by potential nest trees, i.e. trees with cavities. In a 10 km² study site, eight trained observers systematically visited 30 250 m x 250 m plots and recorded tree cavities that appeared suitable for hornbills based on a pre-established list of criteria. Nineteen trees with cavities were located, measured and identified. We anticipated that cavities could go undetected by the observers; we therefore used a zero-inflated process occupancy model to address this measurement error and to analyse data obtained along transects. The observers detected trees with cavities in 10 out of 30 plots, translating into an observed proportion of roughly 33%. However, our model indicated that trees with cavities might actually occupy 25 out of 30 plots, i.e. 82% of the forest patch area. Our modelling approach incorporates imperfect detection through hierarchical modelling and constitutes a quick and cost-effective assessment tool that can be used to investigate the spatial presence of potential nest trees, an important resource for hornbills.

INTRODUCTION

Since the early 1800s, South-East Asia has lost much forest cover due to agricultural expansion, with the introduction of rice paddy (*Oryza sativa*) followed by rubber *Hevea brasiliensis*, oil palm *Elaeis guineensis* and coconut *Cocos nucifera* (Sodhi *et al.* 2004). In the 1950s, the demand for timber increased and dipterocarp trees were heavily harvested (Sodhi *et al.* 2004). Subsequently, 30% of the Bornean forest cover was lost between 1973 and 2010 (Gaveau *et al.* 2014).

The Lower Kinabatangan Wildlife Sanctuary (LKWS) is located on the eastern side of Sabah, Malaysian Borneo. The area is internationally known for its biodiversity and is recognised as an Important Bird Area (IBA). In 2005, 27,000 ha along the Kinabatangan river was designated as a Wildlife Sanctuary. In addition to the sanctuary, there is approximately 15,000 ha of protected forest declared as Virgin Jungle Forest Reserves (Ancrenaz *et al.* 2004). Today, oil palm plantations and their processing mills, villages, farms and a network of roads surround the sanctuary. There are also fragments of degraded forest (approximately 10,000 ha) under private or state ownership (Ancrenaz *et al.* 2015).

There are eight species of hornbill that persist in the regenerating forests of LKWS. These include the critically endangered Helmeted Hornbill *Rhinoplax vigil*, the endangered Wrinkled Hornbill *Rhabdotorrhinus corrugatus* and White-crowned Hornbill *Berenicornis comatus*, three vulnerable species (the Rhinoceros Hornbill *Buceros rhinoceros*, Black Hornbill *Anthraceros malayanus* and Wreathed Hornbill *Rhyticeros undulatus*), the near threatened Bushy-crested Hornbill *Anorrhinus galeritus* and one least concern species, the Oriental Pied Hornbill *Anthraceros albirostris*.

Hornbills are important seed dispersers because they have a long seed retention time (Kitamura 2011) and they regurgitate seeds unharmed (Kitamura *et al.* 2008, Kitamura 2011) as they travel across vast areas (Holbrook *et al.* 2002). Hence, their absence may alter the forest composition (O'Brien *et al.* 1998). Though the high levels of wildlife biodiversity in LKWS have been attributed to high fruit production and low hunting pressure (Boonratana 1993, Boonratana & Sharma 1994), interviews with local community members showed that hornbill populations have declined over the past few decades (HUTAN 2011). In fact, Kaur (2020) reported low sightings of the Helmeted Hornbill and White-crowned Hornbill during boat surveys that were conducted from 2014–2017.

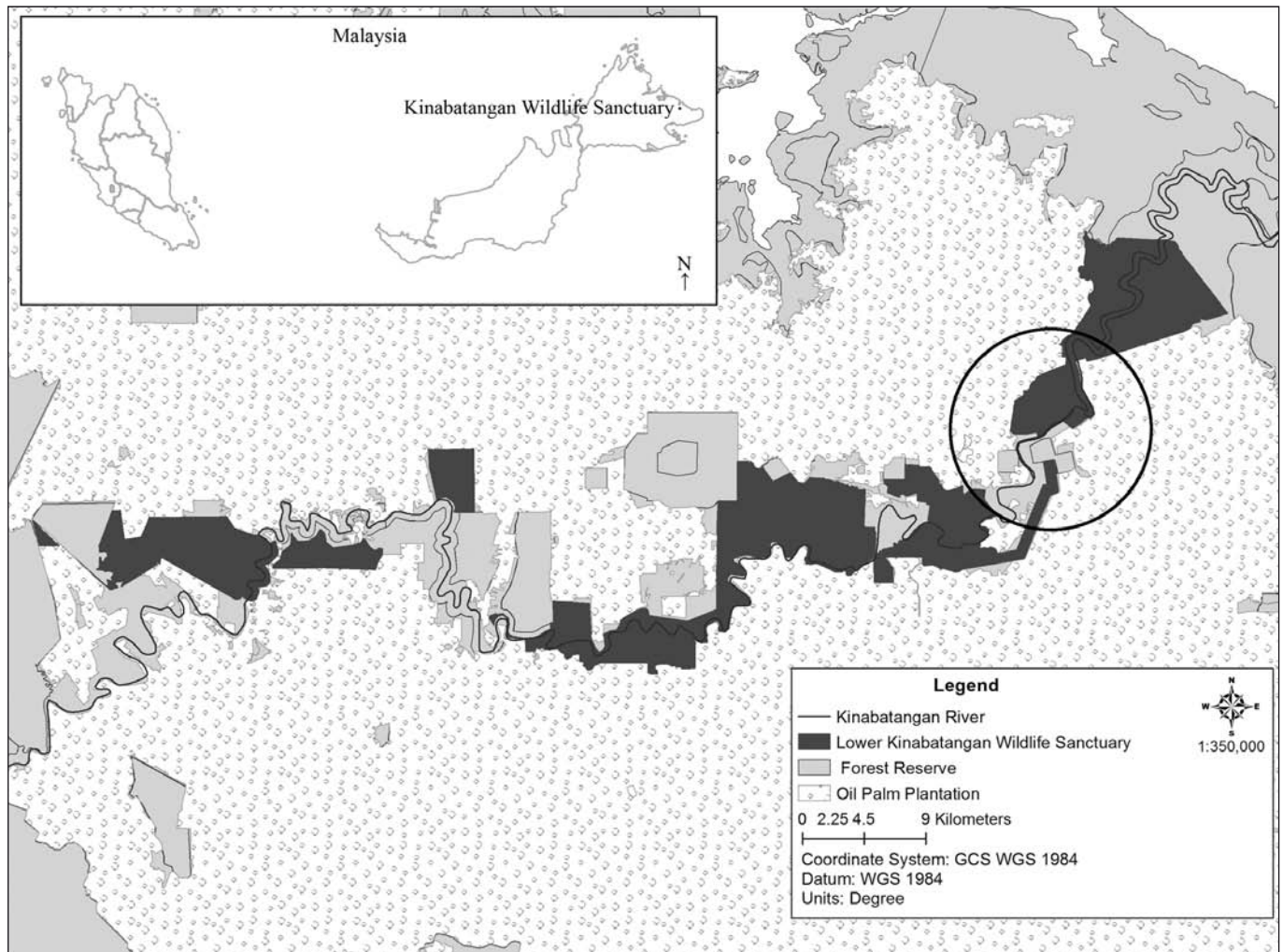
Two studies in the LKWS have reported that many hornbills prefer food plants from the genera *Syzygium* (Myrtaceae), *Litsea* (Lauraceae) (Boonratana 2000, Poonswad *et al.* 2012) and *Ficus* (Moraceae) (Poonswad *et al.* 2012). In the LKWS, the driest months are February and April, receiving about 50 mm of rain (Boonratana 2000). A distinct flowering period was reported in April, followed by the fruiting season in June (Boonratana 2000). The fruiting period coincides with the beginning of the nesting season for six species of hornbills in the Kinabatangan, namely Helmeted Hornbill, Wreathed Hornbill, Black Hornbill, Rhinoceros Hornbill, Bushy-crested Hornbill and Wrinkled Hornbill (Kaur 2020).

In addition to distribution and abundance of food resources, other potential limiting factors for sustaining healthy hornbill populations include the presence of natural tree cavities suitable for breeding and adequate roosting sites (Poonswad 1993, Poonswad 1995, Poonswad *et al.* 1999, Datta & Rawat 2004, Poonswad *et al.* 2013a). Being secondary cavity-nesters, Asian hornbills do not create tree cavities on their own (Chuaihua *et al.* 1998, Datta & Rawat 2004, Poonswad *et al.* 2013b, Pasuwan *et al.* 2015). Dipterocarpaceae are an important family of trees that provide main nesting opportunities for hornbills (Poonswad *et al.* 1987, Chuaihua *et al.* 1998, Jinamoy *et al.* 2014, Poonswad *et al.* 2013b). Mature dipterocarp trees have large girths and their pronounced heights make them susceptible to branch loss during storms. Subsequent fungal infections of the scar tend to form large cavities, creating ideal nesting sites for large bodied hornbills (Poonswad 1995). Cavities may also form through excavation works of woodpeckers and barbets (Chimchome *et al.* 1998, Datta & Rawat 2004).

When a hornbill breeding pair has selected a suitable tree cavity, upon mating the female hornbill will seal herself inside (Kemp 1995). A narrow slit will be preserved and used by the male hornbill to pass food material to the female and the chick (Poonswad 1993). Once a pair selects a suitable tree cavity, they will return to nest in it in following years (Poonswad *et al.* 1987, Kinnaird & O'Brien 2007), as has been documented for the Red-knobbed Hornbill *Rhyticeros cassidix* (Kinnaird & O'Brien 2007) and Helmeted Hornbill (Kaur *et al.* 2018).

A logged forest may offer adequate food for adult hornbills but fewer suitable nest cavities (Meijaard *et al.* 2005). There is also intraspecific competition among hornbill species for tree cavities and interspecific competition through cavity occupation by monitor lizards, king cobras, flying squirrels, bees and wasps (Poonswad *et*

Figure 1. The 10 km² study site as circled, located in Kinabatangan, Sabah, Malaysia.



al. 1987, Datta & Rawat 2004). Hence, the decline in the hornbill population in the LKWS is postulated as a result of the loss of nesting resources.

Although tree cavities are essential to sustain viable populations of the hornbill species, there is limited information available on tree cavities and cavity formation in South-East Asia (Meijaard *et al.* 2005, Cockle *et al.* 2011). In this study, we investigate whether the paucity of suitable cavities may explain the decline in hornbill populations in Kinabatangan by estimating the proportion of forest patch currently occupied by potential nest trees, i.e. trees with cavities. The results of this study can be used to inform local wildlife management authorities about possible adaptive management activities to be undertaken to sustain viable and healthy bird populations (e.g. the need to erect artificial nest boxes).

METHODS

Study site

The LKWS experiences seasonal flooding. Most of its flood-free zone, comprising 60,000 ha of lowland forest, has been converted into agricultural land (Boonratana 2000). Geologically, the LKWS consists of flood-prone alluvium soil, limestone hills and sandstone hills. A majority of the area within LKWS has been logged at least once (Boonratana 2000). The forest experiences a warm, wet and humid climate with an annual precipitation that averages 3,000 mm (Ancrenaz *et al.* 2004).

We conducted three reconnaissance site visits in different patches of the LKWS to select appropriate sampling areas. These sites comprise

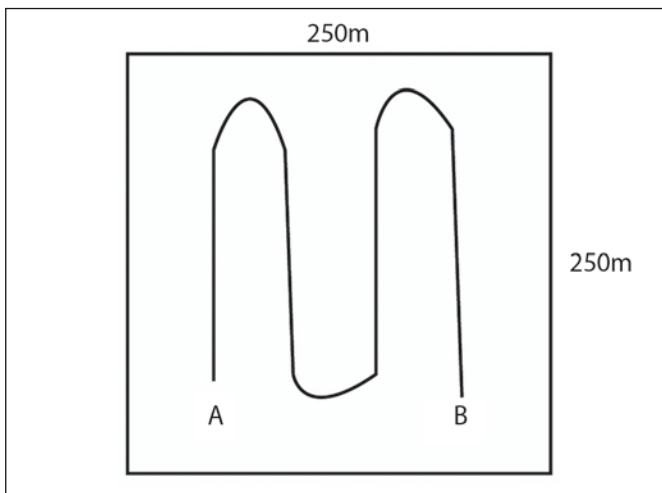
continuous logged forest patches accessible to the observers without entry restrictions imposed by the local government. We ultimately selected one site: a 10 km² long-term study area used by the researchers from NGO HUTAN-Kinabatangan Orangutan Conservation Programme (KOCOP) located in Lot 2 of the LKWS (Figure 1).

Systematic sampling survey

The main survey was carried out in September–October 2017, towards the end of the breeding season of the Rhinoceros Hornbill, Helmeted Hornbill, Wreathed Hornbill, Black Hornbill, Bushy-crested Hornbill and Wrinkled Hornbill (Kaur 2020). This period of time allows for easier nest detection because at the end of the breeding cycle, the chicks are more vocal, and adult pairs become more conspicuous as they move back and forth to the nest to supply food to their chicks (Kaur 2020). In order to reduce observer-specific heterogeneity in detection probability, eight observers were specifically trained before the survey (Chen *et al.* 2009). They learnt to recognise hornbill calls through audio recordings and the eight different hornbill species through photographs. They were also trained to recognise the preferred tree cavities of hornbills through the use of photographs.

A tree cavity deemed suitable for hornbills was recorded if its cavity entrance possessed distinct shapes as described in Poonswad & Kemp (1993). Typical cavity entrance dimensions for Great Hornbill *Buceros bicornis*, Wreathed Hornbill and Oriental Pied Hornbill are 40 cm x 14 cm, 26 cm x 13 cm and 25 cm x 10 cm, respectively (Poonswad & Kemp 1993), and these sizes were incorporated into the list of criteria for on-the-ground estimation during cavity selection. Though Great Hornbills do not occur in

Figure 2. The 'M'-shape transect walked by observers in a 250 m x 250 m plot.



Borneo, they have a similar body size to the Rhinoceros Hornbill. Furthermore, in Thailand, Great Hornbill nest cavities have been used by other hornbill species such as Wreathed Hornbill and Oriental Pied Hornbill (Poonswad 1993). Cavities that lure hornbills tend to have scratch marks at the base of the entrance, along with remnants of old or fresh sealing material (Kaur 2020). Observers were also shown photos of hornbill faeces, feathers and preferred fruits, as these items are commonly found aggregated at the base of a hornbill nest tree (Datta & Rawat 2004).

Prior to the actual survey, a pilot survey was conducted with three types of plot sizes, i.e. 100 m x 100 m, 250 m x 250 m and 500 m x 500 m, to determine their practicality for the survey. We ultimately selected the 250 m x 250 m plots because this size was manageable in terms of effort. This plot size also made it easier to estimate the location of hornbills that were sighted or heard during the surveys and determine if they were indeed within the plot area. A map with 250 m x 250 m plots was overlaid using ArcGIS software and then uploaded into the Garmin GPS devices. The map within the GPS device helped guide the observers to remain inside the selected plot (Figure 2).

Observers were divided into two main groups, each consisting of four observers. The observers used systematic sampling techniques, whereby every alternate 250 m x 250 m plot was surveyed. For each plot, the four observers walked a 1.2 km transect once, at the same pace, from point A to point B following an 'M' shape. In one day, the two teams of observers could complete two to four plots, depending on plot distance and weather. Each team had one observer that used a compass to navigate through the plots and into neighbouring plots while the others searched for cavities with their binoculars. A detection event was defined as a visual sighting of a tree cavity deemed suitable for hornbills, based on the pre-established list of criteria. In each plot, the observers recorded the time of detection of trees with cavities seen along the transect as the response variable. Any hornbill species sighted or heard within the plots were also noted down.

Trees with cavities were marked with blue paint and their location carefully recorded and mapped with a GPS device to help observers locate them again to obtain tree measurements and species identification in a subsequent survey. The observers and a botanist carried out the tree identification surveys in June 2018, February 2019 and May 2019. During these surveys, the observers walked towards the previously located trees with cavities based on the GPS coordinates and any additional trees with cavities that were encountered by chance were recorded. In addition, the height and diameter at breast height (DBH) of the marked trees were recorded using a range finder (Leica Disto D810 Touch) and a measuring tape, respectively.

Statistical analysis

Tree cavities are difficult to detect because thick foliage or branches may cover them. Imperfect detection results in uncertainty and can potentially lead to misleading conclusions and poor wildlife management decisions. To reduce this bias, we examined the bark of all large trees (DBH >0.40 m) with a pair of binoculars. The DBH threshold was chosen because it represents the smallest DBH value documented for a hornbill nest tree (Poonswad *et al.* 1987).

Traditional occupancy methods rely on temporal replicates to estimate detection probability (MacKenzie *et al.* 2002). However, it is becoming increasingly popular to use occupancy models with spatial replication to estimate detection probability over vast geographical areas that are expensive and logistically difficult to survey repeatedly (Whittington *et al.* 2014). Therefore, a transect can be divided into segments and each segment is considered a replicate. However, a loss of information would arise if several detections were recorded in one segment. To address this, Guillera-Aroita *et al.* (2011) proposed that the transect be divided into infinitesimal segments, providing a more natural description of any continuous detection data through a Poisson distribution.

One of the assumptions of such a zero-inflated Poisson model (Guillera-Aroita *et al.* 2011, Kery & Royle 2016) is that the study site must be closed to changes in occupancy (Guillera-Aroita *et al.* 2011). This assumption was met because trees are immobile and each transect was walked within a day. The detection probability, $p:\lambda = \text{LAMBDA} * p$, where LAMBDA is the number of trees with cavities available for detection per unit length if present along a transect. There are no false positives as each transect without trees with cavities is given zero detection. The model includes a parameter, $z[i]$, indicating the presence or absence of trees with cavities and this is the basis of our occupancy estimate.

The occupancy probability and detection probability are assumed constant across sites (Guillera-Aroita *et al.* 2011). In addition, the assumption is that detections occur independently (Guillera-Aroita *et al.* 2011) and cavities that form in trees are indeed an independent occurrence, i.e. the probability of a tree cavity presence on one replicate is not influenced by the presence on other replicates within the same cell.

This hierarchical model addresses a two-layered process simultaneously, the ecological process for the occurrence of trees with cavities and an observational process, the detectability of trees with cavities. The latter is often prone to error (MacKenzie *et al.* 2006, Bornaand *et al.* 2014) as cavities may be hidden by foliage:

Model for presence/absence: $z_i \sim \text{Bernoulli}(\psi_i)$

Number of detections at site i : $n_i \sim \text{Poisson}(L_i * z_i * \lambda_i)$

where n_i is the number of detections at site i , L_i is the time spent at site i , and λ_i the rate per detection of trees with cavities at site i .

We used JAGS (<http://mcmc-jags.sourceforge.net>), a generic Bayesian software package available online, to fit the model using Markov Chain Monte Carlo (MCMC) techniques (Royle & Dorazio 2008) in R software (R Development Core Team 2012). Sample codes and data are available from the corresponding author upon request.

RESULTS

The observers walked 36 km in total and detected a total of six species of hornbills in the study site: Bushy-crested Hornbill, Black Hornbill, Oriental Pied Hornbill, Rhinoceros Hornbill, White-crowned Hornbill and Wrinkled Hornbill (Figure 3).

During the first survey, observers detected trees with cavities in 10 out of the 30 plots. The observed proportion of occupied plots was $10/30 = 0.33$, and this value represents the naïve occupancy estimate $psi \psi_{naive} = 0.33$ (Figure 4).

A total of 14 trees with cavities ($n=14$) were discovered and geotagged. None of the located tree cavities were used by any

hornbill species at the time of the survey. When the model was applied, with a Bayesian prior distribution and the data (priors for occupancy estimates $\psi \sim \text{dbeta}(1, 1)$ and $\lambda \sim \text{dgamma}(0.0001, 0.0001)$), a posterior mean occupancy estimate of $\psi = 0.82$ with a 95% credible interval (0.56, 1) emerged (Figure 5). Based on the JAGS output, the rate of detection of trees with cavities was 0.005.

The occupancy value (ψ) was a higher estimate than the naïve occupancy estimate. In fact, by accounting for imperfect detection, the model indicated that trees with cavities occupied 25 plots, a much larger area than perceived based on the naïve estimates. During the subsequent botanical assessments of the 14 trees with cavities, we recorded five additional cavity-bearing trees. Of these five cavities, three were located inside the systematically chosen plots while the other two were located outside the plots. Though these additional five cavities were not included in the occupancy analysis, these trees were also identified to family or species level, along with the 14 original trees with cavities (Appendix 1).

The mean height of the trees with cavities ($n=19$) was 21.0 m, standard deviation (SD) = 4.9 (height range 13.7–28.4 m) and the mean DBH of the trees was 0.6 m, SD=0.2 (DBH range 0.3–1 m). The mean height of the cavity was 10.3 m, SD=5.8. Only 32% of the 19 trees had cavities occurring higher than 10 m from the ground. The most common tree families and genera with cavities were Sapotaceae, genus *Madhuca* ($n=4$) followed by Lauraceae, genus *Eusideroxylon* ($n=4$). During all surveys, there were no signs of nesting by hornbills in any of the marked trees with cavities. There were no signs of sealing materials at the cavity entrances, no fallen faeces of hornbills and aggregations of regurgitated seeds at the base of the trees, no visits by any hornbills and no calls of chicks.

DISCUSSION

As anticipated, trees with cavities may be easily overlooked in the field, as shown by our observed occupancy estimate ($\psi_{naive} = 0.33$), which was considerably lower than the occupancy estimate obtained by the model ($\psi = 0.82$). In fact, the model suggests that 25 plots were occupied by trees with cavities, as opposed to our field observation of only 10 occupied plots. The results from the model were supported further by the discovery of five additional cavities during the subsequent botanical assessment, suggesting that as effort increases, more trees with cavities could be discovered.

Degraded forests are characterised by an abundance of pioneer tree species from different families, such as Euphorbiaceae, Dilleniaceae, Theaceae, Sterculiaceae and Moraceae (Whitmore 1984). In fact, a vegetation study in the LKWS by Boonratana (2000) also reported on these tree families in a sample of 1,378 trees. Species of the family Euphorbiaceae were the most abundant, followed by Myrtaceae, Rubiaceae, Lauraceae and Dilleniaceae. Pioneer tree species exhibit rapid height and girth growth and tend to have low wood density (Whitmore 1984). These plants are light-demanding species that thrive when a large gap occurs in the forest, creating heterogeneity (Whitmore 1984). Thus, the growth of pioneer species obscures tree cavities, making cavity detection a challenging task from the ground. There are also tree cavities that occur with protruding rims, complicating detection from the ground. Hence, it is plausible that many trees with cavities were easily overlooked.

Perhaps due to their low wood density, pioneer trees are more susceptible to cavity formation than climax tree species because of heart rot, excavators or storm damage. This may explain why cavities appear to be widespread in this young regenerating forest. However, the low wood density and rapid growth of the trees might make their cavities less suitable for long-term hornbill nesting as they are more susceptible to rapid change such as entrance narrowing

Figure 3. The number of plots occupied by hornbill species in the 10 km² study site.

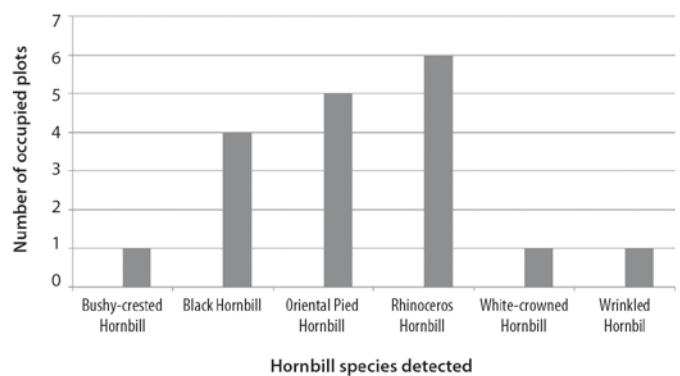


Figure 4. The black dots represent the location of trees with cavities in 30 plots (shaded medium grey) of the 10 km² study site.

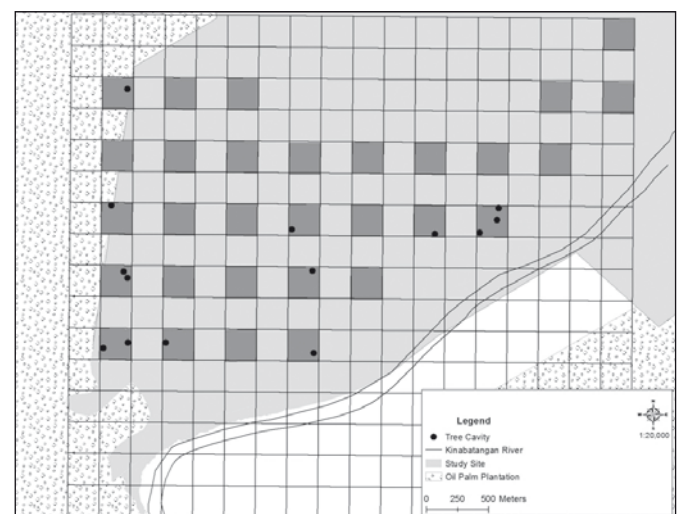
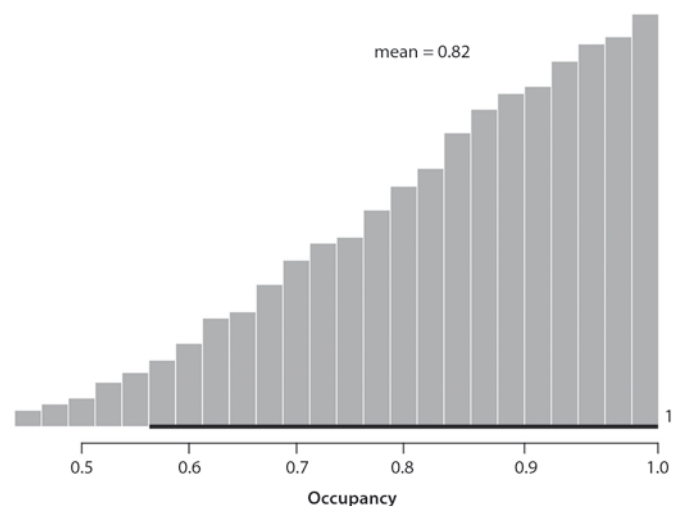


Figure 5. The posterior mean occupancy estimate $\psi = 0.82$ with a 95% credible interval (0.56, 1), reflecting the proportion of sites occupied by trees with cavities in the 10 km² study site.



and deterioration of the cavity floor. These processes are the most common cause for nest deterioration among natural hornbill nests in Thailand (Chuilua *et al.* 1998).

To address imperfect detection, we need to estimate the probability of detection of trees with cavities. This is usually achieved through repeated surveys, which in turn means more field effort and inflating costs (Whittington *et al.* 2014). Ground surveys are also challenging to carry out in most of these degraded

tropical forests characterised by thick undergrowth. Our model is advantageous because it does not require repeated surveys or multiple observers and thus is more easily implemented than traditional site-occupancy models. Therefore, even with limited time, manpower and budget, one can obtain reliable estimates in a short time with these hierarchical occupancy models. We did not include other variables because we were restricted to surveys within 30 plots, a sparse data set. If working with a larger data set, the incorporation of additional variables, such as observer bias, may improve the performance of the model.

Based on the model, cavities appear to be a widespread resource in the study site. However, none of the 19 cavities examined by our team was occupied at the time of the surveys, despite the presence of six hornbill species in the study site. Previous studies at other sites showed that upon closer inspection, 70–80% of cavities that were observed from the ground were not suitable for nesting birds, lacking the internal depth and height (Cockle *et al.* 2010). A limitation of this study is the lack of closer examination of the cavity's features (e.g. precise shape, depth and other parameters that influence breeding suitability). Such evaluation would require climbing trees for closer inspection, which would increase costs, manpower and time resources allocated for the surveys, as well as exposing the team to potential hazards. Hence, we attempted to counterbalance this shortcoming by conducting our survey during the hornbill breeding season as we assumed that high quality cavities would have a higher chance of being occupied and active nests would be more conspicuous.

A hornbill's body size dictates the choice of nest cavity as larger hornbills choose bigger trees with higher cavities (Kinnaird & O'Brien 2007). The mean height of the cavity-bearing trees we recorded was 21 m and the mean cavity height was 10.3 m, while the DBH ranged between 0.3–1.0 m. Cavities formed in trees of such a size range may be too small for large bodied hornbills. In a study in Thailand, Poonswad (1993) divided the forest into three main layers, the lower layer (<15 m), middle layer (15–25 m) and top layer (>25 m). Larger hornbills such as Great and Wreathed Hornbills preferred nesting in middle and top layers whereas the smaller bodied hornbills such as Oriental Pied Hornbill and Austen's Brown Hornbill *Anorrhinus austeni* preferred middle and lower layers. Hence, the over-logged and regenerating forest of Kinabatangan seems to lack the preferred cavity heights and internal cavity sizes to accommodate larger bodied hornbills.

In Thailand, the two main tree genera and families of hornbill nest trees were *Dipterocarpus* (Dipterocarpaceae) and *Syzygium* (Myrtaceae) (Poonswad *et al.* 2013a). In Kinabatangan, in addition to Dipterocarpaceae, tree families such as Rubiaceae, Moraceae, Malvaceae, Anacardiaceae, Acanthaceae and Erythroxylaceae have been reported as preferred nesting trees of hornbills (Kaur *et al.* 2018, Kaur 2020). In our study, none of the 19 detected cavities occurred in dipterocarp trees, an important nest tree family in Thailand. A previous study in the same forest patch also recorded that all known hornbill nest trees, i.e. *Dipterocarpus*, *Shorea*, *Parashorea*, *Cleistocalyx* and *Syzygium*, were young and had not yet formed any cavities (Poonswad *et al.* 2012).

In this study, only two tree species with cavities belonged to families known to be used by hornbills for nesting, i.e. Myrtaceae (genus *Decaspermum*) and Sapotaceae (genus *Madhuca*). For instance, Black Hornbills have nested in *Madhuca motleyana* in the family Sapotaceae (Poonswad *et al.* 2013). The genus *Madhuca* was also used by Bushy-crested Hornbill and Wreathed Hornbill in Sumatra (Sibarani *et al.* 2020). Most of the cavities detected in this study had formed in tree species that are not known to serve as hornbill nest trees, such as Belian *Eusideroxylon zwageri* (Lauraceae), a slow growing tree of high wood density. Despite its reputation for being extremely solid, this tree species is susceptible to cavity formations as we located four such trees with cavities. In

fact, in another study on Borneo, stingless bees had occupied natural tree cavities that occurred in 17 trees of *Eusideroxylon zwageri* (Eltz *et al.* 2003). In other studies in Thailand, trees that tend to form cavities were *Alangium salviifolium* (Cornaceae), *Lagerstroemia* spp. (Lythraceae) and *Vitex* spp. (Lamiaceae) (Pattanavibool & Edge 1996).

The lack of nesting opportunities for large bodied hornbills is also evident by the continued utilisation of artificial nest-boxes in Kinabatangan since 2017. Over a three-year period, a total of five nesting cycles by two pairs of Rhinoceros Hornbills were recorded in two separate artificial nest-boxes erected by HUTAN-KOCP within the area (Kaur 2020). In fact, one of the nest-boxes utilised by a Rhinoceros Hornbill pair for three consecutive years is located directly across the river from our study site. Smaller bodied hornbills such as Bushy-crested Hornbill and Oriental Pied Hornbill were also reported to use artificial nest-boxes in Kinabatangan (Kaur 2020).

These observations may indicate the lack of suitable nesting sites in these forests, particularly for larger hornbill species, which could threaten the long-term viability of hornbill populations. Installing artificial nest-boxes in logged and regenerating forests may be necessary to support and boost the long-term viability of hornbill populations. The existing trees with cavities located in this study will require long-term monitoring. If they remain unoccupied, these cavities will be climbed and evaluated for possible cavity restoration works to make them suitable for smaller-bodied hornbills to nest in. Such conservation efforts have been successful in Thailand (Poonswad *et al.* 2012).

The formation of good quality tree cavities through decay takes a considerable amount of time. Most forestry policies promote the harvest of large mature trees and protect young trees, which can be detrimental to cavity-nesting animals (Cockle *et al.* 2011). Such practices need to be changed because these large mature cavity-bearing trees are an important resource for animals and should be spared and protected (Pattanavibool & Edge 1996, Meijaard *et al.* 2005, Cockle *et al.* 2011).

CONCLUSION

The results of our occupancy model suggest that trees with cavities are rather widespread in the study area. However, our study site is at an early stage of regeneration and all the cavities we identified occurred in pioneer tree species that are not known as nest trees of the hornbills. The low heights of the cavities and their relatively small size make them less suitable as nesting sites for large hornbill species. These existing trees with cavities can be restored to become suitable for smaller-bodied hornbills. For larger hornbill species, we recommend installing artificial nest-boxes to provide breeding opportunities.

Overall, our work shows that it is cost-efficient to conduct rapid nesting resource assessments to inform hornbill conservation strategy. Identifying the presence, relative abundance and overall characteristics of tree cavities, along with tree species identities, is crucial information to decide what management strategy needs to be implemented to sustain the long-term viability of hornbill populations.

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Appendix 1. The species, families, common names and measurements of trees with cavities located in the 10 km² study site.

No.	Tree height (m)	Circumference (m)	Diameter at breast height (dbh) (m)	Cavity height (m)	Family	Species/genus	Common name
1	20.5	1.8	0.6	8.4	Sapotaceae	<i>Madhuca</i> sp.	Nyatoh
2	14.0	0.9	0.3	6.4	Sapotaceae	<i>Madhuca</i> sp.	Nyatoh
3	26.4	1.0	0.3	8.5	Sapotaceae	<i>Madhuca</i> sp.	Nyatoh
4	24.1	1.8	0.6	12.5	Sapotaceae	<i>Madhuca</i> sp.	Nyatoh
5	25.8	3.0	1.0	13.4	Lauraceae	<i>Eusideroxylon zwageri</i>	Belian
6	21.4	2.7	0.9	9.3	Lauraceae	<i>Eusideroxylon zwageri</i>	Belian
7	17.5	1.9	0.6	13.6	Lauraceae	<i>Eusideroxylon zwageri</i>	Belian
8	24.8	2.3	0.7	9.4	Lauraceae	<i>Eusideroxylon zwageri</i>	Belian
9	24.4	1.0	0.3	9.5	Sterculiaceae	<i>Pterospermum macropodom</i>	Tungkulingan
10	24.5	1.8	0.6	7.5	Sterculiaceae	<i>Pterospermum macropodom</i>	Tungkulingan
11	16.7	2.2	0.7	9.6	Myrtaceae	<i>Decaspermum fruticosum</i>	Obah merah
12	16.9	1.5	0.5	8.3	Myrtaceae	<i>Decaspermum fruticosum</i>	Obah merah
13	22.8	1.6	0.5	13.7	Rubiaceae	<i>Neolamarckia cadamba</i>	Laran
14	28.4	1.7	0.5	21.0	Rubiaceae	<i>Neolamarckia cadamba</i>	Laran
15	14.5	2.2	0.7	1.2	Dilleniaceae	<i>Dillenia bornensis</i>	Simpoh gajah
16	13.7	1.2	0.4	3.6	Meliaceae	<i>Toona sureni</i>	Limpaga
17	18.6	1.9	0.6	8.6	Euphorbiaceae	<i>Excoecaria indica</i>	Apid-apid
18	28.3	2.6	0.8	26.1	Anacardiaceae	<i>Pontaspadon motleyi</i>	Pelajau
19	16.5	1.6	0.5	4.8	Bombacaceae	<i>Nessia</i> sp.	Durian monyet