

Long-term monitoring of nesting behavior and nesting habitat of four sympatric hornbill species in a Sumatran lowland tropical rainforest of Bukit Barisan Selatan National Park

Marsya C. Sibarani^{1*}, Laji Utoyo¹, Ricky Danang Pratama², Meidita Aulia Danus³, Rahman Sudrajat¹, Fahrudin Surahmat¹, and William Marthy¹

¹Wildlife Conservation Society-Indonesia Program, Jalan Tampomas no. 35, Bogor 16151 Indonesia

²Universitas Lampung, Jalan Prof. Dr. Soemantri Brodjonegoro No.1, Bandar Lampung 35145 Indonesia

³Bukit Barisan Selatan National Park, Jalan Ir. H. Juanda No. 19, Terbaya, Kotaagung, Lampung, 35384 Indonesia

*Corresponding author: msibarani@wsc.org

Abstract

Hornbills are vulnerable to extinction due to their low reproductive output and dependence on large trees as nesting sites. However, little is known about their breeding behavior in Sumatra, which is important to plan effective strategies to save the nine species from extinction. Here we present the nesting season and nest-site characteristics of sympatric hornbills at Way Canguk Research Station, Bukit Barisan Selatan National Park, Sumatra, Indonesia. We monitored in total 35 tree cavities in two monitoring periods: 23 tree cavities between 2006 – 2009 and 20 between 2015 – 2018; and recorded the nesting activities of hornbills. We also measured the characteristics of nest trees, nest cavities, and vegetation within 20-m radius of the nest trees. We found that there was a significant decrease of nesting frequency between the two monitoring periods, from a mean of 0.058 records/year in 2006 – 2009 to 0.013 records/year in 2015 – 2018. Of eight hornbill species known to occur in the study area, only four were found nesting during the study periods, i.e. Bushy-crested, Helmeted, Rhinoceros, and Wreathed Hornbills. Among the four species, there were no differences in the height of nest cavities, diameter, and height of nest trees. All species preferred emergent trees and trees with big trunks as nesting sites. Wreathed Hornbill preferred nests with more vertically-elongated nest entrance compared to the other three species which were found nesting in oval cavities. Bushy-crested Hornbill seemed

to select nest cavities with entrance facing toward north-east direction, while the other hornbill species did not have preferences. Most tree species that were used by hornbills for nesting also have high timber value, thus are vulnerable to the risk of illegal logging. To ensure the survival of hornbills, sufficient number of tree cavities that are suitable for nesting must be maintained.

Keywords: breeding, bird population, reproductive behaviour, Way Canguk Research Station

Introduction

Ensuring the success of a species' reproduction is important to safeguard the survival of the species. Understanding species' reproductive behavior and breeding habitat suitability are required to plan effective conservation actions (Côté 2003). Hornbills are cavity-nesters that are dependent on the availability of tree cavities for breeding. They are, however, unable to excavate their own nesting cavities (Poonswad 1995), but rather occupy cavities formed by the decay of broken branches or excavated by other birds such as woodpeckers and barbets (Datta and Rawat 2004, Supa-Amornkul et al. 2011).

Hornbills' nesting cavities are usually located in large and tall trees (Poonswad 1995, Mudappa and Kannan 1997, Utoyo et al. 2017), which are rare in logged forests because the trees with such characteristics are also of high timber value (Mudappa and Kannan 1997, Collar 2015).

Hornbills occur sympatrically with a number of other hornbill species across their ranges. As frugivores and cavity-nesters, they have overlapping niche, but some sympatric hornbills also exhibit resource partitioning on foraging strategies and nest cavity preferences. In Sumatra, Helmeted hornbill *Rhinoplax vigil* and Rhinoceros hornbill *Buceros rhinoceros* tend to predominantly feed on figs, while the diet of Bushy-crested hornbill *Anorrhinus galeritus* and Wreathed hornbill *Rhyticeros undulatus* primarily consists of oily drupaceous fruits (Hadiprakarsa and Kinnaird 2004). Helmeted hornbills are found more frequently in the upper canopy relative to the other sympatric species (Hadiprakarsa and Kinnaird 2004). Great hornbill *Buceros bicornis* tend to use larger cavities, while Oriental Pied hornbill *Anthracoceros albirostris* used smaller ones in India (Datta and Rawat 2004). Poonswad (1995) also reported differences in nesting tree diameter, tree height, and nest cavity dimensions among four sympatric hornbills in Thailand.

Compared to the other forest birds, hornbills have distinctively larger body size which is linked to lower reproductive output, longer generation spans, and dependence on large tree cavities (Gonzalez et al. 2013). Therefore, it will take a long time to reverse population declines. Unfortunately, hornbills face high threats of extinction due to habitat loss, habitat disturbance, forest fragmentation, and illegal hunting (Kinnaird and O'Brien 2007). Forest fires are known to be associated with the de-

cline of nesting success in hornbill population (Cahill and Walker 2000) and the population decline of some hornbill species (Anggraini et al. 2000). Helmeted Hornbill is highly hunted for their dense casques that are used for carving—around 2,170 casques were seized from illegal market in Indonesia and China between 2012 and 2014 (Beastall et al. 2016).

The island of Sumatra harbors nine species of hornbills among the 62 hornbill species found globally and among the 13 species found in the Indonesian archipelago. Of the nine species, one is listed as Critically Endangered, two as Endangered, and four as Vulnerable on the *IUCN Red List of Threatened Species* (IUCN 2019). There are only few studies on hornbill nesting behavior in Indonesia (Marsden and Jones 1997, Kinnaird and O'Brien 2007, Rahayuningsih et al. 2017). Particularly, not much is known about hornbill nesting cycle and nesting site characteristics in Sumatra. In this study, we aimed to (1) estimate the nesting period of four sympatric hornbills, and (2) assess the characteristics of the hornbills' nest cavities, nest trees, and nest sites at Way Canguk Research Station (WCRS), one of the last Sumatran lowland rainforests.

Methods

Study area

We conducted long-term tree cavity monitoring at Way Canguk Research Station (WCRS), Bukit Barisan Selatan National Park (BBSNP), Lampung Province, Sumatra, Indonesia (Fig. 1). The research area covers 800 ha of lowland dipterocarp forest which ranges between 15 – 70 m above sea level. The forest is a mixture of intact primary forest and secondary forest disturbed by past forest fires and illegal logging. The annual rainfall during the study periods (2006 to 2018) ranged between 2459 – 4620

mm, with a mean of 3347 ($SD = 644$) mm. The research area experiences two seasons: dry season during March-September (driest month in August with a mean rainfall of 91 mm/month) and rainy season during October-April (wettest month in November with a mean rainfall of 519 mm/month). Eight hornbill species have been recorded in the research area: Black hornbill *Anthracoceros malayanus*, Bushy-crested hornbill, Great hornbill, Helmeted hornbill, Oriental Pied hornbill, Rhinoceros hornbill, White-crowned hornbill *Berenicornis comatus*, and Wreathed hornbill.

Tree cavity monitoring

We recorded the locations of trees with cavities found within the 800 ha research area *ad libitum* during other biodiversity monitoring or research. Each month throughout the year since 2006, we monitored the tree cavities and recorded the occurrence of nesting hornbills. If there were hornbills nesting in a tree cavity, we monitored their activities for three days each month (average interval between visits = 7 days, $SD = 6.9$), 4 – 5 hours per day. We recorded their behavior *ad libitum* and we tried to minimize disturbance by frequent visit as these hornbills are really sensitive (based on our field observation where once they noticed human presence the female will alert the male to not approach the nest).

The monitoring data were only available for 2006 – 2009 and 2015 – 2018. We calculated hornbill nesting frequency (f) during each period using the following formula:

$$f = \frac{\text{number of nesting hornbill}}{\text{monitoring effort}(\text{year})}$$

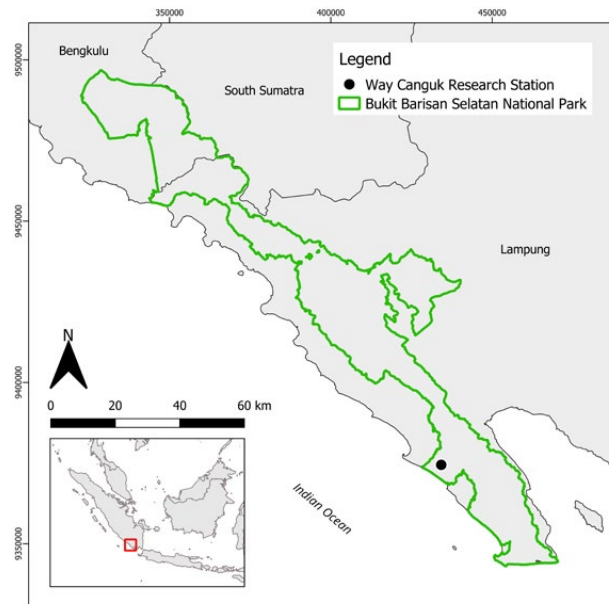


Fig. 1. The location of Way Canguk Research Station in Bukit Barisan Selatan National Park, Sumatra, Indonesia.

We calculated nesting frequencies for each individual tree. To account for unequal monitoring effort for each tree (Fig. 2), we included monitoring effort in the calculation instead of simple counts of nest records. A record of hornbill occupying a cavity was included in the calculation if the hornbills were seen occupying the cavity for a minimum of 2 survey-months. Survey effort was defined as the number of survey-months, and then converted to years. We only calculated nesting frequencies in trees that we monitored for a minimum 24 months in each study period. We then tested for differences between the nesting frequencies in 2006 – 2009 and 2015 – 2018 using Wilcoxon rank sum test.

The duration of nesting cycle was approximated by calculating the difference between the first and last date when the hornbills were observed to occupy the cavity. To estimate the nesting duration, we only used the observation data if we had checked the cavity at least a month before and after the hornbills nesting to allow a more accurate estimation.

Nesting cavity characteristics

We measured the nest tree and cavity characteristics of nests used by any hornbill species. We measured 1) the nesting tree's diameter at breast height (dbh) using a diameter tape at 1.3 m above ground; 2) tree height, nest height from the ground, and height of first branch using a range-finder; 3) and nest entrance orientation relative to compass direction. We also climbed the tree and measured the height and width of the cavity opening. Nest entrance measurements were made when the hornbills were no longer occupying the tree cavity.

We then performed Kruskal-Wallis test for testing the differences in nesting tree diameter, tree height, nest cavity height, and nest opening height:width ratio among the four hornbill species. If we found a statistically significant result ($p < 0.05$), we further ran Dunn's multiple comparison test as a post hoc test to determine species pairs that exhibited significant differences. Orientation angles of nest entrances were treated as circular data. We ran Rayleigh test for circular data for each species separately to examine if the nest entrances for each hornbill species faced random direction (null hypothesis) or faced particular direction (alternative hypothesis; Landler et al. 2018).

Vegetation survey

We surveyed the vegetation surrounding the nesting tree within circular sampling plots of radius 20 m with the nesting tree at the center. We recorded all plants with a dbh ≥ 10 cm. We identified the trees to species level (identification guide: Whitmore 1972) and measured the dbh, tree height, and height of the first branch. We ran Wilcoxon rank sum test to see the differences between 1) nesting tree dbh and the dbh of surrounding trees, and 2) nesting tree height and surrounding tree height.

To describe the vegetation community in nesting sites, we calculated Shannon diversity index, species richness, and tree density in each sampling plot. We then performed Kruskal-Wallis test and Dunn's test to examine differences in vegetation characteristics between nesting sites of the four hornbill species.

Results

Nesting frequency and duration

We monitored 23 tree cavities in 2006 – 2009 and 20 trees in 2015 – 2018 (totaling 35 tree cavities). Among these, 8 trees were monitored in both periods and there were 12 new trees in 2015 – 2018. Fifteen trees found in 2006 – 2009 were no longer monitored because either the trees fell down or the cavities shrank. Of 8 hornbill species known to occur in WCRS, we recorded four species nesting during 2006 – 2018 in 19 tree cavities across the study area (Fig. 2). Between 2006 and 2009, we recorded 19 occurrences of nesting hornbills (mean $f = 0.058$ records/year, $SD = 0.037$), and between 2015 and 2018, there were 10 records (mean $f = 0.013$ records/year, $SD = 0.012$). There was a significant decrease of nesting frequencies between period 2006 – 2009 and 2015 – 2018 (Wilcoxon test, $W = 81$, $p < 0.001$).

Five of 19 nest cavities were used by hornbills multiple times, and the same cavities tended to be re-occupied by the same hornbill species. For example, a cavity in a *Terminalia bellirica* was used four times by the Wreathed Hornbill (three times between 2006 – 2009 and once in 2015). An exception was recorded in 2009 when a nesting pair of Wreathed hornbills in a *Dipterocarpus humeratus* were replaced by Helmeted hornbills. Unfortunately, the tree had fallen down before 2015, so we could not perform nest measurement.

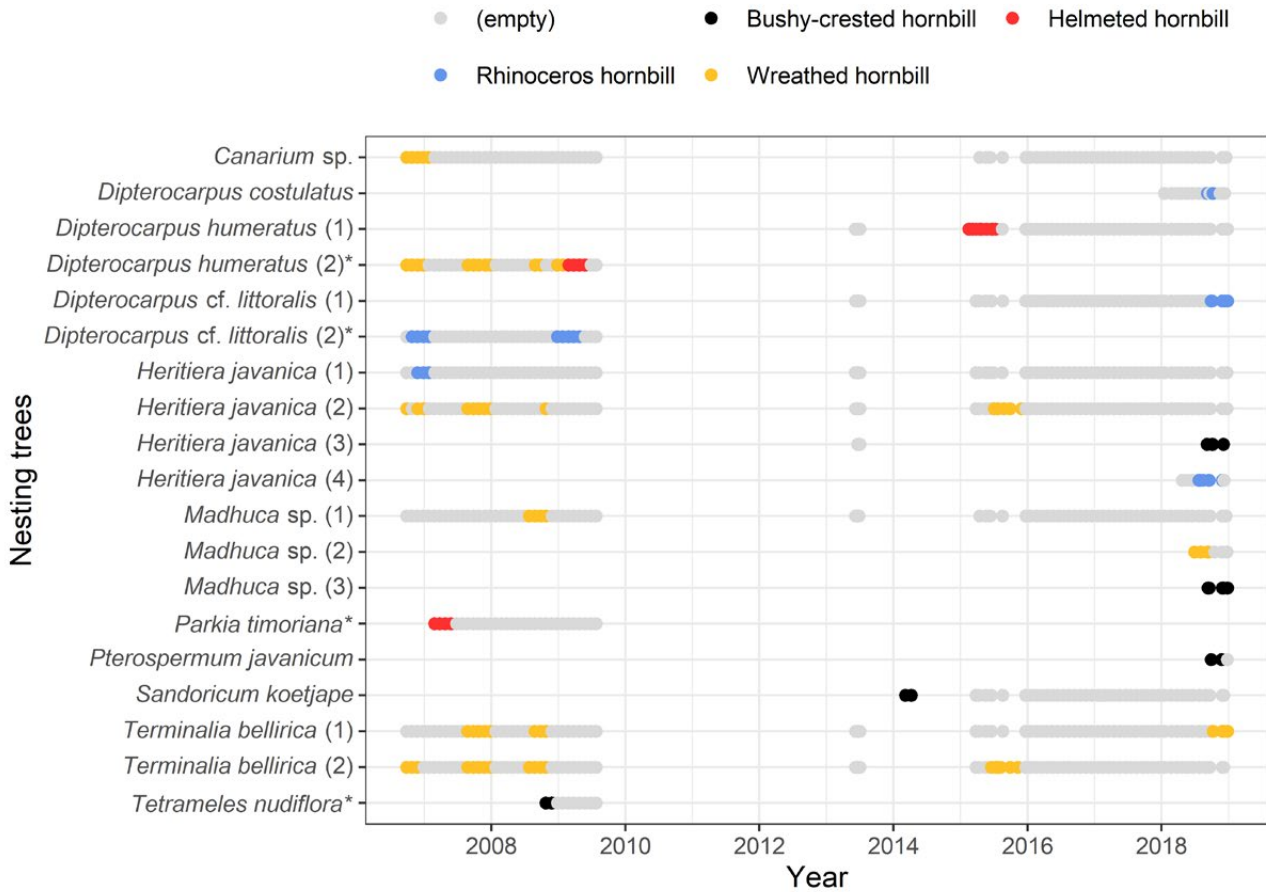


Fig. 2. Nesting cycle of hornbills at Way Canguk Research Station. Tree species with asterisks had fallen down or the cavities were damaged/closed.

Of four hornbill species, nesting period could only be estimated for three species, i.e., the Rhinoceros, Helmeted, and Wreathed hornbills. Of a total of 29 nesting records, we could not estimate the nesting duration on seven records because the cavities were found when the hornbills had already started nesting. All observations of nesting Bushy-crested Hornbill were encountered after they started nesting. Hornbill, Rhinoceros Hornbill exhibited longer nesting durations (Table 1).

In general, Rhinoceros Hornbill started nesting in mid-year and left the nest at the end of the same year or early the next year. Among the four species, Wreathed Hornbill was the most frequently found nesting in the study area. This species usually started nesting between July-August, and then left the nest between October-Decem-

ber. Helmeted Hornbill was recorded nesting in early year (Jan-Feb), and left the nest around midyear. There was no record of the time when Bushy-Crested Hornbill start nesting, but we recorded two occurrences of them leaving the nest in December (Fig. 2).

Other than the 10 records of nesting Wreathed Hornbills, we also twice recorded Wreathed Hornbills visiting tree cavities for approximately 31 days in August-September 2008 and December 2008-January 2009. Subsequently in February 2009, however, the cavity was occupied by a pair of Helmeted hornbills. Other competition events for tree cavities were also recorded on 16 January 2016 and 26 April 2018. On the former date, a pair of Rhinoceros Hornbills was

Table 1. Nest duration approximation

Species	No. of nesting records	Mean (SD) of nesting duration in days	Range in days	Range in days based on previous studies
Rhinoceros hornbill	5	99 (26)	62 – 127	80 – 143 ^a 50 – 111 ^b
Helmeted hornbill	2	118 (40)	89 – 146	172 ^a 140 – 162 ^b 154 – 167 ^c
Wreathed hornbill	10	116 (27)	61 – 149	128 ^a
Bushy-crested hornbill	5	-	-	90 ^a

^aKinnaird and O'Brien 2007

^bKaur et al. 2015

^cChong 2011

observed visiting a tree cavity, but in the next survey-month, a flying squirrel *Petaurista* sp. was seen inside the cavity. In April 2018, a female Wreathed Hornbill entered a tree cavity for two days, but was then disturbed by a pair of Rhinoceros hornbills on the third day. The Wreathed hornbill left the nest subsequently and the cavity was occupied by a pair of Rhinoceros hornbills on 23 July 2018.

Nest cavity and nest site characteristics

Of a total of 20 trees that were monitored during 2015 – 2018, tree and cavity measurements were made only on the 16 occupied nest trees (Appendix 1). The tree cavities occupied by hornbills were at minimum 16.5 m above ground (mean nest height = 31.9 m, *SD* = 9.3 m). Most of the nest cavities (67%) were located higher than the first branch of the trees. In general, the nesting trees were characterized by large trunk size (dbh

range = 56.5 – 185.0 cm, mean = 104.3 cm, *SD* = 37.9 cm) and tall trees (range height = 35.0 – 61.1 m, mean = 47.7 m, *SD* = 7.4 m). We found no evidence of differences in nest cavity height (Kruskal-Wallis test, *N* = 16, *df* = 3, *H* = 5.78, *p* = 0.12), tree diameter (*H* = 5.71, *p* = 0.13), and tree height (*H* = 3.64, *p* = 0.30) used by the four hornbill species.

All nesting trees were emergent trees relative to the surrounding trees (Fig. 3) and were significantly taller than the other trees (Wilcoxon test, *W* = 161, *p* < 0.001). The diameter of nesting trees were also significantly higher than the other trees within the 20-m circular plots (Wilcoxon test, *W* = 228.5, *p* < 0.001).

Of the four hornbills, the size of nesting cavity entrance of Helmeted hornbill was the largest, while the smallest was the Bushy-crested Hornbill

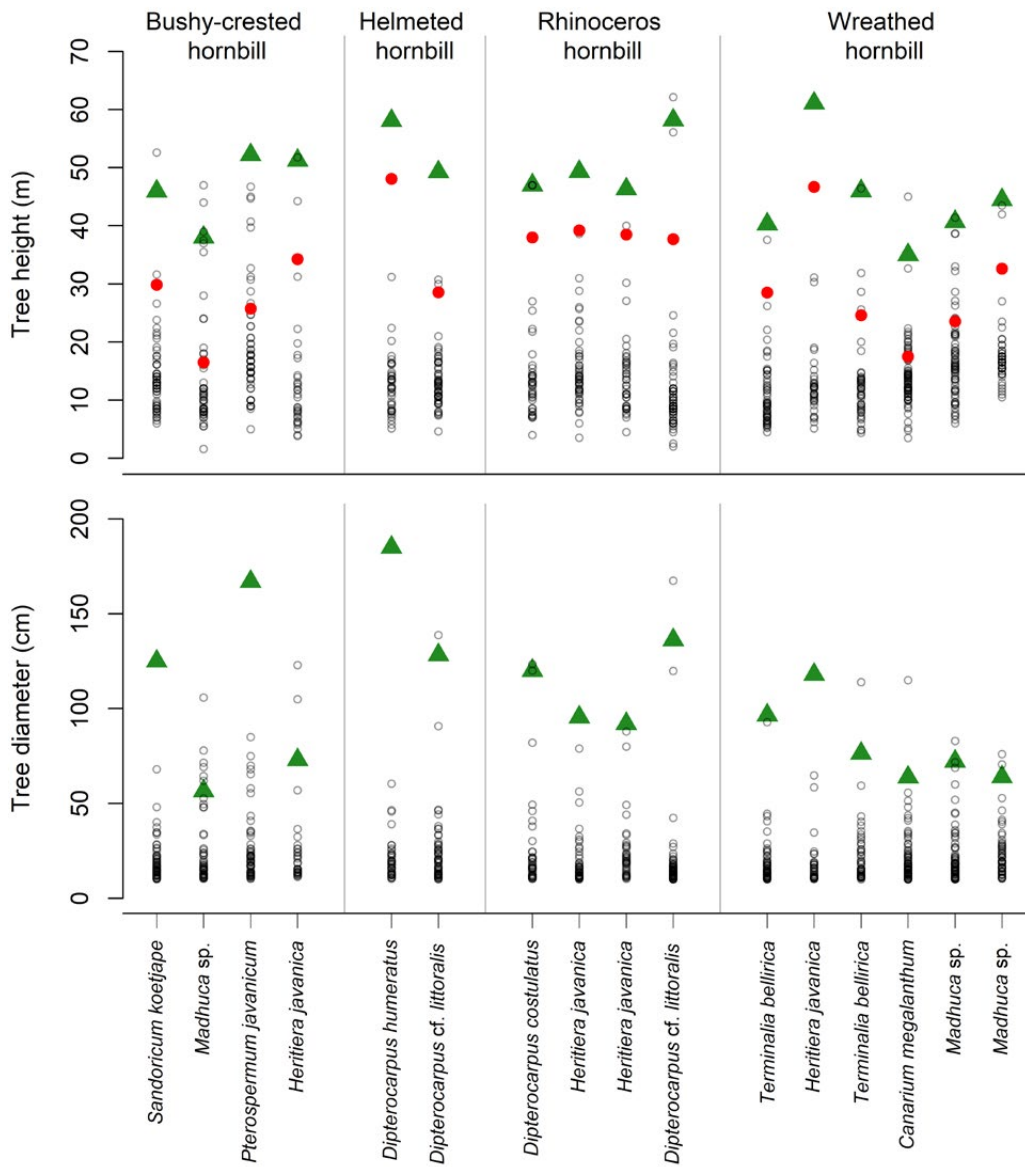


Fig. 3. Nest tree height (upper panel) and diameter (lower panel) compared to other trees surrounding the nest tree. Green triangles represent the height and diameter of the nesting trees. Red circles represent the height of nesting cavities from above the ground. Open black circles represent the other trees surrounding the nest trees within 20-m radius.

(Fig. 4). The ratio of nest entrance height vs. width was only significantly different between Wreathed Hornbill (mean = 2.55, SD = 0.67) and Bushy-crested Hornbill (mean = 0.84, SD = 0.21, Dunn test, $p = 0.0014$). All cavities used by Wreathed hornbill were more vertically elongated compared to other cavities used by the other hornbills, with the nest opening height reached 2.5 times longer than the width (Fig. 5).

Among the four hornbill species, only Bushy-crested hornbill preferred nests with particular entrance orientation, with a mean of 22° relative to compass direction (N = 4, Rayleigh $r = 0.86$, $p = 0.04$). The other three species did not have preference on nest entrance orientation (Helmeted hornbill N = 2, Rayleigh $r = 0.69$, $p = 0.45$; Rhinoceros hornbill N = 4, $r = 0.36$, $p = 0.63$; Wreathed hornbill N = 6, $r = 0.26$, $p = 0.69$; Fig. 6).

Tree species richness around the nesting trees of all hornbill species combined ranged between 15 and 48 species with an average of 31 species ($SD = 8.0$). There were no significant differences of tree diversity (Kruskal-Wallis test, $N = 16$, $df = 3$, $H = 1$, $p = 0.80$), species richness ($H = 0.37$, $p = 0.95$), and tree density ($H = 0.78$, $p = 0.85$) in the surrounding habitat of nesting cavities of the four hornbill species (Fig. 7).

Discussion

This research is a follow-up study of our earlier work (Utoyo et al. 2017) which only presented the nesting cycle and nest site characteristics of Helmeted and Wreathed hornbills in 2015 at WCRS. Here, we add records for Bushy-crested and Rhinoceros Hornbill (pre- and post-2015) and included detailed measurement of the nest site characteristics. In total, we recorded 29 breeding records of four hornbill species (Rhinoceros, Helmeted, Wreathed, and Bushy-crested hornbill), including three records described in Utoyo et al. (2017).

Based on our observation, Wreathed Hornbill tended to occupy vertically elongated cavities, different from Datta and Rawat (2004) who found that Wreathed Hornbill preferred oval cavities. Nest cavity of Helmeted Hornbill was the largest compared to other hornbill species; this might be due to its large body size relative to the other three hornbills. The smallest hornbill, the Bushy-crested Hornbill, used the smallest cavity size. Poonswad (1995) also reported that larger hornbill tended to select nest with longer nest entrance height.

As found in other studies (e.g. Hussain 1984, Poonswad et al. 1987, Poonswad 1995) hornbills tend to nest in holes of live trees, as in our study site. However, the information on the tree

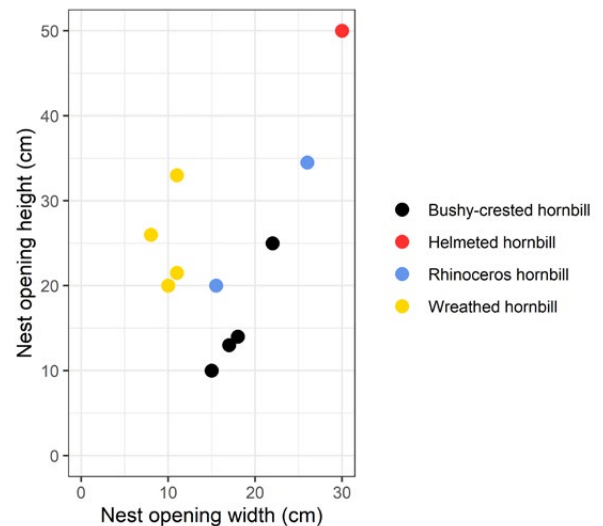


Fig. 4. Cavity opening dimensions (height x width) of the nests used by different species of hornbills.

species used for nesting in Southeast Asian tropical forests is relatively scarce (Poonswad 1995, Kinnaird and O'Brien 2007). Poonswad (1995) recorded five genera (*Dipterocarpus*, *Eugenia*, *Tetrameles*, *Nephelium*, and an unknown genus) utilized by the Wreathed hornbill. From our study, we added four more genera: *Madhuca*, *Canarium*, *Terminalia*, and *Heritiera*. Moreover, in our study site, as in Thailand (Poonswad 1995), hornbills selected the largest and emergent trees. This might be due to the possibility that the largest trees have larger and suitable cavities (Poonswad 1995), but might also reflect the trees available at particular sites (Kinnaird and O'Brien 2007).

We found that the nesting tree characteristics (cavity height, tree diameter, and tree height) and the ratio of nest opening (except between Bushy-crested and Wreathed hornbills) were not different among the four sympatric hornbill species in our study area. There was also no preference in cavity orientation (this study, Poonswad 1995, Datta and Rawat 2004), except for the Bushy-crested Hornbill. On the other hand, Poonswad (1995)



Fig. 5. Photographs of nest cavity entrances.

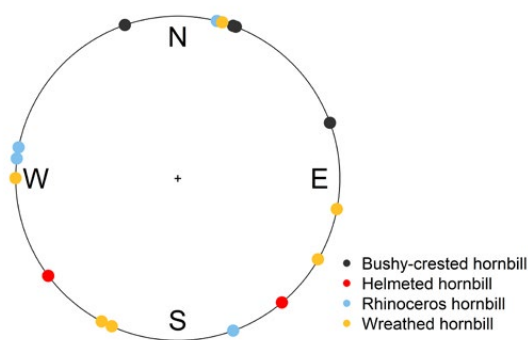


Fig. 6. Nest entrance orientation of four sympatric hornbills.

found differences of nest height, diameter at nest height, nest entrance height, and nest entrance width used by four sympatric hornbill species in Thailand. Similarly, Datta and Rawat (2004) found that the cavity size was the main variable that separated the three hornbill species in their study site in north-east India. Both studies might indicate that there was low competition pressure for nest-sites among the hornbills. In our study site, however, the similarity in nest-tree characteristics among the sympatric hornbills might have caused the three events of nest-site competition between 1) Helmeted and Wreathed hornbills, 2) Rhinoceros Hornbill and *Petaurista* sp., and 3) Wreathed and Rhinoceros hornbills. However, the lack of differences of nest characteristics might also be due to our small sample sizes.

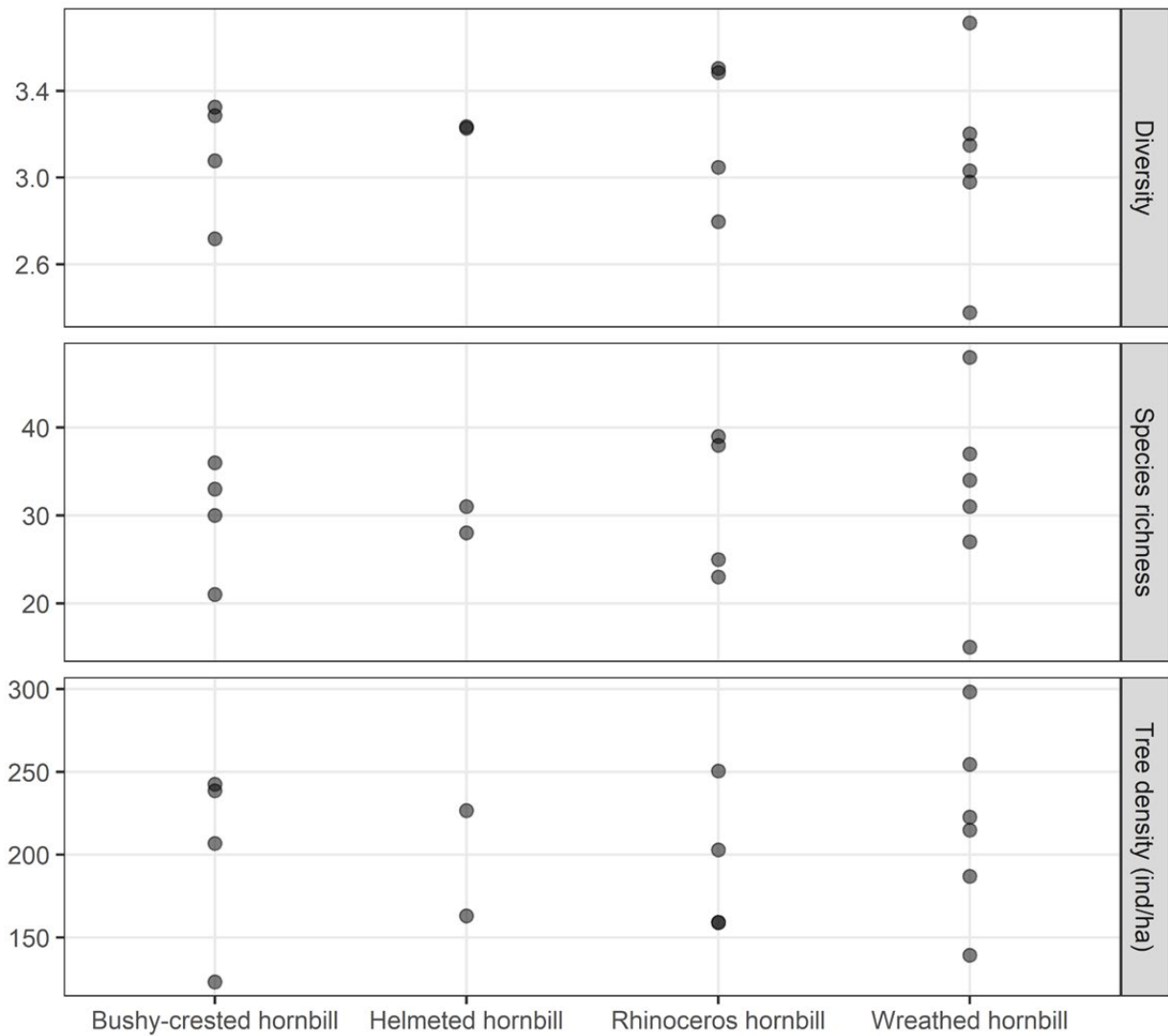


Fig. 7. Community structure of the trees within 20-m radius from the nesting trees. Diversity indices were calculated using Shannon Diversity Index. Species richness is the number of tree species per sampling unit. Tree density is the number of tree stems per hectare.

Kinnaird and O’Brien (2007) summarized the timing of breeding for hornbill species in the aseasonal equatorial region (Sumatra, Peninsular Malaysia, and Borneo) and found that they typically started nesting over the six months’ period beginning in January (although Rhinoceros and Helmeted hornbills begin nesting during the wettest month, and the Bushy-crested and Wreathed hornbills initiate nesting throughout the year). Our results also generally concurred with this general pattern, but not for Rhinoceros and Wreathed hornbill. In addition, when rain

is less seasonal (as in Sumatra) the abundance of trees bearing flowers or fruit crops may provide cues that trigger nest initiation (Kinnaird and O’Brien 2007). We suspected that this was the possible reason for a significant decrease of nesting frequencies between the two monitoring periods (2006 – 2009 and 2015 – 2018). However, to establish this, further investigation of long-term phenology data is required (fortunately, phenology data are available since 1998 onward) and this can be examined in future research studies.

This study is limited because we could not conduct continuous daily observation nor frequent monitoring to avoid unnecessary disturbance to the breeding pair. As a result, we were unable to make an accurate estimation of the duration of the nesting stages. However, this caveat was traded off against the greater number of potential nesting cavities we could observe each month. Another limitation of this study was that we did not measure tree cavities that were not occupied by hornbills to determine their preference of nesting sites.

Conservation implications

Hornbills are threatened across Sumatra mainly due to habitat loss and illegal hunting for their casques. In order to increase their population, we need to ensure that sufficient nesting sites are available. Nesting trees are vulnerable to illegal logging due to their high timber value. For example, tree species of *Dipterocarpus* and *Sandoricum* have hard wood and are suitable for furniture and *Pterospermum* trees are easy to process. However, *Terminalia bellirica* is less preferred for timber because the wood is rather soft and easily attacked by termites (*pers. comm.* with local community). High intensity of illegal logging had occurred in BBSNP, but since 2004 the park has implemented better law enforcement and logging has greatly reduced. The population decline of emergent trees due to past illegal logging may hamper the reproduction cycle of hornbills and increase competition pressure for nesting sites between sympatric hornbill species.

Hornbills are easily targeted by poachers when they are foraging in fruiting trees or during nesting. Fig trees bearing fruits are often visited by hornbills, resulting in higher vulnerability for hunting. Although the information on Helmeted hornbill nesting period in published literature may increase the chance of misuse by hunters,

we believe this information can also inform conservation managers to increase patrolling effort during vulnerable time.

Considering the high risk of extinction to hornbills, we suggest the following conservation measures to safeguard hornbill populations:

- Increasing patrol effort during predicted period of hornbill nesting.
- Law enforcement on illegal logging of large trees in protected areas.
- Regular checks on known, previously-used tree cavities and restoring damaged cavities or maintaining available cavities.

Acknowledgments

We thank our field staff who collected the data in the field since 2006, especially Sukarman and Wiroto. We also thank Bukit Barisan Selatan National Park officials for the permission to conduct this long-term monitoring project, especially the park's forest ecosystem managers for WCRS, including Rikha A. Surya, Tri Sugiharti, Hagnyo Wandono, and Subki. Special thanks to donors (KfW-BBS and anonymous donor) who supported this activity.

References

- Anggraini K, Kinnaird M, O'Brien T. 2000. The effects of fruit availability and habitat disturbance on an assemblage of Sumatran hornbills. *Bird Conservation International* **10**:189–202.
- Beastall C, Shepherd CR, Hadiprakarsa Y, Martyr D. 2016. Trade in the Helmeted Hornbill *Rhinoplax vigil*: The "ivory hornbill." *Bird Conservation International* **26**:137–146.
- Cahill AJ, Walker JS. 2000. The effects of forest fire on the nesting success of the Red-knobbed Hornbill *Aceros cassidix*. *Bird Conservation International* **10**:109–114.
- Chong MHN. 2011. Observations on the Breeding Biology of Helmeted Hornbill in Pahang, Peninsular Malasia. *The Raffles Bulletin of Zoology* **24**:163–165.

- Collar NJ. 2015. Helmeted Hornbills *Rhinoplax vigil* and the ivory trade: the crisis that came out of nowhere. *BirdingASIA* **24**:12–17.
- Côté IM. 2003. Knowledge of reproductive behavior contributes to conservation programs. Pages 77–92 in *Animal behavior and wildlife conservation*. Island Press, Washington, DC.
- Datta A, Rawat GS. 2004. Nest-site selection and nesting success of three hornbill species in Arunachal Pradesh, north-east India: Great Hornbill *Buceros bicornis*, Wreathed Hornbill *Aceros undulatus* and Oriental Pied Hornbill *Anthracoseros albirostris*. *Bird Conservation International* **14**:S39–S52.
- Eaton JA, van Balen B, Brickle NW, Rheindt FE. 2016. *Birds of the Indonesian Archipelago: Great Sundas and Wallacea*. Lynx Edicions, Barcelona.
- Gonzalez JCT, Sheldon BC, Tobias JA. 2013. Environmental stability and the evolution of cooperative breeding in hornbills. *Proceedings of the Royal Society B: Biological Sciences* **280**:20131297.
- Hadiprakarsa YY, Kinnaird MF. 2004. Foraging characteristics of an assemblage of four Sumatran hornbill species. *Bird Conservation International* **14**:53–62.
- Hussain SA. 1984. Some aspects of the biology and ecology of Narcondam Hornbill (*Rhyticeros narcondami*). *Journal of Bombay Natural History Society* **81**(1):1-18.
- IUCN 2019. The IUCN Red List of Threatened Species. Version 2019-3. <http://www.iucnredlist.org>. Downloaded on 20 December 2019.
- Kaur R, Singh S, Ahmad AH. 2015. The breeding biology of the Great Hornbill *Buceros bicornis*, Rhinoceros Hornbill *Buceros rhinoceros* and Helmeted Hornbill *Rhinoplax vigil* in the Temengor Forest Reserve, Perak, Malaysia. *Malayan Nature Journal* **67**:242-259.
- Kinnaird MF, O'Brien TG. 2007. *The ecology and conservation of Asian hornbills*. University of Chicago Press, Chicago.
- Landler L, Ruxton GD, Malkemper EP. 2018. Circular data in biology: advice for effectively implementing statistical procedures. *Behavioral Ecology and Sociobiology* **72**(8):128.
- Marsden SJ, Jones MJ. 1997. The nesting requirements of the parrots and hornbill of Sumba, Indonesia. *Biological Conservation* **82**:279–287.
- Mudappa DC, Kannan R. 1997. Nest-site characteristics and nesting success of the Malabar Gray Hornbill in the Southern Western Ghats, India. *The Wilson Bulletin* **109**:102–111.
- Poonswad P. 1995. Nest site characteristics of four sympatric species of hornbills in Khao Yai National Park, Thailand. *Ibis* **137**:183–191.
- Rahayuningsih M, Kartijomo NE, Retnaningsih A, Munir M, Dahlan J. 2017. Nest Records of Wreathed Hornbill (*Rhyticeros undulatus*) in Gunung Gentong Station, Mount Ungaran Central Java. *Page Journal of Physics: Conference Series*. Institute of Physics Publishing.
- Supa-Amornkul S, Wiyakrutta S, Poonswad P. 2011. Wood Decay Fungi in Hornbill Nest Cavities in Khao Yai National Park, Thailand. *Raffles Bulletin of Zoology* **24**:95–113.
- Utoyo L, Marthy W, Noske RA, Surahmat F. 2017. Nesting cycle and nest tree characteristics of the Helmeted Hornbill *Rhinoplax vigil*, compared to the Wreathed Hornbill *Rhyticeros undulatus*, in Sumatran lowland rainforest. *Kukila* **20**:12–22.

Appendix 1. Characteristics of hornbill nesting trees.

Hornbill species (length cm)	Nest tree species	Tree Family	DBH (cm)	Tree height (m)	First branch (m)	Nest height (m)	Cavity dimensions (height x width in cm)	Entrance orientation (°)
	<i>Pterospermum javanicum</i>	Malvaceae	167.0	52.2	34.7	25.7	13 x 17	341
Bushy-crested hornbill (65 – 70)	<i>Heritiera javanica</i>	Malvaceae	73.0	51.3	28.8	34.3	25 x 22	70
	<i>Sandoricum koetjape</i>	Meliaceae	125.0	46.0	17.6	29.9	14 x 18	21
	<i>Madhuca</i> sp.	Sapotaceae	56.5	38.0	29.0	16.5	10 x 15	20
Rhinoceros hornbill (80 – 90)	<i>Dipterocarpus</i> cf.	Dipterocarpaceae	136.2	58.2	36.3	37.7	34.5 x 26	160
	<i>Heritiera javanica</i>	Malvaceae	95.5	49.3	43.5	39.2	*	277
	<i>Dipterocarpus costulatus</i>	Dipterocarpaceae	120.0	47.0	32.0	38.0	20 x 15.5	14
	<i>Heritiera javanica</i>	Malvaceae	92.0	46.3	25.5	38.5	*	281
Helmeted hornbill (110 – 120)	<i>Dipterocarpus humeratus</i>	Dipterocarpaceae	185.0	58.1	41.1	48.1	50 x 30	140
Wreathed hornbill (75 – 85)	<i>Madhuca</i> sp.	Sapotaceae	72.3	40.7	27.3	23.5	*	120
	<i>Canarium megalanthum</i>	Burseraceae	63.8	35.0	24.0	17.5	*	208
	<i>Madhuca</i> sp.	Sapotaceae	64.0	44.5	18.5	32.6	21.5 x 11	16
	<i>Terminalia bellirica</i>	Combretaceae	96.5	40.3	22.6	28.5	20 x 10	270
	<i>Terminalia bellirica</i>	Combretaceae	76.4	46.0	23.6	24.6	26 x 8	101
	<i>Heritiera javanica</i>	Malvaceae	118.0	61.1	34.8	46.7	33 x 11	204

* No nest entrance measurement because when the measurement survey was conducted, the cavities were still being occupied by hornbills.