Nesting cycle and nest tree characteristics of the Helmeted Hornbill *Rhinoplax vigil*, compared to the Wreathed Hornbill *Rhyticeros undulatus*, in Sumatran lowland rainforest

LAJI UTOYO[1], WILLIAM MARTHY[1,2], RICHARD A. NOSKE[3], AND FAHRUDIN SURAHMAT[1]

[1] Wildlife Conservation Society-Indonesia Program, Jl. Tampomas no. 35, Bogor 16151- Indonesia; [2]Corresponding author: wmarthy@wcs.org; [3]Centre for Biodiversity and Conservation Science, University of Queensland, St Lucia, Qld, 4072.

Summary. Hornbills provide a seed dispersal service for rainforest trees, but the persistence of hornbill populations depends on the availability of old trees that provide cavities for their nests. The Helmeted Hornbill *Rhinoplax vigil* is Critically Endangered, due to both forest destruction and an inhumane illegal trade in their bill casques, yet little is known about its nests and breeding biology. Here we describe the nest tree and external nest characteristics of a pair of Helmeted Hornbills in Bukit Barisan Selatan National Park, Lampung, Sumatra, and compare them with observations of two nests of the Wreathed Hornbill *Rhyticeros undulatus* less than 1 km away. As in a previous study, the Helmeted Hornbill (HH) nest was in a large dipterocarp, and possessed a stump next to the entrance that the male used as a perch when feeding the female or chick. The nest entrance dimensions and bole diameter of the nest tree were much larger than those of the two Wreathed Hornbill (W1 and W2) nests. Egg laying in HH took place in February, while in W1 and W2, eggs were laid much later, between late May and July. The maximum nesting cycle of the Helmeted Hornbill was an astonishing 137 days (4.5 months), close to the minimum period (range, 138-151) for a nest of the species in Peninsular Malaysia. This may be longer than the nesting cycle of the Wreathed Hornbill, but additional data are needed.

Ringkasan. Rangkong adalah penting dalam penyebaran biji-bijian dari pohon-pohon hutan tropis, tetapi populasi yang sehat di alam tergantung ketersediaan pohon-pohon besar sebagai tempat bersarang. Rangkong Gading *Rhinoplax vigil* saat ini berstatus Kritis karena ancaman kerusakan hutan dan aktivitas perburuan burung untuk diambil paruhnya untuk diperdagangkan, tetapi informasi tentang biologi bersarang dan berkembang biak masih kurang. Kami mendeskripsikan karakteristik sarang sepasang Rangkong gading di Taman Nasional Bukit Barisan Selatan, Lampung, Sumatra, dan membandingkannya dengan dua sarang Julang Emas *Rhyticeros undulatus* yang ditemukan < 1 km. Seperti penelitian terdahulu, sarang Rangkong Gading (HH) terletak pada pohon Dipterocarpaceae besar dengan tunggul dekat lobang sarang untuk tempat hinggap burung jantan ketika memberikan makanan. Dimensi lobang sarang dan diameter pohon sarang cenderung lebih besar dibandingkan dengan Julang Emas (W1 & W2). Masa bertelur bagi HH pada Februari, W1 pada akhir Mei dan W2 pada Juli. Total waktu berbiak maksimum untuk HH adalah 137 hari (4,5 bulan), sangat dekat dengan rentang yang pernah tercatat sebelumnya (138-151 hari) di Semenanjung Malaysia. Angka ini mungkin lebih lama dari siklus berbiak Julang emas, tetapi masih dibutuhkan informasi yang lebih banyak untuk memastikannya.

Introduction

Hornbills play an important role as seed dispersal agents for tropical forest regeneration (Kinnaird & O'Brien 2007; Walker 2007; Kitamura 2011; Naniwadekar *et al.* 2015; Corlett 2017). Fruits from at least 205 tree species have been recorded to be part of the diet of nine species of hornbills in Southeast Asia (Shanahan *et al.* 2001; Hadiprakarsa & Kinnaird 2004; Kitamura *et al.* 2002, 2005). Studies of the fate of seeds accumulating underneath hornbill nest

trees (Kitamura *et al.* 2004; Kinnaird & O'Brien 2007) and roosting sites (Kitamura *et al.* 2008) indicate seeds are able to germinate well despite being aggregated under the trees, but as hornbills have large home ranges it is likely that seeds are also being dispersed far from nesting and roosting trees (Naniwadekar *et al.* 2015). For instance, the home range of the largest Asian hornbill species, the Great Hornbill *Buceros bicornis* varies between 3.7 km^2 (breeding season) to 14.7 km^2 (non-breeding season) (Poonswad & Tsuji 2008). The sustainability of hornbill populations depends not only on the availability of food resources, but also suitable nesting sites (Anggraini *et al.* 2000; Naniwadekar *et al.* 2015).

Hornbills are secondary cavity-nesters, unable to excavate their own nest cavities (Poonswad 1995). Tree hollows are usually formed after a branch has broken off a trunk or bough, allowing the invasion of wood-decomposing microorganisms (Hopper & Lennartz 1991; Poonswad 1995; Supa-Amornkul *et al.* 2011). The large size of hornbills demands large cavities for nesting, particularly since the female must live in the nest for up to four months or more, and such cavities are more likely to occur in trees that are old with wide boles (Kinnaird & O'Brien 2007). In Nepali sal forests, the probability of cavities occurring on tree trunks was related to the diameter of the trunks (Bhusal *et al.* 2015).

As the availability of suitable nest sites plays a major role in population recruitment of cavity-nesters (Cody 1985), information about the characteristics of nest trees of hornbills is vital for determining their preferred tree species, which can potentially be used to estimate their breeding density in forested areas. Studies to date suggest that species differ in their selection of nest sites, though there is overlap between them. For example, in India, Great Hornbills preferred elongated nest entrances, while Wreathed Hornbills *Rhyticeros undulatus* preferred oval entrances (Datta & Rawat 2004). In Khao Yai National Park, Thailand, four sympatric hornbill species (Great, Wreathed, Oriental Pied *Anthracoceros albirostris* and Brown Hornbill *Ptilolaemus tickelli*) tended to use elongated nest entrances, but Great Hornbill used entrances that were more elongated than those of the others (Poonswad 1995).

Information on nest tree characteristics is especially important in the case of the Helmeted Hornbill *Rhinoplax vigil*, which is now Critically Endangered due to unsustainably high levels of illegal trade in its unique bill casque (BirdLife International 2016; Collar 2015; Eaton *et al.* 2015; Beastall *et al.* 2016). In Thailand, nests of this species were found to possess a protruding knob or stump next to the entrance, which the male uses as a platform to perch on when feeding the female and chick (Thiensongrusamee *et al.* 2005). Although Thiensongrusamee *et al.* (2005) described the characteristics of 15 nest trees of Helmeted Hornbills found over six years (1994-2000), they did not provide details of their breeding biology, which remains poorly known.

Little is known about the characteristics of nest trees of hornbills in Indonesia. Of the 13 hornbill species that occur in Indonesia, details of nest characteristics are available only for Red-knobbed Hornbill *Aceros cassidix* and Sulawesi Dwarf Hornbill *Penelopides exarhatus* (Kinnaird & O'Brien 2007), Sumba Hornbill *Rhyticeros everetti* (Marsden & Jones 1997; Cahill 2003), and Wreathed Hornbill *Rhyticeros undulatus* (Rahayuningsih *et al.* 2017). Here we describe the characteristics of a nest tree of Helmeted Hornbills, and compare them with those of two nearby nests of Wreathed Hornbills in a lowland rainforest of Sumatra. We also provide an estimate of the duration of the nesting cycle of the Helmeted Hornbill, and compare this with the sole previous estimate for this species (Chong 2011).

Methods

The study area was located in lowland rainforest around Way Canguk Research Station (c. 50 m above sea level; 04°31'–5°57'S, 103°24'–104°43'E), which is part of the 325,000 ha Bukit

Barisan Selatan National Park (hereafter BBSNP), Lampung Province, southwest Sumatra (Fig. 1). The Research Station is located within an area of c. 900 ha of primary lowland forest, which is surrounded by a mosaic of primary forest, burned forest, and areas disturbed by illegal logging and agriculture. From 1998 to 2015, annual rainfall ranged from 2,459 to 4,403 mm, with a mean of 3,343 mm, at the Research Station, and the wettest months were November and December (WCS-Indonesia Program unpubl. data).

We conducted nest searches for hornbills every month in 2015 (January- December 2015), and after identifying the tree species, we measured the diameter of the trunk at breast height (DBH) with a diameter tape, and using a Nikon Aculon AL11 digital range finder, heights of the nest cavity, first branch and top of tree from the ground. To describe the surrounding vegetation, we measured the diameter, total height and height of the first branch of all trees greater than 10 cm DBH within 20 m radius of the nest trees, as well as their distance from the nest tree. For trees with buttresses, the diameter was measured 50 cm above the top of the highest buttress. We estimated the length and width of the nest cavity entrance using the body length of visiting hornbills as a yardstick. The dimensions of the nest tree and nest entrance were compared with those from other studies of hornbills. We also measured the bole diameter and tree height of all trees within a 20 m radius of the nest tree.

We define the nesting cycle as the combination of incubation and nestling periods, from the laying of the first egg to fledging of the first young, but this presents a problem as it is usually very difficult to check the contents of hornbill nests, due to their height above the ground. If the female was already inside the nest, we estimated the egg laying date based on the last date when she was seen outside the nest, and available literature on the interval between the female entering the nest and egg laying. Each nest was checked six to 17 times to ensure we did not miss the day when the female and or chick left the nest. Avian nomenclature in this paper follows IOC World Bird List Version 6.1 (Gill & Donsker 2016).

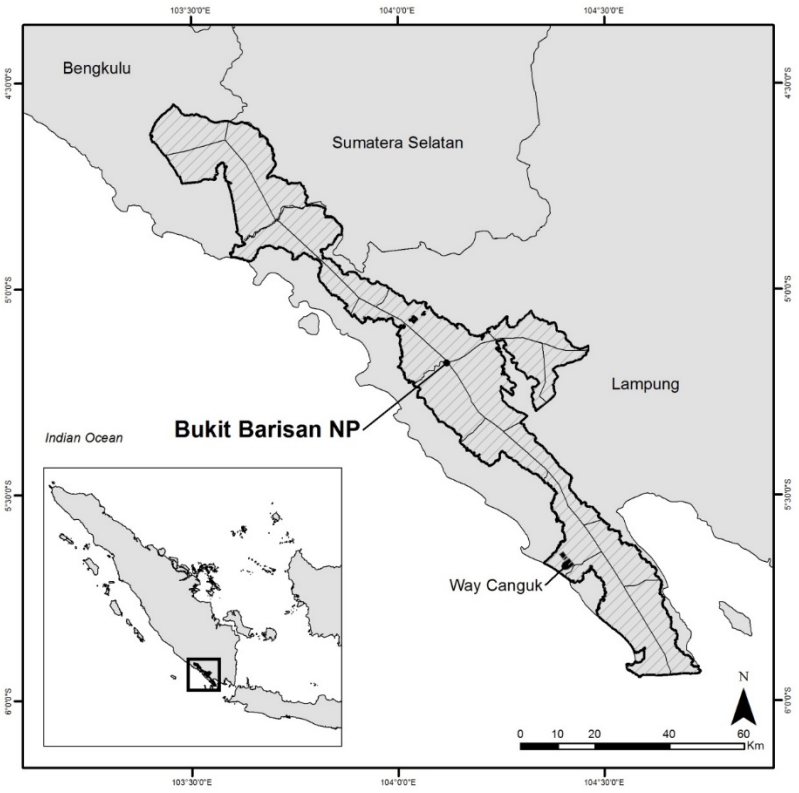

Figure 1. Map of location of the study site at the Bukit Barisan Selatan National Park, Lampung, Sumatra.

Results

One active nest of Helmeted Hornbills and two active nests of Wreathed Hornbills (W1 and W2; Plates 1, 2) were found. All nest cavities were situated above the first branch, in large trees ranging in height from 40 m to 61 m (Table 1, Fig. 2). One of the Wreathed Hornbill nests (W2) was located in secondary forest, while the other two nests were in primary forest. The mean and maximum height of the trees surrounding the Helmeted and W1 nest sites were identical (13 m and 31 m, respectively), while the trees around W2 reached higher (37 m) but were, on average, shorter (11 m) (Table 1).

The Helmeted Hornbill nest was discovered on 14 February 2015, and was observed for a total of 17 days until 11 July 2015. It was located on the main trunk of a tall buttressed *Dipterocarpus humeratus* (Dipterocarpaceae) tree (Table 1, Fig. 2), on which the first branch emerged at 71% of the total tree height. There was a protuberance c. 25 cm to the side of the entrance, which the used as a perch by the male whenever it fed the female. The height of the nest cavity was at 83% of the total height, 7 m above the first branch. The nest entrance was relatively wide (1.7 times higher than wide) and faced the south-east (Table 1). On 14 February both the male and female were observed near the cavity, and on the following day, the female entered and exited the nest cavity twice. From 22 February, we only observed the male, and therefore assumed that the female entered the nest between 15 and 22 February. On 27 June the female was already out of the nest, but the chicks were still in the nest. The next day the situation was the same, but on 11 July the nest appeared empty because we could not hear any noises emanating from the nest or find any birds around the nest tree site. Assuming that the female entered the nest for the last time on 15 February, and the young fledged successfully on 10 July, and allowing nine days for the female to lay the first (or only) egg (see below for explanation), the maximum nesting cycle, from egg-laying to fledging, was 137 days.

Table 1. Characteristics of nests of two hornbill species in Bukit Barisan NP in 2015.

Hornbill species/ site	**Helmeted**	**Wreathed (W1)**	**Wreathed (W2)**
Nest tree			
Tree species	*Dipterocarpus humeratus*	*Terminalia bellirica*	*Heritiera javanica*
DBH* (cm)	185	96	118
Tree height (m)	58.1	40.3	61.1
First branch (m)	41.1	22.6	34.8
Nest height (m)	48.1	28.5	46.7
Nest entrance			
Length x width (cm)	50 x 30	20 x 10	33 x 11
Aspect (degrees)	140	270	204
Surrounding trees			
N	41	35	56
DBH, mean (cm)	20.3	17.9	18.7
DBH, range (cm)	10 – 60	10 – 65	11 - 93
Tree height, mean (m)	12.6	12.5	10.9
Tree height, range (m)	5 – 31	5 – 31	2 - 37
Nest tree compared to surrounding trees			
Mean DBH x 1000	9.11	5.39	6.31
Maximum DBH x 1000	3.08	1.48	1.27
Mean tree height	4.61	3.22	5.61
Maximum tree height	1.87	1.30	1.65

*DBH, diameter of bole at breast height.

Plate 1. Male Wreathed Hornbill perched at entrance to nest W1 in *Terminalia bellirica*, Bukit Barisan National Park, Sumatra, June 2015 (photographer, Laji Utoyo).

Plate 2. Male Wreathed Hornbill perched at entrance to nest W2 in *Heritiera javanica*, July 2015 (photographer, Laji Utoyo).

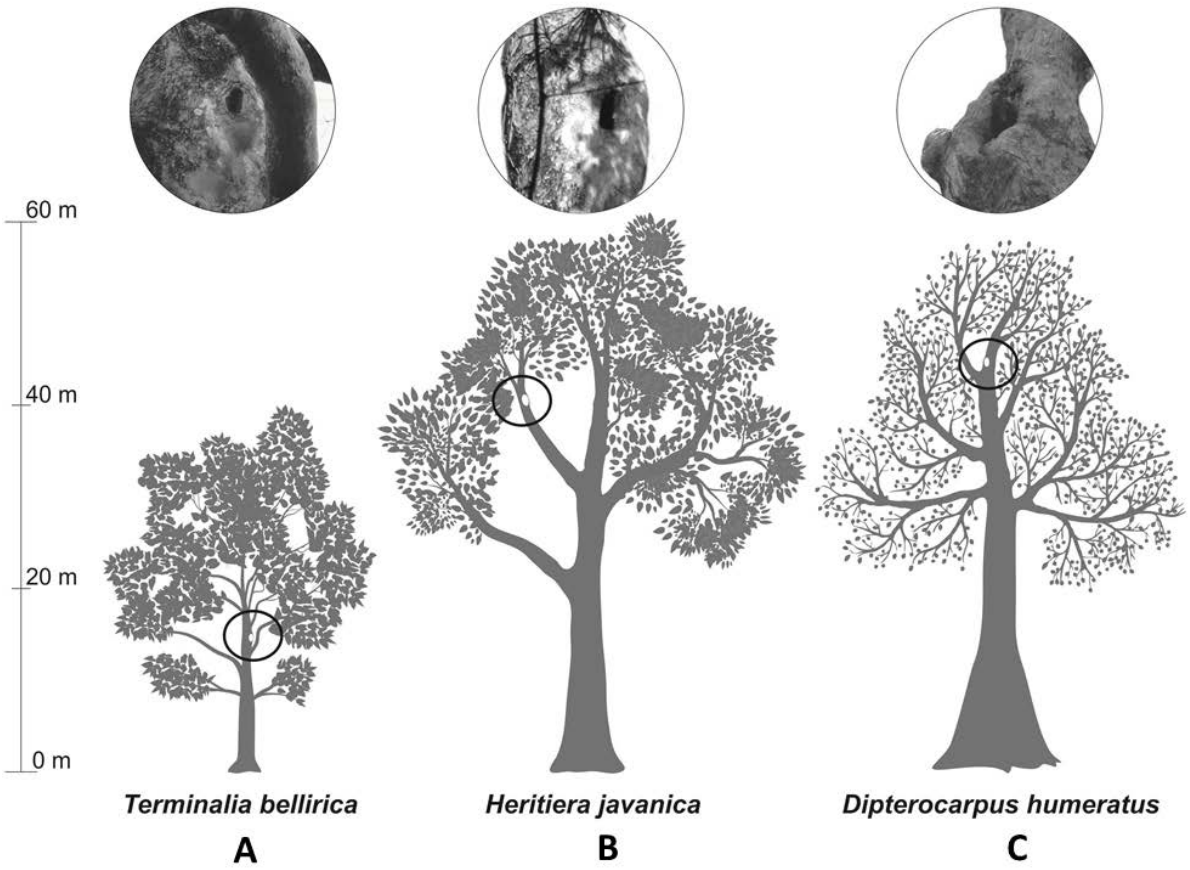

Figure 2. Illustration of the hornbill nest trees and nest locations (encircled), with photographs of the nest cavities, Way Canguk Research Station, Lampung, Sumatra. A-B, Wreathed Hornbill: A, W1; B, W2; C, Helmeted Hornbill (Illustrator: Fahrudin Surahmat).

On 18 June 2015, we found the first nest (W1) of Wreathed Hornbills in secondary forest that was created by a forest fire in 1997. It was located on the main trunk of a *Terminalia bellirica* (Combretaceae; Fig. 2). The first branch and nest cavity were at 56% and 71%, respectively, of the total tree height, the distance between them being 6 m. The nest entrance was a third of the width of the Helmeted's nest entrance, but was similar in its relative width, (two times higher than the wide) and faced west (Table 1). The cavity was already sealed and as only the male was observed outside the nest cavity, we assumed the female to be inside. The situation remained the same on four subsequent visits, the last on 28 September. We did not visit the nest tree again until 10 November, by which time the nest appeared empty. Assuming the nest already had eggs on 18 June and the female brooded until 28 September, the minimum nesting cycle was 103 days.

The second Wreathed Hornbill nest (W2) was found on 4 July 2015. It was located in the second branch of a *Heritiera javanica* (Sterculiaceae) (Fig. 2). The first branch and nest cavity were located at 57% and 76%, of the total tree height, respectively, the distance between them being 11 m. The nest entrance was sealed, and was similar in width to that of W1, but was higher (three times higher than wide) and faced more south-south-west (Table 1). The female was already inside the nest when it was discovered, and was presumed to be inside the nest on four subsequent visits, the last on 30 November. However, by 15 December the nest appeared empty. Assuming that the nest was vacated on the following day (1 December) and the nest was occupied by 4 July, the female was apparently incarcerated for at least 150 days.

Discussion

Nest cycle and breeding season

Little is known about the breeding biology of the Helmeted Hornbill, apart from its breeding season (Kemp *et al.* 2017). In Thailand females are reported to enter nests in February or March, and the young fledge between July and August (Poonswad *et al.* 1999), suggesting a nesting cycle of about five months. The breeding season in Sumatra appears to be longer, females entering nests from November to March, and young fledging from May to August (WCS-Indonesia Program, unpublished data). Our observations of one nest are consistent with the latter breeding season, the female entering the nest in February, and the young fledging in late June or early July. This period corresponds with the breeding seasons of most birds in Sumatra, which starts after the rainy season (September to December) and continues during the dry season (van Marle & Voous 1988).

According to Kemp (2017), sealing of the nest entrance holes of hornbills takes at most a few days. The female then sits in the nest for a pre-laying period of typically 4–6 days, made possible by the male's sperm being stored and nourished by glands in the female's oviduct, as well as an unusually long period of sperm viability after the last copulation. We therefore allowed nine days, comprising 4 days to seal the nest entrance and 5 days to lay an egg, in our calculations of the nest cycle of the nest of Helmeted Hornbills. Large species lay one or two eggs, the second being laid about five days after the first (Kemp 2017). Being confined to the sealed nest cavity, however, the female is forced to start incubation from the time when the first egg is laid, with the consequence that the second egg hatches about five days after the first. Although the Helmeted Hornbill is reported to lay two eggs sometimes, the older and larger nestling is likely to out-compete its sibling for food, resulting in the smaller chick dying of starvation. Thus it is reasonable to define the nest cycle as starting with the laying of the first (or only) egg and ending with the fledging of the first young.

Chong (2011) observed a nest of Helmeted Hornbills in sub-montane primary forest in the Genting Highlands, Pahang, Peninsular Malaysia, during 19 visits from February to July 1998. The nest cavity was situated in the hollowed stump of a large branch of an unidentified tree, at a height of c.30m from the ground. The female started to seal (plaster) the nest entrance on 21 February, but did not complete the sealing work until 6 March, 13 days later. Consistent with Kemp's (2017) general account, the female was incarcerated in the nest by 2 March, four days before completion of the seal. She was still in the nest with the chick on 25 July, but by 8 August both birds had vacated the nest, as the entrance sealing was found to be broken. A pair of Helmeted Hornbills with a recently fledged young, presumed to be the same birds, was seen near the nest area on 4 September, suggesting the nest had been successful. Although Chong (2011) estimated the period over which the female was confined to the nest as 154–167 days, i.e. 160.5 ± 6.5 days, RN re-calculated this period as 147–160 days, i.e. 153.5 ± 6.5 days. Chong added seven days to the maximum estimated period to take account of the 14-day interval between the dates on which the female was first observed sealing the nest entrance, and when the entrance appeared to be completely sealed.

With almost the same number of visits (17) spanning the same months (February to July), our observations of a nest in Sumatra are highly comparable to those of Chong. We assumed that the female entered the nest between 15 and 22 February, but we are not certain whether she was totally confined by the latter date. In addition, the female had clearly left the nest at least 1.5 days before the chick fledged, but we do not know how much longer the chick remained in the nest. We did not notice if sealing had already begun when both adults were observed outside the nest on 14 February. Chong calculated the period of nest incarceration of the female, but allowing four days for completing the entrance seal (as he observed), and

another five days for egg laying, as we did, the nesting cycle took between 138 and 151 days, i.e. 144.5 ± 6.5 days. The minimum period is thus very close to our maximum nesting cycle estimate of 137 days. These estimates are based on the assumption that the females took nine days to form and lay an egg after entering the nest for the last time, but it is conceivable that they laid before the ninth day.

Wreathed Hornbills have been reported nesting in Sumatra in all months of the year except December, whereas in eastern Borneo nesting was restricted to the first half of the year (Kinnaird & O'Brien 2007). At Mount Ungaran, Central Java, Rahayuningsih *et al.* (2017) found the species breeding from August to December over five years (2010-2015), but unfortunately gave no details. In this study, the female of the first nesting pair of Wreathed Hornbills was already in the nest by 18 June, and since the minimum nesting cycle was 103 days, eight days less than the minimum period reported for this species (111–137 days; Kemp & Boesman 2017), it is likely that the eggs were laid at the start of June or in late May. At the nest of the second pair, however, the female was thought to be incarcerated for at least 150 days, much longer than the maximum period reported. This species normally lays two eggs (Kemp & Boesman 2017), but even allowing nine days for the first egg to be laid (see above), and another five days for a second egg, the *minimum* nesting cycle, from laying to fledging of the second young would be 136 days, which is within the reported range for the species. Given the body size difference between the Helmeted and Wreathed Hornbills, however, one might expect the nesting cycle to be shorter in the latter species.

Notwithstanding many uncertainties about the timing of events at W2, egg-laying probably started in the first or second week of July, at least five weeks after laying is assumed to have taken place at W1. It is noteworthy that these two nests of the Wreathed Hornbill were initiated 3–4.5 months after the Helmeted Hornbill nest was initiated. As both species inhabited the same forest, this disparity in their breeding phenology suggests that they depended on the fruits of different tree species for their food supply. These differences suggest that at the very least that forest should contain a diversity of old trees and fruiting tress in order to sustain populations of both species.

Comparison between the two hornbill species in nest characteristics

The only detailed study of nest trees of Helmeted Hornbills was conducted in hill forest (300-535 m asl) at two sites in South Thailand (Thiensongrusamee *et al.* 2005). The most significant feature of all 15 observed nests was that they possessed a knob or stump at the top, bottom or side of the nest entrance, which served as a perch for the male when feeding the female or chick (Thiensongrusamee *et al.* 2005). Males were never observed clinging to the nest entrance. The nest in the present study resembled the Thai nests in this respect, with a stump on the side of the nest entrance, which the male used as a feeding platform. Thiensongrusamee *et al.* (2005) speculated that the requirement of a platform in this species related to its unusually long central tail feathers and heavy head with solid casque, but provided no detailed explanation. When delivering food, males of other hornbill species use their tails to brace against the tree while clinging to the cavity opening, but by using a platform, male Helmeted Hornbills can prevent wear and tear of these feathers, since the tail hangs in mid-air, avoiding contact with trunk (Kinnaird & O'Brien 2007).

Like all but two of the Helmeted Hornbill nest trees in South Thailand (Thiensongrusamee *et al.* 2005), and all five nests in the previous study at BBSNP (WCS-Indonesia Program unpubl. data), the nest in the present study was a dipterocarp. Six of the nest trees in Thailand belonged to the genus *Hopea*, five in *Shorea faguetiana*, and one to each of three other species (*Shorea curtisii*, *Scaphium macropodum* and *Koompasia excelsa*). Mean DBH ranged from 105 to 207 cm, but averaged 158 cm, while tree heights ranged from 26 to

70 m, averaging 45 m. While the Thai dimensions are clearly lower than those of the BBSNP nest, the ratio of tree height to bole diameter is quite similar (mean ratio, 28.1, n=14; vs. 31.4, n=1). Mean nest entrance heights for the two dominant tree species at the Thai site were very similar (29.5 and 30.7 m), representing 69% and 66%, respectively, of total tree heights. This is clearly proportionately lower than the heights of nest entrances of either hornbill species at BBSNP.

Given that female Helmeted Hornbills are larger than female Wreathed Hornbills (mean weight, 2.50 kg and 1.95 kg, respectively; Kinnaird & O'Brien 2007), it may be expected that they select nests with a larger entrance hole. Indeed the nest entrance of the Helmeted was about three times wider than the entrances of either of the two Wreathed nests, and 1.5–2.5 times longer (Table 1). Although we do not know the internal dimensions of the nest, it seems reasonable to suppose that the former species also requires a larger nest cavity than the latter, and that such cavities would normally be found only on the largest trees in the forest. The nest tree of the pair of Helmeted Hornbills in this study was not as tall as that of the second Wreathed Hornbill nest tree (W2), but it was much wider at its base (DBH, 185 vs 118 cm). This is consistent with the findings of Kinnaird & O'Brien (2007) at the same site, though the DBH of the nest trees of both species averaged lower (125 and 102 cm, respectively; Table 2) than those in the current study. The ratio of the DBH of the Helmeted nest tree to the mean DBH of the trees surrounding it (9.1×10^{-2}) was greater than that for either of the Wreathed nests (5.4 and 6.3×10^{-2}), indicating that the Helmeted nest tree was an exceptionally large tree in terms of its girth, which also suggests it was older (Table 1). The two studies in Thailand are not directly comparable since they were conducted in different regions and presumably had different tree floras, yet the nest trees of Helmeted Hornbills averaged 38 cm wider (in DBH) and 13 m taller than those of Wreathed Hornbills (Table 2).

Table 2. Characteristics of nest trees of the two hornbill species from previous studies

Species	Region	n	Mean DBH (cm)	Mean tree height (m)	Mean nest height (m)
Helmeted	Sumatra[1]	5	125	nr	27.0
Helmeted	Thailand[2]	14	158	44.6	30.1[5]
Wreathed	Sumatra[1]	5	102	nr	29.0
Wreathed	Thailand[3]	15	120	31.5	21.1
Wreathed	Central Java[4]	10	119	25.2	14.6

[1] Same site as in present study (Kinnaird & O'Brien 2007), [2] Budo-Sungai Padi National Park, South Thailand (Thiensongrusamee *et al.* 2005), [3] Khao Yai National Park, East Thailand (Poonswad 1995); [4] calculated from data in Rahayuningsih *et al.* (2017, Table 1); [5] estimated from means of each tree species.

Rahayuningsih *et al.* (2017) tabulated data on the characteristics of ten Wreathed Hornbill nests in Central Java. Mean DBH of these nest trees was similar to that at the above localities, but mean tree height and nest height were substantially lower (Table 2), suggesting the Javan forest was of lower stature. Ratios of height to DBH averaged 21.9 m (calculated from their Table 1), somewhat lower than that of Helmeted Hornbills in either BBSNP (31.4) or Thailand (28.1). In this study, the entrance of the Helmeted Hornbill nest was higher, relative to the tree's height (83%), than the entrances of both Wreathed Hornbill nests (71–76%). The first branch of the Helmeted nest tree was also much higher than those of the Wreathed nest trees (Table 1), though this is a typical feature of dipterocarps. Nest entrance heights of Javan Wreathed Hornbills ranged from 8.0 m to 27.0 m, representing 38–90% of their respective tree heights (mean, 58%, Rahayuningsih *et al.* (2017)). This wide range of relative nest heights was evident even when considering one of the four tree species used, *Syzygium antisepticum* (n=6).

The characteristics of Wreathed Hornbill nest trees were thus highly variable, suggesting this species is more flexible in its nesting ecology than the Helmeted Hornbill. Thus, the continued survival of the Helmeted Hornbill in Sumatra, as elsewhere within its range, depends not only on the cessation of hunting, but also on the protection of forests that contain very old dipterocarps or other trees with cavities that are both large (probably greater than 40 cm and 20 cm in length and width, respectively) and have perching platforms (i.e. stumps) beside them.

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References

Anggraini, K., M. Kinnaird & T. O'Brien. 2000. The effects of fruit availability and habitat disturbance on an assemblage of Sumatran hornbills. *Bird Conservation International* 10: 189-202.

Beastall, C., C.R. Shepherd, Y. Hadiprakarsa & D. Martyr. 2016. Trade in the Helmeted Hornbill Rhinoplax vigil: the 'ivory hornbill'. *Bird Conservation International* 26: 137-146.

Bhusal, P., D. Czeszczewik, W. Walankiewicz, M. Churski, R. Baral, B.R. Lamichhane & G. Mikusinski. 2015. Availability of tree cavities in a sal forest of Nepal. *Forest-Biogeosciences and Forestry* 9: 217-225.

BirdLife International. 2016. *Rhinoplax vigil*. The IUCN Red List of Threatened Species 2016. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22682464A92947540.en. Accessed on 17 June 2017.

Cahill, A.J. 2003. Nest-site characteristics of the Red-knobbed Hornbill *Aceros cassidix* and Sulawesi Dwarf Hornbill *Penelopides exarhatus*. *Ibis* 145: E97-E113.

Chong, M.H.N. 2011. Observations on the breeding biology of Helmeted Hornbill in Pahang, Peninsular Malaysia. *Raffles Bulletin of Zoology* Supplement 24: 163-165.

Cody, M.L. (Ed.). 1985. *Habitat Selection in Birds*. Academic Press, New York.

Collar, N.J. 2015. Helmeted Hornbills *Rhinoplax vigil* and the ivory trade: the crisis that came out of nowhere. *BirdingASIA* 24:12-17.

Corlett, R.T. 2017. Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: an update. *Global Ecology and Conservation* 11: 1-22.

Datta, A. & G.S. Rawat. 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 *Anthracoceros albirostris*. *Bird Conservation International* 14(S1): S39-S52.

Eaton, J.A., C.R. Shepherd, F.E. Rheindt, J.B.C. Harris, S.(B.) van Balen, D.S. Wilcove & N.J. Collar. 2015. Trade-driven extinctions and near-extinctions of avian taxa in Sundaic Indonesia. *Forktail* 31: 1-12.

Gill, F. & D. Donsker. 2016. IOC World Bird List (v 6.1). http://www.worldbirdnames.org/

Hopper, G.R. & R.M. Lennartz. 1991. Heart rot and cavity tree selection by Red-cockaded Woodpeckers. *Wildlife Management* 55: 323-327.

Hadiprakarsa, Y.Y. & M.F. Kinnaird. 2004. Foraging characteristics of an assemblage of four Sumatran hornbill species. *Bird Conservation International* 14(S1): S53-S62.

Kemp, A.C. 2017. Hornbills (*Bucerotidae*). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona. www.hbw.com/node/52280. Accessed on 20 May 2017.

Kemp, A.C. & P. Boesman. 2017. Wreathed Hornbill (*Rhyticeros undulatus*). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona. www.hbw.com/node/55926. Accessed on 18 April 2017.

Kemp, A.C., C.J. Sharpe & P. Boesman. 2017. Helmeted Hornbill (*Rhinoplax vigil*). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona. www.hbw.com/node/55911. Accessed on 18 April 2017.

Kinnaird, M. & T. O'Brien. 2007. *The Ecology and Conservation of Asian Hornbills: Farmers of the Forest*. University of Chicago Press, London.

Kitamura, S. 2011. Frugivory and seed dispersal by hornbills (Bucerotidae) in tropical forests. *Acta Oecologica* 37: 531-541.

Kitamura, S., T. Yumoto, N. Noma, P. Chuailua, T. Maruhashi, P. Wohandee & P. Poonswad. 2008. Aggregated seed dispersal by wreathed hornbills at a roost site in a moist evergreen forest of Thailand. *Ecological Research* 23: 943-952.

Kitamura, S., T. Yumoto, P. Poonswad, P. Chuailua, K. Plongmai, T. Maruhashi & N. Noma. 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133: 559-572.

Kitamura, S., T. Yumoto, P. Poonswad, N. Noma, P. Chuailua, K. Plongmai, T. Maruhashi & C. Suckasam. 2004. Pattern and impact of hornbill seed dispersal at nest trees in a moist evergreen forest in Thailand. *Journal of Tropical Ecology* 20: 545-553.

Kitamura, S., T. Yumoto, P. Poonswad, P. Chuailuai, K. Plongmai, N. Noma, T. Maruhashi & P. Wohandes. 2005. Fruit-frugivore interactions in a moist evergreen forest of Khao Yai National Park in Thailand. *Tropics* 14: 345-355.

Marsden, S.J. & M.J. Jones. 1997. The nesting requirements of the parrots and hornbill of Sumba, Indonesia. *Biological Conservation* 82: 279-287.

Naniwadekar, R., U. Shukla, K. Isvaran & A. Datta. 2015. Reduced hornbill abundance associated with low seed arrival and altered recruitment in a hunted and logged tropical forest. *Plos One* 10: e0120062.

Poonswad, P. 1995. Nest site characteristics of four sympatric species of hornbills in Khao Yai National Park, Thailand. *Ibis* 137: 183-191.

Poonswad, P. & A. Tsuji. 2008. Ranges of males of the Great Hornbill *Buceros bicornis*, Brown Hornbill *Ptilolaemus tickelli* and Wreathed Hornbill *Rhyticeros undulatus* in Khao Yai National Park, Thailand. *Ibis* 136: 79-86.

Poonswad, P., V. Chimchome, K. Plongmai, & P. Chuilua, 1999. Factors influencing the reproduction of Asian hornbills. Pp 1740-1755 *in* N.J. Adams & R.H. Slotow (eds.). *Proceedings of the 22nd International Ornithological Congress.* BirdLife South Africa, Durban, South Africa.

Rahayuningsih, M., N.E. Kartijomo, A. Retnaningsih, M. Munir & J. Dahlan. 2017. Nest records of Wreathed Hornbill *Rhyticeros undulatus* in Gunung Gentong Station, Mount Ungaran Central Java. *Journal of Physics: Conference Series* 824: 012061.

Shanahan, M., S. So, S.G. Compton & R. Corlett. 2001. Fig-eating by vertebrate frugivores: a global review. *Biological Reviews* 76: 529-572.

Supa-Amornkul, S., S. Wiyakrutta & P. Poonswad. 2011. Wood decay fungi in hornbill nest cavities in Khao Yai National Park, Thailand. *The Raffles Bulletin of Zoology* 24: 95-113.

Thiensongrusamee, P., P. Poonswad & S. Hayeemuida. 2005. Characteristics of Helmeted Hornbill nests in Thailand. Pp. 51–54 in S. Lum & P. Poonswad, eds. *The Ecology of Hornbills: Reproduction and Populations.* Hornbill Research Foundation, Mahidol University, Bangkok.

van Marle, J. G. & K. H. Voous 1988. *The Birds of Sumatra*. *B.O.U. Check-list 10.* British Ornithologists' Union, Tring UK.

Walker, J.S. 2007. Dietary specialization and fruit availability among frugivorous birds on Sulawesi. *Ibis* 149: 345-356.