The breeding biology of the cooperatively breeding White-throated Brown Hornbill (*Anorrhinus austeni*)

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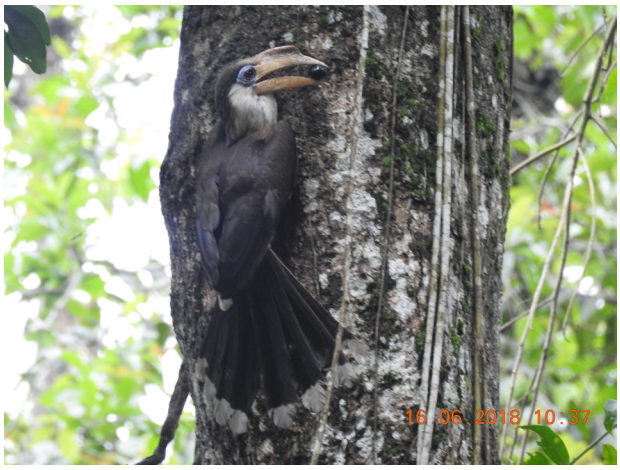
Abstract

We documented the breeding biology of the cooperatively breeding Brown Hornbill Anorrhinus austeni. *We found ten nests from 2017 to 2020. The nesting season was from early March to mid-July. The mean (± SE) nesting duration was 95.4 (± 2.3) days with a range from 92 to 99 days. Overall nesting success was high (91.6%). Most successful nests (83%) produced one chick, with the remaining 17% producing two chicks. Visitation and food delivery rates were higher in the post-hatching period compared to the pre-hatching period. There was inter-annual variation in the food delivered at nests, with a higher proportion of animal matter recorded in 2018 compared to 2019. The mean (± SE) number of helpers at Brown Hornbill nests was 2.2 (± 1.6), ranging from zero to five, and helpers (adult males or juveniles) assisted in bringing food and guarding nests. There was no relationship between number of helpers and nesting success or the number of chicks. The role of helpers may be related to ensuring nesting success through greater vigilance or by enhancing food finding and food delivery, however there may be no incremental advantage from having more helpers. Helpers may also be constrained by limited breeding opportunities and therefore may defer their own breeding and instead, assist the adult pairs. Further research with marked individuals would be required to better understand the role of helpers, and the factors determining the evolution of cooperative breeding behaviour in this species.*

Keywords: cooperative breeding, helpers, nesting, North-east India, rainforest

Introduction

Hornbills are among the 15% of birds that are monogamous (Kemp, 1995), with a unique breeding biology where the female confines and seals herself into a cavity throughout the nesting duration. Within this monogamous breeding system, there is variation with some species exhibiting cooperative breeding (Leighton, 1986; Kinnaird and O'Brien, 2007). Cooperative breeding is a social system in which adults, in addition to a breeding pair, display parental behaviour towards the young. This rare social system is more common among birds as compared to mammals, with just over nine percent of all avian species exhibiting this system (Cockburn, 2006; Keet al., 2016; Koenig, 2017). Among hornbills, the prevalence of cooperative breeding is relatively high. In Asia, the six species that are known to be cooperative breeders are *Anorrhinus austeni*, *A. galeri-*



Adult male Brown Hornbill on a feeding visit to the nest. Photo: Bhaskar Bora.

An adult male Brown Hornbill and a juvenile helper at nest. Photo: Bhaskar Bora.

tus, *A. tickelli*, *Buceros hydrocorax*, *Rhabdotorrhinus exarhatus* and *Berenicornis comatus*. Three more species – Sri Lanka Grey Hornbill *Ocyceros gingalensis*, Mindanao Hornbill *Penelopides affinis* and Mindoro Hornbill *P. mindorensis* are believed to be cooperative breeders, but this is yet to be confirmed (Kinnaird and O'Brien, 2007).

The most common form of cooperative breeding is helpers at the nest—where the social group is the breeding pair and its adult offspring. In hornbills, helpers are the nonbreeding offspring that remain with the parents, forego reproduction, help defend the natal territory, and feed the female and chicks (Witmer, 1993). However, not all nests have helpers (Poonswad *et al*., 1986). Some of the main questions related to the evolution of cooperative breeding are: (1) why do offspring remain with parents rather than disperse and breed; (2) why would parents tolerate offspring staying on territory; and (3) why should helpers assist in feeding young? Previous work has suggested that environmental unpredictability and habitat saturation can favour postponement of dispersal and reproduction. Environmental unpredictability increases the probability of reproductive failure in inexperienced birds (Reyer,1980; Emlen, 1981) and habitat saturation causes shortage of breeding opportunities and resources in suitable habitat (Brown, 1974; Stacey, 1979).

Once this condition of delayed dispersal sets in, it has been postulated that helping behaviour can then evolve through kin selection and helpers benefit in terms of indirect fitness through production of non-descendent kin (Emlen and Wrege, 1988; 1989). The life history hypothesis based on a comparative analysis by Arnold and Owens (1998) suggests that factors such as low adult mortality and low dispersal predisposed certain avian lineages to develop cooperative breeding.

Among hornbills, there are a range of dispersal strategies, which includes early dispersal (African genus *Tockus* and Asian genus *Rhyticeros*), delayed dispersal with no helping (Asian genera *Buceros* and *Anthracoceros*) and delayed dispersal with helping (the two Brown Hornbills, the Bushy-crested Hornbill *Anorrhinus* spp. and the White-crowned Hornbill *Berenicornis comatus* (Kemp, 1976; Leighton, 1986; Poonswad *et al*.,1988). Among cooperative breeding hornbills, Leighton (1986) and Poonswad *et al*. (1988) have speculated that delayed dispersal was a result of

habitat saturation. Parental acceptance seems reasonable only if the offspring contribute to their reproductive success or survival. Most studies suggest that the benefits of allowing helpers on their territory outweigh any losses from competition for food or other resources. In addition, hornbills are secondary cavity-nesters and the availability of suitable cavities could be a limiting factor (Poonswad, 1993). Gonzalez *et al*. (2013) used a phylogenetic framework to assess the effects of climate on the evolution of cooperative breeding in hornbills. They found that cooperative breeding in hornbills is associated with both intra- and inter-annual climatic stability.

Of the nine hornbill species in India, only the White-throated Brown Hornbill (*A. austeni*) is a cooperative breeder. Globally, Brown Hornbills are distributed from Cambodia, Vietnam, Laos, Thailand, China, Myanmar up to parts of north-east India (Kemp, 1995; Poonswad *et al*., 2013; Kinnaird and O'Brien, 2007). Areas located south of the River Brahmaputra in north-east India form the westernmost global distributional limit for the species. In north-east India, Brown Hornbills are currently found in a few localized populations in eastern Arunachal and in eastern and southern Assam (Datta, 2009; Hussain *et al*., 2015; Naniwadekar *et al*., 2015; 2016, Jain and Sumashini, 2020), with records from Nagaland (Choudhury, 2005; 2006; Lotha, 2013), Mizoram (Choudhury, 2005;Ved, 2011) and one hunting record from Manipur (Choudhury, 2009). Within this narrow range, populations have become very rare in some places due to hunting (Choudhury, 2005) and local extinctions have also been recorded (Naniwadekar *et al*., 2015). Information on population trends across its global range is still unknown although it is listed as 'Near Threatened' by the IUCN Red-List (BirdLife International, 2018), and it has been recently categorized as a species of High Conservation Concern in India based on eBird data (SoIB, 2020).

Apart from studies in Thailand, quantitative data on the breeding biology of Brown Hornbills from other parts of its global range is lacking. Our study provides new information on the breeding biology and nesting success of this unique cooperatively breeding hornbill species in India. We describe the role of helpers at nests and examine whether the number of helpers at nests is positively related to nesting success and/or higher chick production. We discuss the possible factors that may have led to the evolution of cooperative breeding in this species.

Methods

Study Area

The study was conducted from April 2017 to July 2020 in the Dihing-Patkai (DP) landscape (approximately 584 km^2; 122 – 475 m above sea level; 27°4'58.22"N to 27°30'15.60"N and 95°17'23.54"E to 95°39'46.84"E) in eastern Assam, north-east India. The vegetation of the landscape is broadly classified as Assam valley tropical wet evergreen forest 1B/C1 (Champion and Seth, 1968) and are among the last remaining forests of this category in Assam. Climate is categorized as a tropical monsoon, receiving an average annual rainfall of 2,226 – 3,644 mm (Kakati, 2012), with most rainfall during the south-west monsoon from June – September. November to February is relatively dry and cool. The mean annual temperature ranges from 6°C to 38°C (Kakati *et al*., 2009). The vegetation in the upper canopy is dominated by two dipterocarp species *Dipterocarpus retusus* and *Shorea assamica*. The middle canopy is mostly dominated by *Mesua ferrea*, *Xanthophyllum* spp., *Castanopsis* spp., *Dysoxylum* spp., and *Magnolia* spp.

The study area lies at the confluence of the

Eastern Himalaya and the Indo-Burma global biodiversity hotspots. The total area of fragmented forests of Upper Assam, for which there are some historical records of Brown Hornbill is 892 km^2. Three other hornbill species (Great Hornbill *Buceros bicornis*, Wreathed Hornbill *Rhyticeros undulatus* and Oriental Pied Hornbill *Anthracoceros albirostris*) also occur in the area. The forests of Upper Assam have faced rapid deforestation in the past owing to conversion for tea cultivation, coal and oil and wood-based industries from the mid 19th century (Sharma *et al.*, 2012). The fringe villages are densely populated with communities dependent on non-timber forest resources, timber, and fodder.

Locating hornbill nests

Our nest searches were based on visual and auditory cues to locate the birds and subsequently following them from a distance to locate their nests. Areas where birds were frequently encountered were also searched intensively for potential nest tree cavities. Trees with cavities were examined and the presence of regenerating hornbill food plants and regurgitated seeds/middens helped to confirm hornbill nests. Our nest searches were conducted between 0500 and 1400 hours. We found eight nests in the DP landscape with approximately 270 km of walking effort, during the breeding seasons of 2017, 2018 and 2019. Information on an additional nest location (BH-9) was received from researchers working in the Doomdooma forest fragment, which we monitored systematically to determine the nesting duration and success in 2019. In 2020, one more nest (BH-10) was located, and though it was not regularly monitored, successful fledgling was recorded on 4th August 2020. This nest was previously used by a Chestnut-bellied Nuthatch (*Sitta cinnamoventris*) pair in 2018 for nesting.

Nest observations

We followed the methods of Poonswad *et al.* (1986) and Datta (2001) to quantify male visitation and food delivery rates and diet at nests. Nest observations were made during the daytime between 0500 hours and 1300 hours. We observed the nest trees from a distance of 35 – 50 m. We used camouflage sheets and nets to conceal our location. Food items delivered at the nest were identified using a Celestron Ultima spotting scope (20–60 x 80), binoculars (Bushnell 10 x 42) and Nikon P900 camera. We calculated visitation and food delivery rates for the pre-hatching and post-hatching period. The exact time of chick hatching was unknown and week four (since nest entry) was assumed to be the hatching time following Poonswad (1993, p. 111). Focal nests were monitored at least two to three times a week, depending on rain and elephant movement. The activity of elephants near the nest trees and heavy pre-monsoon rainfall from February till May in 2018 and 2019 were constraints during nest watches thus limiting the total observation hours.

In 2017, we initiated the study in the last week of April when the breeding season had already begun. We found and monitored three nests that were already active. In 2018, we found three additional new nests followed by three more new nests in 2019. In 2018, we carried out intensive nest watches at four of the nests with 127 hours of observations carried out from April to June (Table S1). In 2019, out of the nine Brown Hornbill nests, seven were active and we monitored the nests from the start of February till mid-July (end of the breeding season) to determine nesting outcomes and nesting duration. In 2019, we carried out intensive nest watches at three nests and occasional nest watches at five nests with an effort of 256.2 hours (Table S1).

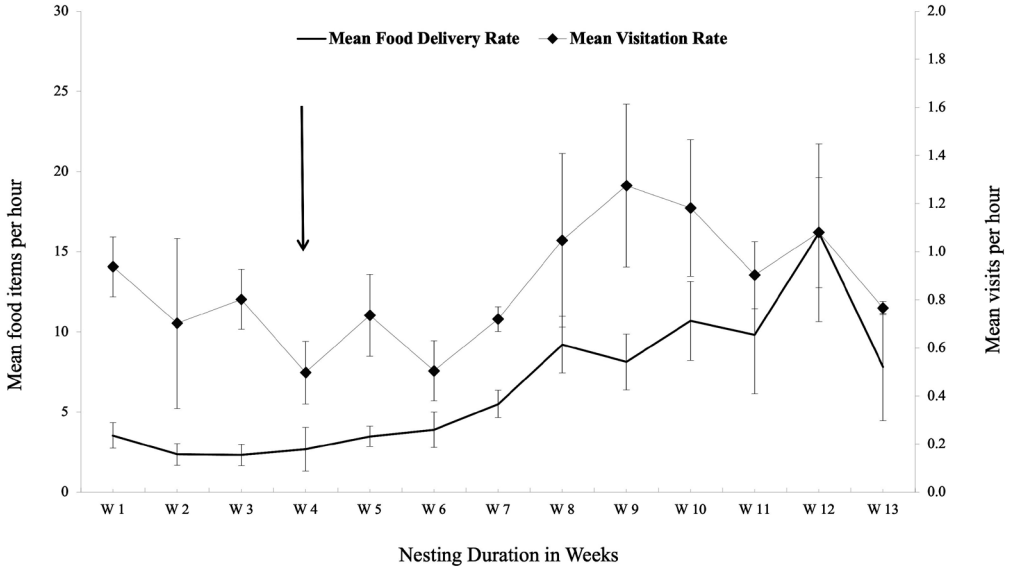


Fig. 1. Mean visitation and mean food delivery rate (± SE) of Brown Hornbill males and helpers at nests during the pre-hatching and post-hatching period in 2019 in the Dihing-Patkai landscape, eastern Assam. The black arrow marks week 4 when the chicks were assumed to have hatched.

Brown Hornbills are sexually dimorphic, males have a pale creamy bill, white cheeks and throat, rufous-brown underparts and white tips to tail and primaries during flight. In females, the head and throat are all dark and more grey-brown with pale streaking on the crown and they lack white tips to the primaries and tail (Ali and Ripley, 1983; del Hoyo *et al*., 2001). Juveniles resemble adult males with paler underparts and can be differentiated by the pinkish orbital skin which is blue in adults. They also have pale brown tips to wing-coverts, yellowish smooth beak, which in adults are dark grey with a well-developed casque.

Although we could not distinguish between individual helpers at the nest as the birds were not tagged or marked, we could determine those which were helpers as they usually visited the nest along with the adult breeding male. At most nests, along with the adult breeding male, other individual adult birds also arrived at the nest simultaneously or within a few minutes of each other. Some of these individuals did not always come directly to the nest tree but perched on surrounding trees. These were the individuals counted as helpers. In some nests, where there were no helpers, only a single adult breeding male came on feeding visits.

Results

Nesting outcomes in 2017-2020

Out of the total 24 nesting instances in all four years, nesting failure was only seen at one nest in 2018, while success could not be confirmed in four instances and nesting was confirmed to be successful in 19 instances. Overall, average nesting success for Brown Hornbill was 91.6%, ranging from 75% in 2018 to 100% in 2019 and 2020.

In 2017, out of three active nests that were

Table 1. Nesting outcomes at Brown Hornbill nests in the Dihing-Patkai landscape, eastern Assam, India during 2017–2018.

Year	Nest ID	Stage nest found	Female exit date	Chick exit date	Fledglings	Status	Comments
2017	BH-1	Chicks had hatched	Between 21 & 28 June	Between 21 & 28 June	NA	NA	Seal was found broken on 28th June and unclear whether nesting was successful
2017	BH-2	Chicks had hatched	Between 21 & 28 June	Between 21 & 28 June	NA	NA	Seal was found broken on 28th June. Unclear whether nesting was successful.
2017	BH-3	Chicks had hatched	02 July	02 July	1	Successful	Visual confirmation with photos
2018	BH-1	19 March found sealed	12 June	17 June	1	Successful	Chick was seen near the nest after fledging.
2018	BH-2	20 March found sealed	Between 15 & 18 June	Between 15 & 18 June	1	Not sure	Female and chick not seen
2018	BH-3	21 March found sealed	21 June	21 June	1	Successful	Visual confirmation
2018	BH-4	20 March nest was active	Between 4 & 7 June	NA	NA	NA	We could not confirm if the nest was successful.
2018	BH-5	Male and female at nest	NA	NA	NA	Female preyed upon between 27th and 30th March 2018	We saw carcass of a Brown Hornbill below nest. The male was seen bringing food and looking inside the empty nest. Feathers found below nest.
2018	BH-6	13 May found full-sealed	NA	12 July	1	Successful	Visual confirmation

NA - Not Available

Table 2. Nesting duration and nesting success of Brown Hornbill nests in the Dihing-Patkai landscape, eastern Assam, India in 2019–2020.

Year	Nest ID	Entry Date	Exit Date	Nesting Duration	Fledgling
2019	BH-1	18 March	22 June	96	2
2019	BH-2	25 March	25 June	92	1
2019	BH-3	Inactive	-	-	-
2019	BH-4	28 March	30 June	94	1
2019	BH-5	Inactive	-	-	-
2019	BH-6	03 April	09 July	97	2
2019	BH-7	*14 April	17 July	94	1
2019	BH-8	NA	26 June	-	1
2019	BH-9	05 April	10 July	96	1
2020	BH-1	16 March	23 June	99	2
2020	BH-2	NA	23 June	-	2
2020	BH-3	Inactive	-	-	-
2020	BH-4	NA	21 June	-	1
2020	BH-5	Inactive	-	-	-
2020	BH-6	NA	NA	-	1
2020	BH-7	NA	20 June	-	1
2020	BH-8	NA	20 June	-	1
2020	BH-9	NA	NA	-	1
2020	BH-10	NA	4 Aug	-	1

**Between 12 and 17 April, however the entry date was assumed to be 14 April.*
NA - Not Available

Table 3. Visitation and food delivery rates (per hour) recorded at Brown Hornbill nests (n = 4) in the Dihing-Patkai landscape, eastern Assam, India in 2018.

Observations at nests	Mean (± SE)
Visitation rate pre-hatching	0.7 (± 0.2)
Visitation rate post-hatching	1 (± 0.1)
Food delivery rate pre-hatching	4.1 (± 1.6)
Food delivery rate post-hatching	7.8 (± 1.6)
Overall visitation rate	0.8 (± 0.1)
Overall food delivery rate	6.3 (± 1.2)

monitored, we confirmed nesting success at one nest (BH-3), and it was unclear whether the other two nests were successful (Table 1). In 2018, out of six known nests, we confirmed one successful fledgling each from three nests (Table 1). A female was found preyed upon in one nest (BH-5), which was confirmed from the feathered remains of the right wing found below the nest tree. In 2019, out of nine known Brown Hornbill nests, seven were active and all seven were successful. Female entry at nests was observed from 18th March till 14th April, while nest exit by female and chicks were observed from 22nd June to 17th July (Table 2). In 2020, out of ten known Brown Hornbill nests, seven were active. Success was confirmed in six out of seven nests. Chick entry dates could not be determined for most nests in 2020 due to the Covid lockdown during that period.

The mean (± SD) nesting duration was found to be 95.4 (± 2.3) days with a range of 92 to 99 days from seven nests (six nests in 2019 and one in 2020) where both entry and exit dates could be obtained (Table 2). A total of nine successful fledglings were recorded from seven nests in 2019. Chicks were seen fledging with the females at the same time, with the females leaving the nest first in all nests. Two fledglings were seen emerging out from two nests, while in the remaining five nests, one chick was seen leaving the nest.

Overall from 2017–2020, the average number of chicks produced was 1.16 chicks (± SD 0.51) per nest (n = 19 nesting attempts from 2017 to 2020, where outcome was known). The total number of chicks produced in the population was 21 from the 19 nesting attempts where outcome was known. In 14 of the nesting attempts, only one chick fledged, while in four of the nesting attempts, two chicks fledged. The outcome or number of fledglings could not be determined at four nests which had been active. Of nests that were successful, 76.5% of nests produced only one chick.

Diet (based on food delivery at nest trees) in 2018

A total of 878 food items were recorded being

Table 4. Number of helpers (excluding main breeding adult male) recorded at Brown Hornbill nests in the Dihing-Patkai landscape, eastern Assam, India in 2017–2020.

Nest ID	2017	2018	2019	2020
BH-1	4	5	5	2
BH-2	3	2	1	1
BH-3	0	1	Inactive	Inactive
BH-4	NA	1	1	1
BH-5	NA	5	Inactive	Inactive
BH-6	NA	3	0	1
*BH-7	NA	NA	2	1
BH-8	NA	NA	4	2
BH-9	NA	NA	4	NA
BH-10	NA	NA	NA	1

**Our field observations suggest that there was overlap in helpers between the BH1 and BH7 nest in 2019.*
NA - Not Available

delivered by the male and helpers at four nests (BH-1, BH-2, BH-3, BH-4) that we had selected for nest observations (Table S1). Six hundred and ninety five items were identified as animal matter (79.4%) and 180 items were identified as fruits (20.6%).

The mean (± SE) visitation rate throughout the breeding season was 0.8 (± 0.1) visits/hour across all nests (n = 4). The mean (± SE) food delivery rate was 6.3 (± 1.2) food items/hour across all nests (n = 4). The mean visitation rate was 1.4 times higher in post-hatching phase (1 ± 0.1 visits/hour) than the pre-hatching period (0.7 ± 0.2 visits/hour). Food delivery rate was also higher in the post-hatching period (Table 3).

Diet (based on food delivery at nest trees) in 2019

In 2019, we recorded a total of 1433 food items in the diet of Brown Hornbills. Out of 1035 food items identified, 52% comprised fruit species belonging to seven plant families and 48% comprised 16 animal food items (Table S2). Overall mean (± SE) visitation rate was 0.89 (± 0.12) per hour (n = 5 nests). Mean (± SE) visitation rate for pre-hatching phase was 0.8 (± 0.1) and the visitation rate during post-hatching period was 0.9 (± 0.1). Mean (± SE) food delivery rate was 6 items (± 0.5) per hour (Figure 1). The mean food delivery rate in the post-hatching phase (7.3 ± 0.8) was 2.7 times higher than the pre-hatching phase (2.7 ± 0.4).

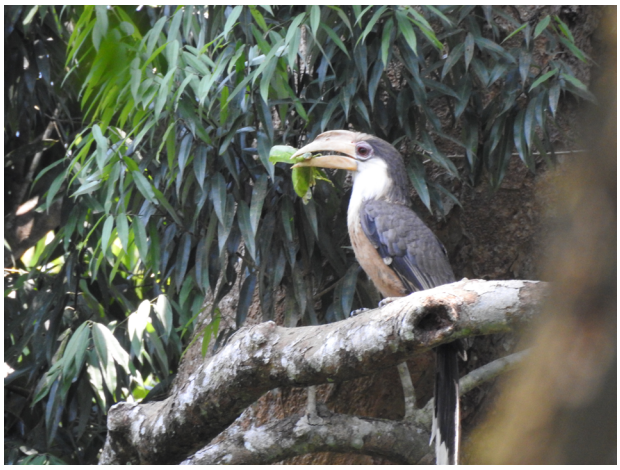
Co-operative breeding: the role of helpers

Out of the 24 breeding instances over four years at ten nests, only on two attempts, nests were seen without helpers, while for one nest in 2020, we had no data on helper numbers. Therefore 91% of breeding instances were with helpers. The mean number of helpers (± SE) was 2.17 (± 1.61) and the number of helpers at nine nests varied from zero to five (Table 4). Helper numbers also varied at some of the nests between years—increased by one in two nests (BH-1, BH-3) and decreased by two in two nests (BH-2, BH-6). In BH-1, the number of male helpers in 2017 was four, which increased to five in 2018. In BH-3 and BH-6, breeding occurred without helpers in 2017 and 2019, respectively, while in other years, breeding was attempted with helpers at the nest.

In the BH-1 nest in 2018, out of 126 visits made by the breeding male and five helpers during 63.4 hours of observations, only four feeding visits were made by a single male without helpers.

In the BH-2 nest, three male helpers were observed in 2017, while in 2018, we saw two helpers and a juvenile (had pink orbital-skin and yellow beak). In 2019, only one helper was seen at the nest. In the BH-3 nest, we did not observe any helper in 2017, while in 2018, we saw a juvenile helper. The adult male made 10 feeding visits to the nest and the juvenile was not seen bringing food on these visits. On two occasions, the juvenile was seen perched behind the nest tree and making alarm calls. The nest was inactive in 2019. During our monitoring visits in 2018 at the BH-6 nest, out of three males, only two were observed bringing food for the female/chicks.

We found a new nest BH-7 in 2019 that was approximately 50 m away from the BH-1 nest. Initially, we saw a pair of Oriental Pied Hornbills visiting and inspecting the BH-7 nest, but finally the Brown Hornbills took over. We also observed there was an overlap of helpers among BH-1 and BH-7. In the first week and the 9th week of the nesting cycle, we observed 1-2 helpers at the BH-7 nest, which were also part of the BH-1 group. We confirmed this by monitoring both nests simultaneously in two teams as these nests were close to each other.



A Brown Hornbill helper at the nest with a leaf insect. Photo: Bhaskar Bora.

We examined if there was a correlation between the number of helpers at a nest and the nesting success and/or the number of chicks produced at that nest. There was no correlation between number of helpers and number of chicks produced ($\rho = -0.20$, $p = 0.42$, $n = 18$) and no correlation between number of helpers and nesting success ($\rho = -0.36$, $p = 0.13$, $n = 19$). The BH-5 which had five helpers is the only nest where there was a failure due to predation of the nesting female. On the other hand, BH-6 which had no helpers produced two chicks.

Discussion

Environmental cues such as photoperiod and light intensity have been found to regulate

seasonal reproduction in tropical birds (Lack, 1950; Wikelski *et al*., 2000). Breeding initiation by three species of large-bodied hornbills in Arunachal Pradesh was found to occur in the pre-monsoon period in March, with the main breeding period (May–June) coinciding with the peak availability of ripe non-fig fruits (Datta, 2001), with chicks fledging in the late wet season (July–August). The Brown Hornbills in our study site also initiated breeding in the same pre-monsoon period (March) with chick fledging in the late wet season (July). Breeding biology studies from across South and South-east Asia, however, shows that there is variation in the timing of breeding by hornbills with respect to geographical location due to latitudinal variation. In some sites, the peak ripe fruit availability occurs towards the end of the breeding season when chicks are about to fledge (Kannan and James, 1999; Poonswad *et al*., 1986, Poonswad *et al*., 1998). In Sulawesi, Indonesia, food resources such as figs and insects are available year-round (Kinnaird *et al*., 1996), yet the cooperatively breeding *Rhabdotorrhinus exarhatus* starts breeding in the wet season (April) with chicks fledging during the dry season in June–July (O'Brien, 1997), whereas the sympatric but larger-bodied *Aceros cassidix* starts breeding in mid-June (Kinnaird and O'Brien, 1999). In Arunachal, the smaller-bodied Oriental Pied Hornbill commences breeding in April, while the two sympatric larger-bodied hornbill species start breeding from March (Datta, 2001; Datta and Rawat, 2004). At some sites, temporal partitioning in the commencement of breeding season between sympatric species may be governed by avoidance for competition of resources.

Breeding biology

In Thailand, the incubation period for Brown Hornbill is known to be 27 days (Poonswad *et al*., 2013) and 30 days (del Hoyo *et al*., 2001), with a nestling period of 66 to 71 days, and a mean nesting cycle of 92.8 ± 6 days (Poonswad, 1993) ranging from 73 to 112 days (Poonswad *et al*., 2013). In our study, we found the nesting cycle to be from 92 to 99 days. Although we could not determine incubation period for all nests, we heard first chick vocalizations after 37 days at the BH-7 nest and believe that the incubation is around 37 days for that nest. Based on that, the nestling period may range from 57 to 62 days. In similar-sized cooperatively breeding *Rhabdotorrhinus exarhatus*, the nesting cycle is shorter (70–90 days), which may have been due to the smaller clutch size (O'Brien, 1997). We do not have information on clutch size from our study, but Brown Hornbills are known to lay 2–3 eggs on average, sometimes laying up to five eggs (Kemp, 1995). In Thailand, on average, Brown Hornbills produced 2.3 chicks with 3.4 helpers, with all helpers being adult males (Poonswad *et al*., 1986). In contrast, we recorded an average of 1.16 chicks fledging (n =19 successful nesting attempts), with an average of 2.17 helpers (2017-2020). Thus, we consistently noted a lower number of fledglings in four breeding seasons compared to that recorded in Thailand in four breeding seasons. Fledging success was 1.8 times lower than Thailand, and would imply that fecundity is also lower in our study site but remained consistent across the four breeding seasons.

A possible explanation for the smaller number of chicks produced could be the lack of quality and quantity of resources available for breeding. These may be exacerbated by the past and ongoing degradation of forests in the area. The vegetation of the landscape is recovering from past logging disturbances, and has been modified in certain patches due to earlier management schemes post-logging. Some of the

hornbill food plant species (*Beilschmiedia* spp., *Syzygium* spp., *Aglaia spectabilis*) and nest tree species (*Magnolia* spp., *Dipterocarpus retusus*, *Shorea assamica*, *Artocarpus chaplasha*) are also important timber species in the area, which have been logged in the past and continue to be illegally logged. For secondary cavity-nesting species like hornbills, the availability of suitable nest cavities could be a limiting factor for breeding success. Hunting of wildlife is prevalent in the region and we have encountered instances of hunting for monitor lizards at tree cavities, bird-traps, gunshots and hides on tree-tops. Brown Hornbills are known to be hunted in adjoining Arunachal Pradesh by tribal communities (Datta, 1999). The forests are also frequented by villagers for collecting firewood, extracting cane and other non-timber forest produce.

Hornbill diet, visitation and food delivery at nests

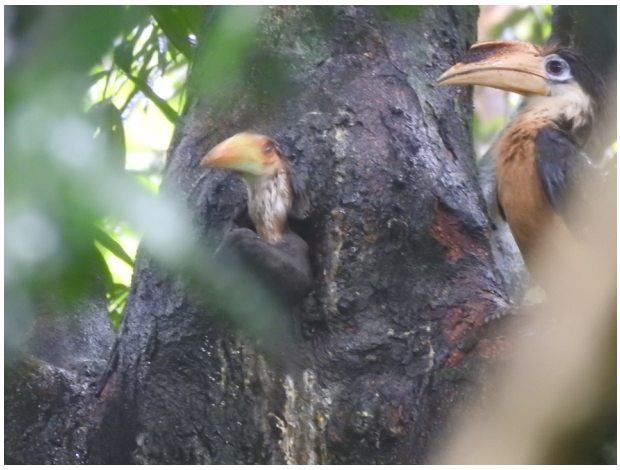
As compared to large-bodied hornbills, the feeding rate of fruits per hour in the smaller-bodied Brown Hornbill and Oriental Pied Hornbills has been found to be relatively low (Poonswad *et al*., 1998). Brown Hornbills fed on animal matter at the highest mean rate (63.5 gm per day) compared to the Great (42.7 gm/day), Oriental (36.8 gm/day) and Wreathed Hornbills (18.7 gm/day) (Poonswad *et al*., 1998). In our study, in the 2018 breeding season, we recorded a higher proportion of animal matter in the diet (79.4%), the reasons for which remain unclear. In 2019, we recorded 48% animal matter in the diet of Brown Hornbills which was similar to that observed in Thailand, where animal matter contributed 40% to the diet (Poonswad *et al*., 2013).

We cannot explain the variation in the proportion of animal matter in the diet between years, but Brown Hornbills are generally known to consume animal matter in higher proportions (Poonswad *et al*., 2004). On the other hand, in the cooperatively breeding *Penelopides exarhatus*, the diet was dominated by fruits (84.6%) with one-third of the fruits being *Ficus* (O'Brien, 1997). In both these studies, males and helpers did not show any difference in proportion of invertebrate prey and fruits delivered at nests (O'Brien, 1997; Poonswad *et al*., 2004); but a male with single helper was found to bring more food than male with three helpers (O'Brien, 1997). Earlier studies also suggest, high diversity of food supplied to nests may increase breeding success (Poonswad *et al*., 1998). We could not collect systematic information on the quantum of food delivery by males and helpers separately at nests. However, food diversity would be dependent on availability in a given area and the helpers' role could be simply to augment the process of locating food resources or increased vigilance at the nest while benefiting from inclusive fitness in return.

Role of helpers: sex, age and identity

In the cooperatively breeding *Anorrhinus galeritus*, both sexes were found to assist in the breeding season which has not been observed in Brown Hornbills (Poonswad *et al*., 1986). Previous studies on Brown Hornbills have reported male helpers at nests, and most of the helpers we observed were also adult males. Two helpers were juveniles; however, the sex could not be determined. The development of adult plumage for immature females takes place at first moult (Kemp, 1995), however the immature period could last up to 2–3 years (Poonswad *et al*., 1986). Hornbills are long-lived and dispersal at an early stage could result in higher mortality in females as suggested by Emlen (1978), generally for long-lived birds. Natal dispersal in cooperatively breeding *Bucorvus leadbeateri*, showed great variability among females and males, 2–24 and 8–96 months, re-

Adult male Brown Hornbill bringing fruits for a chick about to emerge from the nest cavity. Photo: Bhaskar Bora.



A Brown Hornbill fledgling emerges from the nest with the male on watch. Photo: Bhaskar Bora.

spectively (Carstens *et al.*, 2019); but it also signifies that males stay longer than females in natal territories. Moreover, in our study, two nests (BH-1 and BH-7) were located within a radius of approximately 50 meters from each other. Genetic information from these two breeding groups can shed light on genetic relatedness and the possibility of philopatry among male Brown Hornbills which is not known. In either case, this suggests the need to investigate further about the interactions and social organization in Brown Hornbills.

Helpers and nesting success and chick production

Long-term studies suggest that helper numbers may vary from one to five, but presence of two helpers at a nest was efficient in bringing up to 40% of the food to the nest (Poonswad *et al.*, 1998). Presence of multiple helpers may aid in chick development through increased food delivery rates and allow breeding males to invest less in parental care (O'Brien, 1997). In our study, the number of helpers ranged from zero to five, while the number of chicks produced ranged from 1 to 2. We found lone breeding males could raise a similar number of successful fledglings as nests with up to five helpers. Hence, the effect of the number of helpers in terms of higher chick production at individual nest sites is not evident from our study. We could not find any direct benefit of helpers associated with the number of successful fledglings at nests. However, our study had a limited sample size of active nests per year. An extraordinarily large number of helpers (12) were noted at an *Anorrhinus galeritus* nest in Western Malaysia (Styring *et al.*, 2002), which raises further questions as to the function of cooperative breeding in hornbills.

There could be ecological constraints (such as shortage of nest trees/food resources) governing the fate of these younger adults (possibly previous year's offspring) if they leave their natal territories prematurely, which they may compensate by helping behavior. The area also has three other sympatric non-cooperatively breeding hornbill species with which this smaller-bodied species may be competing for nest sites and food resources, although the two larger-bodied species (Great and Wreathed Hornbills) are rarely sighted in the area. Indeed, one instance of possible nest competition was observed when an Oriental Pied Hornbill pair was seen inspecting, entering and cleaning a

nest cavity, which was subsequently taken over by a Brown Hornbill pair. Helpers may also be benefiting from inclusive fitness by participating in cooperative breeding behavior while enhancing foraging efficiency and energy budget in the breeding male. Measuring reproductive success for several groups along with related demographic parameters would be essential to understand the adaptive significance of cooperative breeding behavior. More insights on the evolution of cooperative breeding in Brown Hornbills can be obtained by tagging birds or using telemetry which will also help understand their home range size, degree of territoriality, post-fledging survival and natal dispersal patterns in this highly human-modified yet ecologically important lowland tropical rainforest landscape.

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Table S1. Nest watch effort for visitation/food delivery and diet observations in 2018 and 2019 in Brown hornbill nests in the Dihing-Patkai landscape, eastern Assam, India. NA

Nest ID	Effort in 2018 (hours)	Effort in 2019 (hours)
BH-1	63:35	51:05
BH-2	3:35	29:07
BH-3	13:16	Not applicable
BH-4	47:06	97:10
BH-7	Not applicable	61:23
BH-8	Not applicable	17:34
Total observation hours	127:32	256:19

Table S2. Identity of food items recorded during nest observations in 2018 and 2019 in Brown hornbill nests in the Dihing-Patkai landscape, eastern Assam, India.

Taxonomic category	Food items	Year 2018	Year 2019
Plant	*Aglaia spectabilis* Meliaceae	45	27
Plant	*Dysoxylum gotadhora* Meliaceae	4	37
Plant	*Ficus* spp. Moraceae	16	2
Plant	*Chisocheton cumingianus* Meliaceae	5	1
Plant	*Dysoxylum procerum* Meliaceae	*NR	201
Plant	*Knema* sp. Myristicaceae	2	NR

Taxonomic category	Food items	Year 2018	Year 2019
Plant	*Polyalthia* sp. Annonaceae	NR	17
Plant	*Xanthophyllum* sp. Polygalaceae	NR	14
Plant	*Beilschmiedia* sp. Lauraceae	NR	16
Plant	*Persea*/*Beilschmiedia* sp. Lauraceae	NR	4
Plant	*Sterculia* sp. Malvaceae	NR	61
Plant	*Micromelum* sp. Rutaceae	NR	5
Plant	Unidentified drupe	NR	8
Plants	Unidentified fruit items	108	145
Animal - Arthropod	Unidentified insects	150	362
Animal - Arthropod	Caterpillar	1	5
Animal - Arthropod	Grasshopper	1	1
Animal - Arthropod	Stick insect	2	3
Animal - Arthropod	Mantis	1	NR
Animal - Arthropod	Cicada	3	16
Animal - Reptile	Snake	1	1
Animal - Amphibian	Frog	3	
Animal - Annelid	Earthworm	1	2
Animal matter - unclassified	Egg	NR	9
Animal -	Robber-fly	NR	2
Animal -	Fly	NR	3
Animal - Arachnid	Spider	NR	1
Animal - Arthropod	Bug	NR	7

Taxonomic category	Food items	Year 2018	Year 2019
Animal - Reptile	Skink	NR	1
Animal - Reptile	Lizard	NR	8
Animal - Crustacean	Crab	NR	2
Animal - Bird	Bird	NR	1
Animal - unclassified	Unidentified animal food	532	73

Not recorded

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