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Research Article

Spatial and temporal variation in hornbill densities in Namdapha Tiger Reserve, Arunachal Pradesh, north-east India

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Abstract

Asian hornbill populations are declining across their ranges because of hunting and deforestation. Five of the 32 Asian hornbill species occur in north-east India. However, vital information on their abundance from the region remains scanty. Understanding spatiotemporal variation in densities provides crucial information for formulating effective conservation strategies based on species-specific abundance patterns and population trends. We examined spatiotemporal variation in densities of four hornbill species in the Namdapha Tiger Reserve, a site identified as an important site for hornbill conservation in Asia. We collected data through variable-width line transect sampling (effort=842.1 km) in the non-breeding season from 2009-12 to estimate hornbill densities. We had 458 detections of four hornbill species. We have estimated White-throated Brown Hornbill densities (7.9 birds/km²) for the first time throughout its entire range. The mean Rufous-necked Hornbill densities (6.9 birds/km²) were higher than those reported elsewhere. Great (3.9 birds/km²) and Wreathed Hornbill (16.1 birds/km²) densities were comparable with other sites. The peak densities of all hornbill species in November-December are among the highest reported from Asia. Wreathed Hornbill densities showed temporal variation peaking in November-December (68 birds/km²) and drastically declining by March-April (1.3 birds/km²), indicating seasonal altitudinal movement to low-elevation areas outside the reserve during the breeding season. Our results underscored the spatial variation in hornbill distribution, with low densities of Great and the White-throated Brown hornbills in higher elevations. Our study demonstrates the global importance of Namdapha for hornbills, given its large area and high densities of four hornbill species.

Key words: Eastern Himalaya, Great Hornbill *Buceros bicornis*, Rufous-necked Hornbill *Aceros nipalensis*, White-throated Brown Hornbill *Ptilolaemus austeni*, Wreathed Hornbill *Rhyticeros undulatus*

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Introduction

Asian hornbills (Bucerotidae) are among the largest avian frugivores found in the tropical forests of South and South-east Asia. Hornbills are known to range over large distances [1, 2] and exhibit significant fluctuations over space and time, possibly to track patchily distributed fruiting trees [3]. Given their ability to swallow and regurgitate large seeds unharmed and traverse large distances, hornbills are important dispersers of several large-seeded plants in tropical forests [4]. However, Asian hornbills are hunted for their body parts (casque and tail feathers for traditional attire), for consumption of their meat, and for their body fat, which is believed to have medicinal properties [5-7]. In addition, they face significant threats from logging [8, 9] and habitat fragmentation [10]. Today, only a third of their natural habitat remains, a large proportion of it in a fragmented state and with extraordinarily high levels of threat to their persistence [4, 11].

As a consequence of these anthropogenic pressures, 34% of the 32 Asian species are listed by IUCN [12] as 'Near Threatened,' 19% as 'Vulnerable,' 9% as 'Endangered,' and 6% as 'Critically Endangered,' while only 31% are classified as 'Least Concern.' In addition, IUCN [12] lists the population trends of almost 85% of the 32 species as 'Decreasing.' Several hornbill species are considered to have been locally exterminated from several sites in their global range [13, 14]. Given the declines in hornbill populations throughout their ranges, it is vital to have abundance or density information from sites that are likely to harbor hornbill populations in the long-term. This information will serve as a baseline for monitoring future population trends of hornbill species. Additionally, abundance information is a useful state variable to understand responses of species to natural and anthropogenic disturbances. An understanding of spatial and temporal changes in hornbill densities is useful for identifying areas that are seasonally or spatially important for the different hornbill species, thereby contributing towards devising effective conservation strategies for the different species.

Nine of the 32 species of Asian Hornbills occur in India. Five of these nine hornbill species occur in the tropical and sub-tropical forests of north-east India, where hunting is a major threat to hornbills. These include the Great *Buceros bicornis*, Rufous-necked *Aceros nipalensis*, Wreathed *Rhyticeros undulatus*, White-throated Brown *Ptilolaemus austeni* and Oriental Pied Hornbill *Anthracoceros albirostris*. IUCN has classified Rufous-necked Hornbill as 'Vulnerable' and Great and White-throated Brown Hornbills as 'Near Threatened.' A few Protected Areas in north-east India have been identified as important sites for hornbill populations [1, 13]. However, information on hornbill densities is available only from two sites in Arunachal Pradesh [14, 15]. Abundances of White-throated Brown Hornbill have not been estimated in India, where its distribution is restricted to eastern Arunachal Pradesh, Nagaland, Mizoram, and eastern Meghalaya in north-east India, although encounter rates for the species were estimated from Namdapha Tiger Reserve [16].

In this study, we present estimates of hornbill densities obtained by sampling in four sessions (years) from 2009 – 2012, with a large sampling effort (total effort = 842.1 km) in Namdapha Tiger Reserve. We also compare densities of four hornbill species in both space (three sampling areas varying in elevational range) and time (between months). These density estimates serve as useful baselines for understanding spatiotemporal variation in densities of four hornbill species, monitoring future population trends, and devising conservation strategies for hornbill species in the landscape. We also highlight the importance of Namdapha Tiger Reserve as a globally significant site for conservation of hornbill species, especially the 'Vulnerable' Rufous-necked hornbill.

Methods

Study Area

The study was carried out in Namdapha Tiger Reserve (27°23'30" – 27°39'40"N and 96°15'2" – 96°58'33"E) in Changlang district of Arunachal Pradesh state in north-east India. It is located in the easternmost part of the Eastern Himalaya Biodiversity Hotspot adjoining the Indo-Myanmar Biodiversity Hotspot [17]. The reserve area is 1,985 km² with elevation ranging from 200 – 4,571 m above sea level. Namdapha Tiger Reserve is contiguous with Kamlang Wildlife Sanctuary to the north, Reserved Forests of Jairampur Forest Division to the south and south-west, and Unclassed State forests of Vijaynagar to the east (Fig. 1a). The Noa Dihing River, tributary of the River Brahmaputra, flows from east to the west of the park.

The reserve harbors the world's northernmost tropical rainforests [18]. The vegetation in the park shows transition from tropical and subtropical broad-leaved forest to pine forests, temperate broad-leaved forests, alpine meadows and perennial snow across the elevation gradient. We conducted this study in the lower elevations (below 1,500 m) of the reserve. *Dipterocarpus macrocarpus*, *Shorea assamica* (Dipterocarpaceae), *Terminalia myriocarpa* (Combretaceae), *Altingia excelsa* (Hamamelidaceae), *Schima wallichii* (Theaceae), *Beilschmiedia assamica* (Lauraceae), *Baccaurea sapida* (Euphorbiaceae), *Castanopsis* spp. (Fagaceae) and *Saprosma ternatum* (Rubiaceae) are the dominant tree species in lower elevations.

Five species of hornbills occur in the reserve: the Great, Rufous-necked, Wreathed, White-throated Brown and the Oriental Pied Hornbill. We sampled mainly in the non-breeding season (November to April). The breeding season of hornbills in Arunachal Pradesh is from March-end to early August [19], while in eastern Arunachal Pradesh, breeding commences only in mid- to late April [16]. We sampled in two phases. We carried out Phase I of the sampling (January 2009 – April 2009, November 2009 – April 2010) in three areas (Hornbill Plateau, Ranijheel area and the 58-75 mile area) (Fig. 1a and Table 1), and Phase II (November 2010 – March 2011, December 2011- February 2012) only on the Hornbill Plateau (Fig. 1b and Table 1). Although Hornbill Plateau and Ranijheel area are approximately 5 km (linear distance) apart, we classify them separately because of elevational differences between the two areas (Table 1). We did not classify the trails into different strata based on elevation because some of the trails, especially in the 58 – 75 mile area, spanned a wide elevation gradient starting from 750 to beyond 1,000 m. Hornbill Plateau, where sampling was carried out in both the phases, covers an area of ~15 km² near the western border of the Namdapha, north of the Noa Dihing River. The elevation on the Hornbill Plateau ranges from 550 – 810 m. The Ranijheel area is to the east of the Hornbill Plateau. The elevation of the trails in the Ranijheel area ranges from 780 – 1,450 m ASL. The 58 – 75 mile area is to the south of Noa Dihing River and to the east of the Ranijheel area. The elevation in the 58 – 75 mile area ranges from 710 – 1,310 m (Fig 1a). The terrain of the Hornbill Plateau is relatively flat, while in the Ranijheel area, it is more undulating and hilly, and more steep and hilly in the 58 – 75 mile area. We accessed all the sampling sites on foot.

People living in and around Namdapha Tiger Reserve belong to four different tribal communities. There are Lisu settlements outside the eastern border of the park and in some locations inside the park (Fig. 1a). Chakma, Tangsa and Miju Mishmi settlements are outside the western and south-western boundary of the reserve.

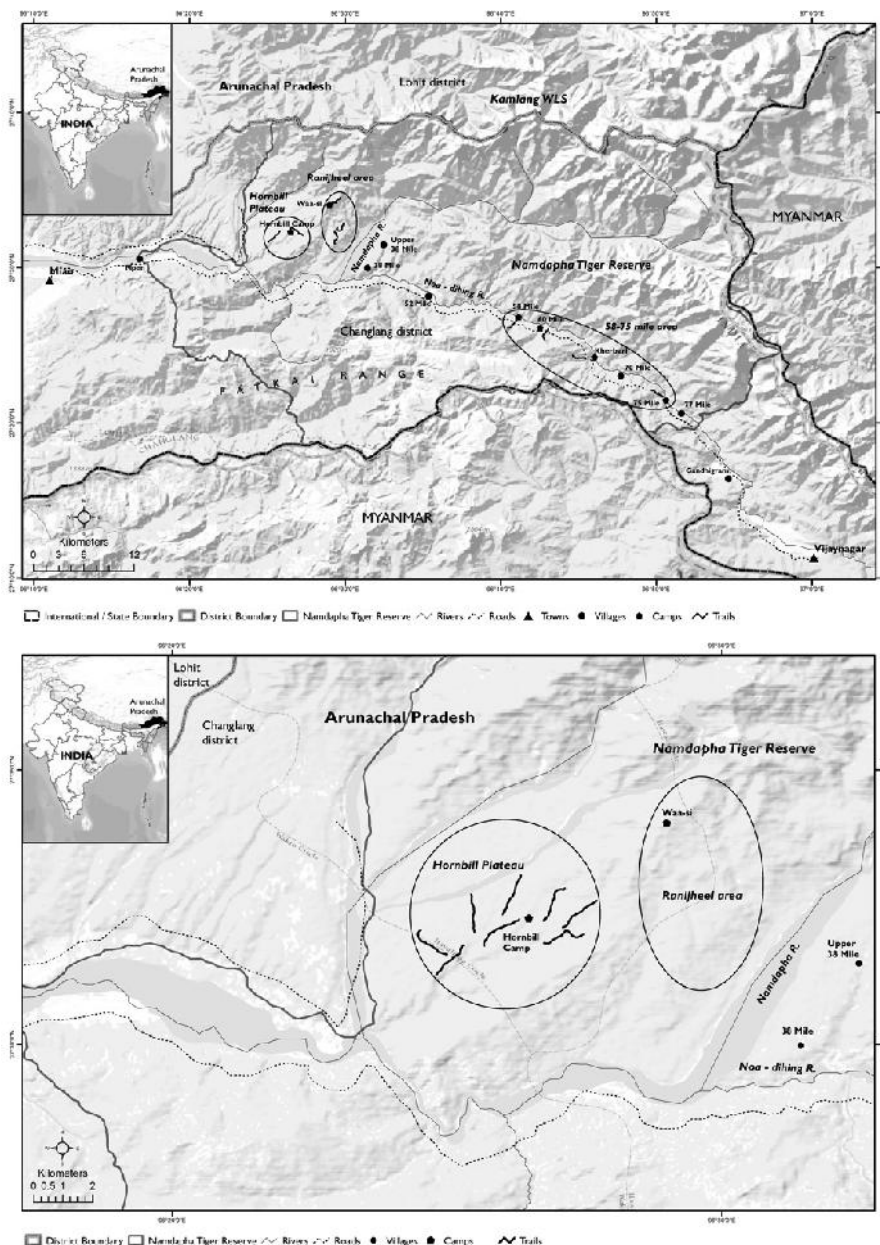


Fig. 1a. Map of the Namdapha Tiger Reserve showing the three sampling areas (enclosed circle/ellipse) with the trails that were sampled during January 2009 – April 2010 (see Methods section for additional details). The map also shows the different Lisu (local community) settlements inside the Tiger Reserve.

Fig. 1b Map focusing on the western portion of the Namdapha Tiger Reserve showing the eight trails that were sampled during November 2010 – February 2012 (see Methods section for additional details) and the Hornbill Camp which served as our base during the period of the study.

Distance Sampling

We used variable-width line transect surveys for sampling hornbills [20]. One or two observers walked each trail in the mornings (0500 – 1100 hr) and/or in the afternoons (1300 – 1700 hr). The average speed of walk was 1.5 km/hr. We recorded species identity, number of individuals, and the perpendicular distance to the centre of the flock following standard line transect protocol [20]. Distances were measured with a Bushnell Rangefinder (Sport 450).

Phase I

In Phase I, we sampled along nine trails (Fig. 1a and Table 1) including two trails on the Hornbill Plateau, three trails on the Ranijheel area, and four trails in the 58 mile – 75 mile area (Table 1). Two of these trails (Waa-si and 75 mile trail) were sampled only from January till April 2009, due to logistic constraints in accessing the sites regularly. We replaced these two trails by two other trails (58 mile and 61 mile) in the same elevation range for sampling from November 2009 – April 2010. The length

of the trails varied from 1.5 – 2 km. In Phase I, the total sampling effort was 470.1 km and the sampling effort along each trail varied from 20 – 86 km (Table 1).

Table 1 Details (elevation, sampling duration, trail length and effort along each trail) of the sampled sites inside Namdapha Tiger Reserve. Sampling in Phase I was carried out from January 2009 – April 2010 and in Phase II was carried out from November 2010 – February 2012.

Region	Trail name	Elevation range (m)	Sampling Duration	Trail length (km)	Effort (km)
Phase I					
58-75 mile area	75 mile	1060 - 1310	Jan-Apr 2009	1.8	25.2
58-75 mile area	65 mile	960 - 1300	Jan-Apr 2009; Feb-Apr 2010	2	38
58-75 mile area	61 mile	720 - 1250	Feb-Apr 2010	2	20
58-75 mile area	58 mile	710 - 860	Feb-Apr 2010	2	20
Ranijheel area	Waa-si	1310 - 1450	Jan-Apr 2009	1.5	33
Ranijheel area	Rajajheel	890 - 950	Jan-Apr 2009; Nov 2009-Apr 2010	2	84
Ranijheel area	Ranijheel	780 - 905	Jan-Apr 2009; Nov 2009-Apr 2010	1.7, 2*	83.9
Hornbill Plateau	Bulbulia	670 - 720	Jan-Apr 2009; Dec 2009-Mar 2010	2	80
Hornbill Plateau	Hornbill	580 - 610	Jan-Apr 2009; Nov 2009-Apr 2010	2	86
				Sub-total	470.1
Phase II					
Hornbill Plateau	1	600 - 650	Nov 2010-Mar 2011; Dec 2011-Feb 2012	1.5	46.5
Hornbill Plateau	2	630 - 670	Nov 2010-Mar 2011; Dec 2011-Feb 2012	1.5	52.5
Hornbill Plateau	3	580 - 620	Nov 2010-Mar 2011; Dec 2011-Feb 2012	1.5	40.5
Hornbill Plateau	4	550 - 590	Nov 2010-Mar 2011; Dec 2011-Feb 2012	1.5	43.5
Hornbill Plateau	5	650 - 750	Dec 2010-Mar 2011; Nov 2011-Feb 2012	1.5	49.5
Hornbill Plateau	6	700 - 810	Nov 2010-Mar 2011; Nov 2011-Feb 2012	1.5	48
Hornbill Plateau	7	650 - 750	Nov 2010-Mar 2011; Dec 2011-Feb 2012	1.5	45
Hornbill Plateau	8	580 - 600	Nov 2010-Mar 2011; Dec 2011-Feb 2012	1.5	46.5
				Sub-total	372
				Total Effort	842.1

* This trail was extended from 1.7 km to 2 km in the sampling session of November 2009 - April 2010.

Phase II

In Phase II, we sampled along eight trails on the Hornbill Plateau (Fig. 1b). The minimum distance between two trails was 500 m, except for two trails that were 300 m apart. Each trail was 1.5 km long. We ensured that no two adjacent trails were walked simultaneously. The total sampling effort during Phase II was 372 km and the total effort along each trail varied from 40.5 – 52.5 km (Table 1).

The total sampling effort for the entire study duration (January 2009 – February 2012) was 842.1 km.

Analysis

Program DISTANCE (ver. 6.0) was used to estimate the densities of four hornbill species [21]. We had only a single detection of the Oriental Pied Hornbill in 842.1 km of sampling effort, which precluded density estimation of this species. We used only direct sightings of perched birds for the DISTANCE analysis. We inspected distance data to detect heaping and outliers. We manually grouped the distance data into intervals for analysis. Sightings were entered as ‘clusters.’ We used size-bias regression ($p = 0.15$) to control for influences of varying flock sizes on detectability. We used standard combinations of series expansion (half-normal, uniform, hazard-rate) and key functions (cosine, simple polynomial and hermite polynomial) [22]. We compared density estimates of the four hornbill species in 1) the three sampling areas (58-75 mile, Ranijheel area and Hornbill Plateau), and 2) three sampling time (months) intervals (November-December, January-February and March-April). Since we had 10 trails for the different analyses, we estimated variance by assuming the distribution of the variance estimate as poisson with overdispersion factor 2 [23]. Since we had less than 40 detections in each of the strata in the two analyses (sampling areas and months) for all species, we estimated the detection probability and cluster size by pooling data from all the strata [23]. We estimated the overall density for each hornbill species in the three sampling areas by taking the mean of stratum estimates weighted by the total effort in the stratum.

Results

Overall density estimates

In 842.1 km of total sampling effort, we sighted 79 flocks of Great Hornbill, 188 flocks of Rufous-necked Hornbill, 150 flocks of Wreathed Hornbill and 41 flocks of White-throated Brown Hornbill (Table 2).

The mean flock size varied from 2.3 birds for the Great Hornbill to 8.2 birds for the White-throated Brown Hornbill (Table 3). The detection probability ranged from 0.34 for Great Hornbill to 0.59 for Rufous-necked Hornbill (Table 3). The overall mean density of Wreathed Hornbill was the highest (16.1 birds/km²) followed by White-throated Brown Hornbill (7.9 birds/km²), Rufous-necked Hornbill (6.9 birds/km²) and Great Hornbill (3.9 birds/km²) (Fig. 2, Table 3).

Monthly variation in hornbill densities

Mean Wreathed Hornbill density declined from 68 birds/km² in November-December to ~ 1 bird/km² in March-April (Fig. 3; Table 2 and Table 3). Though Great Hornbill density also exhibited fluctuations among months, they continued to be present on the Hornbill Plateau. The mean density of Great Hornbill was lower in January-February (2.1 birds/km²) than in November-December (12.7 birds/km²), but it increased again in March-April (5.4 birds/km²) (Table 3). On the other hand, densities of Rufous-necked and White-throated Brown Hornbill were comparable (Fig. 3; Table 3) among the months (November-December, January-February and March-April).

Table 2 Summary of the total effort (km) and number of detections of the four hornbill species in each of the strata across the different months (monthly variation), and across the three sampling areas (spatial variation).

Months	Effort (km)	Great Hornbill	Rufous-necked Hornbill	Wreathed Hornbill	Brown Hornbill
November-December	134.5	41	23	106	12
January-February	260	13	58	33	12
March-April	143.5	20	29	2	15
Total	538	74	110	141	39
Sampling sites					
Hornbill Plateau (550 – 810 m)	538	74	110	141	39
Ranijheel area (750 – 1450 m)	200.9	5	55	9	2
58-75 mile (710 – 1310 m)	103.2	0	23	0	0
Total	842.1	79	188	150	41

Spatial variation in hornbill densities

There was considerable variation in hornbill detections among the three study areas (Table 2). In the 58-75 mile area, we did not detect three hornbill species (Great, White-throated Brown and Wreathed Hornbill), while we sighted 23 flocks of Rufous-necked Hornbills there (Table 2). The densities of the Rufous-necked Hornbill were comparable among the three sampling areas (Fig. 4 and Table 3). The mean densities of Great and White-throated Brown Hornbills on the Hornbill Plateau were 5 and 7 times that in the Ranijheel area (Fig. 4 and Table 3). The estimates of Wreathed Hornbill densities were highest on the Hornbill Plateau. We have opportunistically observed Wreathed Hornbills in the 58-75 mile area in the months of November-January.

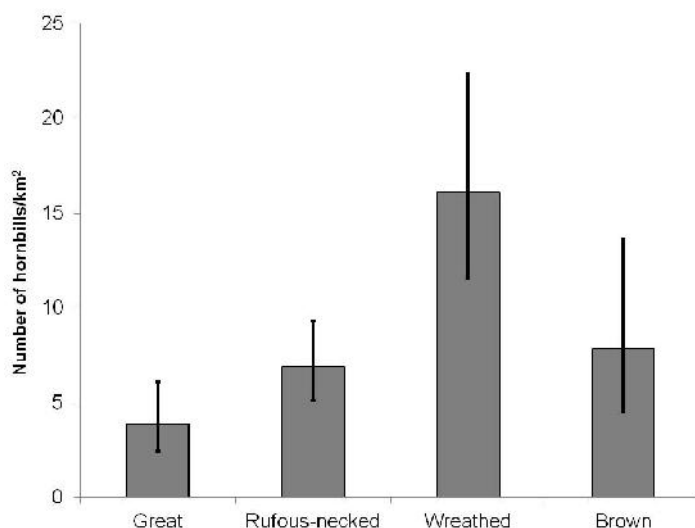


Fig. 2. Overall mean (95% CI) densities of the four hornbill species (Great, Rufous-necked, Wreathed and White-throated Brown Hornbill) in Namdapha Tiger Reserve.

Discussion

Our study demonstrates that Namdapha Tiger Reserve harbours high densities and potentially large populations of four hornbill species, especially the Vulnerable Rufous-necked Hornbill (Fig. 5) and the Near Threatened Great and White-throated Brown Hornbills (Fig. 5) during the non-breeding season from November – April. Wreathed Hornbills (Fig. 5) seasonally visit the area, with densities peaking in months of November and December. The lower elevation forests of the Hornbill Plateau had higher mean densities of the Great and White-throated Brown Hornbills than the higher elevation areas of Ranijheel and the 58-75 mile area.

Table 3 Summary of the mean and 95% Confidence Intervals (CI) of the flock size, detection probability and density of the four hornbill species (Great, Rufous-necked, Wreathed and White-throated Brown Hornbill) across months and sampling areas.

	Mean and 95% Confidence Intervals			
	Great Hornbill	Rufous-necked Hornbill	Wreathed Hornbill	White-throated Brown Hornbill
Flock size	2.3 (1.8-3)	1.7 (1.5-1.9)	5.5 (4.7-6.6)	8.2 (6.4-10.6)
Detection probability	0.34 (0.27-0.42)	0.59 (0.5-0.7)	0.49 (0.42-0.58)	0.51 (0.4-0.66)
Overall density (birds/km ²)	3.9 (2.4-6.1)	6.9 (5.1-9.3)	16.1 (11.6-22.4)	7.9 (4.5-13.7)
Month: Nov-Dec (birds/km ²)	12.7 (7.3-22.2)	4.6 (2.5-8.5)	68 (48.3-95.9)	14 (6-32.9)
Month: Jan-Feb (birds/km ²)	2.1 (0.9-4.8)	6.3 (4.2-9.6)	10.8 (6.3-18.4)	7.3 (3.1-17)
Month: Mar-Apr (birds/km ²)	5.4 (2.6-11.1)	5.5 (3.2-9.6)	1.3 (0.2-6.6)	16.4 (7.5-36)
Area: Hornbill Plateau (birds/km ²)	5.7 (3.6-9)	6.5 (4.6-9.1)	24 (17.2-33.5)	11.7 (6.7-20.5)
Area: Ranijheel (birds/km ²)	1.1 (0.3-3.5)	8.2 (5.3-12.8)	3.3 (1.2-8.9)	1.6 (0.3-8.6)
Area: 58-75 mile (birds/km ²)	0 (0-0)	6.6 (3.5-12.4)	0 (0-0)	0 (0-0)

Throughout Asia, only 7% of forests inhabited by hornbills are under Protected Status, and the average size of these Protected Areas is ~ 350 km² [4]. The geographical extent and connectivity with other Protected Areas and forests in India and Myanmar make Namdapha Tiger Reserve one of the most important areas for hornbill conservation in Asia. The mean densities of the Rufous-necked Hornbill in our study areas were almost twice that of Huai Kha Khaeng Wildlife Sanctuary of Thailand (Appendix 1), a site well known for high densities of Rufous-necked Hornbills [24]. Given the high densities of this species (6-8 individuals/km²) throughout the three sampling sites and more than 1,000 km² of potential habitat (forests below 2,000 m; Fig. 5d), Namdapha harbours a sizeable chunk of the global Rufous-necked Hornbill population. It has been estimated that there has been a 30% decline in the global population size of this species (IUCN 2012). However, based on the results of our study and surveys from Arunachal Pradesh [14], the global population of Rufous-necked Hornbill may need to be revised.

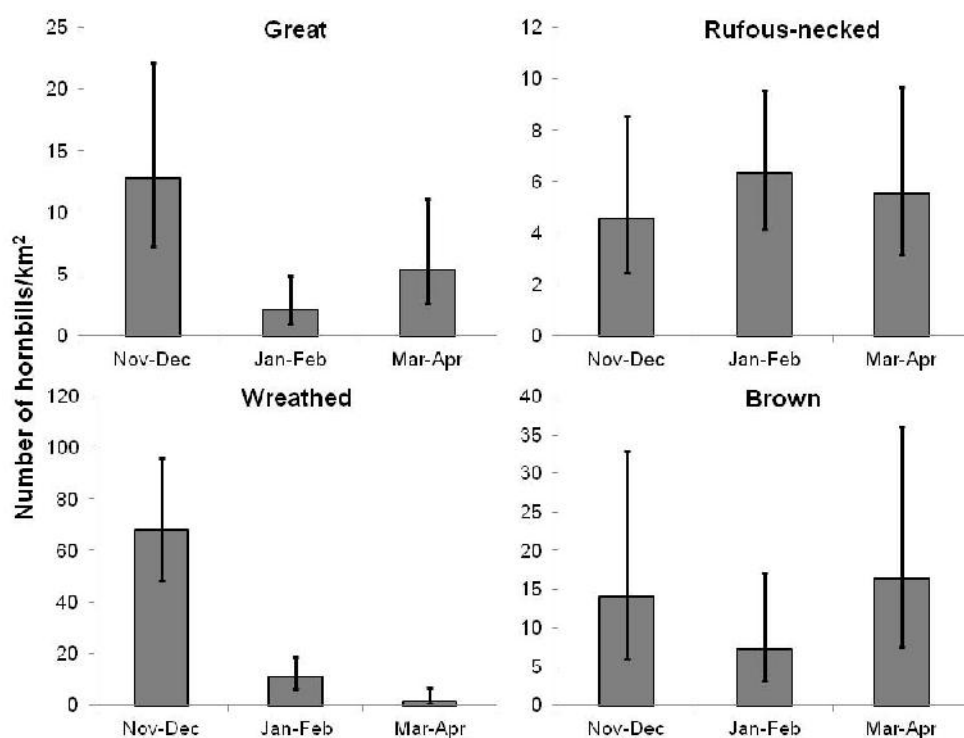


Fig. 3. Mean (95% CI) monthly densities of the four hornbill species (Great, Rufous-necked, Wreathed and White-throated Brown Hornbill) across the months for all sampling sessions (November-December, January-February and March-April).

This is the first study to estimate the density of White-throated Brown Hornbill, although there is limited information on the species' presence in other states of north-east India [25-27]. Namdapha and the adjoining Kamlang Wildlife Sanctuary are the only two Protected Areas in Arunachal Pradesh where the species occurs. Given 450 km² of area in Namdapha which is below 1,000 m ASL, Namdapha potentially harbours a sizeable population of this species.

Mean Great Hornbill density in Namdapha was one-third of that in Pakke Tiger Reserve in western Arunachal Pradesh [15], but still comparable to other sites in Western Ghats, India [10] and Thailand [24]. Great hornbill densities are possibly higher in Pakke Tiger Reserve due to the greater extent of suitable lowland forest habitat, high fig and nest tree densities, and better protection.

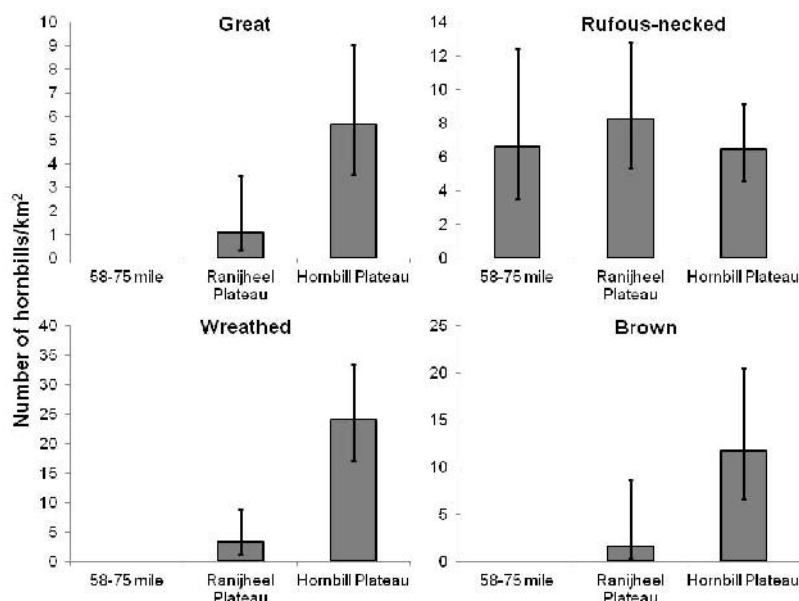


Fig. 4. Mean (95% CI) densities of the four hornbill species (Great, Rufous-necked, Wreathed and White-throated Brown Hornbill) across the three sampling areas (58-75 mile area (710-1350 m), Ranijheel area (780-1450 m), Hornbill Plateau (550-810 m)).

The mean densities of Wreathed Hornbills were comparable in Namdapha and Pakke Tiger Reserves and were generally higher than those reported from other studies (Table 3), except in East Kalimantan [Leighton (1982) as cited in 28]. The aptly named Hornbill Plateau had mean combined hornbill densities of 100 individuals/km² in November-December (Table 3). Apart from two studies [3, 29], which report peak combined densities of 84 individuals/km² and 82 individuals/km² from Sulawesi and Borneo respectively, there are no other reports of such high combined densities of hornbills throughout the range of hornbills in Asia, making Namdapha a globally significant site for ensuring long-term conservation of hornbills.

The monthly density of hornbill species on the Hornbill Plateau varied depending on the hornbill species. Wreathed Hornbill densities peaked in November-December and gradually declined until March-April, before the onset of the breeding season. There are no reports of Wreathed Hornbills breeding inside Namdapha [16]. This is also corroborated by information from local tribes. As in other sites, where they are known to breed in the lowland forests [19], they probably breed in the lowland forests in Lohit District in Arunachal Pradesh, Assam or adjoining Myanmar. It is important to identify the breeding sites and the movement routes of the large wintering population of Wreathed Hornbills. Hornbill densities have been documented to fluctuate with food availability [3]. In lowland forests of western Arunachal Pradesh, the density of hornbill food plant trees in the non-breeding season was one-third that of the breeding season [30]. The Wreathed Hornbills seasonally move to the higher elevations during the non-breeding season [30]. We are probably observing a similar pattern in eastern Arunachal Pradesh, where Wreathed Hornbills, which range over much larger areas (> 170 km²) [24, 31], are probably tracking fruits across a wide elevation gradient (~100 m – 2000 m), unlike the Rufous-necked Hornbill and the sedentary White-throated Brown Hornbill, both of which range over much smaller areas (Rufous-necked Hornbill: 25 km² and White-throated Brown Hornbill: 4.3 – 5.9 km²) [13, 31, 32] and whose monthly densities were comparable. Wreathed hornbills have been recorded in large numbers in the higher elevations of Namdapha (up to 2,000 m) [16, 26]. Our estimates of Wreathed Hornbill densities in the 58-75 mile area are likely to be underestimates, as we were unable to sample during November – December due to logistical constraints.

Great Hornbill density did not exhibit clear trends like the Wreathed Hornbills, but showed monthly fluctuations with highest mean densities in November-December. Like the Wreathed Hornbill, this species is also known to range over large distances (up to 135 km²) [2, 31] probably tracking patchily distributed fruiting figs.

Our study shows that densities of at least two hornbill species (Great and White-throated Brown Hornbill) varied across the elevation gradient (500 – 1450 m) in Namdapha. In north-east India, Great and White-throated Brown Hornbill are common in the lower elevation forests below 1,000 m [8, 15, 16]. The densities of these two species were lower in the higher elevation areas of Ranijheel Plateau and the 58-75 mile area. Since 2003, we have had opportunistic sightings or have heard calls of the Great (seen once and heard twice) and Brown Hornbills (seen on one occasion) in the 58-75 mile area outside distance sampling, indicating that they occur in extreme low densities in this area. The reasons for the absence of these two species from higher areas of Namdapha remain unclear. Densities of Rufous-necked Hornbill were comparable among all the three sampling sites that are spread along a 1,000 m elevation gradient (500-1,450 m). This species is known to prefer the higher elevation areas [1, 13].

Most hornbill species still persist, albeit in lower abundances, outside Protected Areas in Arunachal Pradesh [14]. Protected Areas like the Namdapha Tiger Reserve that harbour hornbill populations at relatively high densities, can potentially serve as a source for adjoining unprotected areas, which experience logging and higher hunting pressures and have low hornbill densities. Given that most

hornbill species are highly mobile and range widely, greater abundances of hornbills inside Protected Areas would also result in greater probability of movement of hornbills between forest areas, resulting in greater rates of seed dispersal and potentially enhanced regeneration of degraded non-protected forests [33].



Fig. 5. Hornbills of Namdapha Tiger Reserve and aerial views of the forest landscape inside the reserve – a) a male Rufous-necked Hornbill, b) A male White-throated Brown Hornbill, c) Flock of Wreath hornbills. Photo credits: Aparajita Datta, Ramki Sreenivasan/Conservation India and Kalyan Varma.

Implications for Conservation

Namdapha is among the globally important sites for conservation due to the high densities of the four sympatric hornbill species, including the Rufous-necked Hornbill (Fig. 5), a species considered 'Vulnerable' by IUCN. Our study highlights the importance of determining spatial and temporal patterns in abundance of hornbill species, because these data can uncover seasonal movements and highlight the need for protection of lowland sites where breeding of certain species like Wreathed Hornbill likely occurs.

Namdapha is known for its high species richness and biodiversity values and is protected in part by natural barriers due to steep terrain. However, it is a Protected Area that is under varied human pressures, which has resulted in park-people conflict, and is poorly managed [34]. From the late nineties there has been a gradual increase in settlements within Namdapha. Forest patches are being cleared for settlements and paddy cultivation (Fig. 5). There is a need for a resolution of the conflict with the local community and better management to ensure that the forests remain intact and continue to harbour hornbill populations in the future. The area around Namdapha is also undergoing rapid transformation from once-forested habitats to settlements, plantations and degraded forests [35, 36]. In addition, the abundance of most vertebrate groups (especially ungulates, large carnivores) is low due to hunting within the park [37]. Hornbills are the only large vertebrate group that occurs in high densities, possibly because they are not targeted for hunting by the particular tribal groups that access the park. Therefore, the value of the hornbill populations inside Namdapha, especially of the more threatened species like the Rufous-necked and White-throated Brown Hornbill, needs to be highlighted.

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Appendix 1. Summary of the mean density estimates of the four hornbill species from several studies across South and South-east Asia. 'na' represents data not available due to natural absence of the species at the site or inability to estimate densities due to low sample sizes.

No.	Site	Mean (95% CI) number of hornbills/km ²				Source
		Great Hornbill	Rufous-necked Hornbill	Wreathed Hornbill	Austen's Brown Hornbill	
1	Namdapha Tiger Reserve, Arunachal Pradesh, India	3.9 (2.5-6.1)	6.9 (5.1-9.3)	16.1 (11.6-22.4)	7.9 (4.5-13.7)	This study
2	Namdapha Tiger Reserve, Arunachal Pradesh India	1.9 (0.6-6.1)	4.39 (2.4-7.7)	2.9 (1-8.35)	na	*Naniwadekar et al. accepted [14]
3	Pakke Tiger Reserve, Arunachal Pradesh, India	11.95 (7.9-18.1)	na	15.14 (10-23)	na	Dasgupta & Hilaluddin [15]
4	Anamalai Tiger Reserve, Western Ghats, India	3.4 & 9.55	na	na	na	Raman & Mudappa [10]
5	Anamalai-Parambikulam Region, Western Ghats, India	1.74 (1.08-2.8)*	na	na	na	Mudappa & Raman [38]
6	Hala Bala Wildlife Sanctuary, Thailand	0.12 (0.08-0.19)	na	0.69 (0.4-1.18)	na	Gale & Thongaree [28]
7	Huai Kha Khaeng Wildlife Sanctuary, Thailand	5.279 (3.39-8.23)	3.69 (2.15-6.33)	11.47 (5.33-24.66)	2.76 (1.14-6.73)	Jomburom et al. [24]
8	Budo Sungai Padi National Park, Thailand	3	na	5	na	Chantarat et al. [39]
9	Thailand	1.88	na	na	na	Poonswad et al. [40]
10	Sungai Tekam, Pahang, Malaysia	na	na	0.7	na	Johns [9]
11	E. Kalimantan, Indonesia	na	na	10-46	na	Leighton [29]
12	Barito Ulu, Central Kalimantan, Indonesia	na	na	0.1	na	McConkey & Chivers [41]
13	Sabah, Malaysia	na	na	3.7	na	Payne and Davies [42]
14	Eukit Barisan Selatan National Park, Sumatra, Indonesia	na	na	7.5	na	Anggraini et al. [43]

* Naniwadekar et al. accepted reported hornbill densities based on 189.9 km of effort from January 2008-April 2009.