

INSIGHTS

Roost site use by Great (*Buceros bicornis*) and Wreathed (*Rhyticeros undulatus*) Hornbill and its implications for seed dispersal

Rohit Naniwadekar¹  | Akanksha Rathore^{1,2} | Ushma Shukla^{1,3} | Aparajita Datta¹

¹Nature Conservation Foundation, Mysuru, Karnataka, India

²Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, India

³INRAE Val de Loire, Research Unit-Forest Ecosystems, Nogent-sur-Vernisson, France

Correspondence

Rohit Naniwadekar, Nature Conservation Foundation, 1311, Amritha, 12th Main, Vijayanagar 1st Stage, Mysuru, Karnataka, India 570017.

Email: rohit@ncf-india.org

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Abstract

We examined roost selection by hornbills using telemetry data and determined its implication for seed dispersal. Roost selection was not influenced by nest/foraging sites. Wreathed Hornbill roosts were mostly close to the river. Hornbills dispersed only 10% of seeds at roosts, but dispersal distances of those seeds were longer.

KEYWORDS

frugivory, GPS telemetry, north-east India, seed dispersal distance

1 | INTRODUCTION

Several terrestrial vertebrates spend a significant part of their life at roosts. Roost selection may be influenced by access to food resources (Johnston-González & Abril, 2019), preference for specific habitats (Zoghby et al., 2016), predation pressure (Bock et al., 2013), or anthropogenic disturbance (Peters & Otis, 2007).

Knowledge about roost selection can have implications for understanding the ecological role played by animals. For example, some frugivorous animals have been reported to clump-disperse seeds at their roosts that are used repeatedly (Datta, 2001; Howe, 1989; Kitamura et al., 2008). Clump-dispersed seeds at communal roosts that are repeatedly used experience high mortality due to negative density dependence (Comita et al., 2014; Datta, 2001; Kitamura et al., 2008). However, if clump-dispersed seeds at roost

sites form only a small proportion of seeds that are dispersed by the frugivore, it may not significantly alter the overall contribution of the frugivore to seed dispersal. Relative proportions of seeds that get dispersed at favorable and unfavorable sites by animals are typically not estimated (Naniwadekar et al., 2019b). This is critical for determining the quantitative and qualitative role of frugivores in seed dispersal (Schupp, 1993).

Hornbills are key avian seed dispersers with interesting roosting ecology. They may roost as singles, in pairs, smaller flocks, or in large communal roosts (up to 2,000 birds) (Poonswad et al., 2013). A telemetry study on Southern Ground Hornbills (*Bucorvus leadbeateri*) in South Africa revealed that the birds preferred riverine habitat for roosting and exhibited site fidelity (Zoghby et al., 2016). In north-east India, hornbills roost on isolated trees, in open riverine grassland areas or on cliff faces with lower tree density, and they exhibit

seasonal differences (Datta, 2001). Given the unique breeding biology of hornbills (Kemp, 1995), nest location can also be expected to influence roosting patterns of birds in the breeding season. Foraging areas may also influence the roosting patterns of frugivorous hornbills because they feed on fruits that usually have patchy distribution (Naniwadekar et al., 2015). Given their unique breeding biology and predominantly frugivorous diet, it is interesting to determine the role of nest and foraging sites in roost site selection. Hornbills mostly scatter dispersed seeds during diurnal foraging (Naniwadekar et al., 2019b, 2021), and relatively, a smaller proportion of seeds can be expected to be clump-dispersed at roost sites.

This study describes the roosting ecology of the Great (*Buceros bicornis*) and Wreathed Hornbill (*Rhyticeros undulatus*) and determines the implication of roosting patterns for seed dispersal. To this end, we (a) describe the patterns of roost site use by four Great Hornbills and one Wreathed Hornbill; (b) explore whether the riverine habitats, nest, and foraging range influences roost site use; and (c) determine the relative percentage of seeds that are dispersed by hornbills at roost and non-roost sites and the dispersal distances of these seeds using simulations. Given the unique breeding biology of the hornbills, we predicted that roosting patterns of hornbills would vary across seasons, and the proportion of seeds dispersed at roost sites will be relatively small.

2 | METHODS

We conducted the study in Pakke Tiger Reserve (area: 861.9 km²; 92°36'–93°09' E and 26°54'–27°16' N) in north-east India. We used GPS tags (Model 'Bird 1A'; e-obs GmbH; Germany) to obtain movement information from four adult, male Great Hornbills (2.2–4 kg) and one adult, male Wreathed Hornbill (1.4–3.7 kg) between October 2014 and May 2016 (Poonswad et al., 2013). Two of the four Great Hornbills (GH3Br and GH4Br) and the Wreathed Hornbill (WH1Br) were breeding individuals. Additional details on study area and tagging methods are in the Supplementary Material and Naniwadekar et al. (2019b).

We used the location of hornbills at 1900 h as the roost location for the day since the mean displacement distances (straight-line distances) between consecutive time points (time interval = 15 min) were shortest for that time (1900 h) for the five hornbills (mean (range) = 23 m (17.9–31.2 m)). This was at least 7.5 times less than displacement distances during the daytime (mean (range) = 172 m (75.5–428 m)). We also calculated the mean displacement distances (straight-line distance) between roosts on consecutive days.

We used hierarchical cluster analysis with complete linkage method implemented through the "stats" package in R (ver. 3.5.3) to identify the cluster of points that were within 200 m from each other (R Core Team, 2019). We considered all roost locations within 200 m of each other as a single "roost site," and the centroid of the locations within 200 m of each other was assigned a unique roost site code. We determined the number of unique roosting sites used

by individual birds, and the mean and the maximum number of nights the particular roost site was used.

We determined the shortest distance of the roost site from the nest (for the three breeding individuals) and from the river/perennial stream (for all five individuals). We used the kernel density estimation method using the library "adehabitatHR" in R to determine the foraging activity range of the individual birds (Calenge, 2006). We used the default "href" function as the smoothing parameter rather than the least square cross validation (LSCV) method (Watts & Turrin, 2017; Worton, 1995). LSCV method tends to estimate smaller home ranges than the href method. Thus, the roost sites would be more likely to be outside the utilization distributions when using the LSCV method than href method. Utilization distribution is a representation of the relative space used by an individual bird within its entire activity range (Worton, 1989). To determine the foraging activity range of the individual hornbills, we used the locations between 0500 and 1700 h for the three breeding birds and one non-breeding individual (GH5NBr) that was tagged in the breeding season. For the non-breeding Great Hornbill tagged in the non-breeding season (GH2NBr), we used the locations between 0600 and 1600 h since the sunrise and sunset are later and earlier in winters, respectively. We then determined the roost locations with respect to the foraging activity ranges of the hornbills.

We simulated patterns of seed dispersal based on empirical data on roost site locations, foraging patterns, and gut passage time, following Naniwadekar et al. (2019b). We estimated the relative percentage of seeds and the dispersal distances of seeds that were deposited at roost and non-roost (other). In each simulation, we selected a random starting point following the distribution of hornbill visitations on fruiting trees as presented in another study (Naniwadekar et al., 2019b). We excluded roost and nest locations of birds from this starting point selection since they were unlikely to be fruiting trees (Datta, 2001). We integrated the movement information with gut retention time data of five medium- and large-seeded plants (Shukla, Naniwadekar, Rathore, & Datta, 2018, 2019) to determine the end location where the hornbill potentially dispersed the seed. To account for the GPS error and canopy extent of large roost sites, if the end location was within 50 m of the roost location for the same day, then the seed was classified as dispersed at the roost site. We determined the dispersal distances of the seeds by measuring the Euclidean distance between the start location of each seed and the location where it was dispersed (roost and non-roost sites). We used chi-square test for independence and Kruskal–Wallis test for detecting differences in proportions of seeds and dispersal distances of seeds dispersed at roost and non-roost sites. Please see supplementary material, Shukla et al. (2018, 2019) and Naniwadekar et al. (2019b), Naniwadekar et al. (2019a) for additional details on gut passage and movement data and the analytical approach.

3 | RESULTS

The number of days of data available for an individual varied between 19 and 72 days (Table S1). Most of the roost sites were inside

the Pakke and the adjacent Nameri Tiger Reserves (Figure S1). The mean distance between roosts on successive nights for the different Great Hornbills varied between 0.13 and 1.05 km (Table S2). For the Wreathed Hornbill, the mean distance between roosts on successive nights was 1.31 km (Table S2). The maximum distance between roosts on successive nights was greater than 1.18 km for the two non-breeding Great Hornbills and less than 0.71 km for the two breeding Great Hornbills (Table S2).

Roosts of Great Hornbills were generally away from the river bank, but those of Wreathed Hornbill were close to the river (Figure 1). The hornbills did not roost near the nests (Figure 1). All the roost sites of the breeding Great Hornbills (GH3Br and GH4Br) (except one for GH3Br) were outside the 50% kernel density utilization distribution (Figure S2). However, eight of the 11 roost locations of GH2NBr and 16 of the 33 roost locations of the GH5NBr were within the 50% kernel density utilization distribution (Figure S2). For the Wreathed Hornbill, six of the 10 locations were outside the 50% kernel density utilization distribution (Figure S2). All hornbills flew long distances after leaving and before arriving at their roosts in the morning and evening, respectively (Figure S3).

Hornbills dispersed 10% (range: 7–17%) of seeds under the roost trees (Figure 2). The estimated percentage of seeds dispersed under the roost trees for the Wreathed Hornbill was 9% (Figure 2a). The

mean dispersal distances of seeds are longer when they are dispersed at roost sites than non-roost sites (Figure 2b).

4 | DISCUSSION

This study describes the patterns of roost use by Asian Hornbills for the first time and demonstrates the implications of such patterns on seed dispersal. Hornbills used some roosts on multiple occasions highlighting some roost site preference. The choice of roost site by hornbills did not appear to be influenced by their nests or foraging sites. However, the single Wreathed Hornbill consistently used roosts close to rivers. Roosting in open, riverine habitats could accord an advantage by enabling relatively easier detection of potential arboreal mammalian predators. Additionally, the nocturnal, arboreal predators of hornbills, like clouded leopards and binturongs, are less likely to use open habitats along the river (Grassman et al., 2005; Tan et al., 2017).

Simulations (based on the hornbill movement, foraging activity, and gut retention time data) for determining patterns of seed dispersal at roost and non-roost sites indicate that hornbills disperse only a small proportion of seeds at the roost sites. Given that hornbills spend a significant proportion of time foraging in

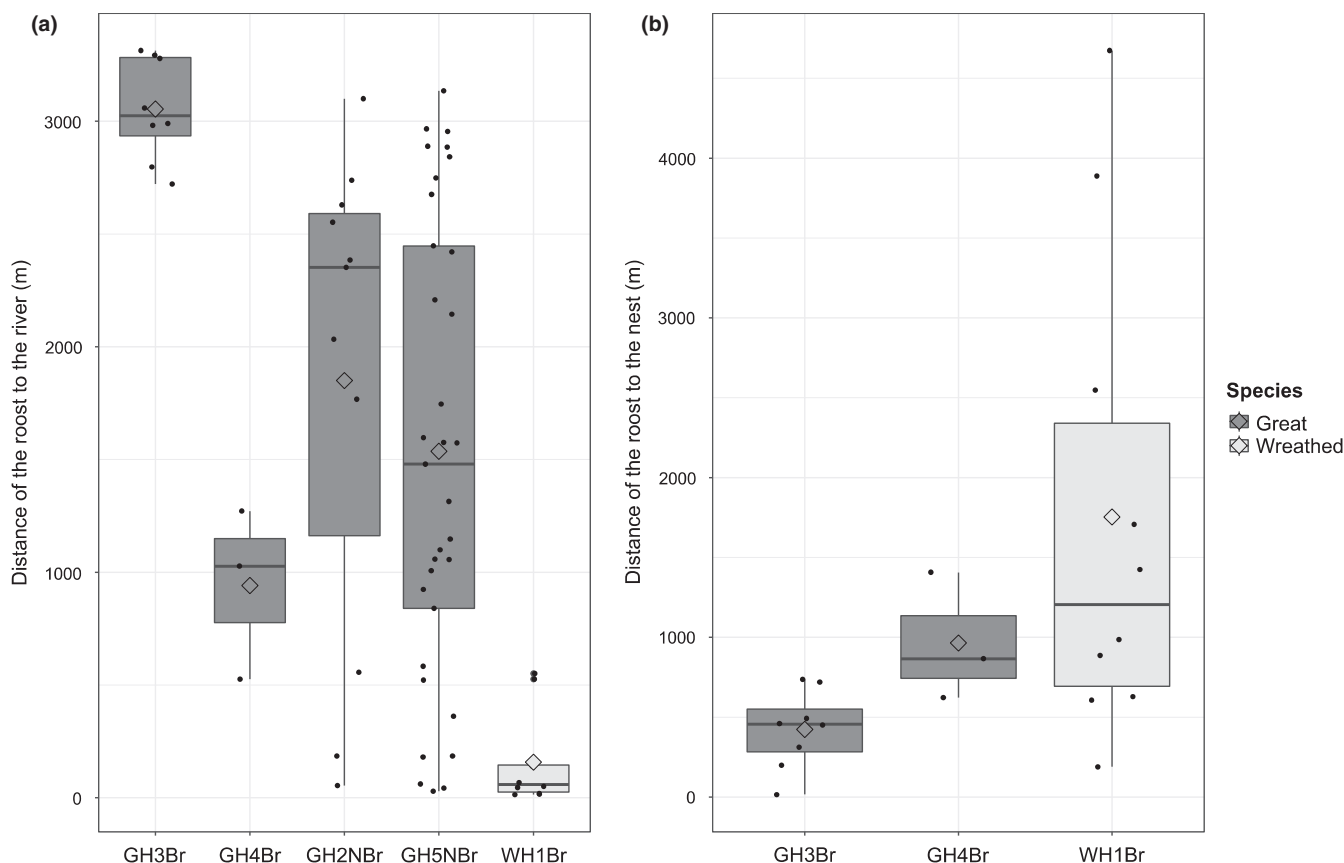


FIGURE 1 (a) Box and whisker plot depicts that the roosts of the Wreathed Hornbill were close to the river while the roosts of Great Hornbills were mostly not near the river. (b) The median distances of roosts from the nest sites were above 400 m for the three breeding hornbills. Black-filled points depict individual data points. Open diamonds depict mean distance. GH indicates Great Hornbill, and WH indicates Wreathed Hornbill. Br indicates breeding birds. NBr indicates non-breeding birds. Numbers are identifiers for individual birds

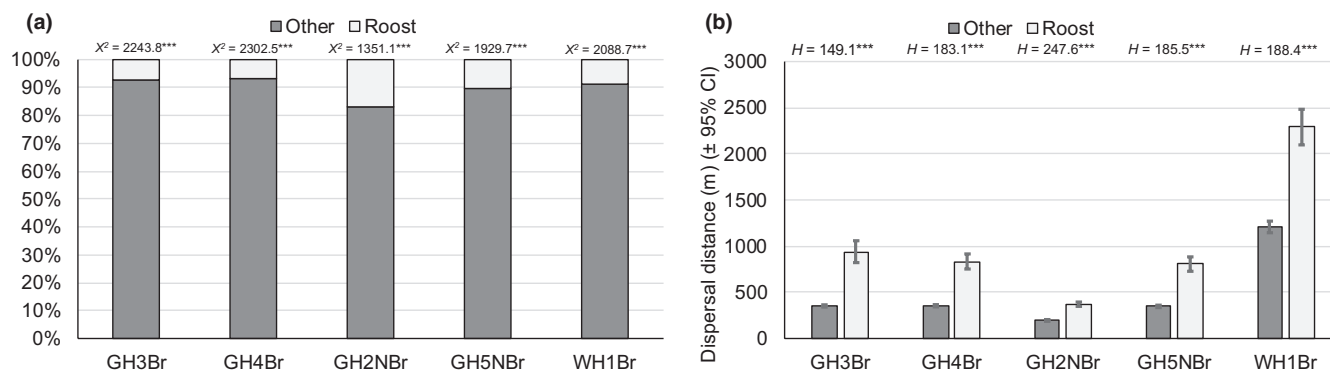


FIGURE 2 (a) Estimated relative percentages of seeds that hornbill dispersed at the roost and non-roost (other) sites. Most of the seeds are dispersed at non-roost sites. (b) Estimated mean (\pm 95% CI) seed dispersal distances when the seed was dispersed at the roost and non-roost (other) sites. Degree of freedom = 1 for the Chi-square test (χ^2) for independence and for the Kruskal–Wallis test (H) and *** denotes $p < .001$. GH indicates Great Hornbill, and WH indicates Wreathed Hornbill. Br indicates breeding birds, and NBr indicates non-breeding birds. Numbers are identifiers for individual birds

the daytime, the bulk of the seeds may be scatter-dispersed away from the roost sites during the daytime (Naniwadekar et al., 2021). Previous studies on clumped dispersal by hornbills at roost sites have been at known communal roosts of hornbills (Datta, 2001; Kitamura et al., 2008). The riverside communal roosts are unsuitable for the establishment of rain forest tree species with hornbill food plant seedlings showing poor survival beyond the first year, and low sapling density and very low tree density of hornbill food plant species likely due to the microsite conditions in these open habitats (Datta, 2001).

Contrary to the Wreathed Hornbill, Great Hornbill roosts were in the forest sites, often away from the river. At least some of these sites were not communal roosts (based on our long-term field observations). Mortality of seeds and seedlings may be lower at these sites than the communal roosts since seeds will not be repeatedly dispersed by hornbills at these sites, indicating that not all roost sites of Great Hornbills may be unfavorable for seedling establishment.

Hornbills are known to mostly carry out long-range seed dispersal (Lenz et al., 2011; Naniwadekar et al., 2019b). Interestingly, the long-flight distances covered by hornbills before arriving at their roost sites resulted in the seed dispersal distances being almost twice as far compared with those seeds dispersed at non-roost sites during the daytime. This long-distance dispersal might be crucial for the maintenance of genetic connectivity between populations of trees and potentially enabling plants to expand their geographic ranges.

Past knowledge on roosting by hornbills has come from direct observations at communal roosts; however, little was known about the roosting patterns of individual hornbills. Despite limited sample sizes, this study has generated novel information on the idiosyncratic roosting patterns of individual hornbills. Given that some of the roost sites may be used for decades, the potential reasons for roost site fidelity need to be identified. This study contributes to current understanding of the context specificity of seed dispersal patterns at roost sites. In future, long-term data on roosting of

multiple hornbill individuals are needed to reveal seasonal patterns in roost use and their implications.

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AUTHOR CONTRIBUTIONS

RN and AD conceived the idea and the study. RN, US, and AR conducted the field work and collected the data. RN and AR analyzed the data. RN wrote the paper. AD critically revised the manuscript. AR and US gave inputs on the manuscript. This work was part of the grants to AD and RN.

ETHICAL APPROVAL

All guidelines for animal care were followed. Ethics clearance was obtained from Nature Conservation Foundation. We followed established methods of the Thailand Hornbill Project team for the tagging of hornbills. Female and juvenile birds were not tagged. Permission for conducting this research was granted by Ministry of Environment and Forest, (F-No. 1-61/2013 WL), National Tiger Conservation

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Movebank Data Repository at <http://doi.org/10.5441/001/1.14sm8k1d> and in Dryad Digital Data Repository at <https://doi.org/10.5061/dryad.5br2q79>.

ORCID

Rohit Naniwadekar  <https://orcid.org/0000-0002-9188-6083>

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SUPPORTING INFORMATION

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