



How far do Asian forest hornbills disperse seeds?

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ABSTRACT

Biotic seed dispersal of plants is a complex phenomenon that is influenced by multiple seed disperser species with implications for plant fitness and range expansions. While inter-species variation has been well-studied, the importance of incorporating intraspecific variation in seed dispersal is increasingly being acknowledged. We compared seed dispersal patterns of breeding and non-breeding great hornbills *Buceros bicornis* and a breeding wreathed hornbill *Rhyticeros undulatus* by combining data on fruiting tree visitations, gut passage time and movement data from tagged hornbills. Seed dispersal probability at nest trees (by breeding males) was low (< 12%) suggesting that males scatter-disperse seeds, unlike breeding females that deposit seeds below nest trees. Median seed dispersal distance of great hornbills was 294 m and 254 m in the breeding and non-breeding season respectively, and, the distribution tail was shorter for breeding birds (2.5 km) than non-breeding birds (13 km). The median and maximum seed dispersal distance by the wreathed hornbill was 1.35 km and 11 km respectively. This study highlights intraspecific variation in seed dispersal patterns across sexes and breeding and non-breeding male hornbills and potential variation between two hornbill species. This is the first study that estimates long-distance seed dispersal by Asian hornbills.

1. Introduction

Seed dispersal is a crucial ecosystem process that ensures the maintenance of tropical tree diversity (Terborgh et al., 2002). Frugivores disperse seeds away from the parent plants thereby potentially reducing mortality due to distance- and density-dependent factors like seed predation, herbivory and competition under the parent trees (Connell, 1971; Janzen, 1970). Seed dispersal by frugivores involves quantitative and qualitative components (Schupp, 1993). The quantitative component deals with the number of seeds dispersed and the qualitative component involves seed handling behaviour, gut treatment of seeds, seed dispersal distances from the parent plant and suitability of seed deposition sites (Schupp, 1993). Seed dispersal distance has implications for range expansions of plant species and maintaining genetic connectivity between populations, which is crucial in the context of increasing habitat fragmentation worldwide. The pattern of seed deposition (clumped/scattered) and suitability of site of seed deposition can further influence the efficacy of seed dispersal (Howe, 1989). In a clumped dispersal scenario, negative density-dependent factors can operate and may have implications for seed germination and establishment (Howe, 1989; Russo and Augspurger, 2004).

Focal observations of frugivores on fruiting trees can enable

estimation of fruit removal (quantitative component) and fruit handling (qualitative component). However, determining seed dispersal distances (qualitative component) is challenging. Certain sites that are habitually used by dispersers e.g. for breeding display, roosting or sleeping sites can be studied for determining the quality of seed deposition sites (Russo et al., 2006; Wenny and Levey, 1998). For vagile animals, determining the seed deposition sites other than those used habitually (for e.g. lekking and roosting/sleeping sites) (Karubian et al., 2012; Russo et al., 2006), is extremely difficult. Movement data combined with gut passage data have enabled an estimation of seed dispersal distances (Holbrook and Smith, 2000; Westcott et al., 2005).

Apart from integrating information from movement and gut passage time data, incorporating disperser behaviour into telemetry studies enables a nuanced estimation of seed dispersal kernels (Kays et al., 2011; Russo et al., 2006; Westcott et al., 2005). Telemetry studies are especially useful to understand long-distance dispersal, as habitats are becoming increasingly fragmented along with climate change, and where dispersal agents can play a critical role in ensuring plant species persistence through dispersal in to favourable habitats (Lenz et al., 2011; Naniwadekar et al., 2019; Nathan et al., 2008).

Temporal differences in disperser behaviour has been demonstrated to influence seed dispersal distances over different times of the day

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(Kays et al., 2011; Westcott et al., 2005). Kays et al. (2011) demonstrated that seeds that were ingested by the toucans in the early mornings or in the afternoons were more likely to achieve significant dispersal versus those that were ingested in the mid-day. Seed dispersal is also influenced by habitat configuration, resource availability and disperser behaviour (Lenz et al., 2011; Pesendorfer et al., 2016). The varying contexts under which animal-mediated seed dispersal occurs makes it a complex and difficult process to predict (Côrtes and Uriarte, 2013). While inter-specific variation in seed dispersal has been studied extensively (Jordano et al., 2007), intraspecific variation and understanding the contextual drivers that influence seed dispersal are relatively understudied (Zwolak, 2018). While there is some evidence of inter-sexual variation in seed dispersal patterns (Karubian et al., 2012), there is limited evidence demonstrating seasonal or context-specific differences in seed dispersal patterns within a species [but see Kitamura, 2011].

Hornbills are among the most important seed dispersers in tropical forests of Asia and Africa and are often referred to as the ‘farmers of the forest’ (Kitamura, 2011). They have a unique breeding ecology. Female hornbills incarcerate themselves in the nest cavities for 3–4 months. During this period, males deliver food (primarily fruits) to the female and the growing chick/s (Kemp, 1995). The incarcerated female and chick/s regurgitate seeds outside nest cavities resulting in clumped seed dispersal under the nest tree (Datta, 2001; Kinnaird, 1998). The clumped dispersal at nest trees often results in high rates of seed predation and seedling and sapling mortality resulting in limited or no net positive effects of seed dispersal (Datta, 2001; Kinnaird, 1998). However, given that male hornbills spend limited time at nest trees during feeding visits, they are expected to mostly scatter-disperse away from parent and nest trees, while they are foraging and perching.

Movement of non-breeding hornbills is not constrained by daily, repeated visits to nest trees. Seed dispersal kernels of juveniles and non-breeding individuals are expected to be different from the breeding hornbills. Given the larger home ranges in the non-breeding season (Poonswad and Tsuji, 1994), they can be expected to disperse seeds at further distances from the parent trees. Moreover, sympatric hornbill species are known to have varying home ranges (Keartumsom et al., 2011). The smaller-sized wreathed hornbill *Rhyticeros undulatus* is known to range over much longer distances (> 170 km²) compared to the larger great hornbill *Buceros bicornis* (> 130 km²) (Keartumsom et al., 2011). African hornbills play a key role in long-distance seed dispersal (Holbrook and Smith, 2000) even in fragmented habitats (Lenz et al., 2011). While Asian hornbills play a key role in the removal of large seeds from fruiting trees (Kitamura et al., 2004; Naniwadekar et al., 2019), their role in long-distance dispersal has not been quantified (Ismail et al., 2017).

In this study, we estimated seed dispersal kernels for two large-bodied Asian hornbills (the great and wreathed hornbill) by incorporating information on fruiting tree visitation patterns during the breeding and non-breeding seasons, gut passage time data and fine-scale movement data obtained from GPS loggers in a tropical forest site in north-east India. We combined information collected from GPS loggers with hornbill visitations patterns on fruiting trees and gut passage

time data to 1) determine relative proportions of seeds potentially dispersed under and away from the nest tree by the breeding male hornbills of both species, 2) compare seed dispersal distributions for breeding and non-breeding great hornbill individuals and, 3) compare seed dispersal distributions by breeding great hornbills with a breeding wreathed Hornbill. We expected that unlike the incarcerated breeding females, breeding males will disperse far fewer seeds at the nest tree. We expected that the movements of breeding hornbills (unlike the non-breeding hornbills) will be constrained due to repeated visits that the male needs to make to the nest trees with implications for seed dispersal distributions. We expected differences in seed dispersal distributions between great and wreathed hornbills since they are known to differ in their diets and ranging patterns.

2. Materials and methods

2.1. Study area

The study was carried out in Pakke Tiger Reserve (PTR; area: 861.9 km²; elevation: 150–1800 m ASL; range: 92°36′–93°09′E and 26°54′–27°16′N), a protected area, in Arunachal Pradesh state which is part of the Eastern Himalaya Biodiversity Hotspot. The intensive study site was in the south-eastern corner of the reserve (Fig. S1). The vegetation is classified as Assam Valley tropical semi-evergreen forest (Champion and Seth, 1968). More than 78% of trees are biotically-dispersed (Datta and Rawat, 2008). Nameri Tiger Reserve in neighbouring Assam state is contiguous with PTR in the south. PTR is surrounded by the Papum and Doimara Reserved Forests which experience significant biotic pressures.

Three species of hornbills including the great *Buceros bicornis*, wreathed *Rhyticeros undulatus* and Oriental pied hornbills *Anthracoceros albirostris* are found here while the rufous-necked *Aceros nipalensis* is found in the higher elevations. The great hornbill is the largest (2.2–4 kg), followed by the wreathed (1.4–3.7 kg), the rufous-necked hornbill (2.2–2.5 kg) and the Oriental pied hornbill (0.6–0.9 kg) (Kemp, 1995). The hornbill breeding season in this area is from March to mid-August. IUCN has classified the great, wreathed and the rufous-necked hornbill as ‘Vulnerable’ and the Oriental pied hornbill as ‘Least Concern’ (IUCN, 2019). Hornbills are the most important dispersers of large-seeded plants (Naniwadekar et al., 2019) and their loss negatively impacts regeneration of large-seeded plants (Naniwadekar et al., 2015c).

2.2. Hornbill visitation patterns on fruiting trees

To determine the hornbill visitation patterns on fruiting trees over the entire day, we carried out focal tree watches on hornbill food plants. We observed 161 focal trees for 21 hornbill food plant species spanning 1025 h between February and June (2015, 2017 and 2018) which coincides with the hornbill breeding season (Table S1). We also carried out 62 focal tree watches for 15 hornbill food plant species spanning 391 h between November and January (2016 and 2017) which coincides with the hornbill non-breeding season (Table S2). The tree watch

Table 1

Details of the six tagged hornbills, date of tag deployment, last date for which data was received, number of days of location data, number of unique locations obtained, GPS error, the status of the tagged bird and the season (breeding or non-breeding) in which the individual bird was tagged. In this area, the breeding season of hornbills is from March (female entry) to mid-August (chick fledging), while the non-breeding season is from September to February.

No	Hornbill species	Code	Date of tagging	Last date of data download	# days	# unique locations	Mean GPS error (m)	Status	Season
1	Great	GH1Br	02-Mar-15	19-May-15	78	3980	15.3	Breeding male	Breeding
2	Wreathed	WH1Br	29-Mar-15	17-Jun-15	80	4707	13.7	Breeding male	Breeding
3	Great	GH2NBr	23-Nov-15	15-Jan-16	53	2607	16.1	Non-breeding male	Non-breeding
4	Great	GH3Br	17-Feb-16	08-Apr-16	51	2962	13.7	Breeding male	Breeding
5	Great	GH4Br	25-Feb-16	15-Mar-16	19	1118	14.9	Breeding male	Breeding
6	Great	GH5NBr	05-Mar-16	10-May-16	66	3901	15.3	Non-breeding male	Breeding

data was collected in the same months for which we had movement data for six birds (Table 1). The hornbill non-breeding season (September to February) is a period of low fruit availability (Datta and Rawat, 2003). The tree watches were done from sunrise to sunset enabling us to determine hornbill visitation patterns on fruiting trees. During the time period when we conducted the tree watches, the sunrise and sunset timings varied between 0430–0610 h and 1620–1800 h respectively. While some tree watches were done over the entire day, some were done over two sessions; the first from sunrise to 11 h and the second (on the next day) from 11 h to sunset (Table S1 and 2). During tree watches, we recorded hornbill species identity, the number of individuals and arrival and departure time of individual birds on fruiting trees. The tree watches were done for many hornbill food plants including figs (*Ficus* spp.), arillate dehiscent capsules (e.g. *Horsfieldia*, *Dysoxylum*) and drupes (e.g. *Beilschmiedia* spp., *Livistona*). For additional details on methods please see Naniwadekar et al. (2019).

2.3. Hornbill movement

The Thailand Hornbill Project team trained us in trapping and tagging hornbills. We used canopy-mounted mist nets on hornbill food plants to trap hornbills. Hornbills were successfully trapped only on fruiting fig trees. The captured birds were measured, weighed and tagged. Only adult male birds were fitted with battery-operated GPS loggers (Model 'Bird 1A'; e-obs GmbH; <https://www.e-obs.de>, Germany). E-obs tags have been successfully used in telemetry studies of hornbills (Lenz et al., 2011), toucans (Kays et al., 2011) and smaller birds (Holland et al., 2009). The weight of the tag was 55 gm which is less than 2% of the weight of great and wreathed hornbills. The tag was fitted like a backpack using Teflon strings (0.55" wide; <https://www.ballyribbon.com>). We did not tag female and juvenile birds as tags could potentially interfere with female entry/exit at nests or the growth of juvenile birds. The data loggers took GPS fixes of these diurnal birds at 15-min intervals between 0300 h and 1900 h (approximately 1 h before sunrise and after sunset in this area) following (Kays et al., 2011; Lenz et al., 2011). The stored data was remotely downloaded using a base station.

Data on gut passage times for great and wreathed hornbills was available from two previous studies (Datta, 2001; Shukla et al., in press). We fed 823 fruits of five large-seeded hornbill food plants (*Aglaia spectabilis*, *Beilschmiedia assamica*, *Livistona jenkinsiana*, *Polyalthia simiarum* and *Syzygium cumini*) were fed to three captive hornbill species (including wreathed hornbill) in Nagaland Zoological Park, Dimapur, Nagaland. Fruits were fed over one to four trials (Shukla et al., in press). Fruit numbers offered in a trial varied between 5 and 17. Of the 823 fruits, 276 were offered to the wreathed hornbill. Twenty nine fruits of two species of *Beilschmiedia* spp. were offered to a captive great hornbill kept in an enclosure in PTR (Datta, 2001). These fruits were offered in a single trial. We pooled the gut passage data for the wreathed and great hornbill and assumed that there were no significant differences in the gut passage time between great and wreathed hornbills. We made this assumption since a) there were no differences in gut passage times between the rufous-necked and wreathed hornbills which are similar-sized (Shukla et al., accepted) and, b) the observed gut retention times are similar to those reported earlier for *Buceros* and *Rhyticeros* hornbills (Kitamura, 2011). We thus had gut passage data for 305 fruits for seven medium- and large-seeded hornbill food plants. The mean gut passage time for the two hornbill species for a range of food plant species was 133 min (range: 18–536 min). Physical activity has been demonstrated to influence the seed retention times in vertebrates (van Leeuwen et al., 2016), therefore, differences can be expected in seed retention times in captive and wild birds, which can in turn influence the seed dispersal kernels.

2.4. Analysis

2.4.1. Hornbill visitation to fruiting trees

We performed Chi-squared tests of independence to investigate whether hornbill visitations were independent of the time of the day (1-h interval) in the breeding and non-breeding season respectively. We also performed Chi-squared tests to investigate whether hornbill visitations in each 1-h interval were independent of the season (breeding and non-breeding).

2.4.2. Hornbill seed dispersal kernels

Following Lenz et al. (2011), we included only those days for which we had more than 30 valid locations to ensure reduced bias in the estimated seed dispersal distances. This resulted in reduction of two days per bird (mean = 2.2; median = 1; range = 1–5). Bird movement is often reduced immediately after tagging (Lenz et al., 2011). To determine this effect, we estimated the mean minimum daily distances moved by each bird. This was done only for those days when we had > 30 locations so that we did not underestimate the mean minimum daily distance. The number of locations obtained on the first day was less than 30 only for GH1Br (breeding great hornbill). We estimated z-scores for the minimum distance moved for each day. If the z-score for either one of the five initial days was less than 2, then it indicated significantly lower minimum distance moved compared to the overall average. For only two individuals (WH1Br and GH3Br), the z-score for the first day (and not the other four days) was less than -2. The first day was dropped from analysis for WH1Br and GH3Br. For the tagged breeding great and wreathed hornbills, we could determine the nest locations. We found that two of our tagged birds (GH1Br and WH1Br) were the males of nest trees we were monitoring as part of our hornbill nest monitoring program. Two other birds that we caught (GH3Br and GH4Br) helped us determine new nest locations. All the nests were in *Tetrameles nudiflora*, which is an important, wind-dispersed nest tree for hornbills (Datta and Rawat, 2004). One of the birds (GH2NBr) was tagged in the non-breeding season (Table 1). Another tagged bird, GH5NBr was determined to be a solitary adult non-breeding male in the breeding season. Typically, all our other breeding birds paired up with their females after release and were either seen with the partner (GH1Br, GH3Br, GH4Br) or were seen at the nest (WH1Br). GH5NBr had arrived alone on the fruiting *Ficus* tree where it was trapped and we always observed it foraging alone.

To estimate the seed dispersal kernel, we combined the gut passage data with the movement data following (Westcott et al., 2008). A random starting point was drawn following the distribution of foraging sightings across the entire day (see Fig. 1). Drawing random locations based on the distribution of foraging observations were more likely to represent fruiting trees. Nest tree locations (and any location in a 20 m radius of the nest tree) were not included in the random start locations. Since we knew the gut passage time for each seed, we assigned a random starting point (drawn as mentioned earlier) to it and the bird's location at the end of the gut passage time corresponded with the displacement distance of the seed from the parent tree. This process was repeated 10 times for each of the 305 seeds for which gut passage time had been obtained. This enabled us to obtain median and maximum displacement distances of seeds and the probability distribution of seeds at different distances from the parent plant. For the breeding birds (GH1Br, GH3Br, GH4Br and WH1Br), we also determined if the final displaced location of the seed was the nest tree (the exact location and any location in a 20 m radius) or a non-nest tree location. The relative frequency of observations at the nest and non-nest sites enabled us to determine the proportion of seeds that are likely to be dispersed at nests by the breeding males. We considered displacement distances of less than 20 m as seed dispersal under the parent tree, distances between 20 and 150 m as short-range dispersal and 150 m and beyond as long-range seed dispersal following Carlo et al. (2013). All the analysis was done in R (R Core Team, 2017).



Fig. 1. Percentage of hornbill visits to fruiting trees at different hours of the day during the hornbill breeding and non-breeding season. Ninety-four and 30 individuals (Great and Wreathed Hornbills) were seen in the breeding and non-breeding season respectively. The number on the x-axis is the first hour of the 1-h time interval. The sunrise and sunset timings varied between 0430 – 0610 h and 1620–1800 h respectively.

3. Results

3.1. Hornbill visitation to fruiting trees

We recorded a total of 94 individuals of wreathed (49 individuals) and great hornbills (45 individuals) in the breeding season and 30 individuals of wreathed (21 individuals) and great hornbills (9 individuals) in the non-breeding season at fruiting trees. Hornbill visitations on the fruiting trees were highest in the morning at around 6 h in the breeding and non-breeding season (Fig. 1). In the breeding season, while activity was higher in the morning, there was some activity throughout the day. In the non-breeding season, there were three distinct periods of activity between 5 and 6 h, 8–10 h and after 14 h (Fig. 1). The relative proportions of sightings across the different 1-h time intervals were significantly different within the breeding season (between 4 h and 17 h) and the non-breeding season (between 5 h and 16 h) (breeding season: $\chi^2 = 40.644$, $df = 12$, $P < 0.001$; non-breeding season: $\chi^2 = 33$, $df = 10$, $P < 0.001$). However, the relative proportions of sightings (between 5 h and 16 h for which comparable data was available for the breeding and non-breeding season) did not differ between the breeding and non-breeding seasons in the 1-h time intervals ($\chi^2 = 25.103$, $df = 20$, $P = 0.2$).

3.2. Hornbill seed dispersal kernels

We tagged five adult males of great hornbill and one adult male of wreathed hornbill. Three male great hornbills (GH1Br, GH3Br, GH4Br) and one male wreathed hornbill (WHBr1) were breeding birds, as determined by observing them subsequently at their nests, one male great hornbill (GH5NBr) tagged in the breeding season was seen singly on multiple occasions after tagging and therefore assumed to be non-breeding male (Table 1). One male great hornbill (GH2NBr) was tagged in the non-breeding season in November (Table 1). GPS tracking data that we obtained for the different individuals varied for each bird. The number of days for which we got movement data for the different birds ranged from 19 to 80 days and the total number of fixes we obtained ranged from 1118 to 4707 (Table 1). The home range of the birds as estimated for the sampling period using the minimum convex polygon method ranged from one to 63 km² (Fig. S1). The three breeding great hornbills had small home ranges that were less than 2 km² (Table 2; Fig. S1). The two non-breeding great hornbills had home ranges of 58 km² and 63 km² (Table 2; Fig. S1). The breeding wreathed hornbill had a home range of 54 km² (Table 2; Fig. S1). However, the mean minimum daily distance (averaged across the sampling period for each bird) moved by the three breeding great hornbills was greater than 6.5 km while it was ≤ 5 km for the non-breeding great hornbills (Table 2; Fig.

S2). The ranging patterns of breeding and non-breeding birds differed (Fig. S3). On the other hand, the mean minimum daily distance moved by the breeding wreathed hornbill was almost 25 km (Table 2; Fig. S2). Four (GH1Br, GH2NBr, GH5NBr and WH1Br) of the six tagged birds moved outside the PTR and Nameri Tiger Reserve in the adjacent Reserved Forests. GH1Br moved outside the park on five different days (1.1% locations), GH2NBr on 22 days (19.2% locations), GH3NBr on four days (0.3% locations) and WH1Br on 25 days (4.4% locations). Mean (range) distance travelled in the Reserved Forests from the protected area boundary for GH1Br was 474 m (87–1247 m), GH2NBr was 616 m (2–2974 m), GH5NBr was 109 m (44–231 m) and WH1Br was 1893 m (56–6077 m).

The seed dispersal kernels generated by breeding great hornbills, non-breeding great hornbills and breeding wreathed hornbill differed (Fig. S4). The breeding great hornbills had a much shorter distribution tail as compared to the non-breeding great hornbills and the wreathed hornbill had a bimodal seed dispersal kernel unlike great hornbills. The seed dispersal probability of a seed under the parent tree (< 20 m from the parent tree) was 0.05 for breeding great hornbills, 0.11 for non-breeding great hornbills and 0.02 for the breeding wreathed hornbill (Fig. 2). Median potential dispersal distance of seeds was 294 m for breeding great hornbills, 254 m for non-breeding great hornbills and 1354 m for the breeding wreathed hornbill (Fig. 3). The maximum potential distance of seed dispersal from the parent tree was 2502 m for breeding great hornbills, 12,860 m for non-breeding great hornbills and 10,828 m for the breeding wreathed hornbills (Fig. 3). Estimated seed dispersal distribution of great hornbills (breeding and non-breeding) was unimodal but for the wreathed hornbill it was bimodal with one peak between 500 and 1000 m and a second one between 4000 and 4500 m from the parent tree (Fig. 2).

In the case of breeding great hornbills, only 7.4% ($N = 9150$) of final locations of the dispersed seed were within 20 m radius of their nest tree indicating that breeding male great hornbills were less likely to disperse seeds at nest trees ($\chi^2 = 6635.5$, $df = 1$, $P < 0.001$) (Figure. S4). The relative proportions of seeds potentially dispersed under nest trees were significantly different for the three breeding great hornbills ($\chi^2 = 171.58$, $df = 2$, $P < 0.001$). It was 3.3% for GH1Br, 7% for GH4Br and 12% for GH3Br (Figure. S4). In the case of the breeding wreathed hornbill, only 1.7% of final locations of the dispersed seed were within 20 m radius of the nest tree (Figure. S4) and wreathed hornbills were less likely to disperse seeds under parent trees ($\chi^2 = 2845.5$, $df = 1$, $P < 0.001$).

4. Discussion

This study shows for the first time that large-bodied Asian forest

Table 2

Details of home range (as estimated by the Minimum Convex Polygon method (MCP)), mean daily distance moved (standard deviation), number of days for which the data was used and the average number of GPS fixes obtained per day (range).

No	Hornbill species	Code	95% MCP (km ²)	Mean daily distance moved in km (SD)	# days of data used	Mean fixes per day (range)
1	Great	GH1Br	1.98	7 (2)	75	52.3 (30–55)
2	Wreathed	WH1Br	54.45	24.8 (6.1)	75	60.5 (40–63)
3	Great	GH2NBr	63.38	3.9 (2.3)	53	48.8 (38–58)
4	Great	GH3Br	1.04	6.6 (1.2)	50	58.2 (41–62)
5	Great	GH4Br	1.51	8.7 (3.1)	19	58 (43–62)
6	Great	GH5Br	57.79	5 (1.4)	66	58.9 (46–63)

hornbills carry out very long-distance seed dispersal. This study uses the information on hornbill visitation patterns on fruiting trees to estimate seed dispersal kernels and highlights the intraspecific differences (breeding and non-breeding individuals) in potential seed dispersal distributions. Breeding male hornbills (great and wreathed) disperse far fewer seeds under the parent or nest trees thereby potentially playing a significant role in scatter-dispersal of seeds, unlike females who have been documented to disperse seeds in a clumped manner under the nest tree (Datta, 2001; Kinnaird, 1998). We found that estimated median seed dispersal distances between breeding and non-breeding great hornbills were similar but seed dispersal distributions of non-breeding great hornbills had a long tail with potential seed dispersal distances of up to 13 km from the parent tree. Estimated median seed dispersal distance of the lone breeding wreathed hornbill was four times larger than the great hornbills, with a maximum estimated seed dispersal distances being almost 11 km from the parent plant.

4.1. Diurnal patterns of hornbill visitation on fruiting trees

Studies have documented frugivore visitation patterns on fruiting trees over time (months) (Bronstein and Hoffmann, 1987) or years (Jordano, 1994). However, information on frugivore visitation patterns on a diverse set of fruiting tree species over a day and across seasons is lacking. Consistent with previous findings on different frugivores (Athreya, 1997), we found a peak in hornbill activity on fruiting trees in the morning and minor peaks in activity in the latter half of the day. There were no differences in hornbill activity over the daytime between the breeding and non-breeding seasons. However, there was low-intensity activity during the whole day in the breeding season, unlike the non-breeding season which had three distinct peaks indicating that hornbills have to likely make frequent forays to fruiting trees as they

have to feed the incarcerated female and/or chick/s. The average daily distance moved by non-breeding birds was consistently lower than the breeding birds, which indicates that the daily hornbill activity in the non-breeding season is likely to be lower than the breeding season. Integrating foraging behaviour into estimating seed dispersal kernels has been shown to improve seed dispersal kernel estimations (Kays et al., 2011; Westcott et al., 2005). Given the objectives of this study, understanding the hornbill visitation patterns has played an important role in estimating the seed dispersal kernels.

4.2. Overall seed dispersal patterns

Our study is the first to estimate seed dispersal distances by Asian hornbills (that weigh > 2000 g). The study demonstrates that like their African counterparts, Asian hornbills are dispersing most of the seeds away from the parent plant and could be dispersing the seeds as far as 13 km from the parent tree. Information on seed dispersal distances exists only from Africa for the smaller-bodied *Ceratogymna* (< 1400 g) and *Bycanistes* (< 900 g) hornbills (Holbrook and Smith, 2000; Lenz et al., 2011). Like the African hornbills, Asian hornbills are dispersing more than 80% of seeds away from the parent plants (Holbrook and Smith, 2000; Lenz et al., 2011). The maximum dispersal distances reported in this study for the two large-bodied Asian forest hornbills are more than twice those reported for *Ceratogymna* hornbills (Holbrook and Smith, 2000) and similar to those reported for *Bycanistes* hornbills (Lenz et al., 2011). The seed dispersal kernels with extremely long tails resembled those reported for African hornbills. However, the peaks for all three categories (breeding and non-breeding great hornbills and wreathed hornbills) between 500 and 1000 m was greater than *Bycanistes* hornbills (Lenz et al., 2011) and smaller than *Ceratogymna* hornbills (Holbrook and Smith, 2000). While the seed dispersal kernels

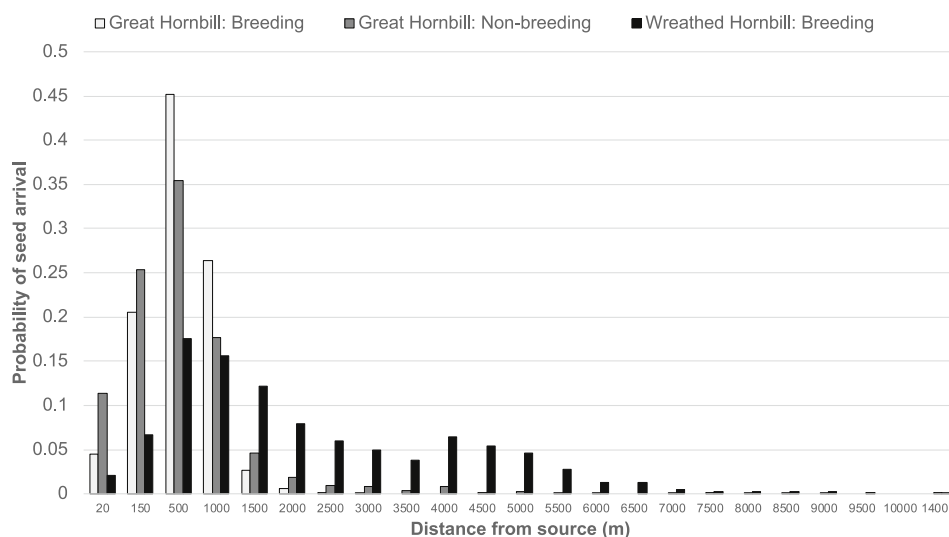


Fig. 2. Seed dispersal distributions generated by breeding Great Hornbills ($n = 3$), non-breeding Great Hornbills ($n = 2$) and breeding Wreathed Hornbill ($n = 1$). The numbers on the x-axis denote maximum value for the respective class. In the second last bin, data has been pooled for 10,000–14,000 m.

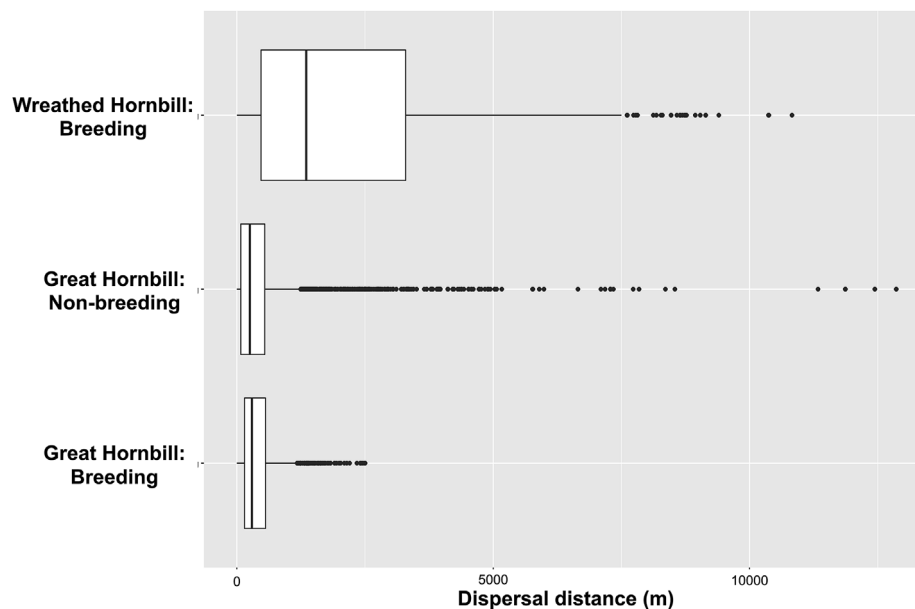


Fig. 3. Boxplot depicting dispersal distances of seeds from parent trees for breeding Great Hornbills and Wreathed Hornbill, and non-breeding Great Hornbills.

were unimodal for the great hornbills, it was bimodal for the wreathed hornbill. Bimodal seed dispersal kernels have been reported for the *Bycanistes* hornbills in fragmented habitats (Lenz et al., 2011). Lenz et al. (2011) hypothesize two different kinds of movement patterns, one within fragments and others across fragments that likely results in the bimodal pattern. It is likely that wreathed hornbills source most of the food items from closer to the nest and a significant part far away from the tree which results in the bimodal pattern. Given the lack of information on fruiting trees, it is difficult to explicitly test this and this needs to be investigated further. Interestingly, four of the six tagged birds left the two adjacent Protected Areas (Pakke and Nameri Tiger Reserve) and frequented the neighbouring Reserved Forests on multiple days. The wreathed hornbill travelled for more than 6 km in the Reserved Forests highlighting the potential role hornbills can play in seed dispersal in degraded forest patches. Despite the ongoing habitat degradation due to logging and habitat conversion, hornbills do breed successfully in these Reserved Forests (Rane and Datta, 2015). Birds whose home range centers are closer to the Tiger Reserve boundaries can be expected to frequent the adjoining Reserved Forests and play an important role in seed dispersal and long-term restoration of these degraded forest patches.

It is interesting to note that the breeding wreathed hornbill (WH1Br) and breeding great hornbill (GH1Br) had nest trees separated by only 670 m and were nesting during similar time periods and yet the smaller-sized wreathed hornbill had a range size 25 times larger and more than four times higher median seed dispersal distances compared to the great hornbills. Unfortunately, we could capture only one wreathed hornbill. Among the hornbill species found in the area, wreathed hornbills were the most difficult to trap as they mostly use the upper canopy (Datta and Rawat, 2003) and are more wary of human presence at fruiting trees compared to other hornbills (pers. obs.). Unlike other hornbills here, they have been documented to potentially exhibit reverse altitudinal migrations (movement to higher elevations in the winter months of the non-breeding season) over relatively large distances to track resource-abundant areas (Naniwadekar et al., 2015a; Naniwadekar and Datta, 2013) and feed more on non-fig fruits, unlike great hornbills that prefer figs (Datta and Rawat, 2003). While movement information might be required from additional individuals to determine consistency of this pattern, it is important to examine the proximate (resource tracking and optimal foraging) and ultimate (evolutionary history) correlates behind this pattern.

This study and others (Holbrook and Smith, 2000; Lenz et al., 2011) highlight the crucial role hornbills play in extreme long-distance dispersal. Hornbills have the longest seed dispersal distances reported for birds and they are the avian equivalent to elephants of the mammalian world, which disperse seeds up to 65 km away from parent trees (Campos-Arceiz and Blake, 2011). While the median seed dispersal distances of hornbills are similar (larger for wreathed hornbills) to other large avian frugivores like the cassowary (Westcott et al., 2005) and primates (McConkey and Chivers, 2007; Russo et al., 2006), they are longer than toucans (Kays et al., 2011) and bats (Abedi-Lartey et al., 2016).

4.3. Intraspecific variation in seed dispersal patterns

Past studies have focused on estimating the mean values (of dispersal distances) for a species, however, it is important to investigate the variation within a species, particularly in the context of seed dispersal patterns, as it has implications for community and landscape dynamics (Snell et al., 2019; Zwolak, 2018). As demonstrated in this study, seeds are not identically distributed by individuals of the same species and the context appears to play an extremely important role in seed dispersal patterns. The first context is, that while incarcerated female and chick/s clump-disperse seeds at the nest (Datta, 2001; Kinnaird, 1998), males continue to scatter-disperse seeds during the breeding season. Clumped seed dispersal may result in high seedling diversity and density (Kinnaird, 1998), however, the positive effects are evened out at the sapling stage with low survival at nest trees (Datta, 2001). Given that more than 50% of the hornbill population (juveniles, sub-adults and male birds) is outside the nests, a significant proportion of the population continues to scatter disperse seeds away from parent plants during the breeding season. Earlier studies have documented sex differences in seed dispersal patterns due to differing behaviour, where males carried out clumped seed dispersal at leks, while females scatter-dispersed seeds (Karubian et al., 2012).

The second context is the difference in seed dispersal patterns of breeding and non-breeding birds. While non-breeding birds ranged over large areas, it did not necessarily translate into longer median seed dispersal distances. The median dispersal distances were marginally smaller for non-breeding birds than the breeding birds. The mean daily distances travelled over the day for the two non-breeding birds was less than that travelled by the three breeding birds. Non-breeding birds do

not have to move between fruiting trees and nests to feed females and chicks, and therefore can reduce energetic costs by moving less frequently. However, they were responsible for occasional long-distance dispersal events that were more than 10 km from the parent tree. Seasonality has been demonstrated to influence frugivore movement patterns. The seed dispersal distance differed seasonally for straw-colored bats which was likely driven by food resource distributions (Abedi-Lartey et al., 2016). However, for hornbills, the non-breeding individual in the breeding season (GH5NBr) and the individual in the non-breeding season (GH2NBr) ranged over large distances and had similar-sized home ranges in similar sampling durations. The hornbill breeding season is associated with peak fruit availability in the area (Datta and Rawat, 2003). Given that the non-breeding individual, unlike the tagged breeding individuals, travelled over a large distance in the breeding season indicates that the possible reasons for ranging might be other than resource distribution and need to be explored further. The general idea that hornbills range more widely in the non-breeding season compared to the breeding season (Poonswad and Tsuji, 1994) itself might depend on the breeding status of the individual. The different contexts of hornbill seed dispersal could have important implications in crucial stages of seed dispersal (scattered versus clumped dispersal by different individuals).

One of the limitations of the study is the number of tagged birds, which limits the generalization of the results and highlights the need to have additional information in the future. However, this study, in conjunction with other studies, demonstrates the superior role of hornbills in seed dispersal vis-à-vis other frugivores. Hornbills have been documented to play a significant quantitative role in fruit removal of large-seeded plants (Kitamura et al., 2004; Naniwadekar et al., 2019) and an important role in scatter-dispersing large numbers of large-seeded species during the non-breeding season (Naniwadekar, 2014). In the wider plant-seed disperser communities, hornbills are especially crucial for large-seeded plants as they provide superior fruit removal and fruit handling role compared to other frugivores (Naniwadekar et al., 2019). Hornbill population declines due to hunting and logging results in lowered scatter-dispersal of large-seeded plants and altered recruitment of important food plants (Naniwadekar et al., 2015c; Sethi and Howe, 2009). This study demonstrates that hornbills play a crucial role in scatter-dispersing seeds in the breeding season and in long-distance seed dispersal thereby facilitating connectivity between plant populations and probably in restoring degraded forests. They are likely to contribute to plant movement in the wake of challenges posed by climate change. Several hornbill species have recently been uplisted to a higher threat category by the IUCN (Birdlife International, 2018). Given the continued threats to hornbill persistence in the region (Beastall et al., 2016; Naniwadekar et al., 2015b), the negative impacts of hornbill loss on plants are potentially immense.

Data sharing

The data used in this study are available from Movebank Data Repository. <https://doi.org/10.5441/001/1.14sm8k1d> (Naniwadekar et al., 2019).

Ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed. Ethics clearance was obtained from the Ethics Committee of the Nature Conservation Foundation that gave suggestions that we complied with. We followed established methods of the Thailand Hornbill Project team and consulted senior wildlife veterinarian Dr. Parag Deka, Aranyak to minimize risk to individual birds. Giving primary importance to bird welfare, we did not tag female and juvenile birds. We obtained research and animal capture permits from the Arunachal Pradesh Forest Department, National Tiger Conservation Authority and the Ministry of Environment and Forests, New Delhi and

conducted the research under the supervision of the PTR forest officers.

Author contributions

RN conceived and coordinated the study, collected the data, carried out statistical analysis, drafted the manuscript; AR participated in data collection and data analysis and gave inputs on the manuscript, US participated in data collection and gave inputs on the manuscript, SC participated in data collection and gave inputs on the manuscript; AD conceived and coordinated the study, participated in data collection and analysis and critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.actao.2019.103482>.

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