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# **Seed dispersal by hornbills, conservation status and the consequences of their decline in tropical forests of Arunachal Pradesh**

A thesis submitted for the degree of

**Doctor of Philosophy**

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# Certificate

The research presented in this thesis entitled "*Seed dispersal by hornbills, conservation status and the consequences of their decline in tropical forests of Arunachal Pradesh*" was conducted by Mr. Rohit S. Naniwadekar, Nature Conservation Foundation, Mysore, Karnataka, under our supervision. It is hereby certified that the thesis submitted is a *bona fide* record of research conducted by the candidate in partial fulfilment of the requirements for his doctoral degree, and has not previously formed the basis for any other degree, diploma or academic qualification in any university.



Aparajita Datta

Guide

Place: Bangalore

Date: 28 February 2014



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Co-guide

Place: Bangalore

Date: 28 February 2014

# Declaration

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I hereby declare that the work presented in this thesis entitled "*Seed dispersal by hornbills, conservation status and the consequences of their decline in tropical forests of Arunachal Pradesh*" has been carried out under the guidance of Dr. Aparajita Datta and co-guidance of Dr. Charudutt Mishra. This work has not formed the basis of the award of any other degree, diploma or any other qualification previously. All the research described herein was carried out by me at Nature Conservation Foundation, Mysore. The particulars given in the thesis are true to the best of my knowledge.

**Place:** Mysore

**Rohit S. Naniwadekar**

**Date:** 28 February

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## Abstract

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Seed dispersal by frugivores is an important mutualistic interaction in tropical forests. As the largest avian frugivores in Asian forests, hornbills are a functionally important group. In this thesis, I have attempted to understand how sympatric hornbill species track resources, the relationship between hornbills and their food plants, its consequences for seed dispersal and how this relationship gets altered in the wake of anthropogenic threats like logging and hunting. My study was carried out in the Namdapha Tiger Reserve, Arunachal Pradesh that harbours five hornbill species.

Great and Brown Hornbill densities were higher in lower elevations while Rufous-necked Hornbill densities were similar in space and time. Wreathed Hornbill densities showed high temporal variation peaking in winter and declining prior to the breeding season. The three large hornbill species (Great, Wreathed and Rufous-necked Hornbill) consistently tracked ripe either fig or non-fig fruit availability in accordance with the representation of the two fruit types in their diets. However, while Wreathed Hornbills tracked fruits at the largest (study area) and intermediate scale (sites within study area), the Great and Rufous-necked tracked fruits at the scale of the fruiting tree. Hornbills were the most important visitors on large-seeded tree species. Hornbill abundance was positively associated with food plant abundance, which resulted in higher seed arrival in areas with higher hornbill abundance with important implications for recruitment of their food plants. However, this relationship was negatively affected by logging and hunting. Logged-hunted site was associated with reduced abundance of hornbill food plants, hornbills, dispersed seeds and altered recruitment of food plants compared to the unlogged-less hunted site. I found that while some hornbill species had higher abundances inside Protected Areas than outside, most species continued to be

present at lower abundances outside. This finding underscores the importance of conserving larger forest landscapes, which encompass a larger area in the state than Protected Areas.

This thesis provides an understanding of how resource tracking by hornbills at multiple scales enables sympatry, a mechanistic understanding of how hornbills govern the spatial distribution of their food plants and the influence of threats like logging and hunting on disrupting the mutualistic relationship between hornbills and their food plants.

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This thesis would not have been possible if not for help from several individuals and institutions. The time I spent at Namdapha will remain unmatched for the diverse array of experiences it provided beyond the domains of academic research. I owe much to the place and its people and, of course, its amazing wildlife.

For a peregrine like me, only Aparajita could have ensured that I see it through to the end of my PhD. She gave me complete freedom and encouraged me to meander through the different walks of ecological research from altitudinal gradient studies to frugivory and seed dispersal in the last few years! She has played several roles from a close friend & philosopher to a sounding board for even my most trivial ideas and, only occasionally was she a 'boss'. I owe her much - for helping me discover the direction of my future research interests and for infusing in me the love for hornbills. Hornbills are amongst the most magnificent beings on this planet. The joys of observing them in field (especially in Arunachal) are unparalleled and worth experiencing at least once in a lifetime if not for a lifetime.

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# Chapter 1

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## Introduction



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**Great Hornbill** *Buceros bicornis*. This thesis is about understanding the relationship between hornbills and their food plants and how it gets altered in the wake of anthropogenic threats like hunting and logging

*"If such great moths were to become extinct in Madagascar, assuredly the Angraecum would become extinct"* (Darwin 1862).

Two centuries ago, Charles Darwin documented close associations between plants and animals and thought about the consequences of their loss. Mutualistic interactions between plants and animals, such as pollination and seed dispersal, benefit both the groups. While plants benefit in reproduction, animals derive nutrition from the nectar and fruits. The evolutionary implications of these associations include morphological adaptations in flowers, fruits, pollinators and frugivores, and the historical range expansions of plants mediated by frugivores. The ecological implications of these interactions include their role in governing the diversity of plants, movement patterns of pollinators and seed dispersers, and eventually, the distribution of plants. The importance of these interactions is underscored by the fact that 90% of plants in tropics are dependent on animals for seed dispersal and pollination (Howe and Smallwood 1982, Jordano 1995, Ollerton et al. 2011). While pollination results in fruit production, seed dispersal marks the end of the reproductive cycle and beginning of the life of a new plant. Thus, the entire cycle from flowering to recruitment of plants has been summarized in what is referred to as the 'seed dispersal loop', highlighting the importance of seed dispersal in regeneration of plants (Wang and Smith 2002). Given such widespread mutual dependency between plants and animals for reproduction and nutrition, their vulnerability to the loss of either one of the two groups cannot be overstated.

Vertebrates play an important role in seed dispersal and a relatively less important role in pollination, which is primarily orchestrated by invertebrates. Seed dispersal by biotic agents assists seeds in moving away from parent plants, under which the conditions for germination and establishment can be hostile due to high predation rates, fungal and microbial infestation and sibling competition. Movement of seeds away from parent plants implies improved chances of recruitment of dispersed seeds due to lower likelihood of predation and competition and it enables the plants

to colonize new habitats. However for seed dispersal to begin, frugivores first need to find fruiting trees. Fruiting trees are patchily distributed in the landscape. Frugivores have to optimize the energy spent in finding fruits and maximize the energy gained by fruit consumption. Thus a frugivore has to make multiple choices from what kind of fruits to eat, which branch to forage on, which fruiting tree to visit, which area or region to forage in and when. These have implications on its movement and therefore the kind of role the frugivore will play in seed dispersal. Thus, distribution of fruit resources can influence distribution of frugivores that in turn influence the seed dispersal patterns and the eventual recruitment of the plant species. This can have implications for the plant-frugivore relationship at longer time-scales.

A tree in fruit can attract a diverse assemblage of frugivores varying in taxonomic affinities and size. On large fruiting trees such as figs (*Ficus* spp.), one can encounter several species of closely related taxa foraging together. However, the role played by different frugivores in dispersal of the seeds can be expected to vary in relation to the absolute and relative abundance of the frugivore, the frequency with which they visit the trees, their ability to handle and disperse seeds, and their foraging behaviour. In general, the size of the disperser relative to the seed size has an important bearing on the potential role it can play in seed dispersal (Howe and Vande Kerckhove 1981, Russo 2003, French and Smith 2005). As compared to smaller frugivores, large-sized frugivores can consume more fruits during a feeding bout (Holbrook and Loiselle 2009). Smaller frugivores would be able to swallow relatively fewer fruits at a time, thereby, limiting the number of seeds that they can disperse. Larger frugivores are also likely to cover longer distances and thus disperse the seeds further away from the parent plant. In case of large-seeded plants, larger frugivores with larger gape sizes might be better at handling the fruits as smaller frugivores would find it difficult to swallow the large seeds and thus are likely to peck or drop fruits under the parent tree (Howe and Vande Kerckhove 1981,

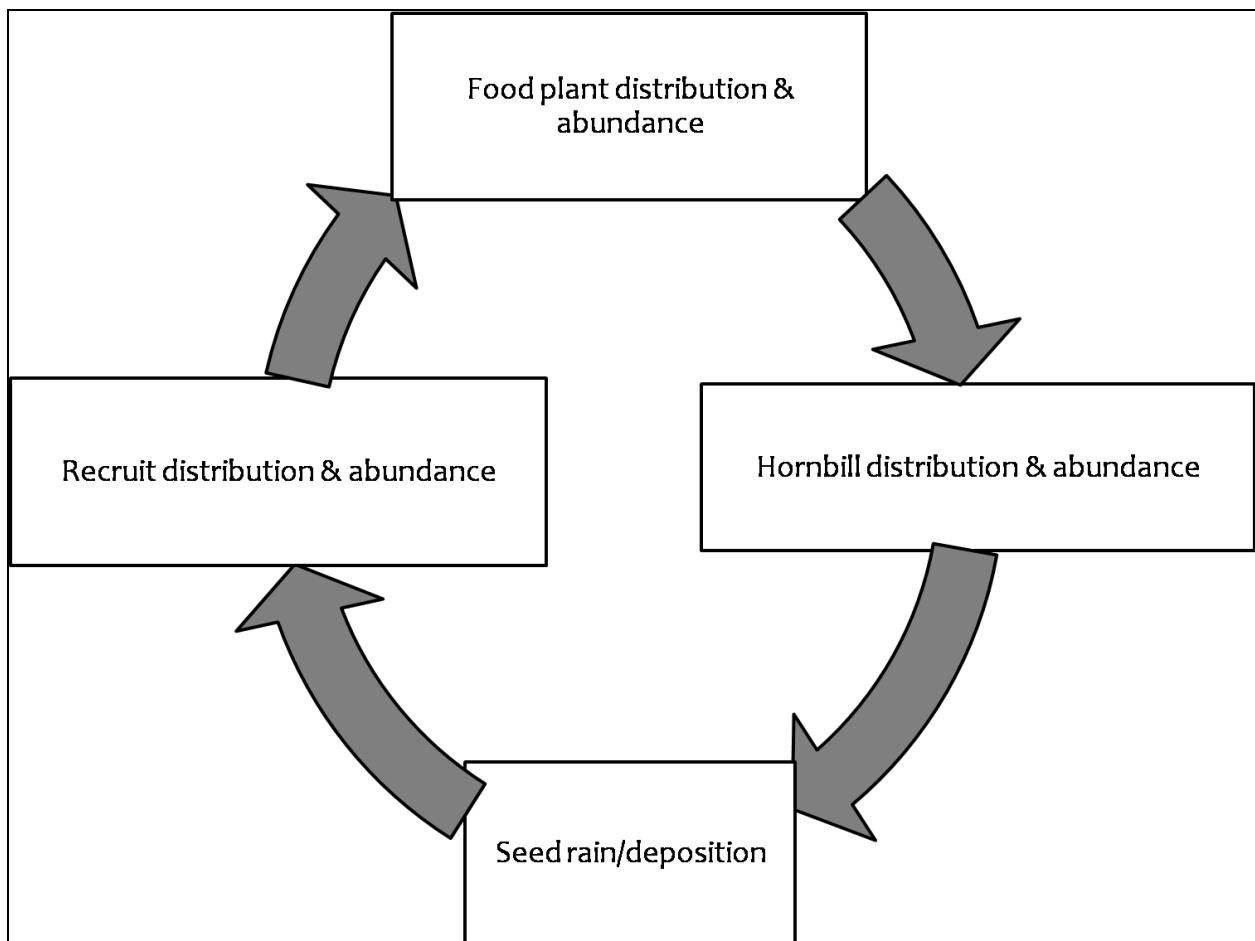
Wheelwright 1985, Burns and Lake 2009). Thus it is expected that large frugivores play an important role in governing the spatial distribution of large-seeded plants that have a smaller assemblage of reliable seed dispersers. Yet, populations of large-bodied frugivores are vulnerable to anthropogenic threats like logging and hunting. Local extinctions of larger vertebrates have been recorded from several sites across tropics (Redford 1992). To paraphrase Darwin, such losses can be expected to result in negative cascading effects on seed dispersal and recruitment, especially in large-seeded plants that have a relatively limited set of large-sized dispersers.

**In this thesis, I attempt to understand the relationship between hornbills, an iconic group of large-bodied avian dispersers in tropical forests, and their food plants. I focus on understanding how hornbill food plants influence the distribution of hornbills, and, in turn, how hornbills influence the distribution of their food plants through seed dispersal (Fig. 1; adapted from Wang and Smith (2002)).**

The studies forming this thesis were conducted in the tropical forests of Arunachal Pradesh state in north-east India, which harbor up to 5 species of hornbills. I focus on understanding the spatial scales at which different species of hornbills track their food resources, and thereby explain how their food plant distribution influences hornbill distribution. I then focus on understanding the role of these large frugivores in governing the spatial distribution of seeds of large-seeded food plants and the implications of such distribution for plant recruitment. I also document the impacts of hunting and logging, two key threats to biodiversity of tropical forests, on the relationship between hornbills and their food plants.

In the subsequent sections, I give a brief introduction to why I chose to study hornbills in Arunachal Pradesh. This is followed by a section on frugivory, seed dispersal and hornbills wherein I briefly introduce the existing knowledge that is

relevant to this study on the relationships between frugivores and their food plants and the role of frugivores in seed dispersal. The last subsection summarizes the negative impacts of disperser loss on seed dispersal. In each sub-section, I additionally summarize existing knowledge obtained from studying hornbills in the respective field.



**Figure 1** The conceptual diagram of this study that explores the relationships between hornbills and their food plants.

## 1.1 HORNBILLS AND ARUNACHAL

Hornbills are the largest avian frugivores found in the tropical forests of Asia, with fruits constituting up to 75–100% of their diet (Kinnaird and O'Brien 2007). Given that up to nine frugivorous hornbill species have been reported to occur in sympatry (Gale and Thongaree 2006), they offer an interesting model system to examine whether sympatric hornbills track resources at different spatial scales.

Hornbills are known to successfully handle and swallow fruits as long as 55 mm in length and 30 mm in width without causing any damage to seeds (Kitamura 2011). They also range over large distances. Wreathed Hornbills are known to cross over open sea to feed on fruiting trees on distant islands in south-east Asia, potentially dispersing seeds at large distances from parent plants (Kemp 1995). It remains unclear whether sympatric frugivore species such as hornbills play a complementary or supplementary role in seed dispersal.

Across their range in south and south-east Asia, hornbills face persecution due to hunting for their body parts that are used to decorate the traditional dresses of local communities and for meat and body fat that is purported to have medicinal value (Bennett et al. 1997, Datta 2002). Their habitat is also under threat from logging pressures (Datta 1998). This makes them a fitting model system to understand consequences of seed disperser loss on recruitment of food plants.

The state of Arunachal Pradesh in north-east India is the only state that still retains large contiguous tracts (>60% of its geographic area) of forests in north-east India (FSI 2009). Hornbills are still widespread in these forests, offering a unique opportunity to study their ecology in relatively undisturbed conditions. At the same time, a large proportion (>80%) of the forests in the state lie outside protected areas. These habitats are undergoing rapid transformations due to logging, habitat conversion and hunting (Kushwaha and Hazarika 2004). The state therefore, also

offers a unique setting to study the impacts of these anthropogenic activities on hornbills.

## 1.2 FRUGIVORY, SEED DISPERSAL AND HORNBILLS

Terborgh (1986) suggested that an animal that has 50% of its total diet comprising of fruits can be called a frugivore. Frugivory is one of the most dominant dietary niches that terrestrial vertebrates occupy in tropical forests. For instance, more than 80% of the avian and mammalian fauna at Cocha Cashu in Peru comprises of frugivores (Terborgh 1986). Amongst the different kinds of resources available in forests, fruits are easily digestible as compared to leaves. They can provide animals with sufficient water, energy and mineral content to reduce their dependence on other resources like animal matter, which although nutritionally rewarding, are difficult to obtain. It is likely that because of these reasons frugivory is one of the most dominant dietary niches.

### *Food plant and frugivore distribution*

Fruiting trees are patchily distributed in space (Loiselle and Blake 1991), and at most sites, fruit availability shows marked variation over time (Van Schaik et al. 1993, Datta 2001). Given this patchy nature of resource availability, fruits and their frugivores have been documented to exhibit synchrony in their abundances over space and time (Thompson and Willson 1979, Burns 2002). Additionally, fruit availability can be expected to vary across a hierarchy of spatial scales from within a fruiting tree, across fruiting trees, across sites within a region and across different regions in the larger landscape (Garcia and Ortiz-Pulido 2004). The need for examining these relationships across these hierarchical scales has been recognized (Garcia and Ortiz-Pulido 2004). Tracking resources at different spatial scales is thought to have implications for the ranging patterns and co-existence of sympatric species dependent on those resources (Inouye 1999).

In the case of hornbills, as much as 75–100% of their diet comprises of fruits (Kinnaird and O'Brien 2007). The fruit availability for hornbills has been documented to fluctuate within and across years (Kinnaird et al. 1996, Anggraini et al. 2000, Datta 2001). This is thought to have an important bearing on hornbill abundances and movements (Kinnaird et al. 1996, Anggraini et al. 2000, Holbrook and Smith 2000, Lenz et al. 2011).

### *Seed rain*

Fruiting plants are dependent on frugivores for dispersing their seeds. A suite of frugivore species usually consumes fruits; indeed, plants would benefit little from depending on a single species for dispersal. Different frugivore species differ in their abundances, visitation patterns on fruiting trees, fruit handling behavior and ranging patterns. Frugivores therefore differ in their ability to disperse seeds. The effectiveness of a seed disperser is measured as the 'number of new adults produced by dispersal activities of a disperser' (Schupp 1993). The effectiveness of a seed disperser is best evaluated by quantifying the number of seeds dispersed (quantitative aspect) and the probability of a dispersed seed producing a new adult (qualitative aspect) (Schupp 1993). The quantity of seeds dispersed is determined by the number of visits the disperser makes to the fruiting plant and the number of seeds it carries away during each visit. The quality of seed dispersal is determined by the treatment the seed receives during fruit handling, in the gut of the disperser and the suitability of deposition sites for germination and establishment of new recruits.

Unlike abiotically-dispersed species whose seed rain patterns can be modeled on the basis of abiotic conditions like wind speed and direction and from height of release (Nathan et al. 2002), it is relatively difficult to model animal-dispersed seed rain as animals exhibit non-random movement and are responsible for spatially aggregated seed dispersal patterns. Apart from factors such as behaviour, age, and sex of the

animal, other important factors that influence frugivore movement patterns is distribution of food resources, nest, roost and display sites. Frugivores have been demonstrated to disperse large number of seeds under their roosting, nesting, leks and sleeping sites (Krijger et al. 1997, Datta 2001, Russo et al. 2006, Kitamura et al. 2008). Frugivores are also known to disperse seeds in disproportionately larger numbers under fruiting trees (Clark et al. 2004, Kwit et al. 2004).

This spatially aggregated seed deposition patterns is thought to have important implications for the spatial distribution of recruits and eventually of adult tree distributions in the long-term. Areas with higher seed rain can create high-density patches of food plants or ‘hubs’ in the long-term (Lazaro et al. 2005). This disparity in the distribution of food plants has implications for resource tracking by frugivores and on the subsequent seed rain patterns that could again be spatially clumped resulting in a positive feedback between distribution of food plants and frugivores.

The relationship between fleshy-fruited plants, frugivores and the eventual distribution of the recruits has been succinctly summarized by Wang and Smith (2002). They describe the chain of processes as the ‘seed dispersal loop’ that includes fruit production, fruit removal, seed dispersal, germination and recruitment. A suite of factors further influences each of these processes. For example, the fruit removal process is influenced by factors like frugivory, diet choice, nutrition, competition, visitation rates, fruit removal rates, and frugivore behavior amongst others (Wang and Smith 2002). Similarly, seed passage time, disperser movement and behavior, and post-dispersal processes such as seed predation and/or seed caching influence the seed dispersal process. In the case of hornbills, seed dispersal has been studied by documenting seed rain patterns and regeneration under nesting and roosting trees (Kinnaird 1998, Datta 2001, Kitamura et al. 2004b, Kitamura et al. 2008), by their visitation patterns on fruiting trees (Kitamura et al. 2004a, Kitamura et al. 2006), by their movement patterns, and estimating the seed dispersal kernels (Whitney et al.

1998, Holbrook and Smith 2000, Holbrook et al. 2002, Lenz et al. 2011), the latter studies having been done mainly for African hornbills.

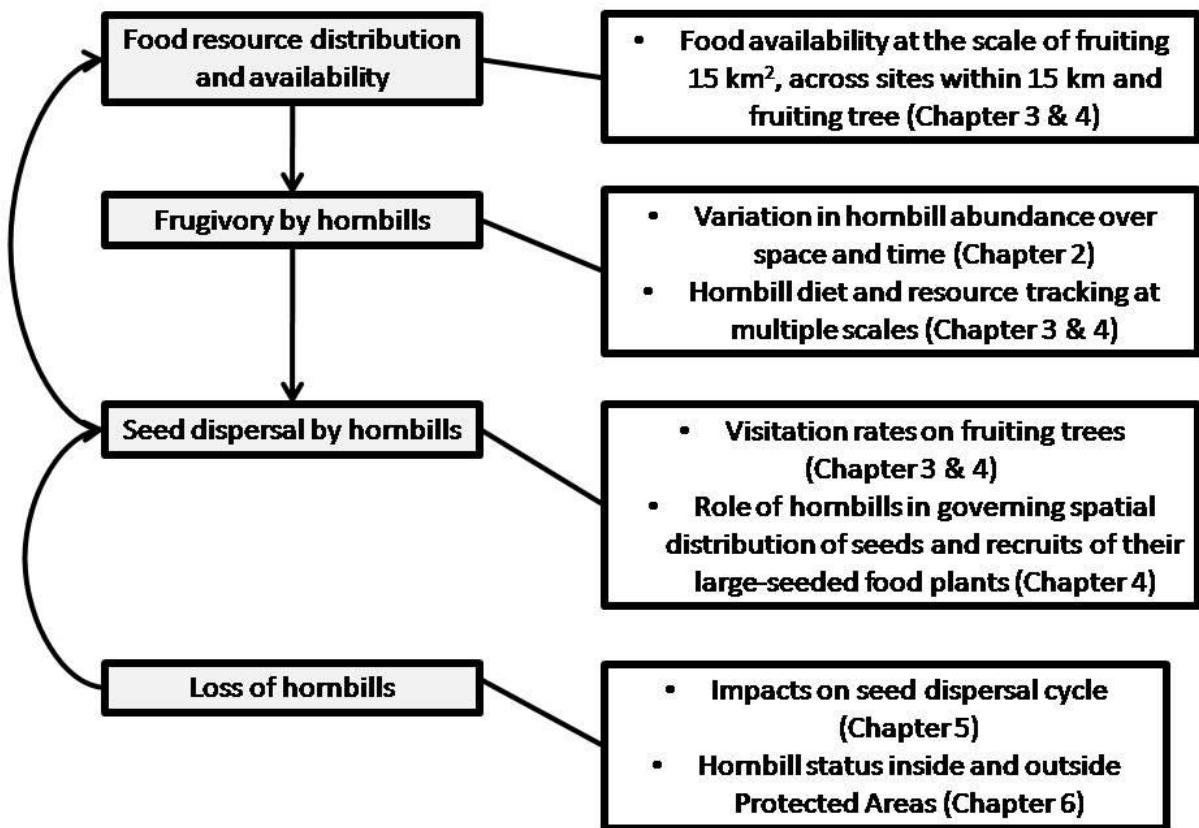
#### *Anthropogenic impacts on the seed dispersal cycle*

Given that the different stages in the seed dispersal loop are dependent on each other, it can be expected that any disruption to the cycle will have cascading effects on the other linked processes. Anthropogenic activities in tropical forests across the world exert pressures on the seed dispersal loop by influencing more than one process. While logging affects fruit availability, loss of frugivores to hunting can affect the fruit removal and seed dispersal stage. Studies have demonstrated that loss of frugivores affects frugivore visitation on fruiting trees (Velho et al. 2012), dispersal distance of seeds away from the parent plants (Forget and Janzen 2007, Sethi and Howe 2009) and abundance and pattern of recruitment (Sethi and Howe 2009, Vanthomme et al. 2010).

Hornbills are known to be negatively affected by habitat fragmentation (Raman and Mudappa 2003), logging (Datta 1998) and hunting (Bennett et al. 1997). Loss of hornbills has been documented to negatively influence dispersal distance of seeds and recruitment of select hornbill food plants (Sethi and Howe 2009, Velho et al. 2012).

### **1.3 STRUCTURE OF THE THESIS**

The broad structure of the thesis is outlined in Fig. 2. The study aims to understand the inter-relationships between food resource distribution and hornbill distribution and their implications for seed dispersal. It also tries to document how these inter-relationships are affected by anthropogenic threats that result in loss of hornbills and their food plants.



**Figure 2** The thesis outline which shows the different themes (shaded in grey) that the thesis addresses and the specific details of the different themes that are addressed in the different chapters of the thesis.

The broad objective of this thesis is to understand the inter-relationships between hornbills and their food plants and how these relationships are affected by anthropogenic threats like logging and hunting. To achieve this broad objective, I first attempt to estimate hornbill densities and understand variation in hornbill abundances over space and time (Chapter 2). Given that the variation in hornbill abundances over space and time can be influenced by the abundance and distribution of their food resources, I then document the diet of three hornbill species and explore the relationship between hornbills and food resource availability across different months in our entire study area (15 km<sup>2</sup>), across different sites within our study area and at the scale of the fruiting tree (Chapters 3 and 4). I then compare visitation patterns of hornbills as compared to other diurnal visitors on their

important large-seeded food plants and to what extent they govern the spatial distribution of their seeds (Chapter 4). Given that hornbills face significant threats in the state of Arunachal Pradesh in north-east India, I attempt to investigate how logging and hunting affect hornbills and their food plants, and the related processes of seed dispersal and recruitment (Chapter 5). Given that a large proportion of hornbill habitat occurs outside Protected Areas in the state of Arunachal Pradesh, I finally document the status of hornbills outside Protected Areas (Chapter 6). I then revisit my findings and discuss the broader relevance as well as the limitations of my work in the Synthesis (Chapter 7).

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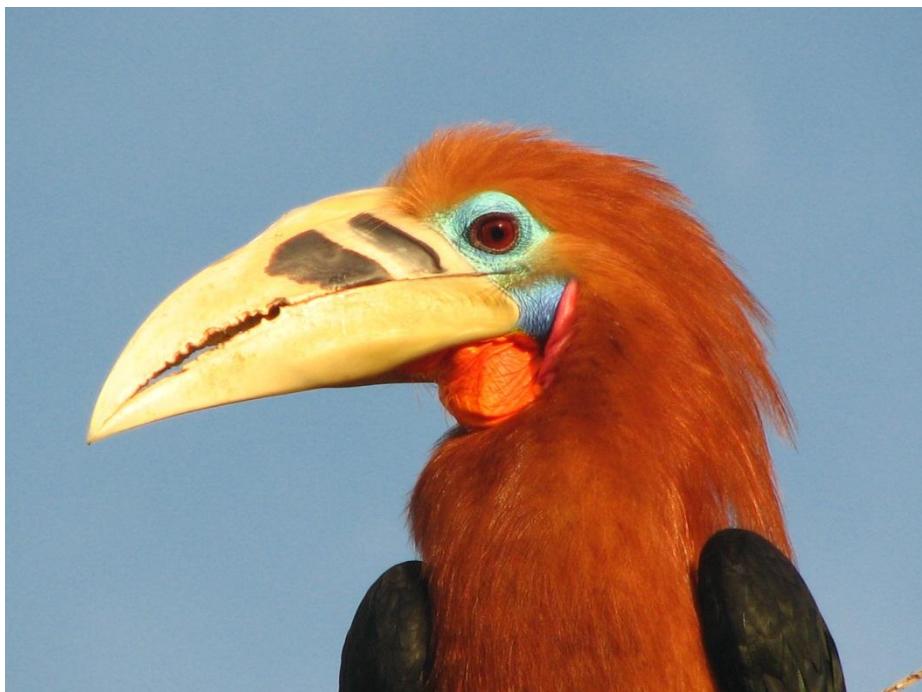
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## Chapter 2

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



**Rufous-necked Hornbill** *Aceros nipalensis*: This is one of the first ecological studies on this globally endangered species from India. This is also the first study to estimate the densities of the White-throated Brown Hornbill from across its geographic range.

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## 2.1 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 ( $7.9 \text{ birds/km}^2$ ) for the first time throughout its entire range. The mean Rufous-necked Hornbill densities ( $6.9 \text{ birds/km}^2$ ) were higher than those reported elsewhere. Great ( $3.9 \text{ birds/km}^2$ ) and Wreathed Hornbill ( $16.1 \text{ birds/km}^2$ ) 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 ( $68 \text{ birds/km}^2$ ) and drastically declining by March–April ( $1.3 \text{ birds/km}^2$ ), 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 *Anorrhinus austeni*,

## Wreathed Hornbill *Rhyticeros undulatus*

### 2.2 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 (Kemp 1995, Keartumsom et al. 2011) and exhibit significant fluctuations over space and time, possibly to track patchily distributed fruiting trees (Kinnaird et al. 1996). 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 (Kinnaird and O'Brien 2007). 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 (Bennett et al. 1997, Aiyadurai et al. 2010). In addition, they face significant threats from logging (Johns 1987, Datta 1998) and habitat fragmentation (Raman and Mudappa 2003). 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 (Laurance 1999, Kinnaird and O'Brien 2007).

As a consequence of these anthropogenic pressures, 34% of the 32 Asian species are listed by IUCN (IUCN 2012) 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 (IUCN 2012) 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 (Poonswad et al. 2013, Naniwadekar et al. in press). 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 *Anorrhinus 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 (Kemp 1995, Poonswad et al. 2013). However, information on hornbill densities is available only from two sites in Arunachal Pradesh (Dasgupta and Hilaluddin 2012, Naniwadekar et al. in press). 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 (Datta 2009).

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.

## 2.3 METHODS

### *Study Area*

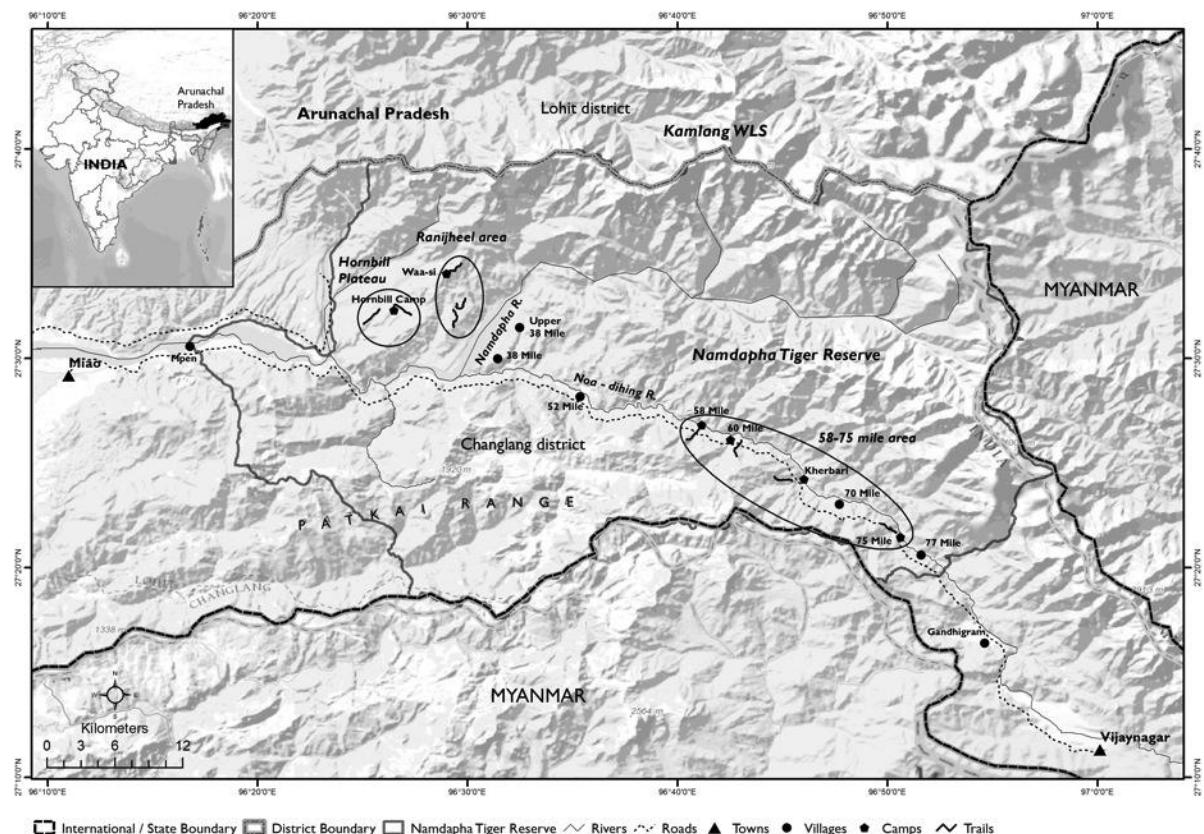
The study was carried out in Namdapha Tiger Reserve ( $27^{\circ}23'30''$ – $27^{\circ}39'40''$ N and  $96^{\circ}15'2''$ – $96^{\circ}58'33''$ E) in Changlang district of Arunachal Pradesh state in north-east India. It is located in the easternmost part of the Eastern Himalaya Biodiversity Hotspot adjoining the Indo-Myanmar Biodiversity Hotspot (Myers et al. 2000). The reserve area is  $1985\text{ km}^2$  with elevation ranging from 200–4571 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 (Proctor et al. 1998). 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 1500 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.

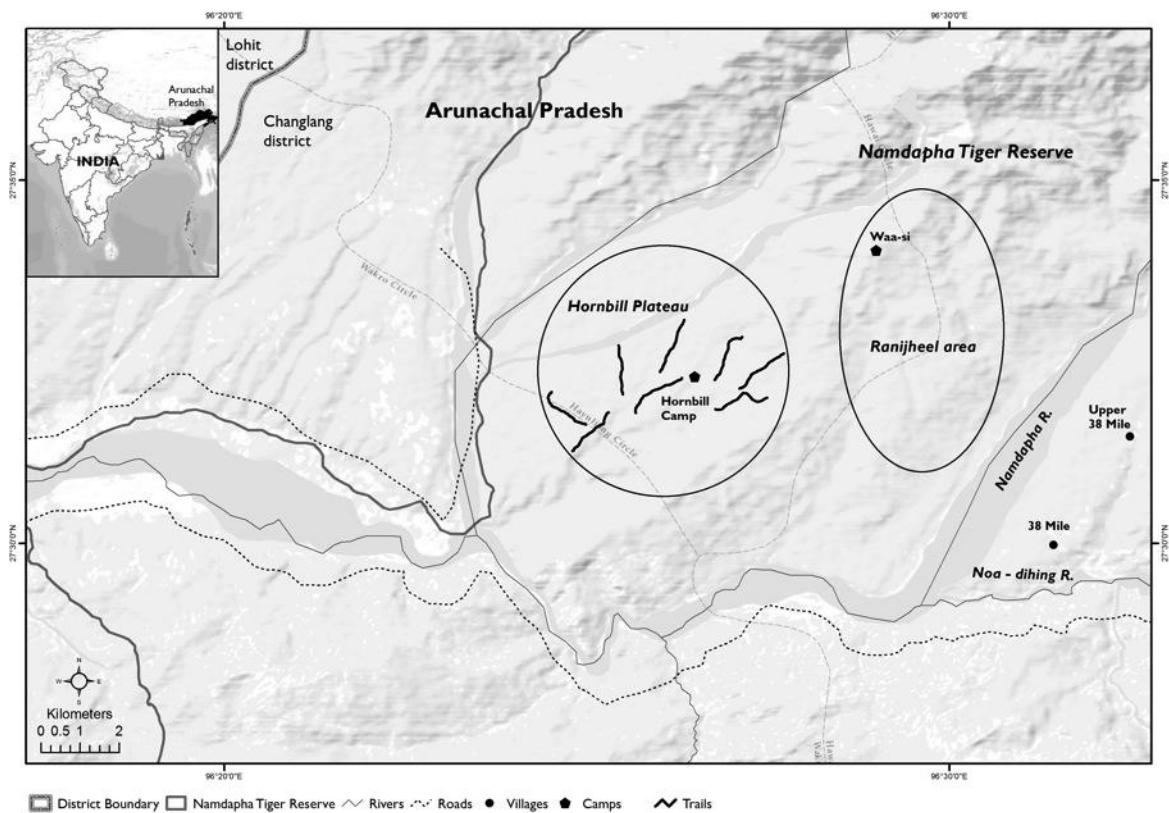
Five species of hornbills occur in the reserve: the Great, Rufous-necked, Wreathed, White-throated Brown and the Oriental Pied Hornbill. We sampled mainly in the non-breeding season (November to April). The breeding season of hornbills in Arunachal Pradesh is from March-end to early August (Datta and Rawat 2004),

while in eastern Arunachal Pradesh, breeding commences only in mid-to late April (Datta 2009). 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 1000 m. Hornbill Plateau, where sampling was carried out in both the phases, covers an area of  $\sim 15 \text{ km}^2$  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 780–1450 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 710–1310 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 southwestern boundary of the reserve.



**Figure 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.



**Figure 1b** Map focusing on the western portion of the Namdapha Tiger Reserve showing the eight trails that were sampled during November–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 (Buckland et al. 2003). 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 (Buckland et al. 2003). 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).

#### *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.

**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)
<b>Phase I</b>					
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
				<b>Sub-total</b>	470.1

<b>Phase II</b>					
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
				<b>Sub-total</b>	372
				<b>Total Effort</b>	842.1

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

### *Analysis*

Program DISTANCE (ver. 6.0) was used to estimate the densities of four hornbill species (Thomas et al. 2009). 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) (Thomas et al. 2010). 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  $\leq 10$  trails for the different analyses, we estimated variance by assuming the distribution of the variance estimate as Poisson with overdispersion factor 2 (Jornburom et al. 2010). 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 (Buckland et al. 2001). 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.

## **2.4 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 ( $16.1 \text{ birds/km}^2$ ) followed by White-throated Brown Hornbill ( $7.9 \text{ birds/km}^2$ ), Rufous-necked Hornbill ( $6.9 \text{ birds/km}^2$ ) and Great Hornbill ( $3.9 \text{ birds/km}^2$ ) (Fig. 2, Table 3).

#### *Monthly variation in hornbill densities*

Mean Wreathed Hornbill density declined from  $68 \text{ birds/km}^2$  in November–December to  $\sim 1 \text{ bird/km}^2$  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 ( $2.1 \text{ birds/km}^2$ ) than in November–December ( $12.7 \text{ birds/km}^2$ ), but it increased again in March–April ( $5.4 \text{ birds/km}^2$ ) (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).

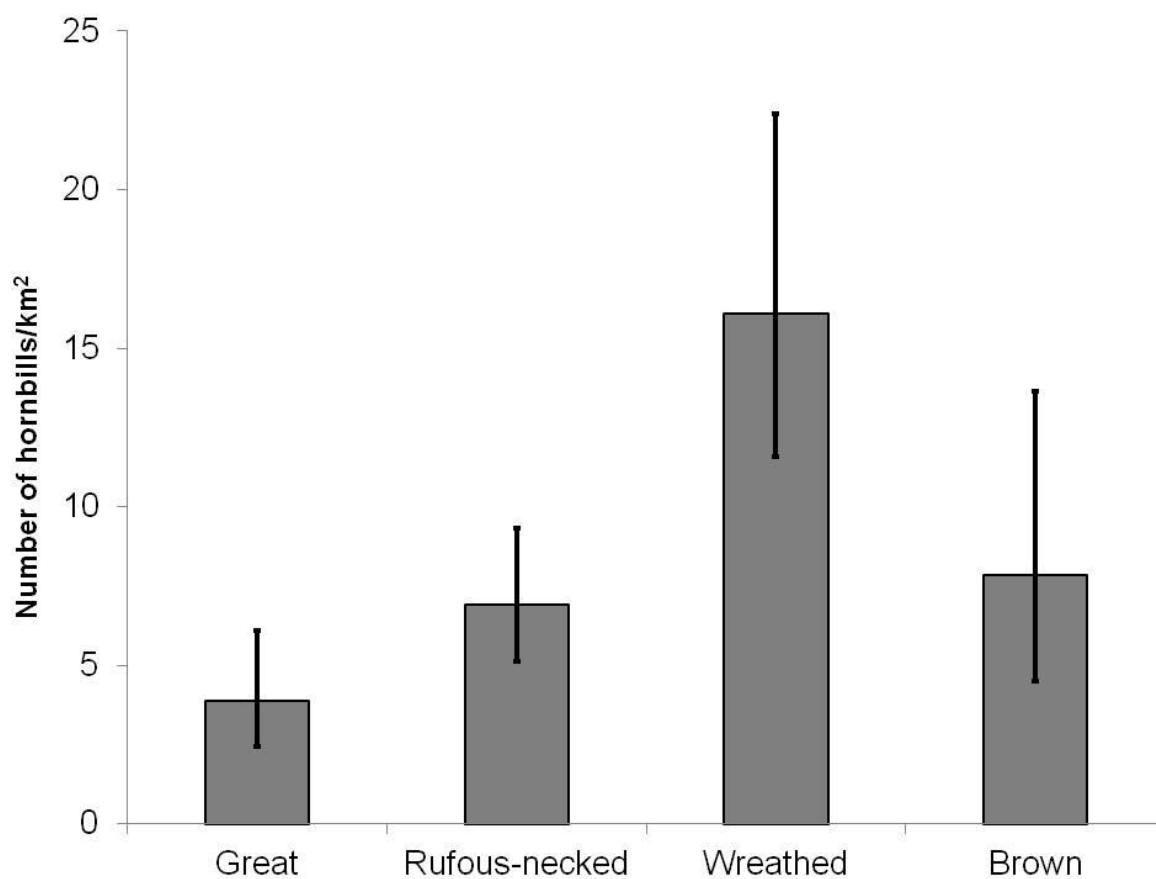
#### *Spatial variation in hornbill densities*

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

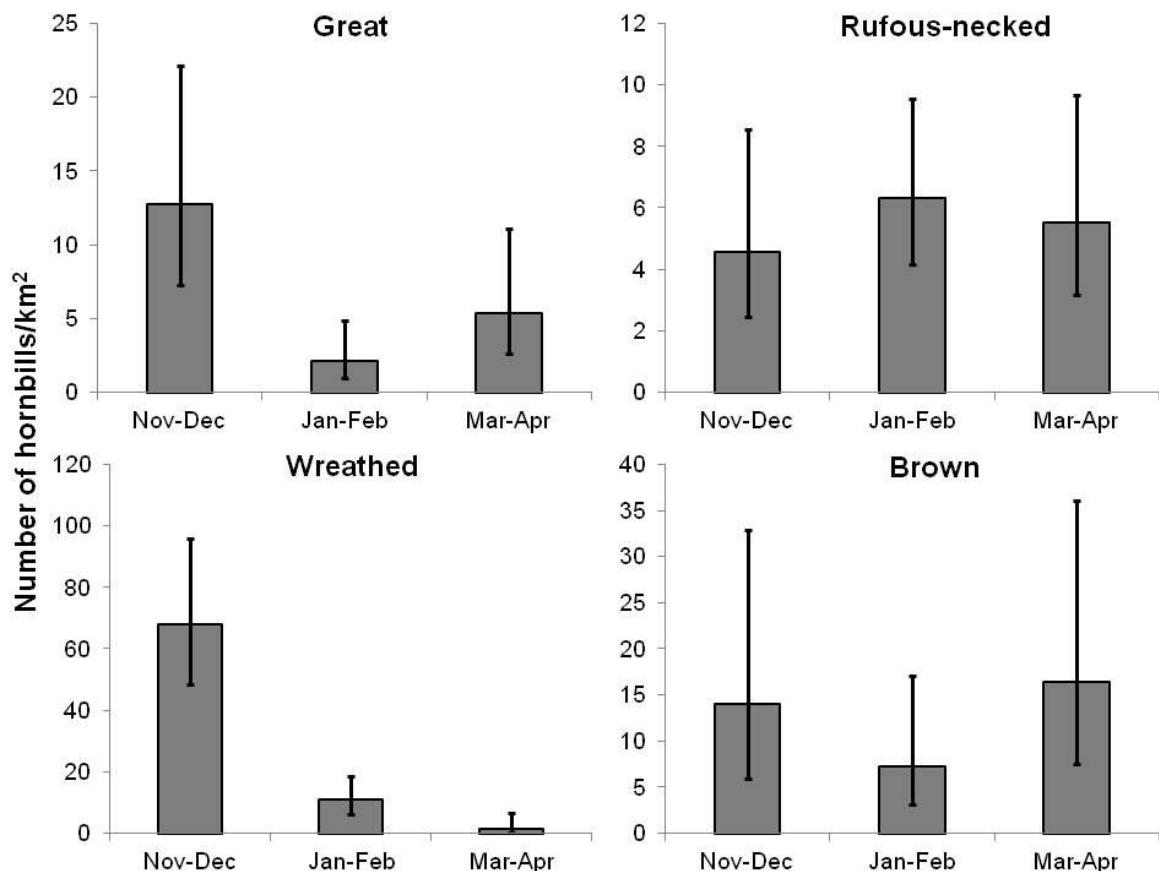
have opportunistically observed Wreathed Hornbills in the 58–75 mile area in the months of November–January.

**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).

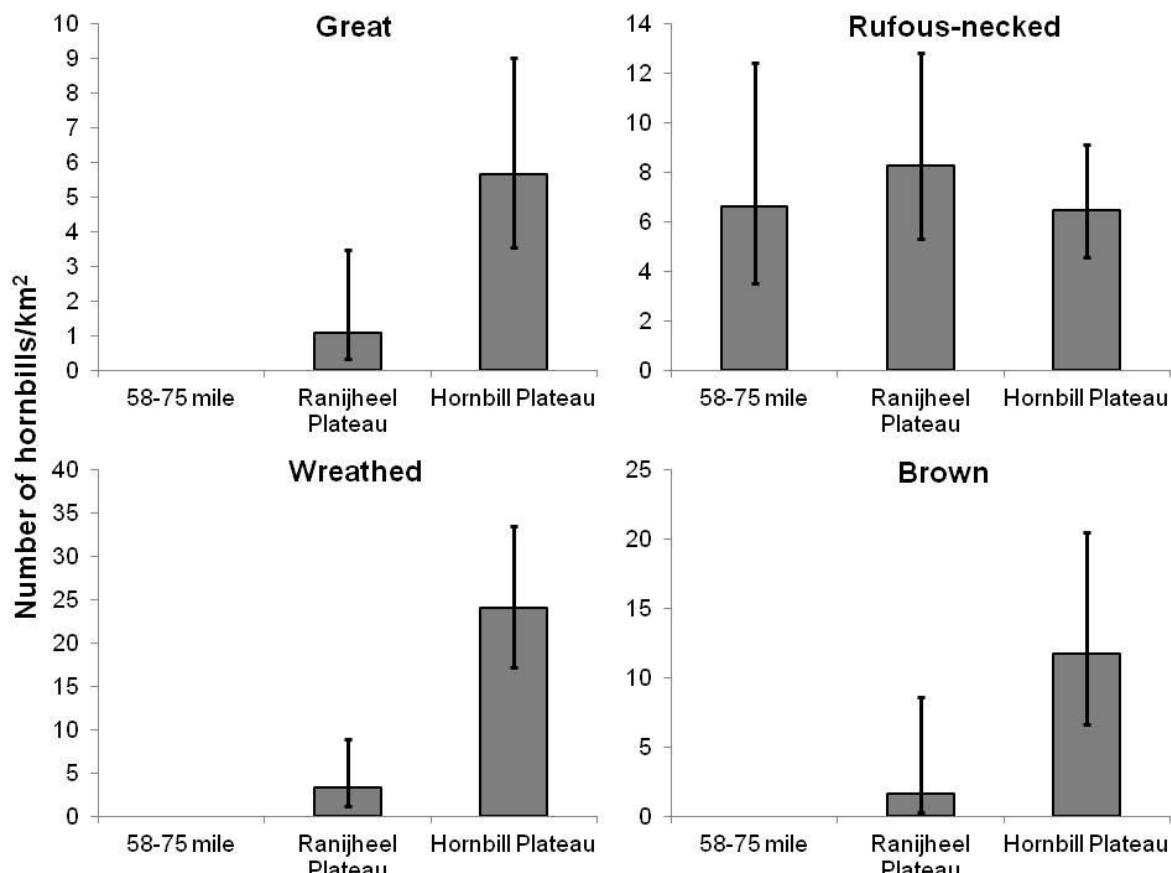
Months	Effort (km)	Great Hornbill	Rufous-necked Hornbill	Wreathed Hornbill	Brown Hornbill
November–December	134.5	41	23	106	12
January–February	260	13	58	33	12
March–April	143.5	20	29	2	15
<b>Total</b>	538	74	110	141	39
<b>Sampling sites</b>					
Hornbill Plateau (550–810 m)	538	74	110	141	39
Ranijheel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



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



**Figure 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).



**Figure 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)).

**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.

	<b>Mean and 95% Confidence Intervals</b>			
	<b>Great Hornbill</b>	<b>Rufous-necked Hornbill</b>	<b>Wreathed Hornbill</b>	<b>White-throated Brown Hornbill</b>
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 <sup>2</sup> )	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 <sup>2</sup> )	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 <sup>2</sup> )	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 <sup>2</sup> )	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 <sup>2</sup> )	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 <sup>2</sup> )	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 <sup>2</sup> )	0 (0–0)	6.6 (3.5–12.4)	0 (0–0)	0 (0–0)

## 2.5 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 and the Near Threatened Great and White-throated Brown Hornbills during the non-breeding season from November–April. Wreathed Hornbills 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.

Throughout Asia, only 7% of forests inhabited by hornbills are under Protected Status, and the average size of these Protected Areas is  $\sim 350 \text{ km}^2$  (Kinnaird and O'Brien 2007). 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 (Jornburom et al. 2010). Given the high densities of this species (6–8 individuals/km<sup>2</sup>) throughout the three sampling sites and more than 1000 km<sup>2</sup> of potential habitat (forests below 2000 m), 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 (Naniwadekar et al. in press), the global population of Rufous-necked Hornbill may need to be revised.

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 (Choudhury 2001, Srinivasan et al. 2010, Ved 2011). Namdapha and

the adjoining Kamlang Wildlife Sanctuary are the only two Protected Areas in Arunachal Pradesh where the species occurs. Given 450 km<sup>2</sup> of area in Namdapha which is below 1000 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 (Dasgupta and Hilaluddin 2012), but still comparable to other sites in Western Ghats, India (Raman and Mudappa 2003) and Thailand (Jornburom et al. 2010). 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.

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 Gale and Thongaree (2006)). The aptly named Hornbill Plateau had mean combined hornbill densities of 100 individuals/km<sup>2</sup> in November-December (Table 3). Apart from two studies (Leighton 1982, Kinnaird et al. 1996), which report peak combined densities of 84 individuals/km<sup>2</sup> and 82 individuals/km<sup>2</sup> 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 (Datta 2009). This is also corroborated by information from local tribes. As in other sites, where they are known to breed in the lowland forests (Datta and Rawat 2004), 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 (Kinnaird et al. 1996). 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 (Datta and Rawat 2003). The Wreathed Hornbills seasonally move to the higher elevations during the non-breeding season (Datta and Rawat 2003). We are probably observing a similar pattern in eastern Arunachal Pradesh, where Wreathed Hornbills, which range over much larger areas ( $> 170 \text{ km}^2$ ) (Poonswad and Tsuji 1994, Jornburom et al. 2010), 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:  $25 \text{ km}^2$  and White-throated Brown Hornbill:  $4.3\text{--}5.9 \text{ km}^2$ ) (Poonswad and Tsuji 1994, Tifong et al. 2007, Poonswad et al. 2013) and whose monthly densities were comparable. Wreathed hornbills have been recorded in large numbers in the higher elevations of Namdapha (up to 2000 m) (Datta 2009, Srinivasan et al. 2010). 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  $135 \text{ km}^2$ ) (Poonswad and Tsuji 1994, Keartumsum et al. 2011) 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 1000 m (Datta 1998, 2009, Dasgupta and Hilaluddin 2012). 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 1000 m elevation gradient (500–1450 m). This species is known to prefer the higher elevation areas (Kemp 1995, Poonswad et al. 2013).

Most hornbill species still persist, albeit in lower abundances, outside Protected Areas in Arunachal Pradesh (Naniwadekar et al. *in press*). 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 (Lenz et al. 2011).

## 2.6 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, 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 (Datta 2007). From the late nineties there has been a gradual increase in settlements within Namdapha. Forest patches are being cleared for settlements and paddy cultivation. 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 (Menon et al. 2001, Yadava et al. 2003). In addition, the abundance of most vertebrate groups (especially ungulates, large carnivores) is low due to hunting within the park (Datta et al. 2008). 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 values 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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## 2.8 APPENDIX

### Appendix 1 Summary of the mean density estimates of the four hornbill species

No.	Site	Mean (95% CI) number of hornbills/km <sup>2</sup>				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	Poenswad 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	Bukit Barisan Selatan National Park, Sumatra, Indonesia	na	na	7.5	na	Anggraini et al. [43]

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

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

# Chapter 3

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## Resource tracking by hornbills at multiple scales: insights from a mid-elevation tropical forest in north-east India



**Wreathed** *Rhyticeros undulatus* and **Rufous-necked Hornbill** *Aceros nipalensis* foraging together on a *Ficus*. This chapter focuses on understanding resource tracking in sympatric hornbill species across different scales in Namdapha Tiger Reserve.

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### 3.1 ABSTRACT

The fruit-tracking hypothesis predicts close links between frugivores and fruit abundance over space and time. Tracking patchily distributed fruit resources across different spatial scales can enable frugivores to co-occur. Hornbills, which are the largest frugivorous birds in Asia, occur in sympatry in most forests. In this study, we documented the diet of three similar-sized hornbill species (Great, Wreathed and Rufous-necked Hornbill) and then examined the relationship between abundance of fruits and hornbills across three scales; at a largest scale of 15 km<sup>2</sup>, at an intermediate scale (3 ha) and on fruiting trees at a mid-elevation forest site. Great Hornbills consumed more figs while Wreathed and Rufous-necked Hornbill consumed more non-fig fruits in their diet. Across two years at the largest scale, Wreathed hornbill abundance and ripe fruit abundance peaked in November–December in the non-breeding season declining by March (onset of breeding season) in mid-elevation forest. At the intermediate scale, we found Wreathed Hornbill abundance was positively associated with non-fig fruit abundance while Rufous-necked Hornbill was negatively associated with non-fig fruit abundance. At the scale of individual trees, Great and Rufous-necked Hornbill visitation was positively associated with ripe fig and non-fig fruit crop size respectively. Prior research has shown that fruit availability peaks in the breeding season (March to August) in lower elevation forests where Wreathed hornbills breed. This information along with the temporal variation in Wreathed hornbill abundance and fruit abundance we found strongly suggests that Wreathed hornbills track peak fruit availability across the elevation gradient in Arunachal Pradesh. Our findings also suggest that the three hornbill species play a complementary role in seed dispersal due to differences in visitation rates, dietary niche breadth, temporal variation in abundance, and occurrence in the mid-elevation forest site.

**Keywords** *Aceros nipalensis*, *Buceros bicornis*, figs, frugivores, fruit crop size, Namdapha, non-fig fruits, *Rhyticeros undulatus*

### 3.2 INTRODUCTION

Up to 90% of tropical plants produce fleshy fruits that are consumed by frugivores (Howe and Smallwood 1982, Jordano 2000). Fruiting is patchy in space and time (Van Schaik et al. 1993, Herrera 1998). The patchiness in distribution of fruits can be observed at a hierarchy of scales. Fruit abundance might vary across different branches on a fruiting tree, across different fruiting trees with varying fruit crops, across sites with differing abundances of fruiting trees or at a regional level where fruiting might vary across larger landscape patches (Garcia and Ortiz-Pulido 2004). Frugivores have to move across space and time to find these patchily distributed resources. The positive association of frugivore abundance with the variation in fruit abundance over space and time is the fruit-tracking hypothesis (Rey 1995, Burns 2002, Burns 2004). Frugivores might be expected to track resources to minimize energy loss in search of food and maximize energy intake through fruit consumption. Such studies have been carried out at single scales across latitudes (Telleria and Perez-Tris 2004), altitudes (Loiselle and Blake 1991), at smaller, geographically homogeneous spatial scales (Herrera 1998, Moegenburg and Levey 2003, Saracco et al. 2005) or across a hierarchy of scales (Sallabanks 1993, Garcia and Ortiz-Pulido 2004, Saracco et al. 2004). However, several studies have also reported absence of relationships between frugivore and fruit abundance as a consequence of conducting the study at a single scale (Garcia and Ortiz-Pulido 2004, Guitian and Munilla 2008), importance of the role played by abiotic factors rather than fruit abundance in governing frugivore abundance (Herrera 1998), overriding role of behaviour in constraining the movement patterns of frugivores (Brown and Long 2006) and idiosyncratic species-specific responses to changes in fruit abundance (Telleria et al. 2008).

Documenting resource tracking at different spatial scales is important. While species can occur through partitioning resources, habitat selection in space and time, a patchily distributed resource across a hierarchy of spatial scales is also thought to

play an important role in enabling several species to co-occur (Kotler and Brown 1988, Kneitel and Chase 2004). The trade-off between energy costs of travelling large distances and patch foraging efficiency can promote coexistence along the axis of heterogeneity in fruit resource distribution along the spatial scale (Kotler and Brown 1988). Thus, while one species will minimize the travelling cost and maximize efficiency in foraging in a patch, others may move between the rich patches thereby incurring additional travel costs.

In Asian tropics, hornbills are the largest avian frugivores. Hornbill diet (75–100%) is dominated by fruits (Kinnaird and O'Brien 2007). Hornbills are known to play an important role in seed dispersal, especially of the large-seeded plants (Kinnaird and O'Brien 2007, Kitamura 2011). Fruit availability for hornbills has been demonstrated to vary over space and time (Kinnaird et al. 1996, Anggraini et al. 2000). At most evergreen forest sites, several species of hornbills occur in sympatry with up to nine species reported to occur in sympatry in Thailand (Gale and Thongaree 2006). Sympatric hornbills depend on a similar set of fruiting plant species; fifty percent of the plant species that Asian hornbills forage belong to only five families that include Moraceae, Lauraceae, Meliaceae, Annonaceae and Myristicaceae (Kitamura 2011). Sympatric hornbill species differ in the relative contributions of figs and non-figs in their diet and have also been demonstrated to differ in preferred foraging areas on fruiting trees (Datta and Rawat 2003, Hadiprakarsa and Kinnaird 2004). While these two factors might aid in reduced niche overlap between sympatric hornbill species, it remains to be explored whether sympatric hornbill species differ in the scale at which they track fruit resources.

In this study, we explore patterns of resource tracking by three sympatric similar body-sized hornbill species, the Great Hornbill *Buceros bicornis*, Wreathed Hornbill *Rhyticeros undulatus* and the Rufous-necked Hornbill *Aceros nipalensis* at three different spatial scales. The three spatial scales are 1) at the largest scale of our study area ( $\sim 15 \text{ km}^2$ ) where we have looked at temporal variation in fruit abundance and

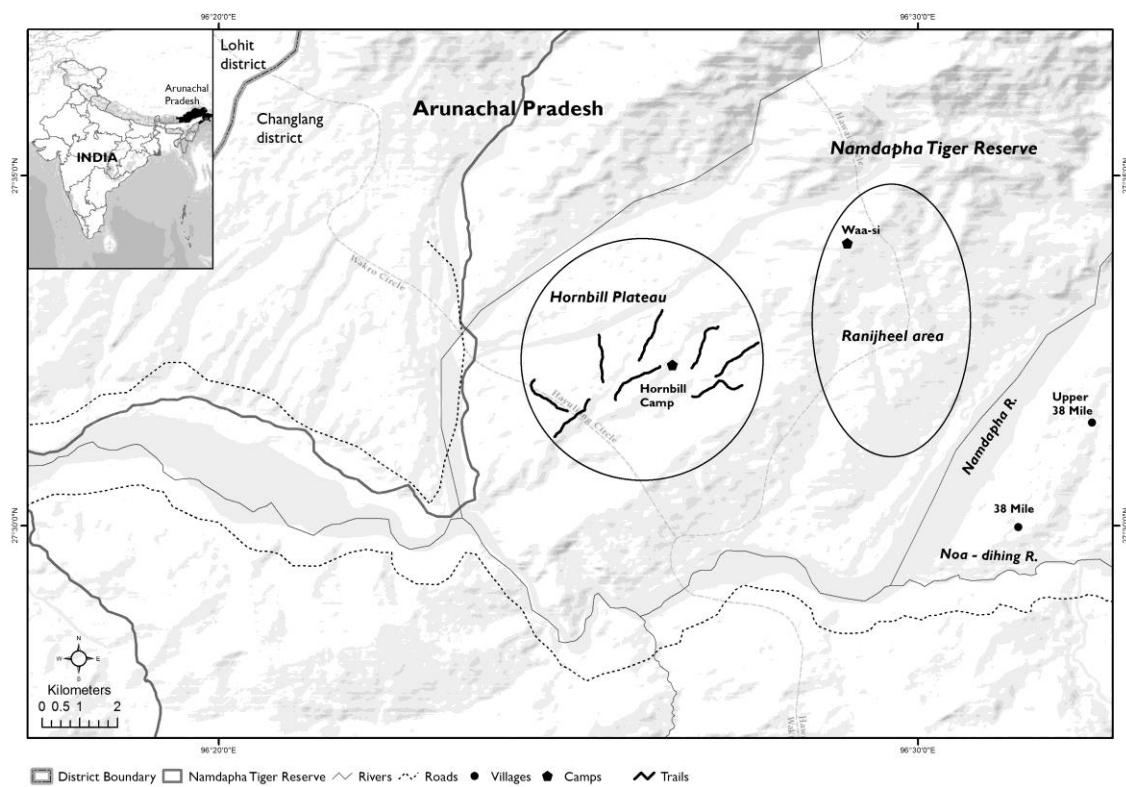
hornbill abundance, 2) at the scale of different sites within this study area, by investigating relationship between fruit abundance and hornbill abundance and 3) at the scale of fruiting tree, by examining the relationship between fruit crop size and hornbill visitation patterns. To this end, we first document the diets of the three species and also compare inter-specific differences in visitation rates and visitation lengths of hornbills. We further explored the implications of diet, visitation patterns and hornbill abundance in determining the role and importance of the three hornbill species as seed dispersers.

### 3.3 METHODS

#### *Study area*

We collected data in the non-breeding season of hornbills (November–March) between November 2009–February 2012 on a 15 km<sup>2</sup> plateau (550–800 m ASL) in the western portion of the Namdapha Tiger Reserve (27°23'30"–27°39'40"N and 96°15'2"–96°58'33"E; area: 1985 km<sup>2</sup>) in Arunachal Pradesh state in north-east India (Fig. 1). The tropical forests of the plateau are dominated by *Altingia excelsa*, *Shorea assamica*, *Terminalia myriocarpa*, *Schima wallichii*, *Beilschmiedia assamica*, *Castanopsis* spp., *Syzygium* spp., *Baccaurea ramiflora* and *Saprosma ternatum*. Four of the five hornbill species in Namdapha: the Great Hornbill (112–150 cm), Rufous-necked Hornbill (99–122 cm), Wreathed Hornbill (84–117 cm) and the White-throated Brown Hornbill *Anorrhinus austeni* (73–80 cm) occur on the plateau. The Oriental Pied hornbill *Anthracoceros albirostris* (60–85 cm) is mostly seen in degraded secondary forests and was rarely recorded on the plateau. Our paper focuses on the three larger hornbill species for which we had adequate observations. However, we also summarize limited foraging observations of White-throated Brown Hornbill as there is a lack of information of diet on this species from India. Hornbill densities are high, although they fluctuate over time (Naniwadekar and Datta 2013). Hornbills in this

area are reported to breed from April onwards (Datta 2009) and our sampling period constitutes the non-breeding season for these species.



**Figure 1** Map of the intensive study area showing the Hornbill Plateau where the fruit tree watches were conducted in the Namdapha Tiger Reserve. Eight trails that were monitored from 2010–12 are also shown.

*Temporal variation in fruit availability and hornbill encounter rates at the scale of the study area*

Considering that hornbill abundances fluctuate on the plateau ( $15 \text{ km}^2$ ) (Naniwadekar and Datta 2013), we assessed the temporal variability in fig and non-fig availability on the plateau. To estimate temporal fluctuation in fruit availability, we monitored 68 fruiting individuals of eight species of hornbill food plants in 2009–10 and 67 individuals of nine species (*Ficus drupacea* was additionally monitored) of hornbill food plants in 2010–11 (Table 1). For five species (*Beilschmiedia assamica*, *Canarium strictum*, *Machilus duthiei*, *Ficus cf. tsjahela*, *Dysoxylum* sp.), we monitored 10 individuals each. We monitored between 3–7 individuals for *Ficus drupacea*, *Chionanthus* sp., *Prunus ceylanica*, *Ficus cf. altissima* (Table 1). These nine species were

represented in 91% of the total number of foraging observations of hornbills (n=246) during time-constrained searches and line transect surveys, while an additional five species made up the remaining foraging observations. These nine species were monitored monthly from November–March in 2009–11. For non-fig fruiting trees, we estimated fruit crop sizes by visually dividing the canopy into four quarters and counting the number of fruits in one of them to estimate tree fruit crop size following Davidar and Morton (1986). For figs, where it was difficult to accurately count individual fruits, we estimated fruit crop size on a logarithmic scale (1,10,100,1000 and so on) following Kinnaird and O'Brien (2007). We also used this data to estimate proportion of trees in fruit in each month of monitoring. We estimated the density of each of the nine food plant species on the plateau using eight belt transects (1500 m × 20 m) along the trails that were sampled for monitoring hornbills from 2010–12 (Fig. 1). In these belt transects, we enumerated thirteen species of hornbill food trees ( $\geq 30$  cm girth at breast height). For estimating fruit availability of food plants for each of the ten months over the two years (November 2009–March 2010 and November 2010–March 2011), we summed the re-sampled (with replacement) estimated fruit availability across all the food plant species during each resample and took the median of 1000 re-samples. For each species, fruit availability in each resample was estimated by multiplying randomly drawn values for tree density, proportion of trees fruiting and the fruit crop size for the respective months. Random values for tree density were drawn assuming normal distribution with mean and standard deviation for each food plant species as determined using belt transects. Random values for proportion of trees fruiting were determined using binomial distribution for the number of trees monitored for each species and proportion of trees that were fruiting in each month. Random values for fruit crop size were determined using a Poisson distribution with mean fruit crop size for each species estimated by averaging the fruit crop sizes of trees that were in fruit for that month. Thus, we estimated the fruit availability for figs and non-fig fruit species separately. For figs,

we estimated fruit availability for two species in 2009–10 and for three species in 2010–11.

We marked and monitored two trails in 2009–10 and eight trails from 2010–11. Our sampling effort was 72 km in 2009–10 and 232.5 km in 2010–11. One or two observers walked the trails in the mornings (0545–1030 hr) and evenings (1200–1600 hr) and recorded hornbill species identity and number of individuals seen during the walk. We estimated the mean and bootstrapped 95% confidence intervals (CI) of encounter rates of the three hornbill species for each month.

**Table 1** Species and number of trees monitored monthly for fruit crops across two years (2009–10 and 2010–11).

Species	Family	Years monitored	No. of individuals monitored in each year
<i>Beilschmiedia assamica</i>	Lauraceae	2009–10, 2010–11	10,10
<i>Canarium strictum</i>	Burseraceae	2009–10, 2010–11	10, 10
<i>Chionanthus</i> sp.	Oleaceae	2009–10, 2010–11	4, 4
<i>Dysoxylum</i> sp.	Meliaceae	2009–10, 2010–11	10, 10
<i>Ficus</i> cf. <i>altissima</i>	Moraceae	2009–10, 2010–11	7, 6
<i>Ficus drupacea</i>	Moraceae	2010–11	3
<i>Ficus</i> . cf. <i>tsjahela</i>	Moraceae	2009–10, 2010–11	10, 10
<i>Machilus duthiei</i>	Lauraceae	2009–10, 2010–11	10, 10
<i>Prunus ceylanica</i>	Rosaceae	2009–10, 2010–11	7, 4

*Relationship between fruit availability and hornbill encounter rates across different trails*

Along the eight trails that were monitored in 2010–11, we had collected information on abundance of hornbill food plant species ( $\geq 30$  cm dbh) and hornbills along the entire length of the trail. Data on proportion of trees fruiting and the mean fruit crop size for each species for each month was available as has been described in the previous section. We therefore estimated fruit availability along each trail for each of the five months (November–March) by multiplying data on number of trees along each trail with data obtained from tree monitoring (described in the previous section) that included proportion of trees fruiting and the mean fruit crop size for each month. We estimated fruit availability for figs and non-figs separately.

We used Generalized Linear Mixed-effect Models (GLMM) with Poisson errors to understand the relationship between counts of hornbills visually sighted along each trail and with fig and non-fig fruit availability separately. There were differences in counts of hornbills across the five months and across the different trails (Table 2), therefore, we incorporated effects of month and trail as random effects in the model. We defined a candidate set of four models with the two predictor variables (fig and non-fig fruit availability) used singly and in conjunction (Johnson and Omland 2004). The candidate set also included an only-intercept model without any predictor for evaluating the influence of predictors on the response variable. The GLMM with trail and month as random effects and fig and non-fig fruit availability as fixed effects indicated over-dispersion in the data. We, therefore, incorporated effects of individual observations as an additional random effect in the model following Elston et al. (2001). We used the Information-theoretic framework for optimal model selection (Burnham and Anderson 2002). The model with the least AIC<sub>c</sub> (Akaike Information Criterion corrected for finite sample size) value was chosen as the optimal model (Burnham and Anderson 2002).

**Table 2** Number of sightings of the three hornbill species across months and trails.

<b>Trail</b>	<b>Great Hornbill</b>	<b>Rufous-necked Hornbill</b>	<b>Wreathed Hornbill</b>	<b>Effort</b>
<b>1</b>	6	6	19	28.5
<b>2</b>	6	6	104	34.5
<b>3</b>	6	4	58	25.5
<b>4</b>	1	5	13	27
<b>5</b>	6	5	37	30
<b>6</b>	9	15	243	28.5
<b>7</b>	3	8	28	28.5
<b>8</b>	2	9	12	30
<b>Month</b>	<b>Great Hornbill</b>	<b>Rufous-necked Hornbill</b>	<b>Wreathed Hornbill</b>	<b>Effort</b>
<b>November</b>	8	4	160	22.5
<b>December</b>	5	2	300	39
<b>January</b>	4	14	37	64.5
<b>February</b>	3	10	10	45
<b>March</b>	19	28	7	61.5

### *Hornbill visitation on fruiting trees*

We conducted 55 fruit tree watches under fruiting fig (n=22; 4 species) and non-fig (n=33; 10 species) trees (Table 3). These fruit tree watches were conducted over the last two years (2010–2012) from November–March each year. We observed the fruiting trees in the morning (0520–1100 hr) and in the afternoon (1230–1545 hr) sitting just beyond the canopy to obtain a clear and maximum view of the entire tree. We abandoned a fruit tree watch if it rained, or if there was disturbance due to

human movement around the fruiting tree. At the onset of each fruit tree watch, we enumerated the number of ripe fruits. During the fruit tree watch, we recorded hornbill species, number of individuals and their arrival and departure times from the focal tree. Hornbill abundances in the study area varied across different months, this could influence the visitation rates on fruiting trees. Therefore, we used ambient hornbill encounter rates (as estimated for each month) for each species as an index for hornbill abundance on the plateau for that particular month. We assumed that encounter rates estimated for a month reflect the ambient hornbill abundance. This measure was used as a predictor for a fruit tree watch that was conducted on a single day. Two trails were monitored in 2009–10 (effort=72 km) while eight trails were monitored in 2010–11 (effort=232.5km) and 2011–12 (effort=144 km). The mean effort per month was 32.3 km (SE:  $\pm$  5.6 km). Based on the month in which the fruit tree watch was carried out, we used the corresponding estimate of the encounter rate of the particular hornbill species for that month.

**Table 3** Hornbill food plant species, fruit type and number of fruit tree watches that were conducted across three years (2009–2012) in the intensive study area (Hornbill plateau) in Namdapha Tiger Reserve.

Species (Family)	Fruit type	Fruiting period	Number of fruit tree watches
<i>Ficus cf. altissima</i> (Moraceae)	Fig	Nov–Mar	2
<i>Ficus drupacea</i> (Moraceae)	Fig	Nov–Mar	4
<i>Ficus nervosa</i> (Moraceae)	Fig	Jan–Apr	1
<i>Ficus cf. tsjahela</i> (Moraceae)	Fig	Nov–Mar	15
<i>Dysoxylum</i> sp. (Meliaceae)	Non-fig: Arillate dehiscent capsule	Jan–Apr	3
<i>Beilschmiedia assamica</i> (Lauraceae)	Non-fig: Drupe	Oct–Feb	4
<i>Beilschmiedia roxburghiana</i> (Lauraceae)	Non-fig: Drupe	Dec–Apr	2
<i>Canarium strictum</i> (Burseraceae)	Non-fig: Drupe	Nov–Apr	4
<i>Chionanthus</i> sp. (Oleaceae)	Non-fig: Drupe	Nov–Apr	2
<i>Machilus duthiei</i> (Lauraceae)	Non-fig: Drupe	Nov–Mar	2
<i>Alseodaphne petiolaris</i> (Lauraceae)	Non-fig: Drupe	Oct–Jan	5
<i>Phoebe</i> sp. (Lauraceae)	Non-fig: Drupe	Oct–Jan	6
<i>Phoebe cooperiana</i> (Lauraceae)	Non-fig: Drupe	?–Nov	1
<i>Prunus ceylanica</i> (Rosaceae)	Non-fig: Drupe	Nov–Mar	4

We compared visitation rates of the each of the three hornbill species on figs and non-figs separately. We carried out separate analysis for the fruiting figs and non-figs as they differ in fruit crop size and seed size. We used mixture models to determine the role of fruit crop size and ambient hornbill encounter rates on visitation patterns of the three hornbill species on fruiting fig and non-fig trees. The motivation behind using mixture models was the presence of excess zeroes in hornbill visitations on fruiting trees. In mixture models, the zeroes are modeled from the count and the binomial process (Zuur et al. 2009). We defined four candidate models with the two predictor variables, fruit crop size and ambient hornbill encounter rates and an intercept-only model. We evaluated these four candidate models with mixture models with Poisson and negative-binomial error structure and ranked them using Akaike's Information Criterion adjusted for small samples ( $AIC_c$ ). We estimated model-averaged coefficients. We interpreted those coefficients for which the 95% confidence intervals did not overlap with zero. We carried out this analysis for all the three hornbill species on fruiting fig trees, however, on non-fig trees, we carried out this analysis only for the Rufous-necked Hornbill since we had limited sightings for the other two species on non-fig fruiting trees (Great Hornbill: 5, Wreathed Hornbill: 7). All the analysis was carried out in R (ver. 3.01.). We used the packages 'lme4' (Bates and Sarkar 2007), 'pscl' (Zeileis et al. 2007), and 'MuMIn'(Barton 2009) for generalized mixed effects modeling, mixture modeling and model averaging respectively.

### 3.4 RESULTS

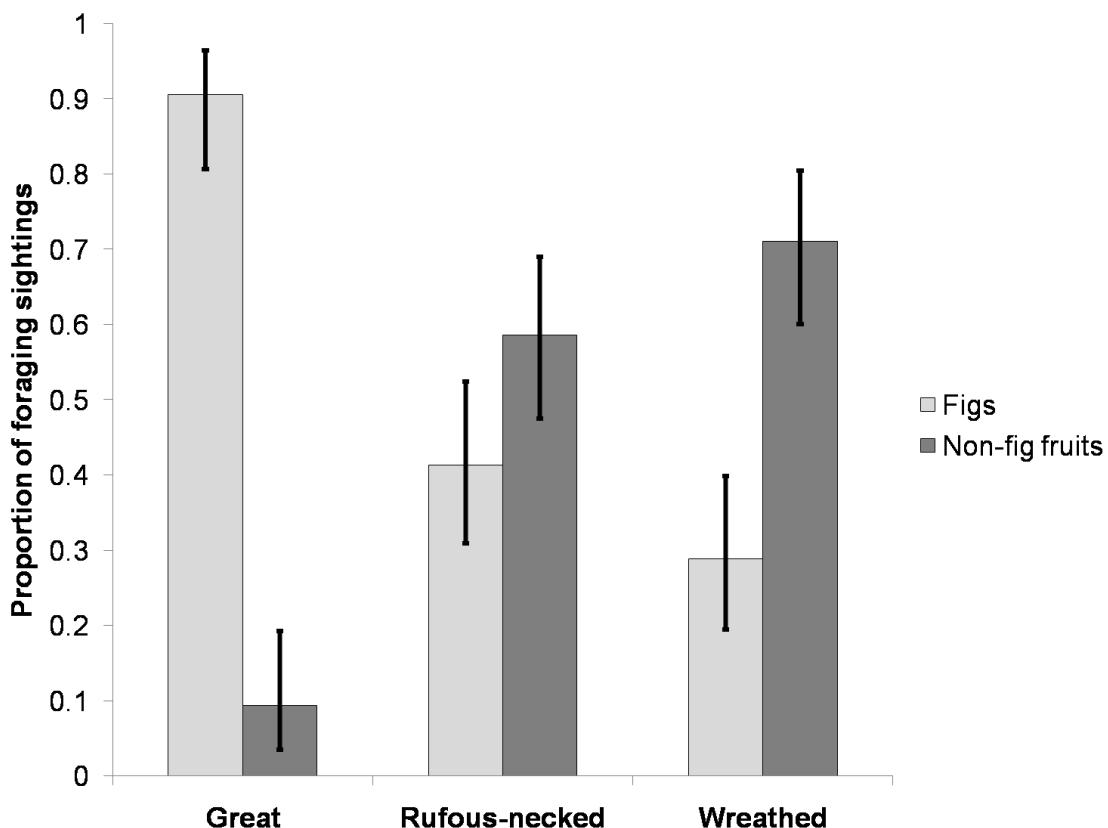
#### *Hornbill diet*

Across the two sampling sessions (2009–11) in the non-breeding season, we identified 20 species of plants belonging to seven families. Lauraceae and Moraceae had the highest representation (Table 4). While Great and Wreathed Hornbill were seen foraging on nine and ten species each, Rufous-necked Hornbill was seen

foraging on 17 species (Table 4). The standardized Levin's niche breadth for the Rufous-necked Hornbill (0.61) was more than 1.5 times that of the Wreathed (0.37) and more than twice that of the Great Hornbill (0.30). Of the total foraging observations on fruits, we saw Wreathed Hornbills feeding on non-fig fruits more than on figs and Great Hornbills feeding on figs more than on non-fig fruits (Fig. 2). While the mean proportion of sightings of Rufous-necked Hornbill feeding on non-fig fruits was more than that of fig fruits, the 95% CI overlapped (Fig. 2). Great Hornbills were observed peeling bark of *Terminalia myriocarpa* on two occasions, possibly foraging for insects. White-throated Brown Hornbill was seen foraging on 12 occasions on 8 different species of plants. They were seen foraging on non-fig fruit items on six of the 12 occasions (Table 4). In addition, we saw White-throated Brown Hornbill foraging on an unidentified large (> 10 cm) katydid.

**Table 4** Summary of number of hornbill sightings seen overall and foraging on different plant species for the three large hornbill species during trail walks and searches.

	Family	Great Hornbill	Wreathed Hornbill	Rufous-necked Hornbill	Brown Hornbill
Total sightings		126	179	220	57
Foraging sightings		64	83	87	12
<i>Beilschmiedia assamica</i>	Lauraceae	0	10	5	3
<i>Beilschmiedia</i> sp.	Lauraceae	0	0	1	0
<i>Beilschmiedia roxburghiana</i>	Lauraceae	0	0	3	0
<i>Machilus duthiei</i>	Lauraceae	1	7	7	0
<i>Phoebe</i> sp.	Lauraceae	0	1	0	0
<i>Cryptocarya</i> sp.	Lauraceae	0	1	3	0
<i>Canarium strictum</i>	Burseraceae	1	34	10	0
<i>Prunus ceylanica</i>	Rosaceae	0	5	11	2
<i>Chisocheton paniculata</i>	Meliaceae	1	0	0	0
<i>Dysoxylum</i> sp.	Meliaceae	3	0	5	0
<i>Chionanthus</i> sp.	Oleaceae	0	1	3	0
Unidentified sp.	Mimosaceae	0	0	3	0
<i>Ficus</i> cf. <i>tsjahela</i>	Moraceae	29	14	11	2
<i>Ficus altissima</i>	Moraceae	15	3	11	1
<i>Ficus drupacea</i>	Moraceae	11	7	10	1
<i>Ficus microcarpa</i>	Moraceae	0	0	1	1
<i>Ficus</i> sp.1	Moraceae	1	0	1	0
<i>Ficus</i> sp.2	Moraceae	0	0	1	0
<i>Ficus</i> sp.3	Moraceae	2	0	1	1
Unidentified climber		0	0	0	1



**Figure 2** Binomial means and 95% confidence intervals of proportion of foraging sightings of the three hornbill species (Great, Rufous-necked and Wreathed) on fig receptacles and non-fig fruits.

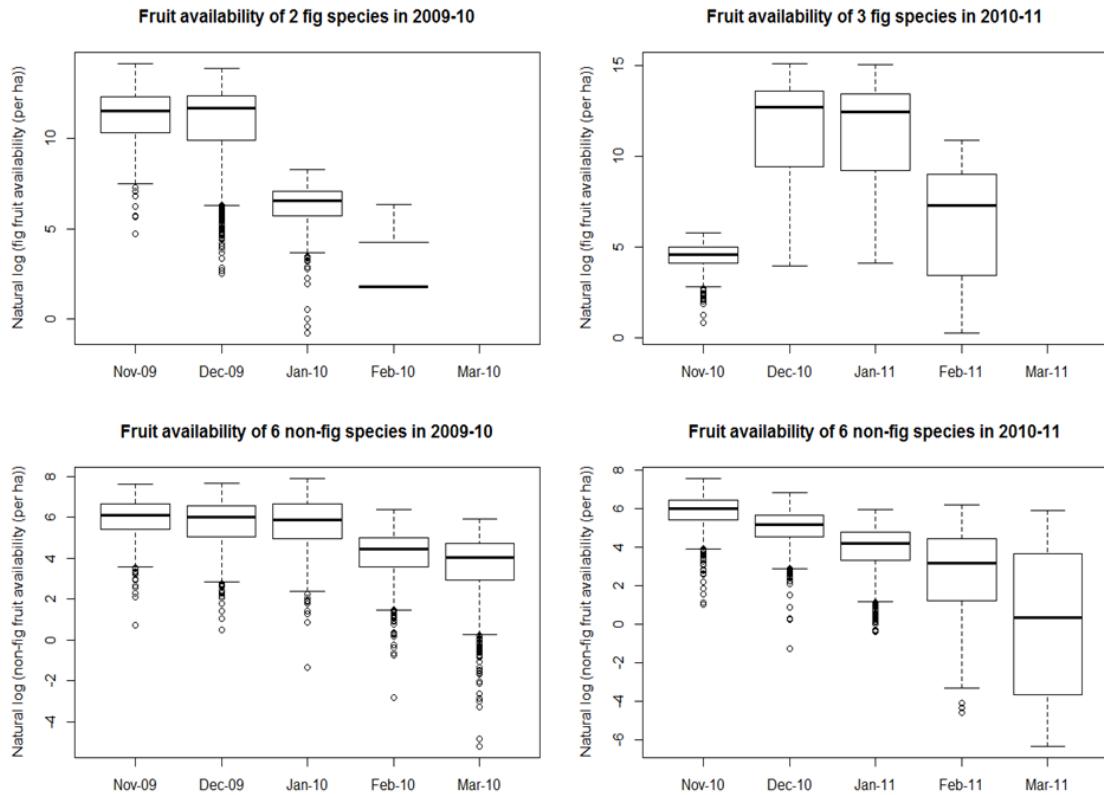
*Patterns in fruiting and hornbill encounter rates across different trails on the intensive study site*

We recorded 13 species of non-fig hornbill food plants in the belt transects. Their mean ( $\pm$  SE) densities ranged from 0.04 ( $\pm$  0.04) trees/ha for *Canarium strictum* and *Aglaia* sp. to 2.5 ( $\pm$  0.8) trees/ha for *Beilschmiedia assamica*. The total density of all the 13 species of non-fig hornbill food plants was 5.7 ( $\pm$  2.4) trees/ha. Of the 118 sightings of hornbills feeding on seven species of figs, 111 were on these three species. The mean ( $\pm$  SE) densities of three species of figs (*Ficus* cf. *tsjahela*, *Ficus* cf. *altissima* and *Ficus drupacea*) of the seven on which hornbills were seen foraging ranged from 0.2 ( $\pm$  0.1) to 0.4 ( $\pm$  0.2) trees/ha. The total density of these three fig species was 0.8 ( $\pm$  0.4) trees/ha.

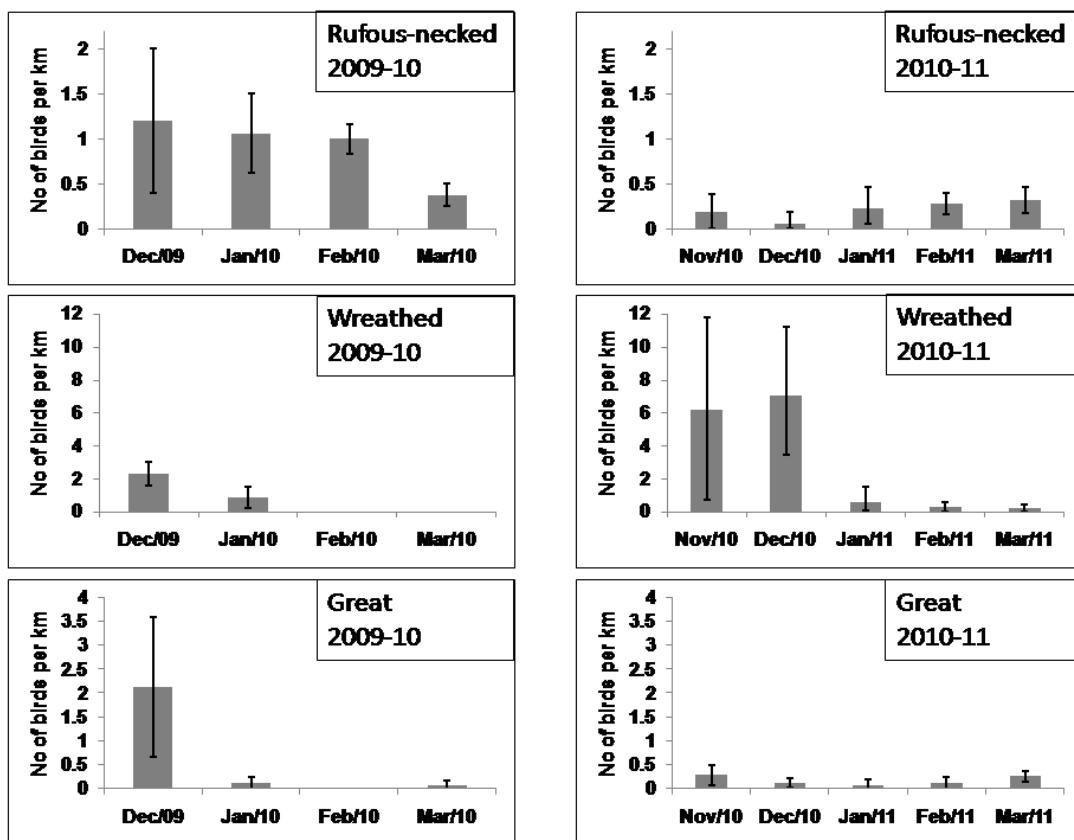
Median (inter-quartile range) fruit availability of two species of figs ranged from 0 to 1,19,700 (20,650–2,32,300) fig receptacles per ha between November 2009–March 2010 and from 0 to 3,27,500 (12,390–7,85,400) fig receptacles per ha for three species of figs between November 2010 and March 2011 (Fig. 3). In both years, the highest median value of fig availability was in the month of December (Fig.3).

The bootstrapped median (inter-quartile range) fruit availability of non-fig fruits ranged from 57 (19–111) to 450 (223–753) fruits per ha in 2009–10 and 1 (0–39) to 408 (226–619) fruits per ha in 2010–11 (Fig. 3). The highest median value for non-fig fruit availability (six species) was in November in 2009–10 and in December in 2010–11.

Hornbill encounter rates differed between sampling sessions (2009–10 and 2010–11) and species. In the case of Wreathed Hornbills, the mean encounter rates declined from December to April consistently across the two years (Fig. 4). Mean encounter rates of Rufous-necked and Great Hornbills declined from December to April in 2009–10 but not in 2010–11 (Fig. 4).



**Figure 3** Natural logarithm of re-sampled ( $n = 1000$  resamples) estimates of fruit availability of fig tree species (two species in 2009–10; three species in 2010–11) and six non-fig tree species across the winter months (Nov to Mar) of two years (2009–11). These nine tree species constituted 91% of the total foraging sightings of hornbills.



**Figure 4** Mean and bootstrapped 95% confidence intervals ( $n = 1000$  bootstraps) of the encounter rates of the three hornbill species, Rufous-necked, Wreathed and Great, across the winter months (December to March) of two years (2009–11).

*Relationship between fruit availability and hornbill abundance across different trails*

There was considerable variation in hornbill detections over space and time as has been summarized in Table 2. We did not find any relationship between Great Hornbill abundance and availability of either figs or non-figs. The intercept-only model was the one with the least AIC<sub>c</sub> value (Table 5a). The 95% CI on the estimates of both fig and non-fig fruit availability overlapped zero (Table 6). However, for Wreathed Hornbills, the model with non-fig fruit availability had the least AIC<sub>c</sub> value (Table 5b). We found a positive relationship between non-fig fruit availability and Wreathed Hornbill abundance. The 95% CI on the estimate of non-fig fruit availability did not overlap zero and its relative variable importance value was 0.69 (Table 6). Interestingly, for the Rufous-necked Hornbill too, the model with non-fig fruit availability had the least AIC<sub>c</sub> value (Table 5c). However, the abundance of Rufous-necked Hornbill was negatively associated with non-fig fruit availability indicating that Rufous-necked Hornbills avoided areas that had greater availability of non-fig fruits (Table 6).

**Table 5** The structure of the different candidate models and  $\Delta AIC_c$  value to identify the influence of fig and non-fig fruit availability on hornbill abundance for a) Great Hornbills, b) Wreathed Hornbills and c) Rufous-necked Hornbills

**Table 5a**

No	Structure	df	AIC <sub>c</sub>	$\Delta AIC_c$
1	Great Hornbill abundance ~ 1	4	113.64	0
2	Great Hornbill abundance ~ Fig fruit availability	5	113.97	0.33
3	Great Hornbill abundance ~ Non-fig fruit availability	5	116.11	2.47
4	Great Hornbill abundance ~ Fig fruit availability + Non-fig fruit availability	6	116.76	3.12

**Table 5b**

No	Structure	df	AIC <sub>c</sub>	$\Delta AIC_c$
1	Wreathed Hornbill abundance ~ Non-fig fruit availability	5	212.77	0
2	Wreathed Hornbill abundance ~ 1	4	214.49	1.72
3	Wreathed Hornbill abundance ~ Fig fruit availability + Non-fig fruit availability	6	215.22	2.45
4	Wreathed Hornbill abundance ~ Fig fruit availability	5	216.39	3.63

**Table 5c**

No	Structure	df	AIC <sub>c</sub>	$\Delta AIC_c$
1	Rufous-necked Hornbill abundance ~ Non-fig fruit availability	5	133.4	0
2	Rufous-necked Hornbill abundance ~ 1	4	134.78	1.38
3	Rufous-necked Hornbill abundance ~ Fig fruit availability + Non-fig fruit availability	6	136.14	2.74
4	Rufous-necked Hornbill abundance ~ Fig fruit availability	5	136.94	3.54

**Table 6** Model averaged coefficients, their associated 95% CI and the relative variable importance values for models examining the relationship between hornbill abundance and fig and non-fig fruit availability for the three hornbill species, Great, Wreathed and Rufous-necked Hornbill.

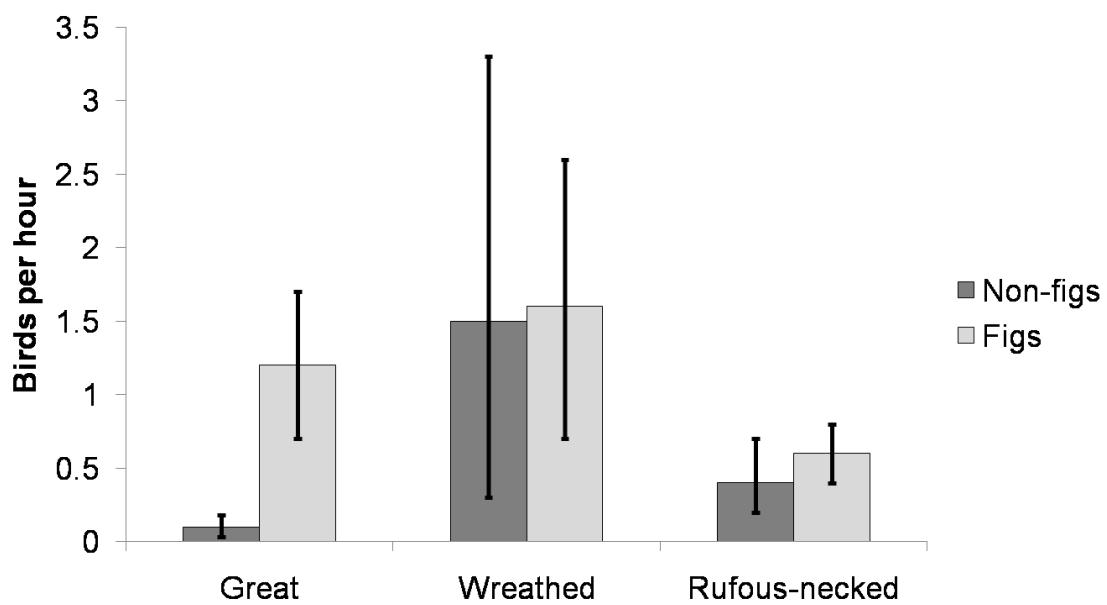
Hornbill species	Variable	Relative importance	Estimate	95% LCI	95% UCI
Great	Intercept		-2.15	-3.04	-1.26
	Fig fruit availability	0.45	-0.08	-0.19	0.18
	Non-fig fruit availability	0.21	-0.02	-0.27	0.23
Wreathed	Intercept		-4.18	-6.69	-1.67
	Fig fruit availability	0.24	0.06	-0.11	0.23
	Non-fig fruit availability	0.69	0.72	0.31	1.14
Rufous-necked	Intercept		-1.43	-2.28	-0.59
	Fig fruit availability	0.22	0.03	-0.06	0.12
	Non-fig fruit availability	0.65	-0.19	-0.37	-0.02

### *Hornbill visitation on fruiting fig and non-fig trees*

We detected hornbills in 38 out of the 55 total fruit tree watches. Great Hornbills were detected in 20 fruit tree watches, Rufous-necked Hornbills in 22, and Wreathed Hornbills in 18. In the 22 fruit tree watches on fruiting figs, we detected hornbills in 20, while we detected hornbills in 18 out of the 33 fruit tree watches on non-fig fruiting trees. Rufous-necked Hornbill was detected on 11 of the 14 species observed in the fruit tree watches while Wreathed and Great Hornbills were detected on nine species. The visitation rate on fruiting figs and fruiting non-fig trees of Rufous-necked hornbill and Wreathed Hornbill was similar (Fig. 5) while the visitation rate of Great Hornbills was higher on figs as compared to non-fig fruiting plants (Fig. 5). The median visitation length on fruiting figs of Great Hornbill was 21 min (range: 2–192 min, n=50), Rufous-necked Hornbills was 26 min (range: 2–74 min, n=24) and Wreathed Hornbills was 23 min (range: 1–73 min, n=67). The median visitation length of Great Hornbills on fruiting non-fig trees was 17 min (range: 2–24 min, n=11), Rufous-necked Hornbills was 10 min (range: 1–45 min, n=20), and Wreathed Hornbills was 45 min (range: 2–81 min, n=55).

Fruit crop size of fruiting figs explained the variation in the visitation rates of Great Hornbills. Visitation rates of Great Hornbills on fruiting figs were positively associated with ripe fruit crop size. The top two models within 2  $\Delta\text{AIC}_c$  units had both fruit crop size as the only predictor (Table 7a). The relative variable importance of ripe fruit crop size of figs was 0.84 (Table 8). The 95% CI on the estimate also did not overlap zero (Table 8). Visitation rates of Wreathed and Rufous-necked Hornbills were not associated with ripe fig fruit crop size (Table 8). The intercept-only models were the top models with the least  $\text{AIC}_c$  value (Table 7b and 7c). Ripe fruit crop size of figs has a relatively low variable importance (< 0.35) and the 95% CI on the estimate for the ripe fruit crop size also overlapped zero for Wreathed and Rufous-necked Hornbills. For non-fig fruiting trees, visitation rates of Rufous-necked Hornbill were positively associated with ripe fruit crop size. The model with the

least AIC<sub>c</sub> value was the one with fruit crop size as the predictor (Table 7d). The model-averaged weight of the fruit crop size was 0.56 and the 95% CI on the estimate of fruit crop size also did not overlap zero (Table 8).



**Figure 5** Mean and bootstrapped 95% confidence intervals ( $n = 1000$  bootstraps) of the visitation rates of the three hornbill species, Great, Wreathed and Rufous-necked, across fruiting fig and non-fig food plants.

**Table 7** The structure of the different candidate models along with model type (Zero-inflated Poisson (ZIP) or Zero-inflated Negative Binomial (ZINB)) and  $\Delta AIC_c$  value to identify the influence of fruit crop size and ambient hornbill encounter rate on a) Great Hornbills on figs, b) Wreathed Hornbills on figs, c) Rufous-necked Hornbills on figs and d) Rufous-necked on non-fig fruiting trees. Analysis for Great and Wreathed Hornbill visitation rates on non-fig fruiting trees was not carried out due to limited detections.

**Table 7a**

No.	Structure	Model	df	AIC <sub>c</sub>	$\Delta AIC_c$
1	Great hornbill visitation ~ Fruit crop size	ZIP	3	109.14	0.00
2	Great hornbill visitation ~ Fruit crop size	ZINB	4	109.24	0.10
3	Great hornbill visitation ~ Fruit crop size + ambient great hornbill encounter rate	ZIP	4	111.59	2.45
4	Great hornbill visitation ~ Ambient great hornbill encounter rate	ZINB	4	112.02	2.88
5	Great hornbill visitation ~ Fruit crop size + ambient great hornbill encounter rate	ZINB	5	112.16	3.02
6	Great hornbill visitation ~ 1	ZINB	3	113.69	4.55
7	Great hornbill visitation ~ Ambient great hornbill encounter rate	ZIP	3	119.22	10.08
8	Great hornbill visitation ~ 1	ZIP	2	130.37	21.23

**Table 7b**

No.	Structure	Model	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
1	Wreathed Hornbill visitation ~ 1	ZINB	3	112.10	0.00
2	Wreathed hornbill visitation ~ Fruit crop size	ZINB	4	113.39	1.29
3	Wreathed hornbill visitation ~ Ambient Wreathed Hornbill encounter rate	ZINB	4	114.01	1.91
4	Wreathed hornbill visitation ~ Fruit crop size + ambient Wreathed hornbill encounter rate	ZINB	5	115.53	3.43
5	Wreathed hornbill visitation ~ Fruit crop size	ZIP	3	164.19	52.09
6	Wreathed hornbill visitation ~ Fruit crop size + ambient Wreathed hornbill encounter rate	ZIP	4	166.93	54.83
7	Wreathed hornbill visitation ~ Ambient Wreathed hornbill encounter rate	ZIP	3	189.90	77.80
8	Wreathed hornbill visitation ~ 1	ZIP	2	190.35	78.25

**Table 7c**

No.	Structure	Model	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
1	Rufous-necked hornbill visitation ~ 1	ZIP	2	78.51	0.00
2	Rufous-necked hornbill visitation ~ Fruit crop size	ZIP	3	80.40	1.89
3	Rufous-necked hornbill visitation ~ Ambient Rufous-necked hornbill encounter rate	ZIP	3	80.44	1.93
4	Rufous-necked hornbill visitation ~ Fruit crop size + ambient Rufous-necked hornbill encounter rate	ZIP	4	80.98	2.47
5	Rufous-necked hornbill visitation ~ 1	ZINB	3	81.21	2.70
6	Rufous-necked hornbill visitation ~ Fruit crop size	ZINB	4	83.42	4.91
7	Rufous-necked hornbill visitation ~ Ambient Rufous-necked hornbill encounter rate	ZINB	4	83.46	4.95
8	Rufous-necked hornbill visitation ~ Fruit crop size + ambient Rufous-necked hornbill encounter rate	ZINB	5	84.37	5.86

**Table 7d**

No.	Structure	Model	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
1	Rufous-necked hornbill visitation ~ Fruit crop size	ZINB	4	93.79	0.00
2	Rufous-necked hornbill visitation ~ Ambient Rufous-necked hornbill encounter rate	ZINB	4	94.12	0.33
3	Rufous-necked hornbill visitation ~ 1	ZINB	3	94.37	0.57
4	Rufous-necked hornbill visitation ~ Fruit crop size	ZIP	3	95.07	1.27
5	Rufous-necked hornbill visitation ~ Fruit crop size + ambient Rufous-necked hornbill encounter rate	ZINB	5	96.07	2.27
6	Rufous-necked hornbill visitation ~ Fruit crop size + ambient Rufous-necked hornbill encounter rate	ZIP	4	97.41	3.62
7	Rufous-necked hornbill visitation ~ 1	ZIP	2	103.83	10.03
8	Rufous-necked hornbill visitation ~ Ambient Rufous-necked hornbill encounter rate	ZIP	3	104.01	10.22

**Table 8** Model averaged coefficients, their associated 95% CI and the relative variable importance values of the two predictors for models examining visitation rates of the three hornbill species (Great, Wreathed and Rufous-necked) as a function of ambient hornbill encounter rates and/or ripe fruit crop size (natural logarithm) for two different fruit types (fig and non-fig trees). Analysis for Great and Wreathed Hornbill visitation rates on non-fig fruiting trees was not carried out due to limited detections.

Hornbill species	Fruit type	Variable	Relative importance	Estimate	95% LCI	95% UCI
Great	Fig	Count(fruit crop size)	0.88	0.23	0.1	0.37
		Count(Ambient Great Hornbill encounter rate)	0.27	0.29	-0.36	0.95
		Count(Intercept)	-	-2.10	-4.23	0.03
		Zero(Intercept)	-	-1.72	-89.46	86.01
Wreathed	Fig	Count(fruit crop size)	0.34	-0.16	-0.36	0.05
		Count(Ambient Wreathed Hornbill encounter rate)	0.27	0.13	-0.18	0.45
		Count(Intercept)		1.44	-1.18	4.06
		Zero(Intercept)		-0.51	-3.25	2.24
Rufous-necked	Fig	Count(fruit crop size)	0.32	-0.07	-0.21	0.06
		Count(Ambient Rufous-necked Hornbill encounter rate)	0.32	0.50	-0.41	1.42
		Count(Intercept)	-	0.23	-0.83	1.29
		Zero(Intercept)	-	-0.11	-1.00	0.78

Hornbill species	Fruit type	Variable	Relative importance	Estimate	95% LCI	95% UCI
Rufous-necked	Non-fig	Count(fruit crop size)	0.56	0.59	0.09	1.10
		Count(Ambient Rufous-necked Hornbill encounter rate)	0.37	1.56	-1.31	4.36
		Count(Intercept)	-	-2.74	-6.53	1.05
		Zero(Intercept)	-	-2.01	- 81.98	77.97

### 3.5 DISCUSSION

We found that the sympatric hornbill species differed in their diets and in the spatial scale at which they track their shared resources. Resource tracking in the three hornbill species was associated with their diets. Species having greater representation of figs in their diets (Great Hornbill) tracked fig fruit availability, while species with greater representation of non-figs in their diet (Wreathed and Rufous-necked Hornbill) tracked non-fig fruit availability albeit at different scales. Wreathed and Rufous-necked Hornbills, which have similar body size and diets, have contrasting patterns of resource tracking. The Rufous-necked Hornbill tracked non-fig fruit availability at the smaller scale of a fruiting tree while the Wreathed Hornbill responded to consistent temporal fluctuations in fruit availability at the intensive study site. Additionally, at the intermediate scale, across different trails in the intensive study site, we found that while Wreathed Hornbill abundance was positively associated with non-fig fruit availability, Rufous-necked Hornbill abundance was negatively associated with non-fig fruit availability.

Sympatric hornbills are known to differ in their diets. While diets of the *Buceros* hornbills are known to be dominated by figs, diets of other genera like *Anorrhinus*, *Aceros* and *Rhyticeros* have greater representation of non-fig fruits that include drupes and arillate dehiscent capsular fruits (Datta and Rawat 2003, Hadiprakarsa and Kinnaird 2004, Kinnaird and O'Brien 2007, Datta 2009). Consistent with these findings, we found that Great Hornbills consumed more figs in their diet while Wreathed and Rufous-necked Hornbills consumed more non-fig fruits in their diets.

#### *How are they tracking resources?*

Two assumptions outlined by Guitian and Munilla (2008) that need to be met in studies focusing on resource tracking by frugivores are that fruits should significantly contribute to the diet of frugivores under focus and fruit production data should be comprehensive and include all the species that can potentially play

an important role in the diet of the frugivores. Our study meets both these assumptions as hornbills are highly frugivorous and our observations include all food plant species that comprise more than 90% of the diet of the three hornbill species.

Given this background, it is interesting to understand the mechanism through which the three hornbill species track their fruit resources. As documented in this study and as has been documented in several past studies (Jordano 1992, Herrera 1998), fruit availability varied across trees, across different sites in the intensive study area and across time over the entire study area. The type of diet appears to play an important role in resource tracking by hornbills, with Wreathed and Rufous-necked Hornbill that had higher representation of non-fig fruits in their diet exhibiting positive relationships with non-fig fruit abundance, while Great Hornbills showed positive relationships with fig fruit abundance albeit at differing scales.

Jetz et al. (2004) suggest that one of the consequences of sharing a resource with competitors is increased home range size. Such behaviour of increased movement should be observed during lean resource periods when there is greater likelihood of competition with other sympatric species. In our study area, the Wreathed Hornbill appears to range over large area which is likely to be a consequence of tracking areas with resource patches with high fruit availability at a large scale. At the largest scale, the peak fruit availability in the middle elevation forest site (500–800 m) of Namdapha was in the months of November–December (winter). Incidentally, this is exactly opposite to that of fruit availability patterns in the lower elevation forests (100 to 300 m). Datta and Rawat (2003) found that during winter, fruit availability in lower elevation forests is low. Thus during the non-breeding season of hornbills (winter months), the lean period in fruit availability in the lower elevation forests coincides with the high fruiting period in the middle elevation forests. Wreathed Hornbills are known to breed in lower elevation forests (Datta and Rawat 2004, Datta 2009). There are no records of Wreathed Hornbills breeding in Namdapha and

our long-term abundance data clearly indicates that Wreathed Hornbills leave Namdapha prior to the onset of the breeding season in March (Datta 2009, Naniwadekar and Datta 2013). Thus, in conjunction with the available data on fruit abundance in lower elevation forests during the non-breeding season of hornbills and the data collected in this study, it appears that Wreathed Hornbills track the peak in fruit availability across the elevation gradient. This possibly explains the long-ranging movement patterns of Wreathed Hornbills which are amongst the highest in Asian hornbills (Keartumsom et al. 2011). For the Rufous-necked and Great Hornbills, we did not see consistent patterns of variation in abundance that matches the fruit availability at the largest scale and these species are unlikely to show predictable movement across elevation. Rufous-necked Hornbill is known to breed in Namdapha (Datta 2009) but there are no reports of it breeding in the lower elevation forests of Arunachal as yet. While we documented similar overall trends in the fig fruit availability across the two years (except in the month of November), bird-consumed figs are generally known to have asynchronous fruiting (Shanahan et al. 2001). Fig fruiting is usually unpredictable over space and time. Great hornbills that mainly consume figs are therefore unlikely to demonstrate predictable movement patterns across large scales when their main fruit resource (figs) exhibit asynchronous fruiting patterns.

At the intermediate scale, where we investigated variation in hornbill abundances across different sites within our intensive study area, we found that sites with high abundances of Wreathed Hornbills also had higher non-fig fruit availability. This indicates that Wreathed Hornbills not only move across the elevation gradient but that they also choose areas with high fruit availability once they are in the middle elevation forest of the intensive study area. Additionally, as compared to the Rufous-necked Hornbill, Wreathed Hornbill had a smaller niche breadth (non-fig fruit species). It appears to depend on a smaller subset of non-fig fruiting plants in the non-breeding season as compared to the Rufous-necked Hornbill. Interestingly,

however, Rufous-necked Hornbill abundance was negatively associated with non-fig fruit availability.

Given that Rufous-necked hornbills do not show seasonal movements and are known to remain resident in smaller home ranges (Tifong et al. 2007), it is possible that during the non-breeding season, when Wreathed hornbill abundances are unusually high, the slightly smaller body-sized Rufous-necked hornbill diversifies its diet to include many more non-fig species to avoid competition with the numerically more abundant Wreathed hornbill at the intermediate scale. We have observed a single Wreathed Hornbill actively chasing a Rufous-necked Hornbill pair from a fruiting fig tree. However, whether the observed pattern of Rufous-necked Hornbill avoiding areas with high non-fig fruit availability that attract Wreathed Hornbills is a consequence of competition (interference/exploitative) remains speculative and needs further investigation.

Kinnaird and O'Brien (2007) suggest that hornbills could feed on trees with large crop sizes to maximize foraging efficiency. In accordance with the prediction, at the smallest scale we found a positive relationship between Great and Rufous-necked Hornbill visitation on fruiting figs and non-figs respectively. Both these hornbills therefore are more likely to visit trees with larger fruit crop sizes. Fruit crop size has been known to be an important factor governing visitation rates on fruiting trees (Saracco et al. 2005, Blendinger et al. 2008, Blendinger and Villegas 2011). For a frugivore, choosing trees with larger fruit crop sizes implies reduced need for moving between trees to find fruits thereby saving energy. Unfortunately, we could not explore the relationship between Wreathed and Great Hornbill visitation on fruiting non-figs due to limited data. For Great Hornbills, lower visitation on non-figs is a likely outcome of their dietary preference. Great Hornbills that were seen feeding mostly on figs also had higher visitation rates on figs as compared to non-figs.

*What are the implications of tracking resources at different scales?*

Kinnaird and O'Brien (2007) synthesized data on resource tracking by hornbills from several forest sites. They consistently found that hornbills tracked fig availability across these sites. In our study, we found that while some hornbill species track figs, some species also track non-fig fruit availability at varying scales. Non-fig fruit availability is a resource which is more predictable than figs. The finding that hornbill species track distinct resources at distinct scales has several implications for each of the hornbill species and for the ecological role they play as dispersers. Firstly, it is likely that the dietary differences and varying abundance patterns at different scales enables the three species to co-occur. One of the mechanisms for co-existence as suggested by Kotler and Brown (1988) is by trading-off travel cost and efficiency in patch foraging. Wreathed hornbills follow a strategy of tracking peak resource availability across the elevation gradient avoiding a period of low resource availability. Thus they are likely to trade-off patch foraging efficiency by incurring large travel costs of finding resources in rich areas across the elevation gradient. On the other hand, Rufous-necked Hornbill with similar diet to Wreathed Hornbill, reduce travel costs while increase foraging efficiency by diversifying their diet and selectively foraging on non-fig trees with larger fruit crops. For the more localized species that continue to remain in the site, periods of low resource availability might have a bearing on the densities and flock sizes in which the species can occur. Tracking peak fruit availability across the elevation gradient might enable Wreathed Hornbills to occur in high densities and to move in large flocks as resource abundance would tend to minimize pressures exerted by intra-specific competition. However, it remains to be understood whether resource tracking at such large scales emerged out of the need for living in flocks or whether flocking emerged as an outcome of tracking resources over large scales.

Tracking different kinds of resources at different scales also has an important bearing on the role played by each of the hornbill species in seed dispersal. Great

Hornbills had lower visitation rates on non-fig fruiting trees as compared to the Wreathed and Rufous-necked Hornbill, which implies that this species plays a limited role in dispersal of non-fig food plants of hornbills as compared to the Wreathed and Rufous-necked Hornbill. Though Wreathed Hornbills visit the intensive study site seasonally, they are numerically abundant and therefore play an important quantitative role in seed dispersal during the time they spent at the intensive study site. However, by only seasonally visiting the middle-elevation forests, Wreathed Hornbills are important dispersers only of species that fruit during the non-breeding season at the site. Rufous-necked Hornbills, on the other hand, are present at the intensive study site throughout the non-breeding season unlike the Wreathed Hornbill. This implies that they are possibly playing an important role in fruit removal and seed dispersal for non-fig fruiting trees throughout the year, especially for species that fruit between March to September. Additionally, given that this species consumes a diverse array of food plant species suggests that it is a relatively more important disperser for more non-fig species as compared to the Wreathed Hornbill. The differences in diet, abundances, dietary niche breadth, and temporal changes in occurrence of hornbill species in the mid-elevation forest site suggests that the three sympatric hornbill species play a complementary role in seed dispersal.

The relationship between hornbill abundance and food abundance also has important implications for the seed dispersal patterns. At the smallest scale of the fruiting tree, Rufous-necked and Great Hornbills are likely to disperse higher number of seeds under trees with large fruit crop sizes. At intermediate scales, Wreathed Hornbills are likely to disperse seeds in areas with greater non-fig fruit availability. This disproportionately higher dispersal service provided by different dispersers has important implications for spatial aggregation of fruiting trees at the scale of a focal fruiting tree and at the larger scale of areas with higher abundance of fruits (Lazaro et al. 2005). At the largest scale, Wreathed Hornbills are also likely to

disperse seeds across the elevation gradient contributing to long-distance dispersal. Thus by tracking resources at different scales, hornbills can play an important role in governing the distributions of their food plant species across a hierarchy of scales.

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# Chapter 4

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## Farming the forest: hornbills govern the spatial distribution of tropical trees



Scatter-dispersed seeds of *Canarium strictum* and *Beilschmiedia assamica* under a fruiting *Ficus drupacea* tree. Hornbills disperse seeds of large-seeded food plants on the forest floor while foraging in the day-time. This chapter documents the role of hornbills in governing the spatial distribution of large-seeds on forest floor

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## 4.1 ABSTRACT

Hornbills are amongst the largest avian frugivores in tropical forests of Asia. Different hornbill species tend to co-occur at relatively high densities in most sites, and are therefore likely to play an important role in seed dispersal. We investigated how the distribution of food plants governs the distribution of hornbills, and together how they influence the spatial distribution of seeds on the forest floor. We specifically asked if hornbills were the most important visitors on a sample of five of their large-seeded food species, and if their abundances were governed by the abundance of food plants. We also tested whether the net arrival of large seeds on the forest floor was associated with hornbill abundance. Finally, we quantified the patterns of recruitment of four of the five species of large-seeded hornbill food plants. We found that hornbills were the most frequent diurnal frugivorous visitors on fruiting individuals of five large-seeded tree species. Compared to other taxa, they had a higher frequency of visits and higher mean flock sizes. Median visitation lengths of hornbills were shorter than known seed regurgitation times, implying that the majority of the seeds they handled were transported away from the parent plants. We found that abundances of the three hornbill species (Great, Rufous-necked and Wreathed hornbill) were positively associated with their food plant abundance, particularly of the canopy non-fig food plants. The net seed arrival on the forest floor was positively associated with hornbill abundance. Areas with presence of canopy hornbill food plants had higher mean species richness of recruits of large-seeded hornbill food plants as compared with plots without canopy hornbill food plants. These tree species may be acting as 'hubs' by attracting large numbers of hornbills enhancing seed arrival that results in a more diverse recruitment under their canopies. Our study demonstrates the important ecological role of hornbills in governing the spatial distribution of their food plants, and generating food plant orchards.

**Keywords:** *Aceros nipalensis*, large-seeded plants, Namdapha, nestedness, recruitment, *Rhyticeros undulatus*, seed arrival

## 4.2 INTRODUCTION

Seed dispersal is considered to be an important processes governing the maintenance of tropical tree diversity (Nathan and Muller-Landau 2000, Condit et al. 2002). Around 70–90% of plants in the tropics are dependent on animals for seed dispersal (Howe and Smallwood 1982, Jordano 2000). In biotic seed dispersal, seeds benefit by ‘escaping’ away from parent plant and the frugivore benefits from the nutrition provided by the pulp/aril surrounding the seed (Herrera 1982, Howe and Smallwood 1982). Two important stages involving the biotic agent in the seed dispersal cycle are fruit removal and seed dispersal (Wang and Smith 2002).

Disperser movements and abundance may be governed by the spatial distribution of fruit resources (Kinnaird et al. 1996, Kimura et al. 2001, Burns 2002). In addition to the abundance and distribution of dispersers, biotic dispersal is influenced by several disperser behaviours such as display (Wenny and Levey 1998), nesting (Kitamura et al. 2004b) and roosting (Kitamura et al. 2008), wherein specific microhabitats or locations get used repeatedly over a long period and become sites for high seed deposition. Thus as a consequence of the abundance, distribution and behavior of the disperser, one can expect spatially aggregated patterns of seed dispersal wherein certain sites receive higher seed rain as compared to others.

Based on observations of fleshy-fruited plants dispersed by frugivores in temperate forests, Lazaro et al. (2005) suggested that plants exhibited clumped and highly nested distributions, with rare species occurring alongside more abundant ones. They suggested that these patterns were mediated by frugivores that tend to spend more time in areas rich in food plants, resulting in spatially clumped seed dispersal patterns. From a frugivore’s viewpoint, a fruit rich patch can occur at different spatial scales, from a single fruiting individual tree to patches spread out in the entire geographic region (Garcia and Ortiz-Pulido 2004). Most studies have focused on understanding the role of frugivores in dispersal at smaller spatial scales (Clark et

al. 2004), and our understanding of the role of frugivores in governing the spatial pattern of seed rain at larger scales in tropical forests is limited (Schupp et al. 2010).

In this study, we have tried to understand the relationship between a group of important avian dispersers, the hornbills, and their food plants. Hornbills are frugivores occurring in tropical forests of Asia, with large proportions (75–100%) of their diets being comprised of fruits. Owing to their ability to handle and regurgitate relatively large sized seeds without damaging them, hornbills play an important role in seed dispersal(Kinnaird and O'Brien 2007, Kitamura 2011).

We examined the distribution patterns of food plants and asked how they influence the spatial pattern of seed rain. We focused on large-seeded hornbill food plants, which have a smaller disperser assemblage, to control for the confounding influences of other non-hornbill frugivores. We compared the relative importance of hornbills as dispersers in relation to other diurnal frugivores by comparing their rates of visitation and fruit removal.

Studies on the role of hornbills have focused on dispersal under nest or roost trees (Kinnaird 1998, Datta 2001, Kitamura et al. 2004b, Kitamura et al. 2008). Quantitative information on the role of hornbills in dispersing seeds over the larger forest landscape as a consequence of their daily foraging movements is lacking.

We hypothesized that by attracting hornbills, their food plants serve as seed dispersal hubs, facilitating spatially clumped seed deposition and recruitment of a diversity of hornbill food plants in their surroundings. We tested whether hornbill abundances were positively correlated with the abundance of their food plants, and whether seed rain on the forest floor was positively associated with hornbill abundance. We also tested if hornbill food plants exhibit a nested distribution with the rare species being associated with the common ones. Finally, we explored patterns in richness and abundance of seedlings (10–30 cm) and saplings (30–150 cm) in an attempt to identify tree species likely responsible for formation of hubs. This is

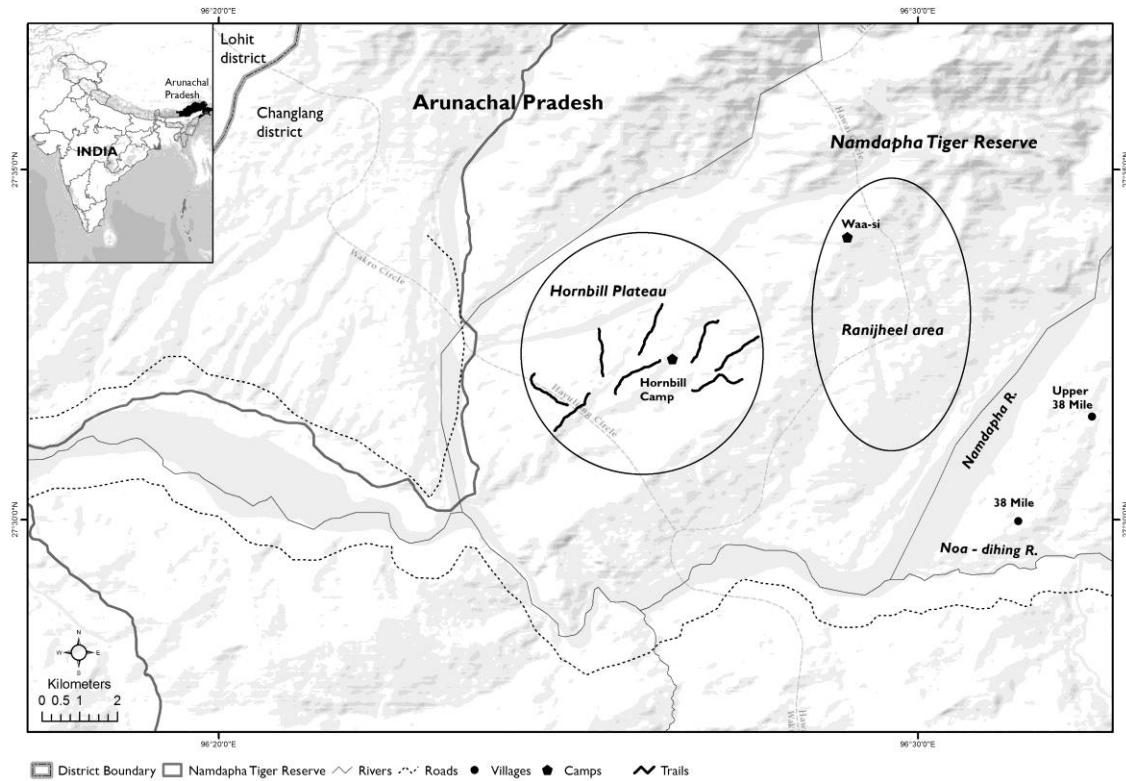
the first study to quantitatively estimate the role of hornbills in scatter-dispersal of seeds on the forest floor and to explore the consequences for forest regeneration and adult food plant distribution.

### 4.3 METHODS

#### *Study Area*

We carried out intensive sampling in two sessions in the hornbill non-breeding season from November 2010–March 2011 (1<sup>st</sup> year) and December 2011–February 2012 (2<sup>nd</sup> year) on the Hornbill Plateau inside the Namdapha Tiger Reserve (27°23'30"– 27°39'40"N and 96°15'2"–96°58'33"E; Fig. 1). Namdapha is located in the easternmost part of the Eastern Himalaya Biodiversity Hotspot (Myers et al. 2000). The area of the Reserve is 1985 km<sup>2</sup> with elevation ranging from 200–4570 m ASL. The Hornbill Plateau, in the western portion of the Reserve, is spread over an area of approximately 15km<sup>2</sup>. Elevation on the plateau ranges from 550–800 m ASL. The forests on the plateau are dominated by *Terminalia myriocarpa*, *Altingia excelsa*, *Shorea assamica*, *Schima wallichii*, *Beilschmiedia assamica*, *Saprosma ternatum*, *Baccaurea ramiflora*. Five species of hornbills, including the Great *Buceros bicornis* (112–150 cm), Rufous-necked *Aceros nipalensis* (99–122), Wreathed *Rhyticeros undulatus* (84–117 cm), White-throated Brown *Anorrhinus austeni* (73–80 cm) and the Oriental Pied Hornbill *Anthracoceros albirostris* (60–85 cm), occur on the plateau (Naniwadekar and Datta 2013, Poonswad et al. 2013). Our study was carried out in the non-breeding season of the hornbills (winter), while the breeding season is from April to August (Datta 2009). We focused on the three larger hornbill species. The Oriental Pied Hornbill was very rare in the area and we detected it only once during transect/trail walks. Additionally, we had very limited information on the diet of White-throated Brown Hornbill. While studies have reported hunting pressures in our study area on mammalian groups like ungulates and carnivores (Datta et al. 2008), hornbills were not hunted in our intensive study site. In fact, their densities on the Plateau were

amongst the highest reported for hornbills across South and South-east Asia (Naniwadekar and Datta 2013).



**Figure 1** Map of the intensive study area showing the Hornbill Plateau where the fruit tree watches were conducted in the Namdapha Tiger Reserve. Eight trails that were monitored from 2010-12 are also shown.

### Visitation rates of frugivores

We carried out focal tree observations on 23 trees of five large-seeded hornbill food species (Table 1) to identify the frugivore assemblages that visited these species. All species fruit during the non-breeding season of hornbills. We observed focal trees from 0600–1000 hr. A single observer sat under or just beyond (up to 15 m) the tree canopy, camouflaged in the undergrowth but with a clear view of a large proportion of the canopy. We identified the visitors, counted the number of individuals, and their arrival and departure times throughout the observation period. Hornbills and Imperial pigeons (*Ducula* spp.) are known to swallow and regurgitate large seeds unharmed (Kitamura 2011). Smaller avian frugivores, on the other hand, peck and drop a large proportion of fruits during foraging (Sethi and Howe 2012). We classified the different visitors/frugivores into four groups – hornbills, pigeons (medium-bodied avian frugivores; 40–50 cm), small-bodied (25–35 cm) avian frugivores (hill mynas, barbets and cochoas), and mammals (primates and diurnal squirrels). Through focal animal observations, we recorded fruit handling behavior of hornbills (35 min) and the small-bodied avian frugivores (44 min). We represented visitation rates of different frugivore groups as the proportion of watches in which each group visited. We compared visitation rates of these different groups using binomial means and 95% confidence intervals (n=25 focal tree watches). We conducted the focal tree observations between November–March (2010–2012) spanning the fruiting season of these tree species (see Table 1 for sampling effort).

Eight trails, each 1.5 km long, were marked on the Hornbill Plateau, and monitored over the two years (Fig. 1). Starting points of trails were placed at least 500 m apart from adjacent trails except two trails that were 300 m apart. Each trail was marked at every 50 m along its entire length. We split all the trails into 500 m segments and considered each of the 24 segments as a sampling unit.

**Table 1** Fruit and seed characteristics of large-seeded tree species observed for frugivore visitation.

Tree species (number of trees observed)	Fruit type	Seed size (mm)		Effort
		Length	Width	
<i>Beilschmiedia assamica</i> (n = 5 trees)	Single-seeded drupe	34.3 ± 2.8	22.9 ± 1.2	34 hr 43 min
<i>Phoebe</i> sp. (n = 6 trees)	Single-seeded drupe	27.8 ± 3.6	16.9 ± 0.96	24 hr 45 min
<i>Canarium strictum</i> (n = 4 trees)	Single-seeded drupe	33.8 ± 0.96	15.1 ± 1.1	15 hr 46 min
<i>Dysoxylum</i> sp. (n = 3 trees)	Lipid-rich arillate capsule	28.3 ± 0.95	17.2 ± 0.5	12 hr 44 min
<i>Alseodaphne petiolaris</i> (n = 5 trees)	Single-seeded drupe	35.6 ± 2.2	17.4 ± 1.0	20 hr 7 min

### *Relationship between hornbill encounters and their food plants*

We enumerated hornbill food trees (girth at breast height (GBH)  $\geq 30$  cm) within 10 m on each side of the eight trails (1500 m  $\times$  20 m). We identified hornbill food plants based on published information (Datta and Rawat 2003, Datta 2009) and from data we collected in our study area as part of the another study (Chapter 3). We later classified the food plants into three categories, 1) figs that are characterized by minute seeds and fruit crop sizes that are usually a few orders of magnitude larger than the large-seeded hornbill food plants, 2) canopy non-fig tree species including *Phoebe* sp. and *Canarium strictum* that attain large sizes ( $>40$  m in height), large-seeded and have fruit crop sizes that can go into several thousands, and 3) small non-fig food plants that including middle-storey trees with medium to large seeds but with fruit crop sizes mostly in hundreds and fewer than 1500 fruits (Table 2).

Information on hornbill encounters was gathered by repeated trail walks along the eight established trails. One or two observers walked trails in the mornings (0530–1030 hr) and/or afternoons (1230–1600 hr) following the standard distance sampling protocol (Buckland et al. 2003). The average ( $\pm$  SD) time required for walking a trail was 1hr10min ( $\pm$  16 min). On detecting hornbills during the trail walk, we recorded the species identity, number of individuals and perpendicular distance of the flock center from the trail. We recorded perpendicular distances using a Bushnell rangefinder (Yardage ProSport 450). The total effort in the first year was 232.5 km (range: 25.5–34.5 km per trail) and 144 km (18 km along eight trails each) in the second year.

We estimated Moran's I autocorrelation coefficient to examine spatial autocorrelation in the response variable (total number of hornbills sighted in each sampling unit) using package 'ape' in R ver. 3.0.1 (Paradis et al. 2004, R Development Core Team 2013). We defined a candidate set of eight models with the three predictor variables used singly and in different combinations (Johnson and

Omland 2004). The candidate set also included an only-intercept model without any predictor for evaluating the influence of predictors on the response variable. In the absence of spatial autocorrelation (if observed Moran's I was within 1.96 SD units of the expected Moran's I coefficient), we used Mixture Models to explore the relationship between encounters of the three hornbill species (total number of hornbills seen in each sampling unit) and the abundance of the three different types of hornbill food plants (figs, emergent non-figs and small non-figs), separately for the two sampling sessions. We did not uniformly detect the three hornbill species in the 24 sampling units over the two years. Since the hornbill detections were variable and we recorded them in 5 to 18 of the 24 sampling units, we used Mixture Models. In mixture modeling, data are divided into two imaginary groups, one containing zeroes called the 'zero mass' and the 'count process' containing the count data (with zeroes and non-zeroes). The zero mass is modeled using the binomial distribution and the count process is modeled using either Poisson or negative binomial distribution. We used the 'offset' function to control for variable sampling effort. We used the R package 'pscl' for the mixture models (Jackman et al. 2012). In case of spatial autocorrelation in the response variable, we additionally performed Generalized Least Square (GLS) analysis with an added spatial correlation structure (Zuur et al. 2009). We ran models with five different correlation structures (exponential, Gaussian, linear, rational and spherical) and compared it with a model without any correlation structure. We used the R package 'nlme' for performing the GLS analysis (Pinheiro et al. 2013). We used the Information-theoretic framework for optimal model selection (Burnham and Anderson 2002). Model with the least AIC<sub>c</sub> (Akaike Information Criterion corrected for finite sample size) value was chosen as the optimal model (Burnham and Anderson 2002). We used the R package 'MuMIn' to determine the AIC<sub>c</sub> values for the different models (Barton 2009).

**Table 2** Information on tree and fruit type, tree height and abundances of the 18 species of hornbill food plants that were detected in the belt transects across the 24 sampling units.

Species	Family	Tree type	Fruit type	Tree height (m)	Mean tree density ( $\text{ha}^{-1}$ ) $\pm$ SE
<i>Canarium strictum</i>	Burseraceae	Canopy non-fig	Drupe	50*	0.04 $\pm$ 0.04
<i>Phoebe</i> sp.	Lauraceae	Canopy non-fig	Drupe	40-50	0.38 $\pm$ 0.22
<i>Ficus altissima</i>	Moraceae	Tree/ Hemi-epiphytic fig	Fig	25-30*	0.21 $\pm$ 0.08
<i>Ficus cf. tsjahela</i>	Moraceae	Hemi-epiphytic fig	Fig	40-50	0.42 $\pm$ 0.16
<i>Ficus drupacea</i>	Moraceae	Hemi-epiphytic fig	Fig	10-15*	0.17 $\pm$ 0.08
<i>Ficus</i> sp. 1	Moraceae	Hemi-epiphytic fig	Fig	20-30	0.04 $\pm$ 0.04
<i>Ficus</i> sp. 2	Moraceae	Hemi-epiphytic fig	Fig	20-30	0.04 $\pm$ 0.04
<i>Polyalthia simiarum</i>	Annonaceae	Small non-fig	Drupe	25*	0.33 $\pm$ 0.14
<i>Alseodaphne petiolaris</i>	Lauraceae	Small non-fig	Drupe	20*	0.13 $\pm$ 0.07
<i>Beilschmiedia assamica</i>	Lauraceae	Small non-fig	Drupe	20-25	2.46 $\pm$ 0.63
<i>Beilschmiedia</i> sp.	Lauraceae	Small non-fig	Drupe	20	0.08 $\pm$ 0.06
<i>Beilschmiedia roxburghiana</i>	Lauraceae	Small non-fig	Drupe	20*	0.08 $\pm$ 0.06
<i>Cryptocarya</i> sp.	Lauraceae	Small non-fig	Drupe	15	0.04 $\pm$ 0.04
<i>Machilus duthiei</i>	Lauraceae	Small non-fig	Drupe	8*	0.42 $\pm$ 0.21
<i>Dysoxylum gobara</i>	Meliaceae	Small non-fig	Dehiscent arillate capsule	15	0.04 $\pm$ 0.04
<i>Dysoxylum</i> sp.	Meliaceae	Small non-fig	Dehiscent arillate capsule	15	1.5 $\pm$ 0.35
<i>Chionanthus</i> sp.	Oleaceae	Small non-fig	Drupe	25-30	0.08 $\pm$ 0.06
<i>Prunus ceylanica</i>	Rosaceae	Small non-fig	Drupe	30	0.08 $\pm$ 0.06

\*Tree height information for these species is from [http://www.efloras.org/flora\\_page.aspx?flora\\_id=2](http://www.efloras.org/flora_page.aspx?flora_id=2), and for the rest from our own observations/data.

#### *Nestedness*

We assessed if the hornbill food plant species followed a nested distribution, i.e. whether sites with species-poor assemblages were subsets of sites with species-rich assemblages. In a perfectly nested assemblage, a rare hornbill food plant species would always be present in sites with a common hornbill food plant species, and would not show a high probability of occurrence in the absence of the latter. We constructed a 2-mode presence/absence matrix with species in columns and sites in rows. We had an 18 (species)  $\times$  24 (sampling units) matrix. Presence of species in sampling unit was determined based on method discussed in the previous section. We used the 'Nestedness Calculator' software to estimate the extent of nestedness in hornbill food plant species distribution (Atmar and Patterson 1995). The software initially organizes the matrix by arranging the food plants species from left to right in decreasing order of the number of sampling units in which they occur. In a perfectly nested matrix, the presences are restricted to the top left corner of the matrix. An isocline is then drawn based on matrix dimensions. In a perfectly nested matrix, isocline separates the occupied area (to the left) from the unoccupied area (to the right of the isocline). Presences to the right of isocline are termed as 'unexpected' and so are the absences to the left of the isocline. Based on the extent of 'unexpected' presences and absences beyond the isocline, matrix temperature is estimated, whose values can range between 0° (perfectly nested community)–100° (Checker board). We compared the observed temperature with the temperature of randomly assembled matrices whose dimensions were similar to the observed matrix and were generated using Monte Carlo simulations ( $n = 1000$  simulations).

*Relationship between seed arrival and hornbill abundance*

On each trail, we established and periodically monitored 200 plots ( $1\text{ m} \times 1\text{ m}$ ;  $n = 1600$  plots) for the arrival of scatter-dispersed seeds on the forest floor. The plots were evenly distributed on either side of the trail throughout its length. Seeds with no trace of pulp were considered as dispersed seeds. These plots were first established in December 2010 and monitored on 7 occasions between January–March 2011 and on 6 occasions from December 2011–February 2012. The plots were monitored at intervals of 8–17 days, except on one occasion when they were monitored after 28–32 days. The total duration for which these plots were monitored varied between 69–75 days in the first year and between 83–84 days in the second year. During each monitoring session, we recorded the species identity and the number of dispersed seeds of the different hornbill food plants in each plot. After enumeration, all seeds were cleared from the plots. We decided not to use above-ground seed traps as some of our nets were taken away or damaged during a pilot study. For the analysis, we considered the seeds of *Canarium strictum*, *Phoebe* sp., *A. petiolaris*, *Beilschmiedia assamica* and *Dysoxylum* sp. as these have large-seeded fruits for which hornbills were demonstrated to be the important dispersers. We expected the arrival of scatter-dispersed seeds on the forest floor to be influenced by hornbill abundance.

We carried out the analyses separately for the two years. We used encounters of hornbills along trails as a measure of hornbill abundance. We used the overall hornbill encounter rate (all three species combined) as a predictor and compared it (using AIC<sub>c</sub>) with an intercept-only model. We examined autocorrelation structure of the seed arrival data using Moran's I. When data were not autocorrelated, we used Generalized Linear Models with Poisson/Negative Binomial error structure. Negative binomial error structure was used for models exhibiting over-dispersion with Poisson error structure (Crawley 2006). We did not use zero-inflated models as there were no sampling units with zero seed arrival.

When data were spatially autocorrelated, we additionally used Generalized Least Squares with different spatial autocorrelation structures to model the variation in seed arrival. We used the overall hornbill encounter rate as the predictor to examine if the pattern persisted even after modeling the spatial autocorrelation. We ran the model with five different correlation structures (exponential, Gaussian, linear, rational and spherical) and chose the one with the least AIC<sub>c</sub> value (Burnham and Anderson 2002, Zuur et al. 2009).

#### *Seed removal*

Seeds arriving on the forest floor are subject to predation/removal by terrestrial animals such as rodents. Therefore we set up plots to estimate the quantum of seed removal. We placed five viable seeds, each of *Canarium strictum*, *Phoebe* sp. and *A. petiolaris*, at every 150 m along the eight trails (5 seeds × 10 points on each trail = 50 seeds on each trail), which simulated scatter-dispersal (i.e. seeds at low densities). The seeds used in the experiment were first tested for viability through the flotation test. We used a black permanent marker to draw a line along the circumference of the seed in the centre. We used markers with alcohol-based ink and without xylene and toluene, and expected the mark to not leave behind any scent after the ink dried. We ensured that the marked seeds were not placed under any fruiting tree to avoid any biases in removal. The seeds of *Phoebe* sp., *A. petiolaris* and *Canarium strictum* were monitored for 84–85 days, 69–70 days and 57–63 days, respectively. Based on the average number of seeds removed from each plot along the trail during the monitoring period, we estimated the percentage removal after 100 days for the three species separately.

#### *Recruit (seedling and sapling) diversity*

In 2011–12, we enumerated seedlings and saplings of four of the five focal species along the eight trails in one sampling session. This included *Beilschmiedia assamica*, *Phoebe* sp., *Canarium strictum* and *Dysoxylum* sp. We were unable to identify *A.*

*petiolaris* recruits. Seedlings and saplings (recruits) were enumerated in belt transects (1500 m × 3 m) along the entire length of the trails. We recorded species identity and the number of individuals of each species. Recruits were classified into two size classes (seedlings: 10–30 cm and saplings: 31–150 cm). The recruitment represented seed arrival patterns of the recent past.

In an attempt to identify the type of food plant that may be responsible for attracting greater richness and abundance of recruits, we explored patterns in recruit richness and abundance across the three food plant categories a) figs b) canopy non-fig food plants c) small non-fig food plants. Considering the limited sample size of recruit species (4 spp.) we did not use formal statistical analysis but we only report broad patterns across the different categories. We report means and SE for the patterns in figs ( $n = 12$  plots) and large canopy non-figs ( $n = 5$ ), which were found in a limited number of plots. We used scatter plots to explore the relationship between the other small non-fig food plants and recruit richness and abundance. Other small non-fig food plants were found across a larger number of plots allowing us to explore the patterns through scatter-plots.

#### 4.4 RESULTS

##### *Frugivore visitation*

During the fruit tree watches (108 hr 5 min hours of observation), we recorded 15 frugivore species, including four hornbill species, the Great Hornbill, Wreathed Hornbill, Rufous-necked Hornbill and the Brown Hornbill; two species of pigeons, the Mountain Imperial Pigeon *Ducula badia* and Ashy Wood Pigeon *Columba pulchricollis*; and five species of small avian frugivores, the Great Barbet *Megalaima virens*, Blue-throated Barbet *Megalaima asiatica*, Hill Myna *Gracula religiosa*, Green Cochoa *Cochoa viridis* and the Purple Cochoa *Cochoa purpurea*. We recorded four mammal species, the Assamese Macaque *Macaca assamensis*, Hoolock Gibbon *Hoolock*

*hoolock*, Red-bellied Squirrel *Callosciurus erythraeus*, and the Malayan giant squirrel *Ratufa bicolor*.

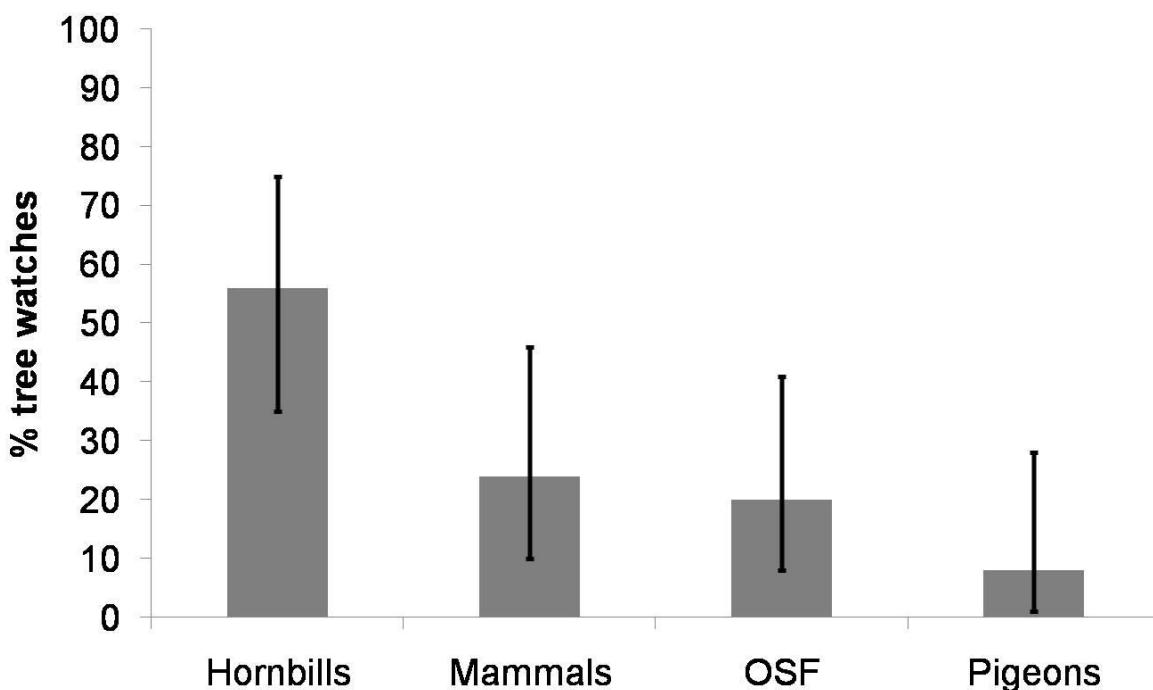
Hornbills were seen in 56% (binomial CI: 35–75%) of the total tree watches, while the mammals were seen in 24% (binomial CI: 10–46%), small frugivores in 20% (binomial CI: 8–41%), and pigeons in 8% (binomial CI: 1–28%) of the total tree watches. The average number of hornbill individuals recorded during a focal tree observation was 10 (range = 0–115; n = 25), while the average number of mammals was 0.4 (range = 0–3; n = 25), small frugivores 1.4 (range = 0–23; n = 25) and pigeons 0.08 (range = 0–1; n = 25). The median visitation length of hornbills on fruiting trees was 28 min, and specifically, 9 min for the Great Hornbill (n = 11 observations), 10 min for Rufous-necked Hornbill (n = 15 observations), and 39 min for Wreathed Hornbill (n = 56 observations).

In our observations of foraging by hornbills (35 min) and small avian frugivores (44 min), we recorded hornbills swallowing fruits 68% (n = 47 fruits) of the times they handled them, while small avian frugivores swallowed only 2% of the times they handled fruit (n = 43). Conversely, hornbills were recorded pecking on fruits or dropping them 15% and 17% of the times, respectively, while the small frugivores were recorded pecking on fruits or dropping them 61% and 35% of the times, respectively (2% of the times we saw them take the fruits in their beaks but did not observe whether they dropped or swallowed the fruits). We had no focal feeding observations of pigeons (that were detected on only one occasion during the fruit tree watch) and mammals. Primates (Assamese Macaque and Hoolock Gibbon) were seen on 3 occasions but did not feed on the fruits.

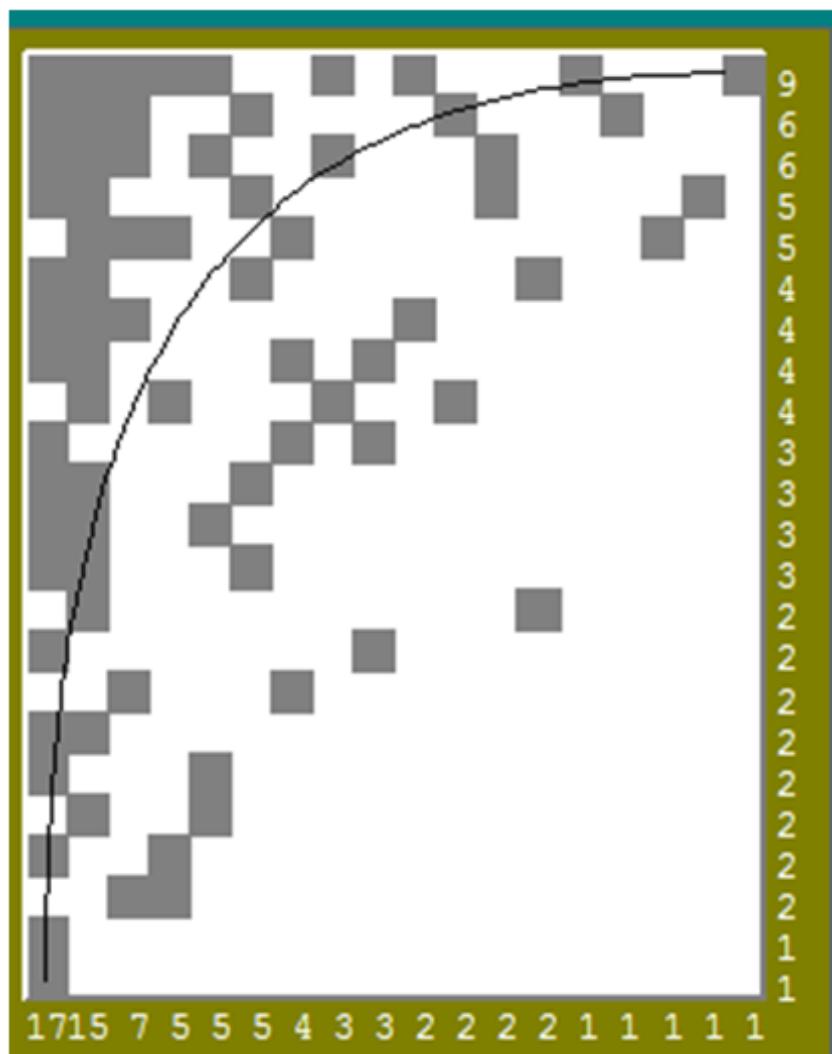
#### Nestedness

Our 2-mode matrix (Fig. 3) comprised of 18 species × 24 sampling units = 432 cells. Of these 432 cells, hornbill food plant species were recorded in 77 cells, the rest being absences. The observed matrix temperature was 15.3°. On the other hand, the

average ( $\pm$  SD) temperature of 1000 random matrices generated using Monte Carlo simulations was  $39.5^\circ$  ( $\pm 5.98$ ). Our observed matrix temperature was more than 4 SD lower than the average temperature of 1000 random matrices indicating nestedness in distribution and abundance of hornbill food plant species. The sampling units with higher species richness of hornbill food plants also had higher overall food plant abundance ( $r = 0.75$ , 95% CI = 0.49–0.88).



**Figure 2** Percentage (95% binomial CI) of the total tree watches ( $n = 23$ ) on which the different kinds of frugivores like hornbills, mammals, other small frugivores (OSF; including barbets, hill mynas and cochoas) and pigeons (including Imperial and Wood Pigeons) were recorded during hornbill fruit tree watches in Namdapha Tiger Reserve.



**Figure 3** The observed matrix of species (columns) and sampling sites (rows) of the hornbill food plant species. The gray cells indicate sites occupied by the respective species. In a perfectly nested matrix, all the occupied cells should be to the left of the isocline.

*Relationship between hornbill encounter rate and their food plant density*

We detected 612 and 203 individual perched hornbills during 2010–11 (total effort = 232.5 km) and 2011–12 (total effort = 144 km), respectively. The number of individuals of Great Hornbill (1<sup>st</sup> year: 39, 2<sup>nd</sup> year: 58) and Rufous-necked Hornbill (1<sup>st</sup> year: 52, 2<sup>nd</sup> year: 45) detected were similar across the two years. We detected higher number of Wreathed Hornbills in the 1<sup>st</sup> year (521) as compared to the 2<sup>nd</sup> year (100). In 2010–11, we detected Great Hornbill in 12, Rufous-necked Hornbill in 14 and Wreathed Hornbill in 18 and Brown Hornbill in 10 of the 24 sampling units. In 2011–12, we detected Great Hornbill in 10, Rufous-necked Hornbill in 12 and Wreathed and Brown Hornbills in 5 each of the 24 sampling units.

We did not detect spatial autocorrelation in hornbill detections in all the analyses for individual species except for the Rufous-necked Hornbill in the second year (Table 3). In the 1<sup>st</sup> year, we detected a positive relationship between abundance of Wreathed and Rufous-necked Hornbills and the abundance of canopy non-fig hornbill food plants (Table 5). In the 2<sup>nd</sup> year, although we detected 100 individuals of Wreathed Hornbills, sightings were restricted to only 5 of the 24 sampling units, indicating high patchiness in the distribution of this species. Variation in Wreathed Hornbill abundance was explained by variation in canopy non-fig food plant abundance and the smaller non-fig food plant abundance. However, given the patchy distribution of hornbills, it is likely that the model exhibited over-fitting and we are cautious about drawing conclusions from this data. In the case of Great Hornbill, variation in their abundances was best explained by the abundance of small non-fig food plants in 2010–11 (Table 5). Intercept only models were selected for Great Hornbill and Rufous-necked Hornbill in 2011–12 (Table 4b and 4d).

**Table 3** Observed and expected (with SD) Moran's I autocorrelation coefficients for the encounter rates ( $\text{km}^{-1}$ ) of three hornbill species and the overall seed arrival (seed arrival of five species that were studied) across the two years (2010-11 and 2011-12).

Hornbill species	Year	Observed	Expected	SD (expected)	Unit SD difference (observed & expected)
Great	2010-11	-0.06	-0.04	0.05	-0.27
Great	2011-12	-0.03	-0.04	0.02	0.73
Rufous-necked	2010-11	-0.01	-0.04	0.05	0.74
Rufous-necked	2011-12	0.14	-0.04	0.04	4.25
Wreathed	2010-11	-0.01	-0.04	0.04	0.88
Wreathed	2011-12	0.02	-0.04	0.04	1.59
Overall seed arrival	2010-11	0.02	-0.04	0.05	1.39
Overall seed arrival	2011-12	0.18	-0.04	0.04	5.23

**Table 4** Structure of models in a mixture model framework (ZIP: Zero-inflated Poisson model, ZINB: Zero-inflated Negative Binomial model) with  $\Delta AIC_c$  values that were used for model selection for identifying variables that explained variation in abundances of a) Great Hornbill in 2010-11, b) Great Hornbill in 2011-12, c) Rufous-necked Hornbill in 2010-11, d) Rufous-necked Hornbill in 2011-12, e) Wreathed Hornbill in 2010-11 and f) Wreathed Hornbill in 2011-12.

**Table 4a** Great Hornbill in 2010-11.

No	Model structure	Model	df	AIC <sub>c</sub>	$\Delta AIC_c$
1	Great Hornbill abundance ~ small non-fig abundance   1	ZIP	3	81.8 0	0.00
2	Great Hornbill abundance ~ 1   1	ZIP	2	82.4 0	0.61
3	Great Hornbill abundance ~ canopy non-fig abundance + small non-fig abundance   1	ZIP	4	82.5 9	0.79
4	Great Hornbill abundance ~ canopy non-fig abundance   1	ZIP	3	83.0 2	1.22
5	Great Hornbill abundance ~ Fig abundance + canopy non-fig abundance + small non-fig abundance   1	ZIP	5	84.1 6	2.36
6	Great Hornbill abundance ~ Fig abundance + small non-fig abundance   1	ZIP	4	84.4 4	2.64
7	Great Hornbill abundance ~ small non-fig abundance   1	ZINB	4	84.7 0	2.91
8	Great Hornbill abundance ~ 1   1	ZINB	3	85.0 1	3.21
9	Great Hornbill abundance ~ Fig abundance   1	ZINB	3	85.0 3	3.23
10	Great Hornbill abundance ~ Fig abundance + canopy non-fig abundance   1	ZINB	4	85.6 1	3.81
11	Great Hornbill abundance ~ canopy non-fig abundance + small non-fig abundance   1	ZINB	5	85.8 2	4.02
12	Great Hornbill abundance ~ canopy non-fig abundance   1	ZINB	4	85.9 2	4.13
13	Great Hornbill abundance ~ Fig abundance + small non-fig abundance   1	ZINB	5	87.6 7	5.87
14	Great Hornbill abundance ~ Fig abundance + canopy non-fig abundance + small non-fig abundance   1	ZINB	6	87.7 7	5.97
15	Great Hornbill abundance ~ Fig abundance   1	ZINB	4	87.9 1	6.12
16	Great Hornbill abundance ~ Fig abundance +	ZINB	5	88.8	7.04

	canopy non-fig abundance 1			4	
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**Table 4b** Great Hornbill in 2011-12.

No.	Formula	Mode	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
1	Great Hornbill abundance ~ 1 1	ZINB	3	91.01	0.00
2	Great Hornbill abundance ~ small non-fig abundance 1	ZINB	4	92.80	1.79
3	Great Hornbill abundance ~ Canopy non-fig abundance 1	ZINB	4	93.91	2.90
4	Great Hornbill abundance ~ Fig abundance 1	ZINB	4	93.91	2.90
5	Great Hornbill abundance ~ Fig abundance + small non-fig abundance 1	ZINB	5	95.80	4.79
6	Great Hornbill abundance ~ Canopy non-fig abundance + small non-fig abundance 1	ZINB	5	96.03	5.01
7	Great Hornbill abundance ~ Fig abundance + Canopy non-fig abundance 1	ZINB	5	97.13	6.12
8	Great Hornbill abundance ~ Fig abundance + Canopy non-fig abundance + small non-fig abundance 1	ZINB	6	99.38	8.36
9	Great Hornbill abundance ~ Fig abundance + Canopy non-fig abundance + small non-fig abundance 1	ZIP	5	138.19	47.18
10	Great Hornbill abundance ~ Canopy non-fig abundance + small non-fig abundance 1	ZIP	4	141.72	50.70
11	Great Hornbill abundance ~ Fig abundance + small non-fig abundance 1	ZIP	4	142.52	51.50
12	Great Hornbill abundance ~ small non-fig abundance 1	ZIP	3	143.19	52.17
13	Great Hornbill abundance ~ 1 1	ZIP	2	148.34	57.32
14	Great Hornbill abundance ~ Canopy non-fig abundance 1	ZIP	3	148.71	57.70
15	Great Hornbill abundance ~ Fig abundance 1	ZIP	3	148.89	57.87
16	Great Hornbill abundance ~ Fig abundance + Canopy non-fig abundance 1	ZIP	4	148.99	57.97

**Table 4c** Rufous-necked Hornbill in 2010-11.

No .	Formula	Model	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
1	Rufous-necked Hornbill abundance ~ Canopy non-fig abundance 1	ZIP	3	88.92	0.00
2	Rufous-necked Hornbill abundance ~ 1 1	ZIP	2	90.22	1.30
3	Rufous-necked Hornbill abundance ~ Fig abundance + Canopy non-fig abundance 1	ZIP	4	91.81	2.89
4	Rufous-necked Hornbill abundance ~ Canopy non-fig abundance + small non-fig abundance 1	ZIP	4	91.83	2.90
5	Rufous-necked Hornbill abundance ~ Canopy non-fig abundance 1	ZINB	4	91.83	2.91
6	Rufous-necked Hornbill abundance ~ Fig abundance 1	ZIP	3	91.91	2.99
7	Rufous-necked Hornbill abundance ~ small non-fig abundance 1	ZIP	3	92.63	3.71
8	Rufous-necked Hornbill abundance ~ 1 1	ZINB	3	92.85	3.93
9	Rufous-necked Hornbill abundance ~ Fig abundance + small non-fig abundance 1	ZIP	4	94.82	5.90
10	Rufous-necked Hornbill abundance ~ Fig abundance 1	ZINB	4	94.82	5.90
11	Rufous-necked Hornbill abundance ~ Fig abundance + Canopy non-fig abundance + small non-fig abundance 1	ZIP	5	95.04	6.12
12	Rufous-necked Hornbill abundance ~ Fig abundance + Canopy non-fig abundance 1	ZINB	5	95.04	6.12
13	Rufous-necked Hornbill abundance ~ Canopy non-fig abundance + small non-fig abundance 1	ZINB	5	95.05	6.13
14	Rufous-necked Hornbill abundance ~ small non-fig abundance 1	ZINB	4	95.54	6.61
15	Rufous-necked Hornbill abundance ~ Fig abundance + small non-fig abundance 1	ZINB	5	98.05	9.13
16	Rufous-necked Hornbill abundance ~ Fig abundance + Canopy non-fig abundance + small non-fig abundance 1	ZINB	6	98.65	9.72

**Table 4d** Rufous-necked Hornbill in 2011-12.

N o.	Formula	Model	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
1	Rufous-necked Hornbill abundance ~ 1 1	ZIP	2	86.21	0.00
2	Rufous-necked Hornbill abundance ~ small non-fig abundance 1	ZIP	3	87.10	0.90
3	Rufous-necked Hornbill abundance ~ Fig abundance 1	ZIP	3	88.10	1.90
4	Rufous-necked Hornbill abundance ~ 1 1	ZINB	3	88.44	2.23
5	Rufous-necked Hornbill abundance ~ Canopy non-fig abundance 1	ZIP	3	88.83	2.63
6	Rufous-necked Hornbill abundance ~ Canopy non-fig abundance + small non-fig abundance 1	ZIP	4	89.48	3.27
7	Rufous-necked Hornbill abundance ~ small non-fig abundance 1	ZINB	4	89.95	3.74
8	Rufous-necked Hornbill abundance ~ Fig abundance + small non-fig abundance 1	ZIP	4	90.00	3.79
9	Rufous-necked Hornbill abundance ~ Fig abundance 1	ZINB	4	90.82	4.61
10	Rufous-necked Hornbill abundance ~ Fig abundance + Canopy non-fig abundance 1	ZIP	4	90.94	4.74
11	Rufous-necked Hornbill abundance ~ Canopy non-fig abundance 1	ZINB	4	91.33	5.13
12	Rufous-necked Hornbill abundance ~ Canopy non-fig abundance + small non-fig abundance 1	ZINB	5	92.64	6.43
13	Rufous-necked Hornbill abundance ~ Fig abundance + Canopy non-fig abundance + small non-fig abundance 1	ZIP	5	92.70	6.49
14	Rufous-necked Hornbill abundance ~ Fig abundance + small non-fig abundance 1	ZINB	5	93.17	6.97
15	Rufous-necked Hornbill abundance ~ Fig abundance + Canopy non-fig abundance 1	ZINB	5	93.96	7.75
16	Rufous-necked Hornbill abundance ~ Fig abundance + Canopy non-fig abundance + small non-fig abundance 1	ZINB	6	96.24	10.04

**Table 4e** Wreathed Hornbill in 2010-11.

No.	Formula	Model	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
1	Wreathed Hornbill abundance ~ Canopy non-fig abundance   1	ZINB	4	183.20	0.00
2	Wreathed Hornbill abundance ~ Fig abundance + Canopy non-fig abundance   1	ZINB	5	185.86	2.66
3	Wreathed Hornbill abundance ~ Canopy non-fig abundance + small non-fig abundance   1	ZINB	5	186.05	2.85
4	Wreathed Hornbill abundance ~ Fig abundance + Canopy non-fig abundance + small non-fig abundance   1	ZINB	6	189.29	6.09
5	Wreathed Hornbill abundance ~ Fig abundance   1	ZINB	4	189.76	6.56
6	Wreathed Hornbill abundance ~ 1   1	ZINB	3	189.97	6.77
7	Wreathed Hornbill abundance ~ small non-fig abundance   1	ZINB	4	191.89	8.69
8	Wreathed Hornbill abundance ~ Fig abundance + small non-fig abundance   1	ZINB	5	192.89	9.69
9	Wreathed Hornbill abundance ~ Canopy non-fig abundance   1	ZIP	3	334.18	150.97
10	Wreathed Hornbill abundance ~ Fig abundance + Canopy non-fig abundance   1	ZIP	4	334.42	151.22
11	Wreathed Hornbill abundance ~ Canopy non-fig abundance + small non-fig abundance   1	ZIP	4	336.73	153.53
12	Wreathed Hornbill abundance ~ Fig abundance + Canopy non-fig abundance + small non-fig abundance   1	ZIP	5	337.63	154.43
13	Wreathed Hornbill abundance ~ Fig abundance   1	ZIP	3	582.79	399.59
14	Wreathed Hornbill abundance ~ Fig abundance + small non-fig abundance   1	ZIP	4	584.04	400.84
15	Wreathed Hornbill abundance ~ small non-fig abundance   1	ZIP	3	661.54	478.34
16	Wreathed Hornbill abundance ~ 1   1	ZIP	2	680.06	496.86

**Table 4f** Wreathed Hornbill in 2011-12.

No.	Formula	Model	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
1	Wreathed Hornbill abundance ~ Canopy non-fig abundance + small non-fig abundance   1	ZIP	4	65.34	0.00
2	Wreathed Hornbill abundance ~ Fig abundance + Canopy non-fig abundance + small non-fig abundance   1	ZIP	5	66.57	1.23
3	Wreathed Hornbill abundance ~ Canopy non-fig abundance + small non-fig abundance   1	ZINB	5	68.57	3.23
4	Wreathed Hornbill abundance ~ Fig abundance + Canopy non-fig abundance + small non-fig abundance   1	ZINB	6	70.18	4.84
5	Wreathed Hornbill abundance ~ Canopy non-fig abundance   1	ZINB	4	70.98	5.64
6	Wreathed Hornbill abundance ~ 1   1	ZINB	3	71.39	6.05
7	Wreathed Hornbill abundance ~ small non-fig abundance   1	ZINB	4	71.59	6.25
8	Wreathed Hornbill abundance ~ Fig abundance + Canopy non-fig abundance   1	ZINB	5	73.91	8.57
9	Wreathed Hornbill abundance ~ Fig abundance + small non-fig abundance   1	ZINB	5	74.21	8.87
10	Wreathed Hornbill abundance ~ Fig abundance   1	ZINB	4	74.25	8.91
11	Wreathed Hornbill abundance ~ small non-fig abundance   1	ZIP	3	80.65	15.31
12	Wreathed Hornbill abundance ~ Canopy non-fig abundance   1	ZIP	3	82.10	16.76
13	Wreathed Hornbill abundance ~ Fig abundance + small non-fig abundance   1	ZIP	4	83.09	17.75
14	Wreathed Hornbill abundance ~ Fig abundance + Canopy non-fig abundance   1	ZIP	4	84.98	19.64
15	Wreathed Hornbill abundance ~ 1   1	ZIP	2	105.62	40.28
16	Wreathed Hornbill abundance ~ Fig abundance   1	ZIP	3	107.63	42.29

**Table 5** Cumulative AIC<sub>c</sub> weight (relative importance) of the explanatory variables from the candidate models and their model-averaged coefficients and 95% CI.

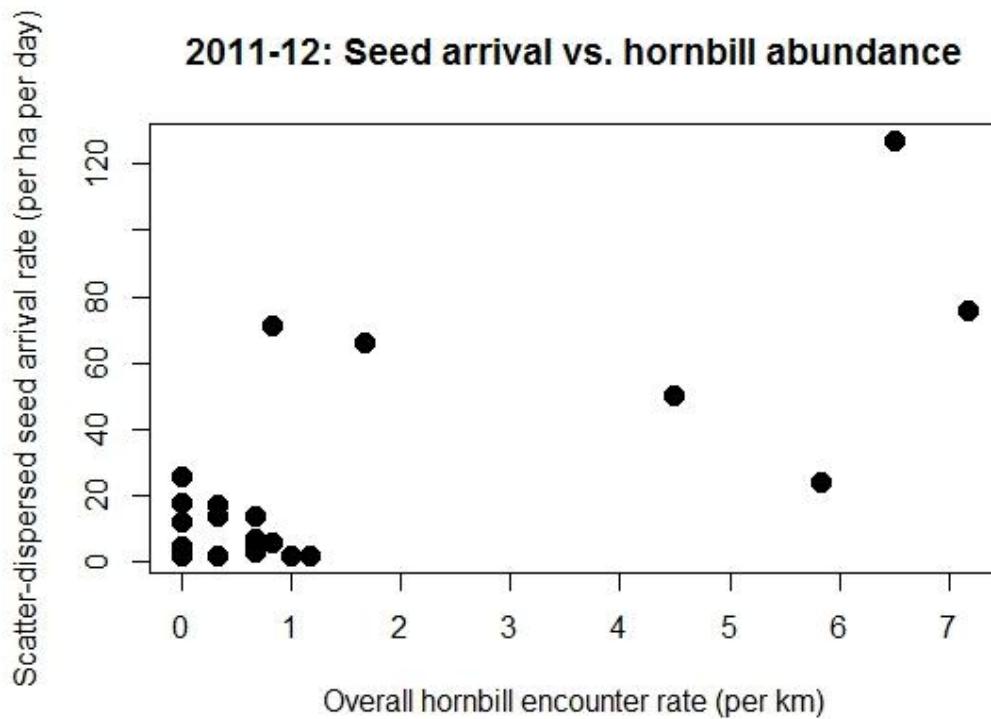
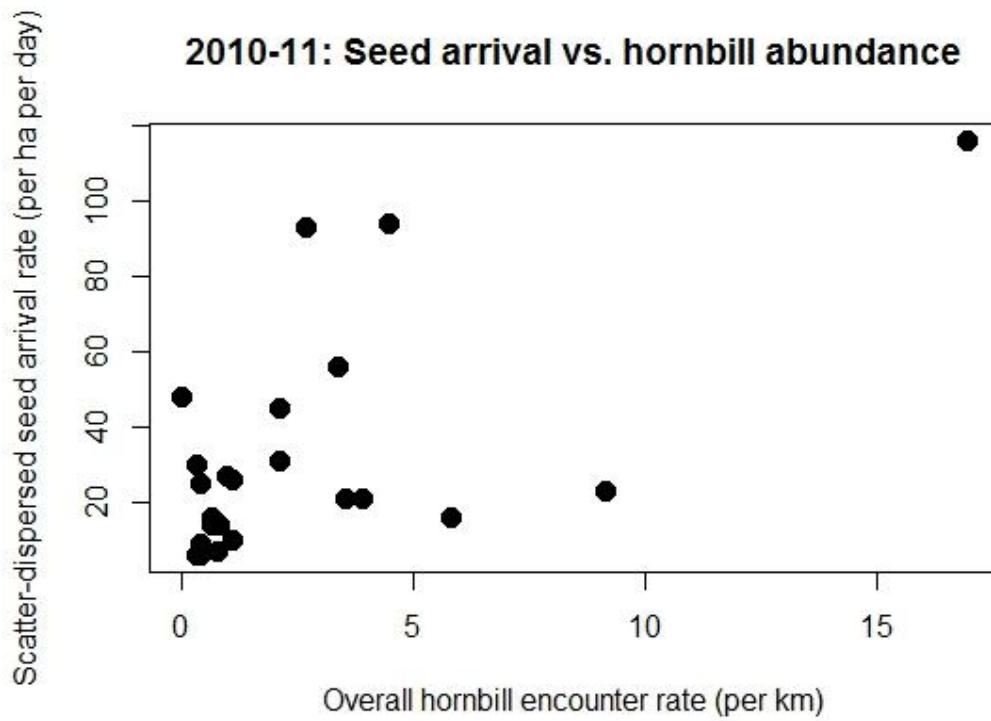
Hornbill species	Year	Variable	Relative Importance	Coefficients	95% LCI	95% UCI
Great	2010-11	Count (small non-fig abundance)	0.57	0.08	0.001	0.16
		Count (canopy non-fig abundance)	0.42	0.19	-0.05	0.42
		Count (fig abundance)	0.23	-0.1	-0.41	0.22
		Zero (intercept)		-0.22	-1.17	0.74
		Count (intercept)		-1.54	-2.41	-0.68
	2011-12	Count (small non-fig abundance)	0.28	0.17	-0.12	0.45
		Count (canopy non-fig abundance)	0.18	0.03	-0.82	0.87
		Count (fig abundance)	0.18	-0.05	-1.23	1.13
		Zero (intercept)		-5.67	-189.78	178.44
		Count (intercept)		-1.14	-2.81	0.53
Wreathed	2010-11	Count (small non-fig abundance)	0.19	0.03	-0.08	0.14
		Count (canopy non-fig abundance)	0.94	0.47	0.15	0.79
		Count (fig abundance)	0.22	0.22	-0.32	0.76
		Zero (intercept)		-1.21	-2.25	-0.17
		Count (intercept)		0.51	-0.06	1.07
	2011-12	Count (small non-fig abundance)	0.93	0.19	0.09	0.29
		Count (canopy non-fig abundance)	0.94	0.33	0.14	0.52
		Count (fig abundance)	0.33	0.18	-0.16	0.53
		Zero (intercept)		1.33	0.34	2.32
		Count (intercept)		-0.52	-1.67	0.64
Rufous-necked	2010-11	Count (small non-fig abundance)	0.19	0.01	-0.07	0.08
		Count (canopy non-fig abundance)	0.61	0.2	0.01	0.39
		Count (fig abundance)	0.22	0.05	-0.26	0.37
		Zero (intercept)		-0.45	-1.32	0.43
		Count (intercept)		-1.12	-1.52	-0.72
	2011-	Count (small non-fig	0.36	-0.11	-0.27	0.05

	12	abundance)				
		Count (canopy non-fig abundance)	0.21	0.04	-0.2	0.28
		Count (fig abundance)	0.23	-0.08	-0.35	0.19
		Zero (intercept)		-0.07	-0.9	0.77
		Count (intercept)		-0.25	-1.1	0.59

### Seed arrival

In the 1600 plots in the first year of sampling, we recorded the net arrival of 408 seeds of 11 species of non-fig hornbill food plants. Of these, 89% (363 seeds) belonged to four of our five focal species (*Canarium strictum* = 217, *Beilschmiedia assamica* = 116, *Dysoxylum* sp. = 25, *Phoebe* sp. = 5, *A. petiolaris* = 0). In the second year, we recorded the net arrival of 538 seeds of 14 species of non-fig hornbill food plants. Of these, 58% (312 seeds) belonged to the five focal species (*Phoebe* sp. = 194, *A. petiolaris* = 55, *Beilschmiedia assamica* = 46, *Canarium strictum* = 9, *Dysoxylum* sp. = 8). In the 2<sup>nd</sup> year, we recorded 181 seeds of *Machilus duthiei*, a small-seeded hornbill food plant also consumed by a diverse array of small-sized frugivores including thrushes (*Turdus* spp.). The mean ( $\pm$  SE) arrival rate of dispersed seeds of the five focal species in the 24 patches was similar across the two years (1<sup>st</sup> year: 32.1 (6.1) seeds day<sup>-1</sup> ha<sup>-1</sup>, 2<sup>nd</sup> year: 23.4 (6.5) seeds day<sup>-1</sup> ha<sup>-1</sup>). While *Canarium strictum* (59.7%) dominated the seed composition in the first year, *Phoebe* sp. seeds (36.1%) were the most commonly recorded species in the second year. Across the 24 patches, seed arrival rates varied from 6 seeds day<sup>-1</sup> ha<sup>-1</sup> to 116 seeds day<sup>-1</sup> ha<sup>-1</sup> in 2010-11 and between 2–75 seeds day<sup>-1</sup> ha<sup>-1</sup> in 2011-12.

In 2010-11, the model with overall hornbill encounter rate as a predictor had lower AIC<sub>c</sub> value as compared to the intercept-only model (Table 6). The net scatter-dispersed seed arrival did not exhibit spatial autocorrelation (Table 3) and was positively associated with overall hornbill encounter rate (Fig. 4a, Table 7). The bootstrapped 95% CIs of parameter estimate of the overall hornbill encounter rate did not overlap with zero (Table 7). The predicted values from the model were correlated with the observed values ( $r = 0.57$ , 95% CI: 0.21–0.79) indicating reasonable model fit.



**Figure 4** Relationship between combined hornbill encounter rate (Great, Wreathed and Rufous-necked Hornbill) and the net arrival of scatter-dispersed seeds across the two sampling years a) 2010-11 and b) 2011-12.

**Table 6** Structure of models in a generalized linear model and generalized least squares framework with negative binomial error structure with  $\Delta AIC_c$  as model selection criteria to examine if variation in seed arrival rates were explained by variation in overall hornbill abundances. In generalized least squares, we examined the relationship using different correlation structures.

Year	Model	Structure	df	AIC <sub>c</sub>	$\Delta AIC_c$
2010-11	GLM-NB	Seed arrival ~ overall hornbill encounter rate	3	176.40	0.00
	GLM-NB	Seed arrival ~ 1	2	181.85	5.45
2011-12	GLM-NB	Seed arrival ~ overall hornbill encounter rate	3	166.82	0.00
	GLM-NB	Seed arrival ~ 1	2	176.84	10.02
2011-12	GLS with no correlation structure	Seed arrival ~ overall hornbill encounter rate	3	188.25	0.00
	GLS with spherical correlation structure	Seed arrival ~ overall hornbill encounter rate	5	188.50	0.25
	GLS with ratio correlation structure	Seed arrival ~ overall hornbill encounter rate	5	189.03	0.78
	GLS with Gaussian correlation structure	Seed arrival ~ overall hornbill encounter rate	5	188.55	0.30
	GLS with exponential correlation structure	Seed arrival ~ overall hornbill encounter rate	5	189.18	0.93
	GLS with no correlation structure	Seed arrival ~ 1	2	204.03	15.78

**Table 7** Coefficients and 95% CI of the overall hornbill encounter rate as obtained from Generalized Linear Models with negative binomial error structure (GLM-NB). Overall hornbill encounter rate was used as a predictor to explain the variation in seed arrival rates. In case of Generalized Least Square (GLS), the coefficients are model-averaged estimates from the set of five models including the model with no correlation structure.

	<b>Model</b>	<b>Parameter</b>	<b>Coefficient</b>	<b>95% LCI</b>	<b>95% UCI</b>
2010-11	GLM-NB	Overall hornbill encounter rate	0.105	0.035	0.196
	GLM-NB	Intercept	-6.109	-6.455	-5.750
2011-12	GLM-NB	Overall hornbill encounter rate	0.316	0.151	0.520
	GLM-NB	Intercept	-6.787	-7.235	-6.299
2011-12	GLS	Overall hornbill encounter rate	4.787	1.991	7.584
		Intercept	4.886	-4.876	14.975

In 2011-12, the net scatter-dispersed seed arrival exhibited spatial autocorrelation (Table 3). The model with overall hornbill encounter rate as the predictor had lower AIC<sub>c</sub> value as compared to the intercept-only model (Table 6). The net scatter-dispersed seed arrival was positively associated with the overall hornbill encounter rate (Fig. 4b, Table 7). The predicted values from the model were correlated with the observed values ( $r = 0.72$ , 95% CI: 0.45–0.87) indicating reasonable model fit. In GLS analysis, the models with and without spatial autocorrelation structure were within 2 AIC<sub>c</sub> units of each other. The GLS analysis also confirmed that the net scatter-dispersed seed arrival rate was positively associated with overall hornbill encounter rate (Table 7).

The overall scatter-dispersed seed arrival was correlated with the overall food plant abundance in 2010-11 ( $r = 0.49$ , 95% CI: 0.11–0.75) and in 2011-12 ( $r = 0.48$ , 95% CI: 0.1–0.75). There was correlation between the spatial pattern of seed arrival in the two years ( $r = 0.69$ , 95% CI: 0.41–0.86) suggesting that patches that experienced high scatter-dispersed seed rain in the first year, also experienced high scatter-dispersed seed rain in the second year.

#### *Seed removal*

There was considerable variation in the seed removal rates among the three species. We did not see any consistent trends in seed removal either across species or across trails (Fig. 5). We did not use seed removal rates to estimate actual seed rain on account of the high associated variation in seed removal rates within a trail and as data for *Beilschmiedia assamica* was not available. The average ( $\pm$  SE) seed removal rates (in 100 days) for *Canarium strictum* and *A. petiolaris* were  $24.2 \pm 6\%$  and  $31.6 \pm 5.6\%$ , respectively. *Phoebe* sp. experienced relatively higher removal rates of  $87.5 \pm 7.3\%$ . The patterns of seed removal across the eight trails (Fig. 5) were similar in case of *Canarium strictum* and *Phoebe* sp. seeds, except trail 5 which experienced higher

mean removal of *Canarium strictum* and lower mean removal of *Phoebe* sp. In case of *Alseodaphne petiolaris*, the pattern of seed removal was variable across different trails.

### *Recruits*

Overall mean ( $\pm$  SE) abundance of recruits (10–150 cm) of *Beilschmiedia assamica* ( $1312 \pm 207 \text{ ha}^{-1}$ ) was highest followed by *Phoebe* sp. ( $207 \pm 88 \text{ ha}^{-1}$ ), *Dysoxylum* sp. ( $110 \pm 33 \text{ ha}^{-1}$ ) and *Canarium strictum* ( $1.2 \pm 0.8 \text{ ha}^{-1}$ ). The overall abundance of seedlings (10–30 cm in height) varied from 2 to 201 (individuals) across the patches and saplings (30–150 cm) from 33 to 533 (individuals). Across the 24 sampling units, the species richness of recruits varied from 1–4 species. While we did not detect any discernible patterns in the case of figs and other small non-figs, we found that plots with presence of canopy non-fig food plants had higher species richness as compared to plots without canopy non-fig food plants (Fig. 6). However, we did not detect any pattern in abundance of seedlings or saplings across the two categories.

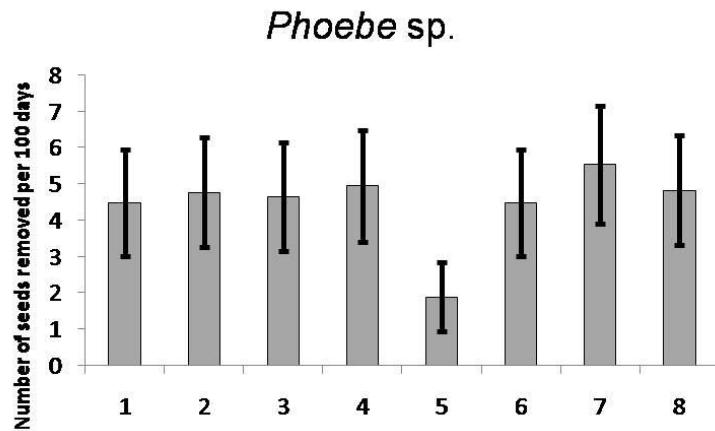


Fig. 5a

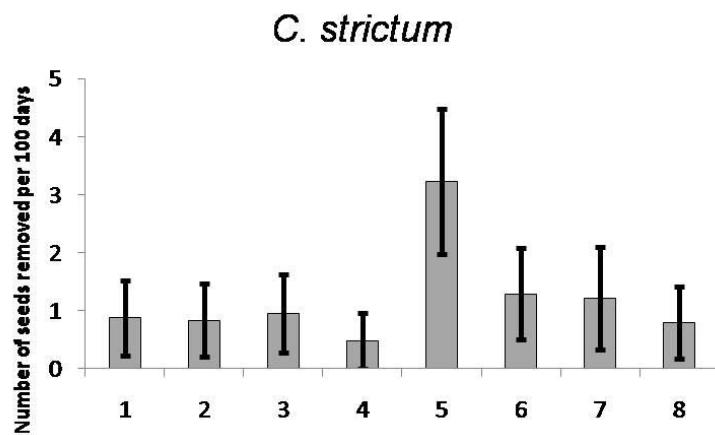


Fig. 5b

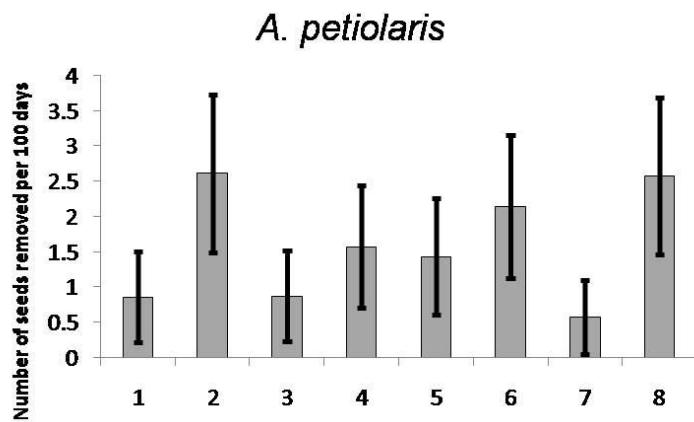


Fig. 5c

**Figure 5** Seed removal rate (per 100 days for three large-seeded species of hornbill food plants a) *Phoebe sp.*, b) *Canarium strictum* and c) *Alseodaphne petiolaris* across eight trails

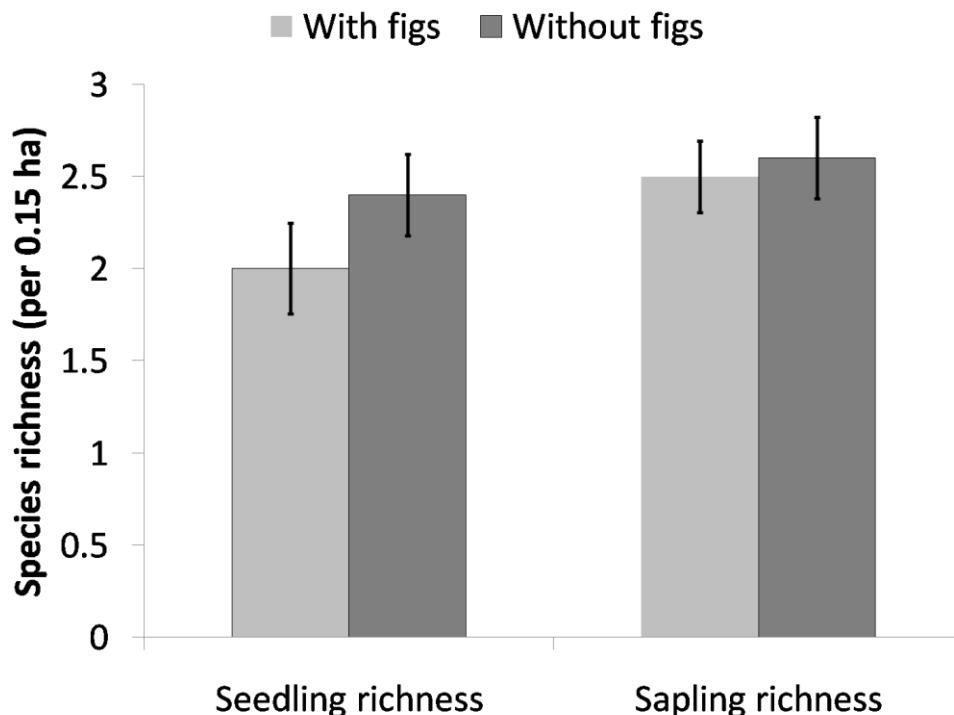


Fig. 6a

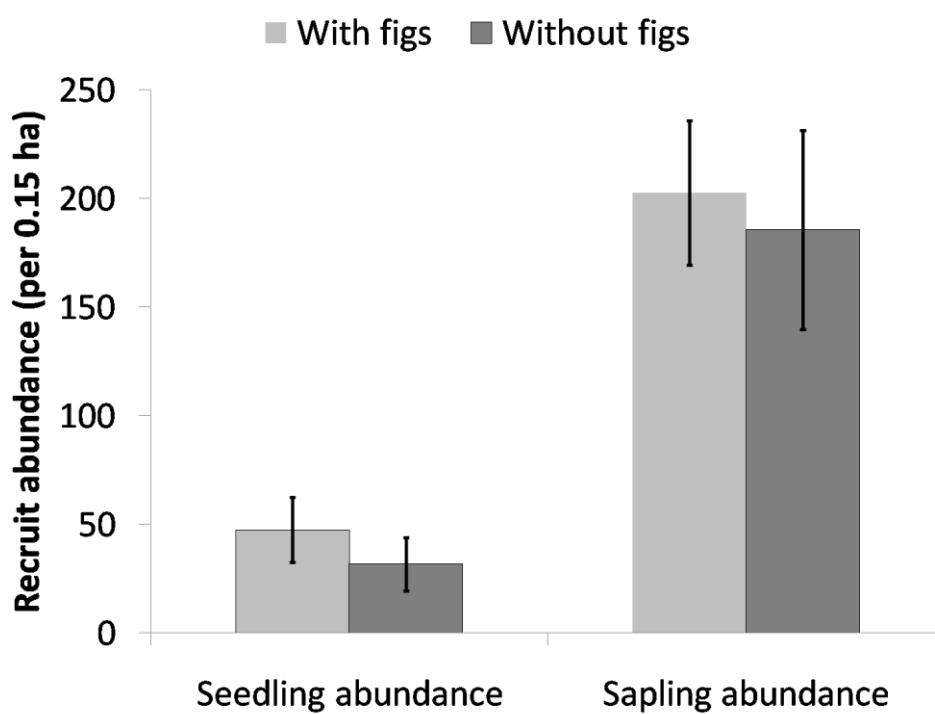


Fig. 6b

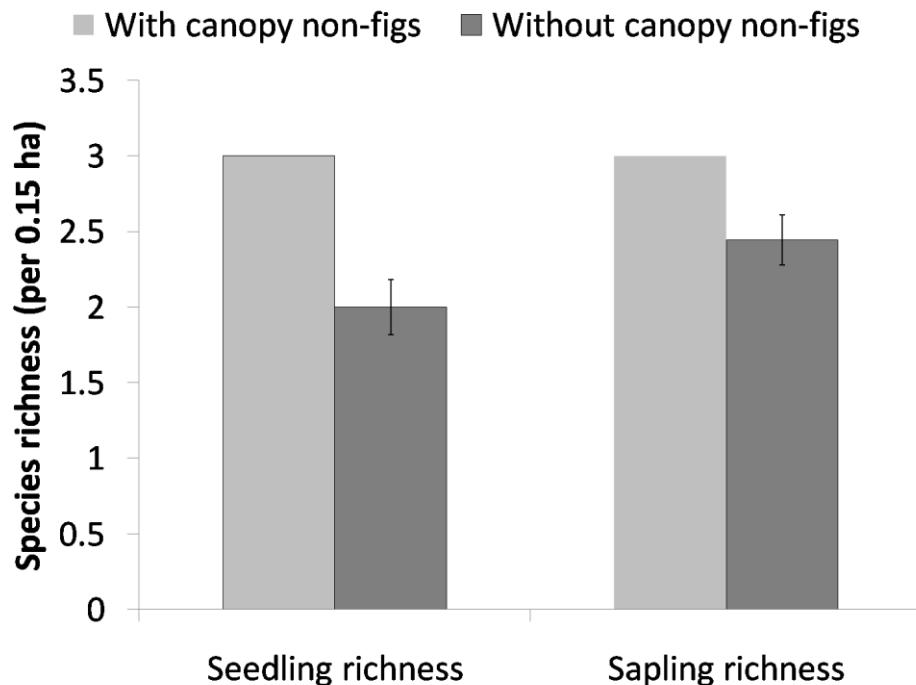


Fig. 6c

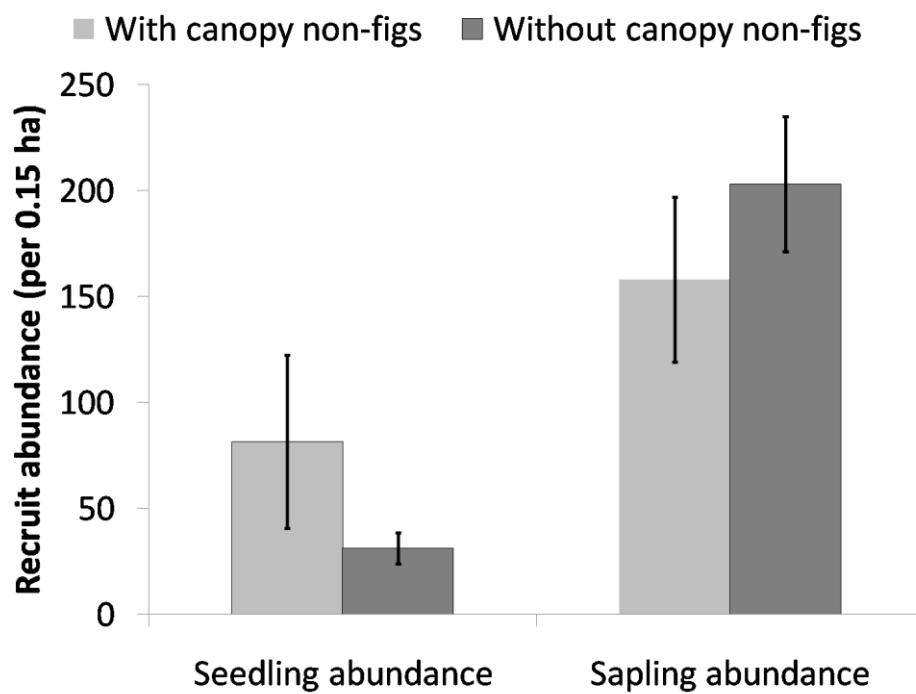
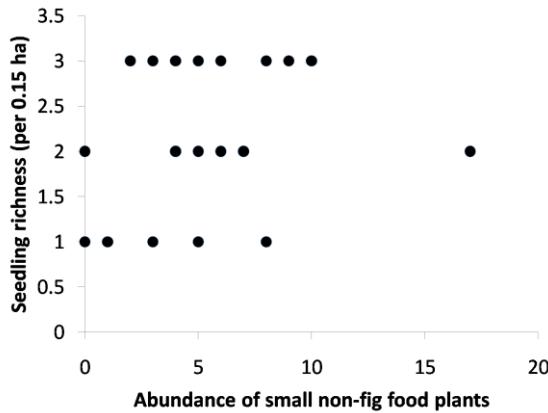
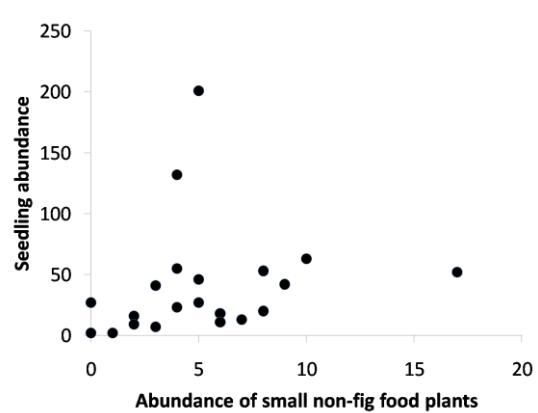
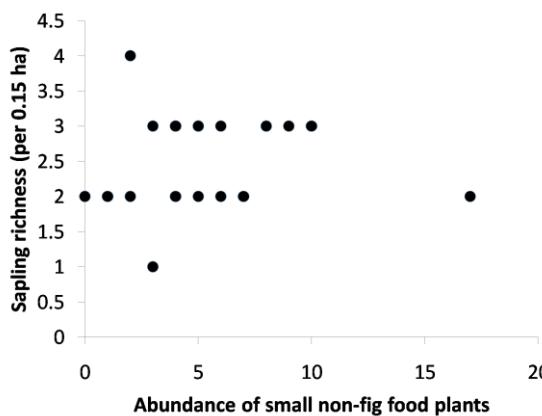
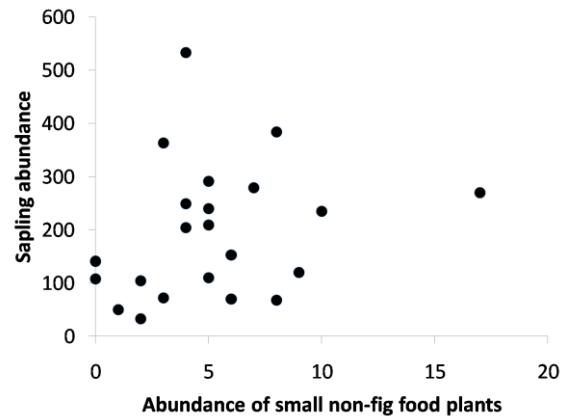


Fig. 6d

**Fig. 6e****Fig. 6f****Fig. 6g****Fig. 6h**

**Figure 6** Comparisons (mean  $\pm$  SE) between species richness and recruit abundance of seedlings (10–30 cm) and saplings (31–150 cm) in plots with and without figs (6a, 6b) and with and without canopy non-fig food plants (6c, 6d). Figures 6e–6h are scatter plots depicting relationship between small non-fig food plants and abundance and richness of seedlings and saplings.

## 4.5 DISCUSSION

Our study shows that hornbills create a spatially heterogeneous distribution of seeds on the forest floor. We found that hornbill food plants, presumably as a consequence, are also patchily distributed into fruit tree 'orchards' (Lazaro et al. 2005). These orchards are characterized by a greater diversity of food plants. We detected a nested pattern in the distribution of hornbill food plants, with the rare species being associated with more common ones. Therefore, these orchards not only offer frugivores with a greater amount of fruits, but also with a greater diversity. The orchards also tended to attract a greater abundance of hornbills.

Hornbills were amongst the most common frugivores in terms of frequency of visits and the number of individuals that visited the fruiting large-seeded trees we observed. Additionally, as compared to smaller frugivores like barbets and cochoas, they swallowed a greater proportion and dropped a smaller proportion of fruits and seeds they handled. Their visitation lengths (10–39 min) on fruiting trees were lower than their known regurgitation or defecation times (> 65 min) (Datta 2001). This underscores their important quantitative (high visitation frequency) and qualitative roles (transporting a majority of seeds away from the parent plant) as seed dispersers in tropical forests. Hornbills thus appear to be responsible for most of the seed dispersal for their large-seeded food plants (Kitamura et al. 2004a, Kitamura et al. 2006, Sethi and Howe 2012).

A majority of studies on seed dispersal by Asian hornbills have focused on their clumped seed deposition patterns below their nest and roost trees (Kinnaird 1998, Datta 2001, Kitamura et al. 2004b, Kitamura et al. 2008). The quality of dispersal when seeds are scattered away from the parent plants in low densities is thought to be better due to reduced density- and distance-dependent mortality (Janzen 1970, Connell 1971). Scatter-dispersed seeds have been reported to have higher survival and recruitment than the clump-dispersed seeds under sleeping trees of spider monkeys (Russo 2005).

Our study, for the first time, quantifies the extent of scatter-dispersal of seeds on the forest floor by hornbills during diurnal foraging movements in the non-breeding season. This kind of scatter-dispersal of seeds as a consequence of foraging activity of hornbills is likely to result in lower probability of density-dependent mortality as compared to under parent trees or under nest/roost trees. However, although seed arrival rates and densities are much lower than under that of the high density seed deposition sites, the ultimate distribution of seeds on the forest floor is relatively heterogeneous. Areas with more hornbill food plants and hornbills have higher seed arrival. From our work, it appears that even single large canopy fruiting trees can have a disproportionate effect on the forest structure through their interactions with hornbills. Large fruiting trees attract a greater abundance of hornbills, which seems to lead to a greater concentration of scatter-dispersed seed rain, ultimately creating fruit orchards of relatively high fruit tree diversity.

Our limited data on recruitment of four of the focal species indicates that areas with high abundances of food plants, especially of the canopy non-fig fruits, were associated with a higher species richness of recruits, hinting towards a positive feedback between the presence of orchards and increased diversity of food plants. However, contrary to our expectation, the abundance of recruits was lower in areas with higher abundances of canopy non-fig food plants. Our data on recruitment was limited to four species, one of which (*Canarium strictum*) occurred at extremely low densities. This precluded our ability to assess the impact of food orchards in influencing recruit abundance. Recruitment of plant species are dependent on a suite of variable factors that include annual variation in fruit availability of particular species, variable life-history traits and variable effect of post-dispersal factors on different species. All these factors may obscure or diffuse the initial template of seed deposition laid down by hornbills. However, we suggest that over the long-term, the repeated arrival of seeds in a patchy manner would still lead to the creation of 'fruit orchards' even if different species are variably affected by post-dispersal factors.

Long-term monitoring of seed and seedling survival will help in determining whether spatially heterogeneous seed arrival indeed results in spatially heterogeneous recruitment patterns.

We suggest that large canopy species like *Canarium strictum* and *Phoebe* sp. are important in tropical forests as, despite being uncommon, they attract large numbers of hornbills and may be responsible for facilitating the dispersal of other hornbill food plant species. Thus, mediated by hornbills, they may play an important role in recruitment of other plants of tropical forests. Unfortunately both these species are preferred timber species and are logged extensively in eastern Arunachal Pradesh. Given that these species occur in low densities and in patches, a closer examination of the loss of these species on hornbills and consequently on recruitment of other hornbill plants is warranted.

Although our data on recruitment patterns are inconclusive, given the positive associations between adult food plant abundance, hornbill abundance and seed arrival and some evidence that some canopy non-fig plants have higher species richness along with the nested pattern of food plant abundance, we conclude that our study has provided the first strong evidence that hornbills, ‘the farmers of the forest’, govern the spatial distribution of their food plants generating ‘fruit orchards’ in tropical forests.

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# Chapter 5

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## Reduced hornbill abundance associated with low seed arrival and altered recruitment in a hunted and logged tropical forest



Hunting and logging are the two main threats that hornbills face across their geographic range in Asia. This chapter focuses on understanding the impacts of these threats on hornbills and seed dispersal

**To be submitted** Rohit Naniwadekar, Ushma Shukla, Kavita Isvaran and Aparajita Datta, 2014. Reduced hornbill abundance associated with low seed arrival and altered recruitment in a hunted and logged tropical forest.

## 5.1 ABSTRACT

Logging and hunting are two key direct threats to the survival of wildlife in the tropics, and also disrupt important ecosystem processes. We investigated the impacts of these two factors on the seed dispersal cycle in a tropical forest in north-east India. We compared abundances of hornbills and their food plants in a site with high logging and hunting pressures (heavily disturbed) with one that had no logging and relatively low levels of hunting (less disturbed). We compared the arrival of five large-seeded tree species of scatter-dispersed seeds and the recruitment of four of those species. Hornbill abundance was 22 times higher in the less disturbed site compared to the heavily disturbed site, while their food plant abundance was two times higher. The arrival of scatter-dispersed seeds was seven times higher in the less disturbed site. Abundances of recruits of two tree species were significantly higher in the less disturbed site. For a third species, abundances of younger recruits were significantly lower while that of older recruits were higher in the heavily disturbed site. Our findings suggest that logging reduces food plant abundance for an important frugivore-seed disperser group, while hunting diminishes disperser abundances, with an associated reduction in seed arrival and altered recruitment of animal-dispersed species in a disturbed site. Based on our results, we present a conceptual model depicting the relationships and pathways between vertebrate dispersed trees, their dispersers, and the two main threats to tropical biodiversity, hunting and logging.

**KEYWORDS** Arunachal Pradesh, frugivores, large-seeded tree species, Namdapha Tiger Reserve, scatter-dispersal

## 5.2 INTRODUCTION

Hunting and logging are amongst the most important threats affecting wildlife in tropical forests (Thiollay 1992, Fa et al. 2002, Corlett 2007). Hunting pressures on vertebrates in the tropics are often unsustainable (Robinson and Bennett 2000, Milner-Gulland et al. 2003) and result in extreme low densities or extirpation of targeted species, such that the forests may remain structurally intact but become functionally defunct (Redford 1992). Animals disperse up to 90% of tree species in tropical forests (Howe and Smallwood 1982, Jordano 2000). Therefore, hunting can disrupt ecosystem processes. The loss of frugivores can affect seed dispersal in several ways — decreased frugivore visitation and lowered fruit removal (Beckman and Muller-Landau 2007, Holbrook and Loiselle 2009), shorter dispersal distances, and increased seed and/or seedling densities under parent plants resulting in density-dependent mortality and lowered recruitment (Howe et al. 1985, Sethi and Howe 2009). Many large vertebrate frugivores targeted by hunting are important seed dispersers (Corlett 2007, Peres and Palacios 2007, Stoner et al. 2007). They are particularly important for large-seeded plants which have fewer effective dispersers (Holbrook and Smith 2000, Kinnaird and O'Brien 2007).

Logging, on the other hand, results in direct changes in forest structure (Cannon et al. 1994), micro-climates (Keenan and Kimmins 1993), fruit abundance (Heydon and Bulloch 1997, Felton et al. 2003) and species composition (Velho et al. 2012). Logging is also often associated with increased hunting pressures (Bennett et al. 2001, Poulsen et al. 2011). Logging can negatively impact frugivores and fruiting plants through the direct loss of mature trees resulting in lowered fruit availability at the community level. The lowered fruit availability could also lead to lower abundance and/or visitation by frugivores, which could lead to lower removal and seed dispersal.

Most of our current understanding of the impacts of hunting and logging on seed dispersal and recruitment has been from the Neotropics (Guariguata et al. 2000, Beckman and Muller-Landau 2007, Forget and Janzen 2007, Nunez-Iturri et al. 2008, Holbrook and

Loiselle 2009), while there are very few studies from Asia (Brodie et al. 2009, Sethi and Howe 2009, Velho et al. 2012). Most studies have focused on either the initial stages of seed dispersal, particularly the fruit removal stage (Beckman and Muller-Landau 2007, Forget and Janzen 2007, Kirika et al. 2008, Holbrook and Loiselle 2009) or comparisons of recruitment across hunted and control treatments (Wright et al. 2007, Terborgh et al. 2008, Sethi and Howe 2009, Vanthomme et al. 2010). Most studies (Beckman and Muller-Landau 2007, Kirika et al. 2008, Holbrook and Loiselle 2009, Markl et al. 2012, Velho et al. 2012) have compared frugivore visitation rates between disturbed and protected sites, but not examined the rate of seed arrival.

In this study we aimed to understand how logging and hunting, through the associated losses of fruiting trees and a key disperser group, affect scatter dispersal and recruitment patterns of large seeded forest trees. We focused on large-seeded plants as they depend on large-bodied frugivores for dispersal. We selected hornbills, which are the largest avian frugivores and dispersers in Asian tropical forests (Kitamura 2011) and five large-seeded tree species (*Phoebe* sp., *Canarium strictum*, *Beilschmiedia assamica*, *Dysoxylum* sp. and *Alseodaphne petiolaris*) as the model system for our study. These large-seeded tree species fruit during winter, the non-breeding season of hornbills (Datta and Rawat 2003). Our study was carried out in the tropical forests of north-east India which face significant threats from logging and hunting (Datta 1998, Sethi and Howe 2009, Aiyadurai et al. 2010). Across most of this region, logging and hunting co-occur (Datta 1998, Sethi and Howe 2009).

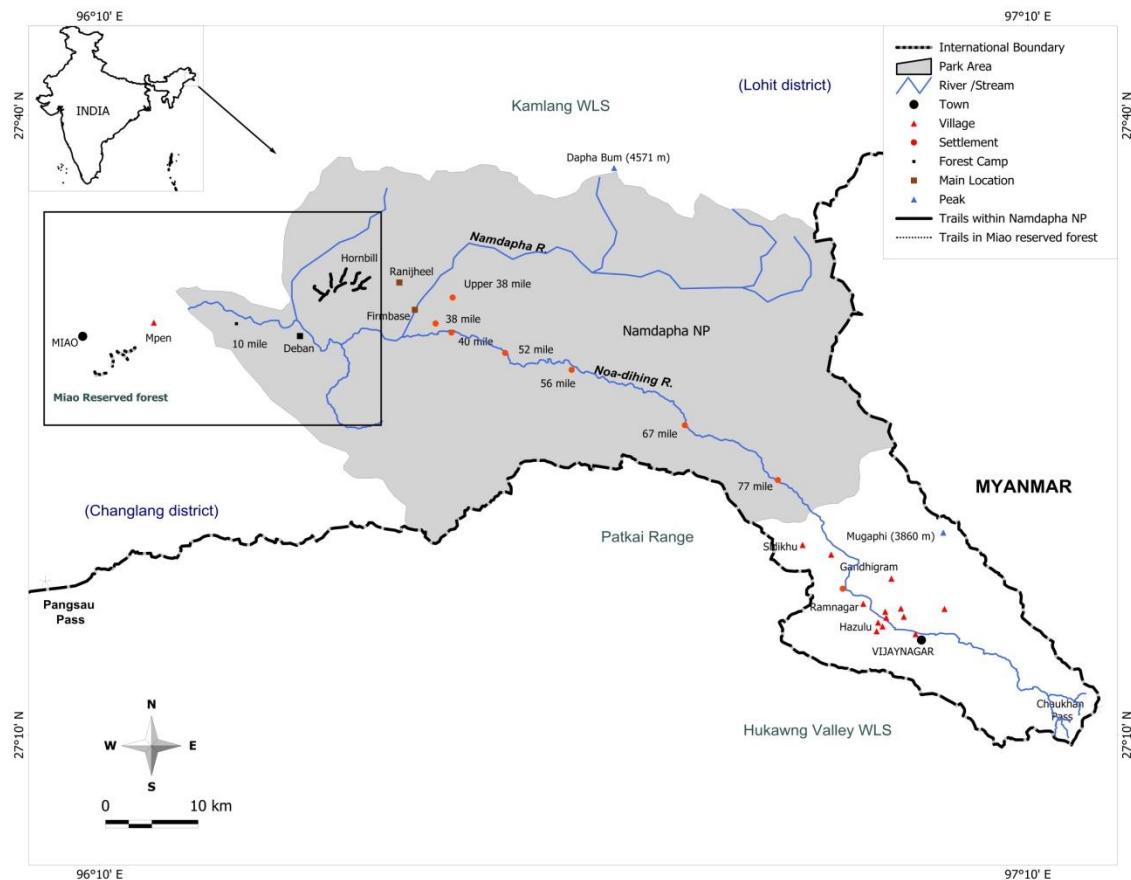
We expected that hunting and logging would negatively impact the abundance of hornbills, their food plants (especially the timber species), and the scatter dispersal of large seeds, fruits of which are primarily consumed by hornbills. These anthropogenic disturbances were also expected to alter the recruitment patterns of large-seeded plants consumed primarily by hornbills. We estimated the extent to which the processes of seed arrival and recruitment were influenced by a combination of hunting and logging through their impacts on the abundances of fruit trees and dispersers. Based on our

results, we present a conceptual model depicting the relationships and feedbacks between vertebrate dispersed trees, their dispersers, and the two main threats to tropical biodiversity, hunting and logging.

### 5.3 METHODS

#### *Study area*

The study was conducted between November 2011 and March 2012 in the Namdapha Tiger Reserve (1985 km<sup>2</sup>; 200–4,500 m above sea level; 27°23'30"–27°39'40"N and 96°15'2"–96°58'33"E) and the adjoining Miao Reserved Forest (121 km<sup>2</sup>; 200 – 1300 m; 27°25'49"–27°30'02"N and 96°8'33"–96°18'59"E) in Arunachal Pradesh, north-east India (Fig. 1). The lower elevations of Namdapha harbor the world's northernmost tropical wet evergreen rainforests (Proctor et al. 1998, Nath et al. 2005). The vegetation in the area is dominated by *Altingia excelsa*, *Terminalia myriocarpa*, *Dipterocarpus macrocarpus*, *Schima wallichii* and *Shorea assamica* (Nath et al. 2005).



**Figure 1** Map of study area. The area shaded gray is the Namdapha Tiger Reserve. The enclosed box shows the intensively sampled area with unbroken lines representing the eight trails in the less disturbed site (Namdapha Tiger Reserve) and broken lines representing the four trails in the heavily disturbed site (Miao Reserved Forest).

More than 490 bird species have been recorded from Namdapha and adjoining areas (Srinivasan et al. 2010). Large avian frugivores with the ability to regurgitate large seeds are represented by five species of hornbills (Great Hornbill *Buceros bicornis*, Rufous-necked Hornbill *Aceros nipalensis*, Wreathed Hornbill *Rhyticeros undulatus*, White-throated Brown Hornbill *Anorrhinus austeni* and the Oriental Pied Hornbill *Anthracoboceros albirostris*, Mountain Imperial Pigeon *Ducula badia*, Great Barbet *Megalaima virens*, Hill Myna *Gracula religiosa*, Green Cochoa *Cochoa viridis* and Purple Cochoa *Cochoa purpurea*). Some of the mammalian frugivores found in the area are Barking Deer *Muntiacus muntjak*, Sambar *Rusa unicolor*, Wild Pig *Sus scrofa*, Hoolock Gibbon *Hoolock hoolock*, Assamese Macaque *Macaca assamensis*, Stump-tailed Macaque *Macaca arctoides*, Northern Pig-tailed Macaque *Macaca leonina* and Rhesus Macaque *Macaca mulatta*.

Our study site, inside Namdapha Tiger Reserve (less disturbed site), was on a plateau (14 km<sup>2</sup>; 500–700 m above sea level) near the western border of the reserve. The other site in Miao Reserved Forest (heavily disturbed site) was c. 10 km<sup>2</sup> with elevation ranging from 400 to 700 m and 20 km straight line distance from our study site in Namdapha.

In spite of a ban on hunting under the Wildlife (Protection) Act, 1972 (Anonymous 1992), wildlife are primarily hunted for food, customary rituals and for trade at different sites in north-east India (Datta 2002, Aiyadurai et al. 2010, Bhupathy et al. 2013). Hornbills are hunted for the upper beak and tail feathers by some tribes (Nyishi, Wancho, Tangsa and Nocte) to adorn their traditional headdresses. Our site in Namdapha was approximately 30 km from the nearest town, Miao and eight km from the nearest village (Deban). Namdapha was designated as a National Park and Tiger Reserve in 1983. Although its legal status as a Tiger Reserve acts as a deterrent to hunters, law enforcement inside the park is inadequate. The two local communities (Lisu and Chakma) living around Namdapha do not target hornbills for hunting as they do not use hornbill body parts in their traditional headdresses unlike other tribes and over a four-year period (2008–2012), we did not detect evidence of hornbill hunting inside Namdapha (Rohit Naniwadekar,

unpublished data). However, some hunting of other mammal groups like ungulates, primates and large carnivores is prevalent inside Namdapha (Datta et al. 2008). In India, timber harvest is banned inside Protected Areas and Namdapha has never been logged. Therefore, we classified Namdapha Tiger Reserve as a less disturbed site with no logging and low hunting pressures (mainly restricted to mammal species).

Miao Reserved Forest is located within one kilometer of Miao town, which is inhabited by several communities (Singpho, Tangsa, Wancho, Nyishi, Nocte, Adi, Lisu, Chakma and Nepali) with some of these tribes using hornbill body parts. Members of some of these tribes hunt ungulates, arboreal mammals, hornbills and small birds with muzzle loader guns (locally fabricated firearms), rifles, air guns or catapults (R. Naniwadekar, pers. obs.). In the past four years (2008–12), we came across four instances of hunting of hornbills (three instances of Great Hornbills and one of Wreathed hornbills being hunted). Miao was notified as a Reserved Forest in 1962 and the earliest record of systematic logging operations is from 1978 (Working Plan, Jairampur Forest Division). A ban on logging through a Supreme Court order was in effect from 1996 till 2008 (Rosencranz et al. 2007). Logging started again in 2009. Selective logging for important timber species is allowed in designated forest areas (Datta 1998, Nath et al. 2005), however, the harvest is often unsustainable (Rosencranz et al. 2007) and has often led to complete loss of forested habitats (Srivastava et al. 2002). Two species of dipterocarps (*Dipterocarpus macrocarpus* and *Shorea assamica*) and *Terminalia myriocarpa* are the most valued timber species. Several hornbill food plants such as *Phoebe* spp., *Canarium strictum*, *Dysoxylum* sp., *Alseodaphne petiolaris*, *Aglaias* spp., *Cinnamomum glaucescens* and *Beilschmiedia* spp. (Datta and Rawat 2003) are also logged (Appendix 1). For forestry operations, tree species are classified from Class A to F in decreasing order of value of timber. We designated the Miao Reserved Forest as a heavily disturbed site because of logging and hunting pressures on all vertebrate groups.

The two sites were similar to each other in geology, rainfall and elevation and forest/vegetation type. The straight-line distance between the furthest sampling sites was

approximately 28 km (Fig. 1). We marked eight trails (each 1.5 km in length) and four trails each in the less disturbed and the heavily disturbed sites respectively. The trails were at least 500 m apart, except two trails in the less disturbed site that were 300 m apart (Fig. 1). However, we never walked two adjoining trails simultaneously. In the heavily disturbed site, we recorded all fallen logs or cut stumps GBH (girth at breast height)  $\geq 100$  cm within 20 m (10 m on each side) along each trail. We consistently recorded the number of hunters (individuals carrying guns) encountered while accessing, walking or returning from the trails for the two sites.

#### *Hornbill food plant abundance*

We identified hornbill food plant species at both sites based on prior information (Naniwadekar unpublished data; Datta and Rawat 2003). We recorded all the known food plants including figs, non-fig trees with drupaceous or arillate dehiscent capsular fruits, which are consumed by hornbills in the non-breeding season (November–March) in 3 ha belt transects ( $1500\text{ m} \times 20\text{ m}$ ) along each trail in both sites. We classified the food plants into logged and not logged based on the list of timber species in the Working Plan of the Forest Department (Appendix 1). We grouped strangler (hemi-epiphytic) figs that are not logged during selective logging operations separately. Hornbills also consume the fruits of the free-standing fig, *Ficus nervosa*, which is logged. We measured food plant abundance as the number of trees ( $\text{GBH} \geq 30\text{ cm}$ ) per 3 ha.

To model the effect of logging on hornbill food plants, we used Generalized Linear Models (GLM) on the count data of hornbill food plants with sites (less disturbed and heavily disturbed), type of hornbill food plant (logged food plants, not logged food plants and strangler figs), and an interaction between these two factors as predictor variables. We initially ran a GLM with Poisson errors but the results indicated over-dispersion in the data. Therefore, we used a negative binomial GLM with a log link.

#### *Hornbill encounter rates*

We carried out trail walks at both sites between December 2011 and February 2012. In the less disturbed site, we walked trails in the mornings (0600–0900 hr) and late afternoons (1300–1500 hr), as hornbill activity is high during these time periods. We had eight trails, which were walked 12 times each. We largely avoided monitoring the same trail twice on the same day, except on seven occasions. In the heavily disturbed site, trails were walked only in the early mornings (0600–0900 hr) as human activity during the day could affect hornbill presence/detection in the late afternoons. One or two observers walked these trails and recorded hornbill species and number of individuals. The species identity was noted on hearing calls. However, we used only the visual detections for the analysis. We monitored each trail four times in a month. The total effort in less disturbed and heavily disturbed sites was 144 km and 72 km, respectively. Since we recorded only seven individuals in three detections in the heavily disturbed site in 72 km of effort, we were unable to estimate detection probability for the two sites separately. However, hornbills are large, striking and canopy-dwelling birds and are unlikely to be missed.

We used Generalized Linear Mixed-effect Models (GLMM) with Poisson errors to compare counts of hornbills sighted between less disturbed and heavily disturbed sites. There were differences in counts of hornbills across the three months (December=173 individuals, January=32 individuals, February=41 individuals; effort=48 km in each month in the less disturbed site), therefore, we incorporated 'month' effects as a random effect in the model. In addition, we walked each trail 12 times during the study duration, there was variation in the total number of hornbill sightings across the different trails (range: 2–105 individuals; effort: 18 km per trail). Therefore, we also used 'trail' as a random effect. In the heavily disturbed site, the total number of hornbill individuals seen was very low throughout the sampling period. The GLMM with trail and month effects as random and site effects (less disturbed and heavily disturbed) as fixed indicated over-dispersion in the data. We, therefore, incorporated individual observations as a random effect in the model following Elston et al. (2001). We used likelihood-ratio tests to test for the influence of random and fixed effects in GLMM.

### Seed arrival rates

In both sites along each trail, we established 200 1 m × 1m plots on the forest floor to record the arrival of scatter-dispersed seeds (1600 m<sup>2</sup> in less disturbed site; 800 m<sup>2</sup> in heavily disturbed site). We monitored these plots every 15 days (except once when the monitoring interval was 29–31 days) from December 2011–February 2012 (five occasions). We monitored the arrival of dispersed seeds of five large-seeded hornbill food plants – *Canarium strictum*, *Phoebe* sp., *Beilschmiedia assamica*, *Alseodaphne petiolaris* and *Dysoxylum* sp. in these plots. After enumeration, we removed all the accumulated seeds. We considered the seeds without any trace of pulp as having been dispersed. We recorded the species identity and the number of seeds in the plot. We did not use above-ground netted seed traps as during an earlier study in the area, our nets had been taken away by people or damaged. While on-ground seed removal/predation by rodents may potentially occur affecting the seed arrival estimates, we feel due to several reasons that this would not affect our study results. First, we had set out paired 1 m<sup>2</sup> above-ground seed traps and ground plots (100 each) and monitored seed arrival rates over 42 days in the same season in 2010–11. Seed arrival rates were estimated to be 0.001 per m<sup>2</sup> per day for seed traps and 0.002 per m<sup>2</sup> per day for ground plots for three of the five study species (*C. strictum*, *B. assamica* and *Dysoxylum* sp.). Second, in a pilot study to estimate rodent seed removal rates, we had set out 400 marked seeds (five seeds each in ten 1 m<sup>2</sup> plots for eight trails) and found that average seed removal was relatively low (14.8%) for one of our study species, *C. strictum*. We do not have information on rodent abundances at the two sites, however, some of the local tribesmen hunt rodents in the heavily disturbed site both with firearms and traps, while there are no hunting pressures on rodents in the less disturbed site, therefore it is unlikely that there would have been greater seed removal by rodents at the heavily disturbed site which could affect seed arrival estimates.

Although seed arrival rates at the less disturbed site were similar between the two years, they differed in species composition (R. Naniwadekar, unpublished data). These

differences are likely to be due to supra-annual variation in fruiting of these species (Datta 2001). Therefore, we did not compare seed arrival rates of individual species at less disturbed and heavily disturbed sites, but compared the overall arrival rates of large seeds of the five focal tree species between both sites. We used GLMM with Poisson errors to compare seed arrival between less disturbed and heavily disturbed sites. There was considerable variation in total number of seeds detected in plots across trails (range: 2–107) and the different monitoring sessions (range: 4–92). We incorporated trails and the different monitoring sessions as random effects. We used natural logarithms of time interval (number of days) between monitoring sessions as offsets to control for differences in time interval between monitoring sessions and trails. The model indicated over-dispersed data. We therefore used individual observations as a random effect.

#### *Recruitment of hornbill food plants*

Along each trail at both sites, we established belt transects measuring 1500 m × 3 m. For two trails in the less disturbed site, we sampled 750 m × 3 m. We recorded recruits of four of the five large-seeded hornbill food plants, *Canarium strictum*, *Phoebe* sp., *Beilschmiedia assamica* and *Dysoxylum* sp. We were not able to identify recruits of *Alseodaphne petiolaris*. We recorded the species identity and number of individuals of the recruits and measured the size to compare the size structure (seedling: 10–30 cm, large seedling: 30–50 cm, sapling: 50–100 cm, large sapling: 100–150) of the recruits between the two sites.

To compare the recruits in four size classes between the less disturbed and the heavily disturbed site, we used GLM on the count data of recruits with sites (less disturbed and heavily disturbed), size of the recruits (10–30 cm, 30–50 cm, 50–100 cm, 100–150 cm) and an interaction between these two factors as predictor variables. We used the natural logarithm of area sampled as an offset to control for varying sampling effort between trails. We detected only 6 and 10 recruits of *Canarium strictum* across all size classes at less disturbed and heavily disturbed sites respectively; therefore, we did not perform statistical analysis for this species. We initially ran a GLM with Poisson errors but the

results indicated over-dispersion in the data, therefore, we used a negative binomial GLM with a log link.

We carried out all the analysis using R Language, version 2.15.1 (R Core R Development Core Team 2013). We used the package ‘MASS’ for carrying out the negative binomial GLMs and package ‘lme4’ (Bates and Sarkar 2007) for the GLMMs.

## 5.4 RESULTS

### *Logging and hunting pressures*

In the heavily disturbed site, the density of cut logs/stumps (GBH $\geq$ 100 cm) was 11±1 logs/stumps per ha (mean ± SD). There was no logging in the less disturbed site. Despite a lower sampling effort in the heavily disturbed site, we recorded hunters (men with guns) on six occasions, while we heard human presence only once in the less disturbed site. Additionally, we saw feathers of Wreathed Hornbills on the forest floor next to a temporary camp in the heavily disturbed site, outside of the trail sampling.

### *Hornbill food plant abundance*

We identified six species of figs and 15 species of non-fig food plants (Appendix 1). Of the 21 hornbill food plant species, ten were timber species (Appendix 1).

The overall abundance of hornbill food plants was two times higher in the less disturbed site as compared to the heavily disturbed site (negative binomial GLM,  $z_{1, 10} = -2.562$ ,  $p=0.01$ ; Fig. 2). The abundance of food plants that were also timber species was significantly higher than non-timber food plants ( $z_{1, 10} = -5.373$ ,  $p<0.001$ ; Fig. 2; Appendix 2) and strangler figs ( $z_{1, 10} = -4.757$ ,  $p=0.01$ ; Fig. 2; Appendix 2) in both sites. Two-way interactions between site and type of food plant were not significant (negative binomial GLM,  $p>0.05$ ).

### *Hornbill encounter rates*

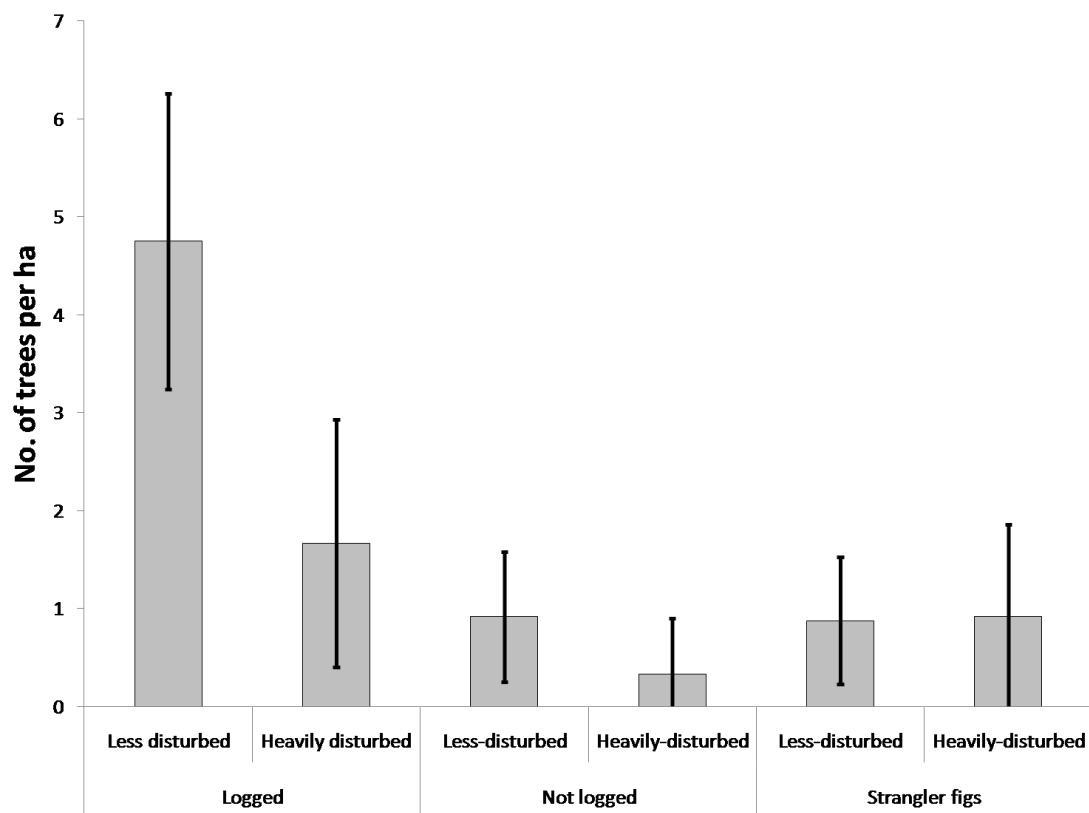
During trail walks, we detected four species of hornbills (Great, Wreathed, Rufous-necked and Brown Hornbill) in the less disturbed site and two species (Wreathed and Rufous-necked Hornbill) in the heavily disturbed site. The total number of hornbills seen across the trails varied from 2–105 individuals at the less disturbed site and 0–6 individuals at the heavily disturbed site. The total number of individuals detected varied across months in the less disturbed site (December: 173, January: 41 and February 32). Overall encounter rates of hornbills was 22 times higher in the less disturbed site as compared to the heavily disturbed site ( $z_{1,10} = -3.123, p=0.002$ ; Fig. 3; Appendix 3).

### *Seed arrival of food plant species*

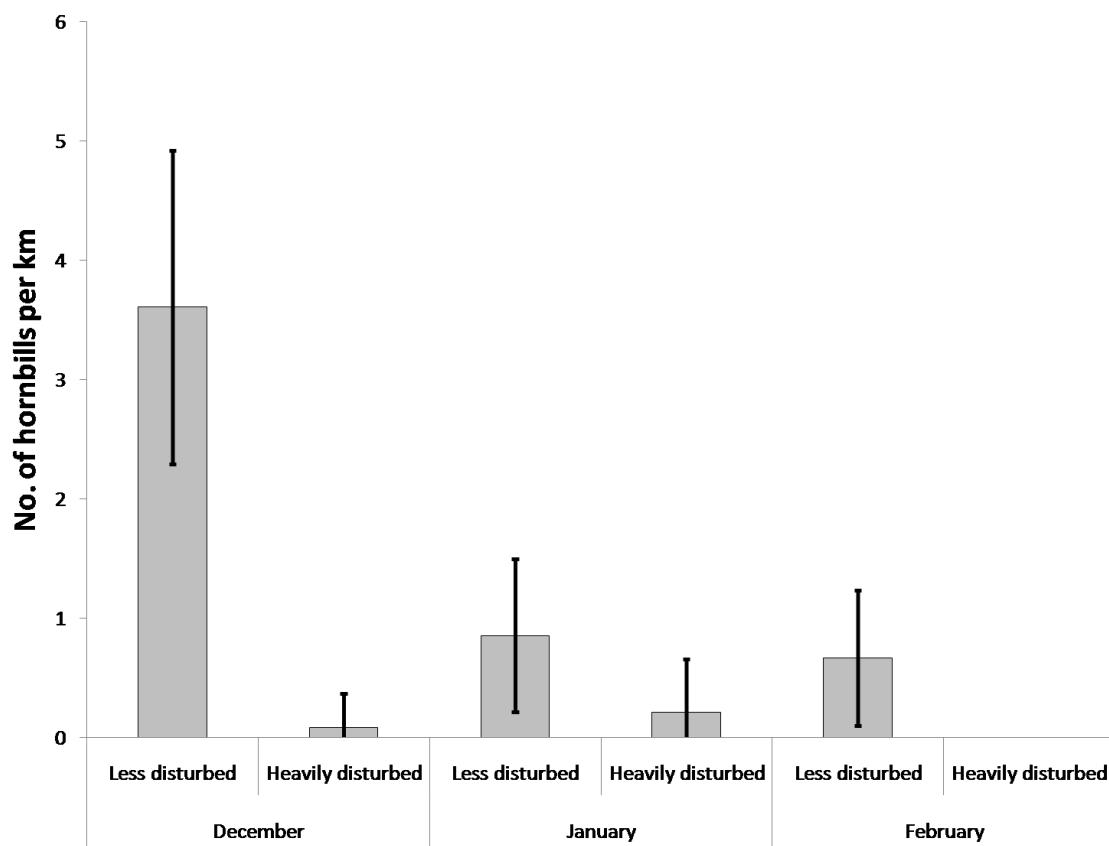
We detected seeds of all the five species (*Phoebe* sp., *Canarium strictum*, *Beilschmiedia assamica*, *Alseodaphne petiolaris*, and *Dysoxylum* sp.) at the less disturbed site and only two species (*Canarium strictum* and *Alseodaphne petiolaris*) at the heavily disturbed site. Scatter-dispersed seed arrival was seven times higher at the less disturbed site as compared to heavily disturbed site ( $z_{1,10} = -2.366, p = 0.018$ ; Fig. 4; Appendix 4).

### *Recruitment of food plant species*

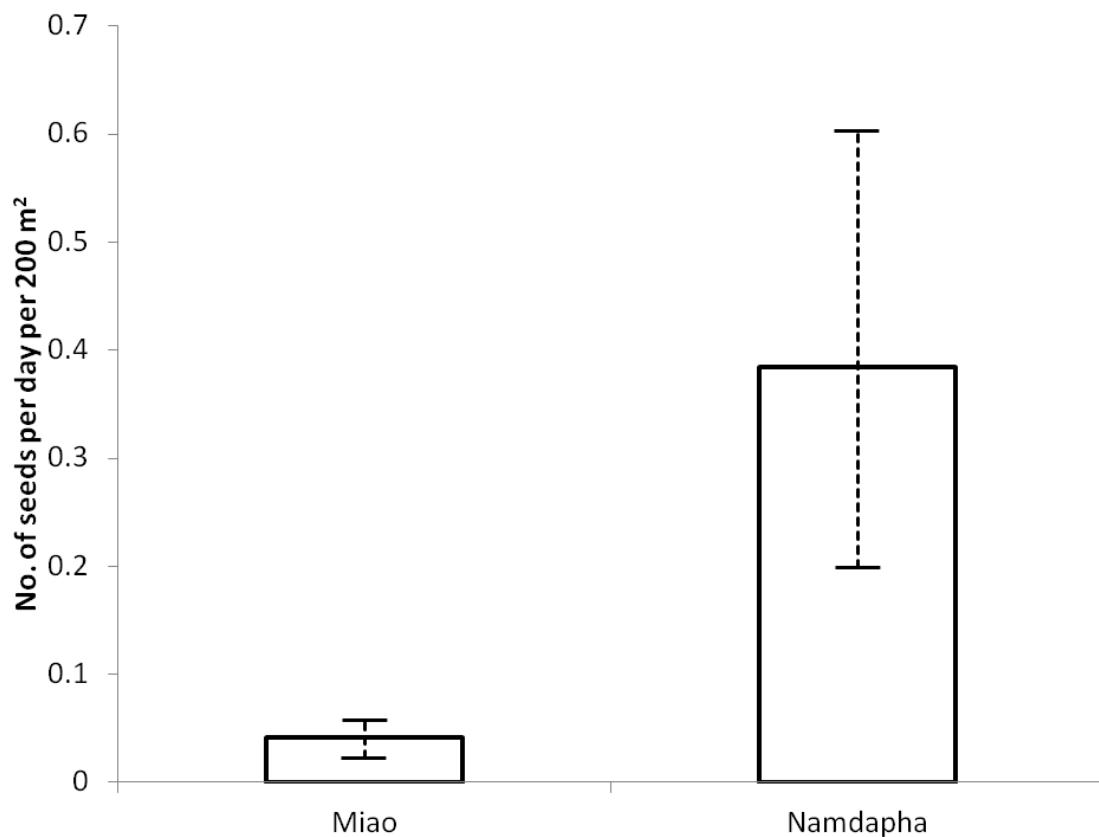
The overall abundance of recruits across all size classes was 20 times higher for *B. assamica* and 48 times higher for *Dysoxylum* sp. in the less disturbed site as compared to the heavily disturbed site (Fig. 5B and Fig. 5C; Appendix 5). The interaction term between size and abundance was not significant in these two species (Poisson GLM, two-way interaction between site and size of recruits was not significant  $p > 0.05$ ). The difference in abundance between less disturbed and heavily disturbed sites was similar for recruits of all size classes in these two species. In contrast, for *Phoebe* sp., the difference between the abundance of small and large-sized recruits was significantly higher in the heavily disturbed site as compared to less disturbed site (Fig. 5A; Appendix 5).



**Figure 2** Number of trees ( $\pm$  95% CI) across the three different categories of food plants (those which are logged, food plants which are not logged and strangler figs) in the less disturbed site (Namdapha) and the heavily disturbed site (Miao).



**Figure 3** Number of hornbills ( $\pm$  95% CI) detected across the sampling period in the less disturbed site (Namdapha) and the heavily disturbed site (Miao).



**Figure 4** Bootstrap mean and 95% confidence intervals of number of seeds per day per  $200 \text{ m}^2$  ( $200 1 \text{ m}^2$  plots per trail) in the less disturbed site (Namdapha) and the heavily disturbed site (Miao).

Fig. 5a

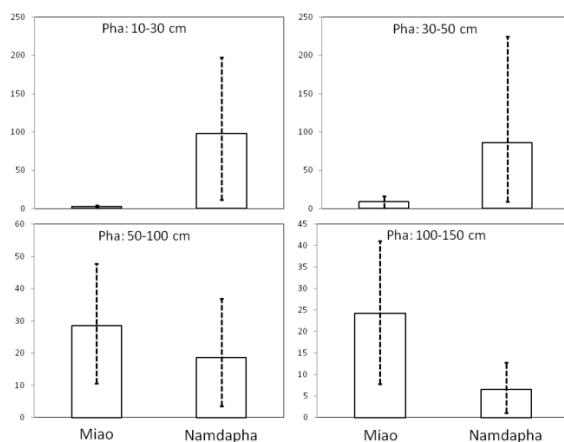


Fig 5b

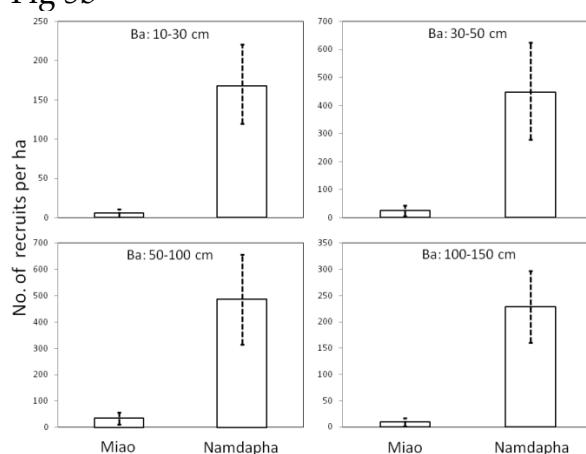
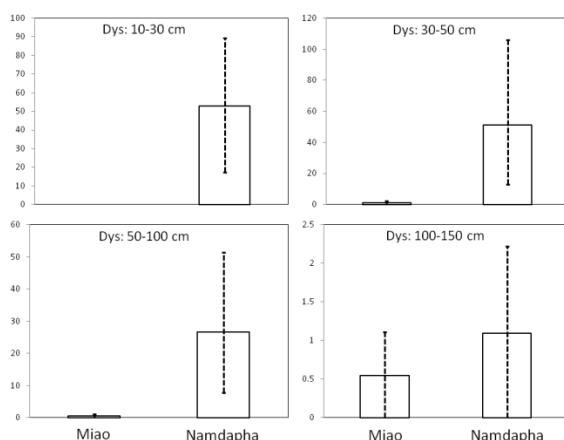


Fig 5c



**Figure 5** Bootstrap mean and 95% confidence intervals of number of recruits per ha in the less disturbed site (Namdapha) and the heavily disturbed site (Miao) for a) *Phoebe* sp. b) *Beilschmiedia assamica* and c) *Dysoxylum* sp. across the four size classes 10–30 cm, 30–50 cm, 50–100 cm and 100–150 cm.

## 5.5 DISCUSSION

We found that the heavily disturbed site had reduced abundances of fruit plants, hornbills and scatter-dispersed seeds, and showed altered recruitment patterns. Our study was restricted to two similar tropical forest sites close to each other (~ 20 km) that differed in the extent of hunting and logging. Due to the absence of more comparable sites representing the less disturbed scenario, we did not have more replicate sites. However, we found that several different stages of the seed dispersal cycle consistently showed differences between our two sites in the predicted direction. This suggests that our findings were robust and that logging and hunting underlay these differences.

In this study, we compared four different stages of the seed dispersal cycle, abundance of food plants, abundance of frugivores, net seed arrival and recruitment patterns of select large-seeded biotically dispersed plants (Fig. 6, open rectangular boxes). The two anthropogenic impacts, logging and hunting, can be expected to differentially impact these four stages. Logging can be expected to have direct impacts (Fig. 6, oval box) on the abundances of plants that are targeted by logging and indirect impacts on frugivores through reduced resource availability (Fig. 6, dark grey box). In the short-term, hunting will have no impacts on food plant abundance. In our study site, timber species that are targeted by logging include abiotically-dispersed species (for e.g. *Terminalia myriocarpa*, *Dipterocarpus macrocarpus*, *Shorea assamica*) and biotically-dispersed species (some examined in this study). Logging of biotically-dispersed species, which is the focus of this study, can alter the abundance of food plants as has been documented in this study. The overall abundance of figs and species that are not logged is lower as compared to abundance of food plant species that are logged. This is despite species richness of plants across the three categories being similar (strangler figs: 5 spp., not logged: 6 spp., logged: 9 spp.). Thus it is clear that logging targets some of the most abundant species of hornbill food plants and can therefore reduce food availability for hornbills. While the frugivore guild is known to be vulnerable to anthropogenic perturbations including logging (Gray et al. 2007, Felton et al. 2008, Markl et al. 2012), studies that have documented reduction

in resource availability as a consequence of these impacts are limited (however see Heydon and Bulloh 1997, Felton et al. 2003). *Canarium strictum* and *Phoebe* sp. are amongst the two important hornbill food plant species that are targeted for logging. They are canopy trees associated with large fruit crop sizes (see Chapter 3). In 2010–11, *Canarium strictum* was represented in 50% and 19% of the foraging sightings of the Wreathed and Rufous-necked Hornbills (see Chapter 3). In 2011–12, when *Canarium strictum* did not fruit *Phoebe* sp. was amongst the most important hornbill food plant (R. Naniwadekar, pers. obs). Additionally, our data from Namdapha, the less disturbed site, indicates that areas with higher abundance of these two species attract higher abundances of hornbills and have higher diversity and abundance of recruits of large-seeded hornbill food plants. Unfortunately, little data exists on the role played by different plant species in the ecosystem. Long-term studies focusing on understanding the importance of different plant species in diet of frugivores and the impacts of logging on the qualitative and quantitative impacts on resource availability for frugivores are therefore needed. In case of hornbills, logging of timber species belonging to the genus *Terminalia*, *Dipterocarpus* and *Shorea* can negatively affect the availability of nesting sites. These hardwood genera are known to be used by hornbills for nesting in Namdapha and other areas in south-east Asia (Kinnaird and O'Brien 2007, Datta 2009). However, this aspect was not examined in the study but is outlined in the conceptual model (Fig. 6).

Hunting of frugivores will result in reduced abundances in the ecosystem (Fig. 6). Amongst the different avian frugivores, hornbills are the largest, they occur in lower densities, have slower breeding rates and take as many as four years to reach sexual maturity (Kemp 1995, Kinnaird and O'Brien 2007). Large-bodied hornbills usually raise a single chick in a year. This makes hornbills vulnerable to hunting pressures exerted for their meat and body parts (tail feathers and casque). The body parts are used by local communities across different areas in north-east India and south-east Asia for traditional reasons (Bennett et al. 1997, Datta 2002). In this study, we found a 22-fold decrease in hornbill abundance in the heavily disturbed site as compared to the less disturbed site. A

combination of both logging and hunting can be expected to result in lower abundances of hornbills in the heavily disturbed site. While logging would have indirect impacts on hornbills through fruit availability, hunting results in direct negative impacts on hornbill populations in the area. Given the difficulty in finding sites with only one of the two anthropogenic disturbances in eastern Arunachal Pradesh, we are unable to tease apart the relative impacts of hunting and logging on hornbills.

Given that logging likely affects food plants of frugivores and hunting impacts the frugivores themselves, negative impacts on the further stages of seed dispersal cycle, including seed dispersal and recruitment, can be expected. Scatter dispersal of seeds as has been documented in this study is mediated by frugivores through fruit removal. While studies have documented reduced frugivore visitation especially, large-bodied frugivores, in sites experiencing anthropogenic disturbances (Forget and Janzen 2007, Holbrook and Loiselle 2009, Velho et al. 2012), estimates of seed arrival of scatter-dispersed seeds have been rarely quantified. In another study in Namdapha, we consistently found positive relationships between hornbill abundance and net seed arrival of four large-seeded plants across two years (Chapter 4). Thus loss of hornbills can be expected to reduce net scatter dispersal of seeds on the forest floor. As per the expectation, we found 7-fold higher seed arrival in the less disturbed site as compared to the heavily disturbed site. However, while net arrival of scatter dispersed seeds can be expected to be negatively influenced by loss of dispersers, it will also be negatively affected by loss of fruiting plants. Seed dispersal will be indirectly influenced by both logging and hunting (Fig. 6). While loss of dispersers results in dispersal limitation and therefore reduced scatter dispersal of seeds, loss of food plants in the first place will result in source limitation. Thus even in the presence of dispersers, logging will negatively affect the scatter-dispersal of seeds and vice versa. In our study, we measured net arrival of seeds (as the arrival of seeds was recorded in plots and not in seed traps), we have not measured the actual seed rain but have measured seeds that remain on the forest floor (net arrival of scatter-dispersed seeds). Secondary dispersal by rodents can be

expected to influence this net arrival of scatter-dispersed seeds differentially across the less and heavily disturbed sites. However, rodents and squirrels face hunting pressures in the heavily disturbed site but not in the less disturbed site. Loss of rodents to hunting is known to reduce secondary seed dispersal and seed predation by rodents (Wright et al. 2000, Wright and Duber 2001, Forget and Janzen 2007). In such a scenario, difference in estimates of net seed arrival in heavily and less disturbed site, can be expected to be conservative. However, we did not quantify these differences across the sites.

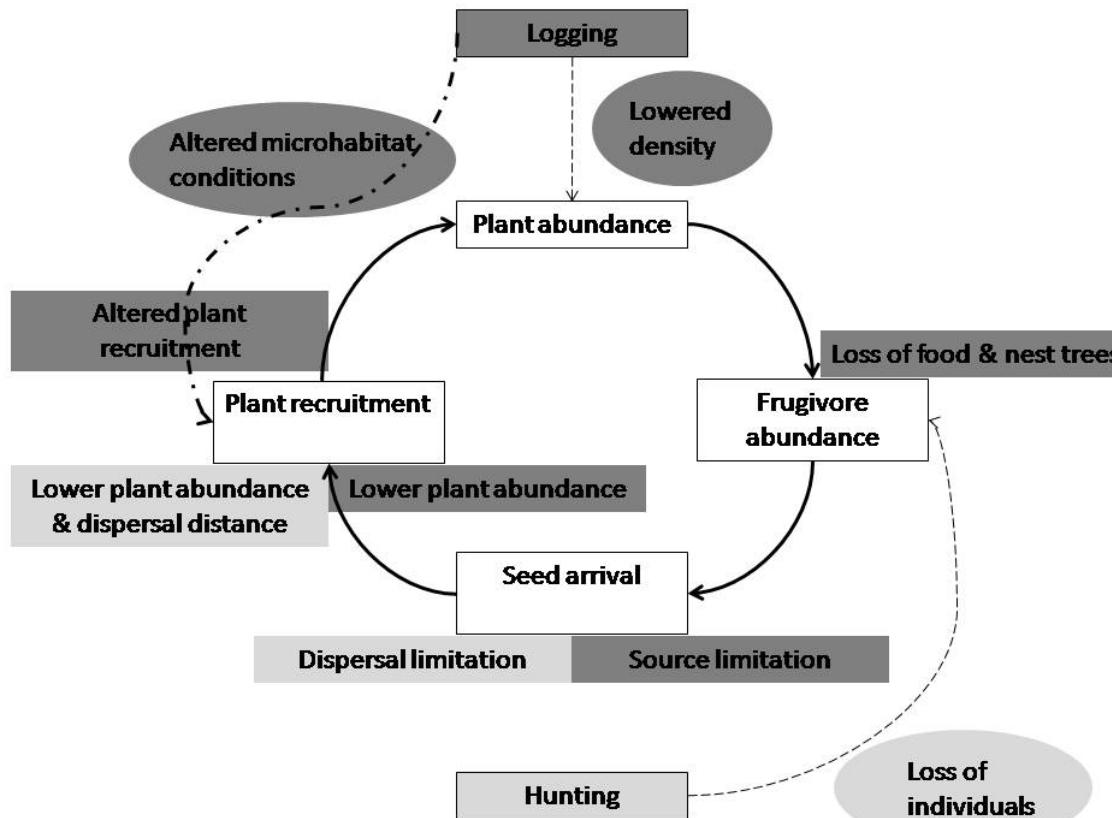
We expected that the lower abundance of hornbills and reduced seed arrival by logging and hunting would have downstream effects by negatively affecting the recruitment of plants. Both hunting and logging will contribute to reduced recruitment mediated by source and dispersal limitation, hunting of frugivores will also additionally result in reduced dispersal distances of seeds. Forests experiencing anthropogenic threats like hunting and logging demonstrate shifts in recruit communities with greater representation of abiotically dispersed species as compared to biotically dispersed species (Terborgh et al. 2008, Velho et al. 2012). We also found that disturbed forests experience lowered recruitment of two large-seeded species *Beilschmiedia assamica* and *Dysoxylum* sp.. This has also been found in other studies in several tropical forest sites (Nunez-Iturri et al. 2008, Sethi and Howe 2009, Vanthomme et al. 2010). Large-seeded biotically dispersed species are known to be particularly vulnerable to these threats as they have a smaller assemblage of frugivores as compared to small-seeded species (Vanthomme et al. 2010, Markl et al. 2012, Velho et al. 2012). Interestingly, for *Phoebe* sp., we found significant interaction between disturbance and recruit size. In the lower size classes, the abundance of recruits was higher in the less disturbed site while in the higher size classes the pattern was reversed. This could be a consequence of poor recruitment in the recent past due to source and dispersal limitation in the heavily disturbed site. For *Canarium strictum*, the abundance of recruits was extremely low as compared to other species at both the heavily and less disturbed site. Recruitment of plants is also dependent on a suite of other factors like micro-habitat conditions (Wenny 2000, Ruger et

al. 2009) and environmental factors (Curran et al. 1999). In fact, improved light conditions is known to enhance recruitment in most (75%) of the plants at a tropical forest site in Panama (Ruger et al. 2009). Thus on one hand while logging can reduce recruitment patterns via source limitation, it can also enhance recruitment of plants through improved light conditions on the forest floor (Fig. 6). Thus in human-modified landscapes, resilience of species to different anthropogenic disturbances can be expected to vary as seen for the four species at our study site.

Reduced recruitment in the disturbed site of certain high value timber species that are animal-dispersed has consequences for long-term persistence of these species and affect the sustainability of timber harvests in logged forests in the long-term. In India, reduced-impact logging, which could improve the sustainability of harvests, is not practiced despite substantial evidence of negative impacts of conventional selective logging practices on wildlife and ecosystem processes (Thiollay 1992, Cannon et al. 1994, Thiollay 1997, Velho et al. 2012). Even the less damaging reduced-impact logging is known to be detrimental to large frugivores (Bicknell and Peres 2010). It is therefore necessary to re-evaluate and modify current logging practices in the tropical forests of north-east India.

Given that tropical forests in north-east India and elsewhere in the world face multiple threats, it is important to understand the combined impacts of multiple threats on ecosystem processes like seed dispersal and recruitment. Frugivores are directly lost to hunting and are also affected by reduced food availability due to logging which can then result in reduced seed arrival and altered recruitment patterns of large-seeded tree species. We summarize the different consequences of logging and hunting in disrupting the seed dispersal cycle into a conceptual model (Fig. 6). At the centre of this framework is the mutualistic relationship between plants and frugivores. The four stages of plant abundance, frugivore abundance, seed arrival and plant recruitment are shown in the four boxes connected with curved solid arrows. This is a shortened version of the ‘seed dispersal loop’ proposed by Wang and Smith (2002). The two anthropogenic threats logging (dark grey box at the top) and hunting (light grey box at the bottom) affect the

different stages directly (color coded oval boxes, broken arrows) and indirectly. The indirect consequences of logging on the different stages are depicted in the rectangular boxes without outlines and arrows. Logging directly impacts target plants by negatively affecting their densities. This indirectly impacts frugivores by reduced fruit (and nest tree) availability, seed dispersal by source limitation and recruitment by lowered abundance of recruits as a consequence of source limitation. Logging also alters the microhabitat conditions and can enhance or reduce recruitment of plants (dashed and dotted line). On the other hand, hunting of frugivores negatively impacts their natural densities indirectly impacting seed arrival by dispersal limitation and plant recruitment by lowered abundance of recruits and lowered dispersal distance of recruits from the parent trees. In the long-term while hunting will have consequences on adult plant abundance it does not have any short-term impacts on abundance of adult plants.



**Figure 6** Conceptual model summarizing the relationship (black solid arrow) across different stages of seed dispersal (shown in open rectangular boxes) and direct (color coded oval box without outline and broken arrow) and indirect (color coded rectangular box without outline) impacts of logging (dark grey rectangular box with outline) and hunting (light grey rectangular box with outline) on the different stages of the seed dispersal. Dashed and dotted line shows additional likely impacts of logging (not explored in this study) on plant recruitment.

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## 5.7 APPENDICES

**Appendix 1** List of hornbill food plants and their timber class (Working Plan, Jairampur Forest Division) categorized into strangler figs, hornbill food plants, which are logged, and hornbill food plants that are not logged. Class A–E represents decreasing order of preference for timber value.

Category	Family	Tree species	Timber Class
Logged	Lauraceae	<i>Phoebe</i> sp.	A/B
Logged	Burseraceae	<i>Canarium strictum</i>	B
Logged	Lauraceae	<i>Phoebe cooperiana</i>	B
Logged	Meliaceae	<i>Dysoxylum</i> sp.	B
Logged	Meliaceae	<i>Aglaia spectabilis</i>	B
Logged	Lauraceae	<i>Alseodaphne petiolaris</i>	C
Logged	Meliaceae	<i>Aglaia</i> sp.	C
Logged	Lauraceae	<i>Beilschmiedia assamica</i>	E
Logged	Lauraceae	<i>Beilschmiedia</i> sp.	E
Logged	Moraceae	<i>Ficus nervosa</i>	E
Strangler fig	Moraceae	<i>Ficus microcarpa</i>	Non-timber
Strangler fig	Moraceae	<i>Ficus drupacea</i>	Non-timber
Strangler fig	Moraceae	<i>Ficus altissima</i>	Non-timber
Strangler fig	Moraceae	<i>Ficus cf. tsjahela</i>	Non-timber
Strangler fig	Moraceae	<i>Ficus</i> sp.	Non-timber
Not logged	Annonaceae	<i>Polyalthia cf. simiarum</i>	Non-timber
Not logged	Lauraceae	<i>Machilus duthiei</i>	Non-timber
Not logged	Lauraceae	<i>Cryptocarya</i> sp.	Non-timber
Not logged	Lauraceae	<i>Actinodaphne angustifolia</i>	Non-timber
Not logged	Oleaceae	<i>Chionanthus</i> sp.?	Non-timber

Not logged	Rosaceae	<i>Prunus ceylanica</i>	Non-timber
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**Appendix 2** Results from the GLM with negative binomial errors comparing hornbill food plant abundance across three categories (food plants which are logged, food plants which are not logged and strangler figs) between the two sites (Namdapha – with no logging and low hunting pressures and Miao – with logging and high hunting pressures). Parameter estimates (intercept and contrasts), standard errors (SE) and hypothesis tests for parameters are shown.

	Estimate	SE	z	p
Intercept (Site – Namdapha; Category – Logged)	2.57	0.19	13.58	<0.001
Site – Miao	-0.7	0.27	-2.56	0.01
Category – Not logged	-1.62	0.30	-5.37	<0.001
Category – Strangler fig	-1.367	0.29	-4.76	<0.001

**Appendix 3** Results from the GLMM with Poisson errors comparing hornbill abundance between Namdapha (with no logging and low hunting pressures) and Miao (with logging and high hunting pressures). Parameter estimates (intercept and contrast), standard errors (SE) and hypothesis tests for parameters are shown.

	Estimate	SE	<i>z</i>	<i>p</i>
Intercept (Site – Namdapha)	1.16	0.59	1.96	0.049
Site – Miao	-3.04	0.97	-3.12	0.002

**Appendix 4** Results from the GLMM with Poisson errors comparing abundance of scatter-dispersed seeds between Namdapha (with no logging and low hunting pressures) and Miao (with logging and high hunting pressures). Parameter estimates (intercept and contrast), standard errors (SE) and hypothesis tests for parameters are shown.

	Estimate	SE	<i>z</i>	<i>p</i>
Intercept (Site – Namdapha)	-2.05	0.54	-3.82	<0.001
Site – Miao	-1.94	0.82	-2.37	0.018

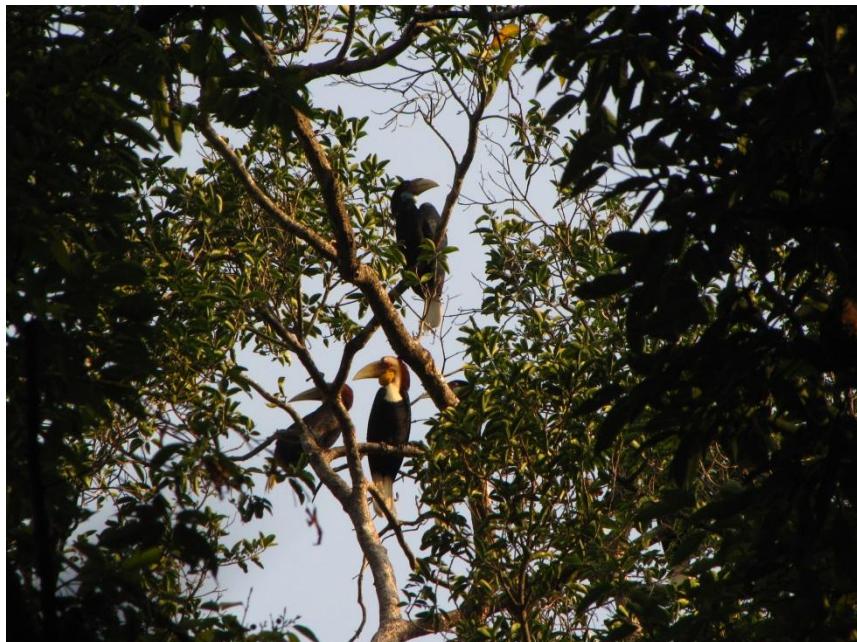
**Appendix 5** Results from the GLM with negative binomial errors, for *Beilschmiedia assamica*, *Phoebe* sp. and *Dysoxylum* sp., comparing recruit abundance between Namdapha (with no logging and low hunting pressures) and Miao (with logging and high hunting pressures) and four size classes (10–30 cm, 30–50 cm, 50–100 cm and 100–150 cm). Three orthogonal contrasts were set for comparisons. Contrast 1: size 10–30 cm vs. other size classes (30–50 cm, 50–100 cm and 100–150 cm), contrast 2: size 30–50 cm vs. other size classes (50–100 cm, 100–150 cm) and contrast 3: size 50–100 cm vs. size 100–150 cm. Parameter estimates (intercept and contrast), standard errors (SE) and hypothesis tests for parameters are shown.

<i>Beilschmiedia assamica</i>				
	Estimate	SE	<i>z</i>	<i>P</i>
Intercept (Site – Namdapha)	-3.49	0.13	-27.18	<0.001
Site – Miao	-2.97	0.24	-12.29	<0.001
Contrast 1	-0.23	0.06	-3.6	<0.001
Contrast 2	0.1	0.09	1.08	0.279
Contrast 3	0.46	0.15	3.01	0.003
<i>Phoebe</i> sp.				
	Estimate	SE	<i>z</i>	<i>p</i>
Intercept (Site – Namdapha)	-5.77	0.33	-17.78	<0.001
Site – Miao	-1.01	0.57	-1.76	0.078
Contrast 1	0.38	0.19	2.05	0.04
Contrast 2	0.70	0.26	2.66	0.008
Contrast 3	0.56	0.47	1.20	0.22968
Site: contrast 1	-0.85	0.34	-2.52	0.012
Site: contrast 2	-1.06	0.46	-2.31	0.021
Site: contrast 3	-0.5	0.79	-0.63	0.53
<i>Dysoxylum</i> sp.				
	Estimate	SE	<i>z</i>	<i>p</i>
Intercept (Site – Namdapha)	-6.31	0.26	-24.66	<0.001
Site – Miao	-3.87	0.66	-5.9	<0.001
Contrast 1	0.29	0.13	2.27	0.023
Contrast 2	0.66	0.19	3.49	<0.001
Contrast 3	1.32	0.38	3.48	<0.001

# Chapter 6

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## Looking beyond parks: the conservation value of unprotected areas for hornbills in Arunachal Pradesh, Eastern Himalaya



Flock of Wreathed Hornbills in a Reserved Forest site in Arunachal. Arunachal continues to harbor vast areas of forest outside Protected Areas. This chapter focuses on understanding hornbill status outside Protected Areas.

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## 6.1 ABSTRACT

The loss of tropical forests and associated biodiversity is a global concern. Conservation efforts in tropical countries such as India have mostly focused on state-administered protected areas despite the existence of vast tracts of forest outside these areas. We studied hornbills (Bucerotidae), an ecologically important vertebrate group and a flagship for tropical forest conservation, to assess the importance of forests outside protected areas in Arunachal Pradesh, north-east India. We conducted a state-wide survey to record encounters with hornbills in seven protected areas, six state-managed reserved forests and six community-managed unclassed forests. We estimated the density of hornbills in one protected area, four reserved forests and two unclassed forests in eastern Arunachal Pradesh. The state-wide survey showed that the mean rate of encounter of rufous-necked hornbills *Aceros nipalensis* was four times higher in protected areas than in reserved forests and 22 times higher in protected areas than in unclassed forests. The mean rate of encounter of wreathed hornbills *Rhyticeros undulatus* was twice as high in protected areas as in reserved forests and eight times higher in protected areas than in unclassed forests. The densities of rufous-necked hornbill were higher inside protected areas, whereas the densities of great hornbill *Buceros bicornis* and wreathed hornbill were similar inside and outside protected areas. Key informant surveys revealed possible extirpation of some hornbill species at sites in two protected areas and three unclassed forests. These results highlight a paradoxical situation where individual populations of hornbills are being lost even in some legally protected habitat, whereas they continue to persist over most of the landscape. Better protection within protected areas and creative community-based conservation efforts elsewhere are necessary to maintain hornbill populations in this biodiversity-rich region.

**Keywords** *Aceros nipalensis*, *Buceros bicornis*, Arunachal Pradesh, community-owned forest, hornbill abundance, Namdapha National Park, protected area, *Rhyticeros undulatus*

## 6.2 INTRODUCTION

Tropical forests harbour 50% of the known global biodiversity (Dirzo and Raven 2003) but these forests are under threat from logging, agriculture and other land-use changes (Curran et al. 2004, Gaveau et al. 2007). The rate of tropical forest loss in Asia is high, estimated at 2.9% during 2000–2005 (Achard et al. 2002, Hansen et al. 2008). Although protected areas are intended to reduce the rates of forest loss (Sanchez-Azofeifa et al. 2002, Naughton-Treves et al. 2005) the current network of protected areas is inadequate for conserving tropical biodiversity (Rodrigues et al. 2004). Therefore there is a need for improved biodiversity conservation in areas outside protected areas (Daily 2001). Forested areas outside protected areas are important as they increase the effective habitat size (Pimm et al. 1988) and act as buffers to reduce anthropogenic pressures on protected areas (Brashares et al. 2001, Laurance et al. 2002).

The state of Arunachal Pradesh in north-east India is part of the Eastern Himalaya biodiversity hotspot. More than 60% of its land area is under forest cover. However, 81.5% of this forested area lies outside the protected area network (FSI 2009) and potentially harbours important and threatened wildlife (Mishra et al. 2006, Aiyadurai et al. 2010). Hornbills are a key ecological group in Asian tropical forests. They are the largest volant frugivores and range over large areas (Keartumson et al., 2011) in search of patchily distributed fruit resources. They play an important functional role as seed dispersers (Datta 2001, Kitamura 2011). Of the 31 species of Asian hornbills nine are found in India, and five of these occur in Arunachal Pradesh: rufous-necked hornbill *Aceros nipalensis*, brown hornbill *Anorrhinus austeni*, great hornbill *Buceros bicornis*, wreathed hornbill *Rhyticeros undulatus* and oriental pied hornbill *Anthracoceros albirostris*. The rufous-necked hornbill is categorized as Vulnerable and the great and brown hornbills as Near Threatened on the IUCN Red List of Threatened Species (IUCN 2012).

In Arunachal Pradesh, as in other parts of south-east Asia, hornbills are hunted for their meat, body parts (casque and tail feathers) and fat (Bennett et al. 1997, Datta 2002, Kinnaird and O'Brien 2007). Given the extensive hornbill habitat that lies outside protected areas, a considerable proportion of the state's hornbill population probably occurs outside these areas. We surveyed 20 sites across the state to assess the status of hornbills within and outside protected areas. We carried out field surveys and key informant interviews, focusing primarily on landscapes outside protected areas, including those under the de facto ownership of local communities as well as those managed by the State Forest Department. We included some sites within protected areas for comparison. We complemented these landscape-level assessments at multiple sites across Arunachal Pradesh with intensive efforts to estimate hornbill density both within and outside protected areas in the eastern part of the state.

### 6.3 METHODS

#### *Study area*

The survey was carried out across the state of Arunachal Pradesh (Fig. 1), which has a human population density of 17 persons  $\text{km}^{-2}$  (country mean  $382 \text{ km}^{-2}$ ) and a decadal population growth rate of 25.92% (country mean 17.5%; Indian Census 2011). There are nine protected areas in the state (two tiger reserves, eight wildlife sanctuaries and one national park), which account for 18.5% of the state's forested area. National parks are 'inviolate' areas, where human residence and activities such as hunting and logging are prohibited. In wildlife sanctuaries subsistence activities such as collection of wood for fuel by local communities and cattle grazing are permitted. The forested areas outside protected areas can be classified as reserved forests or unclassed forests. Logging may be carried out in reserved forests under the working plan prescriptions made for different divisions of the State Forest Department. Unclassed forests, although recorded as forests by the State Forest

Department, are under the de facto control of local tribal communities. Logging is carried out in unclassed forests with the consent of the local communities, using the working schemes of the local Forest Divisions. Indian wildlife is categorized under six schedules in the Wildlife (Protection) Act of India, 1972. Hunting of wild animals in Schedules I–IV is illegal. All five hornbill species are categorized under Schedule I of the Act.

We sampled eight sites in seven protected areas and six sites each in reserved forests and unclassed forests (Fig. 1; Table 1). Our aim was to represent adequately the variability in rates of encounters with hornbills across the three regimes and therefore we placed greater emphasis on surveying several independent sites than on intensive sampling at any one site. We sampled across the entire elevation gradient occupied by hornbills in Arunachal Pradesh (150–2300 m; Table 1).

To obtain more precise information on hornbill abundance in the different administrative regimes we sampled intensively at one site in a protected area (Namdapha National Park), four sites in ecologically comparable reserved forests and two sites in unclassed forests. Intensive sampling resulted in a higher number of detections and allowed us to account for differential detectability between sites, which we were unable to do in the state-wide surveys.

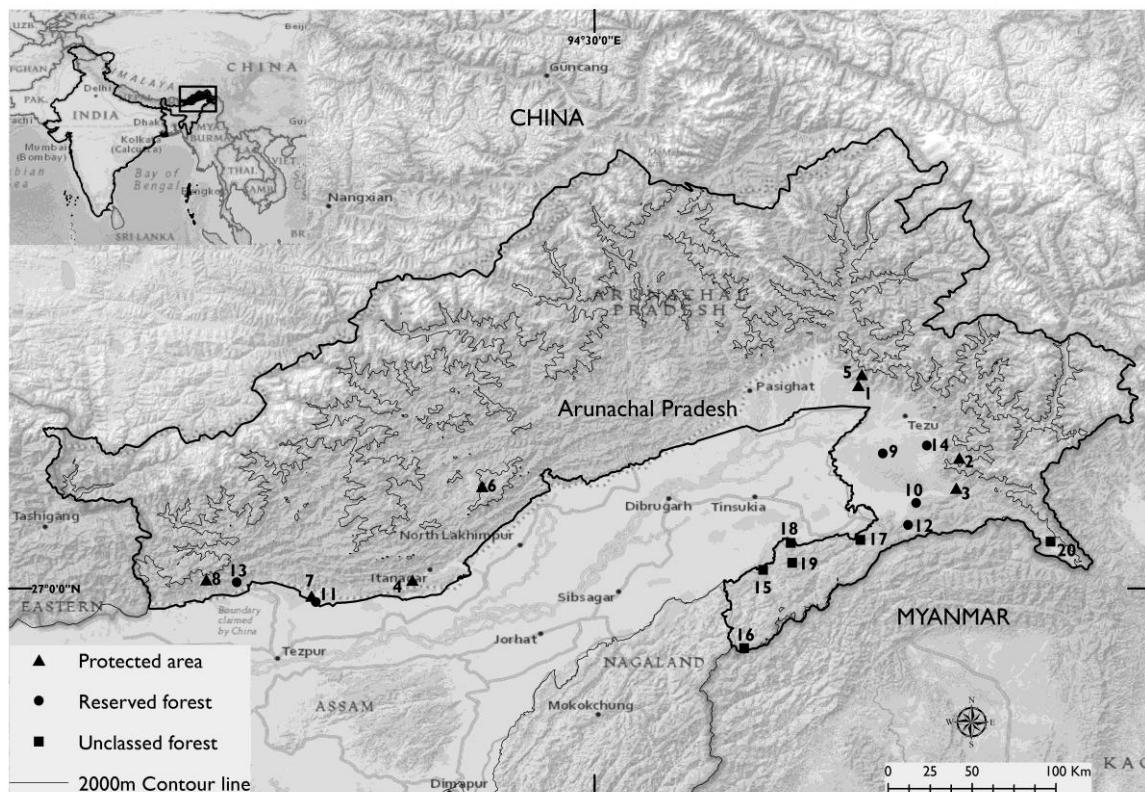
**Table 1** Details of sites sampled for hornbill species in Arunachal Pradesh, north-east India (Fig. 1) during state-wide and intensive surveys, with the site name, trail lengths, name of protected area, reserved forest or unclassed forest, elevational range of sampling, total sampling effort, and sampling period.

No.	Site (trail lengths, km)	Protected area/reserved forest/unclassed forest*	Elevation (m)	Total effort (km)	Sampling period
<b>State-wide surveys</b>					
1	Abango (5)	Mehao WS	400–500	5	Jan. 2008
2	Glao Lake (14, 3, 14)	Kamlang WS	400–1300	31	Feb. 2008
3	Hornbill Plateau (8, 3, 3, 8)	Namdapha TR	500–600	22	Mar. 2008
4	Jotte (5, 7)	Itanagar WS	200–300	12	Apr. 2008
5	Mehao Lake (7, 2, 7)	Mehao WS	400–1750	16	Feb. 2008
6	Monipoliyang-Pange-Tale (6, 9, 9, 6)	Tale WS	1500–2300	30	Mar. 2008
7	Seijusa (2)	Pakke TR	150–300	6	Apr. 2008
8	Sessni (2, 2.5, 2)	Eaglenest WS	1200–1400	6.5	Apr. 2008
9	Madhuban (5)	Tengapani RF	200–250	5	Mar. 2008
10	Miao (6)	Miao RF	350–800	12	Feb. 2008

11	Monai (3.5, 2.1, 3)	Papum RF	150–250	8.6	Apr. 2008
12	Rima (2)	Rima RF	400–750	34	Nov. 2008–Apr. 2009
13	Tipi (5, 2, 1.7)	Doimara RF	200–400	17.4	Apr. 2008
14	Turung (5)	Turung RF	230–250	10	Mar. 2008
15	Hukanjuri (2.5)	UF, Deomali FD	170–250	5	Feb. 2008
16	Konnu (1)	Kanubari UF, Deomali FD	1050–1150	1	Jan. 2008
17	Manmao (4)	Manmao UF, Jairampur FD	700–850	8	Feb. 2008
18	Mopaya (4)	UF, Deomali FD	160–520	8	Feb. 2008
19	Soha (7)	UF, Deomali FD	550–1,150	7	Feb. 2008
20	Yakhulo (1.3)	Vijaynagar UF, Jairampur FD	1200–1400	20.8	Jan.–Apr. 2009
<b>Intensive surveys</b>					
1	Bulbulia (2)	Namdapha TR	550	48	Jan.–Apr. 2009
2	Hornbill (2)	Namdapha TR	500	46	Jan.–Apr. 2009
3	Rajajheel (2)	Namdapha TR	850	50	Jan.–Apr. 2009
4	Ranijheel (1.7)	Namdapha TR	850	45.9	Jan.–Apr. 2009
5	Madhuban 1 (1.5)	Tengapani RF	200–250	33	Jan.–Apr. 2009

6	Madhuban 2 (1.5)	Tengapani RF	200–250	31.5	Jan.–Apr. 2009
7	Madhuban 3 (1.5)	Tengapani RF	200–250	34.5	Jan.–Apr. 2009
8	Madhuban 4 (1.5)	Tengapani RF	200–250	30	Jan.–Apr. 2009
9	Miao (2)	Miao RF	350–700	42	Nov. 2008–Apr. 2009
10	Rima (2)	Rima RF	400–750	34	Nov. 2008–Apr. 2009
11	Turung (3)	Turung RF	230–250	27	Jan.–Apr. 2009
12	Manmao (1.7)	Manmao UF, Jairampur FD	700–850	25.5	Nov. 2008–Apr. 2009
13	Yakhulo (1.3)	Vijaynagar UF, Jairampur FD	1200–1400	20.8	Jan.–Apr. 2009

\*WS, Wildlife Sanctuary; TR, Tiger Reserve; RF, Reserved Forest; UF, Unclassed Forest; FD, Forest Division



**Figure 1** Locations of sampling sites across the state of Arunachal Pradesh, northeast India. The numbers correspond to those in the state-wide survey section of Table 1. The rectangle on the inset indicates the location of the main map in India.

*State-wide surveys*

We sampled hornbill abundance along existing trails at each site during 0600–1300 hr from January to April 2008. Our sampling was carried out mainly during the non-breeding season, which in Arunachal Pradesh is between the end of March and early August (Datta and Rawat 2004). The total effort across all 20 sites was 265.3 km (mean 13.3 km per site). The mean length of trails sampled was 4.4 km (range 1–14 km; Table 1). On sighting a hornbill flock we recorded the species and the number of individuals. Species were also identified by their calls. We used visual and aural detections to calculate hornbill flock encounter rates as the number of flocks (sightings or calls) per km of sampling effort.

Our state-wide surveys were not adequate to confirm the absence of hornbill species at a site. Therefore we conducted semi-structured key informant interviews ( $n=78$ ), with at least two hunters at each site, to ascertain the presence of species that were not recorded during our walks. The interviews were conducted at villages close to the sampling site.

We used the point-centred quarter method (Cottam and Curtis 1956) at 15 sites and 10-m-radius circular plots at five sites to estimate tree density (girth at breast height  $\geq 30$  cm) and total basal area per ha. Every 100 m along the trail we measured the distance to the nearest tree (girth at breast height  $\geq 30$  cm) and its girth, in each of the quarters around the observer. We sampled at 20 such points along the length of the trail except at one site (Konnu), where the distance interval was reduced to 75 m as the trail was short. The circular plots were spaced at 100 m intervals. The number of plots along a trail was 15–35, depending on the length of the trail.

*Intensive surveys in eastern Arunachal Pradesh*

We carried out temporally replicated line-transect surveys along four trails in a protected area (Namdapha Tiger Reserve), seven trails at four reserved forest sites (Tengapani, Turung, Miao and Rima) and one trail at each of two unclassed forest sites (Manmao and Vijaynagar) in eastern Arunachal Pradesh from November 2008 to April 2009 (Table 1). Trail length was 1.3–3.0 km and the total effort along each trail was 20.8–50 km, yielding an overall sampling effort of 486.2 km. One or two observers walked each trail in the morning (0500–1000 hr) and/or in the evening (1300–1700 hr). We recorded species identity, number of individuals and the perpendicular distance to the centre of the flock, following standard line-transect protocol (Buckland et al. 2003). The mean walking speed was 1.6 km per hour. Distances were measured using a rangefinder.

*Analysis of state-wide survey data*

Particular hornbill species are known to occur within a certain range of elevation, therefore we needed to control for the confounding effects of elevation on natural species absence while investigating species responses within and outside protected areas. Based on existing knowledge (Katti et al. 1992, Datta et al. 1998, Kemp 2001) and previous experience we used data only from sites within the known elevational distribution of each species. The great hornbill and brown hornbill usually occur from the plains and low-elevations forests up to 1000 m, although the great hornbill is known to occur up to 2000 m, rufous-necked hornbill occurs between 150–2200 m, but usually within 600–1800 m, while wreathed hornbill occurs mainly among foothills to 2560 m. We omitted data from two protected area sites (Sessni and Monipoliyang-Pange-Tale) and two unclassed forest sites (Yakhulo and Konnu) that were higher than the known preferred elevation range of great hornbill. For the rufous-necked hornbill, we omitted five low-elevation sites, including three in protected areas (Jotte, Seijusa and Abango) and two in reserved forests (Tipi and

Monai). For the wreathed hornbill, we included data from all sites as this species occurs across the entire sampled elevation gradient (150–2500 m).

We used generalized linear models on the count data for hornbill flock detections for comparison across the three site categories (protected area, reserved forest and unclassed forest). The natural logarithm of effort was used as an offset to control for differences in sampling effort between the sites. As generalized linear models with Poisson errors indicated over-dispersion in the data we used a negative binomial model with a log link. We carried out this analysis separately for great, rufous-necked and wreathed hornbills. We did not carry out analysis for oriental pied hornbills, because of a paucity of detections, or brown hornbills, which are geographically restricted to eastern Arunachal Pradesh. Statistical inference was based on model selection using an information-theoretic approach (Burnham and Anderson 2002). For each of the three species we specified and fitted two models (a basic model with only intercept and a second with an administrative category as a predictor). We used the corrected Akaike's information criterion ( $AIC_c$ ) to evaluate the relative fit between two candidate models.  $AIC_c$  is recommended for small sample sizes where the ratio of sample size to the number of parameters is  $<40$  (Burnham and Anderson 2002). The model with the smallest  $AIC_c$  value is the best estimate of the unknown 'true' model based on our data. The administrative regimes were indicators of anthropogenic pressures on each site. To assess independently the effects of logging pressure on each of the sites we also compared tree density and basal area across the three administrative categories.

The data were non-normally distributed and therefore we compared the mean and 95% bootstrapped ( $n=1000$ ) confidence intervals for hornbill encounter rates, tree density and total basal area per hectare across protected area, reserved forest and unclassed forest. We performed all the analysis for hornbill encounter rates and vegetation data in *R v. 2.15.1* (R Development Core Team 2013).

### *Analysis of intensive survey data*

We estimated hornbill densities using *DISTANCE v. 6.0* (Thomas et al. 2009). Distance sampling accounted for variability in detection probability within and outside protected areas. Distance data were grouped automatically by the software. Sightings were entered as clusters. To control influences of varying flock sizes on detectability we used size-bias regression ( $p=0.15$ ). Standard combinations of series expansion (half-normal, uniform, hazard-rate) and key functions (cosine, simple polynomial and hermite polynomial) were used (Thomas et al. 2010). The model with the smallest AIC was chosen as the best model (Burnham and Anderson 2002). Given that we had only three hornbill sightings in unclassed forests over 46.3 km of effort we combined hornbill sightings for unclassed forests and reserved forests and compared overall hornbill densities within and outside protected areas. As the number of sightings of each hornbill species was low we estimated the detection function by pooling the detections of the three large-bodied hornbill species (2000–3000 g). Detections were pooled separately for inside and outside protected areas.

## 6.4 RESULTS

### *State-wide surveys*

Mean rates of encounter of hornbills (95% bootstrapped CI) within protected areas were consistently higher than in reserved or unclassed forests for two of the three species (Table 2), for which models with administrative regime as predictor fit the data better than the basic model ( $\Delta\text{AIC}>4$ ). The mean rate of encounter with the rufous-necked hornbill in protected areas ( $0.45 \text{ km}^{-1}$ ) was four times higher than in reserved forests ( $0.11 \text{ km}^{-1}$ ) and 22 times higher than in unclassed forests ( $0.02 \text{ km}^{-1}$ ) (Table 2). The mean rate of encounter with the wreathed hornbill in protected areas ( $0.24 \text{ km}^{-1}$ ) was more than twice that in reserved forests ( $0.10 \text{ km}^{-1}$ ) and eight times that in unclassed forests ( $0.03 \text{ km}^{-1}$ ). The mean rate of encounter with the great

hornbill was  $0.14 \text{ km}^{-1}$  in protected areas and  $0.11 \text{ km}^{-1}$  in reserved forests, with no encounters in unclassed forests (Table 2).

Key informant interviews indicated that in the 5 years prior to the study the great hornbill was not detected in surveyed areas within two protected area sites (Mehao and Itanagar) and three unclassed forest sites (Table 3) and the rufous-necked hornbill was not detected at two unclassed forest sites. The only species that was reported present at all sites was the wreathed hornbill (Table 3). We considered that reports of non-detection in the previous 5 years by key informants were evidence of apparent extirpation.

Mean tree density (95% bootstrapped CI) was lowest in reserved forests ( $295 \text{ trees ha}^{-1}$ , 95% CI 167–421) followed by unclassed forests ( $504 \text{ trees ha}^{-1}$ , 95% CI 346–641) and protected areas ( $525 \text{ trees ha}^{-1}$ , 95% CI 379–716). Protected areas had higher mean basal area per ha ( $60 \text{ m}^2\text{ha}^{-1}$ , 95% CI 42–80) than unclassed forests ( $42 \text{ m}^2\text{ha}^{-1}$ , 95% CI 35–49) and reserved forests ( $24 \text{ m}^2\text{ha}^{-1}$ , 95% CI 10–39).

#### *Intensive surveys in eastern Arunachal Pradesh*

At our intensively sampled sites; we had 151 detections of five hornbill species across the three administrative regimes (Appendix 1): 85 in the protected area (total effort=189.9 km) and 66 outside the protected area (total effort=278.3 km). Mean flock and individual densities of rufous-necked hornbills were more than eight times higher at the protected area site compared to outside the protected area (Table 4). Mean flock and individual densities of great and wreathed hornbills were more than twice as high in the protected area compared to outside, with overlapping 95% confidence intervals (Table 4).



**Table 2** Results of a generalized linear model, with negative binomial errors, of encounter rates for the great hornbill *Buceros bicornis*, the rufous-necked hornbill *Aceros nipalensis* and the wreathed hornbill *Rhyticeros undulatus* across the three administrative regimes, with AIC<sub>c</sub> and ΔAIC<sub>c</sub> values. Parameter estimates and associated standard errors are given for the rufous-necked and wreathed hornbills and mean and bootstrapped 95% CI are given for all the three species

	Great Hornbill			Rufous-necked			Wreathed		
Model predictor	Only Intercept	Administrative regime		Only Intercept	Administrative regime		Only Intercept	Administrative regime	
<b>AIC<sub>c</sub></b>	70.23	107.97		89.68	78.23		92.01	87.63	
<b>Δ AIC<sub>c</sub></b>	0	37.74		11.45	0		4.38	0	
<b>Status</b>	<b>PA</b>	<b>UF</b>	<b>RF</b>	<b>PA</b>	<b>UF</b>	<b>RF</b>	<b>PA</b>	<b>UF</b>	<b>RF</b>
<b>Estimate</b>				-0.81	-2.47	-1.41	-1.64	-1.62	-0.58
<b>SE</b>				0.58	1.04	0.89	0.49	0.99	0.75
<b>Mean rate of encounter (km<sup>-1</sup>)</b>	0.14	0	0.11	0.45	0.02	0.11	0.24	0.03	0.1
<b>95% CI (n = 1000 bootstraps)</b>	0.00-0.29	0-0	0.03-0.2	0.13-0.79	0.00-0.07	0.01-0.21	0.02-0.61	0.00-0.07	0.06-0.15



**Table 3** Summary of key informant surveys, with the number of potential sites (where each species could be present, based on their elevational and geographical ranges), the number of sites where we detected the species, the number of sites where the species was present according to the key informants but where we failed to detect it, and the number of sites where the species was not seen by key informants in the previous 5 years.

Hornbill species	Potential sites	Detected	Present but not detected	Not seen in previous 5 years
Great hornbill	16	6	5	5
Rufous-necked hornbill	13	9	2	2
Wreathed hornbill	19	11	8	0
Brown hornbill <i>Anorrhinus austeni</i>	12	7	4	1
Oriental pied hornbill <i>Anthracoboceros albirostris</i>	14	3	9	2

**Table 4** Results of *DISTANCE* analysis of the density of great, rufous-necked and wreathed hornbills at the intensively sampled protected area site (Namdapha Tiger Reserve) and outside the protected area (including four reserved forest and two unclassed forest sites).

	Great hornbill		Rufous-necked hornbill		Wreathed hornbill	
	Protected area	Outside protected area	Protected area	Outside protected area	Protected area	Outside protected area
No. of trails	4	9	4	9	4	9
Total effort (km)	189.9	278.3	189.9	278.3	189.9	278.3
Model	Half normal	Uniform	Half normal	Uniform	Uniform	Uniform
Adjustment terms	Cosine	-	-	-	-	-
Detection probability	0.32	1	0.73	1	1	1
Effective strip width (m)	28.76	57	43.86	50	65	80
Flock density ( $\text{km}^{-2}$ )	1.46	0.54	2.64	0.32	0.49	0.2
% CV of group density	46.56	40.93	24.5	60.37	37.9	33.61
95% CI of group density	0.45–4.82	0.22–1.33	1.49–4.67	0.08–1.17	0.15–1.56	0.1–0.43
Mean cluster size	1.56	1.71	1.64	1.67	5.91	6.68
Individual density ( $\text{km}^{-2}$ )	1.88	0.91	4.32	0.54	2.88	1.37
% CV of individual density	48.01	42.07	25.77	61.19	45.97	44.3
95% CI of individual density	0.58–6.1	0.37–2.28	2.43–7.71	0.15–0.96	0.99–8.35	0.56–3.37

## 6.5 DISCUSSION

Our state-wide survey indicates that although hornbills are present outside protected areas, mean encounter rates of the threatened rufous-necked hornbill and wreathed hornbill were lower outside than within protected areas. However, the importance of non-protected areas cannot be discounted as >60% of the land area of Arunachal Pradesh is under forest cover, of which only 18.5% is within the protected area network (FSI, 2009). Almost 60% of the state's forested area lies in the elevation range used by hornbills (<2000 m; Fig. 1; FSI 2009). Thus a significant proportion of the hornbill population in the state probably occurs outside protected areas. Furthermore, individual hornbills are reported to range over areas >170 km<sup>2</sup> to track seasonally varying fruit resources (Kinnaird and O'Brien 2007, Keartumsom et al. 2011). Thus stretches of reserved forests and unclassed forests adjoining protected areas provide habitat contiguity for hornbills.

Hornbills are known to be vulnerable to hunting because of their low natural densities and slow breeding rates compared to other frugivorous birds (Bennett et al. 1997, Kinnaird and O'Brien 2007). Hornbill species respond variably to anthropogenic pressures such as logging: the abundance of oriental pied hornbills is higher in logged habitats, whereas great hornbills are negatively affected by logging (Datta 1998). Our data indicate that in the two administrative regimes outside protected areas the mean rates of encounter with both the rufous-necked and the wreathed hornbill were five and three times higher in the government-regulated reserved forests than in community-regulated unclassed forests, respectively. This was despite higher tree density and basal area in unclassed forests. The lower basal area in reserved forests may be a result of historical logging pressures; other studies have shown that logging is associated with reduced basal area (White 1994, Silva et al. 1995). The community-managed unclassed forests are probably exposed to higher hunting pressures.

Our intensive study in eastern Arunachal Pradesh also revealed that the abundance of the rufous-necked hornbill was significantly higher within the protected area (Namdapha Tiger Reserve) than outside. The densities of great and wreathed hornbill were not statistically different inside and outside protected areas. The importance of habitats lying outside protected areas is underscored by their size. The area of reserved forests in the two forest divisions (Namsai and Jairampur) in eastern Arunachal Pradesh is 1633 km<sup>2</sup>, compared to Namdapha Tiger Reserve's 1985 km<sup>2</sup> (of which c. 1200 km<sup>2</sup> lies in the elevational range of hornbill species). The reserved forests lie entirely below 2000 m, which is the preferred elevation range for hornbills. Based on the estimated densities of great, rufous-necked and wreathed hornbills outside protected areas (Table 4), these two Reserved Forests together could harbour c. 1500, 900 and 2200 individuals, respectively. Similarly, reserved forests in western Arunachal Pradesh (Khellong Forest Division) with breeding populations of four hornbill species encompass larger areas (>1300 km<sup>2</sup>) than nearby protected areas such as Pakke Tiger Reserve (862 km<sup>2</sup>). Arunachal Pradesh as a whole is therefore a globally important region for hornbills.

Given the high density (4.3 individuals per km<sup>2</sup>) of rufous-necked hornbills in Namdapha and the low hunting pressure on the species at this site, Namdapha Tiger Reserve appears to be a stronghold for this globally threatened species. Mean flock densities of great hornbills inside Namdapha (1.45 flocks per km<sup>2</sup>) were comparable with estimates from the Western Ghats (1.74 flocks per sq. km; Mudappa and Raman 2009). The combined densities of the three large hornbill species in the western portion of Namdapha (9.1 individuals per km<sup>2</sup>) were higher than the combined densities of nine hornbill species in Hala Bala Wildlife Sanctuary (5.7 individuals per sq. km; Gale and Thongaree 2006). Our key informant surveys revealed that some hornbill species are no longer detected at protected area sites where they occurred in the past. This indicates that there are significant hunting pressures on hornbills even in protected areas. At five of our surveyed sites, including two in protected areas,

great hornbills are no longer reported. Body parts of the great hornbill (casque, tail feathers and body fat) are highly valued by several tribes across the state (Datta 2002). A single casque and tail feather can be sold for up to INR6000 (c. USD110) and INR1000 (c. USD18), respectively (A. Datta, pers. obs.). The beaks and feathers of the rufous-necked hornbill are also used by different tribes (Datta 2002, 2009) and the species is hunted intensively (R. Naniwadekar, unpubl. data). The rufous-necked hornbill was not detected at two unclassed forest sites, where hunting is a probable cause of their disappearance. We had limited detections of oriental pied hornbills and sampled only a few protected area sites for the brown hornbill, and therefore we are unable to draw conclusions on the status of these species across the three regimes. The presence of hornbills in forested tracts outside protected areas is a promising sign for hornbill conservation in Arunachal Pradesh. However, considering the pressures exerted by anthropogenic activities such as hunting and their potential effect on hornbill abundance, there is a need for dedicated forest management, greater conservation awareness, community involvement and incentive-based conservation practices (Datta et al. 2012) to ensure continued co-existence of humans and hornbills.

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## 6.7 APPENDIX

**Appendix 1** Number of sightings of five hornbill species inside (effort = 189.9 km) and outside (effort = 278.3 km) protected areas during an intensive survey in eastern Arunachal Pradesh.

Species	No. within protected area	No. outside protected area	Total
Great hornbill <i>Buceros bicornis</i>	17	18	35
Rufous-necked hornbill <i>Aceros nipalensis</i>	46	9	55
Wreathed hornbill <i>Rhyticeros undulatus</i>	13	9	22
Brown hornbill <i>Anorrhinus austeni</i>	9	23	32
Oriental pied hornbill <i>Anthracoceros albirostris</i>	0	7	7
<i>Total</i>	85	66	151

## Chapter 7

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# Conclusions and Synthesis

The studies described in the preceding chapters sought to contribute to our understanding of the relationships between hornbills and their food plants. The general conceptual framework for the thesis was presented in the Introduction (Chapter 1). I investigated how the distribution and abundance of food plant species influenced the distribution of hornbills, and how the distribution of hornbills, in turn, affected the seed dispersal and recruitment patterns of food plants. The thesis also examined how these relationships get altered in the wake of anthropogenic perturbations like logging and hunting, which affect the food plants and their dispersers such as hornbills, respectively.

This thesis specifically aimed to understand three broad themes in the context of frugivory and seed dispersal. These were 1) resource tracking by hornbills, an important frugivore group in tropical forests of Asia, at multiple spatial scales, 2) role of hornbill species in seed dispersal and, 3) the status of hornbill populations inside and outside Protected Areas of Arunachal Pradesh, and the consequences of their population decline on the seed dispersal process. In this Chapter, I summarize the main findings of these studies that have enabled a better understanding of resource tracking by hornbills in the non-breeding season (Chapters 2, 3 and 4), their role as dispersers of large-seeded plants (Chapter 4), the consequences of their population decline on the seed dispersal process (Chapter 5), and the status of this ecologically important group of birds inside and outside Protected Areas in the state of Arunachal Pradesh in north-east India (Chapter 6).

## 7.1 MAIN RESULTS

I documented the variation in densities of sympatric hornbills over space and time in Namdapha Tiger Reserve (Chapter 2). I found that the sampled areas in Namdapha Tiger Reserve had a relatively high density of the Rufous-necked Hornbill *Aceros nipalensis* (6.9 birds/km<sup>2</sup>), a species classified globally as Vulnerable in the IUCN's

Red List. The density of the Great Hornbill *Buceros bicornis*, classified as 'Near Threatened' was similar (3.9 birds/km<sup>2</sup>) to other sites in South-east Asia and Western Ghats but lower than those reported from the lowland forests of western Arunachal Pradesh. Chapter 2 represents the first study anywhere in its geographic range to have estimated the density of the White-throated Brown Hornbill *Anorrhinus austeni* (7.9 birds/km<sup>2</sup>), which is classified as Near Threatened.

I recorded a high temporal variation in the abundance of the Wreathed Hornbill *Rhyticeros undulatus* that peaked in November–December (68 birds/km<sup>2</sup>) in my study area, and drastically declined by March–April (1.3 birds/km<sup>2</sup>) when the birds moved out of the study area. On the other hand, the density of Great and White-throated Brown Hornbills exhibited spatial variation, with both species occurring at lower densities at the higher elevations (over 1000 m asl).

In my intensive study site (15 km<sup>2</sup>, 500–800 m asl) for this study in the Namdapha Tiger Reserve, the combined density of the four of the five species (excluding the Oriental Pied Hornbill *Anthracoboceros albirostris*) in November–December was amongst the highest (100 birds/km<sup>2</sup>) recorded for any site in Asia.

I then examined resource tracking by three sympatric hornbill species across different months (Chapter 3). The inappropriateness of the scale of study has been identified as one of the weaknesses of prior resource tracking studies on hornbills (Garcia and Ortiz-Pulido 2004, Guitian and Munilla 2008), therefore, I conducted the study at multiple spatial scales: at the scale of the fruiting tree, across different sites within the intensive study area (intermediate scale), and at the scale of the study area. At the scale of a fruiting tree, I examined the role of fruit crop size in influencing the visitation rates of the different hornbill species on figs and non-fig fruiting trees. I also compared diets, visitation rates and visitation lengths of three sympatric hornbill species on figs and non-fig trees to understand their role in seed dispersal.

I found that the temporal trends in Wreathed Hornbill abundances were similar to the overall fruit availability patterns across the different months at the scale of the study area, peaking in November–December and declining by March. I did not detect any relationship between Great and Rufous-necked Hornbill abundance and fruit availability over the two years at the scale of the study area. At the intermediate scale, I found that Wreathed Hornbill abundances were positively associated with non-fig fruit availability while Rufous-necked Hornbill abundances were negatively associated with non-fig fruit availability. I did not find any relationship between Great Hornbill abundance and fig and/or non-fig fruit availability at the intermediate scale. At the scale of the fruiting tree, Great Hornbills abundances were associated with fruit crop sizes of figs that also had a higher representation (91% of total foraging sightings) in its diet, while the abundances of the Rufous-necked Hornbill were associated with ripe fruit crop sizes of non-fig trees that had a higher mean representation (59% of total foraging sightings) in its diet. I did not find any relationship between Wreathed Hornbill visitation rate and ripe fig fruit crop size.

The median visitation lengths of all the three hornbill species were lower than their known regurgitation and defecation times for large and small seeds, respectively, implying that hornbills carry the bulk of seeds away from the parent plant, improving the chances of dispersal away from the parent plants.

I then investigated whether patches within the forest with higher abundance of food plants attracted a larger numbers of hornbills, and how this influenced the spatial distribution of scatter-dispersed seeds and eventual recruitment of large-seeded hornbill food plants. I first documented that hornbills were the most frequent visitors on fruiting trees of five large-seeded species, suggesting that they represented an important group of dispersers for these trees. I found that the abundances of the three hornbill species (Great, Rufous-necked and Wreathed hornbill) were associated with the abundance of their food plants, particularly that of the canopy non-fig food plants. My study showed that the net seed arrival on the

forest floor was positively associated with the abundance of hornbills. The recruitment of seedlings and the species richness of recruits were positively associated with the abundance of canopy non-fig food plants pointing towards the role played by canopy non-fig food plants in attracting hornbills and thereby resulting in spatially aggregated recruitment of food plants in areas with higher abundance of canopy non-fig food plants. Thus in our study site, patchily distributed ‘orchards’ of canopy non-fig food plants of hornbills attracted greater numbers of hornbills which resulted in greater seed arrival of plants whose fruits are predominantly consumed by hornbills. These orchards were characterized by higher abundances of seedlings belonging to different species.

Having determined the role of hornbills in seed dispersal, I examined the impacts of decline in hornbill populations due to anthropogenic factors (logging and hunting) on seed arrival and recruitment. I compared the abundances of hornbills and their food plants, and the seed arrival rates of five large-seeded hornbill food plants and recruitment patterns for four of these tree species between a logged and hunted (heavily disturbed) site with an unlogged and less-hunted (less disturbed). I found that the abundance of hornbill food plants was higher in the less disturbed site compared to heavily disturbed site. The non-fig food plants that are logged occurred at higher abundance in the less disturbed site compared to non-fig plants that are not logged and the hemi-epiphytic figs. The overall abundance of hornbills was 22 times higher in the less disturbed site as compared to the heavily disturbed site. The arrival of scatter-dispersed seeds on the forest floor was seven times higher at the less disturbed site as compared to the heavily disturbed site. Two of the four focal tree species showed reduced recruit abundances in the heavily disturbed site. For one species, the abundance of smaller-sized recruits was higher in the less disturbed site while the abundance of larger-sized recruits was greater in heavily disturbed site, suggesting reduced recruitment of this species in the recent past.

In the final study (Chapter 6), I compared measures of hornbill abundance (encounter rates and densities) inside and outside Protected Areas at two scales: across the state of Arunachal Pradesh, and at an intensive study site in the eastern part of the state. The state-wide survey indicated that the mean encounter rates of Rufous-necked and Wreathed Hornbill inside Protected Areas were four-times and two-times greater than in Reserved Forests, and 22-times and eight-times greater than in Unclassed State Forests, respectively. The encounter rate of Great Hornbill in Protected Areas was 0.14/km, and 0.10/km in Reserved Forests, with no encounters in Unclassed State Forests. I could not obtain sufficient ( $n = 2$ ) Protected Area sites for the White-throated Brown Hornbill and sufficient detections (detected in only 3 sites) for the Oriental Pied Hornbill. The intensive survey in eastern Arunachal Pradesh indicated that the Rufous-necked Hornbill densities inside Protected Areas ( $4.3 \text{ birds}/\text{km}^2$ ) were higher than outside Protected Areas ( $0.5 \text{ birds}/\text{km}^2$ ). The key-informant surveys revealed the possible extirpation of species like the Great Hornbill at sites inside two Protected Areas and three Unclassed State Forests.

## 7.2 A NOTE ON RESOURCE TRACKING BY HORNBILLS

Hornbill densities have been documented to fluctuate over space and time and sympatric hornbill species are known to occur in differing densities (Kinnaird et al. 1996, Gale and Thongaree 2006). While the role of food availability in governing these fluctuations has been explored (Kinnaird et al. 1996, Anggraini et al. 2000), very little research has focused on the mechanisms that allow sympatric hornbill species to co-occur in a landscape. The only niche axis that has been hitherto explored is that of the diet where sympatric hornbills have been demonstrated to diverge (Datta and Rawat 2003, Hadiprakarsa and Kinnaird 2004). In my study area too, like other areas in south-east Asia, different hornbill species varied in their densities across elevations and months. Wreathed Hornbill densities fluctuated greatly and predictably across the different months while none of the other species

exhibited such dramatic variation in abundances over time. I investigated the role of diet and fruit availability in governing the observed patterns in hornbill abundance.

Fruits form an important component of the diet of hornbills. There is divergence among sympatric species in the contribution of figs and non-fig fruit items in their diets. Consistent with existing literature, I found that Great Hornbills had greater representation of figs, while Rufous-necked and Wreathed Hornbills had a greater representation of non-fig fruits in their diets. Such resource partitioning is an important mechanism underlying the coexistence of species across different foraging guilds including granivorous desert rodents (Kotler and Brown 1988) and herbivorous African ungulates (Jarman and Sinclair 1979).

Great Hornbills tracked fig fruits while Rufous-necked Hornbills and Wreathed Hornbills tracked the abundance of non-fig fruits, as expected from their diets. However, I found differences in the scale at which the three hornbills tracked the resources. At the largest scale, only the Wreathed Hornbill abundance fluctuated consistently with fruit availability. At the intermediate scale, the Wreathed Hornbill exhibited a positive relationship with non-fig fruit availability, while the Rufous-necked Hornbill exhibited negative association with non-fig fruit availability. At the smallest scale, Great Hornbills exhibited a positive relationship with ripe fig fruit crop size while Rufous-necked Hornbills exhibited a positive relationship with ripe non-fig fruit crop size.

In Namdapha, in my intensive study site in mid-elevation forest, the non-fig fruit availability consistently peaked in November-December across both the sampling years. However, in the lowland forests of Pakke Tiger Reserve in Arunachal Pradesh, non-fig fruit availability was consistently low during this period of the hornbill non-breeding season (Datta and Rawat 2003). It is therefore likely that Wreathed Hornbills are tracking this predictability in the non-fig fruit availability patterns across the elevation gradient and the abundance of this resource explains

the high Wreathed Hornbill abundance in my intensive study area during the non-breeding season.

Unlike non-fig fruit availability, bird-dispersed figs are known to fruit asynchronously (Shanahan et al. 2001). Asynchronous fruiting would imply unpredictable spatial and temporal patterns in fruit availability. This would mean that Great Hornbills, which mainly feed on figs, are less likely to show predictable long-distance movement patterns as exhibited by Wreathed Hornbills. During my study, the median fruit availability of figs was highest in November 2009–10, but not in 2010–11 when no fruits (of the three fig species examined) were available. Thus Great Hornbills are less likely to exhibit predictable movement patterns across large scales like the elevation gradient as shown by Wreathed Hornbills.

Tracking resources at different spatial scales is thought to facilitate co-occurrence of species (Inouye 1999, Kneitel and Chase 2004). This is presumably the case with the Wreathed and Rufous-necked Hornbills. Both species have similar diets with higher representation of non-fig fruit items and have similar body size and therefore are likely to compete. I found that while at the largest scale, only the Wreathed Hornbill abundance showed consistent fluctuations with fruit availability, at the smallest scale of the fruiting tree, only the Rufous-necked Hornbill showed a positive relationship with the fruit crop size of non-fig trees. At intermediate scales, I found a contrasting pattern with Wreathed Hornbill showing a positive relationship and the Rufous-necked Hornbill showing a negative relationship with non-fig fruit availability. This opposing pattern observed at the intermediate scale hints at probable competitive interactions in the non-breeding season. Indeed, while I observed Wreathed and Rufous-necked Hornbills feeding together on fruiting fig trees, I have also observed a Wreathed Hornbill chase a pair of Rufous-necked Hornbills from a fruiting fig tree. It is likely that the two ecologically similar species avoid competition by tracking resources at different scales. Kotler and Brown (1988) suggest that when abundance of resources varies spatially, the trade-offs between

travelling cost and foraging efficiency can promote coexistence. I recorded such differences in trade-offs, with the Wreathed Hornbills traveling across the elevation gradient, tracking peak resource availability, and the Rufous-necked Hornbill diversifying its diet and selecting trees with larger fruit crop size.

Apart from enabling co-existence of sympatric species, resource tracking at different spatial scales may have implications for the abundance of hornbill species. Sympatric hornbills with similar diets, such as the Rufous-necked and Wreathed Hornbill, showed more than thirteen-fold difference in peak densities in November–December in my study. Data on densities of hornbills are also available from another site in Arunachal Pradesh, the Pakke Tiger Reserve (Dasgupta and Hilaluddin 2012). In both these studies, Wreathed Hornbill was the most abundant species. Unlike other species, Wreathed Hornbills exhibit long-ranging movements across the elevation gradient and track peak fruit availability in lowland and middle elevation forests, which might enable them to occur in high densities seasonally. On the other hand, species that do not undertake such altitudinal movements presumably experience greater troughs in fruit availability in lowland forests or middle elevations, which could have implications for their densities and flock sizes.

Considering that Wreathed Hornbills seem to undertake local altitudinal movements, it is imperative to conserve the lowland forests that are the preferred breeding areas and middle-elevation forests that are the wintering areas for this species. Lowland forests in Arunachal Pradesh and adjoining Assam have been known to be under severe pressure from habitat loss (Srivastava et al. 2002, Kushwaha and Hazarika 2004). None of the lowland forest habitats around Namdapha in Arunachal Pradesh are under the Protected Area network. In Namdapha, which is spread over almost 2000 km<sup>2</sup>, while Rufous-necked Hornbill and White-throated Brown Hornbill have been reported to breed in the middle-elevation forests (Datta 2009), there are no records of Wreathed Hornbills breeding in the park. The breeding grounds of Wreathed Hornbills that visit Namdapha in

winter in such large numbers need to be identified and anthropogenic threats to these habitats evaluated.

### 7.3 A NOTE ON SEED DISPERSAL BY HORNBILLS

Seed dispersal of fleshy-fruited species is thought to result in spatially heterogeneous seed dispersal patterns (Russo et al. 2006, Levey et al. 2008) due to animal behavior and movements. This applies to specific microhabitats such as nest, roost or sleeping sites (Datta 2001, Kitamura et al. 2004, Russo et al. 2006, Kitamura et al. 2008) where seeds are dispersed in relatively high-density clumps. I estimated the rates of seed arrival on the forest floor as a consequence of the daily diurnal foraging movements of hornbills; a situation where seed arrival is expected to be more scatter-dispersed. I found that even in the larger context of scatter-dispersal of seeds on the forest floor, the rate of net seed arrival (after removal by secondary dispersers) is patchy and spatially clumped, although less so compared to roost and nest sites.

#### *Complementary role of hornbills in seed dispersal*

One of the challenges in the seed dispersal studies is to determine how dependent the plant species is on a particular disperser species. This information is critical for determining the vulnerability of the plant species to the loss of a particular disperser. I did not estimate the dependency of particular plant species on the different hornbills or other species. However, my work provided some indications regarding whether sympatric hornbill species play a complementary or supplementary role in seed dispersal.

Seed disperser effectiveness is typically studied by evaluating the qualitative and quantitative roles of the dispersers (Schupp 1993, Schupp et al. 2010). Amongst the three hornbill species, I found that Wreathed Hornbills and Rufous-necked Hornbills had higher visitation rates on non-fig fruiting plants as compared to the Great

Hornbill that had higher visitation rates on fruiting figs. This suggests some level of complementarity in their functional roles.

Between the two hornbill species that ate more non-figs, the Rufous-necked Hornbills had almost twice the niche breadth compared to the Wreathed Hornbill in the non-breeding season. Thus, the Rufous-necked Hornbill dispersed seeds of a wider array of tree species. While, the Rufous-necked Hornbills remained year-round in the study site, the Wreathed Hornbills visited in large numbers for up to four months. Thus, Wreathed Hornbills are likely to play a quantitatively important role in seed dispersal over a shorter duration during the non-breeding season and for a smaller number of food plant species, while the Rufous-necked Hornbill is important for the dispersal of a diverse array of species over a longer duration.

#### *Hornbill-created fruit orchards*

The number of seeds dispersed by a species, or the quantitative role of a seed disperser, is determined by disperser abundance, frequency and length of visits to fruiting trees, and the rates of fruit removal. On large-seeded food plant species, in relation to other diurnal frugivores, hornbills were detected in larger numbers of fruit tree watches and occurred in greater numbers. Compared to other smaller frugivorous birds like Cochoas, they dropped far fewer seeds below parent trees and therefore, carried most of the handled seeds away from the parent plant. Thus, hornbills appear to have a significant quantitative role in the dispersal of large-seeded plant species as compared to other diurnal frugivores.

This thesis is the first to discover that the patchy or clumped distribution of hornbill food plant species is linked to seed dispersal by hornbills. In a prior study, Lazaro et al. (2005) had found clumped distribution of fleshy-fruited plants in temperate forests and had invoked the role of dispersal by frugivores in determining the observed patterns. My study recorded clumped distribution of hornbill food plants in a tropical forest and demonstrated the role played by the hornbills themselves in

governing the distribution patterns of their food plants. However, unlike the findings of Lazaro et al (2005), where more abundant tree species were acting as 'hubs' and attracting rare species, in my study, the rare canopy non-fig trees appeared to be playing the role of 'hubs' and attracting hornbills, resulting in the spatially-clumped and nested patterns. Unlike temperate forests, tropical forest canopy is distinctly structured. It appears the large fruit crop size in the large canopies of the canopy non-fig trees allows even single trees to act as hubs in tropical forests.

Lazaro et al. (2005) explained the observed nested pattern in tree species abundance and distribution being brought about due to 'hitchhiking' of rare species on abundant ones. In contrast, the nested pattern in my case was perhaps the outcome of the rare species (canopy non-fig food plants) attracting more hornbills and greater diversity of seeds (as can be seen in recruit abundance and richness), resulting in a greater diversity of trees occurring alongside canopy non-fig food plants.

This complex dependency between hornbills and their food plants has important conservation implications. Large-seeded plants are thought to be more vulnerable to anthropogenic perturbations that cause disruption of their seed dispersal compared to small-seeded plants (Vanthomme et al. 2010, Markl et al. 2012). In Arunachal Pradesh, regions outside Protected Areas experience perturbations due to hunting and logging simultaneously. I documented that this leads to reduced abundances of hornbills. While hunting results in the direct loss of hornbills from the forest, logging causes the reduced abundance of their food plants. Canopy non-fig hornbill food trees like *Phoebe* sp. and *Canarium strictum* are amongst the important timber species that are harvested outside Protected Areas. By attracting a disproportionately higher number of hornbills and consequently a diverse array of seeds, they play an important role as 'hubs'. Their loss therefore will have important implications for the persistence of other plant species dependent on hornbills for dispersal. I have demonstrated this by documenting reduced seed arrival and altered recruitment

patterns of large-seeded plants in a site that experiences both hunting and logging as compared to a less disturbed site.

However, despite lower hornbill abundances outside Protected Areas, there is still hope for Arunachal's large forested tracts. The continuing presence of hornbill species, albeit at lower densities, is possibly crucial for the long-term survival and persistence of many tropical tree species in these multiple-use landscapes. While small-seeded tree species have a more diverse assemblage of frugivores and dispersers, large-seeded tree species have a limited assemblage of species like hornbills that disperse their seeds. Given that a larger fraction of the forests in the state lies outside Protected Areas, the maintenance of these forests (even in multiple-use landscapes) depends on survival of hornbill populations. In addition, given the greater extent of forests that are not Protected Areas, they can potentially harbor a larger population of hornbills in the long-term than the few Protected Areas in the state.

#### 7.4 SHORTCOMINGS OF THE THESIS

The absence of site-level replication for the studies on resource tracking and seed dispersal is an important shortcoming in the present thesis. Site level replication would have been desirable, but the lack of control sites that are devoid of anthropogenic threats, and the difficult logistics of field work precluded replication.

Resource tracking by Wreathed Hornbills across the elevation gradient would be best studied by documenting fruit availability simultaneously across lowland and middle elevation forests. However, there were no lowland forest sites near Namdapha. I had initially attempted to sample in the lowland forest of Tengapani Reserve Forest adjoining Namdapha, but the site experienced significant logging pressures, rendering it inappropriate for inclusion in the study.

My work was restricted to the non-breeding season of hornbills, and ideally data from across the year would have allowed me to better understand the intra- and inter-annual variation in fruit availability. It would have also allowed me to draw comparisons on the role of hornbills in scatter-dispersal of large seeds in both the breeding and non-breeding seasons. I faced problems in being able to access the intensive study site during the long rainy season in a high rainfall area like Namdapha, which did not allow year-round fieldwork.

To understand which of the two factors between logging and hunting had a greater role to play in the decline of hornbills it would have been useful to have combinations of sites with differing intensities of logging and hunting. However, hunting and logging co-occur at most sites outside Protected Areas near Namdapha in eastern Arunachal Pradesh. This did not allow me to tease apart the relative influences of logging and hunting.

## 7.5 CONTRIBUTION OF THE THESIS

This thesis is the first to report the densities of the White-throated Brown Hornbill and the second to report the densities of the Rufous-necked Hornbill anywhere in their geographic range across South-east Asia. These species have been classified as 'Near Threatened' and 'Vulnerable', respectively, by the IUCN Red list of Threatened Species (IUCN 2012). Published information on the ecology of the Rufous-necked Hornbills is limited to only one more site (Huai Kha Khaeng National Park) in its geographic range in Thailand (Chimchome et al. 1998, Ouithavon et al. 2005, Tifong et al. 2007). I documented the foraging ecology of Rufous-necked Hornbill for the first time from India, (the second site in its geographic range). This is also the first study to investigate its role in seed dispersal.

In this thesis, apart from exploring co-existence amongst sympatric hornbill species along the axis of diet, I have additionally explored how sympatric hornbill species distribute themselves along the axis of resource availability across increasing spatial

scales. This aspect has not been investigated in earlier studies on resource tracking by hornbills. I found differences in broad diet among the hornbill species which have been documented before. In addition, I found that different hornbill species track resources at varied scales. The latter finding along with diet divergence additionally explains how sympatric hornbill species may co-occur.

This is the first study to demonstrate the role of hornbills in governing the spatial distribution of scatter-dispersed seeds on the forest floor during diurnal foraging movements. I found that the arrival and distribution of seeds (during scatter-dispersal) in the larger scale is also spatially heterogeneous. This has important implications for the spatial organization of hornbill food plants in the long-term. My study is the first to empirically demonstrate that a frugivore group in a tropical forest site is responsible for the distribution of their food plants, which Lazaro et al. (2005) had proposed as a mechanism based on observations of fleshy-fruited plants in temperate forests. Their hypothesis suggests that widespread plant species govern the nested patterns in observed plant distributions. However, my finding suggest that it is the rare but important food plants in the diet of hornbills that may act as 'hubs' attracting more hornbills enhancing seed arrival and recruitment and are responsible for the observed nested pattern of fruiting trees.

My study also showed the impacts of two main threats in tropical forests (hunting and logging) in affecting ecosystem processes like seed dispersal. I found that logging reduces food plant abundance for hornbills, while hunting results in decline in abundances, with an associated reduction in seed arrival and altered recruitment of animal-dispersed species in a logged and hunted site. Based on my results, I present a conceptual model depicting the relationships and pathways between vertebrate-dispersed trees, their dispersers, and the threats they face.

My state-wide assessment of hornbill abundance inside and outside Protected Areas in 20 sites was the first larger-landscape level of the status of hornbills in north-east

India, a region where hornbills are especially vulnerable to human disturbances. I found that while in general, most hornbill species fared better in Protected Area sites, some species like the Great hornbill and Rufous-necked hornbill appeared to have been extirpated from even a few Protected Area sites. Therefore, although I found lower hornbill abundances outside Protected Areas, their continued presence and the fact that a greater proportion of Arunachal's forests lie outside Protected Areas, suggests the conservation of these forests outside the few Protected Area sites is crucial for the long-term persistence of hornbills and important ecosystem services like seed dispersal.

## 7.6 FUTURE RESEARCH

Sympatric similar body-sized hornbills exhibit dietary differences (Datta 2001, Datta & Rawat 2003, Kinnaird & O'Brien 2007), which may serve to reduce niche overlap. This has important consequences for their ranging patterns that also differ substantially. In this thesis, I have investigated resource partitioning and co-existence in relation to diet divergence and fruit availability at different scales. However, the different fruit items differ in their nutrient contribution and therefore it will be interesting to determine how hornbills partition fruits along the axis of nutrient value and energy per unit weight in conjunction with fruit availability. This will provide more insights on the trade-off between movements over large distances *vis-a-vis* foraging in smaller patches.

I made inferences on the complementary role in seed dispersal by the three hornbill species on the basis of their diets, abundance patterns and visitation rates on fruiting trees. Comparative information on fine-scale movement patterns will add another dimension of spatial scale (dispersal distance) at which the three sympatric hornbills disperse seeds. Given the differences in home range sizes and scales of resource tracking by the various hornbill species, differences in dispersal distances of seeds from parent trees can be expected. For example, movement data on the wide-ranging

Wreathed Hornbill will provide insights into the role of Wreathed Hornbills in long-distance dispersal of seeds.

While, in middle-elevation forests (up to 500 m), hornbills occurred at high densities and were important dispersers, especially of the large-seeded plants, both the diversity and density of hornbills declined in the higher elevation areas. Do hornbills continue to play an important role in seed dispersal in high elevation forests (up to 2000 m) or are they replaced by other frugivores? This will require comparisons in overall fruit and seed size across the elevation gradient and determining the relative importance of hornbills in dispersal of large-seeded plants. Given the lower abundance and richness of hornbill species, large-seeded plants in higher elevations could be expected to be even more vulnerable to frugivore loss due to anthropogenic disturbances like hunting and logging. It would be interesting to examine the interaction between elevation and frugivore (hornbill) loss on seed dispersal and recruitment patterns of large-seeded plants.

Hornbill habitats across south-east Asia are experiencing unprecedented levels of habitat loss (Sodhi et al. 2004). Similar trends are seen in parts of north-east India (Srivastava et al. 2002, Kushwaha and Hazarika 2004, Pandit et al. 2007). Several areas in north-east India continue to harbor tropical forests, but information on the occurrence and abundance of hornbills at a regional level is not available. In addition, hunting is a serious threat for hornbills in most parts of north-east India. It is imperative that surveys are carried out across north-east India to identify important areas for hornbills and for generating a baseline for future monitoring.

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