Breeding biology and nesting behaviour of Great Hornbill *Buceros bicornis* in tropical rainforest and human-modified landscapes in Anamalai hills, India


A Report

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By

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EXECUTIVE SUMMARY

Hornbills are among the largest birds of tropical forests. Sixty one species belonging to 14 different genera are distributed in Asia and Africa. Asian tropics are home to 32 species (9 genera) of hornbills. Hornbills are long-lived, large bodied and wide-ranging. They exhibit strong social monogamy and a unique breeding strategy. Hornbills are secondary cavity nesters and thus depend on cavities formed due to falling of branches or wood rot or by primary cavity nesters in large trees. During the breeding season, which lasts for several months, the male singly provides fruits to the incarcerated female and the growing chick. Diet of hornbills is largely comprised of fruits, predominantly figs which are patchily distributed. Thus, persistence of hornbills is determined by presence of large trees suitable for nesting and ample fruit resources in relatively undisturbed tracts in tropical evergreen forests. Hornbills are considered as a 'farmers of the forest' of Asian tropical forests for their role as seed dispersers.

Tropical forests in Asia are being lost at an alarming rate. They are being converted to monoculture plantations of mainly, rubber, tea, coffee and oil-palm. As a consequence of this, the remaining forests are left fragmented and degraded. India is no exception in expansion of agriculture into forest lands. The major plantation crops established in tropical forests are tea, rubber and coffee which were introduced to India in the 18th century. Most of these plantations have been historically established in areas of high biological diversity and value. Unfortunately, the extant hornbill habitat is often juxtaposed with fragmented and thus depauperated forests. Loss of forests is one of the major threats to hornbills apart from hunting.

One such critical area for hornbill conservation is the Anamalai Hills in southern Western Ghats. Spanning across an altitudinal gradient of 600m to 1500m, Valparai plateau is a 220km^2 landscape mosaic of tea, coffee, cardamom, and *Eucalyptus* plantations with interspersed rainforest fragments. Valparai plateau is surrounded by protected areas on all sides. A wide range of wildlife uses this modified landscape including hornbills. Great Hornbills *Buceros bicornis*, the largest of the hornbills, are also known to use this modified landscape. Hornbills have been observed in plantations and forest remnants in Valparai plateau during breeding and non-breeding seasons. I conducted a study from October 2015 to

June 2016 in Valparai and adjoining contiguous forests to understand their breeding biology in human-modified, plantation-dominated landscape.

I compared the breeding biology and nesting behaviour of Great Hornbills in tropical rainforests and human-modified habitat. Great Hornbill nests (n = 8) were observed for 526 hours to collect information on their nesting cycle, nesting success and nest provisioning behaviour during the nesting season. The structure and quality of nesting habitat was assessed by using vegetation sampling methods. I recorded number of visits made by adults, and number and kinds of food items delivered at the nest during nest watches. The nest watches spanned over pre-hatching and post-hatching phases. I also estimated hornbill densities in Valparai plateau by conducting point-count transect surveys at two sites in Valparai plateau. Along with quantifying trade-off between quality and quantity of food delivered, I monitored nesting cycle and nesting success of nests in contiguous forest and modified habitat.

This study showed that the diversity and abundance of hornbill food plants were lower in the modified habitat as compared to contiguous forests. The diversity of food provisioned in modified habitat was lower than in the contiguous forest. A wide variation in breeding cycle and nest provisioning across individuals was documented. There were significant differences in the kind of food items that were delivered at nests across contiguous forests and modified habitats. The present study adds significant information to the existing knowledge about hornbill breeding biology from the western limit of Great Hornbills' distribution range. It is one of the first studies to document the breeding biology of Great Hornbill in human-modified habitat. It also highlights the potential of modified habitats and rainforest fragments that are amidst large forested tracts for conservation of hornbills.

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INTRODUCTION

Biodiversity hotspots occupy only 2.3% of the Earth's land surface but harbour more than 50% of endemic plant species and 42% of vertebrate diversity (Myers et al., 2000). They are characterized by high rates of habitat loss driven primarily by anthropogenic activities (Myers et al., 2000; Tilman et al., 2001; Schipper et al., 2008; Dobrovolski et al., 2013). Forest loss is predominantly driven by land use conversions (Hosonuma et al., 2012). Shrinkage of available forests is followed by a cascade of impacts on biodiversity. At the species level, it results in lowered species abundances and viability, increased extinction probability of vulnerable species, alteration in genetic make-up of a species; and at the community level could lead to decline in overall species richness and breakdown of associations between species (Fahrig, 2003; Brotons et al., 2005; Keyghobadi, 2007; Fahrig et al., 2011). However, despite the increased risks to survival, species continue to use and adapt to their changing environments, including human-modified countryside habitats such as agricultural fields and plantations (Daily et al., 2003; Bhagwat et al., 2008; Billeter et al., 2008). A wide suite of animal species including primates (Riley, 2008), cats (Basille et al., 2009; Athreya et al., 2013), birds (Faria et al., 2007; Anand et al., 2008; Holbech, 2009), bats (Wordley et al., 2015) and other mammals (Sridhar et al., 2008; Dellinger et al., 2013) have been documented to use plantations in human-dominated and fragmented tropical forest landscapes. Understanding factors that enable persistence of species in modified landscapes is a major area of research in applied ecology and conservation biology.

Habitat modification leads to conversion of contiguous, relatively pristine habitats to fragmented habitat patches with altered spatial configuration in terms of area, isolation and increased edge effect (Rand et al., 2006; Fischer & Lindenmayer, 2007). The persistence of wild species in human-modified landscapes may depend on a combination of species traits as well as habitat and landscape attributes. Traits such as body size, home range requirements, breeding biology and diet, may influence species survival. For instance, studies show that the extinction rate for large-bodied animals that have large home ranges is higher as compared to small-bodied fauna (Collar et al., 1994; Hoffmann et al., 2011; Pimm et al., 2014). Habitat and landscape attributes such as degree of fragmentation, the size, quality, and contiguity of remnant forests, and availability of crucial resources such as nesting and feeding sites would be vital for species persistence in modified habitat (Gustafson, 1998; Fischer & Lindenmayer, 2007). In the case of birds, habitat modification can alter pairing and nesting success (Probst

& Hayes, 1987; Burke & Nol, 1998), increase predation pressures on adults and chicks (Jokimäki & Huhta, 2000) and reduce food resource availability (Wilson et al., 1999).

Hornbills are among the largest birds in tropical forests of Asia and Africa. Hornbills are large-bodied, wide-ranging birds that play an important role in seed dispersal (Kemp, 1995; Kemp, 2001; Kinnaird & O'Brien, 2007). They are secondary cavity nesters depending on cavities formed in large trees due to falling of branches, wood rot or by primary cavity nesters such as woodpeckers. They exhibit monogamy and a unique breeding behaviour in which the female seals herself in a tree cavity (nest) after copulation and the male feeds the incarcerated female and young ones over a 2– 4 month breeding cycle. The average nesting period of Asian Hornbills ranges from 39 in the Black Hornbills *Anthracoceros malayanus* to 133 days in the Red-knobbed Hornbills *Rhyticeros cassidix* (Kinnaird & O'Brien, 2007). Asian hornbills are predominantly frugivorous with a small and varying amount of animal matter in their diet (Kemp, 2001; Kinnaird & O'Brien, 2007; Poonswad et al., 2013). Hornbills are known to track patchily distributed fruit resources in space and time (Kinnaird et al.,1996; Whitney & Smith, 1998; Anggraini et al., 2000; Naniwadekar et al., 2015b). The dependence of hornbills on large trees for nesting and patchily distributed fruit resources makes them vulnerable to habitat modification. Hornbills in Asia are primarily found in moist forests, but much of the forests in these regions are fragmented, have high hunting pressures, and are surrounded by areas with high human population densities (Kinnaird & O'Brien, 2007).

Habitat modification is accompanied by loss of native vegetation and altered forest structure with loss of large trees (Lindenmayer & Laurance, 2016). Suitable cavities in large trees are a limiting resource for breeding hornbills. Habitat modification can reduce availability of suitable cavities for hornbills to nest which may play a major role in population dynamics (Cody, 1985; Lindenmayer & Laurance, 2016). Habitat modification is known to reduce the diversity and relative abundance of fruiting trees thereby negatively impacting fruit availability (Tabarelli et al., 1999). Diversity and availability of food resources decreases in disturbed habitats (Whitney & Smith, 1998; Lenz et al., 2011; Sitompul et al., 2004). This can have a significant impact on hornbills that depend on patchily distributed fruit resources.

The behavioural responses to habitat modification can be evaluated through studies on time allocation by birds for activities like foraging, changes in home ranges and in quantity and

quality of food delivered at nest. Behavioural changes may be pronounced during breeding season, particularly if birds have to range more widely in order to meet food requirements in degraded habitats. Since male hornbills have to feed the incarcerated female and young ones, increased home range size could result in changes in nest provisioning behaviour. This in turn could determine the duration of nesting, various phases of the breeding cycle and nesting success. Sumatran hornbills have been reported to avoid highly disturbed areas (Anggraini et al., 2000). Size of forest patches could determine hornbill persistence in fragmented habitat (Raman & Mudappa, 2003). Abundances and densities of Sumba Hornbills were positively correlated to the size of forest fragments (Sitompul et al., 2004). Abundance of food plants determined the persistence of hornbills in forest fragments (Raman & Mudappa, 2003; Naniwadekar et al. 2015a). Hornbill densities have been reported to decline with reduction in tree densities in forest fragments of the Western Ghats (Raman & Mudappa, 2003; Mudappa & Raman, 2009) and in logged forests in northeast India (Datta, 1998). However, our understanding of how habitat modification alters the breeding biology is poor and the only available information is from a study that evaluated nesting success in modified landscape in northeast India (Rane & Datta, 2015).

In this study, I aimed to understand the variation in breeding biology and nesting behaviour of Great Hornbill in relation to natural and human-modified habitats. The objectives of the study were:

1) To assess the impact of habitat modification on forest structure, and density of native trees and hornbill food plants

2) To assess the impact of habitat modification on nesting duration (breeding biology) and quality and quantity of food that is delivered at the nest (nest provisioning).

METHODS

Study Species

Great Hornbill *Buceros bicornis* is the largest hornbill found in Asia and the only hornbill species that occurs in the biodiversity hotspots of the Eastern Himalaya, Indo-Myanmar and the Western Ghats. Western Ghats is the western most distribution limit of the Great Hornbill. The Great Hornbill is a large, conspicuous bird with a bright yellow and black casque on the large bill, loud calls and producing whooshing sounds with every wing-beat during their flight due to lack of under-wing coverts. They are sexually dimorphic—with the male and female Great Hornbills being easily distinguishable—male has red eyes with black orbital skin around whereas female has white eye with red orbital skin (Plate 1–2). The juvenile has blue-grey eyes and a casqueless bill (Plate 3a). Great Hornbills attain sexual maturity at the age of 4–5 years (Poonswad et al., 2013). In northeast India, breeding season begins in March and lasts up to August (Datta 2001). Whereas, in the Western Ghats, breeding season commences in early December and ends in May (Kannan & James, 1997). The Great Hornbill is listed in 'Near Threatened' category by the IUCN Red list (BirdLife International 2015). Their numbers are declining due to hunting pressure and habitat loss. The species is also listed in CITES-Appendix 1 due to their trade as pets and for their body parts, particularly, casque and feathers. In India, Great hornbill is protected under Schedule I of the Wildlife Protection Act, 1972.

Malabar Grey hornbill *Ocyceros griseus*, the smallest hornbill in India, is endemic to the Western Ghats and sympatric with the Great Hornbill in the moist forests of this region. They have a peculiar loud cackling call. They are sexually dimorphic and do not have a casque unlike most other species of hornbills. The males have a larger, orange-coloured bill than the females that have a small, ivory-coloured bill. They breed between February and May (Mudappa 2000). This species is reported to be more adaptable to plantations and forest fragments than the Great Hornbills (Raman & Mudappa, 2003). The population size has not been quantified; but it is believed to be locally common. In this study, I have estimated the density of Malabar Grey Hornbill at two sites with modified habitat on the Valparai Plateau. No other observations or data was collected on Malabar Grey Hornbill during this study.

Study Area

This study was carried out in the Anamalai hill range of southern Western Ghats in the states of Tamil Nadu and Kerala, India. The Valparai plateau (10.26°– 0.37°N and 76.87°–76.99°E) is a 220 km^2 mosaic of commercial plantations and rainforest fragments. The plantations include tea (*Camellia sinensis)*, coffee (*Coffea arabica* and *Coffea canephora*), cardamom (*Elettaria cardamomum*), *and Eucalyptus* spp. along with human settlements. Over 40 tropical wet evergreen forest (rainforest) fragments of varying sizes (0.5ha to 300ha) are interspersed within this plantation landscape (Raman & Mudappa, 2003). The elevation of the Valparai Plateau ranges between 600m and 1500m above mean sea level. The natural vegetation of the plateau is classified as the mid-elevation (600–1400 m) tropical wet evergreen forest of the *Cullenia exarillata – Mesua ferrea – Palaquium ellipticum* type (Pascal, 1988). In the plantations, exotic tree species like silver oak *Grevillea robusta* and *Maesopsis eminii* are planted as shade trees and *Eucalyptus* spp. in woodlots for fuel.

Valparai plateau is surrounded by relatively undisturbed tropical wet evergreen forests that occur in the Manamboli Range of Anamalai Tiger Reserve (ATR), Tamil Nadu and the adjoining Vazhachal Reserved Forests (VRF) in Kerala (10.31°– 10.33°N and 76.70°–76.81°E). The forest is dominated by woody evergreen plant species, with a canopy at around 30 m, and emergent trees such as *Bombax ceiba* and *Tetrameles nudiflora*. Rainforest vegetation includes patches with *Ochlandra* bamboos and *Calamus* canes, and is dissected by numerous streams draining into the Sholayar river. Two major reservoirs, Sholayar and Ambalapara, are situated in this area. The average annual rainfall received across the entire study area is 3000–3500 mm, the bulk of which falls during the south-west monsoon (June to September).

For the purpose of this study, the study region was classified into two strata: modified habitat (MH) and contiguous forest (CF). Modified habitat comprised of the whole of Valparai plateau including tea, coffee, and other plantations and all the rainforest fragments. Vazhachal Reserved Forest and Anamalai Tiger Reserve were classified as contiguous forest. The Great Hornbill nests located in the forests of Anamalai Tiger Reserve (Tamil Nadu) and Vazhachal Reserved Forest (Kerala) were classified as ‘nests in contiguous forest’ (CF). Whereas, nests located in Valparai plateau were classified as ‘nests in modified habitats’ (MH).

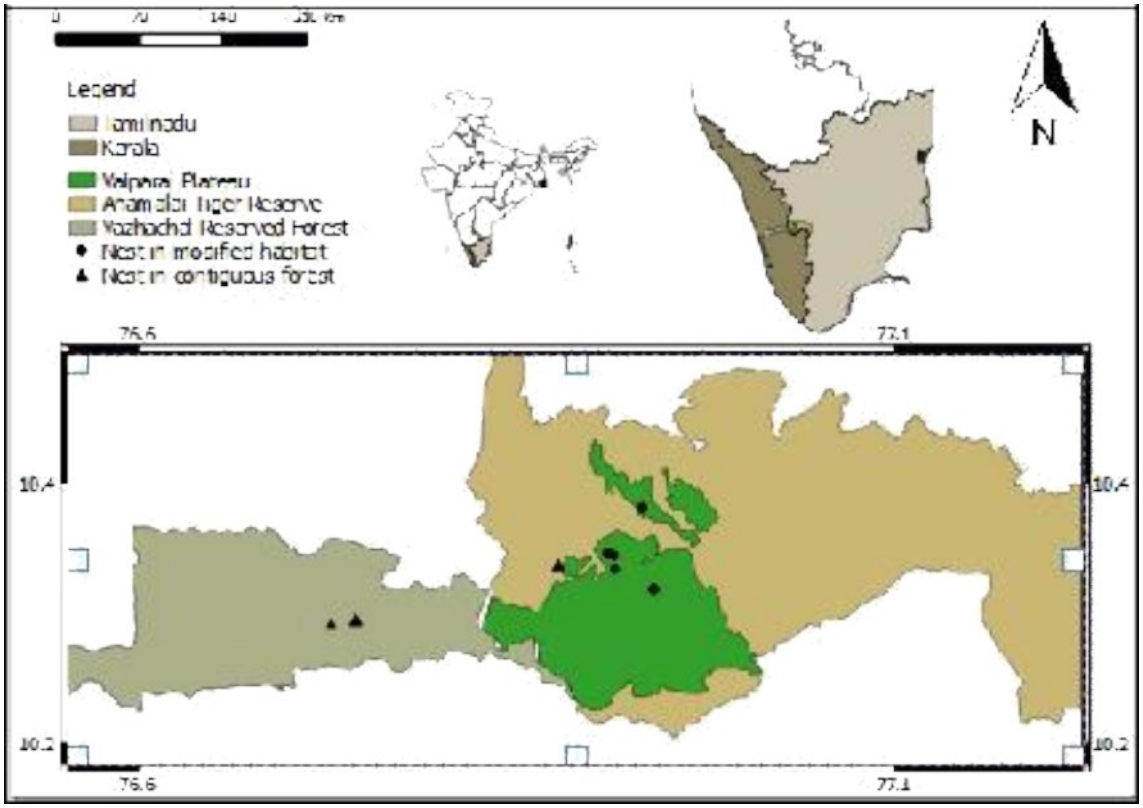

Figure 1. Map showing study area in the Anamalai Hills, Western Ghats, India.

Field methods

Hornbill density estimation

Variable-radius point transect method was adopted to estimate densities of Great and Malabar Grey Hornbills at two sites in the Valparai plateau. Earlier studies in the landscape have documented the abundance of hornbills in contiguous forests and their near-absence in plantations dominated by tea and *Eucalyptus* (Raman & Mudappa, 2003; Sidhu et al., 2010). Therefore, I focused on the coffee plantations adjoining continuous rainforests and rainforest fragments, in two areas—Anali and Manamboli—in the northern part of the Valparai plateau to estimate hornbill densities. Point transects surveys were carried out along a 4 km long trail in both these sites. The Anali trail cut across a matrix of tea, coffee and eucalyptus plantations. The Manamboli trail was within a coffee plantation. Along each trail, 9 points were surveyed for hornbills, with the first point randomly located and subsequent ones placed at a minimum of 200 m aerial distance from each other.

Hornbill detections were recorded over a duration of 10 minutes at each point. Each point transect was surveyed 4 times during mornings (0600h – 0830h) in the pre-nesting season (November – December 2015) and the post-nesting season (May – June 2016). Total survey efforts in both seasons together were 71 and 72 point counts for Anali and Manamboli, respectively. Hornbill species seen, heard or flying were recorded. Time of detection, distance of the bird (in case of single bird) or the distance to the centre of the flock (for a flock of birds) from the point and number of individuals were noted. Whenever possible, age (adult or young one) and sex (male or female) of detected individuals were also recorded. Distance of the hornbills from the point was measured in metres using Bushnell Laser Rangefinder for sightings and estimated aurally for calls.

Nest survey

Prior to the onset of fieldwork, I had planned to monitor at least five nests each in contiguous forests and modified habitat. Apart from the existing knowledge of hornbill nests (Amitha Bachan, 2010), I systematically searched for new nests especially in the modified habitat. In the modified habitat as well as the contiguous forest, I shortlisted (based on logistics and available information) and monitored 13 nests; 10 in contiguous forest and 3 in modified habitat. These 13 nests were regularly monitored from November 2015 to February 2016. With the onset of breeding in December 2015, of the 10 nests in CF only two nests were occupied by breeding pairs, while all three nests in MH were occupied. Three nests, one in CF and two in MH, were discovered during this study by following Great Hornbill pairs at the beginning of the nesting season. Thus, eight nests were selected for the study: three CF nests in ATR (Tamil Nadu) and adjoining VRF (Kerala) and five MH nests located in the Valparai plateau. Among MH nests, four were in coffee plantations and one nest was in a rainforest fragment which included an area of abandoned cardamom and coffee plantation (abandoned about 21 years ago).

Nest tree characteristics

Nest tree parameters and vegetation around the nest were quantified following Kannan & James (1997), Mudappa & Kannan (1997) and Datta & Rawat (2004). The nest tree parameters measured included height of nest tree and height of nest cavity from the ground, girth at breast height (GBH; measured at 1.37 m from the base of the tree). Tree and cavity

height was measured using a Bushnell laser rangefinder and GBH was measured using a measuring tape. The location (main trunk or branch) of the nest cavity on the tree was also noted.

Habitat quality at two scales

I was interested in assessing the quality of habitat in the immediate vicinity of the nest tree (within 15 m around the nest tree) and in the larger area (4.5 km^2) corresponding approximately to the known home range of Great Hornbills during the breeding season (Poonswad & Tsuji, 1991).

Habitat characterisation at the nest site scale was carried out by adopting methods followed by Kannan & James (1997), Mudappa & Kannan (1997) and Datta & Rawat (2004). Circular plots of 15 m radius (0.07ha area) were laid with nest trees as the centre. Within this circular plot, all trees (GBH ≥ 30cm) were counted and identified to species using field guides (Pascal and Ramesh, 1997) and their GBH measured. Average canopy height was estimated at four points in four cardinal directions 5m away from the nest tree. Canopy cover was measured using a convex spherical densiometer at the same four points. Using these measurements, I estimated the tree density (per ha), basal area (m^2/ha), average canopy height and average canopy cover in the immediate neighborhood of the nest.

Given that hornbills range over a large area (c. 4km^2) in the breeding season (Poonswad & Tsuji, 1991), I was also interested in assessing the habitat quality in the larger area (approximately the size of its known home range elsewhere) around the nest site, both in contiguous forest and modified habitats. In a radius of 1200m around the nest tree (area = 4.5km^2), 12 belt transects of 100m × 10m (0.1ha) were laid to measure seven habitat parameters. The 1200m radius was divided into three distance classes of 0 – 400m, 400 – 800m and 800 – 1200m. In each distance class, four belt transects were laid at random locations in each of the four cardinal directions amounting to a total of 12 belt transects around each nest. As some of the belt transects fell in inaccessible terrain, or unvegetated areas such as rocky slopes, reservoirs, and tea plantations; the total vegetation sampling effort for each nest varied between 1ha and 1.2ha. Within each belt transect, trees ≥ 30cm GBH were enumerated and identified to the species level. At 25m intervals along each belt transect,

canopy height was measured using a Bushnell range finder and canopy cover was measured using a convex spherical densiometer.

List of hornbill food plants was collated from available scientific literature on hornbill diet (Kannan & James, 1997; Mudappa, 2000; Datta & Rawat, 2003) and from direct observations during the study period at nests and opportunistic observations. Trees were identified using the field key by Pascal & Ramesh (1987) and based on species known to occur in the study area (Muthuramkumar, et al., 2006). Tree species were also classified into native and non-native (exotic) trees. This data enabled me to estimate total tree species richness, hornbill food-plant species richness, total tree density, hornbill food-plant density and basal area of trees in the larger habitat around the nest tree.

Breeding biology

From November 2015, each nest was visited and searched for signs of activity by hornbill pairs at the nest and around the nest tree periodically until the female occupied the nest and started to seal the entrance (Plate 3b). Entry of the female hornbill in to the cavity marked the beginning of the nesting cycle and it ended when the chick fledged out from the nest (Datta, 2001). Exact dates of female entry for all the nests (except MH-2) were known from monitoring of nests. I classified the entire nesting cycle into pre-hatching and post-hatching phases. In Great Hornbills, eggs are known to hatch after around 50 days of female entering the nest cavity (Poonswad et al., 2004). In field, this can also be confirmed by calls of chicks which can be heard from near the nests. I periodically monitored the nests to hear the chick calls from the nests to ascertain hatching. I classified the entire nesting cycle into pre-hatching and post-hatching phases based on the date the chicks were first heard at the nest. Exact fledging dates were also known for all the nests from periodic monitoring of nests.

Nesting behaviour

I conducted focal nest watches after the female occupied the nest. Nest watches were carried out in the morning, between 0600h and 1300h at all eight nests. In order to minimise disturbance to hornbills by the observer, direct observations were made from a distance varying between 15–60m from the nest tree, using a Vanguard 10×50 binoculars from a hide on the ground, or at one nest, from a platform built on a nearby tree. During the study period,

each nest was visited at least twice every month with 526 hours of observations across the eight nests, of which, 279 hours were during the pre-hatching phase and 247 hours during the post-hatching phase. During each nest observation, I recorded the following: (1) number of visits by the parent bird/s, (2) duration of each visit by the parent bird/s, and (3) number of items of different fruit or animal food species delivered to the nest inmate by each parent bird. While the fruit species that were delivered at the nest could be identified to the species level, animal matter was classified based on the animal group (insect, frog, lizard, snake, mice) to which they belong as species-level identification was difficult. This information was used to calculate visitation rate, food delivery rate, quantification of contribution of different kinds and sizes of food items delivered.

Analyses

Hornbill density estimation

Hornbill detections from point transect surveys were used to estimate population densities of Great Hornbill and Malabar Grey Hornbill in pre- and post-nesting seasons using distance sampling techniques in the DISTANCE program (ver.6.2) following Thomas et al. (2010). All detections were categorised into radial distance classes in metres: 0–20, 20–40, 40–60, 60–80, 80–100, 100–125, 125–150, 150–200 and 200–300 m. Only detections within 150 metres (truncation distance) from the centre of the point were used for estimation of densities. Each detection (cluster) represented an individual or a flock of hornbills foraging or moving together. I estimated cluster density and individual hornbill density. Since I had less number of detections for each species (less than 10) in one survey site in both seasons (pre-nesting and post-nesting), I pooled all the detections from both survey sites for a season. Detection probability was assumed to be invariable across survey sites since both survey sites were in predominantly coffee plantations in modified habitat. Stratification was used to estimate hornbill densities across the two survey sites in each season. Candidate models run were half-normal, uniform and hazard rate to estimate detection probability with *cosine* adjustment terms and standard model selection procedures were followed in DISTANCE to select the best fit models to estimate hornbill density following Thomas et al. (2010). The candidate model with the least Akaike's Information Criterion (AIC) value was chosen for density estimates.

Nest tree characteristics

I used Mann-Whitney U-test to compare, across nests in contiguous forests and modified habitats, GBH of nest trees, height of nest trees, and height of nest cavities. This tests the null hypothesis that the two samples (in this case the different estimated parameters) are from the same population. Unlike parametric tests, this test does not assume that the response variable is normally distributed (Hart, 2001).

Habitat quality at two scales

The mean tree density, food plant density, and basal area were estimated for each nest in CF and MH. Thus, mean of means were used for further comparison. I used Mann-Whitney U-test to compare tree density between contiguous forest and modified habitats in the vicinity of nest trees (within 15m radius of the nest tree) and at the larger habitat scale (within 1200m radius of the nest tree). Similar comparisons were made for basal area and food plant density between CF and MH nests at the larger habitat scale.

Nesting behaviour

Nest-visitation and food delivery rates

Nest watch data on adult visits and number of different food items delivered at the nests was used to calculate the visitation rate and food delivery rate at each nest. This was done to compare the visitation rate and food delivery rate between nests in contiguous forests and modified habitats and between the pre-hatching and post-hatching phases. Visitation rate was estimated as the number of feeding visits per hour calculated as number of feeding visits by parent bird divided by number of hours of observation. Mean visitation rates were calculated for pre-hatching and post-hatching phases separately. Similarly, food delivery rates were calculated by averaging total number of food items delivered divided by the total number of hours of observation at each nest. I used non-parametric Mann-Whitney U-test to compare the visitation and food delivery rates between pre- and post-hatching phases and between the nests in contiguous forests and modified habitats (Mann & Whitney, 1947; Hart, 2001). For the pre- and post-hatching phases, data from all the nests was pooled within each phase as

there was no significant difference in visitation rates between the contiguous forests and modified habitats.

Diversity and quality of food delivered

Nest watch data was used to determine the diversity (species richness) and abundance of fruits delivered at the nest. Broadly, I classified food items delivered as fruits or animal matter. Further, each food item was categorised based on its nutritive quality following classification by Cody (1985) and Corlett (1996) and classified into three different size classes (Gamble & Fischer, 1935; Mudappa unpublished data). Since it was difficult to identify animal matter to the species-level, diversity and abundance of animal matter delivered at the nest was categorized into the animal group to which the item belonged (insect/frog/lizard/snake/bird/mammal). This information was used to determine the percentage contribution of plant and animal matter to the diet of hornbills, the percentage of dietary overlap between nests in contiguous forests and in modified habitats. I used Schoener's Overlap Index to calculate percentage dietary overlap of food items. Additionally, Morisita's dietary overlap index which takes into account the similarity in proportions of different food items in the diets across the nests in contiguous forest and modified landscape was also used (Krebs, 2013). Morisita's index varies between 0 and 1 with 0 indicating no dietary overlap and 1 indicating that the different food items occur in the similar proportions between the two sites (Krebs, 2013).

The fruit items delivered at the nest was classified into figs (all *Ficus* species), lipid-rich and sugar-rich fruits. The figs were considered as a separate nutritional category since more than 70% Great Hornbill diet is comprised of fig species (Datta & Rawat, 2003; Kannan and James, 1997) and apart from lipids and crude protein, figs are a major source for calcium and magnesium which are crucial for egg shell formation and bone development (Kinnaird & O'Brien, 2007; Lamperti et al., 2014). One unidentified fruit was excluded from the analysis. All animal matter was considered as protein-rich food. Based on the fruit sizes, I categorised observed fruits into three size classes: small (≤ 1cm), medium (1–3cm) and large (≥ 3cm) (Mudappa, unpublished data). I categorised animal matter into three size classes as well: small (≤ 10g), medium (10–30g) and large (≥ 30g) based on their body mass.

Rarefaction curves were generated to assess the overall species richness and food plant species richness in contiguous forest and modified habitat. The species richness was calculated by using R package vegan (Oksanen et al., 2016). I performed Chi-squared test of independence to compare between contiguous forest and modified habitat, 1) the relative proportions of fruits belonging to different nutritional categories (lipid-rich, sugar-rich, figs, protein-rich), 2) the relative proportions of fruits belonging to different size classes and, 3) relative proportions of animals belonging to different size classes.

Analysis was carried out in R (version 0.99.893). Packages 'dplyr' (Wickham & Francois, 2015), 'plyr' (Wickham, 2011), 'reshape' (Wickham, 2007), 'reshape2' (Wickham, 2007) were used for organising, summarising and analysing data. However to generate graphs and figures the package 'ggplot2' (Wickham, 2009) was used. Study area map was prepared using Q-GIS spatial mapping tool (URL http://qgis.osgeo.org.).

RESULTS

Hornbill density estimation

In point transect surveys, I obtained 91 detections (201 individuals) of Great Hornbills and 68 detections (99 individuals) of Malabar Grey Hornbill across the pre-and the post-nesting season in the two sites.

Great Hornbill (GH) density

Half-normal model and Uniform model with cosine adjustment term were the best (with the least AIC value) among candidate models for GH density estimates in pre-and post-nesting seasons, respectively. The mean (± SE) cluster size in the pre-nesting season was 2 (± 0.3) and in post-nesting season was 1.8 (± 0.11). The overall mean GH density was 5.4 times higher in the pre-nesting season (mean ± SE: 49 ± 19 individuals/km^2) as compared to the post-nesting season (9 ± 3.5 individuals/km^2; Fig. 2; Appendix 1). However, the magnitude of difference between pre- and post-nesting GH densities varied between the two sampling sites. In Manamboli, GH density was 2.6 times higher in the pre-nesting season (mean ± SE: 26 ± 12.7 individuals/km^2) than in the post-nesting season (8 ± 3.7 individuals/km^2; Appendix 1). In Anali, GH density was 7.3 times higher in the pre-nesting season (mean ± SE: 73 ± 32.4 individuals/km^2) than in the post-nesting season (10 ± 4.8 individuals/km^2).

Malabar Grey Hornbill (MGH) density

The best candidate model (with the least AIC value) selected for MGH density estimation in the pre- and post- nesting season was Half-normal model with cosine adjustment terms. The mean cluster size was similar across the pre-nesting (mean ± SE: 1.6 ± 0.1 hornbills) and the post-nesting seasons (1.4 ± 0.16 hornbills). The overall mean MGH density was 3.5 times higher in the post-nesting season (mean ± SE: 136 ± 42.8 individuals/km^2) as compared to the pre-nesting season (39 ± 15.6 individuals/km^2; Fig. 2; Appendix 2). The magnitude of difference between pre- and post-nesting MGH densities varied across the two sampling sites. In Manamboli, MGH density was 4 times higher in the post-nesting season (mean ± SE: 212 ± 65.4 individuals/km^2) as compared to the pre-nesting season (53 ± 20 individuals/km^2). In Anali, MGH density was 2.3 times higher in the post-nesting season (mean ± SE: 59 ± 21.3 individuals/km^2) than in the pre-nesting season (26 ± 19.6 individuals/km^2).

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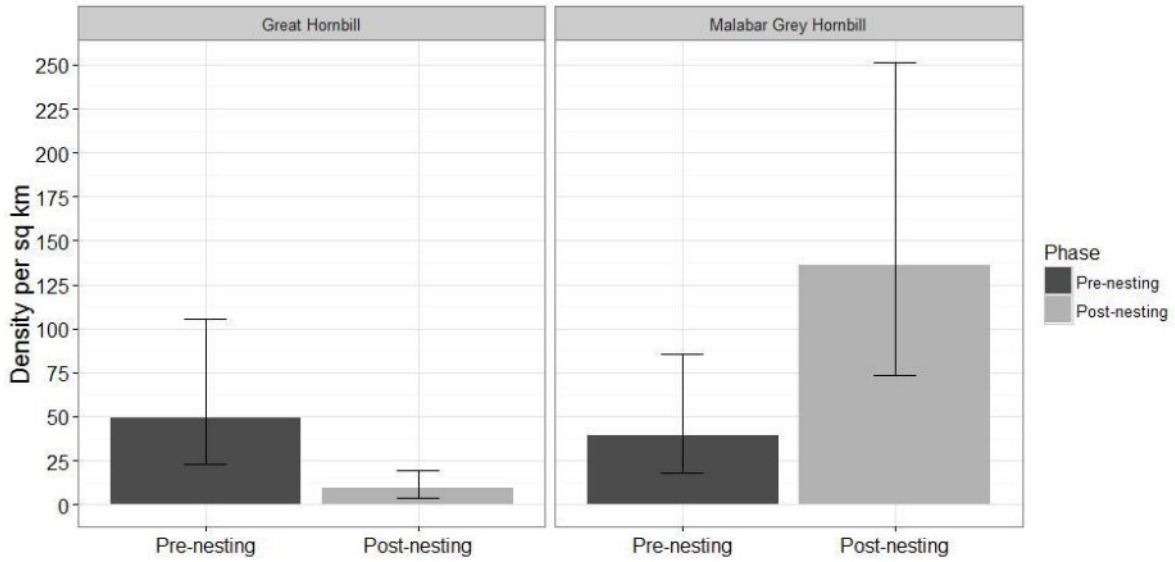

Figure 2. Density estimates (mean ± 95% confidence intervals) for Great Hornbill (GH) and Malabar Grey Hornbill (MGH) during the pre-nesting and post-nesting seasons in the Valparai Plateau, Western Ghats.

Nest tree characteristics

All eight nests of GH were on different tree species (Table 1). While seven of the eight nests were on native tree species, one nest was in a non-native tree species, silver oak *Grevillea robusta*. All nest cavities were on the main trunk of the nest tree. Mean (± SE) girth at breast height (GBH) of GH nests was 7.03m (± 1.88m) in contiguous forests (CF; n = 3) and 3.24m (± 0.3m) in modified habitat (MH; n = 5; Table 1). The nest tree girths did not differ significantly for nests in CF and MH (Mann-Whitney U-test, U = 14, p = 0.071). Mean (± SE) height of the nest trees was 44.7m (± 6.33m) in CF and 33m (± 2.85m) in MH (Table 1). Height of nest trees also did not show significant difference between nests in CF and MH (Mann-Whitney U-test, U = 13, p = 0.143). Mean height of the nest cavity was 29.3m (± 5.90m) in CF and 17m (± 4.18m) in MH (Table 1). Nest cavity heights did not differ significantly across contiguous forest and modified habitat (Mann-Whitney U-test, U = 2.5, p = 0.177).

Habitat quality at two scales

Habitat quality at nest site

The overall mean (± SE) tree density in the immediate vicinity of the nest sites was 705 (± 176) trees/ha in CF and 294 (± 167) trees/ha in MH (Table 1). Tree densities in the vicinity of

nest trees did not differ significantly between CF and MH (Mann-Whitney U-test, $U = 12$, $p = 0.23$). Mean (± SE) basal area in the immediate neighbourhood of the nest tree was 43.8m^2/ha (± 9.7m^2/ha) in CF and 23.7m^2/ha (± 12.7m^2/ha) in MH. The mean basal area did not differ significantly between CF and MH (Mann-Whitney U-test, $U = 12$, $p = 0.25$). Mean (± SE) canopy cover around the nest tree was 80.1% (± 8.4%) in CF and 49.2% (± 10.4%) in MH (Table 1). Mean canopy cover did not differ significantly between CF and MH (Mann-Whitney U-test,

$U = 13$, $p = 0.14$). Mean (± SE) canopy height was 24.9m (± 1.6m) in CF and 27m (± 4.7m) in MH (Table 1). Between CF and MH, mean canopy height did not differ significantly (Mann-Whitney U-test, $U = 5$, $p = 0.57$).

Habitat quality at home range scale

Tree species richness, density, and basal area

I recorded 124 tree species in 3.3 ha of sampled area in contiguous forest and 86 tree species in 5.6 ha of sampled area in modified habitat. Rarefaction results showed that, for an equal sampling effort of 33 plots (3.3 ha) each in CF and MH, 124 tree species were recorded in CF and 72 (SE: ± 0.82) tree-species in MH. Overall species richness was significantly higher (non-overlapping CI) in CF than in MH (Fig. 3). No non-native (exotic) tree species were recorded in CF, while 5 non-native tree species were recorded in MH.

Mean (± SE) tree density (trees/ha) was 1.4 times higher in CF (313 ± 26; range: 285–365 trees/ha) as compared to MH (219 ± 52; range: 123 – 383 trees/ha; Fig. 4; Appendix 3). However, tree density in CF (n = 3) did not differ significantly from tree density in MH (n = 5) (Mann-Whitney U-test, $U = 5$, $p = 0.57$).

Mean basal area (m^2/ha) in CF ranged from 35.9m^2/ha to 51.7m^2/ha (Fig. 5; Appendix 3). In MH, basal area ranged from 21.3 to 48.1m^2/ha. Basal area did not differ significantly between CF and MH (Mann-Whitney U-test, $U= 13$, $p = 0.14$).

Table 1. Summary of the nest tree and nest site characteristics in contiguous forest (CF) and modified habitats (
Ghats

Nest code	**Tree species**	**GBH (m)**	**Tree height (m)**	**Nest height (m)**	**Mean canopy height (m)**	**Mean canopy cover (%)**	**Tree density (trees/l**
CF-1	*Bombax ceiba*	8.96	57	41	27.2	96.9	757
CF-2	*Palaquium ellipticum*	3.27	36	22	21.8	72.9	514
CF-3	*Tetrameles nudiflora*	8.88	41	25	25.8	70.6	543
MH-1	*Mesua ferrea*	3.17	39	25	30.2	87.7	1129
MH-2	*Syzygium gardneri*	2.90	24	03	11.8	37.7	214
MH-3	*Grevillea robusta*	2.56	35	12	40.2	51.2	43
MH-4	*Dysoxylum malabaricum*	3.22	29	21	22.7	27.1	43
MH-5	*Mangifera indica*	4.36	38	24	30	42.5	43

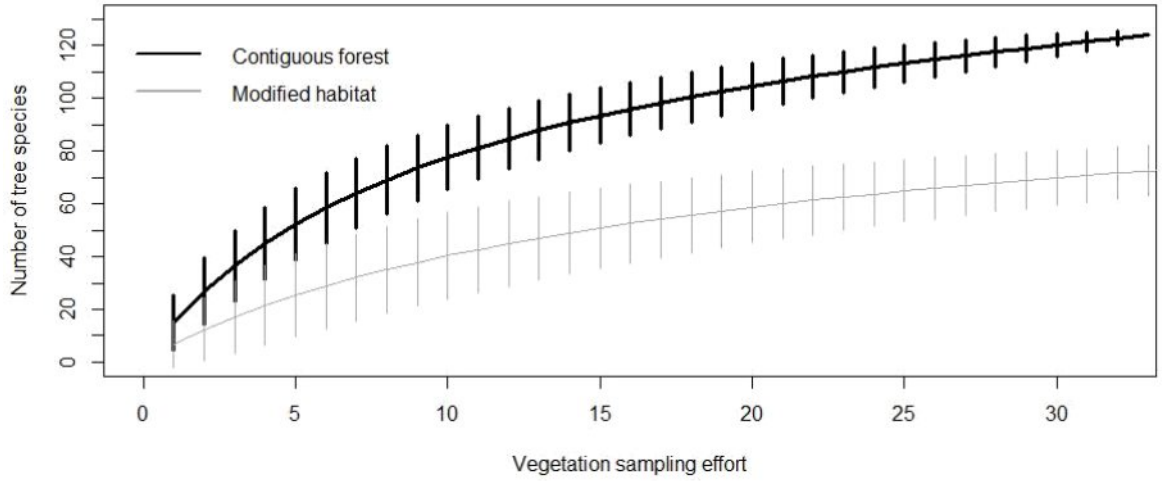

Figure 3. Species accumulation curve and 95% confidence intervals for tree species around nests in contiguous forest (black line) and modified habitat (grey line). The x-axis represents number of vegetation plots.

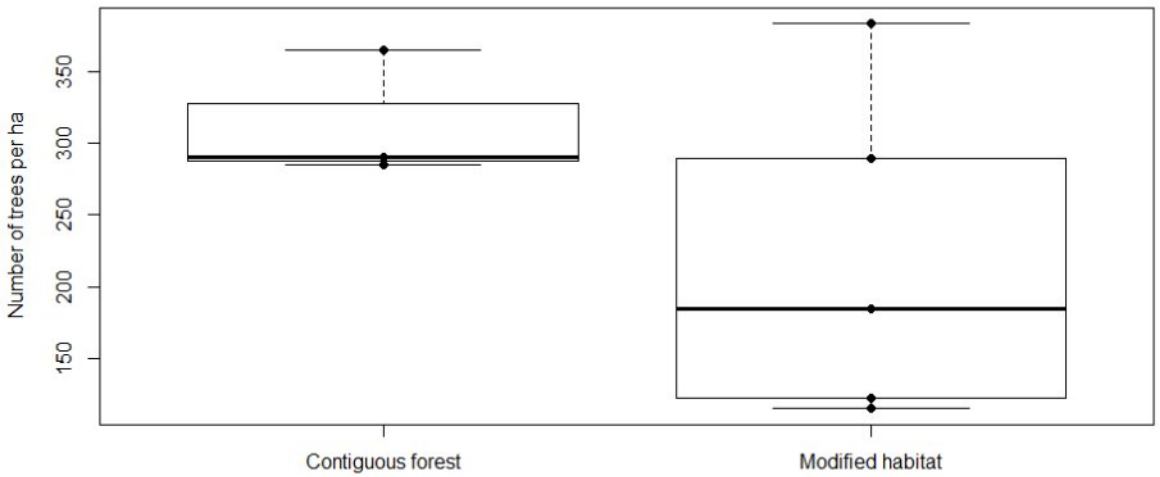

Figure 4. Mean (± SE) Tree density/ha across the contiguous forest and modified habitats in Anamalai hills, Western Ghats.

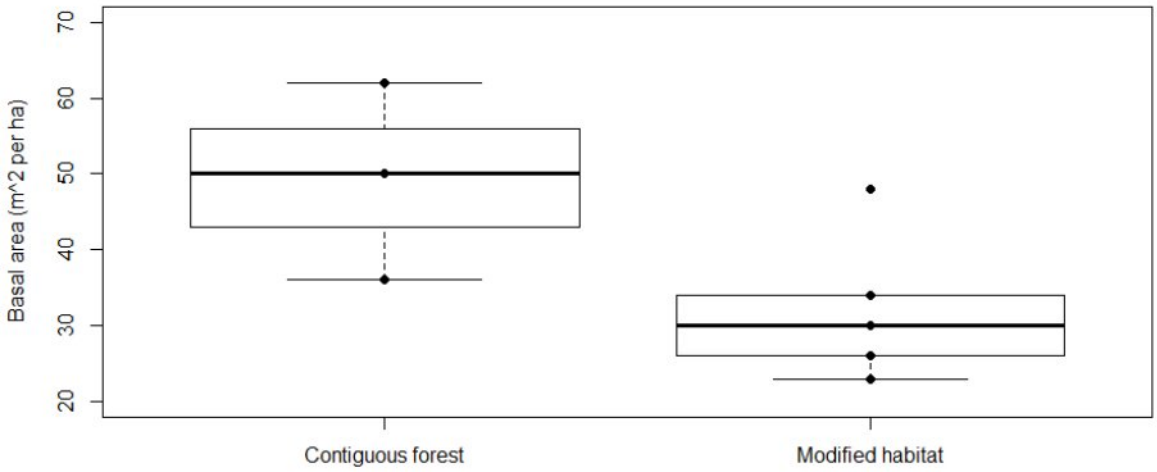

Figure 5. Mean (± SE) basal area (m2/ha) across the contiguous forest and modified habitats in Anamalai hills, Western Ghats.

Food plant species richness across habitats

I recorded 43 species of hornbill food plants across the two habitats. Of the 43 species, 42 species were native and only one species (*Maesopsis eminii*) was a non-native (exotic) food plant species of the Great Hornbill. In CF, all the recorded 36 food plant species were native. In MH, 29 food plant species were found of which 28 were native. Rarefaction curves showed that food plant species richness was significantly higher (non-overlapping CI) in CF than MH as with equal sampling effort, 36 food plant species occurred in CF and 26 (SE: ± 0.26) food plant species in MH (Fig. 6).

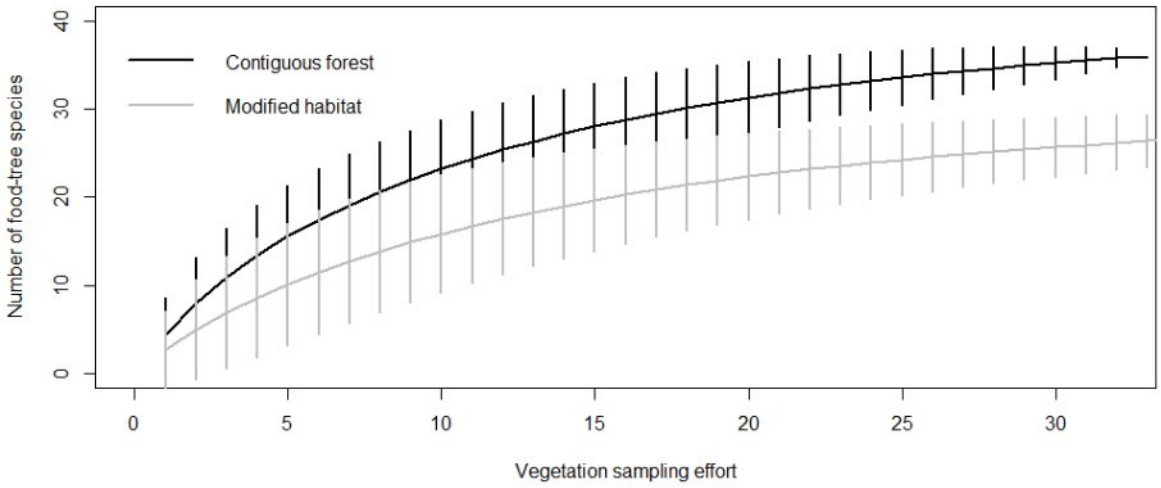

Figure 6. Species accumulation curve and 95% confidence intervals for hornbill food-plant species around nests in contiguous forest (black line) and modified habitat (grey line) habitats. The x-axis represents number of vegetation plots.

Food plant density

The mean (± SE) overall food plant density was 93 trees/ha (± 9.3; range: 81–111 trees/ha) around the three nests in CF and 110 (± 49.6; range: 36–304 trees/ha) around five nests in MH. The overall food plant densities did not differ significantly between CF and MH (Mann-Whitney U-test, $U = 5$, $p = 0.55$). However, the mean density of native food plants was higher in CF (93 ± 9.3 trees/ha) than in MH (43 ± 14.5 trees/ha; Fig. 7; Appendix 3). The density of *Maesopsis eminii*, which is a non-native food plant of Great Hornbill, occurred at a density of 56 ± 41.3 trees/ha in MH but was absent in CF. However, the density of native food plant did not differ significantly between contiguous forest and modified habitat (Mann-Whitney U-test,$U = 13$, $p = 0.143$).

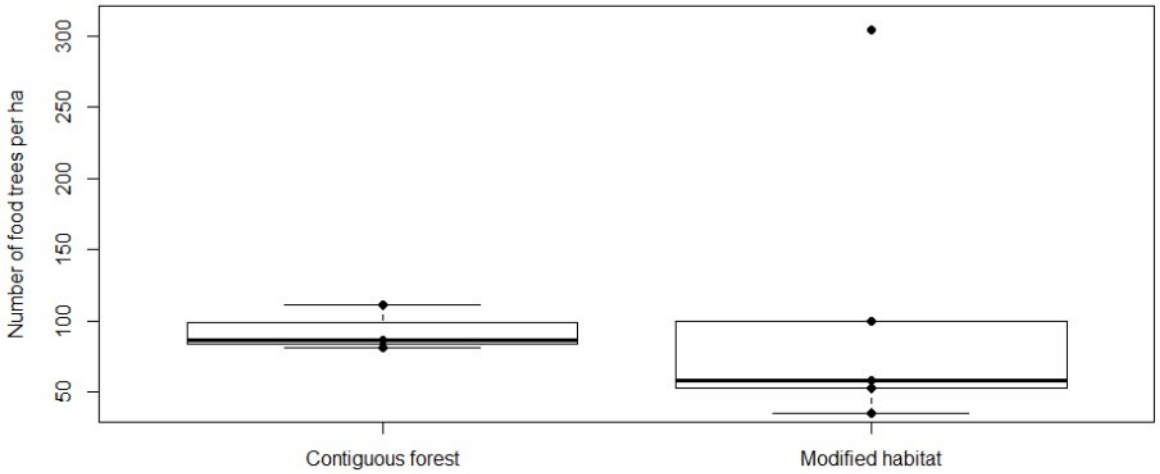

Figure 7. Food tree density per ha across the contiguous forest and modified habitats in Anamalai hills, Western Ghats.

Breeding biology

The nesting season lasted from December 2015 to June 2016 for the eight nests monitored. Nesting commenced in the second week of December in both CF and MH. While five females (Nests: CF-1, CF-3, MH-1, MH-3, MH-5) entered the nest cavity in December, one female (Nest: MH-4) entered on 29 January and one female (Nest: CF-2) entered on 5 February (Appendix 4). One Great Hornbill female nesting in the modified habitat (Nest: MH-4) abandoned the nest 59 days after her entry. The pair was seen around the nest for the rest of the nesting season but the female did not re-enter the cavity. Chicks fledged after 15 April 2016 in MH and CF. The chick of the CF-2 nest fledged on 13 June 2016.

The length of nesting cycle varied between 106 and 130 days across the eight nests monitored. Nesting cycle in CF (n = 3) ranged from 114 to 129 days. In MH (n = 4), nesting cycle ranged from 115 to 130 days. The exact length of nesting cycle for MH-2 nest in MH could not be ascertained but was estimated to be between 106–110 days.

Nesting behaviour

Visitation rate

The overall mean (± SE) visitation rate was 0.6 (± 0.03) visits/hr. In CF mean (± SE) visitation rate was 0.5 (± 0.06) visits/hr, whereas in MH visitation rate was 0.6 (± 0.04) visits/hr. Visitation rates differed significantly between two phases for the pooled data across both strata (Mann-Whitney U-test, $U = 3$, $p = 0.004$).

In CF, mean visitation rate was 1.2 times higher in the post-hatching phase (mean ± SE: 0.64 ± 0.1 visits/hr; n = 14) as compared to the pre-hatching phase (0.52 ± 0.02 visits/hr; n = 12) (Fig. 8; Appendix 5). In MH, mean visitation rate was 1.53 times higher in the post-hatching phase (mean ± SE: 0.78 ± 0.05 visits/hr; n = 20) as compared to the pre-hatching phase (0.51 ± 0.02 visits/hr; n = 13; Fig. 8). Overall visitation rate did not differ significantly between CF and MH (Mann-Whitney U-test, U = 17, $p = 0.5$).

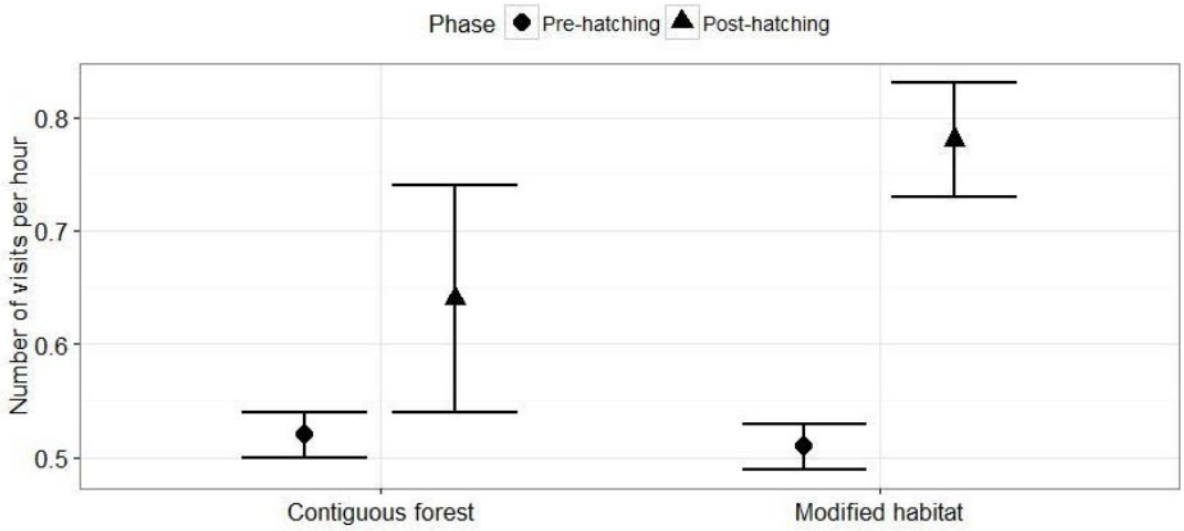

Figure 8. Visitation rate (mean ± SE) by adults in pre-hatching and post-hatching phases in contiguous forest and modified habitat nests (dots and triangles indicate mean whereas error bars indicate standard error) in Anamalai hills, Western Ghats.

Food delivery rate

Overall mean (± SE) food delivery rate was 25.4 (± 4.3) food items/hr across all the nests. In CF mean (± SE) food delivery rate was 27.9 (± 10) food items/hr and in MH it was 23.9 (± 4.34) food items/hr. Food delivery rates did not differ significantly between two phases for the pooled data across both strata (Mann-Whitney U-test, $U = 23$, $p = 0.55$). Food delivery

rate varied across nests from pre-hatching to post-hatching phase (Appendix 5). Mean food delivery rates declined in post-hatching phase in both CF and MH (Fig. 9). In CF, the mean (± SE) quantity of food delivered was 2.3 times higher in pre-hatching phase (38.8 ± 27 food items/hr, n = 12) than in the post-hatching phase (17 ± 8.8 food items/hr, n = 14) food items/hr. In MH, the mean (± SE) quantity of food delivered was only 1.4 times higher in pre-hatching phase (26.1 ± 5.5 food items/hr, n = 28) than in post-hatching phase (18.5 ± 6.1 food items/hr, n = 20) food items/hr; Fig. 9). Overall food delivery rate did not differ significantly between CF and MH (Mann-Whitney U-test, U = 33, p = 0.53).

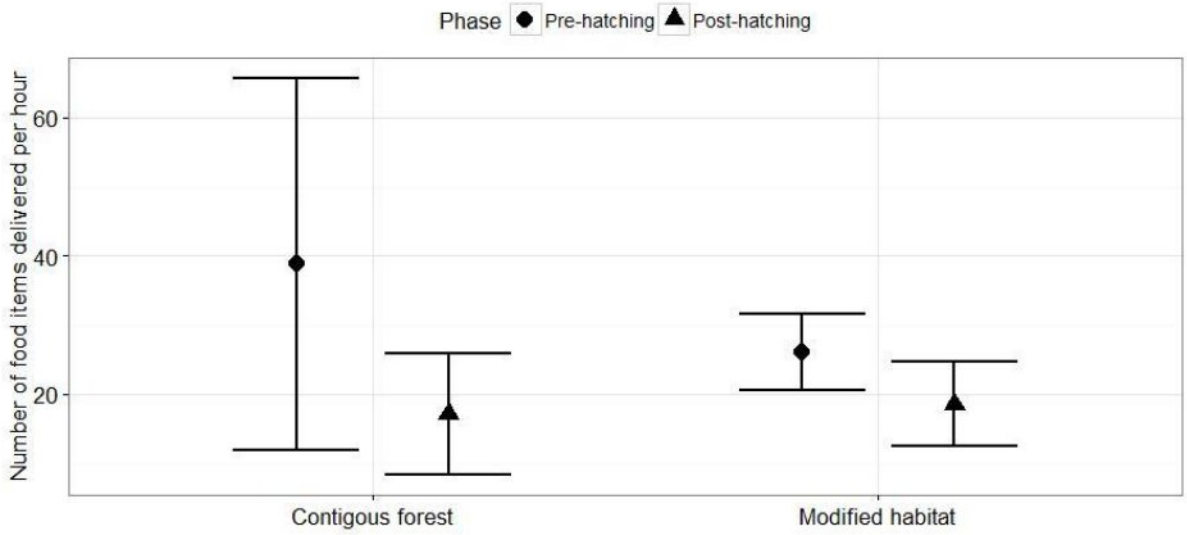

Figure 9. Food delivery rates (mean ± SE) at Great Hornbill nests during pre- and post-hatching phases across nests in modified and natural habitats in Anamalai hills, Western Ghats. (Dots and triangles indicate mean and error bars indicate standard error).

Diversity of food delivered

Over the entire nesting period, adult hornbills delivered 20 fruit species belonging to eight families (Fig. 10; Appendix 6–7) and thirteen kinds of animal matter that included invertebrates like moths, stick insects, mantis, and vertebrates like frogs, skinks, snakes, rodents, small birds and eggs (Fig. 11; Appendix 8). In total, 16629 fruits and 128 animals were delivered in 526 hours of observations across all the nests. Hornbill diet largely comprised of fruits (99%) and a small proportion of animal matter (1%). Among fruits, nearly 50% of the diet comprised of figs.

Ficus microcarpa was the only fruit species that was delivered across all the nests (Fig. 10). Of the total 20 species that were recorded, 6 fruit species—*Syzygium* sp. *Cassine glauca*,

Knema attenuata, *Cinnamomum malabathrum*, *Ficus* sp. 1, *Ficus* sp. 4—were delivered only at nests in contiguous forests and 4 fruit species—*Ficus racemosa, Dysoxylum binectariferum, Ficus* sp. 2, non-fig sp. 1—were delivered only at nests in modified habitats. The percentage dietary overlap between nests in contiguous forests and modified habitat, as calculated using the Schoener's Overlap Index, was 57.5%. However, Morisita's Index for dietary overlap across contiguous forests and modified habitat was 0.84.

Quality of food delivered

Of the 16757 food items that were delivered at the nest, figs comprised 70.4%, lipid-rich fruits comprised 23.7%, sugar-rich fruits comprised 5.1% and protein-rich food items comprised 1% (the unidentified fruit that was delivered once is not included in this calculation). In CF, of 6986 food items that were delivered during the entire nesting season, figs comprised 71.3%, lipid-rich fruits comprised 15.6%, sugar-rich fruits comprised 12.1% and protein-rich food item comprised 1.1%. While in MH, of 9771 food items delivered during entire nesting season, proportions of fig, lipid-rich and sugar-rich fruits were 69.8%, 29.4% and 0.1%, respectively. Protein-rich food items comprised of 0.7% in MH. The relative proportions of fruits belonging to different nutritional categories varied significantly between CF and MH ($\chi^2 = 1502.5$, df = 3, $p < 0.01$).

There was considerable variation in relative proportions of different food items delivered across different nests. The relative proportions of figs ranged from 45-80%, lipid-rich fruits ranged from 10%–54%, sugar-rich fruits ranged from 0%–45% and protein-rich food items ranged from 0.1%–2% across the eight nests monitored.

Mean (± SE) proportion of figs delivered at the nest across all the nests was 1.3 times higher in the pre-hatching phase (75% ± 6.3%) as compared to the post-hatching phase (57% ± 8.8%). At nests in CF, mean (± SE) proportion of figs delivered at the nest was 2.1 times higher in the pre-hatching phase (87% ± 0.4%) as compared to the post-hatching phase (42% ± 16%) (Fig.12). In MH, mean (± SE) proportion of figs delivered at the nest was similar in the pre-hatching phase (87% ± 0.4 %) and post-hatching phase (67% ± 8%).

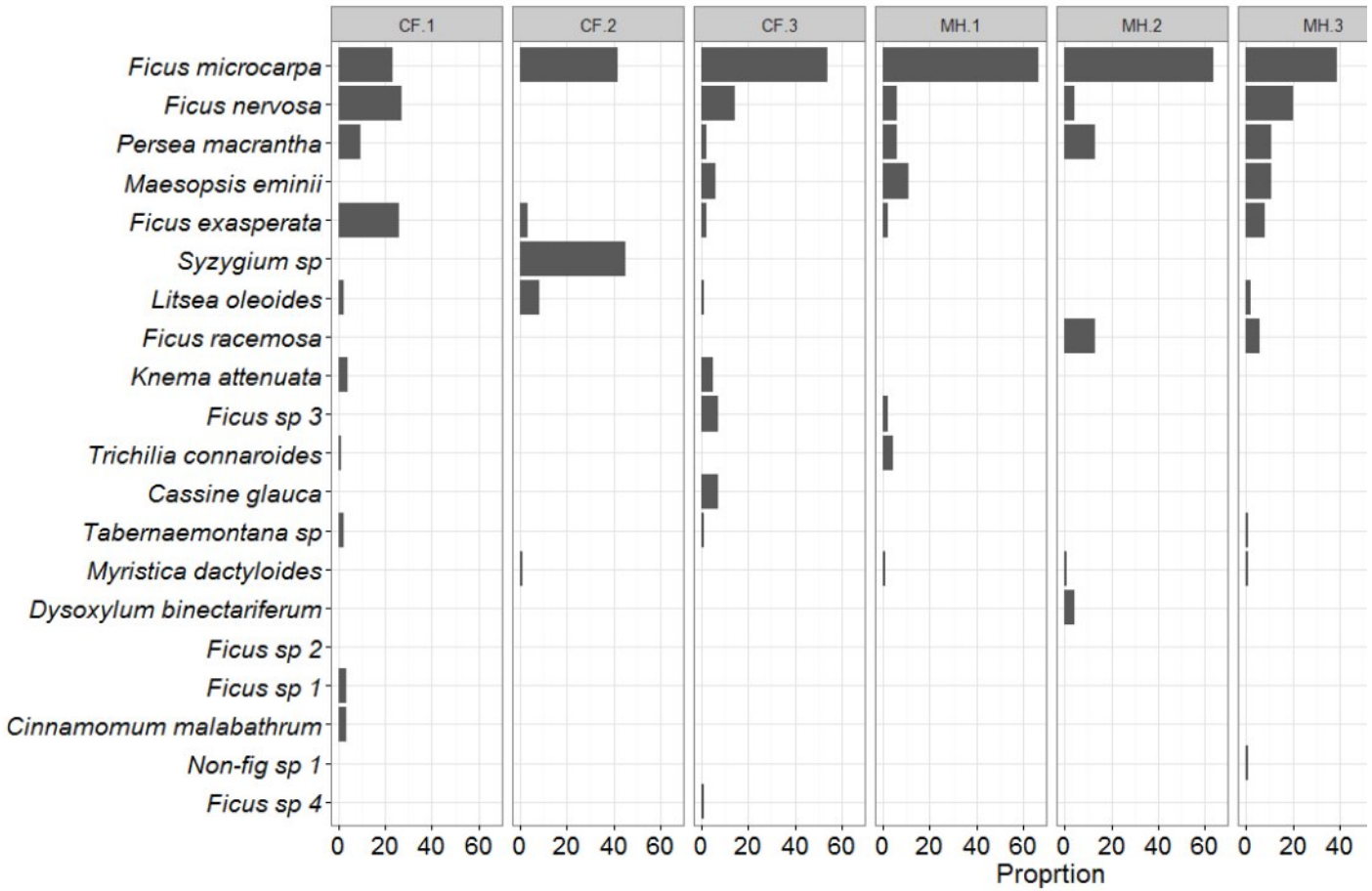

Figure 10. Proportions of different fruit-species in Great Hornbill diet during the breeding season of 2015-16 in

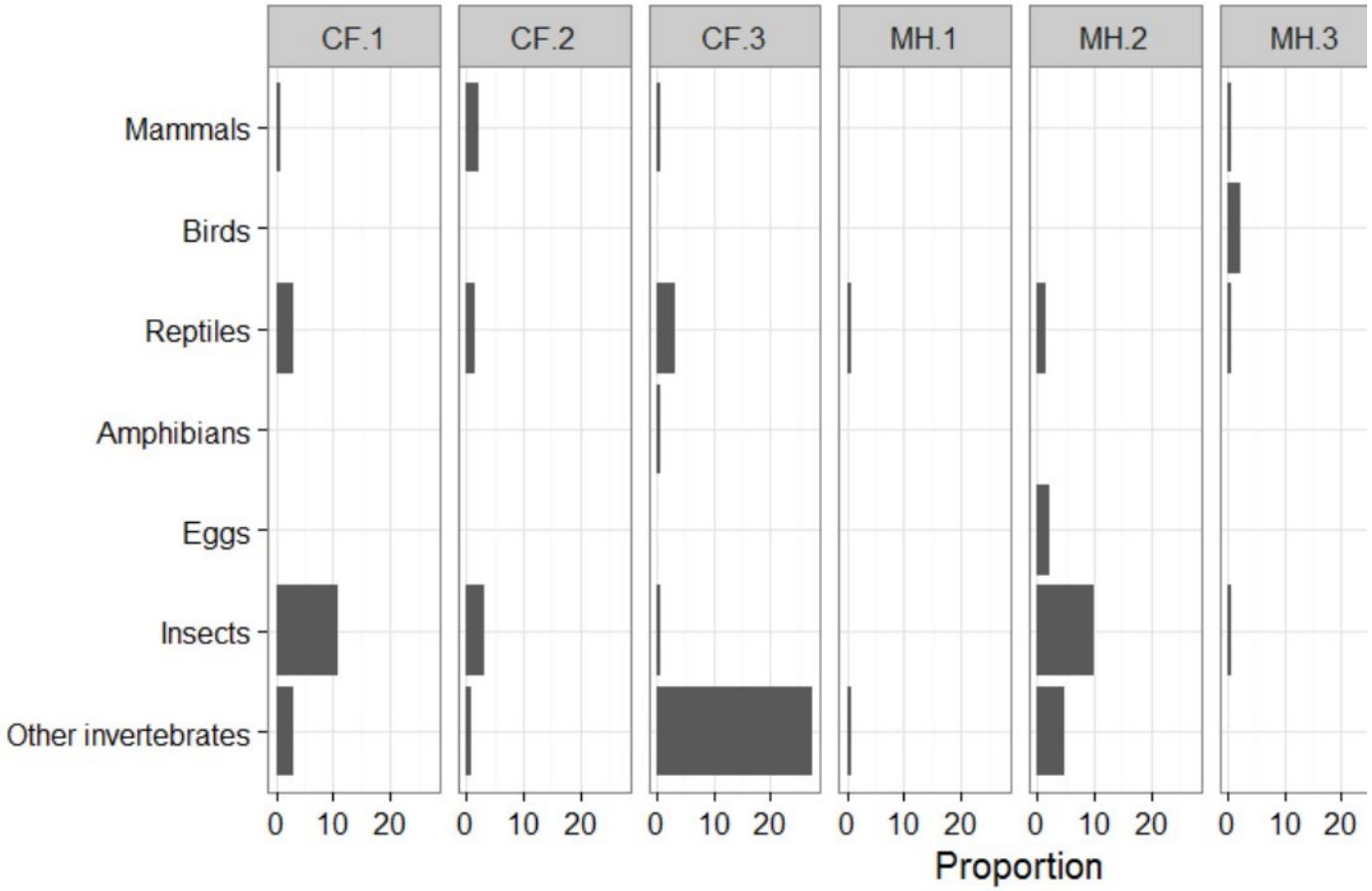

Figure 11. Proportion of different animal groups in Great Hornbill diet during the breeding season of 2015-16 in

Overall proportion of lipid-rich fruits marginally increased during post-hatching phase when compared to pre-hatching phase. Mean (± SE) proportion of lipid-rich fruits in pre- and post-hatching phases was 24.7% (± 6.25%) and 27.8% (± 5.2%), respectively. In pre-hatching phase, mean proportion of lipid-rich fruits in contiguous forest was 13% (± 0.113%) and in post-hatching phase it increased to 23% (± 6.6%). In modified habitat, proportion of lipid-rich fruits did not vary between pre-hatching (30.6% ± 8%) and post-hatching (31.6% ± 8%) phases. (Fig. 12)

Sugar-rich (non-fig) fruits were not provided in pre-hatching phase either in CF or MH. Overall sugar-rich fruit proportion was 14.58% (± 9.5%) in post-hatching phase. In post-hatching phase, proportion of sugar-rich fruits in contiguous forest was 34% (± 17.3%) of overall diet. In modified habitat, sugar-rich fruits were delivered only in post-hatching phase in small proportion (0.9 ± 0.1%).

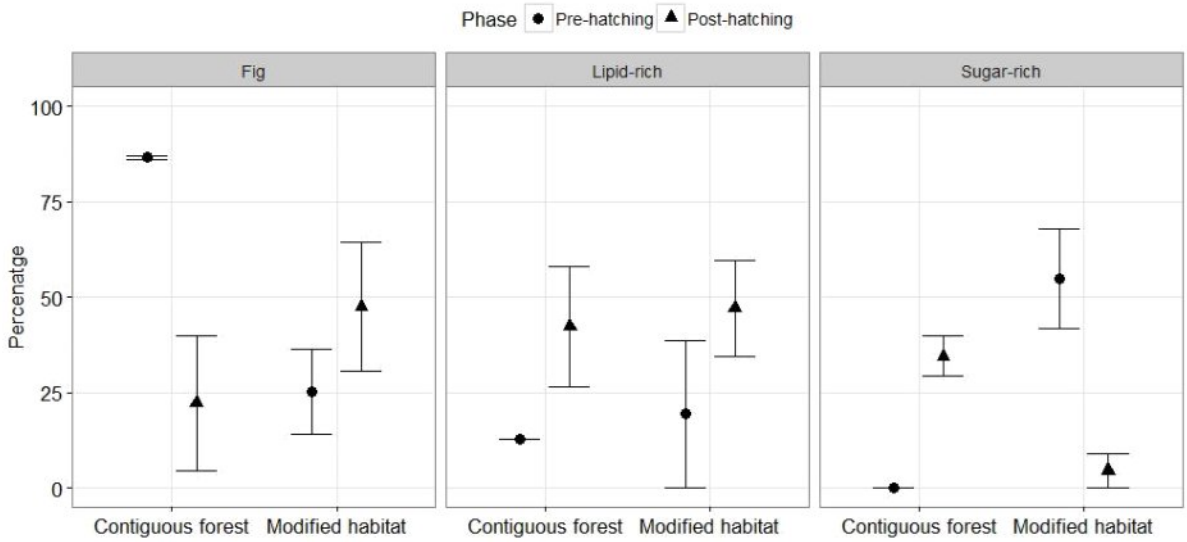

Figure 12. Mean (± SE) proportions of fruits by nutrition category in hornbill diet during pre- and post-hatching phases at nests across contiguous forest and modified habitat in Anamalai hills, Western Ghats. (Dots and triangles indicate mean and error bars indicate standard error).

Of 16629 fruits delivered across eight observed nests, small-sized fruits comprised 51.7%, medium-sized comprised 44% and large-sized fruits were 4.3%. In CF, the proportions of small-, medium- and large-sized fruits were 50.1%, 45.8% and 4.1% respectively. In MH, the proportions of small-, medium- and large-sized fruits were 52.9%, 42.7% and 4.5%,

respectively. The relative proportions of fruits belonging to different size classes varied significantly between CF and MH ($\chi^2 = 16.255$, df = 2, $p < 0.01$).

There was considerable variation in relative proportions of different fruit sizes delivered across different nests. The relative proportions of small-sized fruits ranged from 23%–69%, medium-sized fruits ranged from 17%–73% and large-sized fruits ranged from 0.1%–18%.

In CF, mean (± SE) proportion of small-sized (< 1 cm) fruits was 1.2 times higher in the pre-hatching phase (48 ± 21.3%) than in the post-hatching phase (39 ± 11.3%) (Fig.13). Mean (± SE) proportion of medium-sized (1–3cm) fruits was 1.1 times higher in the post-hatching phase (53.7 ± 12%) than in the pre-hatching phase (49.2 ± 24%). Mean (± SE) proportion of large-sized (>3cm) fruits was 3 times higher in post-hatching phase (7 ± 3.2%) than in pre-hatching phase (2.2 ± 2.2%).

In MH, mean (± SE) proportion of small-sized fruits decreased from pre-hatching (54 ± 5.6%) and the post-hatching phase (39 ± 16%). Medium-sized fruits showed 1.24 times increase in proportions from pre-hatching phase (42 ± 4.9%) to the post-hatching phase (52 ± 17.7%). Proportion of large-sized fruits also increased 2 times from the pre-hatching phase (2.2 ± 1.9%) to the post-hatching phase (8.1 ± 3.7%).

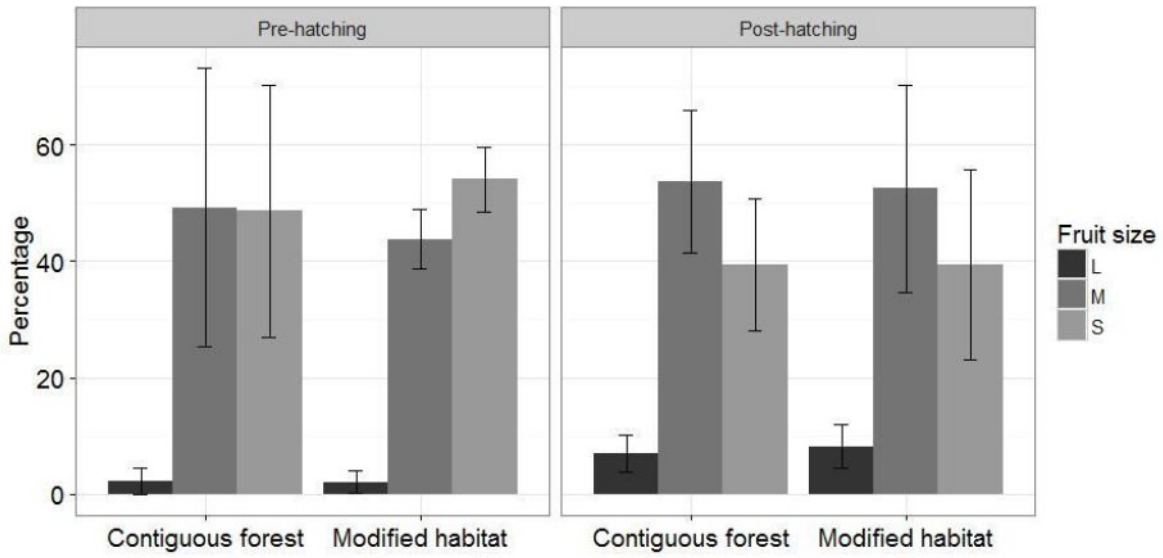

Figure 13. Mean (± SE) proportions of fruits of different size classes (S–small, M– medium, L–large), in hornbill diet of Great Hornbills during pre- and post-hatching phases across nests in contiguous forest and modified habitat in Anamalai hills, Western Ghats.

Of 141 animal matter delivered across eight observed nests, small-sized animal matter comprised 73%, medium-sized animal matter comprised 17.7% and large-sized animal matter were 9.2%. In CF, the proportions of small-, medium- and large-sized animal matter were 77%, 13% and 1% respectively. In MH, the proportions of small-, medium- and large-sized animal matter were 68.2%, 22.7% and 9.1%, respectively. The relative proportions of animal matter belonging to different size classes did not vary significantly between CF and MH (χ^2 = 2.152, df = 2, $p < 0.34$).

There was considerable variation in relative proportions of different sizes of animal matter delivered across various nests. The relative proportions of small-sized animal matter ranged from 40–100%, medium-sized animal matter ranged from 0–50% and large-sized animal matter ranged from 0–40%.

In the CF, during the pre-hatching phase, mean (± SE) proportion of small-sized animal matter in hornbill diet was 2 times higher (95 ± 5.1%) than in the post-hatching phase (49.8 ± 13.3%) (Fig.14). Mean (± SE) proportion of medium-sized animal matter was 8.6 times lower in the pre-hatching phase (3.9 ± 3.9%) than in post-hatching phase (33.7 ± 16.6%) (Fig.14). Mean (± SE) proportion of large-sized animal matter was 12.7 times lower in the pre-hatching phase (1.3 ± 1.3%) than in post-hatching phase (16.5 ±12%) (Fig. 14).

In MH, during pre-hatching phase, mean (± SE) proportion of small-sized animal matter in hornbill diet was 2.1 times higher (90.4 ± 6.6%) than in the post-hatching phase (43.8 ± 15.7%) (Fig. 14). Mean (± SE) proportion of medium-sized animal matter was 8.45 times lower in the pre-hatching phase (3.7 ± 3.7%) than in post-hatching phase (31.3 ± 11.9%) (Fig. 14). Mean (± SE) proportion of large-sized animal matter was 4.2 times lower in the pre-hatching phase (5.9 ± 3.2%) than in post-hatching phase (25 ± 17.7%) (Fig. 14).

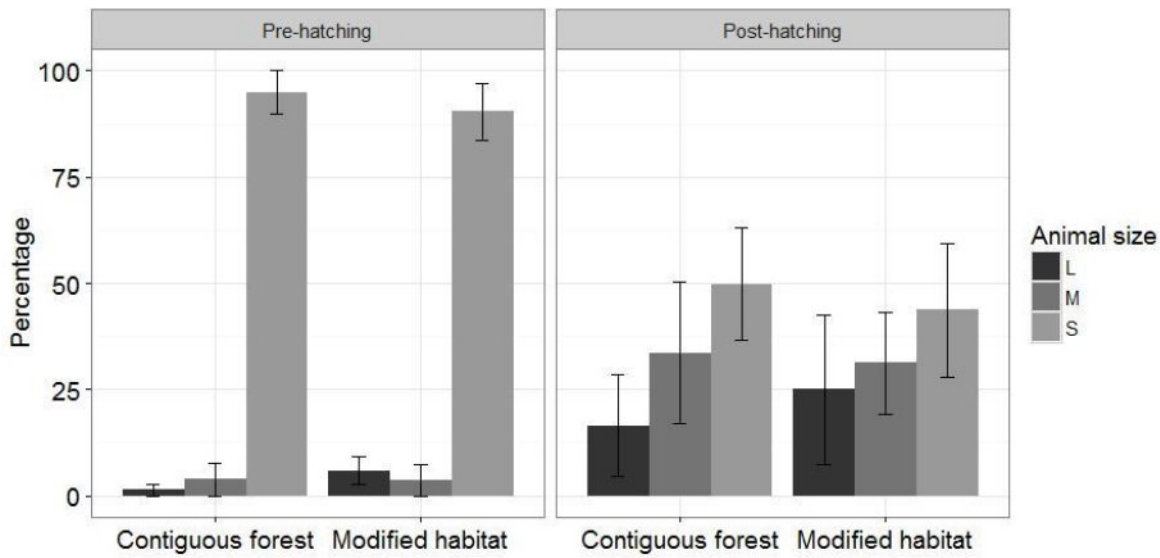

Figure 14. Mean (± SE) proportions of animal matter of different size classes in the diet of nesting Great Hornbills during pre- and post-hatching phases in contiguous forest and modified habitats in Anamalai hills, Western Ghats.

DISCUSSION

As a conspicuous, large-bodied, threatened and wide-ranging bird species of the tropical rainforest canopy, Great Hornbills have posed challenges for research and conservation. Earlier research from the Western Ghats has revealed many aspects of natural history, breeding, behaviour, and ecology of hornbills, but earlier work on hornbill breeding biology has been mostly based on observations at single focal nests (Kannan & James, 1997; Mudappa, 2000). The present study, which aimed to survey ten nests but managed to monitor only eight active nests, builds on earlier research in two significant ways: (a) by documenting variation in breeding biology and nesting behaviour across individual pairs from the westernmost distribution limit of the species; and (b) by expanding the understanding of hornbill ecology and breeding in human-modified habitats. Despite sample size limitations, some key findings include (1) documenting breeding of Great Hornbill in a modified habitat like coffee plantations for the first time; (2) recording a lower diversity of food provisioned in modified habitat than in the contiguous forest; (3) establishing a wide variation in breeding cycle and nest provisioning across individuals; and (4) elucidating nest provisioning pattern of increased nest visitation rate in post-hatching phase with corresponding decrease in food

items delivered – reflecting a trade-off between quantity and quality over the breeding cycle. As the analytical approach was constrained by sample size, I chose a summary descriptive statistics approach with estimation of relevant parameters and basic statistical tests over analytical modelling approach to data analysis.

Nesting success has been demonstrated to decrease in birds nesting in modified habitats as compared to natural habitats (Barber et al., 2001). The present study indicated that Great Hornbills, in spite of having specialized nesting and foraging requirements, were nesting successfully in coffee plantations on the Valparai Plateau. Nesting success in the present study is similar to earlier studies that reported high nesting success of Great Hornbills across its range (Mudappa & Kannan, 1997; Datta & Rawat, 2004; Poonswad et al., 2013; Rane & Datta, 2015). Five active nests of Great Hornbills were found in the coffee plantations, four of which were successful. Only one nest in modified habitat was abandoned for unknown reasons. Hornbills are known to occasionally abandon nests even in primary forests. Earlier studies have reported hornbills using degraded, fragmented and modified habitats (Johns, 1987; Datta, 1998; Marsden & Pilgrim, 2003; Mudappa and Raman, 2009; Naniwadekar, et al., 2015a); and hornbills are also known to breed in degraded forest areas (Rane & Datta, 2015). Here, I report for the first time that Great Hornbills were able to breed in a human-modified landscape of coffee plantations and fragmented rainforests on the Valparai plateau. Certain sites (Anali and Manamboli) within the modified habitat were seasonally important sites for foraging and roosting and they harboured very high densities of both the Great and the Malabar Grey Hornbill. These density estimates are higher than the known density estimates from a wider spatial area on the Valparai Plateau and adjoining forest patches (Raman & Mudappa, 2003; Mudappa & Raman, 2009).

Habitat quality in human-modified habitat was low in terms of tree density, species richness, and hornbill food plant diversity. Other studies in Asian tropics have also demonstrated that anthropogenic factors like logging and land-use conversion causes significant declines in food plant density of hornbills (Datta, 1998; Marsden & Pilgrim 2003). All the nests in modified habitat were located in coffee plantations and forest fragment, none in tea plantations; which suggests that not all monocultures have potential to provide resources for the hornbills. In tea plantation, the canopy is open, small trees are retained for providing shade over tea, thus they lack in presence of large trees. In tea plantations, the canopy is open, small and well spaced trees are retained for providing a sparse shade over tea, and large trees are generally lacking. The main shade tree used in tea plantations is silver oak, which is

not a hornbill food species, and therefore, almost no plant food resources are present in tea monocultures except for very few scattered trees of other species A study in the same area reported low diversity of birds in tea plantations compared to dense and relatively closed canopy plantations like coffee (Sidhu et al., 2010). However, the coffee plantations continued to harbour a significant diversity of native hornbill food plants like *Persea macrantha, Litsea* spp.*, Myristica dactyloides, Dysoxylum binectariferum* and several fig trees. Additionally, some hornbills used two non-native species that have been introduced in the landscape. One of the hornbill nests was in the cavity of *Grevillea robusta*, a tree native to Australia that has been widely introduced in south India as a shade tree. Fruits of *Maesopsis eminii*, a tree native to Africa that has been introduced widely in Valparai Plateau, were extensively eaten by the Great Hornbills, particularly at the onset of the nesting season. *Maesopsis* fruits were delivered at all the nests in human-modified habitat and one nest in the contiguous forest. In Valparai, *Maesopsis* is planted in large numbers as a shade tree particularly in coffee plantations. The presence of *Maesopsis* in Anali and Manamboli likely explains the high density of Great Hornbills at those sites particularly at the onset of the breeding season. Its presence in coffee plantations is likely buffering the otherwise negative consequences of loss of native tree cover in human-modified habitats in Valparai plateau. The juxtaposition of rainforest fragments and relatively large tracts of contiguous primary forests to the modified landscape in Valparai Plateau, in conjunction with no hunting pressures plays an important role in facilitating the use of modified landscape for breeding by the Great Hornbills. The average distance of the nest in modified habitat from the closest forest patch was about 2km. The presence of forest fragments and forests in the vicinity thus likely allows the Great Hornbill to access resources from these undisturbed forest patches.

The variation in nesting duration of the Great Hornbill across all the monitored nests was consistent with the known duration of Great Hornbill from other sites in Asia (Poonswad et al. 2004). The visitation rates of the adult bird/s at the nest significantly increased in the post-hatching phase as compared to the pre-hatching phase. This can be explained by the visitation of both the male and female at the nest in the post-hatching phase, unlike the pre-hatching phase where only the male visits the nest and the female is incarcerated inside. Interestingly, though the visitation rates increased in the post-hatching phase, the mean food delivery rates were lower (but not statistically significant) in the post-hatching phase. This is likely because for a significant duration (4 weeks) in the post-hatching phase fruits for only the chick has to be delivered at the nest as the female leaves the nest. Additionally, unlike in the pre-hatching

phase, the mean proportions of fruits that were lipid-rich and which were larger in size were higher as compared to the pre-hatching phase which points towards the trade-off between quality and quantity of food items that are delivered at the nest. The lowered fruit delivery rate in the post-hatching phase has been reported earlier by Kannan & James (1997). Contribution of animal matter in the diet of Great Hornbills was low and is consistent with findings from other studies on Great Hornbill across its range (Datta, 2001; Poonswad et al. 2004). In this study, the relative contribution of figs was almost 70%, which is similar to that reported in other studies across the Great Hornbill range (Datta, 2001; Poonswad et al. 2004). In the modified habitats, Great Hornbills were able to visit and deliver food items at rates similar to those in the contiguous forests. Great Hornbills in modified habitats are able to source diverse array of fruits. They were also able to deliver fruit items (like lipid-rich fruits) that generally occur in lower abundances even in natural habitats in relatively high proportions. The high proportion of lipid-rich diet in modified habitat could be attributed to a non-native tree species, *Maesopsis eminii*. However, dietary overlap between modified habitat and contiguous forest was 57%; but the relative proportions of common food items provisioned were similar. This indicates that in modified habitat, Great Hornbills are able to provision a diet similar to that in contiguous forest comprising of shared species, which made up a large portion of the diet, but excluded the rare species which even in the contiguous forest did not make up a large portion of the diet. This is likely enabled by the presence of native trees in the coffee plantations and proximity of rainforest patches to the nest. As Great Hornbills are known to range over large distance and track patchily available fruit resources, they can potentially access the resources from the adjoining forests which were found to be at 2km distance from the nests in modified habitat. Sulawesi Red-knobbed Hornbills (*Aceros cassidix*), in degraded and isolated forest patches, were found to track resources from a contiguous forest (Kinnaird et al., 1996); and such large distance foraging is mainly associated to exploitation of patchily distributed figs (Naniwadekar et al., 2015). Also, hornbills showed strong preference for foraging in areas of high resource availability (Whitney & Smith, 1998). This could explain the high hornbill densities estimated in this study are due to abundance of food trees and adjoining larger contiguous tracts of forest.

CONSERVATION IMPLICATIONS

Anamalai hills have been identified as one of the important hornbill conservation areas in the Western Ghats (Mudappa & Raman, 2009). This study highlights the importance of Valparai plateau as a breeding site for Great Hornbills. It is important to emphasise that although Great Hornbills seem to be adaptable to the habitat modification, not all kinds of monocultures or plantations are suitable for them. Considering that hornbills show nest site fidelity, retention of large trees, figs, native trees including hornbill food plants could assure the persistence of these birds in the present landscape. In the current context of large-scale habitat conversion in Asian tropics, this study gives insights into the potential of rainforest fragments and modified habitats for conservation of hornbills. For the modified landscapes across Asia, Valparai plateau, in spite of its imperfections, is an example for retaining biodiversity in modified landscapes. In modified landscapes, retention of native vegetation that serve as important food plants or nesting sites for diverse array of animals is important as shown by earlier studies (Sridhar et al. 2008; Sidhu et al. 2010; Prakash et al., 2012). Additionally, retention of sizeable fragments of old growth forests in modified landscapes can supplement the reduced food availability in modified habitats. The presence of large forested areas of Vazhachal Reserved Forest and Anamalai Tiger Reserve probably play a crucial role in sustaining significant hornbill populations in the adjacent modified landscape. In Valparai Plateau, the matrix of rainforest fragments are potentially serving as bridges in otherwise depauperate and rather homogeneous modified habitats, highlighting the need for identifying and retaining such crucial hotspots in modified landscapes. In the context of hornbills, while this study showcases the ability of hornbills to breed successfully in modified habitats, it is important to understand how modified habitats also influence the movement patterns and home ranges of hornbills, particularly in the breeding season, and understanding the relative contributions of rainforest patches.

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Appendix 1. Summary of the sampling effort and the estimated parameters for the Great Hornbill across the two Manamboli in Valparai Plateau, Tamil Nadu.

Details	**Anali**		**Manamboli**		**Over**
	Pre-nesting	**Post-nesting**	**Pre-nesting**	**Post-nesting**	**Pre-n**
Number of surveys	4	4	4	4	8
Number of points	36	36	35	36	71
Model	Half-normal	Uniform	Half-normal	Uniform	Half-
Adjustment term	Cosine	Cosine	Cosine	Cosine	Cosin
Number of clusters Detected	55	7	15	14	70
Average cluster size	1.8 (0.18)	1.2 (0.10)	1.8 (0.18)	1.2 (0.10)	2.0 (0
Detection probability (SE)	0.33 (0.06)	0.48 (0.13)	0.33 (0.06)	0.48 (0.13)	0.33 (
Effective radial distance, metres (SE)	85.6 (7.7)	103.5 (14.6)	85.6 (7.7)	103.5 (14.6)	85.6 (
Encounter rate (detections/point)	0.95	0.28	0.33	0.22	0.64
Encounter rate % CV	39.4	40.9	45.1	39.5	32.6
Individual density (per km^2) (SE)	73 (32.4)	10 (4.8)	26 (12.7)	8 (3.7)	49 (1
% CV	44.5	50.5	49.6	49.3	38.6
95 % CI	29-182	4-26	9-72	3-21	23-10

Appendix 2. Summary of the sampling effort and the estimated parameters for the Malabar Grey Hornbill across and Manamboli in Valparai Plateau, Tamil Nadu.

Details	**Anali**		**Manamboli**		**Overa**
	Pre-nesting	**Post-nesting**	**Pre-nesting**	**Post-nesting**	**Pre-n**
Number of survey	4	4	4	4	8
Number of points	36	36	35	36	71
Model	Half-normal	Half-normal	Half-normal	Half-normal	Half-n
Adjustment term	Cosine	Cosine	Cosine	Cosine	Cosin
Number of clusters detected	7	10	15	36	22
Average cluster size (SE)	1.83 (0.18)	1.7 (0.13)	1.83 (0.18)	1.7 (0.13)	1.57 (
Detection probability (SE)	0.2 (0.04)	0.12 (0.25)	0.2 (0.04)	0.12 (0.25)	0.19 (
Effective radial distance (SE)	65.78 (7.7)	50.95 (5.6)	65.78 (7.7)	50.95 (5.6)	65.8 (
Encounter rate	0.2	0.28	0.4	1	0.29
Encounter rate % CV	70.35	27.84	28.57	20.41	30.4
Individual density estimate (SE)	26 (19.61)	59 (21.31)	53 (20.05)	212 (65.36)	39 (15
% CV	19.61	36.15	20.05	30.8	39.61
95 % CI	5.96-115.43	28.45-122.12	24.37-112.92	115.04-391.46	18.16-

Appendix 3. Mean (± SE) of the overall tree density/ha, native tree density/ha, basal area (m^2/ha), hornbill food plant density/ha and hornbill native food plant density/ha, around each nest across contiguous forests (CF) and modified habitats (MH) in Anamalai hills, Western Ghats.

Nest code	**Area sampled (ha)**	**Tree density/ha**	**Native tree density/ha**	**Basal area (m^2/ha)**	**Food-plant density/ha**	**Native food plant density/ha**
CF-1	1	285 ± 40	285 ± 40	35.9 ± 7.0	81 ± 1	81 ± 1
CF-2	1.1	365 ± 26	365 ± 26	45.5 ± 7.4	111 ± 2	111 ± 2
CF-3	1.2	290 ± 42	290 ± 42	51.7 ± 8.4	86 ± 1	86 ± 1
MH-1	1	383 ± 70	129 ± 19	48.1 ± 10.7	304 ± 6	44 ± 12
MH-2	1.2	289 ± 55	235 ± 66	28.6 ± 4.3	100 ± 4	100 ± 47
MH-3	1.2	115 ± 21	60 ± 17	24 ± 4.5	53 ± 1	33 ± 9
MH-4	1.1	123 ± 23	69 ± 21	21.3 ± 4.5	36 ±1	21 ± 5
MH-5	1.1	185 ± 32	144 ± 43	35.9 ± 2.9	58 ± 2	32 ± 10

Appendix 4. Nesting cycle of Great Hornbill and the duration of different breeding phases in 2015-16 Anamalai hills, Western Ghats.

Nest code	**Nest monitoring start**	**Nest entry date**	**First time chick seen (days)**	**Fledging date**	**Duration of Nesting cycle (days)**
CF-1	18-Nov-2015	26-Dec-2015	86	18-Apr-2016	114
CF-2	05-Feb-2016	05-Feb-2016	46	13-Jun-2016	129
CF-3	15-Dec-2015	15-Dec-2015	93	16-Apr-2016	123
MH-1	29-Oct-2015	17-Dec-2015	75	15-Apr-2016	120
MH-2	02-Feb-2016	*NA*	50*	28-Apr-2016	106*
MH-3	18-Oct-2015	24-Dec-2015	82	17-Apr-2016	115
MH-4	18-Jan-2016	29-Jan-2016	NA	28-Mar-2016	59
MH-5	18-10-2015	10-Dec-2015	86	18-Apr-2016	130

Note: *- exact date of nest occupation not known thus these are estimated range and values, NA- data not available.

Appendix 5. Visitation and food delivery rates in pre- and post-hatching phases for each Great Hornbill nest in 2015-16 in Anamalai hills, Western Ghats. (n indicates number of focal nest watches (days) carried out at each nest).

Nest code	Pre-hatching phase n (days)	Visitation rate (per hr) Mean (±SE)	Food delivery rate (per hr) Mean (±SE)	Post-hatching phase n (days)	Visitation rate (per hr) Mean (±SE)	Food delivery rate (per hr) Mean (±SE)
CF-1	5	0.50 (± 0.03)	12 (± 8.3)	5	0.82 (±0.07)	8 (± 2.6)
CF-2	1	0	0	5	0.53 (±0.10)	35 (± 8.9)
CF-3	7	0.54 (±0.07)	66 (± 16.7)	4	0.56 (±0.10)	9 (± 7.3)
MH-1	6	0.54 (±0.10)	38 (± 6.9)	4	0.92 (±0.20)	36 (± 15)
MH-2	NA	NA	NA	6	0.69 (±0.08)	27 (± 11.4)
MH-3	7	0.47 (±0.03)	31 (± 4.3)	4	0.63 (±0.17)	12 (± 7.3)
MH-4	7	0.47 (±0.08)	12 (± 5.6)	1	0.81	0
MH-5	8	0.56 (±0.06)	24 (± 7.3)	5	0.82 (±0.05)	16 (± 8)

Note: For MH-2, data was not collected (NA) during pre-hatching phase.

Appendix 6. Summary of diversity of Great Hornbill diet during breeding season across eight nests monitored in Anamalai hills, Western Ghats.

Food Diversity	CF-1	CF-2	CF-3	MH-1	MH-2	MH-3	MH-4	MH-5
Fruit species detected	10	5	11	8	6	10	5	7
Genus	7	4	7	5	4	6	3	5
Families	5	4	6	5	4	5	3	4
Vertebrates	4	3	3	1	1	3	0	2
Invertebrates	3	3	2	1	4	1	1	2

Appendix 7. Number fruits of different plant species provisioned by Great Hornbills across eight nests monitore observations in 2015-16 in Anamalai hills, Western Ghats.

Rank	Species	Family	CF-1	CF-2	CF-3	MH-1	MH-2	MH-3	MH
1	*Ficus microcarpa*	Moraceae	475	543	1923	1709	807	696	108
2	*Ficus nervosa*	Moraceae	564	0	494	153	49	366	387
3	*Persea macrantha*	Lauraceae	179	0	66	156	165	192	389
4	*Maesopsis eminii*	Rhamnaceae	0	0	198	276	0	205	0
5	*Ficus exasperata*	Moraceae	538	39	67	56	0	146	97
6	*Syzygium* sp.	Myrtaceae	0	579	0	0	0	0	0
7	*Litsea oleoides*	Lauraceae	43	106	44	0	0	32	53
8	*Ficus* sp. 3	Moraceae	0	0	257	54	0	0	0
9	*Knema attenuata*	Myristicaceae	80	0	181	11	0	8	8
10	*Cassine glauca*	Celastraceae	0	0	265	0	5	0	0
11	*Ficus racemosa*	Moraceae	0	0	0	0	163	102	0
12	*Trichilia connaroides*	Meliaceae	29	0	0	97	2	0	0
13	*Tabernaemontana* sp.	Apocynaceae	48	0	33	0	0	21	0
14	*Myristica dactyloides*	Myristicaceae	0	11	8	37	10	23	0
15	*Cinnamomum malabathrum*	Lauraceae	57	6	0	0	0	0	0
16	*Ficus* sp. 2	Moraceae	0	0	0	0	0	0	0
17	*Ficus* sp. 1	Moraceae	56	0	0	0	0	0	0
18	*Dysoxylum binectariferum*	Meliaceae	0	0	0	0	54	0	0
19	*Ficus* sp. 4	Moraceae	0	0	22	0	0	0	0
20	Non-fig sp. 1	Unknown	0	0	0	0	0	13	0

Appendix 8. Diversity of animal matter provisioned by Great Hornbills during nesting season of 2015-16 in Ana

Rank	Animal kinds	Group	CF-1	CF-2	CF-3	MH-1	MH-2	MH-3	MH-4	MH
1	Insects	Arthropod	10	0	1	0	3	0	8	0
2	*Calotes* sp.	Reptile	1	1	4	1	2	1	0	1
3	Stick insect	Arthropod	0	1	0	0	10	0	0	0
4	Rat	Mammal	1	3	1	0	0	1	0	2
5	Caterpillar	Arthropod	0	0	0	0	0	0	0	7
6	Moths	Arthropod	4	0	0	0	0	0	0	0
7	Bird chicks	Bird	0	0	0	0	0	3	0	0
8	Eggs	Eggs	0	0	0	0	3	0	0	0
9	Flies/Moth	Arthropod	0	3	0	0	0	0	0	0
10	Skink	Reptile	2	0	0	0	0	0	0	0
11	Snake	Reptile	1	1	0	0	0	0	0	0
12	Mantis	Arthropod	0	0	0	0	0	1	0	0
13	Toad/ frog	Amphibian	0	0	1	0	0	0	0	0
14	Other invertebrates	Arthropod	4	1	35	1	6	0	0	3

PLATE 1: Male hornbill at a nest in modified habitat in Valparai plateau.

PLATE 2: Female hornbill perched on a branch

PLATE 3a: Hornbill fledgling

PLATE 3b: Female hornbill sealing the nest entrance after occupying the nest.