Habitat determinants of nest-site selection by Indian Grey Hornbill *Ocyceros birostris* in an urbanized landscape in Aligarh, Uttar Pradesh, India

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Abstract

We studied nest-site selection by the Indian Grey Hornbill *Ocyceros birostris* in the urban landscape of Aligarh, Uttar Pradesh, during the breeding season from March to July 2022. A total of 21 active nests were documented across five focused intensive study sites. These nests were distributed among 11 tree species. The majority of nesting sites were found on *Eucalyptus tereticornis* (33%), followed by *Holoptelea integrifolia* (10%), *Delonix regia* (9%), *Cassia fistula* (9%), and *Azadirachta indica* (9%). All identified nests were located on living trees. Although *Eucalyptus tereticornis* had the highest number of nests, statistical analysis did not reveal a significant selection for any specific tree species. Multivariate Principal Component Analysis (PCA) revealed that the Indian Grey Hornbills preferred larger trees with greater height and girth at breast height (GBH), located in habitats with higher tree density, diversity, and richness. Shrub cover played only a secondary role, it still exhibited a modest positive association with nest-site selection, possibly because the additional cover and microhabitat complexity offer supplementary benefits. Moreover, we found no significant differences between nest-centered and random plots regarding their proximity to human habitation or roads, underscoring the hornbill's adaptability to urban environments. To support Indian Grey Hornbill populations in urban environments, we recommend preserving and planting native fruit-bearing trees to secure year-round food resources, installing and maintaining artificial nest cavities within green corridors.

Introduction

Hornbills are among the principal frugivores and play a crucial role in seed dispersal (Kitamura 2011; Naniwadekar et al. 2021). Their extensive daily foraging movements in search of fruiting trees enable them to contribute significantly to long-distance seed dispersal, which in turn enhances seed germination and facilitates forest regeneration—processes vital for maintaining ecosystem health and biodiversity (Balasubramanian et al., 2011; Holbrook et al. 2002). As secondary cavity nesters, hornbills rely on naturally occurring hollows or cavities created by primary cavity-excavating species, such as woodpeckers. This dependence makes the availability and selection of suitable nesting sites a critical factor in determining their reproductive success (Kemp 1995; Datta & Rawat 2004; Kasambe 2011). Nest-site selection thus becomes a fundamental component of hornbill's reproduction (Ali & Ripley 1983; Holt & Martin 1997; Losin et al. 2006; van Eerden et al. 2025). During the breeding season, the female seals herself inside the nest cavity and relies entirely on the male to supply food throughout the incubation period and early stages of chick rearing (Kemp 1995; Kitamura 2011; Naniwadekar et al. 2021).

For successful breeding, the nest site must provide protection from predators, maintain optimal thermal conditions for incubation, and lie close to adequate food resources. Both natural and anthropogenic factors that reduce the availability of suitable nesting sites can severely impact reproductive success (Poonswad et al. 1987; Kinnaird & Brend 1999). Conversely, when these resources are abundant, species like the Indian Grey Hornbill *Ocyceros birostris* (hereinafter, IGHO) achieve remarkably breeding success (Santhoshkumar & Balasubramanian 2010; Charde et al. 2011). Therefore, choosing an appropriate nesting site plays a vital role in ensuring breeding success (Ali & Ripley 1983; Holt & Martin 1997; Losin et al. 2006).

Several key factors influence this selection, including the presence of fruiting trees and the availability of suitable nesting cavities. Limited nesting options and ongoing habitat degradation driven by human activities and natural disturbances, further constrain breeding success (Poonswad 1995; Kinnaird & O'Brien 1999). Yet, some unusually adaptive hornbills like IGHO that readily forage in orchards and ornamental plantings, switch to cavities in dead trees, nest boxes, or even concrete walls, and supplement their diet with anthropogenic foods when fruit is scarce (Gadikar 2017). In urban landscapes, where human interference is strongest, securing adequately sized cavities still limits reproduction and may curb local population viability (Datta & Rawat 2004). Similarly, in fragmented forests where large cavity-bearing trees are scarce, competition for nest sites intensifies, underlining the pivotal role of nest-site availability (Wiebe 2011).

The IGHO is the most common and widely distributed hornbill species in India. It occurs in urban areas, rural areas, as well as wooded habitats (Kasambe 2011). Despite its abundance, the species has received limited focused research compared to other Indian hornbills, especially in the context of nesting ecology in urban environments. Although various studies have explored the breeding biology, nest-site selection, and nest tree use of other hornbills (Mudappa & Kannan 1997; Datta & Rawat 2004; James & Kannan 2009; Santhoshkumar & Balasubramanian 2010), this species remain understudied.

We examined the features that enable IGHO to breed successfully in human habitations and the factors that sustain their urban populations within Aligarh, Uttar Pradesh, India. Although rapid development is reshaping the landscape, this adaptable species seems to prosper where three resources coincide: (i) fruit-bearing avenue and orchard trees that provide food year-round, (ii) cavities in mature trees or in man-made structures that substitute for natural nest hollows, and (iii) tolerant human attitudes that minimise direct persecution (Datta & Rawat 2004; Charde et al. 2011; Gadikar 2017). By identifying the specific combinations of food trees, cavity types, and neighbourhood characteristics that predict nest occupancy, our study offers practical guidance for sustaining and even enhancing IGHO populations in increasingly urbanised landscapes.

Hornbills are exceptionally long-lived, field and ex-situ records indicate reproductive lifespans exceeding two decades (Kozlowski et al. 2015); hence, even modest annual gains in fledging success can translate into substantial lifetime reproductive output that can sustain healthy populations.

Study Area

Aligarh District is located in the northern Indian state of Uttar Pradesh (27.483°N–28.017°N, 77.483°E–79.667°E) and spans an area of approximately 3,650 sq. km. It is positioned between two perennial rivers, the Ganga and the Yamuna. Aligarh experiences a monsoon-driven climate with three primary seasons: winter (November to February), summer (late March to June), and the rainy or monsoon season (July to October). Winter nights can be as cool as 10°C, while summer temperatures may peak to 44°C. The district has a high population density, with 1,007 people per sq. km, totalling around 3.6 million residents as per the 2011 Census of India (Government of India 2011).

We conducted this study from March 2022 to July 2022, during the breeding season of the IGHO, thus covering the entire summer months and early monsoon (Ali & Ripley 1983; Santhoshkumar & Balasubramanian 2010). The urban landscape of Aligarh city is characterized by a mosaic of historical buildings, residential quarters, academic institutions, and green spaces with mature trees, which provided an ideal setting to study this species. Based on a preliminary field survey, five sites were selected for intensive study: Aligarh Fort, Naqvi Park, Tar Bungalow Road, and the Engineering and Zoology compounds. (Fig. 1). We selected these sites for their diverse habitat features (Table 1), enabling a comprehensive assessment of the nesting preferences and habitat utilization patterns of the IGHO in an urban environment.

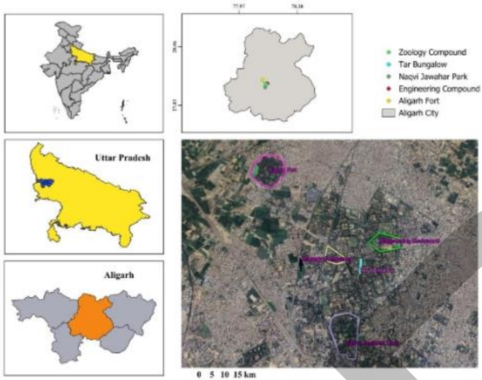

Fig 1. Map of the study area

Table 3: Intensive study site with key habitat features within the study area

Intensive Study Site	Area (in ha)	Key habitat features	Rationale for selection
Aligarh Fort	17.0	A walled heritage complex dominated by mature avenue plantings of flora, Human use is light and mainly diurnal, creating a low-disturbance refuge within the urban matrix.	Represents mature, cavity-rich refuge within the urban matrix
Zoology compound	3.0	Compact academic enclave with double-row plantings of *Polyalthia longifolia*, *Eucalyptus tereticornis*, and *Dalbergia sissoo*.	High anthropogenic disturbance during the day time.
Tar Bungalow Road	10.0	Linear roadside habitat flanked by government bungalows. Avenue trees include large *Ficus religiosa*, *Millingtonia hortensis*, and *Eucalyptus* spp.	Linear corridor linking residential blocks—tests use of roadside avenues
Engineering compound	7.5	Mixed-use campus with lecture blocks interspersed with lawns and remnant groves of *Tectona grandis, Delonix regia*, and *Roystonea regia*.	Constant anthropogenic pressure
Naqvi Park	25.0	A municipal park comprising mature remnant woodland and artificial pond. Floristics are diverse	Highest fruit bearing trees

Methodology

Nest finding

As IGHO depend on tree cavities for nesting, we conducted an extensive search for nest cavities during a single breeding season, from March to July 2022 (Ali & Ripley 1983). Typically, females become incarcerated in mid to late March, and chicks emerge between mid-July and early August (Santhoshkumar & Balasubramanian 2010; Charde et al. 2011).

We located a total of 21 nests within the study area by tracking parent birds or solitary males, inspecting potential trees for cavities, and identifying middens accumulations of regurgitated seeds and faecal matter beneath active nests (Datta & Rawat 2004; Santhoshkumar & Balasubramanian 2010).

Cavities frequently visited by breeding pairs were marked as nesting sites and later confirmed by the presence of incarcerated females. Each nest site was assigned an alphanumeric code, consisting of the abbreviation "N" for nest, the site number, and the intensive study area where it was located. For example, "10NNP" refers to nest number 10 in Naqvi Park (NP).

We adhered to the guidelines outlined in *Indian BIRDS* by Barve et al. (2020) to record all nest-related parameters. These included the GPS location, the tree species for each nesting tree, tree phenology, girth at breast height (GBH), tree height from the ground, canopy cover, nest strata, height from the ground, and distance of each nesting tree from human habitation and nearby roads. During our visits to monitor active nests, we ensured that we maintained an appropriate distance to avoid disturbing the species. To further minimize any potential disruption, we avoided visits during early morning hours.

Nest-habitat sampling

To assess the habitat characteristics influencing nest-site selection by IGHO, we compared the utilized (nest-centered) plots with available (random) plots using the circular plot method. In total, 63 plots were sampled; 21 nest-centered plots and 42 random plots, with two random plots placed 50 m away from each nest-centered plot. Tree species were recorded in 10 m radius plots, and shrub species were documented within a 3 m radius subplot. Tree canopy cover was measured using a 25 × 25 cm gridded mirror divided into 5 × 5 cm sections. At four random locations per plot, the mirror was held 1.25 m above the ground, and grids with over 50% foliage were counted to calculate tree cover percentage (Mudappa & Kannan 1997; Datta & Rawat 2004; Ilyas 2014). Ground cover was estimated using the point intercept method, wherein a meter tape was laid in four directions, and materials such as vegetation, litter, and bare ground were recorded at 5-cm intervals (Ilyas 2014). In each plot, we recorded the species of trees along with their density (count/plot), height, GBH, and canopy cover (Datta & Rawat 2004; Santhoshkumar & Balasubramanian 2010). Additionally, shrub species, their count, and height were noted within a 3 m radius subplot. GBH was measured by fully encircling the tree trunk at 1.37 m height using a measuring tape. Furthermore, we documented the distance of each nest-centered and random plot from the nearest road and human habitation. Finally, a comparison between nest-centered and random (non-nest) plots was conducted to identify the key habitat parameters influencing nest-site selection by IGHO.

Analysis

Data preparation: We applied square root transformation to continuous variables and arcsine transformation to percentage data in order to enhance the normality of the dataset prior to conducting statistical analyses. To identify the habitat variables influencing nest-site selection, we employed both univariate and multivariate approaches. As an initial step, we performed univariate independent sample t-test using IBM SPSS software (Norusis 1990) to assess significant differences in habitat variables between nest-centered plots (n = 21) and random plots (n = 42). This preliminary analysis enabled us to filter out non-informative variables and retain only those showing statistically meaningful group differences. Subsequently, we included these variables in Principal Component Analysis (PCA)[1], thereby improving the clarity, interpretability, and ecological relevance of the extracted components in explaining nest-site selection patterns.

Nest-habitat Principal Component Analysis (PCA): Out of 17 recorded habitat variables, we selected 13 for PCA to examine factors influencing nest-site selection by the IGHO across 63 sampling plots, including both nest-centered and random plots. We excluded highly autocorrelated variables—specifically, tree species, number of tree individuals, shrub species, and number of shrub individuals—to avoid redundancy in the analysis. We applied the Kaiser-Meyer-Olkin (KMO) test and Bartlett's test of sphericity to assess sampling adequacy and data suitability for PCA. We conducted PCA using SPSS software, applying Varimax rotation (Norusis 1990) to extract independent components that represent key ecological gradients. Our primary objective was to reduce data dimensionality and identify variables that explain the greatest variation in nest-site selection. Accordingly, we retained only those components with eigenvalues greater than 1, as they accounted for a substantial proportion of the variance, while discarding those with lower eigenvalues due to their limited explanatory power. Within each retained component, we considered variables with factor loadings $\geq \pm 0.70$ to be ecologically significant (Eni et al. 2012). Additionally, we performed a Chi-square goodness-of-fit test to evaluate whether IGHO exhibited statistically significant preferences for specific tree species when selecting nest sites.

We calculated tree and shrub densities in each sampling plot using the formula: Density = Number of individuals / Unit area. We quantified species diversity and richness using the Shannon-Wiener Diversity Index (H′) and Margalef's Richness Index, respectively, and carried out these analyses in PAST 3 software.

Results

We identified a total of 21 nesting trees, with IGHO utilizing 11 different tree species for nesting **[1, 2]** out of the 86 tree species recorded in and around the Aligarh Muslim University campus (Parveen & Ilyas 2017). Results from the independent sample t-test indicated significant differences in tree density, diversity, richness, height, GBH, and canopy cover between nest-centered and random plots (Table 2).

[1] A male hornbill feeding a brooding female nested inside a cavity on the *Bombax ceiba*. Photo: (Aeiman Hafeez)

[1] Principal Component Analysis (PCA) helps reduce many related variables into fewer, easier-to-understand patterns or gradients.

[2] A female searching for an appropriate nest-site on *Eucalyptus tereticornis.* Photo: (Aeiman Hafeez)

Table 2: Results of independent t-Test between nest-centred plots and random plots
*= $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant ($p \geq 0.05$)

Habitat variables	Nest-centered plots	Random plots	t-value
Tree species	1.8±0.08	1.62±.04	2.03*
No. of individuals	2.38±0.12	2.12±0.08	1.76ns
Tree Density	9.60±0.50	8.23±0.31	2.42*
Tree Diversity	1.16±0.04	1.03±0.03	2.129*
Tree Richness	1.29±0.06	1.13±0.04	2.067*
Mean GBH (m)	1.40±0.04	1.23±0.03	3.1**
Mean Tree height(m)	4.49±0.11	3.59±0.12	4.66***
Shrub species	1.18±0.08	1.12±0.07	0.496ns
No. of individuals	1.83±0.20	1.65±0.16	0.735ns
Shrub density	15.88±2.26	13.49±1.95	0.799ns
Shrub diversity	0.81±0.03	0.81±0.03	-0.188ns
Shrub richness	0.80±0.03	0.81±0.03	-0.201ns
Shrub height	1.19±0.07	1.06±0.06	1.307ns
Canopy cover (%)	39.40±2.40	27.13±1.86	3.921***
Shrub cover (%)	23.89±4.56	20.39±3.26	0.621ns
Distance from human habitation (DFHH)	5.76±0.48	7.35±0.53	-2.219
Distance from road (DFR)	9.95±1.39	10.90±0.85	-0.617

The highest number of nests were observed in *Eucalyptus tereticornis* (33%), followed by *Holoptelea integrifolia* (10%), *Delonix regia* (9%), *Cassia fistula* (9%), and *Azadirachta indica* (9%). The remaining tree species had only one nesting tree each (Fig. 2).

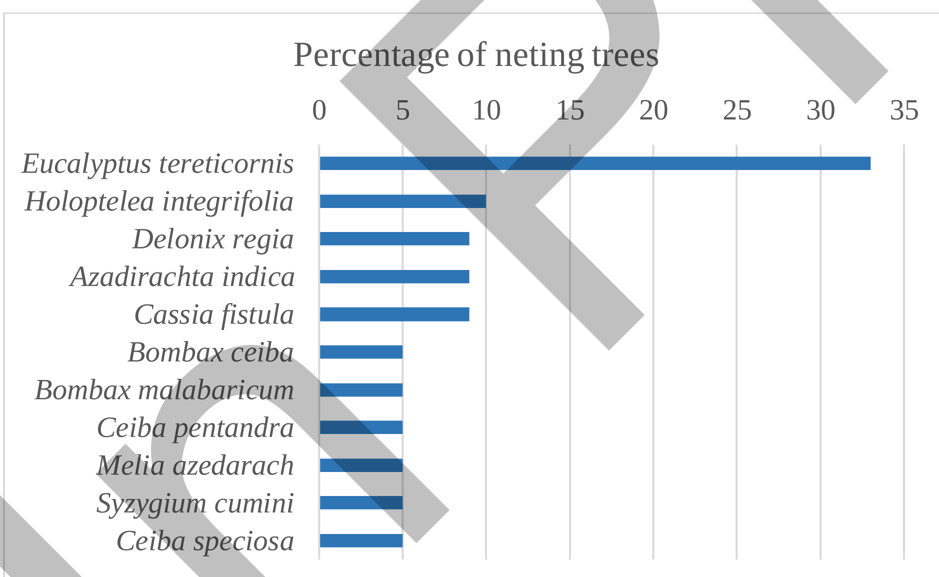

Fig. 2. Distribution of tree species used by Indian Grey Hornbill for their nests in Aligarh city, Uttar Pradesh, India

Most nests (67%) were located in the middle stratum of trees, with 24% in the lower and 9% in the upper stratum, indicating a preference for nesting in the middle canopy layer.

PCA further elucidated the habitat variables influencing nest-site selection. The first four principal components (PCs), each with eigenvalues greater than 1, collectively accounted for 79.87% of the total variance. PC I exhibited strong positive correlations with tree density ($r = 0.849$, $p < 0.01$), tree species diversity ($r = 0.967$, $p < 0.01$), and species richness ($r = 0.948$, $p < 0.01$), explaining 33% of the variance with an eigenvalue of 4.29. Subsequently, PC II showed positive correlation with shrub density ($r = 0.773$, $p < 0.01$), shrub height ($r = 0.875$, $p < 0.01$), and shrub cover ($r = 0.754$, $p < 0.01$) comprising about 26.65% of the variance with (3.465) Eigenvalue loading (Fig. 3). The third component (PC III) accounted for about 12%

variance and is positively correlated with shrub diversity ($r = 0.898$, $p < 0.01$) and Shrub richness ($r = 0.907$, $p < 0.01$) with (1.592) Eigenvalue loading. PC IV had two positively correlated variables GBH ($r = 0.941$, $p < 0.01$) and Tree height ($r = 0.898$, $p < 0.01$) accounted for about 7.97% total variance with (1.036) Eigenvalue (Table 3). Although *Eucalyptus tereticornis* supported the highest number of nests (7 out of 21), chi-square analysis indicated no statistically significant preference for any particular tree species [$\chi^2 = 16.19$, df = 10, $p > 0.05$].

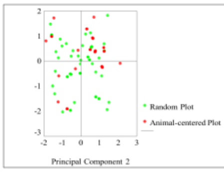

Fig. 3. Ordination diagram from principal component analysis of the nest sites selection by Indian Grey Hornbill based on nest-centred and random plots.

Table 3: Results of Principal component analysis
Variables ≥ ±0.70 are considered significant and are underlined.

Habitat Variables	PC1	PC2	PC3	PC4
Tree density	0.849	0.005	0.298	0.124
Tree diversity	0.967	0.103	0.076	0.049
Tree richness	0.948	0.114	-0.003	0.058
GBH	-0.094	0.029	-0.139	0.941
Tree height	0.239	-0.091	-0.065	0.891
Shrub density	0.177	0.773	0.507	-0.064
Shrub diversity	0.096	0.345	0.898	-0.089
Shrub richness	0.084	0.334	0.907	-0.091
Shrub height	0.163	0.875	0.124	-0.071
Canopy cover	0.195	-0.341	0.393	0.528
Shrub cover	0.082	0.754	0.435	0.039
DFHH	-0.387	0.463	0.065	-0.354
DFR	-0.383	0.448	0.152	-0.314
Eigenvalue	4.29	3.465	1.592	1.036
Variance (%)	33.001	26.653	12.248	7.97
Cumulative variance (%)	33.001	59.654	71.902	79.871

Discussion

This study provides important insights into the nesting ecology of the IGHO. We documented 21 nests across five intensive study sites, all of which were located in live trees—an observation consistent with earlier findings for other hornbill species by Madge (1969), Kemp (1976), Hussain (1984), and Poonswad et al. (1987). Although we initially recorded one nest in a dead tree, it was destroyed during a thunderstorm and therefore excluded from the analysis. Parveen & Ilyas (2017) recorded 86 tree species on the Aligarh Muslim University campus, of which IGHO used only a small fraction (12 %) for nesting. No single tree emerged as statistically preferred even though *Eucalyptus tereticornis* accounted for the largest share of cavities. This absence of species-level selectivity suggests that hornbills exploit whichever large, cavity-bearing trees remain available, reinforcing the need to retain structural diversity rather than focusing on any one "favoured" species. Furthermore, rather than exhibiting species-specific preferences, hornbills appeared to select trees based on structural attributes—particularly taller trees with larger girths—that may offer more suitable nesting cavities. Additionally, hornbills likely favoured commonly available tree species, such as *Eucalyptus*, perhaps due to the scarcity of natural cavities suitable for nesting (Poonswad 1995). As one of the most frequently occurring and structurally suitable tree species across all five study sites, *Eucalyptus* likely met the cavity and size requirements of the species.

Our analysis demonstrates that IGHO do not choose nest sites at random. Trees that supported active nests were significantly taller, thicker, and embedded in stands with greater stem density, species richness, and diversity than control trees, whereas distances to roads and houses did not differ between nest-centred and random plots. One pair even bred in an *Azadirachta indica* cavity just 3 m from a human dwelling and a paved road, confirming that this species can tolerate intense human activity provided structural requirements are met. Similar plasticity in selection of nesting sites has been recorded elsewhere: hornbills in Nagpur nested on street trees within bustling markets (Kasambe 2020), and a pair in Indore in Madhya Pradesh successfully reared young inside a cavity that had formed in a concrete boundary wall (Gadikar 2017). Across sites, therefore, nest-site occupancy appears to be governed primarily by cavity suitability and the local abundance of fruit-bearing trees rather than by a fixed buffer distance from people. These observations, together with earlier work in forested landscapes (Datta & Rawat 2004; Charde et al. 2011), support a two-component framework for hornbill persistence in human-modified habitats: (i) a structural filter, in which nests are restricted to cavities of adequate size, depth, and micro-climate; natural or man-made, and (ii) a forage filter, in which year-round fruit supply and low hunting pressure allow adults to maintain body condition during the prolonged nesting cycle (Mudappa & Raman 2009). Habitat management planning that preserves large cavity-bearing stems, incorporates artificial hollows into mature trees and safe built structures, and retains a diverse mix of native fruiting species should enhance breeding opportunities for this adaptable hornbill in rapidly urbanising landscapes.

PCA revealed that nest tree height and GBH were the primary factors contributing to variation in nest site characteristics. While shrub density, height, diversity, and richness also showed a positive correlation with nest plots, their role appears supplementary, potentially influencing the microhabitat around nest sites. A diverse and dense shrub layer may enhance habitat complexity and stability, indirectly supporting nest site suitability by offering concealment and attracting a wider range of prey items such as insects and small vertebrates, which hornbills are known to consume during the breeding season (Fitzsimons 2019).

The importance of nesting site availability is further emphasized by von Haartman (1957), who noted that for cavity-nesting birds, the number of suitable tree cavities can limit breeding opportunities. In our study area, *Eucalyptus* trees, due to their considerable height and broad girth, likely provide potential nesting cavities. This aligns with findings by Mudappa & Kannan (1997) and Santhoshkumar & Balasubramanian (2010), who observed a preference among IGHO for large, mature trees with wide trunks when selecting nest sites.

Despite increasing urbanization and habitat degradation, our study suggests that the IGHO can persist in urban landscapes like Aligarh, provided certain ecological requirements are met. Specifically, the presence of large trees with broad GBH, along with high density and diversity of fruiting, nesting, and roosting tree species, appears to support hornbill populations in such modified environments. Furthermore, at broader spatial scales, population indices corroborate our site-level observations. The *State of India's Birds 2023* assessment lists the IGHO in the "rapid-increase / stable" category nationally and documents stable trends in Uttar Pradesh as well as long-term increases in Delhi and Uttarakhand (SoIB 2023). These trajectories reinforce our conclusion that, even under intensive urbanisation, IGHO persist and can expand where two ecological conditions are satisfied: (i) the continued presence of large, cavity-bearing stems (or suitable artificial hollows) and (ii) a high local density and diversity of fruit-, nest-, and roost-bearing tree species.

Hornbills remain vulnerable to habitat loss and certain human-induced pressures. While the importance of large trees is well established, our results also highlight the need for further investigation into the role of shrubs in nest-site selection. Although shrub density and diversity were positively associated with nest plots, these features were relatively evenly distributed throughout the study area. As obligate frugivores, hornbills play a vital role in seed dispersal and forest regeneration, acting as ecological engineers within their habitats. Therefore, conserving remnant forest patches and promoting urban green spaces with a diverse and dense tree structure is essential not only for the survival of hornbills but also for maintaining ecosystem processes. In turn, the continued presence of hornbills can contribute to the ecological integrity of these landscapes.

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