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Nest-site selection and nesting success of three hornbill species in Arunachal Pradesh, north-east India: Great Hornbill *Buceros bicornis*, Wreathed Hornbill *Aceros undulatus* and Oriental Pied Hornbill *Anthracoceros albirostris*

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Summary

Nest-site selection by the sympatric Great Hornbill *Buceros bicornis*, Wreathed Hornbill *Aceros undulatus* and Oriental Pied Hornbill *Anthracoceros albirostris* was investigated in a lowland tropical forest in Arunachal Pradesh, north-east India during 1997–2000. Information on two nests of Rufous-necked Hornbill *Aceros nipalensis* in higher-elevation forests is also presented. All species nested in live trees of three tree genera, 83% ($n = 36$) in *Tetrameles nudiflora*, an emergent deciduous softwood, relatively common in lowland foothill forests. No difference was recorded in nest-tree species or nesting habitats of sympatric hornbills, but there were a few differences in structural characteristics of nest-trees. Cavity size was the main variable separating the three species. Great Hornbills used larger cavities while Oriental Pied Hornbills used smaller cavities closer to riverine areas. Nesting was attempted at 64% of known sites and successful fledging of chicks was 80% overall ($n = 72$ nests, pooled over 4 years). Nest-trees in disturbed habitats near human habitation were used but were often abandoned or unsuccessful and 50% of all nest-trees were inactive by the end of the study. Potential large nest-trees had a density of 5.9/ha, that of the two most used species was 1.3/ha, and minimum nest densities of all three species was about 1 pair/km^2. Interference competition for nest-sites was not observed, despite similarity in nest-tree characteristics, low nest density and high loss of nest-trees. Nest-site availability may naturally limit hornbill populations in the area, and additional loss of nesting habitat to human activities may exacerbate limited availability of breeding sites.

Introduction

Hornbills do not excavate their own nest-cavity so selection of suitable nest-sites is critical to breeding success. Competition for cavities and/or loss through natural or human activities further constrains breeding. There have been numerous studies on the nesting biology of Asian hornbills (Poonswad *et al.* 1987, Poonswad 1995, Kinnaird and O'Brien 1999). In India, nest-site selection and breeding biology of Great Hornbill *Buceros bicornis* and Malabar Grey Hornbill *Ocyceros griseus* have been studied in detail in the Western Ghats, southern India by Kannan (1994) and Mudappa and Kannan (1997) respectively.

We determined nest-site characteristics for sympatric Great Hornbill, Wreathed Hornbill *Aceros undulatus* and Oriental Pied Hornbill *Anthracoceros albirostris* in Arunachal Pradesh, north-east India. These species occur mainly in the lowland foothill forest, a habitat of limited extent in this hilly state, easily accessible to and under severe pressure from humans. Most hornbill species are threatened and vulnerable in varying degrees, because of traditional hunting, recent accelerated habitat loss and modification due to logging, shifting cultivation and clearing of land for settlements and agriculture (Datta 1998, Raman 2001). The tropical forests in north-east India have an assemblage of five hornbill species, all of which are listed in Schedule I of the Indian Wildlife Protection Act (1972) (Anonymous 1994): Great Hornbill, Rufous-necked Hornbill *Aceros nipalensis*, Wreathed Hornbill, Oriental Pied Hornbill and Brown Hornbill *Anorrhinus austeni*. Rufous-necked Hornbill is listed as Rare in the IUCN Red Data Book (1990), and among the 10 globally threatened hornbill species (Collar *et al.* 1994), while Great Hornbill and Brown Hornbill are listed under the Lower risk/Near-threatened category (IUCN 1990, Collar *et al.* 1994).

Although traditional analyses of resource selection has been carried out under a univariate framework (Neu *et al.* 1974, Byers *et al.* 1984, Robb *et al.* 1996, Walsh and Harris 1996), recent work (Conner and Adkisson 1976, 1977, Madhusudan and Johnsingh 1998) has used multivariate analyses to examine resource selection (including nest selection) more realistically by considering the interacting effects of several independent and correlated variables.

We used univariate and multivariate analyses to identify variables that determine nest-site selection and contribute to differences in sites chosen by the three sympatric hornbill species. Nesting success and nest-tree loss over the study period are also discussed in the light of natural and man-induced causes of nesting failure and abandonment. The identification of nest-tree species, location and structural characteristics of nest-trees selected by hornbills may help in conservation of these species.

Study area

The study was conducted in Pakke Tiger Reserve (862 km^2, 92°36′–93°09′E and 26°54′–27°16′N) in East Kameng district of western Arunachal Pradesh. The park is surrounded by contiguous forests and delineated by rivers in the east, west and north. Numerous small rivers and perennial streams drain the area. The terrain is hilly, with altitude ranging from 150 m to over 2,000 m above sea level. The central and northern part of the park is relatively inaccessible due to the dense vegetation and hilly terrain. Hunting, fishing and collection of cane and other minor forest products is more common towards the southern boundary.

The area has a tropical climate, with cold weather from November to February. October and November are relatively dry months. The area receives rainfall from the south-west monsoon (May–September) and the north-east monsoon (December–April). The average annual rainfall is 2500 mm, mean (± SD) maximum temperature was 29.3°C ± 4.2 and the mean minimum temperature was 18.3°C ± 4.7 (1983 to 1995, Tipi Orchid Research Centre). May and June are the hottest months.

The general vegetation type of the entire tract is Assam Valley tropical semi-evergreen forest 2B/C1 (Champion and Seth 1968). The forests are multi-storeyed and rich in epiphytic flora, woody lianas and climbers. A total of 343 woody species of flowering plants (angiosperms) have been recorded from the foothill areas of the park, with a high representation of species from the Euphorbiaceae and Lauraceae families (Datta and Goyal 1997, Datta 2001). The intensive study site was located in the south-eastern part of the park near the Arunachal Pradesh–Assam border (150–600 m) with less intensive work in other areas.

Methods

Observations were made from March 1997 to July 2000, over four breeding seasons. Nest entry occurs in mid- to late March, with chick emergence from mid- July to early August. Thirty-six nests were located, 19 during intensive nest searches between February and May each year and 17 by offering monetary rewards to local tribals. Most nest-trees were located by following lone males, searching potential trees for cavities, or middens (piles of regurgitated seeds and fecal matter below active nests) or the presence of seedlings of hornbill food plants and old feathers. Two nests were also located by calls heard during watches at nearby nests.

Habitat quantification followed previous methods (James and Shugart 1970, Kannan 1994, Mudappa and Kannan 1997), using a 15 m circular plot (0.07 ha) with the nest-tree as the centre. The nest-tree species was noted, plus all trees of GBH (girth at breast height) ≥ 25 cm. Canopy cover was quantified using a densiometer, taking 10 readings every 5 m (steps) in the four cardinal directions from the nest-tree. The altitude of the nest-site (using an altimeter) and distances to the nearest road, human habitation and river were also noted.

The nest-tree and cavity parameters measured or estimated were: height of nest-tree and of first branch; distance from and height of tallest other tree in plot; extent of emergence of nest-tree; height of cavity from the ground; location (main trunk, primary, secondary or tertiary branch), position (emergent, upper, middle or lower canopy) and orientation of cavity; cavity width and length; girth of nest-tree above any buttress and at nest cavity. The possible mode of cavity formation was also recorded, based on whether the cavity was on a protrusion of an old broken branch or directly on the main trunk or branch, and on the shape of the hole.

Comparisons of random (non-nest) plots with nest-tree plots were made to determine parameters affecting choices by hornbills. Non-nest plots were located 100 m in a random direction from the nest-tree, with the nearest tree of GBH ≥ 80 cm chosen as the centre. Tree density, canopy cover and centre tree parameters were measured as above.

Nest-tree species and nest cavity availability

The availability and density of potential nest-tree species (species that attain large size or are emergents) were assessed from twenty-one 0.25 ha (50 m × 50 m) vegetation plots (5.25 ha). The availability of potential nest cavities on 180 trees was assessed in fourteen 10 m radius circular plots (0.44 ha). All trees were scanned for the presence of cavities; the height of cavities from the ground was recorded.

Nesting status, attempts and success

Twenty-three nests were monitored intensively, 14 were observed at intervals of 1–2 weeks (data pooled for all 4 years), and a few nests were checked twice each season, once to see whether they were active and once at the end of the breeding season. Nesting success was determined by direct observation of a chick fledging or by indirect evidence of success, such as presence of sealing plaster below the nest, activity of the nest until the end of the breeding season, or the presence of the family group (male, female and newly fledged chick) on or in the vicinity of the nest. Re-use of nests by the same or different species in successive years was also recorded, as was the presence of potential competitors or predators at nest-trees.

Data analysis

The non-parametric Mann–Whitney *U*-test was used to determine differences in 15 univariate parameters (6 nest-tree parameters and 9 nesting habitat parameters) between nest ($n = 31$) and non-nest ($n = 21$) plots. Differences among the three hornbill species in 13 nesting habitat and nest-tree parameters were first ascertained using Kruskal–Wallis one-way ANOVA. The Rayleigh test was used to determine whether nest cavity orientation differs significantly from random (Zar 1974, Batschelet 1981).

A multivariate principal component analysis (PCA) was used to ordinate 12 parameters of nest-site selection by hornbills (SPSS/PC + software using Varimax rotation of factors; Norusis 1990), as depicted by a Pearson's correlation matrix where the factor scores incorporate a known fraction of the variation explained by the original variables. One-way ANOVA and post-hoc multiple comparison tests were used to test for differences between these factor scores. Discriminant function analysis (DFA) was then used to determine which variables contributed most to the differences between species (Pielou 1984).

Kolmogorov–Smirnov one-sample tests, along with histograms of frequency distributions, determined that all variables were normally distributed. Twelve variables for 21 nests were used in the analysis. Sample sizes were small, with multi-collinearity and the risk of autocorrelation between variables, but it was felt that the explanatory power of the analysis would be compromised if some of the variables were dropped. DFA was used to explore differences among hornbill species in nest-site selection and which variables were important in discrimination, despite some of its assumptions not being met.

Results

Nest-trees

Thirty-six nest-trees were located of which 11 were Great Hornbill nest-sites (one cut down), 6 were Oriental Pied Hornbill sites (one cut down), 17 were Wreathed Hornbill sites (1 uprooted in a storm, 2 cut down) and 2 were Rufous-necked Hornbill sites (1 old and inactive). Of these, 19 were located in Arunachal Pradesh and 15 in border areas of Assam. Twelve nests were in dense forest, 9 in open forest and 14 in highly degraded edge forest.

Nest-site characteristics

Nest-trees differed significantly from trees at the centre of non-nest plots in size, height, emergence, girth, height of the first branch and large-tree density, but not in canopy cover, distance to tallest tree or overall tree density. Almost all nest-trees were emergent and the tallest tree in the plot (30), with nest holes located only in the upper (91%) and mid-canopy (9%). Cavity orientation was random (Rayleigh test, $r = 0.3437$, $P > 0.05$, $n = 22$ nests) and most holes were located on the main trunk (56%) or in a broken branch off the main trunk (19%). Other nests were located on primary (12.5%), secondary (9%) and tertiary (3%) branches. The shape of the nest-cavity varied from elongated (11 nests) through oval (14) to round (7).

There was overlap in nest-tree species, with *T. nudiflora* most important (30/36 trees) followed by *Ailanthus grandis* (3 trees) for the three lowland hornbill species. The two nests of the highland Rufous-necked Hornbill were in *Terminalia myriocarpa* and *Altingia excelsa.* Structural characteristics of nest-trees differed little among the lowland hornbill species, except in cavity length ($\chi^2 = 9.43$, df = 2, $P = 0.009$) and girth at nest cavity ($\chi^2 = 4.83$, df = 2, $P = 0.08$). Cavity length differed between Great Hornbill and both Wreathed Hornbill ($U = 13$, $P = 0.033$) and Oriental Pied Hornbills ($U = 0$, $P = 0.006$). Wreathed and Oriental Pied Hornbill also differed in girth at nest cavity ($U = 12.5$, $P = 0.034$). Oriental Pied Hornbill nest-trees and nest cavity heights tended to be highest, while Wreathed Hornbill nests tended to be in denser forests and farther from disturbance. Great Hornbill nest holes tended to be more elongated (63.6%) and those of Wreathed Hornbill tended to be oval (53.3%).

Data for a PCA on 12 variables came from 21 nests (seven trees were cut down before measurement and eight could not be measured for all parameters) (Table 1). Four components explained 73.1% of the total variance (Table 2). The first explained 32.3% and was correlated with aspects of nest-tree size (tree height, emergence, girth and cavity height above ground), the second explained 18.2% and was correlated with aspects of remoteness (tree density and distances to road, human habitation and rivers), the third explained 12.6% and was correlated with cavity size (width and length) while the fourth explained 10% and was correlated with tree stoutness (height of the first branch and girth at cavity). Mean first factor scores for each of the three lowland hornbill species indicated that Oriental Pied Hornbill nested higher in taller and larger trees than the other two species. On the second factor, nests of Great Hornbill were in dense, less disturbed forest, of Oriental Pied Hornbill in more open and disturbed habitats, and of Wreathed Hornbill in areas of intermediate disturbance. On the third factor, as the size of the hornbill increased so did the cavity size, from Oriental Pied to Wreathed to Great Hornbill. The relationships among the three species were tested statistically using the factor scores. There was no difference among species in factor scores 1, 2 and 4. There was a significant difference between species in factor 3 (one-way ANOVA, $F = 7.52$, $P = 0.004$). Post-hoc tests showed that the difference was between Great Hornbill and both Wreathed ($P = 0.031$) and Oriental Pied Hornbills ($P = 0.005$).

In a DFA, the first function explained 77.9% of the variance (eigenvalue 2.68) and the second 22.1% (eigenvalue 0.76). The canonical correlation with the first function was 0.85, while the canonical correlation with the second function was

Table 1. Pearson's correlation coefficient matrix between nest-tree variables for four sympatric hornbill species.

	Tree density	Tree height	Height of first branch	Nest-hole height	Girth at cavity	Emergence	Cavity width	Cavity length	GBH	Distance to river	Distance to road	Distance to habitation
Tree density	1.00	0.186	0.446*	0.121	0.203	0.226	−0.437*	−0.161	0.156	0.255	0.725*	0.554*
Tree height		1.000	0.195	0.883*	−0.034	0.604*	−0.034	−0.172	0.466*	−0.054	0.340	0.433*
Height of first branch			1.000	0.123	0.367	0.265	−0.053	−0.071	0.068	0.051	0.315	0.174
Nest-hole height				1.000	−0.341	0.393*	−0.189	−0.135	0.389*	−0.118	0.262	0.321
GBH at cavity					1.000	−0.058	−0.162	0.049	−0.147	0.006	0.333	0.262
Emergence						1.000	0.084	−0.042	0.500*	0.310	0.281	0.285
Cavity width							1.000	0.340	−0.109	0.018	−0.484*	−0.268
Cavity length								1.000	−0.068	0.197	−0.200	−0.204
GBH									1.000	0.214	0.237	0.118
Distance to river										1.000	0.546*	0.362
Distance to road											1.000	0.872*
Distance to human habitation												1.000

GBH, girth at breast height.
*Significant at $P \leq 0.05$.

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Table 2. Summary statistics of the principal component analysis for nest variables of sympatric hornbill species.

Nest-tree variable	Communality	PC1		PC2		PC3		PC4	
		r	*C*	*r*	*C*	*r*	*C*	*r*	*C*
Tree density	0.668	0.113	−0.035	0.657*	0.200	−0.290	−0.105	0.373	0.130
Tree height	0.870	0.903*	0.345	0.053	−0.114	−0.171	−0.046	0.151	0.105
Height of first branch	0.735	0.213	0.089	0.102	−0.129	0.020	0.084	0.824*	0.581
GBH	0.505	0.651*	0.234	0.224	0.069	0.074	0.089	−0.159	−0.140
Nest-hole height	0.815	0.840*	0.315	−0.014	−0.104	−0.318	−0.163	−0.088	−0.066
Girth at cavity	0.697	−0.289	−0.123	0.206	−0.016	−0.006	0.044	0.756*	0.501
Emergence	0.709	0.747*	0.286	0.248	0.028	0.267	0.236	0.135	0.081
Cavity width	0.687	0.073	0.111	−0.392	−0.135	0.727*	0.435	−0.002	0.120
Cavity length	0.536	−0.113	−0.004	−0.017	0.056	0.723*	0.451	0.006	0.052
Distance to river	0.873	0.014	−0.058	0.794*	0.430	0.464*	0.342	−0.167	−0.240
Distance to road	0.962	0.204	0.025	0.890*	0.324	−0.258	−0.071	0.247	−0.001
Distance to habitation	0.713	0.270	0.018	0.733*	0.253	−0.251	−0.077	0.200	−0.005
Eigenvalue		3.879		2.183		1.512		1.197	
% of variance explained		32.325		18.192		12.598		9.973	

r, Pearson's correlation coefficient; *C*, factor score coefficient; GBH, girth at breast height.
*Correlation significant at $P \leq 0.05$.

0.66. Function 1 was most highly related to cavity size and distance to river, while function 2 was related to nest-tree size (Figure 1). Distance to river, cavity length and width were the three most important variables in discriminating

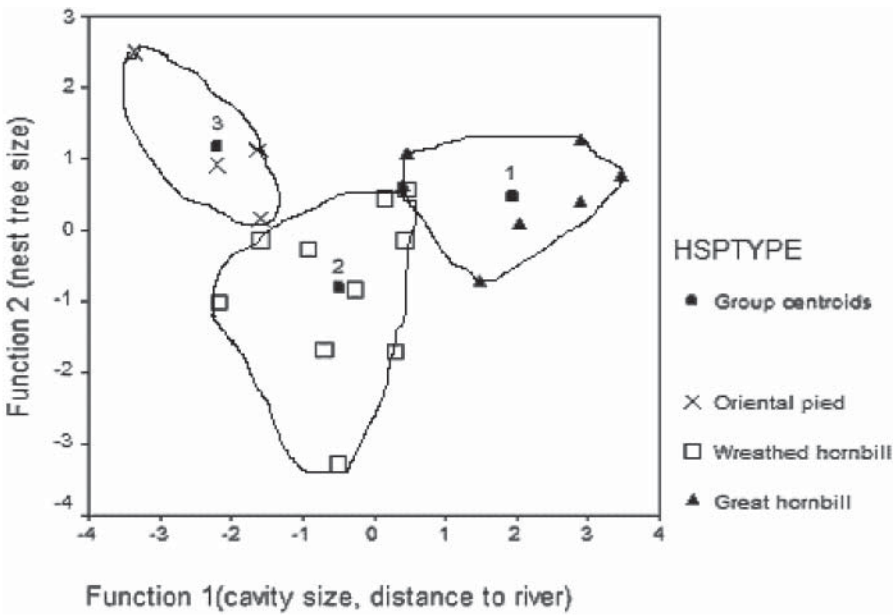

Figure 1. Canonical discriminant functions for hornbill nests that distinguish among the three species. Function 1 was related to cavity size and distance to a river with increasing values from left to right, while function 2 was related primarily to nest-tree size with increasing values from bottom to top.

among the three species. However, the difference between group means was not statistically significant for either of the functions.

Potential nest-tree species and cavity availability

A list of tree species in the study area large enough to contain a hornbill nest was compiled (Poonswad 1995, Chimchome *et al.* 1998; Table 3). Of 25 candidate species, only two (*T. nudiflora* and *Ailanthus grandis*) were used for nesting in the study area. Both were emergent softwoods with large girth, relatively common, with *T. nudiflora* the most common. Of 11 other softwood species (Table 3), no large trees of seven species were recorded in the plots; the remaining four combined were uncommon (1.14 trees/ha). Of 25 potential nest species, large trees of 16 species were available at 5.9 trees/ha, with the two recorded nest species comprising 1.33 trees/ha and no large trees of the remaining nine species being recorded in the plots (Table 3).

Of the 180 trees sampled in 0.44 ha, potential nest cavity availability was estimated at 2.3/ha.

Table 3. Potential nest-tree species, tree characteristics and availability for sympatric hornbill species.

Tree species	Tree height	Wood type[a]	Foliage type	Overall tree density/ha	Tree density/ha (GBH ≥250 cm)
Ailanthus grandis[*b]	Up to 40 m	Softwood	Deciduous	1.52	0.19
Altingia excelsa[*b]	18–20 m	Hardwood, but rots easily	Deciduous	2.28	1.14
Alstonia scholaris	Large	Softwood	Evergreen	0.38	0
Amoora wallichi	Middle-sized	Hardwood	Evergreen	7.42	0.57
Artocarpus chaplasha	Large	Moderately hard	Deciduous	0.95	0.19
Canarium resiniferum	Large	Softwood	Evergreen	4.19	0.38
Cinnamommum cecidodaphne	Large	Soft to moderately hard	Evergreen	0.76	0.19
Duabanga grandiflora	Tall	Softwood	Deciduous	0.76	0
Dysoxylum hamiltonii	Large	Moderately hard	Evergreen	0.19	0.19
Garuga pinnata	Large	Moderately hard	Deciduous	2.66	0.19
Garuga gamblei[+c]	Large	Softwood	Deciduous	0	0
Gmelina arborea	Large	Softwood	Deciduous	0.57	0.38
Litsea chinensis	Middle-sized	Moderately hard	Evergreen	1.33	0.19
Mesua ferrea[c]	Large	Hardwood	Evergreen	0	0
Michelia champaca[+c]	Large, tall	Softwood	Evergreen	0	0
Michelia sp.	Large	Softwood	Evergreen	0.57	0
Phobe cooperiana	Middle-sized	Moderately hard	Evergreen	1.33	0.19
Sapium baccatum	Up to 50 m	Softwood	Deciduous	0.19	0
Schima wallichi	Large	Moderately hard	Evergreen	1.71	0.38
Sterculia alata	Large	Softwood	Deciduous	11.62	0.19
Stereospermum chelonoides	Large	Hardwood, no heartwood	Deciduous	4.57	0.19
Terminalia myriocarpa[*+bc]	Very large	Hardwood	Evergreen	0	0
Tetrameles nudiflora[*b]	Up to 50 m	Softwood	Deciduous	1.9	1.14
Toona sp.	Large	Softwood	Deciduous	0.19	0
Vitex pentaphylla	Large	Hardwood	Deciduous	2.47	0.19

GBH = Girth at Breast Height.
[a] Gamble (1985).
[b] recorded nest tree species in plots.
[b] not recorded in plots, but present in area.

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Mode of cavity formation

Eight nest cavities were located in offshoots formed by the breaking of a branch and subsequent heart rot, while 12 were enlarged after initial excavation by a primary cavity-nester such as a woodpecker or barbet. At least eight species of woodpeckers and four species of barbets occur in the area and seem to facilitate formation of cavities suitable for hornbills. Holes formed by woodpeckers are commonly seen on *T. nudiflora*, often several one below the other, and they are known to select softwoods such as *Mangifera*, *Albizzia* and *Erythrina* for excavation (Ali and Ripley 1987).

Nest competitors and predators

A yellow-throated marten *Martes flavigula* was seen below an active nest of Wreathed Hornbill in 1997 and in the vicinity of an inactive Great Hornbill nest-site in 2000. Two monitor lizards occupied a Wreathed Hornbill nest-site in 2000 and hornbills did not nest there that year. Monitor lizards were also seen outside five cavities in *T. nudiflora*, *Pterospermum acerifolium*, *A. grandis* (2) and *G. arborea* trees. Other hole-nesting birds seen using cavities in *T. nudiflora* were Hill Myna *Gracula religiosa* (4 trees), Red-breasted Parakeet *Psittacula alexandri* (3 trees), Broad-billed Roller *Eurystomus orientalis* (1 tree) and Great Slaty Woodpecker *Mulleripicus pulverulentus* (2 trees). Hill Mynas were also seen inspecting cavities of nesting hornbills.

Nesting attempts and nesting success

Eighteen (51%) nest-sites were inactive by the end of the study period, while the rest were still active at the end of the study (Table 4). Of 69 cavities known to have been available during 1997–2000, (excluding broken or cut trees), 48 (70%) were used in nesting attempts, and 21 (30%) were not used. Thirty-seven of 48 (84%) of the attempts were successful (Tables 4 and 5). In 1997, attempts were

Table 4. Loss of hornbill nest-trees due to natural causes and human activities (1997 2000) in Arunachal Pradesh, India.

	Great Hornbill	Wreathed Hornbill	Oriental Pied Hornbill	Rufous-necked Hornbill
Total nests recorded	11	17	6	2
Nest-tree cut	2	4	1	
Nest-tree breakage		1		
Occupation by other animals		1		
Nest-entrance shrinkage		2[b]		
Repeated human disturbance and degradation of habitat	2[a]	2[b]	1	1?
Cavity flooding	1[a]			
Unknown (nest-floor sinking?)	1	2		1 (very old)
Total nest-trees lost	5	10	2	2

[a]One Great Hornbill Nest was possibly affected by disturbance and cavity flooding.
[b]These two Wreathed Hornbill nests became inactive possibly due to disturbance, but in following years the nest-cavity also shrank, through disuse.

Table 5. Number of hornbill nests located, nesting attempts and nesting success of the three sympatric hornbill species during 1997–2000.

	1997	1998	1999	2000
Total known nests	7	19	21	25
Nesting attempts	4	16	11	14
Successful nests	3	13	9	12
GH nests	2	8	8	8
Nesting attempts (GH)	1	6	6	4
Successful nests (GH)	1	5	3	3
WH nests	4	11	12	13
Nesting attempts (WH)	3	10	4	6
Successful nests (WH)	2	9	3	5
OPH nests	1 old, inactive	None known	1	4
Nesting attempts (OPH)	None known	None known	1	4
Successful nests (OPH)	None known	None known	0	3

GH, Great Hornbill; WH, Wreathed Hornbill; OPH, Oriental Pied Hornbill.

made in 67% of sites ($n = 6$) with 75% successful ($n = 4$). In 1998, 20 attempts were made (85%) and 15 were successful (81%, $n = 15$). In 1999, nesting was attempted at only 59% of sites ($n = 22$), but success was high (82%, $n = 11$). In 2000, attempts were made in 67% of nests ($n = 21$) and success rose to 86% ($n = 14$), despite many nests having become inactive by then.

We tested for differences in tree density and distance to human habitation and roads (indicators of disturbance) between active nests, (whether successful or not) and inactive nests in a given year. There was a significant difference in tree density and distance to habitation between active and inactive nests ($U = 522$, $P = 0.044$ and $U = 531.5$, $P = 0.055$ respectively).

Nesting density

Thirteen active nests of three species were found in the 12 km^2 of the intensive forest study area, a density of 1.08 pairs/km^2. Wreathed Hornbill nesting density was 0.5 pairs/km^2, Great Hornbill 0.33 pairs/km^2 and Oriental Pied Hornbill 0.25 pairs/km^2. Our preliminary observations suggest that nesting habitat of hornbills is likely to be restricted mainly to lowland foothill forests between 150 m to 600 m in this area. At higher elevations in this area there appear to be few suitable nest-tree species, with the result that nesting densities were unlikely to be uniform across the park.

Discussion

Selection for nest-sites

The singular importance of one tree species as a nest-site for hornbills has not been reported in other studies. However, the importance of *T. nudiflora* and other members of the genus as nest-trees for hornbills and other bird species has been reported (Java: Mardiastuti *et al.* 1996, Sumba: Marsden and Jones 1997, Thailand: Chimchome *et al.* 1998, Narcondam: Ravi Sankaran, pers. comm.),

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along with selectivity on a few other tree species (Western Ghats, southern India: Kannan 1994, Thailand: Poonswad 1995, Sulawesi: Kinnaird and O'Brien 1999). On the other hand, in Africa, Kemp (1976) found no selectivity in nest-tree species selected by small *Tockus* hornbills using common trees.

Although tree species was the most important criterion during this study, hornbills also chose trees with particular structural characteristics (tallness, high cavities, commonness, emergence, softwood, agents for easy cavity formation). The nesting habitat around the nest-tree did not seem to be as important as the characteristics of the nest-tree itself. Multivariate analysis showed that most of the variation in nest-site characteristics could be explained by nest-tree size, degree of disturbance and, thirdly, cavity size. The only differences among hornbill species were in selection for cavity size, which was according to body size, as found in Thailand (Poonswad 1995). Discriminant function analysis showed that species differences in cavity size and distance to river were the most important variables in differentiating between the species. The shape of the cavity entrance may also be an important criterion for selection, with Great Hornbill nest entrances more elongated (also noted by Poonswad 1995), Wreathed Hornbill nests more oval, and Oriental Pied Hornbill nests more round.

Nest cavity availability and nesting density

The availability of cavities in this study was estimated at 2.3/ha, compared with 10 cavities/ha reported for Malabar Grey Hornbill (Mudappa and Kannan 1997). The availability of the two most important nest-tree species was 1.3/ha even though the nesting density was only 1 pair/km^2. Cavity and nesting density compares well with just less than 1 pair/km^2 for four sympatric species in Thailand (Poonswad *et al.* 1987), but is lower than the 5.6 cavities/km^2 for Black-and-white Casqued Hornbills *Ceratogymna subcylindricus* in Uganda (Kalina 1988) and the nesting densities of Narcondam Hornbill *Aceros narcondami* (2.8 pairs/km^2, Ravi Sankaran pers. comm.) and Sulawesi Red-knobbed Hornbill *Aceros cassidix* (10 pairs/km^2, Kinnaird *et al.* 1996).

The high degree of overlap among hornbill species and the importance of a single tree species for nests suggest that availability of nest-sites may be a limiting factor, exacerbated by competition from monitor lizards, flying squirrels, wasps, bees, snakes and several other hole-nesting birds. However, the low nesting density relative to cavity and tree species availability suggests that nests are not limiting, although estimates are from a small sample size.

Nest-tree loss and threats to hornbills and their nesting habitat

More than half of the nest-trees were inactive by the end of the study. There was loss of nest-trees due to natural causes such as nest hole shrinkage, occupation by other cavity-dwelling animals and breakage, similar to what Chuailua *et al.* (1998) found in Thailand. Five were lost due to cutting of the nest-tree and eight were abandoned because of human disturbances.

An important finding of this study was that hornbills will nest in logged forests or even degraded forest, though the nesting attempts are usually hampered by human disturbance and unsuccessful. This suggests that hornbills would nest successfully in such marginal habitats if further degradation of or disturbance at the nest-site could be halted. Given the apparent limitation of suitable nesting trees and that hornbills will nest in marginal habitats, it is necessary to widen the scope of conservation plans to include the 70% of forests that occur outside the existing protected area network (national parks and sanctuaries) of Arunachal Pradesh. Special measures for protection of reserve forest areas from habitat loss and degradation will go a long way to ensuring the long-term conservation of hornbills.

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