The Wilson Journal of Ornithology 121(3):485–492, 2009

NESTING HABITAT OF THE GREAT HORNBILL (*BUCEROS BICORNIS*) IN THE ANAIMALAI HILLS OF SOUTHERN INDIA

DOUGLAS A. JAMES[1,3] AND RAGUPATHY KANNAN[1,2]

ABSTRACT.—Anecdotal evidence suggests the endangered Great Hornbill (*Buceros bicornis*) needs mature, large old-growth trees for nesting. We tested this hypothesis by measuring vegetation characteristics at 24 nest sites in southern India and compared these data with that obtained from equal numbers of unused forest sites. Characteristics significantly different from surrounding forest at hornbill nesting sites were several properties related to size of trees. The nesting habitat characteristics of the species stress the importance of mature forests with emergent trees for nests of the Great Hornbill. Trees used by Great Hornbills for nests, compared to unused trees, averaged 18.5 m taller, 0.85 m greater in diameter, and emerged more above the forest canopy by 12.7 m. Canopy height, canopy cover, and number of large trees >75 cm DBH were greater at nest sites than at unused sites by 5.79 m, 3.15%, and 1.63 trees, respectively. *Received 7 February 2008. Accepted 26 January 2009.*

The Great Hornbill (*Buceros bicornis*) is the largest of the nine species of hornbills (Family Bucerotidae) occurring in India (Ali and Ripley 1968). Basic breeding biology and habitat information is available from southern India (Kannan 1994; Kannan and James 1997, 1998, 1999, 2007, 2008; James and Kannan 2007). It is an endangered species (CSE 1982), listed in Schedule I (most protected) of the Indian Wildlife (Protection) Act of 1972 (MOEF 2006) due to being affected by a variety of problems ranging from destruction of its wet forest habitat to poaching of adults and squabs from nests (Ali and Ripley 1968). The bird is ~120 cm long and ~3 kg in mass, and is believed to have the problem of finding large trees with natural cavities sufficiently large to accommodate the nesting female and young during their confinement. Large scale destruction of forests and selective commercial removal of large trees in peninsular India is suspected to have reduced the availability of optimal nesting sites (Ali and Ripley 1968).

Several authors have commented on the apparent highly specialized nesting requirements of the Great Hornbill. The species is widely believed to depend on tall, old growth trees for nesting. The literature is replete with anecdotal references to its dependence on mature forest vegetation (Hume 1890; Bingham 1897; Prater 1921; Baker 1927, 1934; Ali 1936; Ali and Ripley 1968; Kemp 1995). However, systematic studies have not been conducted concerning the bird's habitat. All conjecture concerning the nesting habitat of the species amount to an untested and unproven hypothesis. Some quantitative information on nesting habitat is available from Thailand (Poonswad 1995), but only a few environmental factors were considered in that study, and empirical procedures comparing nest sites to non-used forest sites were not performed. Comparison between used and non-used sites within the same general vegetation type is essential for identifying habitat features associated with forest nesting sites compared to surrounding forest stands (Conway and Martin 1991). One study, (Datta and Rawat 2004), repeated our earlier work (Kannan 1994) and incorporated unused sites but the results combined four species of hornbills.

Cavity-nesting birds often are affected by land management practices (Gysel 1961, Haapanen 1965, Hunter 1990, Conway and Martin 1991, Mudappa and Kannan 1997). Selective removal of large trees in the Western Ghats in India, our study area, could limit populations of large birds such as hornbills by diminishing nesting opportunities. A detailed description of the critical habitat is the first step in any attempts to ameliorate this situation. An examination of habitat factors using multivariate statistics is essential in describing the habitat-niche of an organism (James 1971) since habitat is an important component of the niche of an organism (Hutchinson 1957, Root 1967). Vegetation factors have been used in multivariate procedures to analyze niche-dimensions of birds (Cody 1968, James 1971, Shugart and Patten 1972, Posey 1974, White and James 1978, Rotenberry and Wiens 1980, James 1992).

The objectives of this study comparing nest sites with unused forest sites were to: (1) use

[1] Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA.
[2] Current address: Department of Biology, University of Arkansas—Fort Smith, Fort Smith, AR 72913, USA.
[3] Corresponding author; e-mail: djames@uark.edu

multivariate statistics to test the hypothesis that Great Hornbills use the largest trees for nesting, (2) ascertain forest patch characteristics associated with nest sites, (3) identify nest tree species, (4) obtain information on nest cavity dimensions and related issues, and (5) investigate suitability of the overall forest for accommodating hornbill nests.

STUDY AREA

The study was conducted between 1991 and 1993 in the vicinity of the village of Top Slip (10° 25′ N, 76° 50′ E) in the Indira Gandhi Wildlife Sanctuary, Tamil Nadu State, in the Anaimalais, which are a part of the hills extending along the southwestern coast of peninsular India (the Western Ghats). The sanctuary has a variety of vegetation types ranging from bamboo (*Bambusa arundinaceae*) and open deciduous forests to southern tropical wet evergreen forests (Champion and Seth 1968). The entire Anaimalai range is a vast mosaic of habitats altered for human use such as tea and teak monocultures, hydro-electric projects, and settlements interspersed with a few large and several small patches of fragmented native forests. The study was conducted in the wet evergreen forest habitat the Great Hornbill usually inhabited.

Nests found were widely separated, many kilometers apart, scattered in a vast region extending across the boundaries of two states, Kerala and Tamil Nadu. Areas between nests often exhibited a mosaic of landscapes. Nests were in patches of forest that varied greatly in size.

METHODS

Twenty-four nests of Great Hornbills were found by local tribal people who were rewarded for their efforts with cash payments. Nests were found within an area covering ~300 km^2. A profile of the habitat used for nesting was developed by measuring different vegetation characteristics around each of the 24 nest trees following James and Shugart (1970). Circular vegetation plots measuring 0.07 ha (15-m radius) were established around the nesting tree, and 17 vegetation features were measured within these plots. Four orthogonal transects were established from the center of each plot with the direction of the first transect chosen by the random twist of a compass dial. Color flagging was used to mark transects and center trees. Shrub density was measured by counting the woody stems intersecting a meter stick held at waist height (1 m) along each transect. Ground and canopy cover were measured by making 40 vertical overhead and ground sightings through a tube with cross hairs, and recording the proportion of sightings in which the cross hair point intersected green vegetation (Winkworth and Goodall 1962). Ten sighting points were made at random positions along each of the four transects. Diameter at breast height (DBH) of the center tree was measured using a diameter tape, and diameter size classes (15–30, 31–45, 46–60, 61–75, 76–90, 91–105, and ≥106 cm DBH) of all woody stems (>15 cm DBH) within the circular plot were measured using a Reach Stick (James and Shugart 1970). Average canopy height, height of the center tree and the tallest tree in the plot, height of the lowest limb of the center tree, and height of projection of the center tree above the rest of the canopy (emergence) were measured in meters using a clinometer. Distance of the center tree to the nearest large tree (≥60 cm DBH) was measured by pacing. The center tree was identified to at least genus when possible.

Information recorded for nest trees included: height of the nest cavity (m), distance of the cavity from the nearest branch (m), cavity orientation (compass degrees), diameter of the trunk at the nest (m), and cavity opening width and length (cm). The last three dimensions were estimated due to inaccessibility of nests. Notes or sketches of the shape of the cavity and overall nature of the habitat were also taken. The distance of the nest from the nearest road and settlement was estimated using 1:100,000 Government of India topography maps of the area.

Data gathered from nesting sites were compared to an equal number (24) of samples from unused areas in which a center tree was located at random in the general area of each nest tree. These samples were positioned by starting at the center tree of a nest plot and pacing a distance of 75 m in a direction chosen randomly by twisting a compass dial. The nearest tree at the end of this distance with a DBH ≥20 cm was designated the center tree, and the 17 vegetation characteristics measured at the nest site were measured in a plot centered at the selected tree. We observed that the 75-m distance to the unused area was sufficient to evade the forest structure influence of the nesting sites but remained within the same general forest type. Data were analyzed using univariate analysis of variance (ANOVA), and principal components (PC) and stepwise discriminant function analyses (SAS Institute 1985).

TABLE 1. Analysis of 17 vegetation characteristics in the nesting habitat of Great Hornbills. Underlined values represent significant difference between unused and nest site measurements.

Characteristics	Nesting plot $\bar{x}$	Unused plot $\bar{x}$	P[a]
Shrub stems/60 m^2	60.30	59.65	>0.05
Canopy cover, %	86.08	82.93	>0.05
Ground cover, %	42.60	40.54	>0.05
Average canopy height, m	30.94	25.15	0.019
Tallest tree in the plot, m	44.76	34.12	0.0001
Center tree height, m	43.75	25.27	0.0001
Center tree diameter DBH, m	1.329	0.479	0.0001
Nearest tree >40 cm DBH, m	8.48	8.12	>0.05
Center tree height lowest limb, m	21.75	10.86	0.0001
Center tree emergence, m	12.81	0.12	0.0001
Trees 15–30 cm DBH, *n*	8.29	10.00	>0.05
Trees 31–45 cm DBH, *n*	3.29	3.16	>0.05
Trees 46–60 cm DBH, *n*	1.50	2.04	>0.05
Trees 61–75 cm DBH, *n*	0.75	0.95	>0.05
Trees 76–90 cm DBH, *n*	0.75	0.25	0.0098
Trees 91–105 cm DBH, *n*	0.79	0.25	0.0304
Trees ≥106 cm DBH, *n*	1.20	0.62	0.0153

[a] Univariate Analysis of Variance (ANOVA), nesting vs. unused plots.

RESULTS

Significant characteristics governing Great Hornbill nest habitat selection were those that reflected size and maturity of the nesting tree and its patch of forest (Table 1). Features significantly greater for nest trees used by hornbills compared to center trees at unused sites were nest tree 18.5 m taller, 0.85 m greater in diameter, lowest limb 10.9 m higher, and 12.7 m more in emergence above canopy. Significant factors greater in nest tree plots than unused plots were canopy height 5.9 m higher, tallest tree 10.6 m taller, and large trees >75 cm DBH 1.63 more in number (Table 1). These findings support the presence of larger trees and a more mature lofty forest at the nest site in comparison to the general nature of the surrounding forest.

Principal component (PC) I, accounting for 66% of the total variance, was highly correlated with nest tree height, height of the tallest tree in plot, diameter of the nest tree, height of the lowest limb, and emergence above the canopy of the nest tree (Table 2). These vegetation features were directly related to the size of the center tree. PC I, designated as ''center tree size'', was the most important factor involved in hornbill nest habitat selection. PC II accounted for an additional 18% of the total variance and was highly correlated with shrub density (Table 2). The third factor (PC III), accounted for 6% of the total variance and represented a correlation with ''cover'', both canopy and ground cover interacting inversely. Together, the first three factors accounted for 90% of the total variation (Table 2) in the data set, and represented most of the realized nesting-niche space of the hornbill.

Hornbill nest sites compared to unused forest plots were strikingly separated along the axis representing large tree sizes at the nest site (Fig. 1), but were not separated with respect to the other habitat axes (Figs. 1, 2). This lack of separation of nest and unused sites along the shrub and cover axes indicates these vegetation characteristics were not important in nesting habitat choice by hornbills. Nest plots were positioned distinctly towards the end of the axis representing greater center tree sizes (Figs. 1, 2), whereas the unused area plots were grouped towards the other end of the continuum. Combined, PC I and II accounted for 84% of the total variance, a large proportion of the nesting niche (Fig. 1).

Principal components analysis does not indicate the significance of the differences between nest and unused areas. Thus, stepwise discriminant function analysis was performed resulting in identification of four characteristics that maximize the difference between hornbill nesting and unused sites. These characteristics were center tree height, diameter of center tree, height of the lowest limb, and number of trees in the plot >105 cm DBH; all were greater in value at the nest site. These differences were significant at *P*

TABLE 2. Correlations of vegetation characteristics with the first three principal components for nest data of the Great Hornbill. Underlined values represent high correlations with their respective principal component.

Characteristics	Correlations with principal components I	II	III
Shrub density	0.085	0.992	0.086
Canopy cover	0.128	0.137	0.519
Ground cover	0.326	0.245	−0.887
Average canopy height	0.197	−0.022	0.255
Tallest tree in plot	0.632	−0.029	0.167
Height of nest tree	0.742	−0.100	0.275
Diameter of nest tree	0.998	−0.028	0.011
Distance to the nearest large tree	0.131	0.022	0.04
Height of lowest limb	0.565	0.002	0.156
Nest tree emergence over canopy	0.634	−0.089	0.099
Trees 75–90 cm DBH, *n*	0.169	−0.077	0.335
Trees 91–105 cm DBH, *n*	0.189	−0.150	0.087
Trees >106 cm DBH, *n*	0.320	−0.020	0.185
Total variance, %	66	18	6
Cumulative total variance, %	66	84	90

= 0.0001, 0.0024, 0.0349, and 0.063, respectively, documenting the overwhelming importance of large, old-growth trees and mature forests for hornbill nest-site selection.

Analysis of nest tree size categories compared to those available in unused plots of the surrounding forest (Fig. 3) showed that nest trees were in the large size categories while available trees in the overall forest structure were predominantly smaller in size. However, there were some large trees remaining in the forest suitable for Great Hornbill nests (Fig. 3).

The mean bole diameter at the level of the nest cavity was less than the mean DBH of nest trees, but greater than the DBH of center trees in unused plots (Tables 1, 3). The dimensions of the cavity

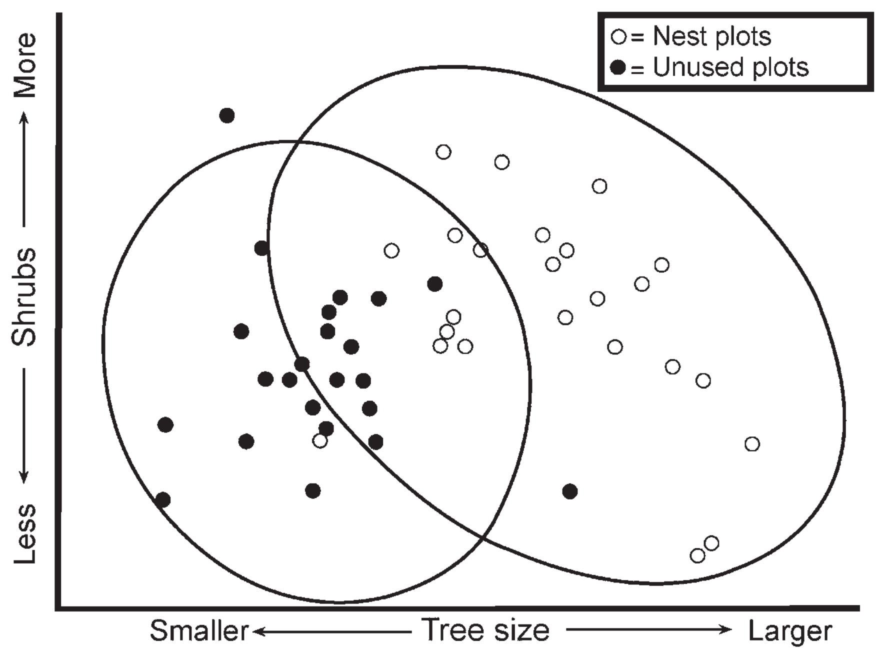

FIG. 1. Ordination with 95% confidence ellipses of nest plots of the Great Hornbill and unused plots based on scores of the first (abscissa) and second (ordinate) principal components.

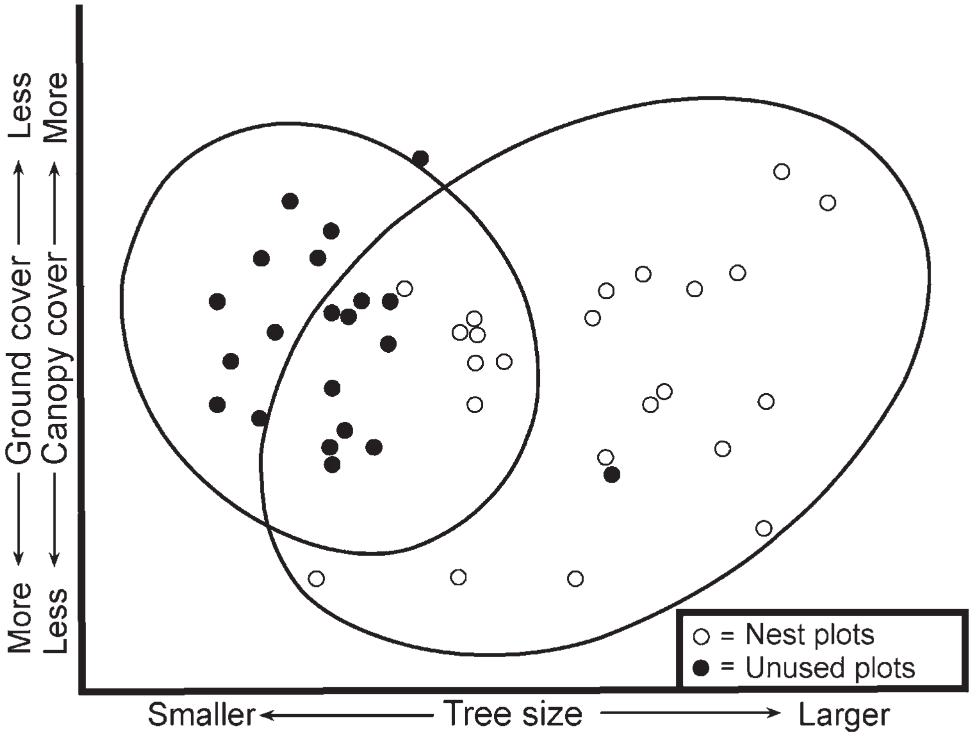

FIG. 2. Ordination with 95% confidence ellipses of nest plots of the Great Hornbill and unused plots based on the scores of the first (abscissa) and third (ordinate) principal components.

entrance demonstrated the propensity of hornbills to choose cavities with a vertical slit entrance. Nest sites were also far from the nearest road and human settlement, the immediate trunk area around the cavities was mostly branchless, and the mean height of the nest cavity from the ground was 22.0 m (Table 3). Eight of the 24 nests (33.3%) were oriented east-south-easterly direction, supporting the hypothesis of nonrandom orientation (X^2 = 11.58, α = 0.05, df = 7). Nests occurred in 12 tree species representing 10 families (Table 4). Six nests were in trees and families that were unidentified.

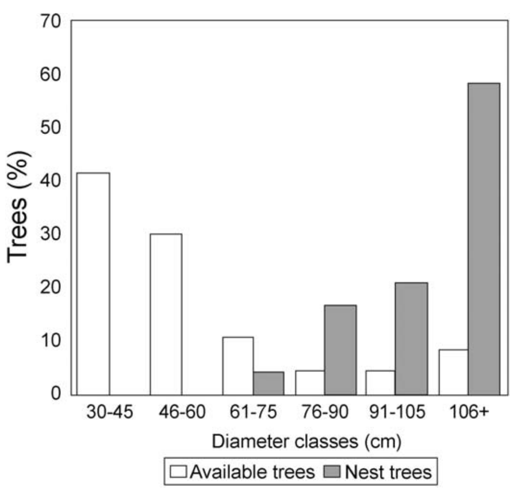

FIG. 3. Percentages of trees (by diameter classes) comparing nest trees (n = 24) with available trees ≥30 cm DBH (n = 177) in the unused plots.

DISCUSSION

Our study provides empirical presentation of the actual nesting habitat of the Great Hornbill based on evidence from multiple plots and measurements comparing nest sites with forest habitats lacking nests. These results support the hypothesis that nest trees of Great Hornbills are large in several dimensions and protrude significantly above the canopy compared to other trees in the forest (Tables 1, 2; Figs. 1, 2). Additionally, the grove of trees around the nest tree also consisted of larger trees than in the overall forest (Table 1). Datta and Rawat (2004), using methods of our previous studies (Kannan 1994, Mudappa

TABLE 3. Specific nest tree characteristics for the Great Hornbill.

Characteristics	*n*	Mean ± SD	Min–Max
Diameter at nest, cm	15	92.6 ± 47.16	50–240
Cavity height, m	24	22.02 ± 6.43	11.21–40
Nearest branch to nest, m	22	2.94 ± 2.36	0–10
Cavity width, cm	24	16.07 ± 5.36	7.5–25
Cavity length, cm	24	35.31 ± 19.6	12.5–100
Distance to nearest road, km	24	2.92 ± 4.19	0.10–20
Distance to nearest settlement, km	24	2.48 ± 1.67	0.5–8

and Kannan 1997), studied the Great Hornbill in northeastern India grouped with other hornbill species. They found that hornbills selected large tall emergent trees for nest trees compared to center trees in non-nest plots, and that the Great Hornbill nested in more dense forests than other hornbills. This replication and confirmation of our big tree hypothesis is a requirement of scientific methodology. However, their analysis combined several hornbill species making it difficult to identify specific nest tree requirements of Great Hornbills or of any of the other hornbill species studied.

Our investigation also compared sizes of nest trees ($n = 24$) in the vast study area with sizes of other trees ($n = 177$) present in forests where nest trees were located (Fig. 3). Tree sizes in the surrounding forest were calculated by summing the tree size categories ≥30 cm DBH across all trees encountered in the 24 unused plots. Percentages of nest trees were in the largest size categories while percentages of trees in the surrounding forests were predominantly in smaller categories. However, there were unused trees in the forest that were nest tree size (Fig. 3). Efforts should be made to preserve these larger trees to serve as future nesting trees for Great Hornbills.

TABLE 4. Tree species with Great Hornbill nests.

Family Scientific name	Number of nests
Lauraceae	
Alseodaphne semecarpifolia	2
Bombacaceae	
Cullenia excelsa	1
Bombax ceiba	2
Combretaceae	
Terminalia bellerica	3
Datiscaceae	
Tetrameles nudiflora	1
Myrtaceae	
Unidentified	1
Guttiferae	
Garcinia sp.	1
Sapotaceae	
Chrysophyllum sp.	1
Palaquium ellipticum	2
Lythraceae	
Lagerstroemia lanceolata	2
Meliaceae	
Aglaia sp.	1
Rhizophoraceae	
Carallia integrimma	1
Unidentified	6

The nesting habitat characteristics of the Great Hornbill clearly show the importance of protecting old growth forest stands with large trees for the conservation of this species. The habitat niche of the hornbill is narrow emphasizing its vulnerability to extinction. Habitat specialization is one of the key factors that make an organism prone to extinction (Terborgh and Winter 1980). The Great Hornbill is a large bodied frugivore, dependent on a fluctuating, patchily available fruit resource, making it vulnerable to extirpation (Terborgh and Winter 1980; Strahl and Grajal 1991; Kannan 1994; Kannan and James 1997, 1999, 2007). Protection of large expanses of old growth forests is important for conservation of the Great Hornbill.

The significant tendency of Great Hornbills in our study to choose nest cavities oriented eastward may be an evolved response protecting from southwest monsoon gusts that blow from the west by May–June near the end of the breeding cycle, when chicks fledge. The selection of a wide variety of nesting trees with no one taxon predominating (Table 4) showed that tree size alone was important (Table 1, Fig 3). Any large tree with a suitable large cavity qualified as a nest tree.

ACKNOWLEDGMENTS

Financial support for field work in India was provided by Ornitholidays (through the Oriental Bird Club, U.K.) and the New York Zoological Society (now The Conservation

Society). Travel grants came from R. Balachander, the Arkansas Andubon Society Trust, and the University of Arkansas. Field work in India was greatly assisted by Divya Mudappa and Gary Neaville. We especially thank the Tamil Nadu Forest Department for permission to work in the forests of the state. T. E. Martin, A. C. Kemp, V. Santharam, J. E. Johnson, and K. G. Smith gave valuable advice during phases of the project. Shekar Dattatri introduced us to the tribal people of Anaipandam and Lorie Livingston helped with plotting the confidence ellipses. The Kadar tribal people of the Anaimalai Hills had a major role in the project by discovering most of the nests.

LITERATURE CITED

ALI, S. 1936. The ornithology of Travancore and Cochin. Journal of the Bombay Natural History Society 39:3–35.

ALI, S. AND S. D. RIPLEY. 1968. Handbook of the birds of India and Pakistan. Volume 1. Oxford University Press, Bombay, India.

BAKER, E. C. S. 1927. Fauna of British India. Second Edition. Volume 4. Birds. Taylor and Francis, London, United Kingdom.

BAKER, E. C. S. 1934. The nidification of the birds of the Indian Empire. Volume 3. Taylor and Francis, London, United Kingdom.

BINGHAM, C. T. 1897. The Great Indian Hornbill in the wild state. Journal of the Bombay Natural History Society 11:308–310.

CENTRE FOR SCIENCE AND ENVIRONMENT (CSE). 1982. The state of India's environment, 1982. A citizen's report. Centre for Science and Environment, New Delhi, India.

CHAMPION, F. C. AND S. K. SETH. 1968. Forest types of India. Government of India, Calcutta.

CODY, M. L. 1968. On the methods of resource division in grassland bird communities. American Naturalist 102:107–147.

CONWAY, C. J. AND T. E. MARTIN. 1991. Habitat suitability for Williamson's Sapsuckers in mixed-conifer forests. Journal of Wildlife Management 57:322–328.

DATTA, A. AND G. S. RAWAT. 2004. 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*. Bird Conservation International 14:S39–S52.

GYSEL, L. W. 1961. An ecological study of tree cavities and ground burrows in forest stands. Journal of Wildlife Management 25:12–20.

HAAPANEN, A. 1965. Bird fauna of the Finnish forests in relation to forest succession. Annales Zoologica Fennici 2:154–196.

HUME, A. O. 1890. The nests and eggs of Indian Birds. Second Edition. Volume 3. R. H. Porter, London, United Kingdom.

HUNTER JR., M. L. 1990. Wildlife, forests, and forestry. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

HUTCHINSON, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

JAMES, D. A. 1992. Measuring shrubland vegetational structure using avian habitats as an example. Proceedings of the Arkansas Academy of Science 46:46–48.

JAMES, D. A. AND R. KANNAN. 2007. Wild Great Hornbills (*Buceros bicornis*) do not use mud to seal nest cavities. Wilson Journal of Ornithology 119:118–121.

JAMES, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bulletin 83:215–236.

JAMES, F. C. AND H. H. SHUGART JR. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

KANNAN, R. 1994. Ecology and conservation of the Great Pied Hornbill (*Buceros bicornis*) in the Western Ghats of southern India. Dissertation. University of Arkansas, Fayetteville, USA.

KANNAN, R. AND D. A. JAMES. 1997. Breeding biology of the Great Pied Hornbill (*Buceros bicornis*) in the Anaimalai Hills of southern India. Journal of the Bombay Natural History Society. 94:451–465.

KANNAN, R. AND D. A. JAMES. 1998. Forest management and the conservation of the Great Pied Hornbill (*Buceros bicornis*) in southern India. Proceedings of the Second International Hornbill Workshop, Bangkok, Thailand.

KANNAN, R. AND D. A. JAMES. 1999. Fruiting phenology and the conservation of the Great Pied Hornbill (*Buceros bicornis*) in the Western Ghats of southern India. Biotropica 31: 167–177.

KANNAN, R. AND D. A. JAMES. 2007. Phenological studies of hornbill fruit trees in tropical rainforests: methodologies, problems, and pitfalls. Pages 155–166 *in* The active management of hornbills and their habitat for conservation (A. C. Kemp and M. I. Kemp, Editors). Proceedings of the Fourth International Hornbill Conference, Mabula Game Lodge, Bela-Bela, South Africa CD-ROM. Naturalists & Nomads, Pretoria, South Africa.

KANNAN, R. AND D. A. JAMES. 2008. Fig trees (*Ficus*), captive elephants, and conservation of hornbills and other frugivores in an Indian wildlife sanctuary. Journal of the Bombay Natural History Society 105: In press.

KEMP, A. C. 1995. The hornbills: Bucerotiformes. Oxford University Press, New York, USA.

MINISTRY OF ENVIRONMENT AND FORESTS, GOVERNMENT OF INDIA (MOEF). 2006. The Indian Wildlife (Protection) Act, 1972, as amended up to 1993. www.envfor.nic.in/legis/wildlife/wildlife1.html (accessed May 2006).

MUDAPPA, D. C. AND R. KANNAN. 1997. Nest-site characteristics and nesting success of the Malabar Gray Hornbill in the southern Western Ghats, India. Wilson Bulletin 109: 102–111.

POONSWAD, P. 1995. Nest site characteristics of four sympatric species of hornbills in Khao Yai National Park, Thailand. Ibis 137:183–191.

POSEY, A. F. 1974. Vegetational habitats of breeding birds in Ozark shrubby old fields. Dissertation. University of Arkansas, Fayetteville, USA.

PRATER, S. H. 1921. Notes on ten young Indian hornbills. Journal of the Bombay Natural History Society 28:550–552.

ROOT, R. B. 1967. Niche exploitation by Blue-gray Gnatcatchers. Ecological Monographs 37:317–350.

ROTENBERRY. J. T. AND J. A. WIENS. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61:1228–1250.

SAS INSTITUTE. 1985. SAS user's guide: statistics. Version 5 Edition. SAS Institute Inc., Cary, North Carolina, USA.

SHUGART, H. H. AND B. C. PATTEN. 1972. Niche quantification and the concept of niche pattern. Pages 283–325 *in* Systems analysis and simulation in ecology (B. C. Patten, Editor). Volume 2. Academic Press, New York, USA.

STRAHL, S. D. AND A. GRAJAL. 1991. Conservation of large avian frugivores and the management of neotropical protected areas. Oryx 25:1.

TERBORGH, J. AND B. WINTER. 1980. Some causes of extinction. Pages 119–133 *in* Conservation biology–an evolutionary-ecological perspective (M. E. Soulé and B. A. Wilcox, Editors). Sinauer Associates Inc., Sunderland, Massachussetts, USA.

WHITE, D. H. AND D. A. JAMES. 1978. Differential use of fresh water environments by wintering waterfowl of coastal Texas. Wilson Bulletin 90:99–111.

WINKWORTH, R. E. AND W. A. GOODALL. 1962. Crosswire sighting tube for point analyses. Ecology 43:342–343.