AN ECOLOGICAL STUDY OF SYMPATRIC HORNBILLS AND FRUITING PATTERNS IN A TROPICAL FOREST IN ARUNACHAL PRADESH

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IN

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BY

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CERTIFICATE

I have great pleasure in forwarding the thesis of Aparajita Datta, titled **"An ecological study of sympatric hornbills and fruiting patterns in a tropical forest in Arunachal Pradesh"** for acceptance of the degree of **Doctor of Philosophy** in **Wildlife Science**. The thesis embodies original findings and interpretation of facts. This research was carried out by Ms. Datta under my supervision, and has not been submitted in part or full to any other University/Institution for the award of any degree.

(G. S. Rawat)
Ph. D. Guide

Dedicated to both my grandfathers
Arun Kumar Datta and Sitesh Roy, who
enriched my childhood

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Goutam Narayan

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SUMMARY

The tropical forests in north-east India have a diverse assemblage of hornbills (Bucerotidae), ranging from the cooperatively breeding Brown hornbills (*Anorrhinus* spp.) to the monogamous and territorial Great hornbill (*Buceros bicornis*). The biology of most of these species remains largely unknown. Hornbills are known to be largely frugivorous, and believed to be important seed dispersal agents in tropical forests. Are all hornbills equally frugivorous? Which fruit or animal species do they feed upon? Where do they nest? How important is their functional role as seed dispersers in the tropical forest habitats in which they occur? Focussing on three sympatric species, the Great hornbill (*Buceros bicornis*), the Wreathed hornbill *(Aceros undulatus*), and the Oriental Pied hornbill (*Anthracoceros albirostris*), in a lowland semi-evergreen forest of Arunachal Pradesh, this study attempted to answer these broad questions about hornbill biology. In addition, the dispersal syndromes of tree species were evaluated, and their patterns of flowering and fruiting examined. The study was conducted in the lowland semi-evergreen forests of Pakhui National Park, western Arunachal Pradesh.

A small proportion of the forest trees in the lowland semi-evergreen forest was found to be wind-dispersed. Flowering and fruiting peaks of these wind-dispersed species were bimodal and coincided with the relatively drier periods in the year. Most tree species (64%) were found to be animal-dispersed. The forest has a diverse array of frugivores, with frugivorous birds possibly being the most important group of dispersers. Plant families such as Lauraceae and Meliaceae that have fruits adapted for dispersal by birds, were especially species rich. In contrast to the wind-dispersed species, flowering of bird-dispersed species occurred throughout the year with no discernible peak. The fruiting peak of these species was unimodal, with most trees fruiting between May-July. Fruit scarcity occurred in the period between September and January (end of monsoon and winter). Most species had fairly synchronous fruit production and most species produced fruits annually, though a palm *Livistona jenkinsiana* showed supra-annual fruiting. One species, *Polyalthia simiarum* had two fruiting peaks and consequently, ripe fruits of this species were available for 9-10 months in a year. Inter-annual variability in overall fruiting patterns was high, while flowering patterns between years were more similar. However, fruiting patterns of bird-dispersed species were similar between years, though there was variation in fruiting intensity with a failure of fruiting of several species belonging to the Meliaceae and Myristicaceae in 1999.

Peak fruit abundance of bird-dispersed species occurred between May and July, which also coincides with the breeding season of resident frugivorous birds such as hornbills, barbets, and hill myna. Compared to wind-dispersed species, the fruit abundance of bird-dispersed species was more uniform, suggesting that there is some degree of staggering of bird-dispersed species that may be driven by competition for dispersers. Null model analysis with a set of 7 bird-dispersed species whose fruiting occurred between February and August showed that fruiting patterns of these species are indeed significantly segregated. But a quantitative test of the hypothesis did not yield a significant negative correlation between similarity in disperser

guilds and similarity in fruit ripening schedules of these species. This, however, does not mean that fruiting patterns are unaffected by dispersers. While climatic factors may be the main force dictating the timing of fruiting at a broad-level, the staggered fruiting pattern detected for a set of bird-dispersed species points to a competitive structuring of fruit ripening times within the limits imposed by climate.

Hornbills consumed 80 fruit species mainly belonging to Lauraceae, Meliaceae, Annonaceae, and Myristicaceae. Fruits formed over 90% of their diet. They are estimated to disperse about one-fourth of the tree species recorded in the area. There is also evidence that hornbills may be the sole dispersers of several large-sized fruits of some Meliaceae, Myristicaceae, and Lauraceae. The quality of seed dispersal by hornbills is high in terms of how they process and handle seeds; hornbill-regurgitated seeds are viable and occasionally do show enhanced germination. The relatively long gut-retention times and the propensity of depositing seeds away from parent fruiting trees while foraging in the forest also suggest quality dispersal. However, seed deposition patterns below nest and roost trees are spatially clumped, compromising the quality of dispersal due to increased seed predation and density dependent mortality. Seed densities as well as seed predation rates at perch trees are much lower than that under nest or roost trees, suggesting that hornbills play a more efficient role as seed dispersers at perch trees. Though seedling density of hornbill food plants below nest and roost trees was very high, suggesting successful dispersal, a high degree of mortality also occurred at the seedling stage. Seedling density of hornbill food species was considerably higher than that of non-food species and it is also significantly higher in front of the nest cavity than at the back of the cavity. But these differences disappear at the sapling stage, by which time further thinning out reduces sapling density by orders of magnitude than those of seedling densities. Roost trees are generally located in open areas near rivers and streams (away from the forest and unsuitable for plant recruitment) and seedlings rarely survived beyond the first year. The comparatively low sapling density and the very low tree density of hornbill food species around roost trees also corroborated this. Seedlings and saplings fare marginally better at nest trees. The patterns of seedling survival below nest, roost and parent trees were not very different. Although seed deposition patterns are clumped at roost trees, part of what hornbills consume is scatter dispersed below perch trees during the day. In the breeding season too, the seed deposition patterns of breeding males and non-breeding adults and juveniles are scattered as they regurgitate and drop seeds over a wider area. Therefore, though overall, hornbills are effective dispersers, the quality of dispersal is relatively poor at nest and roost trees due to the spatially clumped seed rain that results in high seed and seedling mortality.

The breeding season for all the three hornbill species commenced in the dry hot period (March-April) preceding the rainy season. Contrary to what most existing studies have reported, the breeding season did not end before the onset of heavy rains, but, instead, continued through the rainy season (July-August), with both the chick and female remaining incarcerated in the nest cavity through heavy rains. The nesting cycle of the Great hornbill lasted 110-129 days (n = 8), and 120-140 days (n = 9) for the Wreathed hornbill. The nesting cycle of Oriental Pied

hornbill was estimated to be 93-97 days (n = 2), though exact dates of nest entry and sealing could not be observed for this species. The incubation period for the Great hornbill was estimated to be 45 to 55 days, and 40 to 45 days for the Wreathed hornbill. Great hornbill females emerged out of the nest cavity after 88 to 109 days, while in Wreathed hornbill and Oriental Pied hornbill, they emerged together with the chicks, having remained incarcerated throughout the duration of the nesting cycle.

Fruits dominated in the diet of all three species (over 90 % contribution) throughout the breeding season, though animal matter increased marginally in the post-hatching period. A total of 42 plant species and 16 invertebrate and vertebrate species (7 beetle species, two species each of lizard, bird, and rodents, one species of snake, crab, and flying squirrel) were recorded in the breeding season diet of hornbills. Lipid-rich fruits of the Meliaceae, Myristicaceae, Lauraceae, and Annonaceae were especially important in the hornbills' diet. Though a wide variety of non-fig fruit species were eaten, ten species contributed over 90% of the non-fig fruit diet. Although, there were differences in the overall contribution of figs, non-fig fruits and animal matter in the diets of the three hornbill species, there was overlap in the food species consumed. There were no discernible differences in non-fig fruit species consumption among the three hornbill species. Differences in non-fig diet composition were more pronounced between the years. This was possibly due to the differences in relative availability of different fruit species in the 4 years.

Hornbills were recorded to feed on fruits of 49 plant species in the non-breeding season, though the patterns in ripe fruit availability suggested fruit scarcity. Several non-fig species were rare in the lowland habitat and hence there was a seasonal low in ripe fruit availability. However, this did not constrain the hornbills' diet, and they possibly move to higher areas for foraging, during this season. Hornbill species showed some differences in the proportional contribution of figs, non-figs and animal matter in the diets, as well as in the foraging strata used. However, overlap in non-fig fruit species consumed was high and again, ten species contributed to over 90% of the non-fig diet.

All the hornbill species nested only in live trees of five genera. Eighty-three percent of nest trees (n = 36) were on *Tetrameles nudiflora*, an emergent deciduous softwood tree that is relatively common in lowland foothill forests. Several characteristics of this tree species make it an ideal nest tree for hornbills. No significant difference was noted in the nest tree species and nesting habitats used by the three sympatric hornbills, though there were some differences in structural characteristics of the nest trees used. Cavity size seemed to be main variable that separated the 3 species in nest site choice; the Great hornbill used larger cavities than the two smaller species, while the Oriental Pied hornbill used smaller-sized cavities in trees closer to riverine areas. Of the known nest trees, nesting attempts were made in 64%, while overall nesting success (successful chick fledging) over a 4-year period was 80%. Hornbills also used nest trees in disturbed habitats near human habitation, but these nests were often abandoned or unsuccessful. Fifty-one percent of nest trees (n = 36) were inactive at the end of four years,

mainly due to human-related disturbances. The minimum nesting densities of all three species together was about 1 pair per km^2. Despite the high similarity among the three hornbill species in nest tree characteristics, the relatively low nesting density and high loss of nest trees, inter-specific interference competition for nest sites was not observed. Nevertheless, the availability of suitable nest sites may be a limiting factor for hornbill populations in the area. The current rates of loss of nesting habitat in foothill lowland forests to human activities further exacerbate the problem.

Communal roost sites used by hornbills were on isolated deciduous trees either in successional grassland habitats adjoining rivers, or near steep cliff faces and mud banks near small perennial streams. These areas were away from the forests, where hornbills forage and nest. Roost sites shifted periodically, with each site being used up to two months at a stretch. Communal roosting occurred at the same sites in both the breeding and non-breeding seasons. Breeding males also joined the roosting flocks, an observation that has not been reported earlier. The non-territorial Wreathed hornbills roosted in larger numbers than the territorial Great hornbills. The Wreathed hornbills usually arrived at roosts at least half an hour earlier than the Great hornbill, which came in only after sunset. The size of roosting flocks is much larger than diurnal foraging flocks. It is argued that the primary benefit of communal roosting seems to be tied to food-finding and sharing of information and not to other purported benefits such as avoiding predation. Hornbills roost in much larger flocks in the non-breeding season when food resources are scarce. In the fruit-rich breeding season, Wreathed hornbills form relatively smaller aggregations at roost sites and few Great hornbills join communal roosts. An analysis of hornbill species across the world, suggests that the occurrence of communal roosting seems to be related to frugivory and non-territoriality.

Chapter 1. Introduction

Hornbills (Bucerotiformes) are large and conspicuous birds of the tropical forests of Asia and Africa. They are brightly coloured, have loud calls, and characteristically large bills and casques. Due to their predominantly frugivorous diet, hornbills have always been considered important agents of seed dispersal in the tropical forest. The tropical forests in north-east India have a diverse assemblage of hornbills, ranging from the cooperatively breeding primarily insectivorous Brown hornbill (*Annorhinus austeni*) to the monogamous territorial Great hornbill (*Buceros bicornis*). The biology of most of these species remains largely unknown. What do these birds eat? Is their food availability variable in space and time? How do they cope with seasonal lows in food availability? What are their nesting requirements? Where do they roost? What allows several species of hornbills to co-exist in the same forest? Are they indeed efficient seed dispersers? This thesis is amongst the few attempts to understand the biology and ecology of resource partitioning in a sympatric hornbill assemblage. The study sought to address academic questions regarding the evolution of fruiting patterns, seed dispersal and hornbill biology, that have important conservation implications.

Several aspects of the ecology of three sympatric hornbill species, the Great hornbill, Wreathed hornbill (*Aceros undulatus*), and the Oriental Pied hornbill (*Anthracoceros albirostris*) (Plates 1a, 1b) in the lowland tropical semi-evergreen forests of Arunachal Pradesh were studied, including their diets, breeding biology, nesting, and roosting requirements (see Appendix 1 for a brief outline of the study species). The mechanisms that allow these species to co-exist were examined. The community-wide phenological patterns of forest tree species were also examined, and thereby the seasonal highs and lows in food abundance for hornbills and other frugivores identified The dispersal syndromes of forest trees were studied and the importance of biotic and abiotic factors in driving the evolution of fruiting patterns was examined. It was also a major focus of the study to evaluate the role and effectiveness of these hornbills as seed dispersers, an important ecosystem function given the high degree of habitat loss, modification and hunting that has accelerated in recent years in north-east India.

Most studies on hornbills in India that have been conducted so far, have focussed on a single species or mainly examined their breeding biology (Hussain 1984, Kannan 1994, Mudappa & Kannan 1997). None of the species that occur in north-east India, have been studied in India, apart from the Great hornbill in south India (Kannan 1994). Comparative studies on sympatric species provide an understanding of the ecological context of co-existence and resource partitioning.

In this chapter, an overview of hornbill biology is presented with a discussion of their phylogenetic and evolutionary relationships. The distribution of Asian hornbills is presented, and the status of Indian hornbills and threats to their conservation identified. Finally, the organization of the thesis is outlined.

1.1. AN OVERVIEW OF HORNBILLS

Hornbills (Order Bucerotiformes) are confined to the Afrotropical, Indomalayan and Australasian regions. There are a total of 54 recognized species, two ground hornbills in the Bucorvidae family and 52 'true' hornbills in the Bucerotidae. Most hornbills occur in tropical forests; only 13 species occur in more open savannah and woodland habitats, of which 12 are found in Africa and one in India (Kemp 1995).

Hornbills are secondary cavity-nesters like their close relatives, the hoopoes (Order Upupiformes), the trogons (Order Trogoniformes), and the rollers, kingfishers and bee-eaters (Order Coraciiformes) (Kemp 1970, 1976a). They use natural cavities in trees, crevices in rock faces or holes in mudbanks and have a peculiar and unique nest hole sealing habit with the female incarcerated in the nest during the breeding season. She remains there for most of the nesting period, leaving only a thin slit through which the male passes food to her and the chicks (Kemp 1970, 1979, Kemp & Kemp 1972, Smythies 1986). The two ground hornbill species (*Bucorvus* spp.) do not seal the cavity and may even excavate holes (Kemp & Kemp 1980, Kemp 1988a). Hornbills are generally monogamous as a consequence of the dependence of the female and young on the male for food, and the inability of the male to provision two females simultaneously (Leighton 1986). In most species, the female also moults her flight feathers while in the cavity, growing them back while she incubates the egg and broods the chicks, though often there is no moult or only a partial moult (Kemp 1995). Though most species are omnivorous, fruits account for a major part of the diet, especially of Asian forest hornbills (Leighton 1982, Poonswad *et al.* 1983, 1988, Kinnaird *et al.* 1996).

Hornbills attain their greatest diversity in South-east Asian forests. This co-existence is largely possible due to specializations in diet, divergence in size, differences in grouping and spacing behaviour and partly due to diversity of fruits and fruit production patterns in these forests (Leighton & Leighton 1983). Hornbills range in size from the Dwarf Red-billed hornbill (*Tockus camurus*) (111 g) to the Southern Ground hornbill (*Bucorvus leadbeateri*) (4191 g) in Africa. Body size ranges for Asian species, are narrower with the smallest being the Malabar Grey hornbill

(310 g) and the North Sulawesi Tarictic hornbill (*Penelopides exarhatus exarhatus*) (350 g) and the largest being among the *Buceros* genus: Javan Great rhinoceros hornbill (*B. rhinoceros sylvestris*) (3314 g), Helmeted hornbill (*B. vigil*) (3060 g) and Great hornbill (3007 g) (Kemp 1995).

Most hornbill species are highly vulnerable mainly due to their primarily frugivorous diet and the consequent dependence on a resource which may be patchy in time and space, their specialized nesting requirements, and the reported nomadic behaviour of some species (Leighton & Leighton 1983, Poonswad & Tsuji 1994, Suryadi *et al.* 1998) and dependence on large tracts of primary forests. Most species have a prolonged breeding season of up to four months, producing only a few young (one chick for most species and up to 4-5 for some of the smaller species) per season and some species have, in fact, been found to breed once every alternate year (Leighton 1982).

1.1.1. Phylogeny, evolution and biogeography

Hornbills have been considered to be a monophyletic group on the basis of some unique anatomical and morphological features such as the possession of a casque on top of the bill, fusion of the first two neck vertebrae (axis and atlas) that support the skull, presence of an accessory supraoccipital condyle along with the normal basioccipital condyle, bi-lobed kidneys and prominent eyelashes (Kemp 1995 and references therein). The orders that are most closely related to hornbills are the Upupiformes (hoopoes) and the Coraciformes (rollers, kingfishers and bee-eaters) that share several physical, behavioural, anatomical, and morphological features (Kemp & Crowe 1985). Hornbills have in fact, only been separated recently from the Coraciformes into a new order based on molecular studies (Sibley & Ahlquist 1991).

The ground hornbills have now been separated from other hornbills into a separate family, the Bucorvidae, on the basis of 26 characters (Kemp 1995). The two ground hornbills are the earliest surviving offshoots, with fossil evidence from the mid-Miocene in Morocco, some 15 million years ago (Olson 1985 cited in Kemp 1995). There are few fossil records for the remaining hornbill species in the Bucerotidae. The genera can be easily distinguished, but relationships are not clear, and have been the subject of change and debate. While 14 genera were recognized earlier (Sanft 1960), nine are now recognized, though some of these are divided into subgenera to highlight the differences. Based on cladistic analysis, the earliest offshoot appears to be the radiation of the 14 small African *Tockus* species, which are most similar to the hoopoes and woodhoopoes in their biology (Kemp & Crowe 1985). The three

Ocyceros species of the Indian subcontinent are closely related to, and were earlier placed in the *Tockus* genus. The *Ocyceros* again show some affinities with the Indomalayan genus *Anthracoceros*. Some of the larger *Anthracoceros* spp. share similarities with the very large hornbills of the Indomalayan genus *Buceros*. Within the four species of *Buceros*, the Helmeted hornbill is aberrant in being the only hornbill with a solid heavy casque and was earlier placed in a separate genus, *Rhinoplax*. The closest relatives in Africa seem to be the seven medium- to large-sized hornbills (*Ceratogymna*), five of which were earlier in the genus *Bycanistes*. The remaining three genera, *Anorrhinus*, *Aceros,* and *Penelopides* are all Indomalayan and their relationships with other genera are not clear. The least derived are the three *Anorrhinus* species (two species were considered a single species in the genus *Ptilolaemus*). *Anorrhinus* show their closest affinity with the two other Indomalayan genera, *Aceros* and *Penelopides*, in having distinct adult female plumage. There are five small species of *Penelopides* in the Philippine islands and the 11 larger *Aceros* (of which nine were previously placed in the genus *Rhyticeros* and one in the genus *Berenicornis*) are more widespread.

Evolutionary pathways of hornbills have been determined from three main sources: 1) the distribution and relationships of the host-specific parasitic feather-lice (*Mallophaga*) found on hornbills. The evolution and speciation of the lice parallel that of their avian hosts closely and thus can be used to discern relationships (references cited in Kemp 1995), 2) DNA analysis from different species (Sibley & Ahlquist 1991), 3) comparison of the number and structure of chromosomes. The DNA analysis also largely supports the branching pattern suggested by cladistic and parasitic analysis (Kemp 1979, 1988b, Kemp & Crowe 1985), though all genera have so far not been analysed. Chromosomal studies have only been carried out for a few hornbill species (references cited in Kemp 1995).

Inadequate comparative ecological information for many species hinders the understanding of relationships among hornbills. The evolution of dark skin in chicks, plumage patterns such as all-white tail feathers, and white underparts in unrelated genera, complicate discerning evolutionary pathways. The development of the casque, the resemblance of adults to immature(s) of either sex, and cooperative breeding occurs in unrelated genera with no obvious pattern. Female emergence before chick fledging occurs in some species, in other genera, females stay with the chick(s) till fledging. These similarities in some traits in unrelated genera and the difference between otherwise related genera might best be explained by examining the ecological conditions, and the life-history of the species and discerning possible underlying selection pressures for different traits.

Past climatic changes, vegetation distribution and landmass movements are instructive in understanding species origins and radiations, and understanding evolutionary relationships and current distribution patterns. The distribution of plant families such as Lauraceae, Palmae, Burseraceae and Meliceae, and Moraceae, important sources of hornbill food, especially in Asia might be important correlates of their evolution, given the importance of fruits in the diet of hornbills and their role as seed dispersers (Leighton & Leighton 1983, Becker & Wong 1985).

The Indomalayan region has remained largely forested since the Miocene (20 million years ago). Land availability can be inferred from continental drift where landmasses were in a state of flux along with climatic changes that resulted in sea level fluctuations. Many landmasses that are separated now, would have been interconnected when the sea levels were lower (Dingle & Rogers 1972, Siesser & Dingle 1981, Dingle *et al.* 1983, Miller & Fairbanks 1985). Such evidence is important for understanding the connections and separations in the islands of South-east Asia across the Sunda shelf that are indicative of the distributions of several South-east Asian hornbill species. The distributions of the *Penelopides* also reflect the connections across the Philippine islands. For areas in Africa and South-east Asia that lie on the same plate, the distributions of species may have resulted due to movement as a response to changes in climate and vegetation. In some cases, such as the islands of Malesia, which are in different tectonic plates separated by deep water channels, colonization (eg. Philippines, Sulu, Sulawesi, Sumba, Palawan and New Guinea) would have been possible only by flight. Speciation would have occurred afterwards and in the Philippines, a new genus *Penelopides* with new species developed on adjacent islands. The genus *Aceros* seem to be the most successful colonists and wide-ranging travellers. This might be noticed even from the long-range movements and daily flights of mainland *Aceros* species such as the Wreathed hornbill (Leighton & Leighton 1983, Poonswad & Tsuji 1994). In fact, apart from the *Penelopides*, *Aceros* species are the only ones that occur on single islands separated by the sea and several species are superficially similar in appearance. The genus has colonized islands such as Sumba in the Lesser Sundas, Sulu, Sulawesi and Narcondam in the Andaman Sea. The fauna of the Andaman and Nicobar Islands show stronger affinities with Malesia than India being closer to the South-east Asian mainland. India has only two other *Aceros* species that occur in north-east India, at the periphery of the South-east Asian region (Ripley & Beehler 1989). The only hornbill to reach the Australasian region is also an *Aceros* species, where its range extends from the Moluccas through New Guinea to the Solomons.

In Africa, expansion and contraction of lowland and montane evergreen forests occurred in the past (Moreau 1966) and these changes may have resulted in so many African species (thirteen of 23) becoming savanna-dwelling, while only one out of 31 in Asia occupies savanna. The separation of forest patches and isolation may have led to radiation and subspeciation among forest *Tockus* and *Ceratogymna*. The distribution patterns of hornbills in the Indian subcontinent may have also arisen as a result of changes in distribution of forest-savanna mosaics (Ripley & Beehler 1990).

1.1.2. Distribution patterns, sympatry and species richness of hornbills in Asia

There seem to be three main areas of origin of hornbill species in the Indomalayan region, namely, species restricted to the South-east Asian mainland forests, species in the Sunda shelf forests and species that occur in the various island archipelagos. Indonesia and Thailand are the richest with 14 and 13 species respectively. Thailand has several species, the two Brown hornbill species (*Anorrhinus* spp.) and the Rufous-necked hornbill (*Aceros nipalensis*) that occur only in the South-east Asian mainland forest. Indonesia has several endemic island species such as two species in Sulawesi, one in Sumba and one in extreme eastern Indonesia. While Indonesia's richness in species may be partly attributed to its longitudinal spread over several islands where speciation has occurred at a faster rate, Thailand's diversity may be attributed to its wide latitudinal spread, incorporating mainland species as well as species which occur in the true tropical rainforests of Malaysia. The number of species in Malaysia is surprisingly lower (9), though the region is famed for its rainforests. This maybe because the islands of Malaysia are less spread out than those of Indonesia and because species that occur in the South-east Asian mainland forests and endemic island species do not occur here.

Species such as the Helmeted hornbill, Rhinoceros hornbill, Sunda Wrinkled hornbill (*Aceros corrugatus*), Malay Black hornbill (*Anthracoceros malayanus*), Bushy-crested hornbill (*Anorrhinus galeritus*), and the White-crowned hornbill (*Aceros comatus*) are found only in the centre of the Malaysian region, and their distribution borders Thailand and Indonesia. On the other hand, species such as the Wreathed hornbill, Great hornbill, and Oriental Pied hornbills are more widespread, reaching as far west as India. The distribution of the Plain-pouched hornbill (*Aceros subruficollis*) is imperfectly known, but it is likely to be restricted to the South-east Asian mainland forests. The number of hornbills reported in other South-east Asian countries such as Myanmar, Cambodia, Laos, Vietnam and southeast China ranges from 4 to 6 mainland hornbill species. The rest of the species are island species, of which two species each in the genera *Anthracoceros* and the *Aceros* are restricted to only one or two islands in the Philippines. There are also four smaller species belonging to the *Penelopides* genus restricted to the Philippines. Two other island species also belong to the genus *Aceros*, one being the Narcondam Wreathed hornbill (*Aceros narcondami*) (in India but closer to South-east Asia geographically) and the other being the only hornbill species in the Australasian region, Papuan Wreathed hornbill (*Aceros plicatus*).

India is home to nine species of hornbills, of which two are endemic. Occurrence of a tenth species, the Plain-pouched hornbill, doubtful so far, is now believed highly unlikely (Rasmussen 2000). Because of its position in between the Afrotropical and Indomalayan realms, there are two species of the *Ocyceros* genus with affinities to the African *Tockus* genus as well as Indomalayan genera such as *Anthracoceros* (2 species), *Buceros* (1 species), *Aceros* (3 species) and *Anorrhinus* (1 species). Of the two *Ocyceros*, the Malabar Grey hornbill (*O. griseus*) occurs only in the tropical moist forests of the Western Ghats, while the other, the Indian Grey hornbill (*O. birostris*) has a widespread distribution over the Indian subcontinent, and is the only hornbill species in India not confined to forest. Of the two *Anthracoceros* species, the Oriental Pied hornbill (*A. albirostris*) occurs in northern and north-east India, Nepal, Bhutan and Bangladesh, while the Malabar Pied hornbill (*A. coronatus*) occurs in the Western Ghats, Sri Lanka, Eastern Ghats, central India and up to some areas in Bihar and Orissa. These two species might overlap at the extremities of their distributions. Sri Lanka has one endemic hornbill species, the Sri Lankan Grey hornbill *Ocyceros gingalensis*.

The Great hornbill occurs in north, north-east and south India, apart from Nepal, Bhutan and Bangladesh. Two *Aceros* (Wreathed hornbill and Rufous-necked hornbill) and *Anorrhinus austeni* (Austen's Brown hornbill) species in India are restricted to north-east India showing their biogeographical affinity with South-east Asia. The other species, *A.narcondami* is restricted to a single island (Narcondam) of 6.8 km^2 in the Bay of Bengal, which is physically closer to Myanmar than to the Indian mainland. Interestingly, the two larger-sized monogamous *Aceros* species are more widely distributed within north-east India than the smaller cooperatively breeding Brown hornbill, which is restricted to areas in upper Assam and eastern Arunachal Pradesh, south of the Brahmaputra river. Its distribution is also inadequately known and the factors responsible for its localised occurrence within north-east India, and its present rarity would be interesting to determine.

The north-eastern region of India has the highest diversity of hornbill species (5) in India, though the number of sympatric species are not as high as in the South-east Asian forests. It is interesting to note that in India, hornbill species of the same genus never overlap in their range, and have disjunct distributions. It is possible that species in the same genus are more likely to have greater overlap in resource requirements resulting in greater competition leading to parapatric or allopatric distributions. Though resource overlap between different genera also occurs, fine-scale differences in resource partitioning might better enable co-existence. Hornbill diversity and abundance could be related to plant diversity and abundance and the co-existence of similar sized species could be related to abundance of resources. Where resource availability is greater, more species could co-exist, where it is less, greater divergence in size may be required for species to co-exist.

An important factor that might explain patterns of distribution is the number of sympatric species in a given area. Within India, a total of nine hornbill species occur, but in any given area, no more than four occur together. For instance, the Oriental Pied hornbill and Great hornbill occur in foothill forests in northern India, and the Indian Grey hornbill is also found in some areas. In the south (Western Ghats), the Malabar Grey hornbill, Malabar Pied hornbill, and the Great hornbill occur together. But in most areas, only two of these species occur together. Only in north-east India, where plant diversity is greater (Chowdhury *et al*. 1996), there are five species, but here too, in most areas no more than four species co-exist together probably because of fine-scale differences in habitat preference among species.

In the South-east Asian countries such as Thailand and Indonesia, which are richer in plant diversity and abundance (especially of families of Lauraceae, Meliaceae and Myristicaeae) than Indian rain forests, although there are a total of 13 to 14 hornbill species, in any given forest, there are a maximum of three to six co-existing species. Similar patterns in other countries would be interesting to document and correlate. The first level of analysis might be absolute plant species richness, then hornbill food plant diversity or alternatively species richness of families of important hornbill food plants such as Lauraceae, Palmae, Burseraceae, Meliaceae, Annonaceae, and Moraceae. Finer level analysis could look at food plant density from different areas, as well as the availability of nest tree species and nest cavities.

An interesting point to clarify is whether species at the extremities of their distributional range occur at lower densities compared to their abundance in the centre of their distributional range. Examples are Brown hornbills in India, possibly even the Great hornbill in north India and the Western Ghats, the Wrinkled hornbill, Malay Black hornbill and White-crowned hornbills in Thailand and the Rufous-necked hornbill in Nepal. All these hornbill species are very rare, highly endangered or locally extinct in these parts of their range. They are at the extremities of their distributional range and may have originally occurred at lower population densities resulting in greater vulnerability to human impacts. The other explanation that can be invoked for greater vulnerability and rarity may be specialised habitat or resource requirements, but that seems unlikely given that some of these species are not rare throughout their range.

But the relative importance of these factors would be difficult to ascertain given the current pressures of hunting and habitat loss.

1.1.3. Conservation status of hornbill species and threats to hornbills in India

The conservation status of hornbills in India is largely uncertain. Five species of hornbills are listed in Schedule I of the Indian Wildlife Protection Act (1972) (Anonymous 1994): the Great hornbill, Rufous-necked hornbill, Wreathed hornbill, Narcondam hornbill, Oriental Pied hornbill and the Brown hornbill. Surprisingly, the endemic Malabar Grey hornbill and the generally rare Malabar Pied hornbill are not listed at all. The Rufous-necked hornbill is listed as 'rare' in the IUCN Red Data Book (1990), while the Great Hornbill, Brown hornbill and the Malabar Pied Hornbill are listed under the Lower risk/Near threatened category (IUCN 1990). Other Indian species are not listed. Collar *et al.* (1994) lists ten globally threatened hornbill species, of which two species occur in India, the Rufous-Necked hornbill and the Narcondam hornbill, while three species (Malabar Grey hornbill, Malabar Pied hornbill and the Brown hornbill are listed as ‘near threatened’.

The most threatened or rare hornbills in India are the Malabar Pied hornbill, Brown hornbill, Rufous-necked hornbill, and the Narcondam hornbill. All four have restricted distributions, which is the main reason for concern in the first place. The Narcondam hornbill is considered vulnerable simply because the global population of the species is confined to a single small island and any future habitat loss, catastrophe or disease could wipe out the population. The Malabar Pied hornbill has a patchy distribution and is often confined largely to riverine forest patches within deciduous forests. The reasons for its rarity are still to be determined, but hunting and habitat loss are major contributing factors in some areas, such as in Bihar and Orissa (Bivash Pandav, *pers.comm.*). The Brown hornbill and Rufous-necked hornbill are threatened because of habitat loss and hunting in north-east India. The other five hornbill species have wider distributions, but are locally rare or even extinct in some parts of their range. Among these, the species of immediate concern is the Great hornbill, mainly because of hunting, habitat loss, modification and fragmentation. The species is naturally less abundant in the Western Ghats and northern India, than in north-east India, probably because these areas are in the western limits of its overall range. Though they do persist in fragmented rainforest patches to some extent, natural rarity is also aggravated by habitat fragmentation and loss (Raman & Mudappa 2001). Some degree of poaching also occurs in the Western Ghats (Kannan 1994). In northern India, though no population survey or study has been carried out, it is not so common. In north-east India, especially in Arunachal Pradesh, it is more common, but the species faces severe hunting pressure and is locally extinct in some areas. The Wreathed hornbill in India, though restricted to the north-east, is locally abundant in many areas, but is also affected by hunting and habitat loss. Within north-east India, the status of hornbills is probably better in Arunachal Pradesh, where they are more commonly sighted in many areas than in other states like Mizoram, Nagaland and Meghalaya where hunting and habitat loss to *jhum* (shifting cultivation) and logging has been greater (Raman *et al.* 1998, Raman 2001, Pawar & Birand 2001). The Malabar Grey hornbill, though endemic to the Western Ghats is quite common in modified and fragmented habitats and is even able to breed in habitats modified by man (Raman & Mudappa 2001). The Indian Grey hornbill is the species with the widest distributional range in India and is a common bird even in city gardens, parks, woodlands and agricultural tracts. The Oriental Pied hornbill faces some hunting pressure but is relatively widely distributed in India. It is a generalist in habitat choice and is often able to breed and survive in degraded habitats. It is less common in northern India, and is hunted in north-east India, though less than the larger hornbill species.

Historically, hornbills have also been subjected to hunting all over their range, adding to their vulnerability (Bennett *et al*. 1997). The fact that they still remain in Arunachal Pradesh is largely due to the existence of tracts of forest that may soon become small islands in a landscape mosaic created by different land-use patterns such as *jhum* and logging. At present, some forest areas exist outside sanctuaries and national parks, and therefore contiguous patches of forest still remain. Even though habitat modification and fragmentation due to *jhum* and logging are serious threats (Katti *et al.* 1992), hornbills are able to persist in logged and secondary forest patches in part due to their mobility and as long as there is proximity to primary forest areas (Johns 1987, 1989, Datta 1998a, O'Brien *et al.* 1998a).

Hornbills are especially vulnerable in north-east India due to the traditional value of these birds for their feathers, beaks, casques, flesh and supposed medicinal value of their fat, among many tribal groups (Plates 2a, 2b). A major conservation issue is the existence of hunting for several species (particularly of the Great hornbill) by various tribal communities in Arunachal Pradesh. Many areas, especially in eastern and central Arunachal Pradesh have such high hunting pressure that the Great hornbill has become extremely rare or locally extinct. The *Nishis* in the Seijusa area of East Kameng have certain taboos on hunting these birds in the breeding season (Datta 1998a). The Great hornbill is also the state bird of Arunachal Pradesh and most tribes have myths and stories about hornbills that form an important part of their folklore. The *Nishis*, *Adis*, *Apatanis*, *Mishmis*, *Wanchos*, *Tangsas* and *Lisus* all have their own names for the different hornbill species. The *Nishis* use a wooden replica of the Great hornbill as part of their traditional *Nyokum* harvest festival. The Great hornbill is the most valued and hunted by most tribal groups, followed by the Rufous-necked hornbill. *Nishis* wear the upper beak or both the casque and beak as part of traditional ceremonial headgear, and up to Rs. 2000 ($ 45) can be paid for hornbill beaks and casques. *Wanchos* adorn themselves with the feathers, particularly the tail feathers of the Great hornbill. Great hornbill feathers were earlier traded for pigs, mithun horns and wild boar tushes, but now, for money mainly from Myanmar (*pers. obs.*). Hornbill feathers are a matter of prestige, not everyone can possess them. Great hornbills are now not seen in most of Tirap district, and are believed to be locally extinct. Among the *Wanchos*, feathers are most highly prized, worn by the *raja* (king) and other important people in the community. Two body feathers are bought for Rs. 260, while a single tail feather costs between Rs. 600 to Rs. 1600. *Wanchos* consider the Great hornbill and Rufous-necked hornbill to be more beautiful and the tail feathers of these are considered showier than those of the Wreathed hornbill. The head and neck feathers of the Rufous-necked hornbills are also used to adorn *Wancho* headdresses. Among the *Wanchos*, women wear the feathers of the Oriental Pied hornbill during traditional dances. Wreathed hornbill feathers are not used. *Nishis* in Lower Subansiri district also use hornbill feathers during dances, though paper substitutes were also being used (*pers. obs.)*. Apart from the meat that is consumed, the fat of all hornbill species is used for medicinal purposes. *Mishmi* women in Dibang valley are only allowed to eat rat and hornbill meat, and no other meat. In Dibang valley, the Wreathed hornbill is hunted more; while the Great hornbill is hunted very rarely, because of its rarity. The two other smaller species, Brown hornbill and the Oriental Pied hornbill, are hunted much less (mainly for food) being smaller in size and less spectacular, though evidence of hunting of brown hornbills was seen in eastern Arunachal Pradesh.

1.2. THE BACKGROUND AND SCOPE OF THE STUDY

1.2.1. Flowering and fruiting phenology

The seasonal and annual variations in flower and fruit availability are important factors that regulate the life-histories of animals, and it was imperative to understand the patterns of fruit availability for hornbills and other frugivores. In addition, to get a better understanding of the abiotic and biotic factors that determine flowering and fruiting, the community-wide phenological patterns of wind and animal-dispersed species were examined. Phenological studies in Indian tropical forests have been largely conducted in deciduous forests and evergreen forests in south India (Prasad & Hegde 1986, Murali & Sukumar 1994, Ganesh & Davidar 1999, 2001). Such studies in North-east India are few or restricted to a few species of interest (Shukla & Ramakrishnan 1982, Barik *et al.*1996).

While environmental factors may be the primary force influencing phenology (Frankie *et al.* 1974), strong seasonality in fruiting patterns have been found in forest types with differing rainfall and climatic regimes (Medway 1972, Hilty 1980, Foster 1982a, Leighton & Leighton 1983, van Schaik 1986, van Schaik *et al.* 1993). This suggests that other factors (biotic) may also influence fruiting patterns in forests with a high percentage of animal-dispersed tree species (Snow 1965, Smythe 1970, Mckey 1975, Wheelwright 1985a). Four hypotheses have been put forward to explain evolution of fruiting schedules. It has been predicted that fruiting schedules of tree species that share common dispersers should be staggered to avoid competition for dispersers (competition avoidance hypothesis) (Snow 1965). Alternatively, temporally aggregated fruiting phenologies may occur when abundance of seed dispersal agents vary seasonally or when synchronous fruiting enhances dispersal (enhancement hypothesis) (Rathcke & Lacey 1985, Poulin *et al.* 1999) or to minimise seed loss by seed predators (predator satiation hypothesis) (Janzen 1971). Gautier-Hion (1990) suggested that fruiting patterns of fleshy and dry fruits may be related to wet and dry conditions respectively (optimal time of ripening hypothesis). Evidence from previous studies (Leighton & Leighton 1983, Kannan & James 1999) suggested that there was staggered fruiting of hornbill food plant species and this idea was tested during this study.

Another important aspect of the study was identification of critical resources that sustain the frugivorous community during lean fruiting periods in these forests. Most plant species in tropical forests occur in low densities, being rare and scattered in distribution (Hubbell 1979, Hubbell and Foster 1983). Seasonality in fruit production leads to the reliance of frugivores on a few species such as figs (Terborgh 1986). These keystone species provide critical resources during seasons of fruit scarcity (Howe 1977, Gilbert 1980) playing a more crucial role in sustaining a community of frugivores than those in fruit during peaks in production in the forest. It has been suggested that a disappearance of a pivotal resource or of a vertebrate disperser could result in the extinction of other plants dependent on these animals for seed dispersal (Howe 1984a), though Janzen & Martin (1982) suggested that such tight mutualisms are unlikely. Most studies have stressed that a majority of plant species are dispersed by a large set of alternative consumers that can take over from one another in seed dispersal, and this lack of specificity precludes close co-evolution between plant and vertebrate species (Herrera 1985), and therefore, extinction of single vertebrate species or pivotal species is unlikely. On the other hand, many studies have highlighted the existence of dispersal syndromes, suggesting a greater degree of seed disperser specificity (Janson 1983, Corlett 1996, Kitamura 2000, Poulsen *et al. in press*). It is important to identify such resources, existing mutualisms, and determine the degree of specificity, before human-caused disturbances in most areas lead to the extinction of a substantial proportion of tropical flora and fauna. Dispersal mutualisms may be especially important in tropical forests where up to 90% of tree and shrub species bear fruits adapted for animal dispersal (Frankie *et al.* 1974). A high degree of seed disperser specificity has profound implications for the conservation of many primary forest species (Howe 1984a).

1.2.2. The role of hornbills as seed dispersers

Hornbills are important seed dispersal agents of figs, lipid-rich berries/drupes and capsular fruits in tropical forests (Kinnaird 1998, Whitney *et al.* 1998, Holbrook & Smith 2000, Kitamura 2000). It has been asserted that large hornbills are the sole dispersers of many primary forest species with capsular dehiscent fruits because of their large gape size and ability to split open husks (Leighton & Leighton 1983, Becker & Wong 1985, Kannan & James 1999). Hornbills have large gapes, which is associated with specialized frugivory and are able to pry open capsular fruits that other frugivores cannot handle. Hornbills also move over large distances, hence possibly regurgitating and defecating seeds far away from the parent tree with possible beneficial effects on seed germination and survival (Whitney *et al.* 1998, Holbrook & Smith 2000). They are also selective feeders and being large-bodied, feed on more fruit per feeding bout than other smaller frugivores. Some hornbill species are wide-ranging and show nomadic behaviour during lean fruiting periods, and being specialized frugivores, could help in the regeneration of degraded secondary forests (Whitney & Smith 1998). Therefore they could help in maintaining high species diversity in both undisturbed and managed forests by ensuring the dispersal of several primary forest species.

Till recently, observations of hornbills, as seed dispersal agents were anecdotal. It has been hypothesized that their extinction could lead to a chain of extinctions of various tree species that are partly or wholly dependent on them. The severity of this would depend on the relative importance of hornbills as the major dispersers of particular species.

1.2.3. Ecology and social organization of hornbills

Comparative studies of sympatric species with similar biology but which vary in ecological characteristics are useful in understanding the ecological, behavioural and demographic factors that result in different grouping patterns (Jarman 1974, Clutton-Brock & Harvey 1984, Leighton 1986, Krebs & Davies 1991). Studies on hornbills in Asia and in Africa have found differences in the grouping patterns of several sympatric species and related it to specific ecological constraints (Kemp 1976a, Leighton 1982, Leighton & Leighton 1983).

Leighton (1986) found that five Bornean species maintain year-round territories. The Rhinoceros hornbills were found in pairs, sometimes with a dependent helper, in territory sizes *ca.* 7-8 km^2. *Anthracoceros* was found to be territorial and living in pairs with up to two juveniles. *Aceros* is not territorial, and though, mostly found in pairs during the breeding season, they move in large flocks during the non-breeding season. Its range size is considerably larger than that of *Buceros*, despite its smaller body size (Leighton 1986, Poonswad & Tsuji 1994) and it is even nomadic at times. The Great hornbill in southern India and in Thailand is also territorial and largely a fig fruit specialist (Kannan 1994, Poonswad & Tsuji 1994). The Brown hornbill has been reported to have a co-operative breeding system with helpers (Poonswad *et al.* 1987). The greater flocking behaviour and nomadic tendencies of *Aceros* have been postulated to be due to their specialised diet of lipid-rich fruits that are patchy in space and time (Leighton & Leighton 1983, Tsuji *et al*. 1987, Poonswad & Tsuji 1994). They were not found to feed on figs or animal matter to a great extent. Therefore, during fruit-poor times they track fruit resources over larger areas (Leighton & Leighton 1983). Other species were seen to adopt the strategy of switching to non-fruit items or to aseasonal foods such as figs (Leighton & Leighton 1983). More recent studies suggest that fluctuations in resource availability can also lead to flexibility in social organization and flocking patterns, with facultative territoriality by normally territorial species like *Buceros* (Hadiprakarsa & Kinnaird 2001). This is also evident from larger communally roosting flocks seen in generally resource-poor times.

1.2.4. Previous studies on hornbills in India

The ecology and conservation status of the hornbill species have not been studied in north-east India, except for records of sightings as part of avifaunal and other surveys (Katti *et al.* 1992, Datta 1998a, Singh 1995, 1999). It is important to determine the role of hornbills as seed dispersers in these forests, the extent of mutualism existing in these forests, and the lean fruiting periods and the critical resources that sustain frugivores at these times. An understanding of the preferred foraging, nesting and roosting requirements of each hornbill species is also necessary to outline a conservation strategy for these birds. Due to several recent studies in South-east Asia, one can make certain generalizations regarding hornbill social organization and ecology, but a comprehensive picture can only be ascertained from more studies over the species range. Some of these species have been studied in Thailand, Indonesia and Malaysia (*viz.,* Leighton 1982, Leighton & Leighton 1983, Poonswad *et al.* 1983, 1986, 1987, 1988, 1998, Tsuji *et al.* 1987, Kinnaird & O'Brien 1993, 1999, Poonswad & Kemp 1993, Witmer 1993, Poonswad & Tsuji

1994, Suryadi *et al.* 1994, 1996, 1998, Poonswad 1995, Kinnaird *et al.* 1996, Tsuji 1996, Marsden & Jones 1997, O'Brien 1997, O'Brien *et al.* 1998a).

No comparative ecological study of sympatric hornbills has been carried out in India. Ecological studies on hornbills in India have focussed on the Great Hornbill (Kannan 1994, Kannan & James 1997, 1999) and on the nesting habitat and breeding biology of the Malabar Grey hornbill in southern India (Mudappa & Kannan 1997, Mudappa 2000). Short duration studies on the Narcondam hornbill have been conducted during the breeding season (Hussain 1984). The Malabar Pied hornbill has been the focus of an earlier study (Reddy 1988, Reddy *et al.* 1990, Reddy & Basalingappa 1995), while currently its diet and breeding habits are being studied in a riverine forest in Tamil Nadu (Balasubramanian & Saravanan 2001).

1.3. ORGANIZATION OF THE THESIS

This chapter gave an overview of hornbill biology, evolution, distribution patterns, species diversity, and sympatry and the context of the study and the theoretical background to the questions that are addressed. The conservation status and threats to hornbills in India were also outlined. In Chapter 2, the state of Arunachal Pradesh is introduced, followed by a description of the location, vegetation, major fauna and climate of the study area. A brief description of the methods used in individual components of the study is also outlined in this chapter. The next two chapters deal with fruit availability patterns, and the role of hornbills as seed dispersal agents. The first component of the study (Chapter 3) describes the extent of seasonality and annual variability in fruit production in these forests and attempts to evaluate the importance of abiotic and biotic factors that may have shaped flowering and fruiting phenologies. It assesses year-round fruit availability for hornbills and other frugivores, and identifies the alternatives available to them during lean seasons. The dispersal syndromes in these forests based on fruit types and characteristics are also described. In Chapter 4, the role of hornbills as seed dispersers is examined in terms of both the quality and quantity of dispersal. The post-dispersal fate of seeds and seedlings below different types of deposition sites used by hornbills is examined to determine how effective hornbills really are in seed dispersal capabilities. The existence of seed disperser specificity between hornbills and some of their food plants is also highlighted. Chapter 5 deals with the breeding biology and diet of hornbills during the breeding season. The importance of fruits in the diet is highlighted again and a comparison of the breeding biology and degree of overlap in diet of the three sympatric species is made. Chapter 6 is essentially a description and comparison of the non-breeding season diet of the three species. In Chapter 7, the nesting requirements, and nest site selection of the three species are described.

The degree of overlap and/or differences in requirements of these sympatric species is compared to understand the biology of individual species and factors that result in different grouping and spacing patterns of sympatric species. In the last chapter (Chapter 8), characteristics of hornbill roosts are described. An attempt is also made to understand the ecological correlates of the occurrence of communal roosting in hornbills worldwide (based on a literature review and primary data) in the light of existing hypotheses regarding communal roosting.

1.4. OBJECTIVES OF THE STUDY

The broad objectives of the study are outlined below, while detailed objectives are given in each individual chapter

1. To determine the seasonal and annual variations in flower and fruit availability in a semi-evergreen forest of Arunachal Pradesh.
2. To determine how effective hornbills are as seed dispersers in terms of both quality and quantity of dispersal.
3. To describe and compare the breeding biology of three sympatric hornbill species.
4. To characterize the diet composition of three sympatric hornbill species during the breeding and non-breeding season.
5. To determine the nest site characteristics of three sympatric hornbill species and the degree of overlap in nest site characteristics among these species.
6. To describe the characteristics of roost sites used by hornbills and roosting behaviour of three sympatric hornbill species.

Chapter 2. Study Area and Methods

2.1. STUDY AREA

2.1.1. Arunachal Pradesh: Land, biological diversity and people

The state of Arunachal Pradesh (AP; 26°28'– 29°30'N and 91°30'– 97°30'E) covers an area of 83,743 km². Lying in the Eastern Himalayan region, and originally a part of Assam state, AP has remained relatively isolated from the rest of India by virtue of its geographical position and inaccessible terrain. It is situated in the north-easternmost part of India and is surrounded by international boundaries of Bhutan to the west, Tibet to the north and Myanmar to the east., To the south, it is bordered by the states of Assam and Nagaland. It was known in earlier times as the North-East Frontier Tract and subsequently as the North-East Frontier Agency (NEFA). Early explorers into the region have left vivid descriptions and fascinating accounts of the customs, lifestyle and culture of its diverse tribal people (Ward 1941, Shukla 1959, Elwin 1999, Fürer-Haimendorf 1962, 1982, 1983). Large areas of tropical evergreen forests still exist in the state, in part due to low human population density (*c.* 10 per km^2) (Nanda 1992). The state has great biological significance as a result of the diversity of habitats it harbours and its unique position at the confluence of the Palaearctic and Indo-Malayan biogeographical realms (Mani 1974, Rodgers & Panwar 1988), spanning a wide altitudinal range from 100 m to over 6000 m. Although, precipitation is generally high, there can be great variation in amount of rainfall from place to place. Kaul & Haridasan (1987) have identified six forest types in the state. Arunachal Pradesh has the world's northernmost tropical rain forests (Whitmore 1998). Plant diversity is very high, and it is estimated that 7000-8000 species of flowering plants occur here, nearly 50% of the Indian flora (Chowdhury *et al.* 1996). Over 500 species of orchids have also been recorded from the state (Rao & Hajra 1986, Chowdhury 1998). Mammalian species richness (100 species) is high. Of the 1200 bird species in India, nearly 600 species have been recorded from AP (Singh 1995, 1999), and it is recognised as an important endemic bird area (Stattersfield *et al.* 1998). It is one of the world's global biodiversity hotspots (Mittermeier *et al*. 1998, Myers *et al.* 2000) and is also considered to be one of the 200 globally important ecoregions (Olson & Dinerstein 1998). Most of the ecological research has been restricted to surveys of rare species (Katti *et al.* 1990, 1992, Kaul & Ahmed 1993, Athreya & Johnsingh 1995, Kumar & Singh 1998) or largely of avifauna (Singh 1994, 1999, Athreya *et al.* 1997). Recent herpetofaunal surveys have yielded several new species, range extensions and first records from India (Athreya *et al.* 1997, Captain & Bhatt 1997, Pawar & Birand 2001). These few surveys and ecological studies (Datta & Goyal 1997, Datta 1998a, this study) conducted in the state have yielded important discoveries (Kumar & Singh 1998) and information, but many areas still remain unexplored.

More than 25 ethnic groups inhabit the state, most of who traditionally subsisted mainly on hunting and shifting cultivation. They have benefited from laws formulated first by the British and later on by the Indian government, restricting the entry of non-tribals to the area (Elwin 1959). As a result, most of the land area is under tribal ownership, and traditional practices still persist. Though 11% of the geographical area has been brought under the protected area network (Govt. of AP 1998), the imposition of regulations on hunting has not been successful. The forests and resources therein are not viewed as finite by most tribal groups, and with forests being the only source of revenue in this hilly state, bans or controls on logging are resented by the local people. The main sources of revenue for the state were forest-based industries till 1996, after which the Supreme Court banned logging. There were nearly 200 active timber mills during 1994-1995 (Duarah 1995). As a result, within a span of ten years, deforestation has occurred in many areas (FSI 1995, 1997, 1999), and combined with shifting cultivation, this has resulted in severe loss of forest cover in certain districts (e.g., Tirap district in eastern AP). Moreover, hunting has led to the local extinction of several species of wildlife in some areas. The transition from a subsistence economy to a market economy and consumerism due to increasing exposure of the youth to outside influences, threatens this ecologically fragile region. In the absence of any other industry, and pressures to restart logging, the future of some of the last remaining forest areas seems bleak. Conservation efforts, however, have ignored the complexity of this situation and attempted to achieve their goals exclusively through a centralised government machinery. While this system has worked to some measure, there is now a need to actively involve local people in conservation efforts.

AP has 9 wildlife sanctuaries and 3 national parks covering an area of 9246 km² (11.4 %). About 82% of the geographical area is actually forested, albeit the recorded forest area is about 62% of the total area (FSI 1999), of which, 9815 km² (11.7 %) is classified as Reserved Forest (RF). Protected forests, village reserve forests and unclassed state forests constitute the remaining forests. The latter, where tribal people have several rights, comprise the largest area, approximately 35,802 km² (about 43% of the geographical area). Only 18% of the forest area is under the protected area network.

Of the 25 tribal groups with distinct linguistic and cultural identities in the state some have converted to Christianity while most practise an animist religion with a belief in *Donyi-Polo* or the Sun-Moon God. The *Monpa*, *Sherdukpen*, *Khampti* and *Singhpho* are largely Buddhists. Some of the major tribal groups are the *Adi*, *Apatani*, *Mishmi, Monpa*, *Nishi*, *Nocte, Tagin, Tangsa* and *Wancho*. Historically, the *Nishi, Sulung, Aka, Miji* and the *Sherdukpen* have inhabited East and West Kameng districts in western AP. The main tribal groups in Tirap and Changlang districts in eastern AP are the *Wancho, Nocte, Singhpho, Tangsa* and *Lisu*. The latter tribe also inhabit Myanmar, Thailand and other South-east Asian countries.

2.1.2. Location of the study area

The study was carried out in the foothill forests of Arunachal Pradesh, Eastern Himalaya. The intensive study was conducted in Pakhui National Park (NP) (Plate 3) in East Kameng district of western AP (Fig. 1).

Pakhui NP (862 km^2, 92°36' – 93°09'E and 26°54 – 27°16'N) was declared a sanctuary in 1977, and was earlier part of the Khellong Forest Division. It was notified as a National Park and Tiger Reserve in 1999.

Towards the south and south-east, the sanctuary adjoins reserved forests and Nameri NP (349 km^2) of Assam. To the east, lies the Pakke River and Papum Reserve Forest; to the west it is bounded by the Bhareli or Kameng River, Doimara RF and Eagle's Nest Wildlife Sanctuary, and to the north again by the Bhareli River and the Shergaon Forest Division. Both Papum (1064 km^2) and Doimara RF (216 km^2) along with Amartala RF (west of Doimara RF) fall in Khellong Forest Division. Thus, the park is surrounded by contiguous forests on most sides. Selective logging on a commercial scale occurred in these reserve forests till 1996.

The main rivers and streams in the area are the Pakke, Bhareli, Nameri, Khari and Upper Dikorai, all of which run in a southerly direction. The sanctuary is delineated by rivers in the east, west and north. In addition, the area is drained by a number of small rivers and, perennial streams of the Bhareli and Pakke Rivers, both of which are tributaries of the Brahmaputra. The terrain of Pakhui NP and adjoining areas is undulating and hilly. The altitude ranges from 150 m to over 1500 m above sea level. The sanctuary slopes southwards towards the Brahmaputra valley. Higher hills exist in the northern areas of the sanctuary. Seijusa, the sanctuary headquarters, located on the boundary between Assam and Arunachal Pradesh, is 60 km away from Tezpur (the nearest town and airport) in Assam. The western part of Pakhui NP has another range at Tipi, which can be approached along the Tezpur-Bomdilla road via Bhalukpong, situated 5 km before Tipi. The divisional headquarters of Khellong Forest Division is at Bhalukpong, with several ranges in the 3 RFs.

A vast portion in the central and northern part of the sanctuary is relatively inaccessible due to the dense vegetation, hilly terrain and the lack of trails. Consequently, few people including local tribals venture into the interior of the forest. The Bhareli River acts as a barrier to human disturbance, though occasionally local tribals (*Akas*) do cross over to hunt or cut cane and trees. A village (Mabusa, *ca.* 100 ha) near the southern boundary of the sanctuary was relocated outside the park on the other side of the river in 1994. Two small villages exist in the extreme northern end of the park towards Seppa. Towards the southern boundary adjoining Pakke River, access is much easier since the river is fordable most of the year. Instances of hunting and trapping of birds is more common in this area. In addition, villagers from Assam regularly enter the NP, adjoining RFs and Nameri NP to collect cane (*Calamus tenuis,C. erectus, C. flagellum,* and *C. floribundus*), dhuna *(Canarium strictum*), agar *(Aquillaria malaccensis)* and other minor forest products. Illegal fishing is also a major disturbance in the bigger perennial streams towards the southern boundary. But most of Pakhui NP, except the forests near the southern boundary, has relatively undisturbed primary forest.

2.1.3. Geology and Soil

The area consists of comparatively new alluvial deposits of clay, sand, silt, and shingles (Sen 1978). The soils on hills have a moderately deep, moist, fertile, loamy upper layer covered with humus. Shallow soils are common with underlying rocks and boulders. Sub-soil in the foothills consists of mostly boulders and pebbles, under a layer of sandy loam over which lies a layer of humus. The soil is generally porous in nature, despite the heavy rainfall the area receives.

2.1.4. Climate and rainfall

The study area has a tropical and subtropical climate, with cold weather from November to February. It receives rainfall from the south-west monsoon (May-September) and the north-east monsoon (December-April). October and November are relatively dry. May and June are the hottest months. The monsoon lasts till September, but occasional rains occur throughout the year. The south-west monsoon is responsible for more than three-quarters of the annual rainfall. Winds are generally of moderate velocity. Thunderstorms occasionally occur in March-April. The average annual rainfall is 2500 mm. The mean (± SD) maximum temperature was 29.3°C ± 4.2 and the mean minimum temperature was 18.3° ± 4.7, based on data from 1983 to 1995 recorded by the Tipi Orchid Research Centre. Rainfall patterns, temperature and humidity during the study period are described in greater detail in Chapter 3.

2.1.5. Vegetation

The general vegetation type of the entire tract is classified as Assam Valley tropical semi-evergreen forest 2B/C1 (Champion & Seth 1968). At places, evergreen and semi-evergreen vegetation types merge. The forests are multi-storeyed and rich in epiphytic flora and woody lianas. The vegetation is dense, with a high diversity and density of woody lianas and climbers. A total of 234 woody species of flowering plants (angiosperms) have been recorded from the lowland areas of the park, with a high representation of species from the Euphorbiaceae and Lauraceae families (Datta & Goyal 1997), but at least 1500 species of vascular plants are expected from Pakhui NP, of which 500 species would be woody (G.S. Rawat, *pers. comm.*). The forest has a typical layered structure and the major emergent species are Bhelu *Tetrameles nudiflora,* Borpat *Ailanthus grandis* and Jutuli *Altingia excelsa* (Singh 1991). The forest types include tropical semi-evergreen forests along the lower plains and foothills dominated by Kari *Polyalthia simiarum,* Hatipehala *Pterospermum acerifolium,* Karibadam *Sterculia alata,* Paroli *Stereospermum chelonioides*, *Ailanthus grandis* and Khokun *Duabanga grandiflora* (Singh 1991, Datta & Goyal 1997). The tropical semi-evergreen forests are scattered along the lower plains and foothills, dominated by *Altingia excelsa*, Nahar *Mesua ferrea*, Banderdima *Dysoxylum binectariferum*, *Beilschmedia* sp. and other middle storey trees belonging to the Lauraceae and Myrtaceae. These forests have a large number of species of economic value (Singh 1991).

Subtropical broadleaved forests of the Fagaceae and Lauraceae dominate the hill tops and higher reaches. Hill slopes here are dominated by *Mesua ferrea* and Hingori *Castanopsis* spp. Moist areas near streams have a profuse growth of bamboo, cane and palms. About eight species of bamboo occur in the area (Singh 1991), in moist areas in gullies, in areas previously under settlements, or subjected to some form of disturbance on the hill slopes. At least 5 commercially important cane species grow in moist areas, along with Tokko *Livistona jenkinsiana,* a species used extensively by locals for thatching roofs. Along the larger perennial streams, there are shingle beds with patches of tall grassland, which give way to lowland moist forests with Outenga *Dillenia indica* and Boromthuri *Talauma hodgsonii*. Along the larger rivers, isolated trees of Semal *Bombax ceiba* and two species of Koroi *Albizzia* are common. A list of plant species recorded and identified during this study is given in Appendix 2.

2.1.6. Fauna

Datta *et al.* (1998) have recorded 256 bird species from the area. The major avifaunal groups are forest birds such as three species of hornbills, the Great hornbill (*Buceros bicornis*), Wreathed hornbill (*Aceros undulatus*) and the Oriental Pied hornbill (*Anthracoceros albirostris*), the species that were the focus of this study. A fourth species, the Rufous-necked hornbill (*Aceros nipalensis*) was sighted only at higher elevations in Papum RF and forests between Pakke ka Sangh and Rilo (around 1500 m elevation) and in Khellong (*ca*. 800-900 m). It was never sighted within Pakhui NP in the lowland forest intensive study site, but probably occurs in the higher northern areas of the park. Three pheasant species were also recorded in the area (Datta 2001). The major frugivorous/granivorous birds are 8 species of bulbuls (*Pycnonotus*), 5 species of mynas (*Acridotheres*), 4 species of green pigeons (*Treron)* and Mountain Imperial pigeon *Ducula badia*, 4 species of doves (*Streptopelia*, *Macropygia* and *Chalcophaps*), 4 barbet species (*Megalaima*), and 3 parakeet species (*Psittacula* and *Loriculus*). Apart from this, broadbills, cuckoos, the red-headed trogon (*Harpactes erythrocephalus*), two leaf bird (*Chloropsis*) species, fairy blue bird (*Irena puella*), 2 oriole species (*Oriolus*), and 4 species of flowerpeckers (*Dicaeum*) were also recorded.

The area has a great diversity of mammalian fauna. The larger herbivore fauna found here include elephant (*Elephas maximus*), gaur (*Bos gaurus*), sambar (*Cervus unicolor*), barking deer (*Muntiacus muntjak*) and wild pig (*Sus scrofa*). Goral (*Nemorhaedus goral*) and serow (*Nemorhaedus sumatrensis*) occur in the higher areas of the park. The carnivore fauna includes the tiger (*Panthera tigris*), leopard (*P. pardus*), clouded leopard (*Neofelis nebulosa*), wild dog (*Cuon alpinus*) and smaller cats. Several species of viverrids and mustelids, including the binturong (*Arctictis binturong*) and the yellow-throated marten (*Martes flavigula*), both putative predators of hornbills, also occur here (Datta 1999a). Three primate species *viz.*, rhesus macaque (*Macaca mulatta*), Assamese macaque (*M. assamensis*) and capped langur (*Trachypithecus pileatus*), and four squirrel species, the Malayan giant squirrel (*Ratufa bicolor*), Pallas red-bellied squirrel (*Callosciurus erythraeus*), hoary-bellied squirrel (*C. pygerythrus*) and Himalayan striped squirrel (*Tamiops macclellandi*) are the most commonly encountered mammals (Datta & Goyal 1997). Several amphibian species, three species of turtles (Datta 1998b), and at least 10 species of snakes, including both the reticulated python (*Python reticulatus*) and Burmese python (*Python molurus bivittatus*) were also recorded during the course of this study and a previous study (Datta & Goyal 1997). Among lizards, the monitor lizard (*Varanus benghalensis*), tokkay gecko (*Gekko gecko*) and the spotted forest skink (*Sphenomorphus maculatus*) are commonly seen.

2.1.7. Intensive study sites in Pakhui NP

The total area where the study was carried out covered 54 km^2 in the south-eastern portion of the park (Fig. 2), but most of the intensive work was carried out within a smaller area of 12 km^2 near Seijusa.

2.1.7.1. Seijusa: One of the intensive study sites was in forests near Seijusa on the south-eastern boundary of the park bordering the Pakke River, covering approximately 12 km^2 (Fig. 2). This area lies in the extreme south-eastern part of the sanctuary near the AP-Assam border. The study site was in lowland forest with altitude ranging from 150 m to 600 m. The forest here is relatively drier than that in Tipi or Khari area. Some bamboo occurs on the hill slopes, but cane and palms were less abundant. Makrisal *Schima wallichii* was common on hill slopes. The most common species were *Polyalthia simiarum*, *Chisocheton paniculatus,* several *Litsea* and *Phoebe* species, as well as deciduous species such as *Sterculia alata*, *Pterospermum acerifolium*, *Stereospermum chelonoides* and *Tetrameles nudiflora*. A part of the forest near the Seijusa area (*ca*. 4 km^2) has undergone some selective felling in the past (about 20-25 years ago) as is evident from the presence of old cut tree stumps and information from local tribals and Forest Department personnel.

2.1.7.2. Khari, Upper Dikorai and Pukhri : Khari is located 12 km, west of Seijusa at the junction of the Khari and Lalung *nalas* (small streams), near the southern boundary of the sanctuary (Fig. 2). Further west, along the southern boundary of Pakhui NP lies the Upper Dikorai, a large perennial stream that joins the Bhareli further downstream. A 12 km trail runs along a plateau from Khari *nala* and goes down to Upper Dikorai. There are undisturbed forest patches in this area with dense forest dominated by palms, canes and bamboos, dissected by steep gullies and small streams. Pukhri is a small natural pond on a plateau in dense undisturbed forest about 12-14 km to the north of Khari *nala*. The forests near Khari have numerous steep gullies, cliff faces and perennial streams, where canes and palms are abundant, and bamboo clumps occur along the slopes. The species on the hill slopes were largely *Mesua ferrea* and *Castanopsis* spp. *Dillenia indica* was common near the stream banks. Human settlements along with some cultivation existed here in the past as, evinced by abandoned clearings and gaps with thick weedy undergrowth. Cane extraction on a commercial basis occurred here till 1991. Occasionally cane-cutters enter the forests here from the adjacent RFs of Assam. The Nishi community that is now settled in Darlong village and some other villages, used to live in the area before, but were forced to leave and settle outside because of the periodic outbreaks of malaria and other diseases (D.N. Singh, *pers. comm.*). This area has not undergone selective felling in the past. Khari area is not subject to disturbance at present except for occasional cane-cutters, *agar* and *dhuna* collectors, and fishermen, entering the forests mainly from Assam. Due to the presence of signs of past disturbance, in the form of weedy undergrowth, open patches and clearings, and bamboo, the forest here has been categorized as semi-disturbed secondary forest. Ten phenology plots were established in these 3 areas. Opportunistic observations, nest and roost tree searches, counts at roost sites, and hornbill sightings were recorded during monthly visits to these areas. About 3 to 6 days in a month were spent in these areas.

2.1.8. Other study sites

Namdapha Tiger Reserve (TR) (Plate 3) in Changlang district, eastern AP, was another study site where 4 short duration visits (November 1997: 4 days, November 1998: 16 days, March 1999: 18 days, October 1999: 4 days were made to assess hornbill abundance and habitat, quantify vegetation, hornbill food tree density, and make observations on diets of the two other hornbill species, *viz.* Rufous-necked hornbill, and the Brown hornbill. Searches for nest trees were also carried out. Hornbill nests were also located during surveys in **Papum and Doimara RF**, West Kameng district, and in unclassed state forests in the **Pakke Ka Sangh** area in East Kameng district. Several nests were also located in Nameri NP (Assam), adjacent to the south-eastern boundary of Pakhui NP (Fig. 2).

2.1.9. Previous studies and surveys in the area

Apart from the present study, there has been no other continuous, long-term ecological study in Pakhui NP. All other work, apart from two other studies in the area (Datta & Goyal 1997, Padmawathe 2001), have been observations from short visits or as part of larger surveys for various faunal groups (Singh 1991, Athreya & Johnsingh 1995, Atherya & Karthikeyan, unpublished manuscript). Studies on the flora and vegetation have been largely restricted to botanical surveys by the State Forest Research Institute, Itanagar and the Botanical Survey of India (Chowdhury *et al*. 1996). The Orchid Research Centre at Tipi, has been conducting extensive studies on orchids and propagating them using tissue culture techniques. Currently, the Indian Institute of Remote Sensing, Dehra Dun, has undertaken a vegetation survey based on remote sensing techniques. A recent 6-month study compared distribution and abundance of vascular epiphytes in different forest types and also looked at host specificity of epiphytes and environmental correlates of epiphyte abundance (Padmawathe 2001). A six-month study on the responses of arboreal mammals to selective logging was carried out in 1995-96, where (Datta & Goyal 1997) squirrel and primate abundances were compared across different strata, based on logging history. Similar data were also gathered on hornbill and pheasant abundances and their responses to logging (Datta 1998a, 2001). Observations on smaller carnivores, some other mammals and turtles in the area have also been published (Datta

1998b 1998c, Datta 1999a, 1999b). Faunal studies in Pakhui NP started with a short survey for the clouded leopard as part of a survey covering other areas of AP (Athreya & Johnsingh 1995). Periodic short visits are made by scientists from universities in north-east India to survey amphibians. Otherwise, avifaunal and mammal studies have been restricted to sighting records and species lists in the area (e.g., Singh 1991, Datta *et al.* 1998). There has been a recent survey by Pawar & Birand (2001) in the area for amphibians, reptiles and avifauna.

2.2. GENERAL METHODS

A brief summary of the methods used for each individual component of the study is outlined here, while a detailed description is given in individual chapters.

2.2.1. Phenological study

The phenology of all tree species in the plots was monitored once a month within 21 randomly placed 0.5 ha plots in the intensive study site. All trees of Girth at Breast Height (GBH) ≥ 30 cm were enumerated, tagged and the GBH of all individuals in the phenological sample were measured. A total count was made of the number of trees of each species in flower, unripe and ripe fruit every month. Flowering and fruiting of the 1899 trees in these plots was monitored from February 1997 to July 2000, except in June and December 1999. The phenology of all tree species in the plots was recorded for a comparison of the flowering and fruiting patterns of wind-dispersed and animal-dispersed species. Since figs were not adequately represented in the plots, densities of fig trees were also determined along trails, where all fig trees were marked and tagged.

2.2.2. Seed dispersal

The effectiveness of hornbills as seed dispersers was assessed by determining both the quantity and quality of hornbill seed dispersal. A combination of (1) germination experiments with regurgitated and fallen (controls) seeds of non-fig hornbill food species, (2) estimation of gut retention times for 16 food species using 2 captive hornbills, (3) seed counts at middens below hornbill nest trees (breeding season) for 3 years, roost trees and perch trees (non-breeding season) and (5) seedling and sapling counts below nest/roost/perch trees, were used to determine the importance of hornbills as seed dispersers. Seedlings were tagged and their survival monitored below hornbill nest trees (1998, 1999) and roosts trees (1999) and compared with seedling survival below parent trees of ten food plant species of hornbills. The post-dispersal fate of seeds dispersed by hornbills was also monitored below nest and perch trees, by determining rates of seed predation/removal by rodents and insects. The gape width, bill length, bill width, and bill depth of selected frugivorous birds were measured at the Bombay Natural History Society Museum to examine relationships between gape size and fruit sizes consumed by frugivores in the area.

2.2.3. Diet of hornbills: breeding and non-breeding season

During the 4 breeding seasons (1997-2000), nests of the three hornbill species were observed to obtain information on diet profile of each species, degree of frugivory, frequency, amount and biomass of different fruit species in the diet and the relative contribution of figs, non-fig fruits and animal matter in the diet of the three sympatric species. The data were obtained from observations of food items delivered at the nest by the male and from the regurgitated seeds below the nest trees (middens). During the non-breeding season, a diet profile was obtained from a combination of opportunistic records, observations at fruiting trees and by following foraging hornbills whenever possible. Quantitative information on composition of non-fig diet species in the non-breeding season was obtained from seed counts below perch and roost trees. Fruit dimensions and weights of fruits (food species) were measured.

2.2.4. Breeding biology

For a comparison of differences in the breeding biology of the three hornbill species, nests of each species were monitored in the four breeding seasons. Nest trees were located by following lone males, inspecting large trees with cavities for evidence of use by hornbills, presence of regurgitated seeds and food matter below nests, or the regeneration of seedlings of hornbill food plants under potential nest trees. Nest monitoring provided information on the nest entry and dates of initiation of breeding, incubation period, length of the nesting cycle, visitation rates by males, number of chicks fledged, dates of chick fledging, fledging success and diet during the breeding season for each species.

2.2.5. Nest site selection and nesting success

For an understanding of factors determining nest site selection and the degree of overlap in nest site characteristics of the three hornbill species, several nest tree and nesting habitat parameters were measured or estimated at hornbill nest trees. The following nest site variables were recorded: tree species, girth at breast height (GBH), height of the nest tree, height of nest cavity, height of the first branch of nest tree, emergence of nest tree, distance to road, distance to human habitation and distance to river. The canopy cover, altitude at ground level of the nest tree, position of nest hole in the forest strata, the location of the nest on the tree, cavity orientation (degrees), and the general shape of the hole were also recorded. The diameter of the trunk at the nest cavity, cavity width, and cavity length were visually estimated. In addition, all trees of GBH ≥ 30 cm were measured and enumerated around the nest sites, taking the nest tree as the centre of a 15 m radius circular plot to determine the characteristics of the nesting habitat used by the different hornbill species. Random circular plots of similar size were selected 100 m away from the nest, taking the nearest tree above 80 cm GBH as the centre tree and similar habitat variables were measured in these plots. This provided information on preferred nest site parameters for each species. Nesting success (nests in which chicks fledged successfully) over the four breeding seasons was also recorded at the nest trees. The reasons for abandonment of nest trees, unsuccessful nesting and causes of nest tree loss were also ascertained whenever possible.

2.2.6. Roost sites and communal roosting by hornbills

All hornbill species fly to roosting sites at dusk and remain there till daybreak. Roost sites were located by following hornbills in the direction in which they flew in the evenings and looking for signs of use under potential roost trees. Local people also provided information on traditional roosting areas. The species, group size and composition (age and sex), time of arrival, and direction from which they came were noted. Counts at roosts were made usually from 1600 to 1800 hrs (dusk). Opportunistic observations on the behaviour and movement of the birds were also made. Counts at communal roosts were made in 1997,1998 and 1999 during the non-breeding season and in the breeding season of 2000. Use of the roost sites in the breeding season was also ascertained indirectly by the presence of regeneration of hornbill food plant species (that are available and consumed only during the breeding season), below roost trees. At the roost sites, structural characteristics of roost trees such as GBH, tree height, height of the first branch, distance to river, road, and habitation were noted. Circular radius plots of 15 m were laid around individual roost trees (taking the roost tree as the centre tree) to determine tree density and species composition around roost trees. All trees ≥ 10 cm GBH were enumerated and measured. The characteristics of roost sites were compared with other vegetation plots laid randomly in the forest.

2.2.7. Data analyses

All statistical analysis was carried out using EXCEL, SPSS/PC (Norusis 1990) and STATISTICA. Descriptive statistics and non-parametric tests were used wherever appropriate

(Zar 1974, Siegel and Castellan 1988). Equivalent parametric tests were also used for some analyses. For testing hypotheses with the phenology data, Mantel tests (Manly 1994) and ECOSIM (a software package) by Gotelli & Entsminger (2000) were used. Principal Component Analysis and Discriminant Function Analysis were used to understand nest site selection by hornbills (Pielou 1984). Cluster analysis was used to understand patterns in diet overlap between hornbill species. Several indices were used to look at diet breadth, similarity, and overlap (Magurran 1988, Krebs 1989).

Chapter 3. Flowering and fruiting phenology of a tropical forest

3.1. INTRODUCTION

The rhythms of flower and fruit production control the activities of many pollinators and frugivores (Leigh & Windsor 1982). Frugivorous animals such as hornbills are especially affected by variable fruit availability patterns that affect their breeding, activity, and movement patterns.

The phenology of flower and fruit production of tropical trees is influenced by several environmental factors such as temperature, light, rainfall, relative humidity, as well as edaphic and biotic factors (Janzen 1967, Frankie *et al.* 1974, Opler *et al.* 1976, Rathcke & Lacey 1985, Kinnaird 1992, van Schaik *et al*. 1993). It is now well documented that even in tropical evergreen forests, there are marked temporal variations in flowering and fruiting. Peaks and troughs in resource availability have been recorded in many Neotropical (Foster 1982a, Terborgh 1983, Levey 1988), South-east Asian, and African forests (Medway, 1972, Leighton & Leighton 1983, Gautier-Hion *et al.* 1985, van Schaik 1986). Variation in rainfall appears to be a key factor driving patterns in flowering and fruiting (Hilty 1980, Foster 1982a, Borchert 1983). Solar radiation and minimum temperature are other factors that have been found to be important in peaks of leaf flush and onset of flowering (Ashton *et al.* 1988, Tutin & Fernandez 1993, Chapman *et al*. 1999). Strong seasonality has been found in forests with different types of climate and rainfall (Foster 1982a, Leighton & Leighton 1983, van Schaik *et al.* 1993, Struhsaker 1997, Justiniano & Fredericksen 2000) suggesting that biotic factors may be also influencing fruiting patterns in forests with a high percentage of animal-dispersed tree species (Snow 1965, Smythe 1970, Wheelwright 1985a, Terborgh 1990).

Four main hypotheses have been put forward to explain the evolution of fruiting patterns. The **competition avoidance** hypothesis holds that staggered fruiting seasons should be likely among sympatric species of plants having a common pool of dispersers so as to minimize competition for dispersers (Snow 1965, McKey 1975, Wheelwright 1985a), but see Terborgh (1990) for a critical discussion. Competition among fleshy-fruited plants for avian seed dispersers has been suggested to be high (Stapanian 1982). The efficiency of dispersal depends on number of seeds removed and deposited and if more are produced than can be dispersed, it is wasteful. Therefore, staggered fruiting of species will increase chances of dispersal. Leighton & Leighton (1983) and Kannan & James (1999) suggested that food species of hornbills especially of the large-seeded fruits of the Meliaceae, Myristicaceae, Lauraceae, and

Annonaceae had staggered fruiting patterns, in accordance with the competition avoidance hypothesis.

Alternatively, temporally aggregated fruiting schedules may occur when abundance of seed dispersal agents varies seasonally and therefore synchronous fruiting enhances dispersal (**enhancement hypothesis**) (Rathcke & Lacey 1985, Poulin *et al*. 1999) or to satiate seed predators (Janzen 1971). The **predator satiation** hypothesis holds that trees should synchronize fruiting schedules to overwhelm seed predators and therefore there should be a clumped distribution of fruiting periods (Janzen 1971). Gautier-Hion (1990) tested this hypothesis in Gabon and could not find conclusive evidence to prove or disprove it. This hypothesis maybe true for South-east Asian forests where there is heavy arboreal seed predation, a large number of pre-dispersal seed predators and pronounced masting behaviour of several tree families (Leighton & Leighton 1983, Terborgh 1990, Sakai *et al.* 1999).

Another hypothesis that, fruiting patterns are simply related to optimal environmental conditions for ripening (Gautier-Hion 1990**)** was tested by comparing the fruiting patterns of wind-dispersed (dry fruits) and bird-dispersed (generally fleshy fruits, but also dehiscent capsular fruits) species. Her evidence from Gabon suggests that dehiscent dry fruits mature in the dry season facilitated by dry climatic conditions and fleshy fruits mature in the rainy season where moisture helps building up of carbohydrates and lipids.

Terborgh (1990) concluded that this hypothesis might hold true for certain Neotropical and African forests that have strong annual fruiting rhythms and lower seed predation rates. He concludes that the competition avoidance hypothesis could be a weaker selective force in selecting timing of fruiting than the other two hypotheses. A problem in testing these hypotheses is the difficulty of distinguishing between the last three since all predict clumped fruiting peaks and the major problem with testing the first hypothesis is to determine the sets of plant species that share dispersers. In addition, it has usually been found that most plant species are consumed by a variety of animals and thus the occurrence of sets of species sharing similar dispersers is unlikely (Herrera 1985, Terborgh 1990, Gautier-Hion 1990). Another reservation expressed about the application of this hypothesis is the plethora of studies documenting seasonal concentration of fruit production and hence a non-uniform pattern unlike that predicted by the competition avoidance hypothesis (Terborgh 1990).

Null models have been used to test whether observed phenological overlap, in flowering or fruiting patterns in guilds or communities (purportedly driven by pollinators or dispersers) are indeed segregated/aggregated or not different from random simulations, but the evidence is equivocal and results depend on the kind of model used (Fleming & Partridge

1984, Ashton *et al.* 1988, Pleasants 1980, 1990, Poulin *et al.* 1999). Generally, most tests of these hypotheses have been carried out for flowering patterns in a community (Ashton *et al.* 1988, Pleasants 1980, 1990) and only one recent study tested these hypotheses with regard to fruiting patterns (Poulin *et al.* 1999). In general, the influence of pollinators in selection of flowering times is believed to be greater than that of dispersers in driving fruiting schedules of plant species (Wheelwright & Orians 1982, Herrera 1985, Howe & Westley 1988). The caveats with testing these hypotheses are that they are also evoked/modified to explain synchrony/asynchrony in flowering phenologies, circumventing the problem of circularity, channelization of events following from each other, therefore separately attributing selective factors to an already set process/path may be inappropriate (Rathcke & Lacey 1985).

Notwithstanding the multiplicity of fruit consumers of most plant species, plant-animal mutualisms are especially important in tropical forests where up to 90% of tree and shrub species bear fruits adapted for animal dispersal (Frankie *et al.* 1974, Howe & Smallwood 1982). Such estimates of the proportion of animal-dispersed species are unavailable for tropical forests in India, apart from a recent study in the Western Ghats (Ganesh & Davidar 2001). It has been found that hornbills with their large gape sizes are the sole dispersers of many primary forest species (especially of the Meliaceae and Myristicaceae) with capsular dehiscent fruits (Leighton & Leighton 1983, Becker & Wong 1985, Kannan & James 1999, this study, see Chapter 4).

Most plant species in tropical forests occur in low densities, being rare and scattered in distribution (Hubbell 1979, Hubbell and Foster 1983). Apart from low abundance and seasonality of fruit production, inter-annual variation in fruiting patterns and the supra-annual fruiting patterns of many species results in varying patterns of resource abundance for frugivores. Failure of fruiting can cause large-scale mortality and famine (Foster 1982b, Wright *et al.* 1999). Seasonal lows of fruit production leads to the concentration of frugivores on a few species such as figs and some other keystone species (Terborgh 1986, Lambert & Marshall 1991, Gautier-Hion & Michaloud 1989, Kannan & James 1999, Kitamura 2000, Peres 2000). These are known as keystone or pivotal species, since they provide critical resources during annual periods of fruit scarcity and help to support the frugivores community and ensure that frugivore populations are maintained (Howe 1977, Gilbert 1980). These resources play a more crucial role in sustaining a community of frugivores than those available during fruiting peaks. It has been speculated that a disappearance of a pivotal resource or of a vertebrate disperser could result in the extinction of other plants dependent on these animals for seed dispersal, but the answers are equivocal (Janzen & Martin 1982, Wheelwright 1991a). Howe (1990) points out that it is imperative to determine whether such mutualisms exist in some areas, identify pivotal species before disturbances lead to extinctions of tropical flora and fauna, in case such tight mutualisms do exist.

Phenological studies in Indian tropical forests have been largely restricted to drier deciduous forests and to evergreen forests in south India (Prasad & Hegde 1986, Murali & Sukumar 1994, Ganesh & Davidar 1999). Detailed studies on the seasonal and annual variations in community-wide flowering and fruiting patterns of lowland tropical semi-evergreen and evergreen forests in north-east India are lacking, apart from a few studies (Shukla & Ramakrishnan 1982, Barik *et al.* 1999). No previous study has assessed the community-wide patterns of ripe fruit availability for vertebrate frugivores in these forests.

In this chapter, the dispersal modes of tree species in a lowland tropical semi-evergreen forest in Arunachal Pradesh are identified, to understand the extent of importance of animal dispersal. The community-wide seasonal and annual variations in patterns of flower and fruit availability of wind- and animal-dispersed tree species are described, and the environmental correlates of flower and fruit production identified. The seasonal and annual variations in patterns of ripe fruit availability for hornbills are also discussed. Competing hypotheses that seek to explain the evolution of fruiting patterns using a set of bird-dispersed species that share common dispersers are evaluated. Finally, the results are compared with patterns found in other tropical forests to discern commonalities and divergences and the reasons therein.

3.2. OBJECTIVES

1. To determine the dispersal modes of tree species in the area and the percentage of wind-dispersed and animal-dispersed species
2. To compare the flowering and fruiting patterns of wind-dispersed and animal-dispersed tree species and to identify the environmental correlates of flower and fruit production
3. To determine whether there are marked seasonal and annual variations in flower and fruit availability
4. To evaluate hypotheses relating to evolution of fruiting patterns in the light of observed patterns
5. To determine year round patterns in ripe fruit availability for hornbills and identify lean season resources

3.3. METHODS

3.3.1. Phenology plots

Phenology studies have used a diverse array of plot sizes (Chapman *et al.* 1994), but for adequate representation of plant taxa in the sample plots, a plot size of 0.25 ha was considered sufficient (Leighton & Leighton 1983, Kinnaird *et al.* 1996). Twenty-one phenology plots of 0.25 ha each (5.25 ha) was laid in the study area to monitor flowering and fruiting patterns. The phenology of all tree species (wind-dispersed and animal-dispersed) within these plots was recorded once a month. Plants with girth at breast height (GBH) ≥ 30cm were taken in the sample (usually considered as trees in tropical rain forests) and their GBH measured. Every tree was tagged with aluminium tags marked with paint indicating the tree species and number in the plot. Many common tree species were identified with the help of local assistants. Specimens were also collected and field botanists (S.F.R.I, Itanagar, W.I.I, Dehradun) familiar with the flora of the region, confirmed identity. All plants not identified in the field were collected and assigned a temporary code. Phenological data on lianas and shrubs were not collected although four liana species were subsequently identified as hornbill food plants.

Since figs were not adequately represented in the plots (only 16 individuals in 21 plots), all adult fig trees were counted and tagged within 30 m of both sides of 3 trails (total area covered was 48 ha) and their density estimated, but the phenology of these individuals could not be monitored systematically every month.

A total of 1899 trees were enumerated in the study plots, belonging to 165 species. Twenty-five of these species remain unidentified. Two to three people monitored the study plots every month from February 1997 to July 2000, barring the months of July and December in 1999, when no monitoring was done. Field assistants helped in data collection. All plots could not be always monitored every month, consequently, the pool of trees monitored for phenology varied in every month. In addition, 48 trees in the total sample died during the study, and were removed from the total sample from the month when they were found dead onwards, when calculating monthly availability and proportion of trees in flower and fruit. At the end of the study period, there were 1851 trees in the study plots.

The phenophases recorded were the presence/absence of flowers, unripe fruit, semi-ripe fruit and ripe fruit, and scored as 1 if any or all of these reproductive phases were present and as 0 if absent. This provided a total count of the number of trees of each species in flower or fruit in every month. The number of individuals sampled per species varied from 1 to 142, though further analysis was restricted to species represented by a minimum of 4 trees

(Fournier & Charpantier 1975). Thirty-one per cent of species were represented by 10 or more individuals.

3.3.2. Meteorological data

Rainfall and temperature data were obtained from records maintained by the Tipi Orchid Research Centre over the last 15 years. Tipi is at a distance of about 35 km from Seijusa, (the intensive study site) as the crow flies. Relative humidity was recorded with a hygrometer at the basecamp at Seijusa. Rainfall and temperatures were also recorded in Seijusa from 1998 but not recorded accurately for all days in every month, so in order to make consistent comparisons; the data from Tipi were used.

3.3.3. Feeding records and observations

Extensive information on hornbill diet was available as part of this study (detailed in Chapters 4, 5 and 6). Additional observations at fruiting trees and opportunistic feeding records on frugivorous birds were made (*ad libitum* records, > 100 records) during the 4 years to obtain an idea of the fruit species and fruit types consumed by them. Sighting records of mammals at fruiting trees and indirect evidence from scats, dung, and droppings, as well as seed caches or regurgitated seed piles provided information on the types of fruits eaten by mammals. The dispersal modes of some tree species were established by examining fruit characteristics (Brandeis 1906, Kanjilal *et al.* 1934, Grierson & Long 1984) and from literature (Ridley 1930, Snow 1981).

3.3.4. Data analysis

The percentage of trees in each of the phenophases was obtained for every month between February 1997 and July 2000, after accounting for the total number of trees that were sampled in each month and discounting any dead trees. Similarly, based on the area sampled, monthly densities of trees with ripe fruits (number of trees with ripe fruits per ha) were also obtained. Flowering and fruiting patterns of all species together, and of wind-dispersed and animal-dispersed species separately, were examined graphically.

Annual variations in flowering and fruiting patterns and intensity (in terms of the number of species in flower and fruit, monthly percentage of trees in flower, unripe and ripe fruit) were examined graphically. Friedman's test (Non-parametric tests for k- related samples) was used to test for differences between years in flowering and fruiting patterns of wind-dispersed and bird-dispersed species. Since a comparison of all months in all years could not be made because of lack of data for some months, the non-parametric Wilcoxon matched pairs signed rank test (2 related samples) were also used to make pair wise comparisons between years (Zar 1974).

Flowering and fruiting patterns of wind and bird-dispersed species were also compared using correlation tests. The influence of environmental parameters such as monthly rainfall, monthly minimum and maximum temperatures, monthly relative humidity, the total number of rainy days in each month, the preceding month's rain, and the total rainfall in the previous 6 months on production of flowers and fruits were tested using Spearman's rank correlations.

Null model analysis was carried out to determine whether fruiting patterns of the set of bird-dispersed species are different from that expected from randomly generated fruiting patterns. ECOSIM (Gotelli & Entsminger 2000), a software program developed especially for data on phenological overlap or body size differences/size ratios was used. The program tests whether patterns in flowering or fruiting times are aggregated, segregated, or random. The program has been used to test whether peak flowering times in a guild of coexisting plant species are segregated in time (Stiles 1977). In this case, it was used to test similar hypotheses about fruiting times in a guild of coexisting plant species.

A measure known as 'variance in segment length' was used. This measure tests the hypothesis that species sizes (or flowering/fruiting phenologies) are evenly spaced (Poole and Rathcke 1979). So if species are evenly spaced, the variance in segment length should be small. A variance of zero indicates perfectly even spacing of all species in the guild. If competition has led to unusual spacing of species, the observed variance should be significantly less than expected by chance (segregated). Alternatively, if the variance is significantly large, some species are very similar in fruiting times and others are very different in fruiting times (aggregated). An upper and lower limit can be specified (based on prior knowledge) that set the limits the values can take, since species are generally constrained to fruit within a particular time of the year. Each simulation generates its own overlap index. An observed index of overlap is calculated and the statistical probability is determined by determining the number of times the value exceeded (aggregated) or was lower (segregated) than simulated index values by 1000 simulations.

3.3.4.1. Evolution of fruiting patterns: testing hypotheses

1. Sets of plant species that share common dispersers are expected to show staggered or dissimilar fruiting patterns so as to avoid competition for dispersers.

   Prediction: A uniform or staggered fruiting pattern

2. If disperser abundance is seasonal, then species that share dispersers may favour aggregated or synchronous fruiting patterns to enhance dispersal

Prediction: A clumped or aggregated fruiting pattern

These hypotheses were tested by listing the presence/absence of 20 tree species in the diet of 15 major frugivorous bird species in the study area. Quantitative information on diet was available for the three hornbill species only, but based on *ad-libitum* sightings and opportunistic observations over a period of 4 years, some knowledge of the diet composition of 12 other frugivorous birds was available. The analysis was first carried out with 20 fruiting tree species for which information existed on consumers and phenological patterns. The analysis was also repeated with a smaller subset of 8 bird (resident species) and 7 tree species that fruit during the breeding season of these birds (March to August). These species were chosen because they are all large lipid-rich fruits that are mostly capsular dehiscent fruits (Meliaceae and Myristicaceae), two were lipid-rich fleshy drupes (Lauraceae and Annonaceae) that are primarily consumed by hornbills and other frugivorous birds during the breeding season and these plant species are thus likely to compete for dispersers during this time.

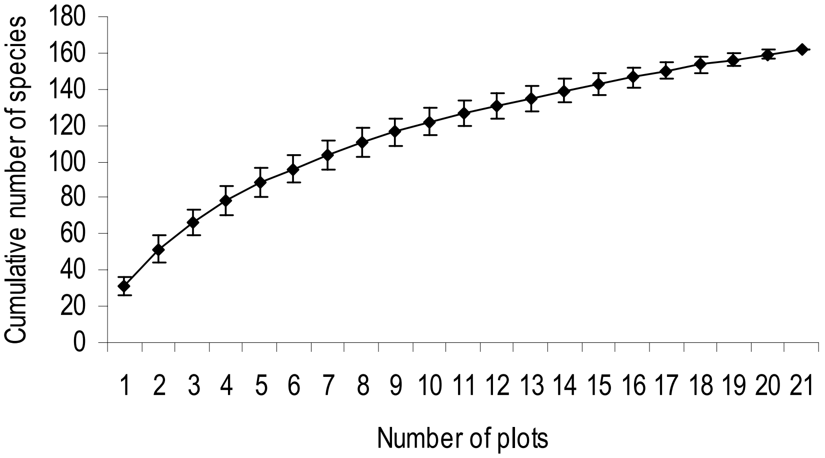
A similarity matrix between the 20 tree species and also the smaller subset of 7 species in their avian consumers was calculated (Sorenson's Index, Krebs 1989). The similarity in fruiting schedules of these species was determined through a matrix of correlation coefficients of ripe fruit availability (% trees in ripe fruit of each species every month) over 40 months. These two matrices were correlated using Mantel tests (Manly 1994). If the competition avoidance does play a role in influencing fruiting schedules of these species, a negative correlation was expected, i.e. tree species that share similar bird dispersers should ripen out of synchrony with each other to avoid competition, while those that do not share dispersers may or may not ripen synchronously. On the other hand, a significant positive correlation was expected if fruiting schedules of these species are aggregated as a response to seasonally high abundance of frugivorous birds.

3.4. RESULTS

3.4.1. Phenology sample

A total of 165 species belonging to 48 families were recorded in 5.25 ha. The total number of species ranged from 17 to 42 per plot. The most common families were Lauraceae (16 species), Euphorbiaceae (14), Moraceae (11), Meliaceae (9). The families Sterculiaceae and Verbenaceae were represented by 5 species each. Twenty-three families were represented by a single species, nine families by 2 species, and nine more families by 3 species and one family by 4 species. Twenty-five species could not be identified. To determine, if the sampling had been adequate, to represent the species richness of the area, the number of new species added per plot was calculated using Estimate S 5.0.1 (a freely downloadable software, Colwell 1994-2000). A randomised cumulative species area curve showed that the number of new species added had nearly stabilized with 21 plots (Fig. 1), though new species were still being added.

Fig. 1. Species accumulation curves for vegetation plots



3.4.2. Dispersal modes

Of the 165 species, 92 species were confirmed to be animal dispersed; an additional 14 species are also likely to be animal dispersed based on fruit characteristics (Appendix 2). Therefore, 64% of the tree species in the area were identified as animal dispersed species. 21 species (13%) were wind-dispersed species, while one more species could possibly be wind-dispersed. Some of the animal-dispersed and wind-dispersed species could also be partly gravity-dispersed. The dispersal modes of 37 species remained unknown. Of the animal-dispersed species, 57 were largely bird-dispersed. The list of plant species, their dispersal modes and major consumers are given in Appendix 2.

3.4.2.1. Wind-dispersed species

Though there were 21 wind-dispersed species (356 individuals), six species were represented by only 1-2 individuals and fruiting was not recorded in these. Therefore, the analysis was restricted to 15 species (349 individuals). Apart from the species with fruits and seeds that are obviously adapted for wind dispersal, a few species have dry indehiscent fruits with no discernible edible fleshy part and were therefore, considered to be wind-dispersed.

Some of these species may be partly gravity-dispersed and the seed may be edible and consumed by pre-dispersal and post-dispersal seed predators such as arboreal squirrels and terrestrial rodents.

3.4.2.2. Animal-dispersed species

Though there were 92 animal-dispersed species and possibly an additional 14, further analysis was carried out with 35 species (938 individuals) that were largely bird-dispersed, for which there were adequate sample sizes of at least 4 or more trees for each individual species.

3.4.2.2.1. Mammals

Mammalian frugivores included four species of diurnal arboreal squirrels, three species of primates, five species of civets, sambar, barking deer, wild pig and elephant and an unknown number of frugivorous bat species.

The diurnal arboreal squirrels were Himalayan striped squirrel, hoary bellied squirrel, red-bellied squirrel and the Malayan giant squirrel that are generally pre-dispersal seed predators. Some of the fruit species consumed by squirrels are *Terminalia bellirica, Mangifera sylvatica, Spondias* sp. *Talauma hodgsonii*, *Duabanga grandiflora*, *Xerospermum glabratum*, and one *Aglaia* sp. Squirrels mostly consume the seeds, but may occasionally drop intact seeds while feeding. Squirrels also eat the pods of *Bauhinia purpurea*, which is largely wind-dispersed.

Porcupines and other unidentified terrestrial rodents ate the fruit pulp and seeds of several species below hornbill nest trees (detailed in Chapter 4) and below fruiting trees, especially of *Dysoxylum binectariferum*, *Horsfieldia kingii*, *Pygeum acuminatum*, *Beilshmedia* spp., *Cryptocarya* sp., *Amoora wallichi* and *Chisocheton paniculatus*. Sometimes seeds and fruits were carried away, though usually seeds were chewed up below the tree itself. Rodent seed caches of *Turpinia pomifera* were found in hollows at the base of tree trunks. These species are generally post-dispersal seed predators and may potentially act as secondary dispersers when they fail to retrieve seed caches.

Of the three species of primates, the capped langur is largely a folivore, while the other 2 species were not so commonly encountered in the area and their abundance/occurrence seemed to be seasonal. Encounter rates of these species were generally low (Datta 1998a). The rhesus macaque is mainly a terrestrial, generalist primate that frequents human-impacted landscapes and forest edges. Direct observations of primates eating fruits other than figs were not made, but fruit species that are known to be consumed by primates are *Garcinia* sp. and possibly some of the Meliaceae and Annonaceae (Leighton & Leighton 1983, Kitamura 2000).

Civets were observed feeding on several species of strangler figs and two species of cauliflorous free-standing figs, *Gynoecardia odorata*, (a cauliflorous fruit), *Vitex* sp. and fruits of several unidentified climbers.

Fruit species consumed by the ruminants and non-ruminants were characteristically different from that eaten by birds or other mammal groups. Seed piles of these species left by sambar or barking deer were commonly found. These species were *Gmelina arborea*, *Turpinia pomifera, Canarium* sp., *Diospyros* sp. *Cheirospondias axillaris*, *Spondias mangifera*, and *Baccaurea ramiflora*. Elephants consumed the fruits of *Dillenia indica*, but the species is also thought to be largely water-dispersed (Ridley 1930).

Apart from these mammals, bears also occur in the area. However, no direct or indirect evidence of their fruit consumption could be ascertained during the study. Some genera (*Cinnamommum.* and *Phoebe*) that have been previously recorded in the diet of bears from South-east Asian forests (McConkey & Galetti 1999, Kitamura 2000), also occur in the study area. Mammals consumed the fruits of at least 34 tree species.

3.4.2.2.2. Birds

Of the 256 bird species recorded in the area (Datta *et al.* 1998), there were about 45-50 frugivorous bird species. Feeding records/observations were made only for the more frugivorous birds such as hornbills, barbets, pigeons, doves, some bulbul species, hill myna and fairy bluebird. A list of fruit species consumed and dispersed largely by birds is given in Appendix 2. About 57 species were largely bird-dispersed (34.5% of all species in the phenology sample).

The important bird-dispersed fruit families were Lauraceae, Meliaceae, Annonaceae, Rutaceae, Styracaceae, Myrtaceae, Moraceae, Myristicaceae, Rosaceae, Sterculiaceae, Bignoniaceae, Burseraceae, and Euphorbiaceae. Several unidentified lianas and the palm *Livistona jenkinsiana* were also recorded in the diet. Fruit types consumed commonly were figs, single-seeded fleshy drupes, single or multi-seeded berries, and multi-seeded arillate capsules, usually black, blue-black, red, orange and yellow in colour when ripe.

3.4.2.2.3. Hornbills

Ripe fruits of 75 plant species (including 9 fig species and four liana species) were recorded in the diet of three species of hornbills. Five other species, *Cinnamommum* *cecidodaphne, Litsea monopetala, L. chinensis*, *Phoebe cooperiana* and a *Syzygium* sp. were not directly recorded in hornbill diet, but are likely to be hornbill food species based on fruit characteristics, literature (Poonswad *et al.* 1998) and local tribal information. Of these, only 45 species (56%, including the five potential species) of hornbill food plant species were recorded and monitored in the study plots. The flowers of a single species, *Oroxylum indicum* were once recorded in the diet of Oriental Pied hornbills (see Appendix 3a for a list of hornbill food plant species). Therefore, hornbills consume and possibly disperse 26% of the 165 tree species. But given that 234 tree species were recorded in a vegetation study over a wider area in an earlier study (Datta & Goyal 1997), it is estimated that about 30% of the plant species in the area maybe consumed and dispersed by hornbills.

The most important families in the diet of hornbills were Lauraceae (19 species), Moraceae (10), Meliaceae (6), Myrtaceae (2), Myristicaceae (2), Annonaceae (2), Euphorbiaceae (2), and Rosaceae (2). *Livistona jenkinsiana* (a palm) and four species of lianas (*Gnetum ula*, *Derris* sp., and two unidentified species) were also recorded in the diet. One species each of Burseraceae, Icacinaceae, Sterculiaceae, Styracaceae and Rubiaceae were also consumed (Appendix 3a). Several other species that were recorded only once or very few times belonged to Rutaceae (2), Anacardiaceae (1), Elaeocarpaceae (1), Urticaceae (1) and Verbenaceae (1). Sixteen species could not be identified to family level, while 11 could not be identified to species. Plates 4a-4c depict the fruits and seeds of several hornbill food species.

Forty non-fig species (excluding 5 possible food species) are consumed by hornbills during the non-breeding season (August to February). Of these, 20 were recorded in phenology plots. Of these, only 13 fruit exclusively in the non-breeding season, 6 species mainly fruit in the breeding season and are also available partly available in the non-breeding season. Thirty-eight non-fig species were consumed during the breeding season of hornbills (March to July). Of these, 23 species were recorded in the phenology plots. Of these, 18 species are exclusively available in the breeding season, 4 species largely fruit during the non-breeding season, but a few regurgitated seeds were found at nests, just before or near the end of the breeding season. One species, *Polyalthia simiarum* was available in both seasons and was important in the diet in both seasons (Chapters 5 & 6). Fruiting of 5 of the 9 fig species that were recorded in the diet was largely asynchronous, and fruits of these species were recorded in the diet in both seasons.

3.4.2.3. Density and distribution of hornbill food plant species

Forty-five (40 non-fig species and 5 fig species, including potential species) of the 80 food plant species of the hornbill food species were recorded in the study plots. Eighteen of the thirty-eight non-fig species (47%) that fruit and are consumed exclusively during the breeding season were represented in the phenology plots, while only thirteen out of the 40 non-fig species (32%) that fruit and are exclusively consumed during the non-breeding season were recorded in the plots. The total sample of hornbill food trees in the phenology sample was 856 trees (45 food species).

Adult tree densities of hornbill food plants varied from 0.19 trees/ha to 22.47 trees/ha for the most common species. Eighteen species were <1 tree/ha, 18 others were < 5 trees/ha, five were < 10 trees/ha and four species occurred at densities > 15 trees/ha. All the food plant species were highly clumped (variance to mean ratio > 1) in distribution (Appendix 3a). The combined tree density of all 45 species was 161trees/ha. Mean (± SE) tree density of all hornbill food plant species was 163 ± (17.28) trees/ha, while density of animal-dispersed food plant species was 236 ± (17.74) trees/ha (n = 21 plots). The overall mean tree density (of all tree species) was 363 ± (21.92) trees/ha.

Of the 45 hornbill food plant species, density of all tree species eaten during the breeding season (including 5 fig species) was 132 trees/ha, while density of all tree species (including 5 fig species) eaten during the non-breeding season was 71 trees/ha. One species, *Polyalthia simiarum*, has two fruiting peaks in the year, and is thus available for 8-10 months in a year and is therefore included in the estimates for both seasons.

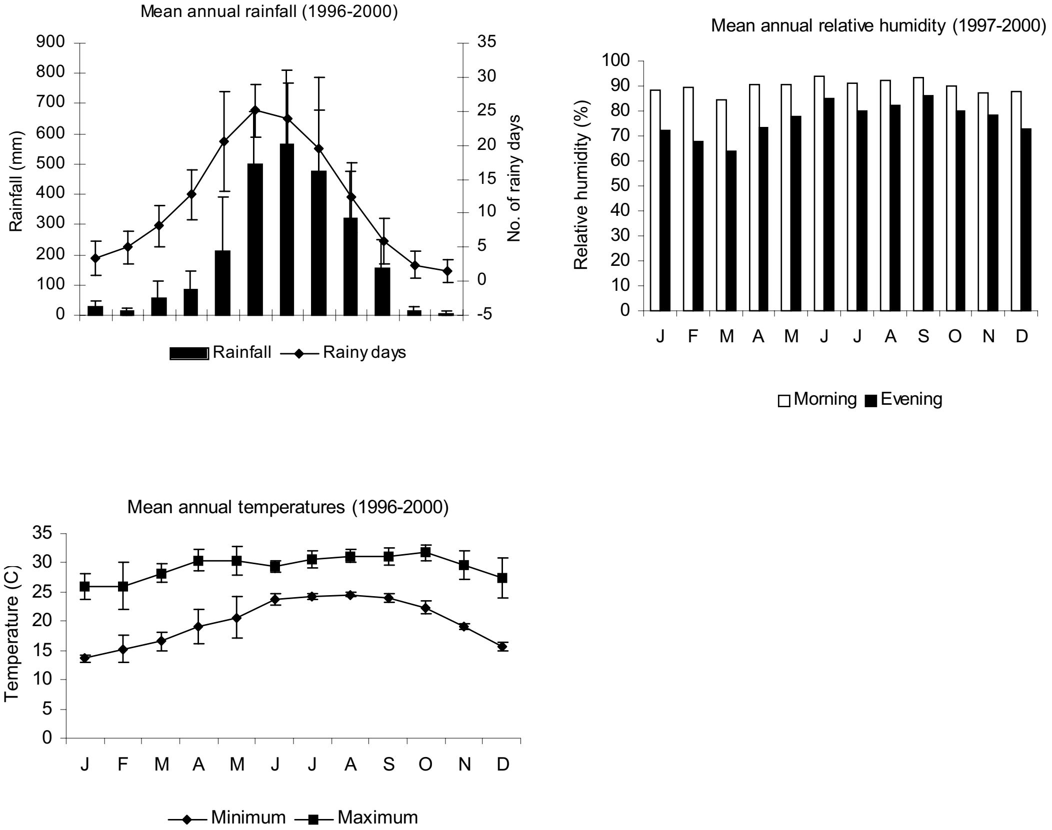
About 25 species of figs (Appendix 4) were recorded in the study area, though all of these were not represented in the phenology plots or trails. Seven were free-standing figs, and the rest were small, epiphytic climbers, or stranglers. Sixty-six fig trees belonging to 18 species were recorded along 3 trails in a total area of 48 ha. Eight of these species remained unidentified. Only 2 species of free-standing figs were represented on trails. The overall mean estimated fig density for the 3 trails was 2.35 ± (0.96) per ha.

Eight fig species (16 individuals) were recorded in the study plots. Of these, three species were free-standing and the rest were strangler figs. Two of the free-standing fig (2 individuals) species were cauliflorous and consumed by mammals. Overall fig density was 3 trees/ha, while strangler fig density was 1.5 trees/ha. The density of hornbill-consumed fig species was 2.7 trees/ha.

3.4.3. Climatic and rainfall patterns

Both the south-west and north-east monsoon is prevalent here. The average annual rainfall is 2500 mm. Most of the rainfall occurs between June and September (south-west monsoon), with some winter rain from December to February. March to May is hot, and some thunderstorms and showers occur in April-May. There were pronounced annual fluctuations in the total amount and the distribution of rainfall (Fig. 2). The total number of rainy days varied annually from a low of 125 in 1997 to a high of 157 in 2000. The number of rainy days in each month varied from a mean of 1.4 days (1996-1999) in December to 25 days in June. Annual rainfall during 1996 -2000 varied from 1782 mm in 1997 to 3546 mm in 1998 with a mean of 2424.3 ± (751.40) mm for a 5 year (1996-2000) period (Fig. 2). Maximum rainfall occurs during the months of June to August with about 500 mm rainfall in each of these months. Mean annual maximum temperature over a five-year period was 29°C ± (1.97), while mean annual minimum temperature was 20°C ± (3.93). January was the coldest month with a mean minimum temperature of 14°C, while May to August was hot with mean maximum temperatures around 30-32°C (Fig. 2). Mean annual relative humidity (in the mornings) was around 90%, with March being the driest month and June, the month with highest humidity. Mean annual relative humidity (in the evenings) was around 77% with March and June again being the least and most humid months respectively (Fig. 2).

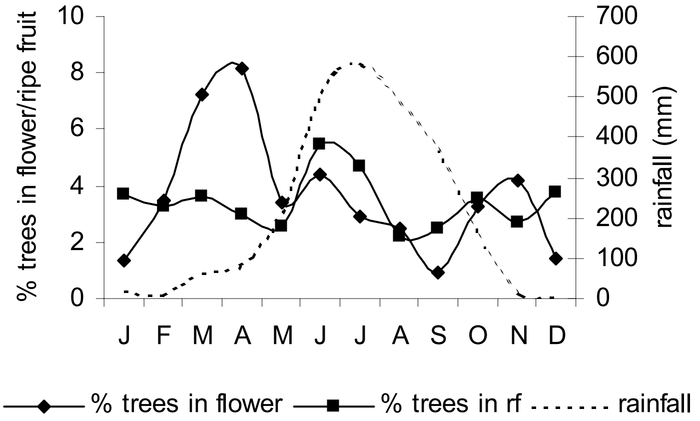
Fig.2. Rainfall, temperature (1996-2000) and relative humidity (1997-2000) in Pakhui NP.



3.4.4. Seasonality in flowering and fruiting patterns

Overall, flowering was unimodal with a major peak before the monsoon in March-April (relatively dry and hot season), though there was a minor peak in November-December (Fig. 3). Fruiting peaked between April and July (hot season to monsoon) (Fig. 3). Fruit scarcity occurred during the period between August and February (end of monsoon and winter, also the non-breeding season).

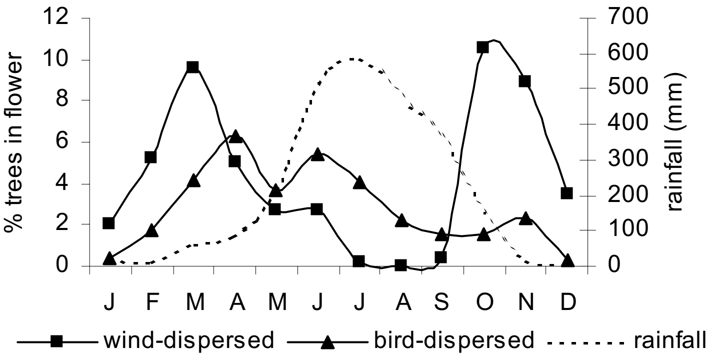
Fig. 3. Overall annual flowering and fruiting patterns for all species (1997-2000)



The flowering and fruiting peaks of the 15 wind-dispersed and 35 bird-dispersed species were dissimilar (Fig. 4a & 4b). Flowering peaks of wind-dispersed species were bimodal, occurring during the relatively dry months, February to April and October to December, while flowering of bird-dispersed species occurred throughout the year (Fig. 4a). Fruiting of wind-dispersed species was also bimodal, peaking in drier months, while the fruiting peak of bird-dispersed species was unimodal, with most middle-storey trees that produced bird-dispersed fruits maturing during the wet season (May-July) (Fig. 4b). Though there was a pronounced fruiting peak in the wet season of bird-dispersed species, ripe fruits of several other bird-dispersed species were available throughout the year. All the larger, arillate capsular fruit species belonging to the Meliaceae and Myristicaceae ripened between March and May, while many fleshy drupaceous fruits of the Lauraceae, Annonaceae and other families ripened between July and December. The lean fruiting season for hornbills was in the non-breeding season from August to February (Fig. 4c).

Fig. 4a-4b. Flowering and fruiting patterns of wind-dispersed and bird-dispersed species

a) Flowering patterns



b) Fruiting patterns

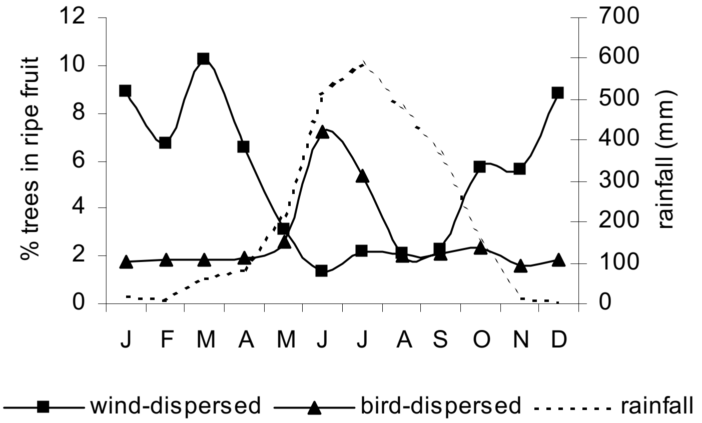
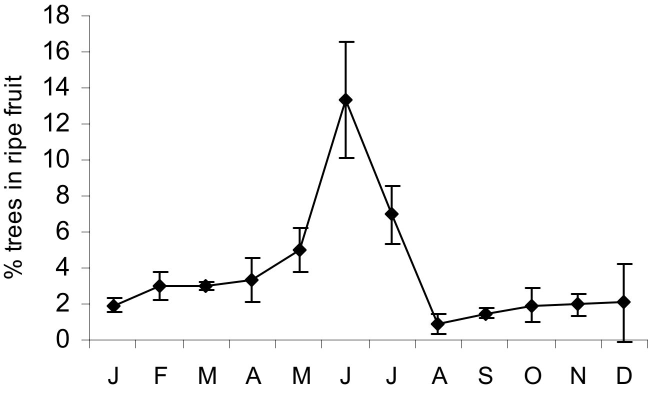


Fig. 4c. Fruiting patterns of hornbill food plants (1997-2000)

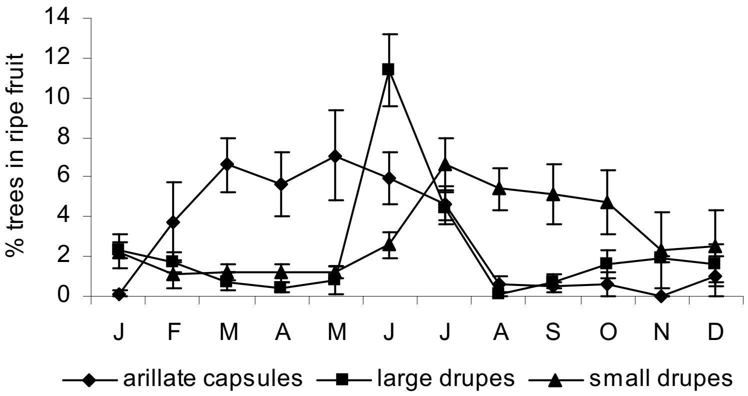


3.4.4.1. Seasonality in ripe fruit availability of different fruit types

The fruit ripening times of fleshy succulent drupes and that of arillate dehiscent capsules were plotted separately (Fig. 4d). Most arillate dehiscent capsular fruits of 7 species belonging to Meliaceae and Myristicaceae ripen during the latter part of the dry season early during the overall peak in bird-fruit abundance. Most fleshy drupes ripen during the wet season. There are also differences in fruit ripening times of larger and smaller fruit drupaceous fruits.

Apart from *Amoora wallichi* that ripens between May and July, all the other 6 species ripen between February and June, before the onset of the main monsoon. On the other hand, the peak fruit ripening times of the large drupaceous fruits of the Lauraceae (5 species) and Annonaceae (1) are in June and July during the period of most heavy rainfall. Three of the large to medium-sized drupes (*Pygeum acuminatum* (Rosaceae), *Livistona jenkinsiana* (Palmae) and *Canarium resiniferum* (Burserarceae) consumed by hornbills ripen between October and February (Fig. 4d).

Fig. 4d. Fruiting patterns of arillate dehiscent capsules and drupes (1997-2000)



The smaller drupes and berries of 10 species ripen between July and November. Hornbills consume only four of these species, the rest are consumed by smaller frugivorous birds such as bulbuls, orioles, barbets, mynas, bar-tailed cuckoo doves, fairy blue birds and chloropsis.

The fruit ripening times of the large drupes were similar between years, though intensity of fruiting differed. Ripe fruit availability of hornbill fruits was distinctly lower in 1999, when there was no recorded fruiting of 3 important lipid-rich arillate fruit species of the Meliaceae and Myristicaceae (*Aglaia* sp., *Dysoxylum binectariferum, Horsfieldia kingii*) and the lipid-rich drupes of two *Cryptocarya* species. In fact, only 6 hornbill food species were recorded fruiting during the breeding season in 1999, while in 1997 and 1998, 10 species were recorded fruiting in the phenology plots. Two to three percent of trees of the large drupes were in ripe fruit in 1999, while 8-14% of trees were in ripe fruit in 1997, 1998, and 2000 during the breeding season.

In 1999, apart from *Polyalthia simiarum* (Annonaceae) and *Phoebe lanceolata* (Lauraceae), there were practically no other lipid-rich fruits of any other species available. In June-July, regurgitated seeds of only these 2 species were found below hornbill nest trees, while in 1997, 1998, and 2000, many more species were being consumed (detailed in Chapter 5). Though, low fruiting of these drupes (apart from *Polyalthia*) was recorded even in 1998, this may have been because fewer drupaceous trees were monitored compared to the other years.

Fruit ripening times of arillate capsules were less similar between years, though overall peak was between February and June, there was some inter-year variation in the pattern. Some of this may have arisen due to incorrect classification of ripe fruits. Though fruits of 3 species were not available in 1999, trees of one species *Amoora wallichii* contributed to the relatively high percent of trees in ripe fruit in 1999 (9%), while it varied between 7 to 14% in 1997, 1998, and 2000.

The availability of small drupes and berries were also lower in 1999 (7%), compared to that in 1997 and 1998 (about 9%). These fruits also ripened slightly later in 1999 between August and October and declined sharply in November, while in 1997 and 1998, the peak was in July and declined more gradually.

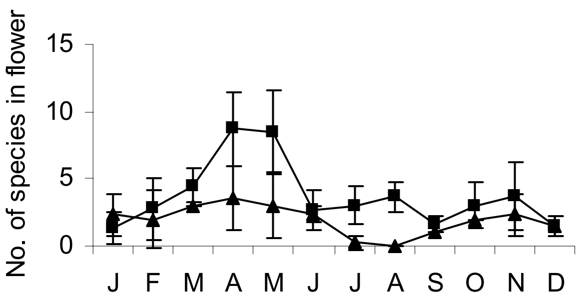
3.4.4.2. Temporal and annual patterns in flowering and fruiting

The number of species in flower of bird-dispersed species reached a peak in April (9), but there were a few species in flower throughout the year (1-13). The number of species in flower of wind-dispersed species showed 2 peaks, in March-April (25) and again in Oct-November (33). There was a total absence of flowering of wind-dispersed species in July and August (Fig. 5a). There was low inter- annual variation in the mean monthly number of species in flower of wind and bird-dispersed species.

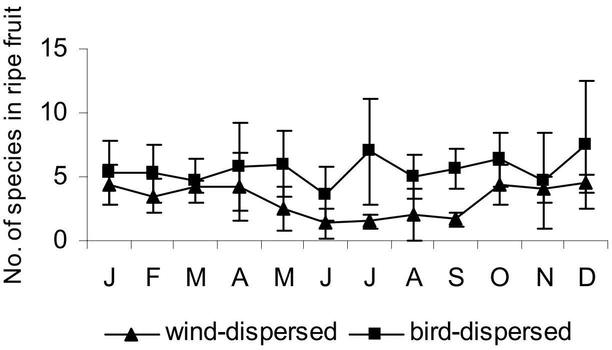
The number of species in ripe fruit of bird-dispersed species seemed to show a uniform pattern throughout the year, the largest number being in July (7) and December (7). The number of species in ripe fruit of wind-dispersed species was bimodal with peaks in March-April (5 species) and in November-December (4 species) (Fig. 5b). There was a greater annual variation in the mean monthly number of species in fruit for wind-dispersed species than for bird-dispersed species.

Fig. 5a-5b. Seasonal and annual variations in number of species in flower and fruit of wind-dispersed and bird-dispersed species

a) Flowering



b) Fruiting

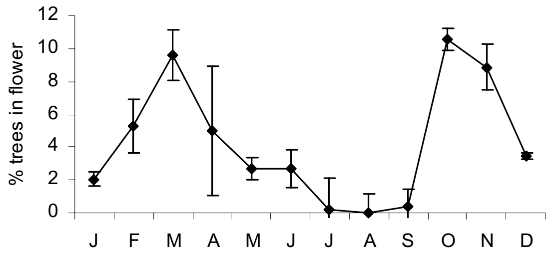


Though the general patterns of flower and fruit availability were similar between years, there were annual variations in fruiting intensity. Fig. 6a shows the inter-annual variability in flowering of wind and bird-dispersed species (in terms of % trees in flower) and Fig. 6b shows the inter-annual variability in fruiting of wind and bird-dispersed species (in terms of % trees with ripe fruit). Fruiting patterns of bird-dispersed species were similar between years, though there was variation in fruiting intensity, with a failure of fruiting of some species belonging to the Meliaceae and Myristicaceae in 1999.

Several individual hornbill food species such as *Horsfieldia kingii*, *Aglaia* sp., *Cryptocarya amygdalina*, *Chisocheton paniculatus*, *Dysoxylum binectariferum* were not recorded fruiting every year. However, most species had fairly synchronous fruit production and most species produced fruits annually, though a palm *Livistona jenkinsiana* showed supra-annual fruiting. It fruited in the winter of 1997-98 and did not bear fruit in 1998-99. Trees of this species were monitored only till February 1999, fruiting of this species was not observed either in the study area or recorded in hornbill diet in the winter of 1999-2000.

Fig. 6a. Seasonal and annual variations in flowering patterns of wind-dispersed and bird-dispersed species (1997-2000).

Wind-dispersed



Bird-dispersed

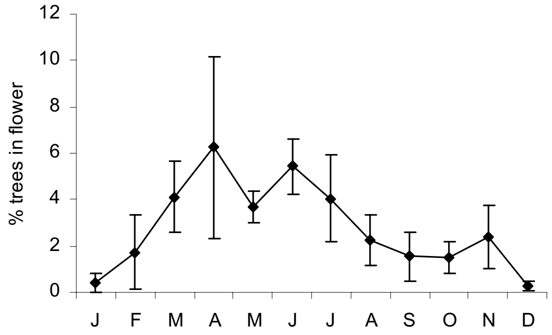
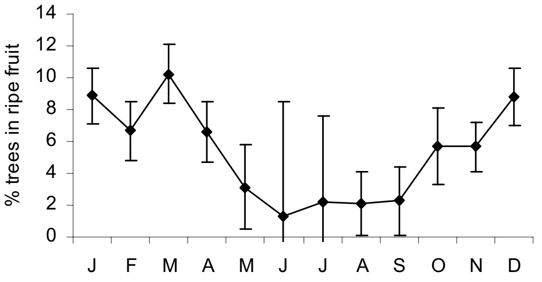
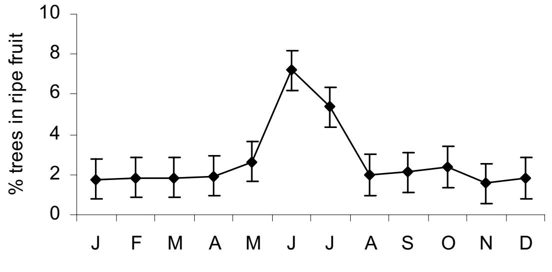


Fig. 6b. Seasonal and annual variations in fruiting patterns of wind-dispersed and bird-dispersed species (1997-2000).

Wind-dispersed



Bird-dispersed



One species, *Polyalthia simiarum* had two fruiting peaks annually with a major one in June-July and a minor one between December and February. Ripe fruits of this species were available 9 months in the year. But the bimodal fruiting pattern was not recorded in the winter of 1997-98; no ripe fruits were recorded from October 1997 to May 1998. In all other years, there were two fruiting peaks.

The fruit characteristics, fruiting phenology and annual variations in ripe fruit availability of 11 hornbill food plant species are detailed in Appendix 5.

3.4.5. Density of trees with ripe fruit: temporal and annual patterns

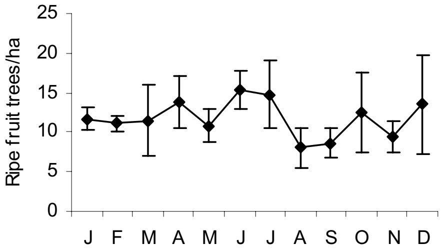
Overall ripe fruit tree density between years varied in intensity. The peak months of fruiting also showed variation in that during 1997, the peak fruit tree density occurred between June and July, while in 1998 and 2000, the peaks occurred between March and May. In 1999, there was low fruiting during most of the months, though in October, there was a peak in fruit tree density (Fig. 7a).

Fruiting patterns of only animal-dispersed species were less variable, the peak of fruiting occurred between April and July in 1997, 1998 and 2000. In 1999, there was a low in fruiting (Fig. 7b). Fruiting peaks of wind-dispersed species was bimodal and occurred between February and March and again in December. In 1999, fruiting peak of wind-dispersed species was delayed and occurred in May (Fig. 7c).

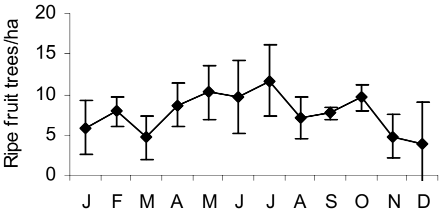
Fruiting patterns of bird-dispersed species was similar between years (1997-1999) with a peak between May to July, and fruit availability was also similar. In 2000, fruit availability was more uniform for the first 6 months (Fig. 7d). Fruiting patterns of hornbill-dispersed species were similar between years with the peak in June and relatively low fruiting in 1999. In 2000, ripe fruit availability was higher and also more uniform during the first 6 months of monitoring (Fig. 7e). Fruiting patterns of only mammal-dispersed species differed between years, the peak being in July in 1997, May in 1998 and in April-May in 2000. There was a near complete failure of fruiting of mammal-dispersed species in 1999 (Fig. 7f).

Fig. 7. Ripe fruit tree density

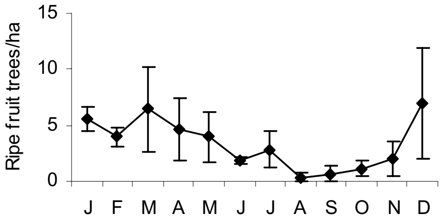
a) All species



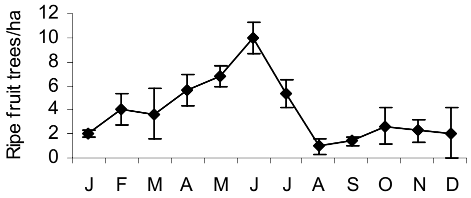
b) Animal-dispersed species



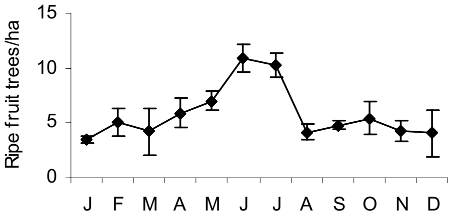
c) Wind-dispersed species



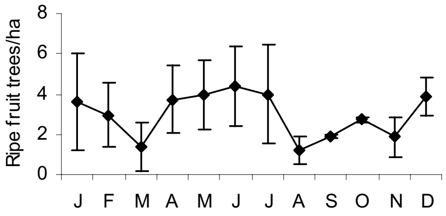
d) Hornbill-dispersed species



e) Bird-dispersed species



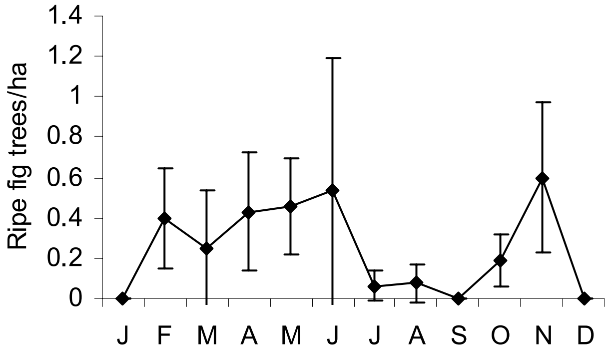
f) Mammal-dispersed species



3.4.5.1. Ripe fruit availability of figs

Out of the 8 fig species recorded in the plots, only 3 out of five strangler fig species and one free-standing fig species consumed by hornbills bore ripe fruits. Asynchronous fruiting ensured the availability of fig fruits almost throughout the year (Fig. 8).

Fig. 8. Ripe fruit availability of figs (1997-2000)



3.4.6. Differences between years in patterns and intensity of flowering and fruiting

There was no difference in both flowering and fruiting patterns of bird-dispersed species or in flowering and fruiting patterns of wind-dispersed species between the 3 years (Friedman's ANOVA, n = 9 months compared).

Since comparisons could not be made for all 12 months in the 4 years together because of missing values, pairwise comparisons (Wilcoxon matched pairs signed rank test for 2 related samples) between years were made to determine if there were any particular years that differed in flowering and fruiting of wind and bird-dispersed species.

There were no differences in flowering and fruiting of wind-dispersed species between any of the pairs of years. There was a significant difference in flowering of bird-dispersed species between 1999 and 2000 (Wilcoxon matched pairs signed rank test, $z = -0.1992$, $p = 0.046$). There was a difference in fruiting of bird-dispersed species between 1997 and 1998 ($z = -0.249$, $p = 0.013$) only.

Flowering patterns of wind-dispersed species in 1997 and 1999 were significantly positively correlated with each other ($r_s = 0.899$, $p = 0.001$, $n = 9$). Fruiting patterns of wind-dispersed species in 1997 and 1999 ($r_s = 0.886$, $p = 0.019$, $n = 6$) and 1999 and 2000 ($r_s = 0.899$, $p = 0.015$, $n = 6$) were positively correlated to each other.

Flowering patterns of bird-dispersed species in 1997 and 1998, and 1998 and 2000 were positively correlated to each other ($r_s = 0.809$, $p = 0.003$, $n = 11$ and $r_s = 0.857$, $p = 0.014$, n = 7, respectively). Fruiting patterns of bird-dispersed species between years were not correlated with each other.

3.4.7. Environmental correlates of flower and fruit production

To identify possible climatic factors that may affect flower and fruit production, monthly rainfall over 40 months (Feb 1997 to July 2000), the total rainfall in the previous 6 months, number of rainy days in each month, monthly minimum and maximum temperature were correlated with percent trees with flower, and unripe and ripe fruit. The flowering and fruiting patterns of 15 wind-dispersed species (in terms of number of species in flower/ fruit and percent of total trees in flower/fruit) were negatively correlated with monthly rainfall and number of rainy days in each month (Table 1a). Flower and fruit production was also negatively correlated with minimum temperature (Table 1a). The flowering patterns of 35 bird-dispersed species (in terms of number of species in flower/fruit and percent of total trees in flower/fruit) were not correlated with monthly rainfall, number of rainy days in each month or minimum and maximum temperatures. But flowering of bird-dispersed species was negatively correlated to the total rainfall in the previous 6 months. Fruit production was positively correlated with rainfall, (r_s = 0.306, p = 0.056) and more strongly so, with the number of rainy days (r_s = 0.343, p < 0.05, Table 1b). Fruiting of bird-dispersed species was also negatively correlated to the total rainfall in the previous 6 months.

Table 1a. Correlates of flower and fruit production in wind-dispersed species

Parameter	Rainfall	Minimum temp.	Maximum temp.	Rainy days	Previous 6 months rain	N
No. of species in flower	-0.395*	-0.349*	-0.94	-0.447**	-0.340*	40
% trees in flower	-0.416**	-0.384*	-0.105	-0.460**	-0.118	40
No. of species in fruit	-0.376*	-0.405**	-0.139	-0.490**	0.107	40
% trees in fruit	-0.392*	-0.507 **	-0.249	-0.463**	0.183	40

** Correlation significant at p < 0.05*
*** Correlation significant at p < 0.01*

Table 1b. Correlates of flower and fruit production in animal-dispersed species

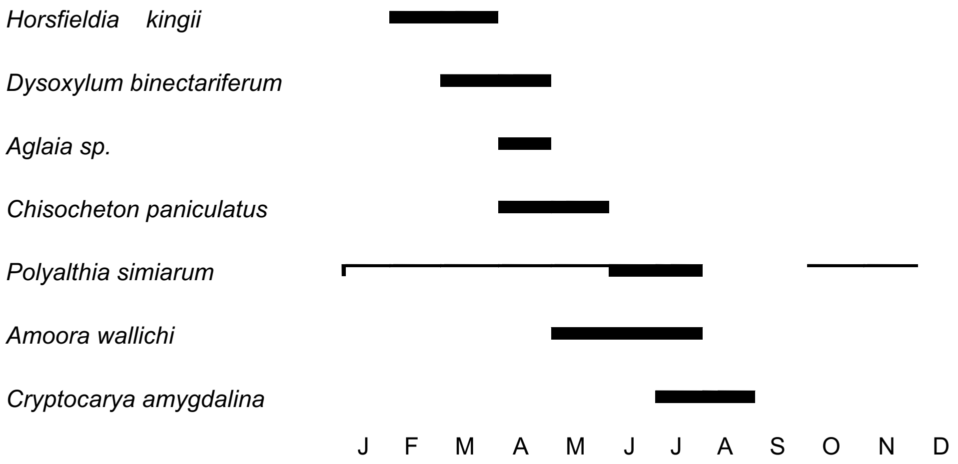
Parameter	Rainfall	Minimum temp.	Maximum Temp.	Rainy days	Previous 6 months rain	N
No. of species in flower	-0.035	-0.231	-0.088	-0.015	-0.539**	40
% trees in flower	0.238	-0.150	-0.213	0.279	-0.579**	40
No. of species in fruit	0.055	0.030	-0.052	0.058	-0.073	40
% trees in fruit	0.306 (0.056)	0.163	-0.047	0.343*	-0.379*	40

** Correlation significant at p < 0.05*
*** Correlation significant at p < 0.01*

3.4.8. Evolution of fruiting patterns: testing hypotheses

Null model analysis was first carried out using 7 bird-dispersed tree species that have their fruiting peaks between February and August (Fig. 9). The potential limits of their fruiting times were set between January and September (9 months).

Fig. 9. Peak fruit availability of 7 bird-dispersed species



The model re-orders the peak fruit ripening times of the species in order to calculate the segment lengths (distance) between adjacent species and then calculates the overall variance in segment length for the set of species. A small variance in segment length suggests segregation, while if the variance is high it is aggregated. The observed index is compared to the number of times it was smaller or greater than 1000 simulations (based on a prior set probability), to determine the statistical significance of the pattern. In this case, the probability was set at 0.05. Therefore, if the fruiting schedules are statistically indistinguishable from random, then the observed index will not be either significantly smaller or greater than the simulated indices.

The observed index (variance in segment length) was 0.16667 and was smaller than the simulated index 971 times, generating a tail probability of 0.029. Since the observed variance in segment length was lower than the simulated indices 971 out of 1000 times, the fruiting schedules of these species were significantly segregated. Therefore, there is a regular or even spacing of fruiting schedules that does not occur by chance alone.

Peak fruit abundance of bird-dispersed species occurred between May and July, which also coincided with the breeding season of resident frugivorous birds such as hornbills, barbets, and hill myna. But, importantly, fruit availability of bird-dispersed species was more uniform, which suggested that there is some degree of staggering of bird-dispersed species throughout the year that may be driven by factors other than climatic conditions. The competition avoidance hypothesis predicts a more uniform fruiting pattern if fruiting schedules are indeed staggered. But a quantitative test of the hypothesis showed that there was no significant negative correlation between similarity in disperser guilds and similarity in their fruit ripening schedules ($r = 0.054$, $p = 0.43$, 5000 iterations, Mantel test). Similarly, with the smaller subset of 7 species there was no significant correlation in similarity in disperser guilds and similarity in fruit ripening schedules of these 7 tree species ($r = 0.22$, $p = 0.14$, 5000 iterations).

3.5. DISCUSSION

3.5.1. Dispersal modes of tree species and their relation to fruiting patterns

The majority of tree species in the study area were animal-dispersed species, which underlines the potential importance of dispersers in driving fruiting schedules. Estimates from other tropical forest regions are even higher (Frankie *et al*. 1974, Howe & Smallwood 1982) and range from 72-76% in Barro Colorado Island, Panama (Foster 1982a) and Hong Kong (Corlett 1996) to 85-90% in Costa Rica and Thailand (Frankie *et al* 1974, Kitamura 2000). Frugivorous birds were the main dispersers in the study area, followed by several groups of mammals.

Since most animal-dispersed species have fruits that are fleshy, the environmental conditions necessary for ripening differed from that of wind-dispersed species that have dry fruits with winged seeds. In addition, wind-dispersed species are more likely to be driven largely by optimal environmental conditions for dispersal of seeds than animal-dispersed species. Therefore it is interesting that patterns in flowering and fruiting of wind and animal-dispersed species differed substantially in expected ways. While most flowering and fruiting of wind-dispersed species peaked in the dry season, fruiting of bird/mammal-dispersed species peaked in the wet season. In addition, the fruiting schedules of animal-dispersed species maybe also driven by competition for dispersers or by seasonal changes in disperser abundance (Foster 1982a), they are likely to differ from that of wind-dispersed species. The fruit availability of animal-dispersed species was more staggered and uniform over the year than that of wind-dispersed species.

3.5.2. Fruit resource partitioning among vertebrate frugivores

Studies of dispersal syndromes in different tropical forest regions have generally found that though many fruits are eaten by a wide array of consumers, there are discernible fruit characters and types that are consumed by subsets of faunal groups. Therefore, it has generally been found that fruits consumed by ungulates, rodents, and elephants are similar and are usually drupes, dull-coloured (often greenish-yellow when ripe) with a dry fibrous flesh and well-protected seeds (Gautier-Hion *et al.* 1985, Corlett 1998, Kitamura 2000). A recent study found that there is little overlap in fruit types and species consumed by primates and hornbills in Cameroon (Poulsen *et al.* in press), unlike the results of Gautier-Hion *et al.* (1985) in Gabon who found that there was greater similarity in fruit types taken by birds and primates than by primates and other mammals. Generally, bird fruits are bright coloured (predominantly black and red), have a succulent pulp and can be berries, drupes, or arillate dehiscent capsular fruits (Jordano 1995, Corlett 1996). Many primate fruits have been found to be often multi-seeded, protected with an outer indehiscent and inedible covering often relatively hard that are almost never consumed by hornbills or other birds. These differences in fruit types eaten may be due to ease of handling, while primates can remove the covering manually, hornbills would have to peck at these fruits to access the edible pulp. Hornbills always swallow fruits whole. Even within birds, there is a partitioning of fruits consumed, which is largely dependent on fruit size and accessibility. For instance, though larger frugivores such as hornbills are not limited by gape size and can consume a wider range of fruit sizes, smaller frugivores such as bulbuls are unable to handle large fruits effectively (Chapter 4). At most, they are able to peck at the fruit pulp. Fruit resources are also partitioned based on life form; bulbuls and other smaller frugivores are the main consumers of fruits of understorey trees and shrubs that hornbills usually do not access (Leighton & Leighton 1983). Green pigeons largely consume figs and are actually seed predators of figs (Lambert 1989b) as are parakeets (Jordano 1983).

Unlike the generalization that has been oft repeated in the recent literature that most species are consumed and dispersed by a wide array of animal species, there are several fruit species that are currently consumed and dispersed by hornbills and Mountain Imperial pigeon, especially among the large-sized fruits of the Meliaceae and Myristicaceae. This has been noted previously by Leighton & Leighton (1983), Becker & Wong (1985), Kannan & James (1999), and Kitamura (2000). Primates were never observed to feed on these species. In addition, the abundance and diversity of primates was low in the study area. There were only 2 species of frugivorous macaques, one of which (rhesus macaque) is found more commonly in forest edges, secondary forest, and human-impacted landscapes. Barbets, hill myna, fairy blue bird and green pigeons consumed some of the drupaceous fruits of the Lauraceae, Annonaceae, and Rosaceae eaten by hornbills, but were never observed to feed on the larger, arillate dehiscent capsular fruits of the Meliaceae and Myristicaceae.

Arboreal squirrels are largely seed predators, very rarely consuming pulp and can act as dispersers only indirectly by dropping unharmed fruits and seeds while feeding. Terrestrial rodents may act, as secondary dispersers by storing seed caches that are later not retrieved, especially in Neotropical forests (Forget 1996, Forget and Milleron 1991, Sanchez-Cordero & Martinez-Gallardo 1998), or mainly as seed predators (Blate *et al.* 1998, Diaz *et al.* 1999). Evidence of food hoarding by terrestrial rodents in Asian tropical forests have been few (Yasuda *et al.* 2000).

The area is rich in viverrid species (Datta 1999a), and the palm civets are known to be highly frugivorous (Corlett 1998, Mudappa 2001). The colours of fruits taken by civets are generally green, and yellow or white, though they do eat 2-3 species (*Vitex pentaphylla*, *Gnetum ula*) that were also consumed by hornbills. The role of bats in dispersing fruits, the number of frugivorous bat species and characteristics of bat-eaten fruits in the study area are unknown, though apparently the drupaceous black fruits of *Polyalthia* are consumed by bats (Kashmira Kakati, Charudutt Mishra, *pers. comm.*).

Overlap in fruit species used was greatest for strangler figs that are eaten by a wide range of birds and mammals. Given that non-fig fruit species seem to be partitioned among few vertebrate consumers in the area, it is likely that fruiting schedules maybe driven to some extent by dispersers.

3.5.3. Seasonal patterns: peaks and troughs in flower and fruit availability

Flowering of bird-dispersed species was negatively correlated with total rainfall in the previous 6 months. Therefore, a dry period before the onset of flowering seems to be a cue for flowering in bird-dispersed species. Flowering of wind-dispersed species was negatively correlated with monthly rainfall, number of rainy days, and minimum temperature. Minimum temperature was also implicated as an important determinant of flowering in South-east Asian and African tropical forests (Ashton *et al.* 1988, Tutin and Fernandez 1993).

The major abiotic factors that have been identified as cues for flowering are photoperiod, temperature, and moisture (see Rathcke & Lacey 1985, Chapman *et al.* 1999). In seasonal tropics, flowering is often induced by rainfall (Borchert 1983 Augspurger 1982, Opler *et al.* 1976, Foster 1982a). Flowers in many plants are produced after a sequence of cues that may be several months apart. Studies in the seasonal tropics have also found that flowering of wind-dispersed species peaked in the dry months, when environmental conditions were suitable.

Most plant species (angiosperms) in the tropics are animal-pollinated (insects, bats and birds, Howe & Westley 1988). The concentration of flowering in one season maybe due to higher pollinator abundance during that period. Wind-pollinated species have been found to flower in the dry season in the tropics, when winds are strongest and trees are leafless (Frankie *et al.* 1974, Foster 1982a). The availability of pollinator abundance may affect flowering times of animal-pollinated species, but it can be vice versa, so it is difficult to separate cause and effect.

Overall fruiting patterns showed seasonal variations with a peak fruiting period between April and July (hot season to monsoon). Fruiting of wind-dispersed species showed a bimodal pattern, with species that flowered in the first peak, ripening during the second flowering peak and vice versa. Therefore, fruiting of wind-dispersed species seemed to be concentrated during the two relatively drier times of the year. Practically, no flowering or fruiting of wind-dispersed species was recorded during the monsoon. Fruiting of wind-dispersed species thus seems to be driven by optimal environmental conditions for ripening as first suggested by Gautier-Hion *et al* (1990). Other studies have also found that in the seasonal tropics, fruits of wind-dispersed species ripen during the dry season (Foster 1982a, Howe & Smallwood 1982, Janzen 1967, Lieberman 1982, Putz 1979, Smythe 1970, Kitamura 2000). There was no fruiting of wind-dispersed species late in the rainy season. Fruiting patterns of the bird-dispersed species was unimodal, with a pronounced peak between May to July. Several studies in seasonal tropics have found that fruit ripening of animal-dispersed species occurs in the wet season (Leighton & Leighton 1983, Kinnaird *et al.* 1996, Kinnaird & O'Brien 1999,) that coincided with the breeding season of hornbills and other birds. Foster (1982a) found that there was a fruiting peak in the wet season and a second peak that corresponded to influx of bird migrations as in temperate regions. He also found a late rainy season depression in fruiting as during this study. In temperate areas, species with fleshy fruits ripen during the autumnal bird migration, similarly in Panama, the second fruiting peak occurs in autumn when birds arrive. When seeking to implicate biotic factors such as dispersers in driving fruit ripening times, there is a problem of circularity, that is, is seasonality of disperser availability a cause or effect of fruiting times? Thus it may be argued that birds have timed their breeding or seasonal influx into habitats based on seasonal differences in ripe fruit availability and not that plants have adjusted their fruiting schedules in response to dispersers.

Abiotic factors have been generally believed to be unimportant in stimulating fruit ripening (Rathcke & Lacey 1985 and references cited therein), but factors such as humidity and moisture may influence secondarily by affecting fruit metabolism. Fruit dehiscence, abscission and dispersal may also be affected by climatic factors (Lacey 1980, Van der Pijl 1972). Ripe fruit availability was concentrated in the rainy season and fruiting of these species was correlated weakly with monthly rainfall and more strongly with number of rainy days. The negative correlation with the total rainfall in the previous 6 months, suggests that lower rainfall (a dry period) in the months before fruiting (when these species are in flower) is important. Studies ranging from Neotropical, African, and South-east Asian forests have also noted that the peak of animal-dispersed fleshy fruits occurs in the rainy season (Foster 1982a, White 1994, Kitamura 2000) or at the end of the rainy season (Chapman *et al.* 1999). These patterns seem to support Gautier-Hion's optimal time of ripening hypothesis that fleshy (most animal-dispersed species) fruits ripen during the wet season when there is enough moisture, while dry fruits (wind-dispersed species) ripen during drier weather. This is especially obvious when the fruiting patterns of wind-dispersed and animal-dispersed species are plotted together, their peaks occur at different times in the year. Fruiting patterns were correlated to rainfall for bird-dispersed species, (similar to seasonal tropics) which maybe the optimal time of ripening, but generally there was no correlation with environmental factors, but humidity and moisture might help fruit ripening mechanisms. Fruiting of wind-dispersed species was related to dryness that is suitable for dehiscing and dispersal. This is also borne out by the fact that when the fruit ripening times of arillate dehiscent capsular fruits (that are bird-dispersed) were plotted separately from fleshy bird-dispersed fruits, notwithstanding the overall peak of bird-dispersed species being in the wet season), these dehiscent fruit species of the Meliaceae and Myristicaceae, except one (*Amoora wallich)* ripened during the dry season or early wet season. Therefore, among bird-dispersed species also, the fruits that are dehiscent and not fleshy generally ripen before the onset of the main wet season.

The overall clumping of ripe fruit availability during the wet season that correlates with climatic factors seems to therefore, negate the hypotheses of disperser-driven fruiting schedules. But despite the peak in ripe fruit availability of bird-dispersed species in the wet season, there were fruits of several other species available throughout the year, albeit much lower in terms of availability. The peak in fruit abundance in the wet season coincided with the breeding season of resident frugivores such as hornbills, mynas, barbets and bulbuls. Most of the species that ripened during the relatively fruit-poor time in winter were smaller-sized fruits that were also consumed by a wider array of bird species, when there is an influx of altitudinal migrants.

3.5.4. Annual patterns: variations in flower and fruit availability

Though the general patterns of flower and fruit availability were similar between years, there were greater annual variations in fruiting intensity, while flowering patterns between years were more similar.

Most species had fairly synchronous fruit production and most species produced fruits annually, with the exception of the palm, *Livistona jenkinsiana*, which showed supra-annual fruiting schedules. The fruiting patterns of the 20 bird-dispersed species were similar between years, though there was variation in fruiting intensity with a failure of fruiting of some species belonging to the Meliaceae and Myristicaceae in 1999 that may have been due to the general failure of fruiting in that year which was related to unusual weather conditions. These species fruited in all other years, and therefore are not necessarily species that normally fruit biennially or supra-annually.

The suspicion that animal-dispersers are important selective forces in shaping fruiting schedules of plant species is further reinforced by the striking similarity in fruiting patterns between years of bird-dispersed and hornbill-dispersed species. The variability was much greater for wind-dispersed species. Most studies, till date, on the other hand, have found high variability in fruiting patterns between years. Though all species did not fruit every year, there was still similarity in patterns between years.

3.5.5. Fruits for hornbills: seasonal lows and keystone resources

Seasonal lows for hornbills are largely due to spatial differences in ripe fruit availability. Interestingly, there were actually lower numbers of food species (in the phenology sample) available during the breeding season of hornbills (that coincides with the wet season peak in fruit abundance) than in the non-breeding season (relatively fruit-poor times), but the percent trees in ripe fruit and ripe fruit tree density were much higher in the breeding season. This was because tree densities of non-breeding season diet species of hornbills and consequently ripe fruit abundance of these non-breeding food species was much lower (nearly 3 times less) than the abundance of species fruiting in the breeding season. This poor representation of non-breeding species in the phenology data may be either an artefact of inadequate sampling and restriction of study plots to lowland forest. The poorly represented non-breeding season species may be rare or stragglers in the lowland habitat and possibly occur only in higher elevations of the study area. Indeed, hornbill abundance in the lowland forest especially of the more wide-ranging, non-territorial, highly mobile Wreathed hornbill *Aceros undulatus* was lower during this period and they had probably moved to higher elevations during the non-breeding season.

Thus the seeming fruit scarcity during the non-breeding season may not actually be the case and there maybe just a spatial difference in fruit availability of some non-breeding season tree species that maybe more abundant in higher elevation forest patches. This would mean that for hornbills and other wide-ranging frugivores, there is essentially only a spatial difference in fruit availability and no real period of fruit scarcity. Hornbills and pigeons are wide-ranging, large, mobile birds that can track changing local fruit availability and access fruit resources over large areas (Leighton 1986, Kinnaird *et al.* 1996, Suryadi *et al.* 1998, Poonswad & Tsuji 1994).

Hornbill species such as the Wreathed hornbill, possibly respond by increasing home ranges and moving to higher altitudes. In addition, fewer, foraging Wreathed hornbills were sighted during the non-breeding winter season in the lowland forest (Datta, A. unpubl. data). These daily movements need not entail major nomadic movements, since hornbills come back to roost in large numbers during the non-breeding season in the lowland areas. During surveys in areas above 1000 m, local tribals in several districts reported that the Wreathed hornbills are only seen during the winter months that corresponds to the low in fruiting in the lowland habitats. The Great hornbill, which is territorial even in the non- breeding season (Poonswad & Tsuji 1994), has smaller home ranges despite a larger body size, and probably relies more on available resources in the lowland forest habitat as well as aseasonal year-round resources such as figs. The role of figs as keystone resources in this area also seems to be important, though detailed phenological study of figs was not carried out. Fig diversity (25 species) and density (2.7 /ha) is relatively high and figs exhibited asynchronous fruiting patterns. Another important lean season resource is *Polyalthia simarum* that fruits nearly 9 months in the year and was ranked as the most important non-fig species in terms of its contribution to the diet (Chapter 5 & 6). It is also one of the most common species in the area, and unlike fruits of the Lauraceae and Meliaceae, it has relatively short maturation times. In addition, during a poor fruiting year (1999), Wreathed hornbills relied almost exclusively on this species during the breeding season. *Polyalthia simiarum* may serve as a lean season resource for hornbills because it is a common food species, and is available and consumed throughout the year and even fruited in 1999, during a general failure in fruiting of several food species.

3.5.6. Evolution of fruiting patterns

Snow's seminal paper that described a case of staggered fruiting patterns to support his competition avoidance hypothesis has been subsequently argued to be not different from random patterns (Gleason 1981). Similarly, Stile's (1977) data on flowering phenologies has been shown to be random (Poole & Rathcke 1979, Gleason 1981), but following Stiles (1979) suggestion that there were 2 groups of bloomers, subsequent re-analysis suggested that flowering is indeed segregated (Cole 1981, Fleming & Partridge 1984). Null model analysis has thus been used in a number of studies, but results are often equivocal and depend on the kind of overlap index used (Pleasants, 1988, 1990, Fleming & Partridge 1984, Poulin *et al.*1999).

In general, most studies have tested the competition avoidance hypothesis with reference to flowering phenologies and pollinators and have found patterns to be aggregated or random. Fewer studies have tested the hypothesis with reference to dispersers and fruiting patterns as was suggested by Snow (1965), Smythe (1970) and McKey (1975). Interspecific competition among plants for dispersers has not been studied, though anecdotal evidence regarding undispersed fruits is present (Herrera 1981, Howe & Smallwood 1982). Fruiting patterns are generally believed to be aggregated, but such studies have not statistically tested the patterns with a random model. They have usually shown that peaks in fruiting occurred at particular times in the year. The only suggested case of segregation was later found to be statistically indistinguishable from random (Gleason 1981). Another overlooked fact is that, these studies have looked at community-wide fruiting patterns and over a whole community, species maybe constrained to fruit within certain environmentally favorable seasons. But the key is to identify a disperser guild that consumes a similar set of trees species and then look at their fruiting patterns. Staggering may occur even within a given season, for instance, during this study, the fruiting peak of several large-sized bird fruits was between March and July, which falls within the breeding season of hornbills and other resident frugivores. But within this period there was finer staggering of the peak ripening times of the species. One of the major problems is of teasing out the importance of environmental factors and disperser-related hypotheses because predictions are similar, except in the case of the competition avoidance hypothesis. In this study, there was a peak in fruiting and flowering that corresponded well with appropriate environmental factors (as suggested by the optimal time of ripening hypothesis), and which thereby suggests a clumping or aggregation during a favourable time of the year. But, due to several lines of evidence outlined below, it is suspected that fruiting patterns of a set of medium to large-sized fruit species that are important food species during the breeding season of resident frugivores are segregated.

If interspecific interactions are determining synchrony or asynchrony in fruiting times, then fruiting schedules should be fairly consistent between years. Fruiting schedules of bird and/or hornbill dispersed species was found to be generally consistent between years. Few long-term studies exist, but most studies have found irregular fruiting patterns within and between years and species, and such occurrences would negate the purported interactions between plants and their dispersers. In fact, the purported inconsistency in fruiting between years found in most studies may be an artefact of looking at the community as a whole and not looking at patterns separately for wind and animal-dispersed species.

Null model analysis with the set of 7 bird-dispersed species whose fruiting occurs between February and August showed that fruiting patterns of these species are indeed significantly segregated. But the demonstration of a segregated pattern does not necessarily imply that the schedules are disperser-driven.

A further test trying to relate fruiting schedules of these species with disperser guilds showed that there was no significant negative correlation between similarity in diets of bird species and similarity in fruit ripening schedules. Therefore, the results may seem contradictory, in that, though a segregated pattern is indicated, there was no relation to suggest that species that share similar consumers/dispersers are the ones that are most different in fruiting times.

This does not provide conclusive evidence that fruiting patterns are unaffected by their bird species consumers. Firstly, this is a simplistic and crude way of determining whether plant species that share dispersers avoid competition by staggering fruiting times. Competition may have structured fruit ripening times in response to a different disperser guild in the past. It is suggested that while climatic factors may be the main force dictating timing of fruiting at a broad-level, within these limits, the staggered fruiting pattern detected for a set of bird-dispersed species that ripen during the breeding season of resident frugivores points to a competitive structuring of fruit ripening times. Segregated fruiting may be beneficial to plants with large fruit crops taken by sedentary dispersers, while aggregated fruiting may benefit plants if produced during periods of high bird abundance (Stapanian 1982). During this study, the peak ripe fruit abundance of large-sized fruits coincided with the breeding season of resident frugivores, while relatively smaller-sized fruits were available during winter months, when there is an influx of migrants. A recent study by Poulin *et al.* (1999) that tested these hypotheses found that both synchrony and asynchrony could occur depending on the disperser guild and their abundance. While species in one genus had aggregated fruiting schedules timed with peak abundance of 6 major bird species consumers supporting the enhancement hypothesis, the species in the other genus that were the major resource for two resident manakins had segregated fruiting times, supporting the idea suggested by Stapanian (1982).

Fine-scale differences in fruit ripening times of tree species may be difficult to pinpoint with monthly phenological data on number of trees in ripe fruit. It would be easier to detect through weekly data on actual ripe fruit availability on sampled trees as well as diets of bird species that are tracking fruit availability. This seemed to be true from the diet of hornbills, where one or two fruit species were important at any given time thus showing that in terms of the contribution to the dispersers' diet, species were staggered temporally. Therefore, while there may be a broad overlap in fruiting schedules of species (that depends on optimal environmental factors), within that period, species may show a less detectable staggering.

3.6. CONCLUSIONS

To conclude, the high percentage of tree species in the area that have fruits adapted for animal dispersal and the wide range of frugivorous animals in the area, highlights the importance of the functional roles that frugivores play in these forests.

Overall fruiting peaked between April and July. Fruit scarcity occurred during the period between September and January (end of monsoon and winter). Most bird-dispersed species had fairly synchronous fruit production and most species produced fruits annually, though a palm *Livistona jenkinsiana* showed supra-annual fruiting. One species, *Polyalthia simiarum* had two fruiting peaks in the year with a major one in June-July and a minor one between October and February. It is abundant in the lowland habitat and was available to frugivores during a failure of fruiting of several species in 1999 and therefore, is an important lean season resource. Inter-annual variability in overall fruiting patterns (all species) was high, while flowering patterns between years were more similar. However, fruiting patterns of bird-dispersed species were similar between years, though there was a failure of fruiting of several species belonging to the Meliaceae and Myristicaceae in 1999. The seasonal low in ripe fruit abundance in the non-breeding season of hornbills was probably restricted to the lowland habitat, since the number of diet species consumed by hornbills in this season was high, despite the fruit scarcity. Many species that are consumed by hornbills in the non-breeding season were either not recorded in phenology plots or low in abundance in the sampled lowland habitat. The flowering and fruiting peaks of wind- and bird-dispersed species were dissimilar. Flowering and fruiting peaks of wind-dispersed species was bimodal, occurring during the relatively dry months, February to April and October to December, while flowering of bird-dispersed species occurred throughout the year. The fruiting peak of bird-dispersed species (mostly fleshy fruits) was unimodal, maturing during the wet season (May-July), but ripe fruits of several other bird-dispersed species were available throughout the year. Ripe fruit availability of wind-dispersed species was negatively correlated with rainfall, while the reverse was true for bird-dispersed species. Among bird-dispersed fruits, there seemed to be a difference in the peak ripe fruit abundance of different fruit types. Almost all the species with larger arillate dehiscent capsules belonging to the Meliaceae and Myristicaceae ripened between March and May (relatively dry), while fleshy drupes of the Lauraceae, Annonaceae and other families ripened between July and December (mostly wet season). The difference in the peak fruit ripening times of wind- and bird-dispersed species and of dehiscent arillate capsules and fleshy drupes suggests that optimal climatic conditions are important factors that determine fruit ripening. Peak fruit abundance of bird-dispersed species occurred between May and July, which also coincides with the breeding season of resident frugivorous birds. But, importantly, fruit abundance of bird-dispersed species was more uniform that that of wind-dispersed species throughout the year, which suggested that there is some degree of staggering of bird-dispersed species that may be driven by dispersers. Null model analysis with a set of 7 bird-dispersed species with large fruits whose fruiting occurs between March and August (breeding season of resident frugivores) showed that fruiting patterns of these species are indeed significantly segregated. However, a quantitative test of the hypothesis showed that there was no significant negative correlation between similarity in disperser guilds and similarity in fruit ripening schedules of these 7 tree species. Similarly, with a larger subset of 20 species there was no significant correlation. It is suggested that while climatic factors may be the main force dictating timing of fruiting at a broad-level, within these limits, the staggered fruiting pattern detected for a set of bird-dispersed species points to a competitive structuring of fruit ripening times. The peak ripe fruit abundance of large-sized fruits coincided with the breeding season of resident frugivores, and showed a staggered fruiting pattern during that time. Segregated fruiting may be beneficial to plants with fruit crops taken by sedentary dispersers. Species maybe constrained by intrinsic and abiotic factors to fruit in a particular “optimal” time or season, therefore, there could be peaks of fruiting in a given season when fruiting is conducive for most species, but within that period, species may show a less detectable staggering.

Chapter 4. The effectiveness of hornbills as seed dispersers

4.1. INTRODUCTION

Seed dispersal by animals is known to be important for 50 to 90% of canopy trees in Neotropical forests, while nearly 100% of shrubs and small trees produce fleshy fruits that are dispersed by animals (Howe & Smallwood 1982). In Paleotropical forests 35-48% of large trees and 70-90% of small trees are animal dispersed. Numerous studies have documented the role of vertebrates in effectively dispersing seeds (Howe & Smallwood 1982, Janzen 1983). Plants benefit from seed dispersal either through escape from density-dependent mortality near parents (Janzen 1970, Connell 1971) or by colonizing gaps where regeneration is favourable (Howe & Smallwood 1982). While evidence for density-dependent mortality has been shown in numerous studies, it does not preclude the advantage of dispersal away from the parent tree, even if there is no density-dependent mortality, simply because offspring will need space and nutrient requirements, already used up by the parent tree. In addition, studies have shown that another cause of higher seedling mortality below parent trees is the presence of host-specific soil pathogens near the parent tree. Seedling survival has been found to be higher away from parent trees as well as below trees of other species (Augspurger & Kelly 1984, Packer & Clay 2000).

These two hypotheses are not mutually exclusive and for either or both reasons, dispersal by animals is important for recruitment of tree populations (Howe 1984a). Schupp (1993) stated that there are two components to dispersal efficacy of any potential seed disperser – quality and quantity. In terms of quality, it is important to determine how the disperser handles the fruit and processes the seeds. It is also imperative to determine the sites of seed deposition and how suitable they are for germination and recruitment. In terms of quantity, it is important to determine how often a potential disperser visits a tree and how much fruit is removed and the total numbers of seeds dispersed. A disperser could consume great quantities of a particular fruit species and yet may not be an effective disperser if all seeds are deposited in sites unsuitable for germination and recruitment. To be an effective disperser, fruits have to be removed regularly; seeds should be unharmed and deposited in 'safe' sites for germination. Therefore, ideally, the fate of deposited seeds needs to be monitored till germination and recruitment to evaluate the effectiveness of any dispersal agent.

While some studies have deduced effective seed dispersal by demonstrating the enhanced germination success of frugivore-processed seeds versus control seeds (Izhaki &

Safriel 1990, Medellin 1994, Izhaki *et al.* 1995, Graham *et al.* 1995, Malo & Suarez 1995), others have relied on fruiting tree visitation patterns and fruit consumption to show possible dispersal by frugivores (Howe & De Steven 1979, Howe 1980, Howe & Vande Kerckhove 1979, 1981, Wheelwright 1991b, Howe 1993). But increasingly, recent studies have demonstrated, quantitatively, the effectiveness of seed dispersers, by tracking the fate of deposited seeds through to at least the seedling stages or looking at the role of secondary dispersers in re-arranging the seed shadow (Andresen 1999, Asquith *et al.* 1999).

The chances of a tight co-evolution occurring between trees and their animal dispersers are believed to be unlikely (Wheelwright & Orians 1982) because, even if seeds are being removed and dispersed, the chances of a seed germinating and recruiting into an adult plant is fraught with uncertainty because of mortality factors at every stage of its life-history, which are not under the plant's control. Several studies have also stressed that most plant species depend on a wide array of vertebrate consumers for seed dispersal, and consequently, diffuse coevolution is the norm (Howe 1984b, Herrera 1985). There has been no example of any single plant species dependent solely on one single disperser. In fact, even the one celebrated example of the extinct dodo and the tamblacoque tree (Temple 1977) has now been argued to be unlikely (Witmer & Cheke 1991). On the other hand, there are a few examples of certain animal taxa that are the principal effective disperses of seeds of certain plant species, (despite consumption by many more visitors) and hence they are critical to the persistence of these plants. This may be especially true of toucans, guans, birds of paradise, and hornbills (Beehler 1983, Howe *et al.* 1985, Howe 1981, 1989, Howe & Van de Kerckhove 1981, Leighton & Leighton 1983, Becker & Wong 1985, Coates-Estrada & Estrada 1988). Apart from this, the mutualisms existing between flowerpeckers and tanagers with mistletoes, manakins and the Melastomataceae (Snow 1965, Snow 1981, Reid 1989) are classic examples of possible co-evolution. Dispersal syndromes have identified many tree species as having fruits adapted for dispersal by certain faunal groups (Janson 1983, Gautier-Hion *et al.* 1985, Jordano 1995, Corlett 1996, Nakanishi 1996, Poulsen *et al. in press*). Increasingly, current faunal assemblages are becoming depauperate in many forest regions and therefore, in present-day conditions, it may be true that some tree species depend on a limited set of effective dispersers. Frugivorous birds and bats have been shown to be instrumental in rebuilding a forest ecosystem in Krakatau over a period of 100 years, which demonstrated the importance of dispersal in forest restoration (Whittaker & Jones 1994).

Detailed studies of plant-frugivore interactions and fruiting phenologies are not so extensive from Paleotropical forests, apart from a few (Lambert 1989a, Leighton & Leighton

1983, Becker & Wong 1985, Kitamura 2000), carried out in South-east Asia. In Indian forests, there have been a few studies in recent years (Borges 1993, Ganesh & Davidar 1999, 2001, Kannan & James 1999).

Hornbills have always been considered as important dispersers in tropical forests based on anecdotal observations. In recent years, some studies have provided more evidence for dispersal with quantitative data. While Kinnaird (1998) demonstrated that there was a higher density of hornbill food plants below Sulawesi red-knobbed hornbill nests in front of the nest cavity than behind the cavity, Whitney *et al.* (1998) demonstrated that there was enhanced germination success of several food plants after passing through the hornbill's gut and that a substantial proportion of seeds were dispersed away from parent trees. They also found a high density of seeds at hornbill middens. Obviously, the fact that large numbers of seeds are being deposited at particular sites should make one question how effective the dispersal is. High seed densities would lead to competition, density-dependent mortality, increased pathogen and rodent attack such as occurs below parent fruiting trees (Coates-Estrada & Estrada 1988)

Some fruit consumers fulfil all the criteria of an effective disperser by depositing seeds in favourable recruitment sites (directed dispersal) (Voysey *et al.* 1999a, 1999b, see Wenny 2001 for a review of directed dispersal). On the other hand, several frugivores may indirectly cause mortality by either deposition in unsuitable sites or by depositing thousands of seeds in a spatially contagious manner (Snow 1962 cited in Howe 1984a). Krijger *et al.* (1997) showed how social behaviour of manakins could lead to aggregation of seeds at lek sites, which are unsuitable sites for germination and recruitment. Therefore the seed shadow produced by lekking manakin males is disadvantageous for Melastomataceae survival. Previous literature had often cited the strong ecological relationship between manakins and the Melastomataceae family as a clear example of plant-frugivore mutualism (Charles-Dominique 1993, Stiles & Rosselli 1993, Snow 1965). This parallels the situation below hornbill nests where seeds of all fruits consumed by nesting females and the young are regurgitated and deposited below nest trees. Similarly, at roost trees where a large number of birds perch for the whole night, all seeds are regurgitated in a small area below the roost tree. Therefore, it becomes important to monitor the fate of dispersed seeds and seedlings to determine actual survival. The mere presence of thousands of seeds does not tell the whole story. Hornbills might be better dispersers while they forage in the forest and perch at trees for shorter times where the seed rain is lower. Holbrook & Smith (2000) have found that foraging hornbills range widely, have long gut passage times and that seeds are dispersed at great distances from parent trees. But it may be argued that tree species that are being dispersed in clumped conditions by hornbills might be better adapted to survive in clumped conditions, as expected by Howe (1989). In addition, despite the high degree of clumping at nests and roosts, escape from soil pathogens near parent trees might still be better for seed and seedling survival.

In this study, both the quality and quantity components of dispersal by hornbills were investigated. Germination experiments with regurgitated and control seeds, estimation of gut passage times and dispersal distances, and monitoring the fate of dispersed seeds and seedlings provided the basis for determining the quality of hornbill dispersal. The quantity component was determined from seed counts at middens below perch trees, nest and roost trees used by hornbills. Apart from this, the relationship between gape sizes of hornbills and some of the other major frugivorous birds in the study area and the fruit sizes consumed by them were examined, to determine whether hornbills were the major consumers and dispersers of large-sized fruits.

4.2. OBJECTIVES

1. To determine how effective hornbills are as seed dispersers in terms of both quality and quantity of dispersal
2. To evaluate the post-dispersal fate of seeds and seedlings and identify the post-dispersal mortality factors

4.3. METHODS

4.3.1. Frugivory by hornbills and other birds: gape size limitations

Hornbill food plant species were known from 4 years of observations at nest trees, fruiting trees, counts at middens below nest, roost and perch trees (detailed in Chapter 5 & 6). Based on opportunistic observations and sightings (> 100 records) and fruit tree watches over the 4-year study period, a list of fruit species consumed by other frugivorous birds was also recorded.

The gape width, bill length, bill width and bill depth of 8 frugivorous birds that occur in the study area were measured using digital callipers at the Bombay Natural History Museum, Mumbai to determine if there was any relationship with gape size and fruit sizes consumed by frugivores. Gape width is defined as the distance between two commissural points. Bill measurements were taken of the Great hill barbet (*Megalaima virens*), Lineated barbet (*Megalaima lineata*), Blue-throated barbet (*Megalaima asiatica*), Hill myna (*Gracula religiosa*) and Fairy bluebird (*Irena puella*), and the three hornbill species, the Great hornbill, Wreathed hornbill, and the Oriental Pied hornbill. Bill measurements of 5 other hornbill species, the

Rufous-necked hornbill, Malabar Pied hornbill, Narcondam hornbill, Plain-pouched hornbill and the Indian Grey hornbill, were also taken. Bill measurements of an important large frugivore, the Mountain Imperial pigeon (*Ducula badia*) and green pigeons (*Treron* spp.) found in the area were not taken, but obtained from Kim McConkey (*unpubl. data*). Fruit dimensions (length, and two diameters (henceforth, referred to as width and depth) and wet fruit weights (edible pulp/flesh along with seed) of 32 species (food species) were measured using a digital calliper and an electronic balance.

4.3.2. Gut passage times

Gut passage times are a measure of the efficiency of seed dispersers, the logic being that the longer the processing time, the greater the likelihood of seed deposition being away from the fruiting (parent) trees and higher the chances of dispersal away from the parent tree. Regurgitation times for thirteen non-fig fruit species and defecation times for three fig species were determined using two captive hornbills (a female Wreathed hornbill and a Great hornbill male) housed in an enclosure near the base camp. Ripe fruits were fed to these two hornbills and the length of time from consumption to regurgitation or defecation was noted for each fruit that was fed.

4.3.3. Germination experiments

Germination experiments were carried out to check seed viability as well as to determine if there were any differences in germination success of regurgitated vs. fallen (control) seeds. Fallen seeds are those that are collected from fallen fruits that have not passed through the hornbills’ gut. Hornbill-regurgitated seeds of 37 food plant species were collected below nest trees, roost trees and perch trees or from seeds that were regurgitated by the captive hornbills. Seeds were also collected from fallen fruits below parent fruiting trees of some of these species, and the fruit pulp was removed manually. Both fallen and regurgitated seeds were planted in homogenized soil in exposed seedbeds near the forest edge in a fenced enclosure. The environmental conditions for both treatments were similar and seeds were monitored till germination. Germination experiments were terminated after 3 months. Experiments were carried out with different sets of species as and when they were fruiting and available. For a few species, experiments were repeated. The number of germinated seedlings at the end of each experiment was counted. Seed viability, that is the proportion of regurgitated seeds that germinated was calculated for all these species. Statistical comparisons of germination success of regurgitated and fallen seeds using Chi-square tests could be made for

12 tree species for which there were adequate sample sizes. For 18 species, only seed viability was assessed because not enough seeds from fallen fruits could be collected.

4.3.4. Dispersal distances

Hornbill seed deposition follows three main patterns. The most visible and obvious locations are below nest trees in the breeding season where the seeds of all fruits that the female and chicks consumes are regurgitated in a small area in front of the cavity. Hornbills roost communally throughout the year, albeit in smaller flocks in the breeding season and these are also major sites of concentrated seed deposition. The last scenario is the most difficult to assess, which is at perch trees when they are foraging in the forest in the daytime. In the breeding season, this includes the breeding males and the non-breeding adults and juveniles that presumably deposit seeds in a more scattered manner during foraging. During the non-breeding season, seeds are scatter-dispersed by hornbills while foraging in the daytime.

The determination of the fate of seeds and subsequent seedling survival below nest and roost trees is relatively easy once these locations are known, but determining the locations of fruiting trees that are regularly visited by hornbills and following their movements and seed deposition patterns is more difficult.

Direct measurements of distances of seeds dispersed by frugivores are rare, because of the difficulties and often the near impossibility of following animals in a natural forest. Ideally it would be necessary to mark or radio-tag animals to track their movements. Hornbills are extremely mobile birds and wary, therefore it is often difficult to follow birds greater than 200-300 m in a dense forest. It would disturb the birds and affect their behaviour and movement patterns. An alternate way of determining dispersal distances was devised by observing foraging hornbills and noting the trees to which they flew to and checking below the trees for deposited seeds, after they had flown away. An estimate of minimum dispersal distances for a small sample (n = 125 trees) could be procured in this way. The method by which this was done is detailed below:

1. The location of fruiting trees in a small patch of 0.75 km^2 in the intensive study area were known and hornbills were regular visitors, so by checking all known fruiting trees and known perch trees, an estimate of dispersal distances could be obtained. These data were collected primarily in the non-breeding season between (September to February) mainly in 1998-99.

   The dispersal distances estimated are only a minimum dispersal distance, since dispersal distances greater than 500 m would be difficult to detect by this method.

Another indirect measure of dispersal distances comes from the observation at roost sites, where hornbills were seen to fly from distances greater than > 2 km to roost sites.

2. By watching hornbills at fruiting trees and collecting regurgitated seeds of fruit species eaten previously, below these fruiting trees as well as regurgitated seeds of that particular fruiting species. Seeds of other species, eaten previously by hornbills are deposited below the crown of the next visited fruiting tree depending on the time spent at the tree. The seed rain below the parent fruiting species includes seeds from fallen fruits as well as those deposited by hornbills and other frugivores. Seeds that were positively identified as having been dropped by hornbills were counted to get a measure of percentage of seeds dropped by hornbills below parent trees. Seeds from fallen fruits usually can be easily identified, because they retain the rotting pulp and to make sure that these were not included in the seed counts on subsequent days, fallen seeds and fruits were removed from under the crown everyday after the fruiting trees were located. Once the location of a fruiting tree and its nearby perch trees are known, these trees were checked everyday for seed rain.

4.3.5. Seed densities below perch, nest, roost trees

Seed densities below 21 nest trees of hornbills were estimated in different-sized rectangular plots (based on area of seed rain at each of these nest trees) during three breeding seasons 1998-2000. Seed counts were made below 4 nest trees in 1998, 7 nest trees in 1999 and 10 hornbill nest trees in 2000. The average plot size was 29.85 m^2 and ranged from 16 m^2 to 42 m^2. Seed densities were estimated below 9 Great hornbill nest trees, 8 Wreathed hornbill nest trees and 4 Oriental Pied hornbill nest trees.

Seed densities were estimated below 90 perch trees used by hornbills in 25 m^2 plots. Seed rain was also estimated below two big *Ficus* trees that were used as both food and perch trees. Plot sizes below these two fig trees were 64 m^2 and 100 m^2. Seed rain estimates below perch trees were carried out only in the non-breeding season.

Seed rain was estimated at 3 roost trees by counting the seeds in 25 m^2 plots. In addition, seeds counted on the first day were subsequently removed and counts were again made on successive days to obtain an estimate of seed rain per day at roost trees.

4.3.6. Post-dispersal seed predation

One of the advantages of dispersal away from parent trees is escape from seed predators. Therefore, to test if seeds suffered greater predation below fruiting parent trees compared to known hornbill perch trees, seeds of fruit species were placed below perch trees and fruiting parent trees and their fate was monitored over 7 to 15 days. Seeds of 5-6 species were used in these experiments and a total of 560 seeds were placed below the crowns of 8 fruiting parent trees and 5 perch trees. In most cases, seed predation could be directly inferred, since remains of seeds and fruits wholly or partly damaged and eaten by rodents were found. In a few cases, seeds simply disappeared and were assumed to have suffered seed predation, though they might have been cached.

4.3.6.1. Seed predation at nest trees: 1998

To examine whether differential seed predation was a factor in low seedling densities of some of the hornbill food plant species, seeds of 6 species were collected and placed in clumps below one Wreathed hornbill nest tree (*Tetrameles nudiflora*) in 1998 and their fate monitored from April to early June. The number of seeds damaged due to predation by rodents and invertebrate predators were counted as well as those remaining intact. Rodent damage to seeds is easily noted, since seeds are thoroughly chewed up into small pieces or gnawed partly where the incisor marks are clearly visible. Invertebrate damage can be identified from the holes bored through the seeds by the larvae of beetles. Seeds of only four species were used, *viz. Polyalthia simiarum*, *Dysoxylum binectariferum*, *Horsfieldia kingii*, and *Aglaia* sp. Very few ripe fruits of the other two species, *Amoora wallichii* and *Chisocheton paniculatus* were available during the study period, therefore the fate of a few available seeds of these species could be monitored only for two weeks.

Data on levels of seed predation in general, were obtained by checking the middens of 6 other Wreathed hornbill nest trees and 3 Great hornbill nest trees periodically (every 10-15 days). The proportion of damaged to undamaged seeds was quantified here. The proportion of damaged seeds was calculated. Chi-square tests were also used to determine if levels of seed predation were significantly different between species.

4.3.6.2. Seed predation at nest trees: 1999

Rodent seed predation rates were also monitored directly below nest trees in 1999 on 43 days during the breeding season. Seed predation rates below two Wreathed hornbill nest trees were monitored on 24 days and on 19 days below 4 Great hornbill nests during the breeding season from April to July. Seed predation rates were monitored for 5 days in April, 10 days in May, 10 days in June, 8 days in July. Total seeds of different species were counted on each day and the number of seeds that were intact and unharmed and those that were chewed up were noted separately, thus giving the proportion of seeds preyed on by rodents for each species below each of the hornbill nest trees.

4.3.6.3. Seed rain and accumulation below nest trees

Seeds falling below the nest tree crown were counted in five 1-m^2 plots below 6 nest trees in 1999. These seeds were counted at intervals of 1-7 days. Here seeds were not removed at all, and allowed to accumulate throughout the breeding season. An unknown proportion of seeds were lost due to rotting and predation. The number of species that made up the seed rain in that breeding season was noted, and finally the number of species that finally germinated was tallied.

4.3.7. Regeneration at nest trees

Seedlings were enumerated in 13 plots laid at the front and at the back of hornbill nest cavities. Seedlings were grouped into hornbill food species and non-food species. The effect of hornbill dispersal was examined by comparing the seedling density of hornbill food plant species at the front of the cavity (where seed rain is high) and at the back of the cavity (little or no seed rain). Since the bulk of the seeds regurgitated by the female and chick fall in front of the nest, it was expected that there would be a high seedling density of food plant species at the front compared to the back, while there would be no such difference in seedling densities of non-food species. If seeds deposited by hornbills do germinate and establish as seedlings, this would give evidence for effective dispersal. All seedlings were identified and counted in 2-m or 5-m radius plots both in front of the cavity and behind the cavity.

4.3.8. Advanced regeneration: sapling densities below nest trees

Saplings of hornbill food species and non-food species were also enumerated at the front and back of the nest cavity (n = 13 plots) to ascertain whether the high seedling densities of the first year are maintained or whether there is drastic thinning out, blurring the effects of hornbill dispersal.

4.3.9. Regeneration below roost trees

Seedlings and saplings of hornbill food plant species were also enumerated in 5-m radius circular plots below 9 and 11 roost trees respectively. Tree density of hornbill food plant species around hornbill roost trees were enumerated in 15-m radius circular plots (n = 15) with the roost tree as the centre.

4.3.10. Seedling densities: nests, roosts and parent trees

Seedlings were counted in 5-m radius plots around 50 parent trees of 10 major non-fig fruit species that are consumed by hornbills. Sample sizes for each of these tree species varied from only 1 tree for 1 species to 7 trees for 2 species and were dependent on the availability of suitable adult trees that were capable of seed production. All seedlings and saplings were enumerated in the plots. The seedling height (measured up to the apical bud), the total number of leaves, and number of leaves affected by herbivory were noted. Seedlings were also counted below 21 nest trees of the three hornbill species (9 Great hornbill nests, 8 Wreathed hornbill nests and 4 Oriental Pied hornbill nests).

4.3.11. Seedling survival: nests, roosts and parent trees

A subset of 502 seedlings was tagged below the 50 parent trees of 10 species. Ten to twenty seedlings were tagged in each plot. In cases, where there were less than 10 seedlings within the plot, all were tagged. All seedlings were tagged and numbered consecutively. Seedlings were monitored from September – December 1998 to July 2000 (21 to 23 months). Towards the end of March 1999, due to the occurrence of a fire, 122 seedlings died. The data has been analysed first with the whole dataset as well as separately, after removing all seedlings that died due to fire, which, incidentally, is a rare occurrence and not an important mortality factor in these forests.

A total of 314 seedlings of 11 species were tagged and monitored below 5 nest trees in 1998-99 for 23 months. At the end of the 1999-2000 breeding season, 433 seedlings belonging to 4 species (97% of 2 species only) were tagged and monitored below 6 nest trees and monitored for 10 months (August 1999 to May 2000). A total of 110 seedlings below 3 roost trees were tagged and seedling survival was monitored for 8 months (October 1999 to May 2000). The seedling cohorts that were tagged below nest trees and parent trees in 1998 were not monitored from the time of germination, but about 2-4 months after. The seedling cohorts tagged below nest and roost trees in 1999, were monitored from the first month of germination. Therefore comparisons of seedling survival, survivorship and mortality rates can only be made among the seedling cohorts of nest and roost trees in 1999 and separately for the seedling cohorts of nest trees and parent trees in 1998.

4.4. RESULTS

4.4.1. Frugivory in hornbills and gape size

Hornbills are largely frugivorous and consume a wide variety of fruit types. These include sugar-rich figs (Moraceae), lipid-rich arils of capsular dehiscent fruits (Meliaceae and Myristicaceae), lipid-rich fleshy single-seeded drupes (Lauraceae, Annonaceae, Rosaceae, Burseraceae, and Palmae) and also sugar-rich watery berries or small drupes of several other families (detailed in Chapter 5 & 6).

Fruits of eighty species (including 9 fig species) were recorded in the diet. About 26% of the tree species recorded in the study area (Appendix 2). While four food plant species were climbers, all the other species are middle storey or upper canopy trees. No shrub species was recorded in the diet of hornbills in the area. Fruits are swallowed whole after testing with the beak for ripeness and softness and seeds of all non-fig species are regurgitated out after processing in the proximal gut. Seeds are always regurgitated intact, smooth, and undamaged, with the pulp having been cleanly removed. The tiny seeds of figs are defecated along with the faeces. Sometimes, the small seeds of *Sterculia villosa* may also be voided out in the faeces.

Gape width ranged from 9 mm for the fairy blue bird to 23 mm for the Great hill barbet, while the minimum gape width of a hornbill species was 36 mm for the Oriental Pied hornbill (Table 1a).

Table 1a. Gape widths of frugivorous birds

Bird species	**N**	**Gape width (mm)**
Great hill barbet *Megalaima virens*	17	23.08 ± 0.25
Lineated barbet *Megalaima lineata*	20	17.50 ± 0.24
Blue-throated barbet *Megalaima asiatica*	20	15.71 ± 0.17
Hill myna Gracula religiosa	20	13.77 ± 0.34
Fairy bluebird Irena puella	20	8.99 ± 0.09
Great hornbill *Buceros bicornis*	3	121.66 ± 14.24
Wreathed hornbill *Aceros undulatus*	3	49.66 ± 3.09
Rufous-necked hornbill *Aceros nipalensis*	1	55.75
Plain-pouched hornbill* *Aceros subruficollis*	3	45.80 ± 0.33
Narcondam hornbill* *Aceros narcondami*	1	34.54
Oriental Pied hornbill*Anthracoceros albirostris*	19	36.01 ± 0.45
Malabar Pied hornbill* *Anthracoceros coronatus*	4	42.23 ± 0.74
Common Grey hornbill* *Ocyceros birostris*	4	48.75 ± 1.43
Mountain Imperial Pigeon *Ducula badia*	-	*ca.* 26 mm

** hornbill species that do not occur in the study area*

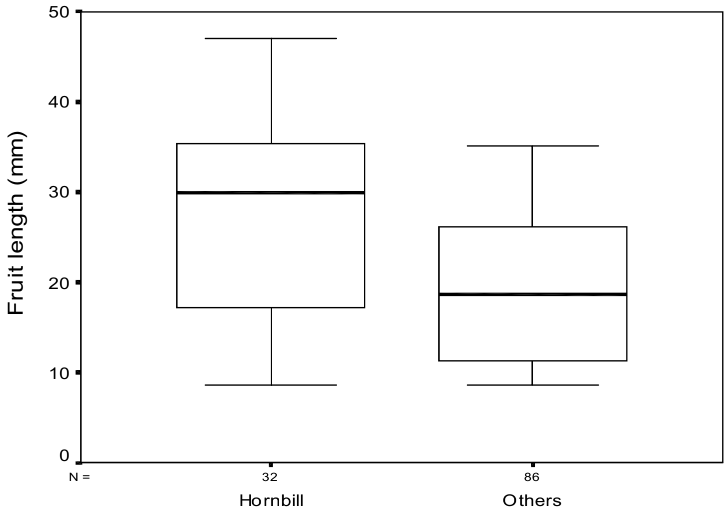
Fruit weights consumed by hornbills ranged from 0.5 g to 46 g. Fig fruits ranged in size from 1 g for *Ficus altissima* to 46 g for *F. hookeri.* While non-fig fruit weights ranged from less than 1 g for *Litsea* sp. and *Sterculia villosa* to up to 19-20 g for *Canarium resiniferum, Beilshmedia, Alseodaphne*. Fruit lengths can range from 7.5-10 mm in some small fig fruit species, *Stryrax serrulatum,*and *Sterculia villosa* to 48-52 mm in *Beilshmedia*, *Horsfieldia kingii,* and *F. hookeri.* Fruit widths ranged from 6 mm to 43 mm and fruit depths from 6 mm to 25 mm. Of the fruit species consumed by hornbills, the smaller frugivorous birds consumed a smaller subset of food species, because they were limited by gape size. But the smaller frugivorous birds also consume many other fruit species not often consumed by hornbills. There was a significant difference in the fruit sizes consumed by hornbills only and those taken by both hornbills and the smaller frugivores (Mann-Whitney U test, p< 0.001) for fruit weight, fruit length, width and depth) (Table 1b).

Table 1b. Size and dimensions of fruits (Mean ± S.E.) consumed by hornbills and other frugivorous birds in the study area

	Fruit weight (g)	**Fruit length (mm)**	**Fruit width (mm)**	**Fruit depth (mm)**
Overall (all fruits)	11.15 ± 0.44 *n = 474*	26.44 ± 0.46 *n = 596*	19.11± 0.27 *n = 552*	16.04 ± 0.36 *n = 269*
Hornbills only	10.13 ± 0.38 *n = 120*	35.58± 0.41 *n = 174*	23.88 ± 0.28 *n = 173*	19.47 ± 0.23 *n = 141*
Both hornbills and other birds	7.85 ± 0.38 *n = 339*	23.96 ± 0.55 *n = 420*	17.13 ± 0.33 *n = 393*	16.53 ± 0.38 *n = 127*

The range of fruit sizes consumed by the smaller frugivores is much narrower than the range of fruit sizes that hornbills are able to swallow and consume because of their large gape size and the method of handling fruits (Fig. 1).

Fig.1. Fruit sizes consumed by frugivorous birds. Hornbills (3 species) and Others (5 species)



Barbets and hill mynas were seen to eat fruits of *Livistona jenkinsiana*, *Pygeum acuminatum* and the smaller-sized *Beilshmedia*, while fairy blue birds were seen to peck even on the medium-sized fruits of *Livistona jenkinsiana.* Only the Mountain Imperial pigeon was seen to feed on fruits of *Horsfieldia kingii* once. Barbets are known to have considerably larger gape sizes compared to overall body size (Snow 1981), an indication of specialized frugivory. However, based on the limited observations, it is unlikely that they are able to swallow and feed on the larger arillate capsular fruits of Meliaceae, Myristicaceae and larger drupes of Lauraceae. The fruit weights and dimensions of 27 food plant species of hornbills are given in Table 2.

Table 2. Fruit weights (wet mass) and dimensions of 27 food plant species of hornbills in Pakhui NP

Tree species	**Fruit weight (g)**	**Fruit length (mm)**	**Fruit width (mm)**	**Fruit depth (mm)**
Actinodaphne obovata	3.35, *n = 40*	19.21, *n = 35*	16.58, *n = 35*	-
Aglaia sp.	-	30.52, *n = 7*	25.44, *n = 7*	20.33, n = 7
Alseodaphne peduncularis	11.47, *n = 19*	39.41, *n = 19*	21.20, *n = 19*	20.60, *n = 19*
Amoora wallichi	4.79, *n = 19*	37.91, *n = 27*	24.58, *n = 27*	19.97, *n = 27*
Beilshmedia sp.	5.59, *n = 22*	35.12 *n = 22*	16.20, *n =22*	15.74, *n = 22*
Beilshmedia sp.	7.16, *n = 25*	24.34, *n = 9*	22.63, *n = 9*	19.40, *n = 9*
Beilshmedia sp.	13.14, *n = 45*	26.41, *n = 35*	24.59, *n = 23*	-
Canarium resiniferum	14.60, *n = 15*	40.20, *n = 15*	25.65, *n = 15*	-
Chisocheton paniculatus	12.12, *n = 13*	35.30, *n = 24*	27.85, *n = 24*	20.16, *n = 24*
Cryptocarya amygdalina	-	29.47, *n = 23*	19.39, *n = 23*	-
Cryptocarya sp.	-	30.66, *n = 13*	22.09, *n = 13*	-
Dysoxylum binectariferum	13.14, *n = 45*	30.67, *n = 19*	24.98, *n =1 9*	18.85, *n = 13*
Ficus altissima	3.16, *n = 22*	18.64, *n =19*	17.29, *n = 19*	-
Ficus clavata	0.66, *n = 15*	-	-	-
Ficus hookeri	24.93, *n = 30*	39.90, *n = 35*	30.38, *n = 35*	22.19, *n = 5*
Ficus macclellandi	4.51, *n = 34*	18.61, *n = 10*	16.68, *n = 10*	16.18, *n = 10*
Ficus nervosa	1.75, *n = 25*	12, *n = 35*	10.91, *n = 35*	-
Ficus sp.	-	13.67, *n = 15*	12.81, *n = 15*	-
Ficus sp.	-	11.74, *n = 8*	10.57, *n = 8*	-
Ficus sp.	-	8.59, *n = 10*	8.34, *n = 10*	-
Horsfieldia kingii	9.06, *n = 21*	35.79, *n = 18*	21.57, *n = 16*	21.29, *n = 5*
Litsea sp.	0.9, *n = 21*	15.72, *n = 39*	11.57, *n = 39*	-
Litsea panamonja	-	20.68, *n = 10*	11.61, *n = 10*	-
Polyathia simiarum	4.94, *n = 16*	32.71, *n = 13*	20.29, *n = 13*	18.86, *n = 13*
Pygeum acuminatum	7.71, *n = 34*	26.11, *n = 9*	18.37, *n = 9*	17.19, *n = 9*
Sterculia villosa	-	10.54 *n = 11*	6.34, *n = 11*	6.26, *n = 11*
Unidentified species	-	34.16 *n = 6*	22.38, *n = 6*	21.14, *n = 6*

4.4.2. Gut passage times

Gut passage times (including all fruits, n =147 feeding sessions, 665 fruits) ranged from 15 minutes to 244 minutes with a mean of 73 minutes ± 36.59 (SD). The mean regurgitation time for non-fig fruits was 75 minutes ± 37.72 (n = 134 feeding sessions). The median gut passage time was 63 minutes. The mean defecation time for fig seeds was 56 ±

14.25 (n = 13 feeding sessions) and ranged from 32 to 84 minutes. The median defecation time was 56 minutes. Gut passage times for the 16 food species are given in Table 3.

Table 3. Gut passage times (Mean ± SD) for 13 non-fig and 3 fig fruit species consumed by hornbills (using 2 captive hornbills), n = 147 feeding sessions with 665 fruits

Food species	**Gut passage time (minutes) (Mean ± SD)**
Actinodaphne obovata	109.67 ± 41.53
Beilshmedia sp.	127.92 ± 46.39
Beilsmedia sp.	60.76 ± 12.69
Cryptocarya amygdalina	33.30 ± 14.98
Cryptocarya sp.	61.83 ± 18.47
Dysoxylum binectariferum	73.75 ± 22.25
Chisocheton paniculatus	84.25 ± 36.07
Pygeum acuminatum	130 ± 20.95
Litsea panamonja	26.50 ± 16.26
Polyalthia simiarum	28.55 ± 8.16
Sterculia villosa	63, n = 1
Actinodaphne sp.2	63, n = 1
Beilshmedia sp.3	61.89 ± 14.57
Ficus nervosa	59.75 ± 16.03
Ficus altissima	54.20 ± 4.92
Ficus hookeri	55.25 ± 22.32

4.4.3. Germination experiments: regurgitated vs. control seeds

A total of 1858 seeds belonging to 37 species were used for germination experiments, out of this, a total of 601 seeds germinated. A total of 1319 seeds regurgitated by hornbills were used, of which 440 seeds germinated (33%), while 161 control seeds (from fallen fruits) germinated out of a total of 539 seeds (30%).

Germination success of regurgitated seeds varied from 12% to 90% (Table 4). Regurgitated seeds were viable and germinated in 18 species. However, relative germination success of regurgitated seeds of these species could not be compared with that of fallen seeds, because of inadequate samples of fallen seeds. Seeds of 7 species failed to germinate, but this was probably due to small sample sizes for these species. Germination success was higher for hornbill-regurgitated seeds for 5 food species in a one set of experiments that were carried out, *viz. Polyalthia simiarum* (χ^2 = 5.6, df =1, n = 30), *Pygeum acuminatum* (χ^2 = 14.3, df = 1, n = 132), *Beilshmedia* (χ^2 = 5.04, df = 1, n = 17), *Livistona jenkinsiana* (χ^2 = 4.01, df = 1, n = 33), *Canarium strictum* (χ^2 = 25, df = 1, n = 68). There was no difference in success for seven other species.

Table 4. Germination success (% germinated seeds) of regurgitated and fallen seeds of some hornbill food plant species (the percentages given are based on total seeds used for each of these species)

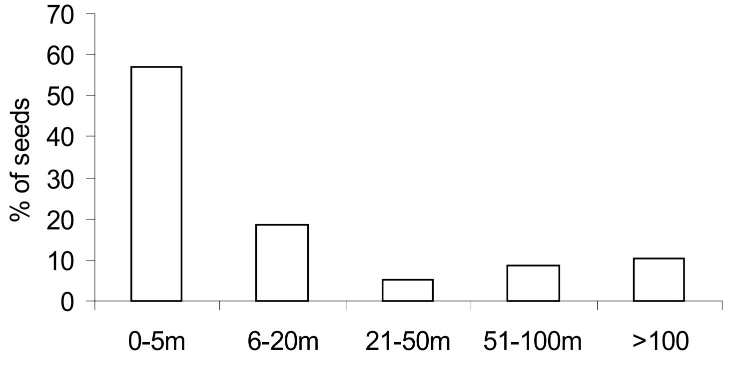
Food species	Regurgitated seeds	Fallen seeds
Aglaia sp.	13.63	33.3
Actinodaphne obovata	22.43	32
Amoora wallichi	37.97	-
Beilshmedia sp.*	11.53	12.96
Cryptocarya sp.	33.84	70.58
Chisocheton paniculatus	62.31	51.40
Canarium resiniferum	64.70	5.88
Dysoxylum binectariferum	27.41	31.57
Litsea panamonja	30	40
Livistona jenkinsiana	70.58	33.33
Horsfieldi kingii	41.17	33.33
Sterculia villosa	90	70
*Polyalthia simiarum**	39.49	43.75
Beilshmedia sp.	17.94	20.23
Phoebe/ Persea	69.76	50
Phoebe lanceolata	80.55	-
*Pygeum acuminatum**	60.29	59.64

**These 3 species showed significantly higher germination success for regurgitated seeds in one set of experiments, but when all seeds of the species from different experiments are pooled, then differences disappeared.*

4.4.4. Dispersal distances

A total of 3085 seeds belonging to 26 species deposited by hornbills below 257 individual trees were counted (n = 470 occasions). Dispersal distances could be estimated for a subset of these (n = 125 trees) since one could not be sure of the seeds' source tree in all cases. Forty-three percent of the seeds (n = 1245) were deposited > 5 m away from parent trees, while 25% of seeds were deposited > 20 m away from parent trees (Fig. 2a). The mean number of seeds (in any particular dispersal event) deposited below perch trees was 10 seeds ± 1.5, while the mean number of seeds dropped below parent trees was 11 ± 1.5, the number of seeds deposited > 100 away was much smaller (5 ± 2.55).

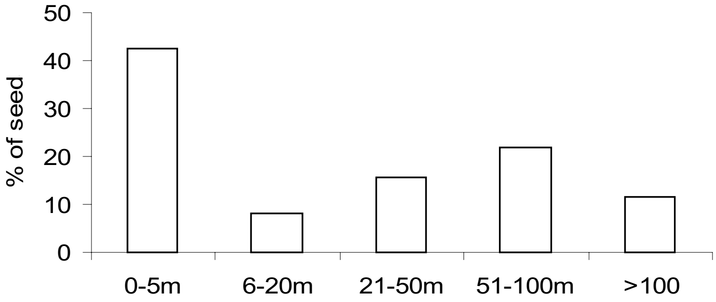
Fig. 2a. Percentage of seeds deposited by hornbills in distance classes from parent fruiting trees, n = 125 dispersal events, 1245 seeds



Seed dispersal distances ranged from 5 m to 400 m from the parent fruiting trees. The mean dispersal distance was 118 m ± 18.32 (SE), but this is not an appropriate measure, since the estimation is restricted towards the detection of dispersal distances of less than 500 m, whereas hornbills do fly much greater distances in the course of a day. The modal dispersal distance might be a better measure to use in this case (300 m), while the median was 50m. This estimate should be taken as being indicative of the minimum dispersal distances and also a measure of what proportion of seeds are deposited below parent trees versus further away.

If the dispersal instances below parent trees are removed, then the mean dispersal distance is 146 m ± 19.07 and the median is 100 m, (n = 52 dispersal events). 42% of the time seeds were deposited greater than 50 m away. Dispersal distances of seeds from a fruiting *Alseodaphne* varied from 5 m to 500 m and the mean dispersal distance was 84 m ± 19.45 (n = 36 dispersal events). Forty-two percent of *Alseodaphne* seeds (n = 184 seeds) were deposited within 5 m of the parent tree, while 48% of seeds were deposited > 20 m away from the parent tree (Fig. 2b). The mean number of seeds of *Alseodaphne* deposited below a particular perch tree (in any particular dispersal event) was 5 ± 1.11 and ranged from 1 seed to 28 seeds.

Fig. 2b. Percentage of seeds of *Alseodaphne* deposited by hornbills in distances classes from a fruiting tree of *Alseodaphne peduncularis*, n = 36 dispersal events, 184 seeds



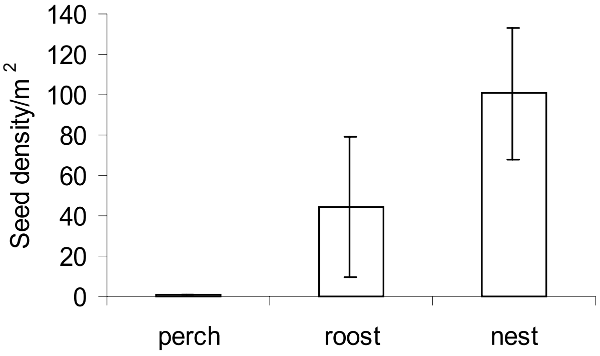
4.4.5. Seed deposition and seed densities below perch/roost/nest trees

Mean seed densities below perch trees used by hornbills (over a 2-3 week period) were about 1/m^2 ± 0.16 (Fig. 3a) while the median seed density was 0.24/m^2 (n = 92 trees, 2622 seeds). The mean number of seeds deposited per day was 7 seeds ± 0.57. The number of species that can accumulate below perch trees ranged from 1 to 9 species depending on the frequency and intensity of use of these perch trees by hornbills over a period of time. Hornbills used particular perch trees in the vicinity of fruiting trees for up to 2-3 weeks.

Seed rain at roost trees was estimated to be 115 seeds per day. Given that these roost sites can be used regularly for 2-3 months, the total accumulated seed rain below individual roost trees can range from 6900 to 10,350 seeds (Plate 5). The mean seed density below roost trees was 44/m^2 ± 34.76, (n = 3 roost trees) (Fig. 3a).

Seed rain at nest trees occurs from March to August (breeding season of hornbills). A total of 68,203 seeds of 21 to 27 food plant species made up the seed rain at 27 nests from 1998 to 2000 (Plate 5). The mean seed density below nest trees was 100/m^2 ± 32.73 (n = 20 nest trees) (Fig. 3a).

Fig. 3a. Density of hornbill-regurgitated and deposited seeds at perch trees (n = 92), nest trees (n = 20) and roost trees (n = 4).



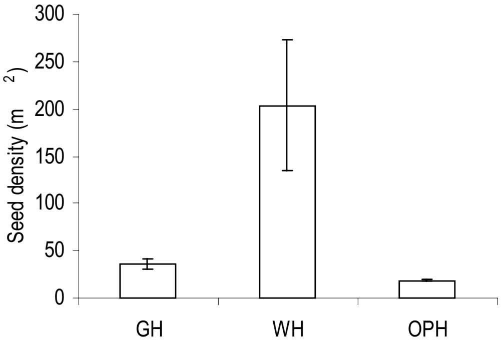
4.4.5.1. Differences in seed deposition among hornbill species

Seed densities were highest below Wreathed hornbill nests, since the Wreathed hornbill feeds on a greater proportion of non-fig fruits than the other two hornbill species (Fig 3b).

4.4.6. Seed predation: parent trees, perch trees and nest trees

Seed predation rates at parent trees (n = 8) were much greater (74% ± 11.99) than at

Fig. 3b. Seed density: nest trees of the three hornbill species.
Great hornbill (n = 9 trees), Wreathed hornbill (n = 8 trees), Oriental Pied hornbill (n = 3 trees)



perch trees (n = 5 trees) (9% ± 6.12) (Fig. 4).

Fig. 4. Seed predation: parent trees (n = 8 trees, 281 seeds) vs. perch trees (n = 5, 279 seeds).

In 1998 in one experiment, eighty percent of *D. binectariferum* seeds were lost due to seed predation below the nest tree, while only 27 % were lost at a location 100m away from the nest tree. There were a significantly greater number of seeds lost below the nest tree compared to further away (χ^2= 13.72, df =1, $p < 0.05$, n = 55).

Rodent seed predation were observed on two species in 1998 below one Wreathed hornbill nest tree. The level of rodent seed predation on the rare species, *H. kingii* was very high (88%, n = 18 seeds), while *D. binectariferum*, also a relatively rare species, suffered considerable seed predation (42.35%, n = 85). Rodent seed predators did not attack the most common species (*P. simiarum*) but about 38% of seeds (n = 79) were bored with small holes by beetle larvae. But even seeds of *Polyalthia simiarum* that are bored by larvae, often germinate successfully. At one count below a nest tree, while 87% of *P. simiarum* seeds with holes were viable, forty percent of seeds had germinated despite being bored with holes, n = 210. Very limited seed predation was noted on another rare species, an *Aglaia* sp., n = 15 seeds.

Chi-square tests indicated that the most rare species (*H. kingii*) suffered a significantly greater seed predation than the most common species (*P. simiarum*), (χ^2 =15.24, df =1, $p < 0.05$, n = 97). There was significantly greater predation on *D. binectariferum* compared to that on *P. simiarum* (χ^2 = 12.88, df =1, $p < 0.05$, n = 103).

Below 4 other nest trees monitored every 2 weeks, rodent damage was relatively lower. Rodents chewed up 15% of *H.kingii* seeds, while 25% seeds of *D. binectariferum* suffered damage due to rodents, beetles or rot. On the other hand, 99% of seeds of

P.simiarum, the most common species, were intact, of which about 24% were germinating. Ninety-five percent of *Aglaia* seeds, a rare species were intact, of which 16% were germinating. None of the *H.kingii* and about 6% of the *D. binectariferum* seeds was germinating.

In 1999, due to a general fruiting failure, hornbills consumed fewer non-fig species. Consequently, the seed rain below nest trees consisted mainly of seeds of 6 non-fig species. *P. simiarum* was never eaten by rodents, but was attacked by insects. The other five were subjected to rodent predation in varying degrees. Four belonged to the Meliaceae and were large-seeded species (arillate capsular fruits), and the single species of Lauraceae (drupaceous fruit) suffered negligible seed predation. Of the four Meliaceae species, only 2 seeds of a single species were recorded under a Great hornbill nest tree once. A total of 1310 seeds were counted below all nest trees, where 20% of all seeds were chewed up by rodents. The percentage of seeds lost due to rotting was not quantified. Seed rain was of 5-7 species at 4 Great hornbill nests (mean – 6.5), but seedlings of only 1-4 species recruited (mean – 2.25). Seed rain was of 10-11 species (n = 2 Wreathed hornbill nests), but seedlings of only 2 species recruited below the nests. Seedling density at Great hornbill nests in 1999 was 3.3/m^2 ± 1.75 (SD) and ranged from 2.2/m^2 to 5.8/m^2. Seedling density at Wreathed hornbill nests was higher (32.2/m^2 ± 19.23 (SD) than that at Great hornbill nests) and ranged from 18.6 m^2 to 45.8 m^2.

4.4.6.1. Seasonal differences in seed predation rates at nest trees

Limited observations also suggested a possible seasonal difference in seed predation rates. In 1998, seeds of *D. binectarierum* suffered heavier predation in April (hot, dry season) (26.5%), while in May-June (rainy season) only 16% were lost. The percentage loss was significantly greater in April than in May (χ^2 = 8.87, df =1, $p < 0.05$, n = 620). There seemed to be a monthly difference in levels of seed predation, with the highest rates of seed predation in April (76%), followed by May (48%), June (34%) and July (6%). The monthly difference could have been as a result of differences in rodent abundance, activity and seed predation rates or simply because one of the species that fruits and is available in July does not suffer much seed predation by rodents. Rates of seed predation were also different for different food species with the highest predation on seeds of *Dysoxylum binectariferum* (78%), followed by *Chisocheton paniculates* (72%), *Amoora wallichi* (60%) and negligible predation on *Phoebe lanceolata* (4%) and none on *Polyalthia simiarum.*

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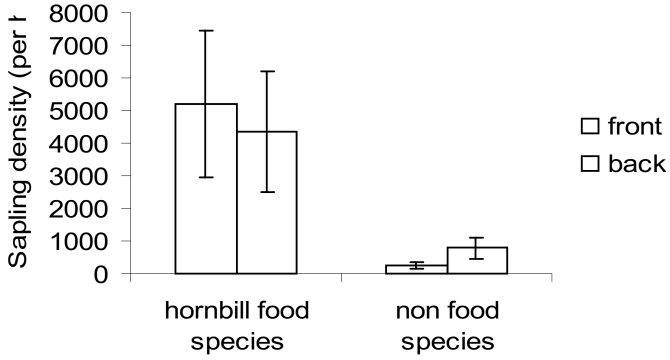
4.4.7. Regeneration at nest trees

Fig. 5a shows the higher seedling density of hornbill food plants in front of the cavity as compared to the back of the cavity, while there was no difference in seedling density of non-food species between the front and back of the nest cavity. It also shows the high seedling density of food plants below nest trees suggesting successful dispersal. Fig. 5b shows that the difference still holds for sapling density of food plants between front and back of the cavity, but sapling density is reduced by orders of magnitude compared to seedling density.

Fig. 5a. Regeneration below nest trees: seedling density at front and back of nest cavity

Fig. 5b. Regeneration below nest trees: sapling density at front and back of nest cavity



4.4.8. Seedling densities below parent trees

Seedling density of 9 food species below parent crowns is shown in Fig. 6a. This demonstrates the wide variability in seedling densities between food plant species below parent trees. It also shows that in three of these species (*Beilshmedia assamica, Cryptocarya amygdalina* and *Polyalthia simiarum*), seedlings germinate and recruit below parent trees in several orders of magnitude higher than in the other species. Interestingly, when one compares seedling density of 6 of these food species (consumed during the breeding season) below both nest trees and parent trees (Fig. 6b), two of these species, *viz. Cryptocarya* sp. and *Polyalthia simiarum*, have much higher seedling density below parent trees than below nest trees. They are also both the highest ranked in terms of abundance below both nest trees and parent trees (Fig. 6b). These species suffer little or no seed predation and seem to be able to germinate well in clumped conditions below parent crowns and therefore also do well below nest trees where similar clumping occurs albeit with a mixture of other species.

Interestingly, in three species, *viz. Chisocheton paniculatus, Horsfieldia kingii*, and *Amoora wallichi,* seedling density is comparatively higher at nest trees, though negligible below parent trees. These species are subject to seed predation by rodents and show overall low seedling densities below both parent and nest trees, but seem to fare marginally better at nest trees. Seedling density at parent trees was highly variable, varying from nil (some trees of *Horsfieldia kingii* and *Amoora wallichi*) to greater than $12/m^2$ below some trees of *Cryptocarya* sp. and *Beilshmedia* sp.

Fig. 6a. Seedling density below parent tree crowns of 9 hornbill food plant species.

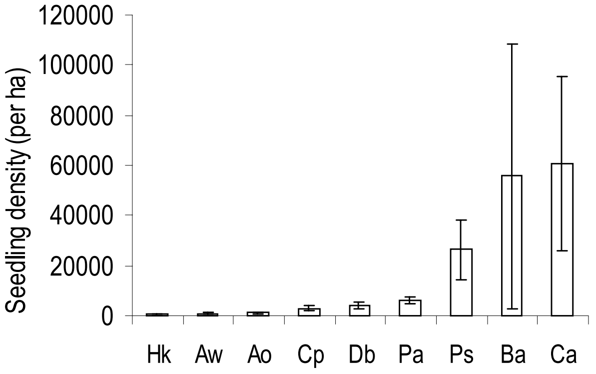
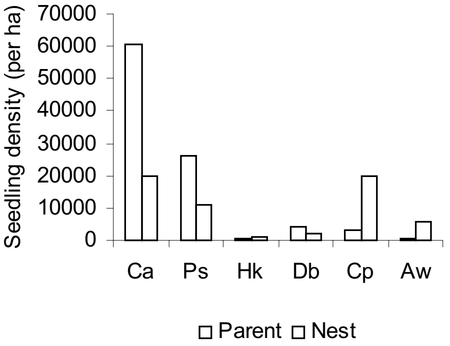


Fig. 6b. Seedling density of 6 hornbill food species: parents vs. nest trees

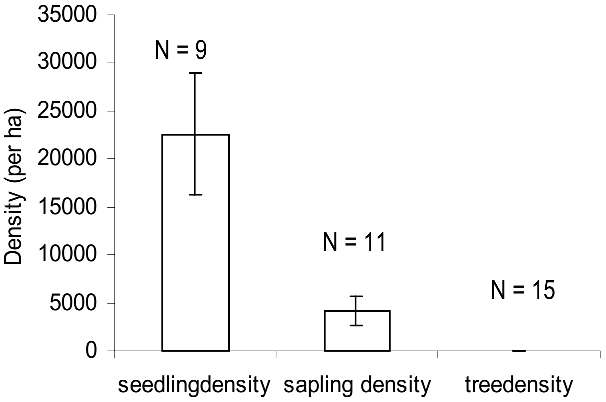


Hk = *Horsfieldia kingii*, Aw = *Amoora wallichi*, Ao = *Actinodaphne obovata*, Cp = *Chisocheton paniculatus*, Db = *Dysoxylum binectariferum*, Pa = *Pygeum acuminatum*, Ps = *Polyalthia simiarum*, Ba = *Beilshmedia assamica*, Ca = *Cryptocarya amygdalina*

4.4.9. Regeneration at roost trees

Mean seedling density at roost trees was 22,598 per ha ± 6382, n= 9 roost trees. Fig. 7 shows the high seedling density of food plant species at roost trees (high initial recruitment), the much reduced sapling density (4165 per ha ± 1512, n = 11 roost trees) and the nearly zero tree density (84 per ha ± 18, n = 15 plots) of food species. Therefore, though seeds germinate and there is high initial seedling density, sapling density is reduced 5-fold, while tree density is reduced a further 49-fold from sapling density.

Fig. 7. Regeneration at roost trees: seedling, sapling and adult stages.



4.4.10. Roost trees and nest trees: seedling survival

At roost trees, while 83% of the seedlings were alive after 3 months, only 35% of seedlings were surviving after 8 months. Unfortunately, seedlings could not be monitored for a longer period. The main causes of mortality were fire, herbivory by cattle, inundation, dessication and shading (due to weed growth forming a dense canopy over seedlings).

Fig. 8a shows the seedling survivorship curve ($\log_{10}lx$) at roost and nest trees in 1999. The survivorship curve does not show a steep decline since 35% seedlings were still alive at the end of the 8-month monitoring period at roost trees. In 1999, 433 seedlings were tagged below 6 nest trees and monitored for 9 months. There was 31% seedling survival in the 1999 seedling cohort at the end of the 9-month monitoring period.

4.4.11. Parent trees and nest trees: Seedling survival

Fig. 8b shows the seedling survivorship below parent trees and nest trees in 1998. Seedling survivorship was low at parent trees, only 13% of seedlings survived at the end of 23 months of monitoring. Towards the end of March 1999, due to the occurrence of a fire (a very rare event in these forests), 122 seedlings died due to the fire. The data have been analysed first with the whole dataset as well as separately after removing the seedlings, which died due to fire. If the fire-affected seedlings are removed, 18% of seedlings survived at the end of 23 months. Similarly, after 6 months of monitoring, a fire in March 1999 destroyed most seedlings tagged in 1998 below 3 of the 5 nest trees. Only 9% seedlings survived at the end of 23 months of the cohort tagged in 1998, but if the fire-affected seedlings are removed, percent survival was much higher (28%).

Fig. 8a. Seedling survivorship below nest and roost trees in 1999.
n = 110 seedlings, below 3 roost trees, 433 seedlings below 6 nest trees

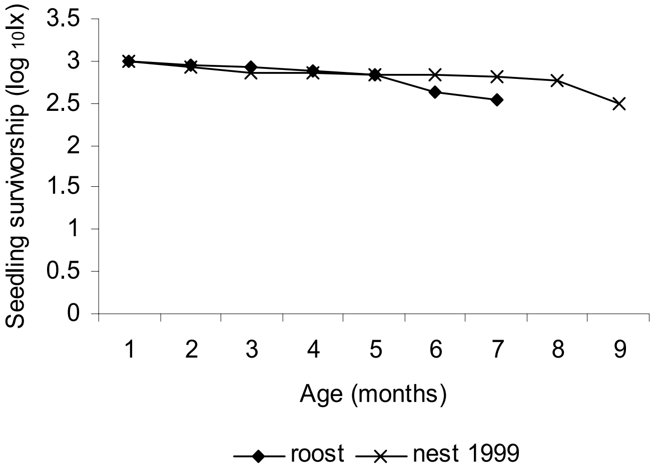


Fig. 8b. Seedling survivorship below parent and nest trees in 1999.
n = 314 seedlings below 5 nest trees and 502 seedlings below 50 parent trees

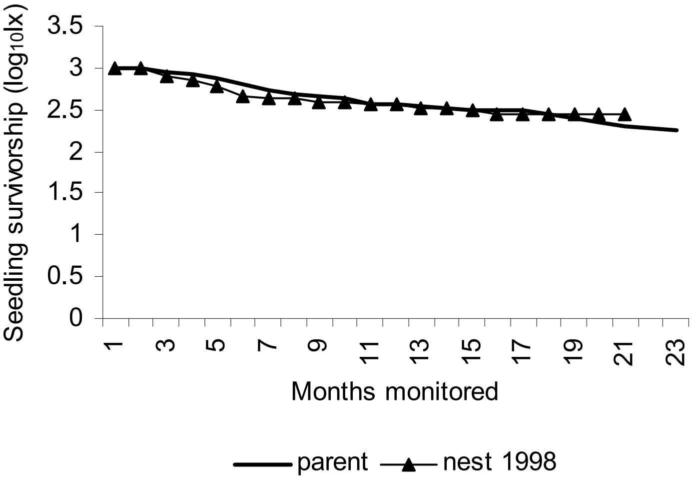
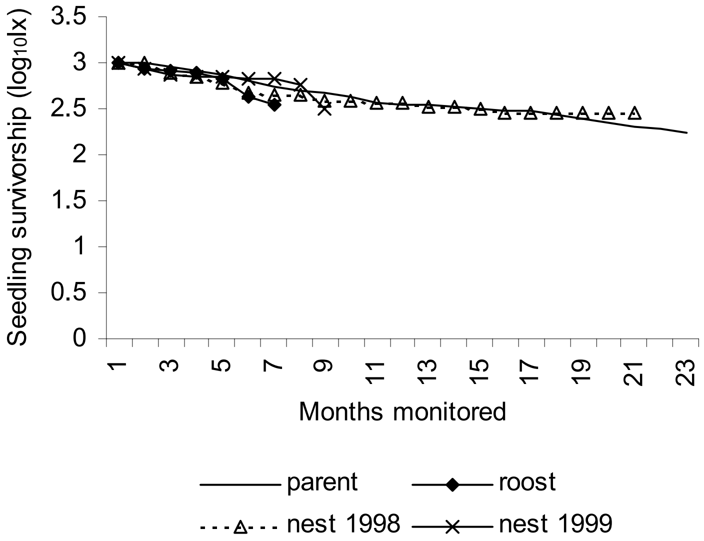


Fig.8c shows the comparative seedling survivorships at parent trees, roost trees and nest trees. The decline in survivorship seems to follow the same pattern and there does not seem to be any difference between the three scenarios.

Fig. 8c. Seedling survivorship: parents, roosts, nests



4.4.12. Differences in seedling survival: nests, roosts, and parent trees

Pair-wise Mann-Whitney U tests were used to test for differences between seedling survival after 1 year and 2 years for seedlings below nest trees and parent trees in 1998, and at 7 months between the seedling cohorts below roost trees and nest trees in 1999. There were no statistical differences in either of the two comparisons.

4.4.13. Age-specific mortality rates

Fig. (9a) depicts the age-specific mortality (qx) of the seedlings below roost trees and nest trees in 1999 and like the survivorship curves, there does not appear to be much difference, except that mortality rates were comparatively higher at roost trees. The seedlings below roost trees and nest trees in 1999 had higher mortality rates, at about 8 months; around the time that monitoring was terminated for these seedling cohorts.

The seedlings below nest trees and parent trees in 1998 had essentially similar rates of mortality, though it was slightly higher for nest trees (Fig. 9b). By the end of monitoring at 23 months, mortality rates were low and the highest mortality for both these conditions occurred after 5 months from the start of monitoring. These seedlings were not monitored exactly from birth, but 2-4 months after germination.

Fig. 9a. Age-specific mortality rates of seedlings below hornbill nest trees and roost trees in 1999.

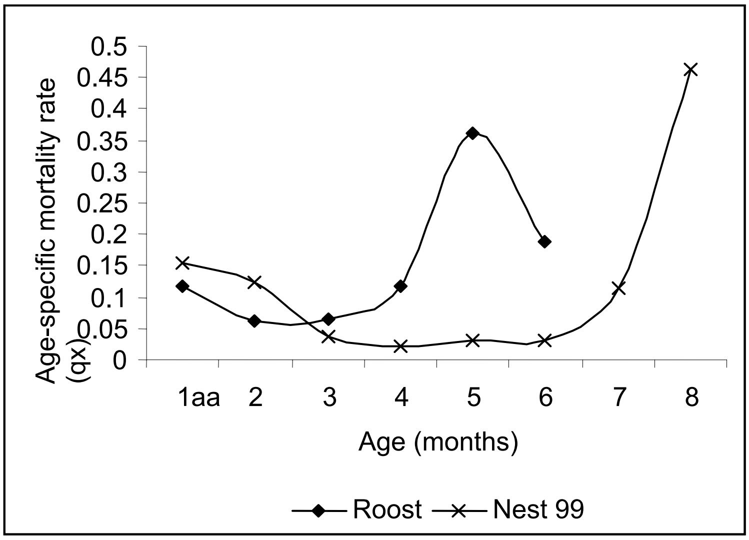
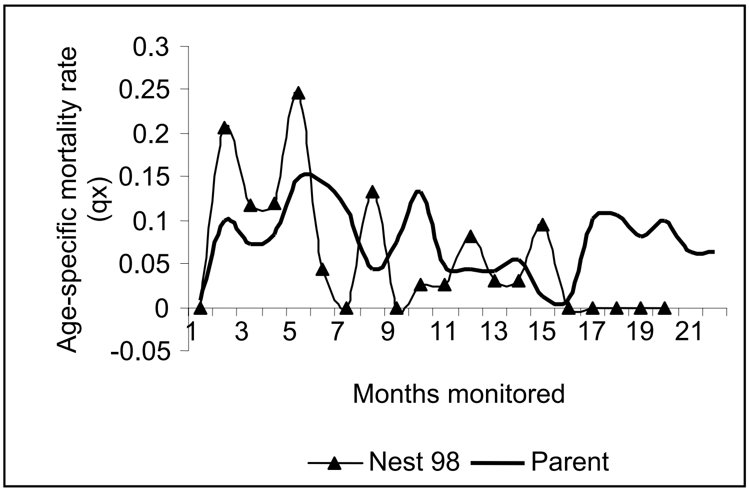


Fig. 9b. Age-specific mortality of seedlings below nest trees and parent trees in 1998. Seedlings were not monitored from germination, but after 2-4 months



The mortality schedules of seedlings (dx) below each of these conditions were log-transformed and a quadratic term (log-polynomial) fitted to standardize and smooth the shape of the mortality curve (Caughley 1977). The mortality schedules of seedlings below roost trees in 1999 (monitored from germination) were low in the first few months, but increased steadily till the end of the monitoring period (Fig. 10a). The mortality schedules of seedlings at nest trees were similar (Fig. 10b), but had a lower mortality than at roost trees, though by the end of the monitoring period, it was higher than at roost trees. The mortality schedules of seedlings at nest trees and parent trees in 1998 were monitored 2-4 months after germination and therefore are not comparable with the seedling cohorts of 1999. The mortality schedules of seedlings below nest trees in 1998 were lower (Fig. 10c) than that of seedlings below parent trees for up to 15 months (Fig. 10d), but then mortality schedules of seedlings below nest trees increased, while mortality schedules of seedlings below parent trees did not show such a drastic decline after this period.

Fig. 10a. Mortality schedules of seedlings below roost trees in 1999, $r^2 = 0.53$, $p = 0.22$

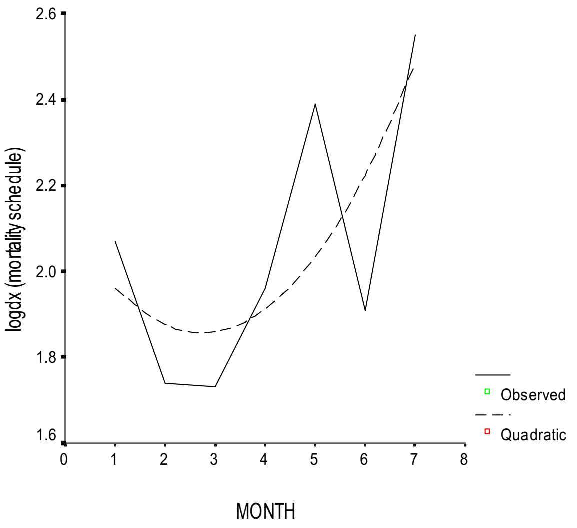


Fig 10b. Mortality schedules of seedlings below nest trees in 1999, $r^2 = 0.88$, $p = 0.002$

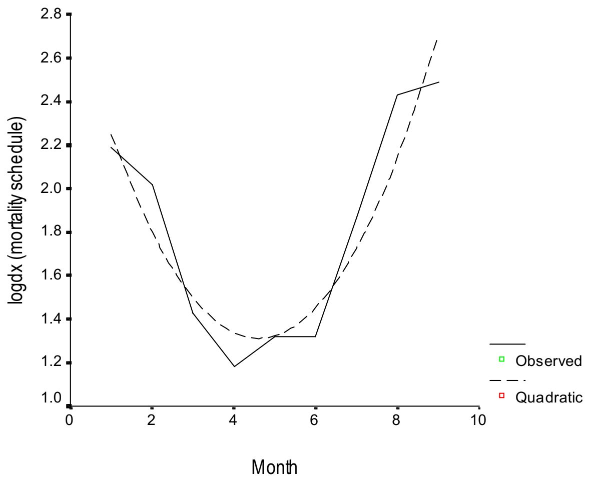


Fig. 10c. Mortality schedules of seedlings below nest trees in 1998, $r^2 = 0.77$, $p = 0.001$

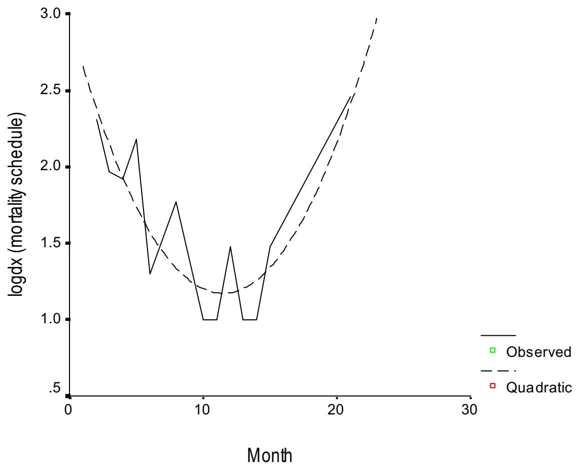
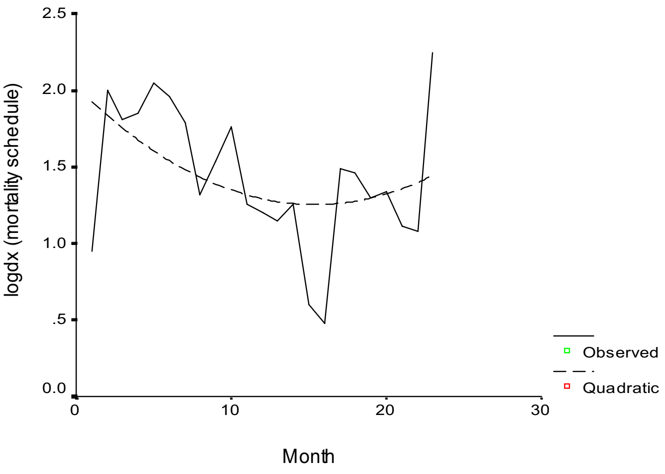


Fig. 10d. Mortality schedules of seedlings below parent trees, $r^2 = 0.19$, $p = 0.12$



4.5. DISCUSSION

4.5.1. Frugivory, gape width and the importance of pan-tropical genera of Meliaceae, Myristicaceae, and Lauraceae

At least seven to ten food plant species (mainly of the Meliaceae, one species of Myristicaceae and some of the larger Lauraceae) were consumed largely by the three hornbill species. Though smaller frugivores have been observed to feed on some of these larger fruit species on occasion, they are not able to swallow the larger fruits like hornbills. They often feed on fruits by pecking at the pulp, unlike hornbills, which toss the fruit and swallow it whole. The only other large frugivore, apart from hornbills, is the Mountain Imperial pigeon (*Ducula badia*) that may be able to consume some of these large fruit species. Levey (1987) had classified frugivores on the basis of their fruit-handling techniques and distinguished between mashers or peckers and gulpers or swallowers. Frugivores that swallow or gulp fruits whole, are likely to be better dispersers because of the way they handle fruits. There are three species of green pigeons (*Treron* genus), which were largely recorded feeding on fruiting figs and very rarely on some of the non-fig species such as *Cryptocarya* spp. It is well known that green pigeons are seed predators of fig seeds because seeds get destroyed in the gizzard of these birds (Lambert 1989b, Jordano 1993).

The relationship of frugivory with gape size was first demonstrated by Wheelwright (1985b) who found that smaller frugivorous birds are limited by gape size, restricting the consumption of larger fruits, while the larger frugivorous birds could eat a much wider range of fruits and were not gape-limited. The absence of other large frugivorous birds in the study area and the large size of these seeds suggest that hornbills are the principal consumers of these species. The dependence of hornbills on these large-seeded Meliaceae, Myristicaceae has been documented in the literature before by Leighton & Leighton 1983, Becker & Wong 1985, Kannan & James 1999).

Specialized frugivores have an upper size limit, which is similar across regions (toucans and cotingas in Neotropics, hornbills in Africa and South-east Asia, large fruit-pigeons in Australasia. The upper size of frugivores may have limited the size of such fruits or vice versa. An upper size limit of 70 mm by 40 mm for oval fruits is the general rule. Some specialized frugivores have very wide gapes in relation to their overall size, undoubtedly an adaptation to allow swallowing of the largest fruits available. Members of the three families with importance to specialized frugivores are consistent in having large seeds, with high protein and fat content (Snow 1981).

A considerable degree of seed predation by rodents (porcupines and other unidentified species) below hornbill nest sites was noted, but a few instances of seed removal or disappearance also occurred. Therefore they could presumably also act as secondary seed dispersers, as has been found extensively in Neotropical forests (Forget 1990, 1993, 1996, Forget & Milleron 1991, Forget *et al.* 1994, 1998, 1999*,* Wenny 1999). Yasuda *et al.* (2000) have recently reported food-hoarding behaviour among nocturnal rats and a diurnal ground squirrel in Malaysian rain forests. They could also possibly help by reducing the high seed densities below nest trees by carrying away seeds.

Other frugivorous mammals in the study area include several species of civets and bats, three species of primates, sambar, barking deer, wild pigs and elephants. The characteristics of fruits and the fruit types taken by these mammals are different (for the most part) from those taken by hornbills, though some of the hornbill food species maybe also consumed by some mammal species. Diurnal arboreal squirrels (*Callosciurus* spp. and *Ratufa* sp.) that are largely pre-dispersal seed predators could presumably disperse some seeds of these species inadvertently while feeding (see Becker & Wong 1985), but no instances of squirrels feeding on seeds or fruits of these species were recorded either during this study or a previous study in the same area (Datta & Goyal 1997). This also holds true for the three primate species in the area, one (capped langur) of which is primarily a folivore, and one (rhesus macaque) is a generalist species that is more common in degraded areas or near human habitation. The third species, Assamese macaque was rarely sighted.

Snow (1981) surveyed the plant families and genera in the diet of frugivores and found that fruits eaten by specialized frugivores are generally large, with large seeds and high nutritive quality. Three families are especially important in this respect, *viz.* Lauraceae, Burseraceae and Palmae. Other such as Annonaceae and Myristicaeae are also important for tropical frugivorous birds (also mammals). Many of these genera are similar and pan-tropical and are of outstanding importance to frugivores world-wide. These genera include *Knema*, *Horsfieldia*, *Myristica*, and *Polyalthia*, which are important for specialized frugivores such as hornbills especially in South-east Asia and Australasia. Lauraceous fruits are especially important in the Neotropics, South-east Asia, and Australasia and are considered as archetypal fruits adapted for dispersal with thin layer of nutritious flesh enclosing single large seed (berries). Other genera listed by Snow (1981) are drupes of the *Elaeocarpus* and arillate capsules of *Sloanea* (Elaeocarpaceae), *Sterculia* in Sterculiaceae, *Trema* in Ulmaceae, *Ficus* in Moraceae and *Cecropia* in Urticaceae (in Neotropics). Figs are important everywhere and some birds feed only on figs. Other important families listed by Snow (1981) are Sapindaceae and Meliaceae, where fruits are arillate and in others such as the Burseraceae and Anacardiaceae, fruits are drupaceous. Rutaceae and Myrtaceae are also important. The two main fruit types produced by selection for dispersal by frugivorous birds are drupes and arillate capsules. Arecoid palms with fleshy fruits are also important in the Neotropics, South-east Asia and Australasia. Many of these important families occur widely and several genera are common, despite the fact that the frugivore assemblage that feeds on them is different. This suggests that the fruits of these pantropical genera had adapted for consumption and dispersal by pre-existing frugivores, prior to the current frugivore fauna (Snow 1981, Fleming 1991).

4.5.2. The quality and quantity of seed dispersal by hornbills

4.5.2.1. Germination experiments

Though seeds of 30 species were found to be viable, germination success varied vastly and although in one set of experiments, seeds of five species showed enhanced germination, overall, for most species, there was no significant beneficial effect. But seed passage through the hornbills' gut is not harmful and seeds are never damaged. A previous study of African forest hornbills found that passage through the hornbill's gut is largely beneficial, though again, the effects were variable for different tree species (Whitney *et. al.* 1998). The evidence for enhancement of seed germination due to passage through an animal's gut has been mixed and is generally considered a less important aspect of the benefit of seed dispersal as compared to seed movement away from the parent plant (Traveset & Willson 1997). While many studies have found that defecated or regurgitated seeds germinate better than control seeds (Izhaki & Safriel 1990, Izhaki *et al.* 1995), others have found no evidence for such enhancement (Izhaki *et al.* 1995), while a few have found delayed germination or lowered germination (references cited in Traveset & Willson 1997). The removal of pulp can enhance germination (Izhaki & Safriel 1990, Witmer & Cheke 1991). Uneaten fallen mature fruits are rapidly attacked by fungi (Traveset & Willson 1997) and may be prone to becoming unviable compared to regurgitated seeds.

4.5.2.2. Gut passage times and dispersal distances

Gut passage times of non-fig fruits in general, were more than an hour, while that of fig fruits were about an hour, though there was wide variability. Although, extensive information on time spent by hornbills on visits to fruiting trees was not collected, the few observations, suggest that hornbills did not stay more than half an hour on a single visit, even on fig trees with large fruiting crops. Visits to the fruiting trees of middle-storey non-fig tree species are usually of even shorter duration, because they usually take a few fruits and fly off to nearby perches. Fruits of the Meliaceae and Myristicaceae usually ripen slowly and on any given day, only a few ripe fruits are found on individual trees, therefore visiting hornbills leave after plucking a few fruit. The only other previous study on gut passage times for wild hornbills (*Ceratogyma* spp. in Cameroon) found much longer processing times (51 to 765 minutes) and also that it was positively related to seed size (Holbrook & Smith 2000). Home ranges varied from 925 to 4,472 ha and maximum seed dispersal distances were 3 to 6 km. The seed shadows for 8 food species suggested that 80% of seeds were being deposited > 500 m from parent trees (Holbrook & Smith 2000). Sun *et al.* (1997) found that three species of turacos were effective dispersers as seed dispersers due to the long gut retention times and the fact that 80% of seeds were deposited away from the parent tree.

Maximum seed dispersal distances could not be estimated for hornbills during this study, but a reasonably high proportion of seeds do get removed away from parent trees when hornbills are foraging in the forest. As pointed out by Whitney *et al.* (1998), hornbills scatter-disperse seeds most of the year, while in the long nesting season, seeds accumulate beneath nest trees, so here they act as clump-dispersers.

According to Howe's (1989) theoretical predictions, species that are generally clump dispersers should show higher levels of resistance to herbivores, pathogens, and seed predators that are sources of density-dependent seed or seedling mortality, but it did not seem from this study that all species dispersed in clumps by hornbills during the breeding season showed similar levels of resistance to seed predators. Species that are consumed in the non-breeding season are also partly clump-dispersed at roost trees. All species consumed by hornbills are partly scatter-dispersed and partly clump-dispersed, so there are no hard divisions between these two. A species like the hornbill can be both a scatter-disperser (perch trees) and a clump-disperser (nest and roost trees), therefore definitions of plant species as being scatter-dispersed and clump-dispersed may be an over-simplication. An extension of Howe's (1989) paper is that species that are generally clump-dispersed should also show greater clumping as adults. But both kinds of deposition patterns can occur for all food plant species of hornbills and, all hornbill food species show clumped adult distributions (Appendix 3). In any case, most tropical forest trees generally show a clumped distribution pattern (Condit *et al.* 2000). Several assumptions would have to be made to infer that the patterns of seed deposition would eventually translate into similar spatial patterns in adult trees. In a test of this hypothesis, Davidar (1983) found that though seed deposition patterns of two mistletoe species differed (one clumped, another singly), adults of both were distributed singly.

4.5.2.3. Hornbill deposition sites: the fate of seeds and seedlings

As already pointed out, deposition of seeds by hornbills at nest trees and roost trees, results in high seed densities due to seed accumulation over a long period. Therefore, at these sites, a high degree of density-dependent mortality at the seed stage (due to seed predators) is likely, as generally occurs below parent trees. While, seeds here may arguably, not suffer mortality due to host-specific soil pathogens that are generally found below parent trees, the fact that seeds of so many species accumulate in a small space will very likely result in competition for resources. While all mortality factors to seeds could not be examined during this study, seed predation rates were found to be high. What complicates matters further, is that there seemed to be differential rates of seed predation on food species, with those suffering less seed predation more common as seedlings (Datta *et al. in press*, and *unpubl. data*). Differential rates of seed predation for different tree species have been demonstrated in a number of studies (Notman *et al.* 1996, Diaz *et al.* 1999). The seeds of *Polyalthia simiarum*, the most common seedling species below hornbill nest trees and indeed one of the most common adult food tree species, were not preyed on by rodents, possibly due to seed toxicity (Pierre-Michel Forget, *pers. comm.*). Wenny (1999) demonstrated that secondary dispersal by scatter-hoarding rodents can re-arrrange the seed shadow of bird-consumed Meliaceae fruit species, resulting in changes in recruitment patterns and that buried seeds had higher germination success. However, there are also high rates of seed predation, so they ultimately have effects that are both positive/negative for dispersal.

The higher seed predation rates in summer than in the wet rainy season, also suggests that rodents may vary in their impacts on seed banks and it could be either related to fluctuations of rodent populations (Gonzalez *et al.* 1989, Meserve *et al.* 1991). Inter-annual variations in fruit crops also affect the latter (Gonzalez *et al.* 1989, Ostfled *et al.* 1996, Murua & Gonzalez 1986). Hence during years of peak abundance, seed-eating rodents may have the potential to modify composition of the seed bank in forests and differentially affect recruitment. This seemed to be the case in 1999, when there was a failure in fruiting or poor fruiting of several species, and though seed rain of up to 11 species occurred below nest trees, recruitment of seedlings of only 2 species (that were not preyed on by rodents) occurred. The level of seed predation is greatly influenced by the availability of alternate and more desirable food sources in the community (Forget 1993, Forget *et al.* 1994). The high seed predation rates suggest that post-dispersal consumption of seeds by rodents affect forest regeneration. Several studies have suggested that differences in plant species seedling recruitment as a result of rodent food choices can partly determine long-term floristic composition in forests (Diaz *et al.* 1999, Wenny 1999).

Of the seeds that do germinate and recruit into seedlings, there is again thinning out due to herbivory, shading effects, and less visible causes such as competition between seedlings for resources. Despite the levels of seed loss due to seed predation, there is high seedling density of food plant species below hornbill nest cavities (especially at the front), therefore one can simply leave it at that, and conclude that hornbills are "good" dispersers. But due to the above-mentioned mortality factors to seedlings, there is a further thinning out at this stage, resulting in a reduced sapling density, when the differences in density of hornbill food species and non-food species at the front and back of the cavity disappear. Obviously in the limited space around the nest cavity, where both seed and seedling densities are so high, only few can survive to adulthood.

Given that, there is such a high degree of wastage of seeds, hornbill seed dispersal especially at nest trees during the breeding season is inefficient from the plant's point of view. On the other hand, the males and non-breeding adults and juveniles do scatter-disperse seeds while foraging in the forest during the daytime. But since hornbills were also found to roost communally even in the breeding season (primarily the Wreathed hornbill), a large number of seeds are again deposited below roost trees. In the non-breeding season, hornbills primarily scatter-disperse seeds in the daytime, but use communal roost sites at dusk where seed deposition patterns are clumped (Chapter 8).

The roost sites that were located and used by hornbills are in successional grassland areas with scattered deciduous trees of *Bombax ceiba* and *Albizzia* spp., next to big rivers or perennial streams (Chapter 8). Seed predation was not a mortality factor in this open roosting habitat. Habitat difference in rates of seed predation and rodent abundance has been reported (Diaz *et al.*1999). Seedling densities are high at roost trees (less so than below nest trees). But both abiotic and biotic factors played a role in preventing successful regeneration at these roost sites. Floods inundate these areas, and fires and cattle grazing are common. In addition, these areas are open, with a high degree of insolation and may not provide ideal conditions for recruitment and growth of the shade-tolerant primary forest species that form part of the hornbills' diet. The few poles and trees of hornbill food species that occurred at these roost sites were of *Bridelia* sp. that is a pioneer species of the Euphorbiaceae family common in open degraded secondary habitats. It was only recorded in the diet of the Oriental Pied hornbill and other smaller frugivorous birds. Therefore, in reality at these roost sites, there is practically no regeneration of hornbill food plants, despite the enormous seed rain. These roost sites have been used by hornbills over 4 years (*pers.obs.*) and presumably even longer (local tribal knowledge) and if there was successful regeneration, the habitat would have reverted to a forest. This demonstrates the unsuitability of these roost sites as viable recruitment foci for primary forest species. One roost site was on a steep cliff face adjacent to a perennial stream. At this roost site, regeneration of food plant species was better than at roost sites in the successional grassland habitat. Presumably, if hornbills also use roosts in other kinds of more suitable forest habitats in the area, regeneration of food plants may be better.

Seedling mortality near parent trees is reported to occur due to pathogens. Greater distance from parent trees and reduced seedling density lead to reduced levels of disease in seedlings resulting in higher survival and establishment (Augspurger & Kelly 1984, Packer & Clay 2000). Therefore, seed dispersal by hornbills away from parent trees to nest trees can still result in higher seedling survival because at least these seeds are escaping pathogens associated with parent trees. But no such effect was seen overall; in that survival at parent trees (of all species overall) and nest trees did not differ significantly. But there was a great degree of variability in seedling density among all the ten tree species, in that while a few species (*Polyalthia simiarum*, *Cryptocarya* sp. and *Beilshmedia* sp.) had very high seedling densities immediately below parent trees, and interestingly had the highest seedling densities below nest trees suggesting that seedlings of these species do well in clumped conditions. The other species (*Amoora wallichi*, *Dysoxylum binectariferum* and *Horsfieldia kingii*) had nil or very low seedling densities below parent trees. These species also survived better below nest trees as compared to below parent trees, but had lower seedling densities than the earlier three species. These species generally do not seem to do well in clumped conditions, but still do better at nest trees than parent trees. Similiar findings were reported for a species of *Aglaia* in Malaysia (Becker & Wong (1985), where they found higher survival away from parents.

The Janzen-Connell hypothesis has postulated that maintenance of tree species richness in tropical forests is possible due to the effects of seed predators, herbivores, allelopathy, and soil pathogens that prevents establishment of offspring near parent trees (Janzen 1970, Connell 1971). Recently Connell (1978) withdrew his support for the hypothesis based on field studies that showed that seed and seedling mortality is not invariably higher near conspecifics adults. Clark & Clark (1984) reviewed studies and found that most evidence supports the Janzen-Connell hypothesis. Hubbell (1979) challenged the hypothesis on empirical and theoretical grounds. An emerging consensus and review of more such comparative studies might show that there are no such hard and fast rules that apply to all species equally, and that while some species might do better in clumped conditions, others may not. The factors resulting in such differences would need to be investigated in more detail. Howe's model (1989) predicted that trees with seeds dispersed in clumps (aggregated) will not suffer density-dependent predation, and will have higher survival of seeds near the parent trees, than other trees that are scatter-dispersed. This seems to be the pattern found in this study based on preliminary evidence.

Reid (1989), Bustamante & Canals (1995) suggested that efficiency and effectiveness are two components of the quality of dispersal. Efficiency is the probability that a seed dispersed by a vector will land in a safe site and germinate; while effectiveness is the proportion of seedlings in a plant population that a seed vector is responsible for disseminating. If hornbills are judged by these two parameters, then they can be considered as both effective and efficient, but these two definitions fail to take into account that ultimately it is seedling survival that matters. Thousands of seeds may germinate, but of those seedlings few survive to sapling stage. There are several mortality factors operating at every stage. The title of Janzen's (1986) paper, "*Mice, big mammals and seeds: it matters who defecates what where*" could be re-phrased to apply to hornbills and seeds: "*it matters who regurgitates, what, how many, where*". The fact that there is death of seeds below roost and nest trees, thinning out of seedling and saplings at nest trees, and near zero regeneration at roost trees, seems to suggest that hornbills are possibly more effective and better dispersers at perch trees where accumulated seed rain, seed density, and seed predation rates are much lower. This implies that dispersal by hornbills to perch trees that are scattered and unpredictable in space and time are relatively "better" sites for seeds, since they escape the heavier mortality at the seed stage below parent trees. Seeds and fruits accumulate below parent trees when the individual is fruiting, and rodents and other seed predators learn the location of these fruiting trees. On the other hand, seeds deposited below perch trees, have a better chance of escaping predation since they are unpredictable in space and time. Detectability is also lower, since seed accumulation and densities are lower. But subsequent regeneration or survival of seedlings at perch trees could not be monitored as part of this study. Therefore, that part of the story remains unanswered. Scatter-dispersed seeds can also occur singly on the forest floor and determining the fates of scatter-dispersed seeds may be of primary importance to the population dynamics and life-history of tree species. The only recent study to have monitored the fates of isolated seeds, found very high rates of seed predation even on isolated seeds, contrary to expectations (Blate *et al.* 1998).

4.6. CONCLUSIONS

The effectiveness of three species of hornbills, the Great hornbill (*Buceros bicornis*), the Wreathed hornbill (*Aceros undulatus*) and the Oriental Pied hornbill (*Anthracoceros albirostris*) as seed dispersers were examined. A combination of (1) germination experiments with regurgitated and fallen seeds of 18 hornbill food species, (2) estimation of gut retention times for 16 food species using 2 captive hornbills, (3) seed counts below 27 hornbill nest trees (breeding season) for 3 years, 12 roost trees and 92 perch trees (non-breeding season) and (5) seedling and sapling counts below nest/roost/perch trees, indicated the importance of hornbills as seed dispersers. Seedling survival was also monitored for 8 to 23 months below 11 nest trees (1998, 1999) and 4 roost trees (1999) and compared with seedling survival below 50 parent trees of 10 hornbill food plant species. Eighty plant species (including 9 fig species) were recorded in the diet of hornbills mainly belonging to the Lauraceae, Meliaceae, Annonaceae and Myristicaceae. Hornbills dispersed about 26% of the tree species recorded in the area. There is also evidence that hornbills are possibly the sole dispersers of several large-sized fruits of some plant species. Seeds regurgitated by hornbills are viable and germinated more successfully compared to control seeds in 5 of the food species, while in others there was no detectable difference. The relatively long gut-retention time of ingested fruits and the propensity of hornbills to move away from fruiting trees after harvesting fruit suggested that they disperse seeds away from the parent trees. But seed deposition patterns below nest and roost trees are spatially contagious compromising the quality of dispersal due to increased seed predation and density dependent mortality. Seed densities at perch trees are much lower than that under nest or roost trees and seed predation rates are also lower suggesting that hornbills play a more efficient role as seed dispersers at perch trees. Though seedling density below nest and roost trees is very high, suggesting successful dispersal, a high degree of mortality at the seedling stage also results in an enormous wastage. Seedling density of hornbill food species is considerable higher than non-food species and it is also significantly higher in front of the nest cavity than at the back of the cavity. But these differences disappear at the sapling stage, by which time further thinning out reduces sapling density by orders of magnitude than those of seedling densities. Roost trees are generally located in open areas near rivers and streams (away from the forest and unsuitable for plant recruitment) and seedlings rarely survived beyond the first year. This was also corroborated by the comparatively low sapling density and nearly zero tree density of hornbill food species around roost trees. Seedlings and saplings fare marginally better at nest trees. The patterns of seedling survival below nest, roost and parent trees are discussed. Although seed deposition patterns are clumped at roost trees, part of what hornbills consume is scatter dispersed below perch trees during the day. In the breeding season too, the seed deposition patterns of breeding males and non-breeding adults and juveniles are scattered as they regurgitate and drop seeds over a wider area. Therefore, though overall, hornbills are effective dispersers, the quality of dispersal is relatively poor at nest and roost trees due to the spatially clumped seed rain that results in high seed and seedling mortality.

Chapter 5. Comparative breeding biology and diet of sympatric hornbills

5.1. INTRODUCTION

Most studies on hornbills have focused on the breeding biology of species possibly because of the unique behaviour of nest sealing and prolonged nest incarceration, unseen in any other bird species. Yet, in spite of the plethora of descriptive natural history studies, studies that have tried to understand the formation and maintenance of pair bonds, reasons for monogamy and for prior female emergence in some hornbills, environmental and behavioural correlates of nesting success, and the evolution of cooperative breeding in some hornbill species are few. These are restricted to Africa, where it has been possible to do experimental manipulations or has been easier to observe in their open desert or savannah habitats (eg. Boix-Hinzen *et al.*2001).

Out of the 23 hornbill species that occur in Asia, as many as 18 species have been studied to some extent. The breeding biology of at least 10 species has been studied in detail (Madge 1969, Leighton 1986, Poonswad *et al.* 1983, 1987, 1998, O'Brien 1997, Kinnaird & O'Brien 1999). A lot of the information on breeding biology of several Asian hornbill species is available from birds that have been successfully bred in captivity (Stott 1951, Poulsen 1970, Choy 1980, Hutchins 1979, Golding & Williams 1986). In India, most studies on hornbills have looked at the breeding biology of single species, such as the Great hornbill (Kannan 1994, Kannan & James 1997), Malabar Grey hornbill (Mudappa 2000), and the Narcondam hornbill (Hussain 1984).

Reproduction is energy-demanding and therefore has to be timed to coincide with suitable environmental conditions (Lack 1968). Environmental cues may be crucial for birds to anticipate or initiate breeding activity, even in seemingly less seasonal environments such as tropical forests (Wikelski *et al.* 2000). Reproductive patterns have usually been found to be distinctly seasonal in tropical forests and are thus believed to be timed with peak food availability (Wikelski *et al.* 2001).

The resource partitioning mechanisms, degree of diet overlap among sympatric hornbills in the breeding season as well as the differences or commonalities in the breeding biology of each species leads to a greater understanding of how sympatric species co-exist and the differing constraints on each species. In addition, a comparison of the nesting chronology, breeding patterns and diet of similar hornbill species in different geographical regions, allows generalizations about the biology of these species and reveals patterns that lead to greater insights into differing ecological constraints on breeding.

Studies on the breeding biology and the diet of sympatric hornbills till now have been restricted to studies in Thailand. Three of these species, the Great hornbill, Wreathed hornbill and Oriental Pied hornbill were the focus of the current study. No previous information exists on the breeding cycle and diet of these species in India, apart from anecdotal observations that suggest that breeding occurs during April-May (Ali & Ripley 1987).

In this chapter, the nesting cycles of the three species are described. The visitation rates and food delivery rates by male hornbills in different phases of the cycle is described and comparisons of the breeding biology of the three species are made. Comparisons are also drawn with data from other studies and related species. The relationship between nesting success and diet diversity, rates and quantum of food delivery, and food availability are examined. Other possible correlates of nesting success such as disturbance, predation, weather and nest damage are discussed. The nesting success between years and hornbill species is examined. Other questions such as why Wreathed hornbill females stay inside throughout the breeding cycle unlike the females of the Great hornbill are addressed. The timing of breeding and period of peak fruit availability is also described and compared with findings from other studies. The breeding season diet of the three species is described and differences between species in their diet and annual variation in diet is examined. The diet breadth and diet overlap of the three species is examined. The importance of fruits, especially non-fig fruits in the diet is highlighted.

5.2. OBJECTIVES

1. To describe and compare the breeding biology of three sympatric hornbill species.
2. To determine and compare the diet composition, overlap, and niche breadth of the three species in the breeding season.
3. To determine the importance of food species in the diet based on its availability and contribution to diet.
4. To determine whether diet diversity and food availability is related to successful nesting attempts.

5.3. METHODS

5.3.1. Nest monitoring

The nesting cycle is defined, as the period starting from female imprisonment to the fledging of young. In the pre-nesting phase, known nest cavities were visited and searched for signs of sealing, visits and activity by hornbill pairs, for seeds and other food matter regurgitated below nest trees. This was done from end of February to April. It is difficult to observe the initial hornbill activity before commencement of breeding. Opportunistic records of nest visiting, and inspection, courtship display, preparation of nest cavities, female imprisonment, entry, and nest sealing were kept. Copulation was never observed.

After female entry occurred, 1-3 observers monitored nests during the breeding seasons of the study period (1997-2000). Nest watches were made during the day for variable periods. Nest watches ranged from 1 to 7 hours (mean 3.5 hours) per day. Observations were mostly carried out in the morning from 0600-0700h till 1300h, though some observations were also made in the afternoons from 1400h to 1700h. Sampling periods of less than an hour were excluded from the analysis of visitation rates. Observations were made from ground hides or platforms from 20 to > 50 m from the nest trees using 7X42 binoculars or a spotting scope. During each sampling period, on each visit by the male to the nest, the number, type and species (whenever possible) of food items delivered, the duration of the visit, and the total number of visits during each sampling/observation period were recorded. Hornbills can store many food items, especially fruits (> 100, in case of figs) in their gular pouch and therefore, are multiple prey loaders, and can deliver many food items during a single feeding visit. Food items are regurgitated by the males and passed one by one to the female. Food items can be identified when the male presents its profile while regurgitating seeds, and brings them out in its beak. At most nests, hornbills either cling to the entrance using their tail as a brace or they perch on knob-like projections on the cavity. Observations on other activities like nest cleaning, sealing, regurgitation, excretion, female and chick vocalizations, and the behavior of the male during nest visits were recorded. Observations on behavioural interactions with other hornbill species or any other animals (such as potential nest cavity competitors or predators) seen at nest trees were also made. The occurrence of moulting was ascertained from old discarded feathers found below hornbill nest trees, either after nest inspection and cleaning by hornbills prior to nest entry or sometimes found during the nesting cycle.

Midden counts were made at the end of each observation session. Nest watches were made on a total of 23 nests over a 4-year period (Table 1). At 14 other nests, midden counts were made to obtain additional information on diet and the condition of nesting.

5.3.2. Diet in breeding season

The most commonly used method for characterising hornbill diet in the breeding season has been by observations of male visits to the nest and identifying the type of food delivered. Earlier studies have not quantified the diet from middens, but mainly used it to corroborate food species identity or acquire additional information on species consumed. During this study, several problems were faced in identifying the fruit species fed (at least 4-5 species had black fruits, fruit sizes of several are similar, and some small fruits that were delivered could also be missed). Though most often during any period, only 2-3 non-fig species were delivered, nevertheless, there was often scope for error, in judging the species of non-fig fruit, therefore for non-fig fruit species, midden counts were relied on. While insect matter and crabs were detected below the nest often, crabs were not observed so frequently during nest watches. Unknown, new or rare fruit species would also be missed if diet were determined only from nest watches. Nest watches were sometimes made at distances of about 40-60 m from a hide in the ground and nest cavities were at heights > than 15 m, therefore food species identity could not be definitive. Hornbills are heavily hunted in the area and are extremely wary at nest trees. They are sensitive to noise, and it becomes difficult to observe them if the hide is too close to the nest tree.

The diet is thus described from a combination of two methods, i.e. middens and nest watches. The advantage of doing this was that many more non-fig species and rare food items in the diet could be recorded by relying on middens. But the number of fig fruits consumed cannot be assessed from middens, since figs are multi-seeded; therefore to determine the proportional contribution of figs, non-figs and animal matter, and to determine food delivery rates, one has to rely on nest watches. In 1997 and 2000 breeding seasons, diet was determined from both methods. In 1998 and 1999, though the number of food items delivered at nests was recorded, the food species was not recorded during nest watches. Contribution of figs to the diet was also estimated in 1999 by from the amount of *Ficus* seeds in fresh defecation below the nest trees. A known number of medium-sized fig fruits were fed to two captive hornbills to see how much defecation is produced from figs of that size to help in this subjective estimation. Additionally, another way to assess relative importance of figs and animal matter in the diet was by counting the number of days in which there were fresh fig defecations and insect remains out of the total number of midden count days.

Therefore, for determination of diet, intensive midden counts were relied on more than nest watches. Seed counts at middens are less disturbing, because the midden can be collected after the observation period in 2-10 minutes by two observers. The area of the seed rain can be marked out initially and periodically cleared of leaf litter and the regurgitated seeds can be collected. The counted seeds were removed from below the nest.

All fruit species consumed during the breeding season were collected for identification. Fruits and seeds were weighed wet with an electronic balance to the nearest 1 g and measured (longest length, width, and, depth) with digital callipers. Fruits > 2 cm in length were defined as being large, while fruits between 0.5 – 2 cm were considered medium-sized fruits, small fruits were < 0.5 cm in length. Here, fruits are defined as the part that is selected and swallowed by hornbills (along with seed) and not the whole fruits. Fruits were also classified by morphology – such as drupes (both single-seeded fleshy fruits with or without an outer skin), dehiscent arillate single or multi-seeded capsules, berries, and figs. Apart from figs, most food species recorded were single seeded fruits, so a count of the number of seeds below the nest approximates the total numbers of fruits. In the study area, four species of the Meliaceae have large dehiscent capsular fruits that bear 3-4 seeds that are partly or wholly covered by the edible aril. Similarly, the whole fruit of *Sterculia villosa* has an outer covering that splits on ripening, exposing the seeds; the edible part is a very thin black layer on the seeds. Hornbills pluck out all these arillate seeds singly and swallow them, regurgitating each seed singly, therefore each arillate seed was considered as a single fruit.

5.3.3. Data analysis

5.3.3.1. Breeding biology

Descriptive statistics were used to depict the length of breeding cycle, incubation period and other parameters of the breeding biology. The nesting cycle was divided into the pre-hatching phase (egg-laying to chick hatching) and the nestling or post-hatching phase (chick hatching to chick fledging), based on estimated dates of chick hatching as well as information from previous literature on these species.

The weekly visitation rates and food delivery rates of the three hornbill species were calculated based on the number of visits and number of food items delivered in the total number of hours sampled per week for each species. Differences between the visitation rates and food delivery rates in pre and post-hatching phases of the nesting cycle were also tested for statistical significance using Mann-Whitney U tests (Seigel & Castellan 1998). The food delivered at nests was broadly classified as fig, non-fig fruits and animal matter for analysis and differences between the rates of delivery of these food types during the two phases of the nesting cycle are depicted graphically.

5.3.3.2. Diet in the breeding season

Overall diet richness (total number of species recorded) of each hornbill species was represented simply by the total number of fig, non-fig and animal species recorded in the diet from both middens and nest watches.

Niche breadth (for non-fig species) of each of the three hornbill species was calculated using Levins measure (Levins 1968), standardized to a scale of 0-1 as suggested by Hurlbert (1978). The total number of non-fig species eaten at least once by at least one of the hornbill species in the 4 breeding seasons was used to calculate the index. Overlap in diet of different pairs of species (for non-fig species) was assessed using Pianka (1973) index, which is a modification of the MacArthur and Levins (1967) index. The latter is an asymmetrical index, which, for any given pair of species, separately estimates the extent to which the diet of the first overlaps on the second and the second on the first. Pianka (1973) devised a modification of the previous index that is similar but symmetrical between species, so overlap between two species is identical.

Importance in the diet was represented in two ways:

1. By number of fruits of each species (middens)
2. By total biomass of each species (middens)

Similarity in non-fig diet composition between hornbill species and differences between years was also examined by calculating the Morisita's similarity index (Morisita 1959 cited in Krebs 1989) for all nests for all years. This index was formulated for counts of individuals and varies from 0 (no similarity) to 1 (complete similarity). A cluster analysis was run on the similarity matrix to examine whether there were intra and interspecific/annual differences in non-fig species diet composition. The seed count data at middens of 24 hornbills nests (1997-2000) were used for this analysis. Though midden count data was available from 32 nests, only data from 24 nests that were observed during most of the nesting cycle and where sample sizes of seeds were > 100 were used for calculating the non-fig diet similarity matrix. To determine the relationship between resource use (non-fig fruits) and foraging patterns in the breeding season, the spatio-temporal variation in resource availability was determined in a semi-quantitative manner following a method suggested by Heithaus *et al.* (1975).

5.4. RESULTS

5.4.1. The nesting cycle

The details of the number of hours of observation of 23 hornbill nests during the 4 breeding seasons are given in Table 1.

Table 1. Nest watches for the three hornbill species during 4 breeding seasons (1997-2000)

Year	Non-intensive nests	Intensive nest watches	Total hours of observation	Great hornbill		Wreathed hornbill		Oriental Pied hornbill	
				Nests	Hours	Nests	Hours	Nests	Hours
1997	-	2	277	-	-	2	277	-	-
1998	6	4	276	2	109	2	167	-	-
1999	4	6	232	3	68	2	148	1	16
2000	4	10	682	3	239	4	325	4	118
Total	14	23	1467	8	416	10	917	5	134

Intensive nests – Nests that were observed regularly on a weekly basis for nest visitation, food delivery rates and midden data, Non-intensive nests – visited only occasionally to check nesting status and obtain additional information on diet.

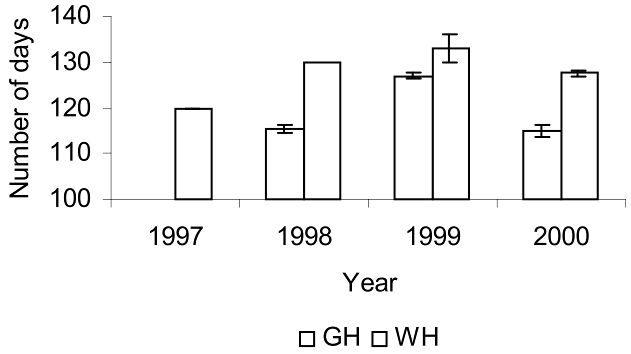
The breeding season spanned 20-22 weeks (March to August), though pre-breeding activities such as courtship and nest inspection were observed from January onwards. The females entered the nest cavities only in March. Courtship feeding was seen in Great hornbills, where males presented females with fruits. Both Great hornbill and Wreathed hornbill pairs were seen visiting nest trees, and inspecting nest cavities during January-February. Great hornbills were also observed chasing away other hornbills that arrived on nest trees.

In 1997, 1998 and 2000, nesting initiation occurred in mid to late March, while in 1999, nesting commenced earlier in 1st week of March (Fig.1). In 1999, there was a long dry period with practically no rainfall for 3-4 months in the winter and nesting may have been initiated earlier, in response to an early and prolonged dry spell, while in the other three years, distribution of rainfall was normal in the preceding winter months. Nesting initiation coincides with peak flowering (March-April) in the area and a relatively dry period in all years. In general, the breeding cycle and chick fledging coincided with periods of high fruit availability (Fig. 1), but immediately after fledging, there was a seasonal low in fruit availability in the lowland habitat (detailed in Chapter 3 & 6).

The length of the nesting cycle, (from female nest entry and sealing to chick fledging) varied between species (Table 2). The nesting cycle of the Great hornbill ranged from 110 to129 days, while that of the Wreathed hornbill was 120 to140 days. The exact length of the nesting cycle of the Oriental Pied hornbill could not be ascertained, but it was estimated to be 93-97 days. The length of the nesting cycle and breeding initiation varied between years and was longer for both Great hornbill and Wreathed hornbill in the 1999 breeding season. The length of the nesting cycle was longer in 1999 for Great hornbills (127 days) as compared to 115 days in 1998 and 2000.

Length of nesting cycle showed less variation between years for Wreathed hornbills, though again in 1999, the cycle was longer than the other years (Fig. 2). 1999 was an unusual year in that, nesting initiation was earlier than other years, there were fewer nesting attempts by Wreathed hornbills, and the length of the nesting cycle was longer than other years especially for the Great hornbill (Fig. 2). Nest entry dates of the Great hornbill were earlier than that of the Wreathed hornbill in all years, though there was yearly variation in initiation of nesting (Table 2). There was within-year synchrony in nest entry dates and fledging dates for both the Great hornbill and Wreathed hornbill.

Fig. 2. Length of nesting cycle: variation between species and years



In most years, Wreathed hornbills initiated breeding in the 3rd-4th week of March, barring 1999, when nesting commenced early in the 1st week of March. Great hornbills showed a similar pattern of nesting initiation dates, except that they commenced nesting about a week earlier than Wreathed hornbills. Thus, in most years, nest entry occurred between the 2nd to last week of March, though in 1999, nest entry occurred earlier in the 1st week of March. The length of the nesting cycle in Great hornbills was shorter by about 2 weeks. Great hornbills usually were out of the nest by mid-July, while Wreathed hornbill nesting often continued till 2nd week of August.

Females sealed themselves in nest cavities using mainly their faeces that were composed mainly of fig seeds, fruit pulp, and insect chitin. Wood chips, down feathers, shreds of *Polyalthia* seeds and little mud were also present in the sealing plaster. The weight of the sealing plaster was 534 g at one Wreathed hornbill nest. Males did not participate in nest-sealing activity nor were they seen to bring mud for sealing. Partial moult or no moult was noted in both the larger hornbills species. It was not possible to determine the exact dates when eggs were laid or when chicks hatched, but it was assumed that egg-laying occurred 2-3 days after nest entry. Chick hatching was estimated to be between 40-55 days for both the larger hornbills. Chick calls were first heard 73 days and 43 days after nest entry at one Great hornbill nest and one Wreathed hornbill nest respectively. In the Great hornbill, female emergence occurred 88 –109 days (mean 96 days) after the date of nest entry and nestlings remained in the nest alone for about 8 to 37 (mean 24 days). Nestlings continued to be fed by both adults until fledging when it was approximately 65-80 days of age. Chick emergence and fledging occurred earlier for the Great hornbill than the Wreathed hornbill. All the three hornbill species produced a single chick, though the Oriental pied hornbills are known to produce more than 1 chick.

5.4.1.1. Nest visitation and food delivery rates at Great hornbill nests (1998-2000)

In 1998, two Great hornbill nests were observed from the 3rd week of nesting. Male visitation rates increased after chick hatching around the 6th week reaching a peak in the 9th and 11th week of nesting. In 1999, there was no discernible peak in visitation rates following chick hatching. Visitation rates by the males to the nest were also lower in 1999 compared to other years. In 2000, visitation rates were steady during most of the nesting cycle, increasing marginally after chick hatching and again during the 15th week after female emergence (Fig. 3a).

Food delivery rates on the other hand were more similar between years, though the peaks of food delivery varied between years. In 1998, peak food delivery rates occurred around week 11, and a second peak was in week 7-8. In 1999, peak food delivery occurred late in the nesting cycle in week 15. In 2000, peak food delivery occurred around week 7-8 and remained mostly steady throughout the rest of the cycle (Fig. 3a). Visitation rates were largely uniform for most of the nesting cycle (about 1 visit in 2 hours, but increased marginally around weeks 7-8, week 11 and again around week 15 (Fig. 3a). The mean visitation rate in the pre-hatching phase (commencement of nesting to week 6) was 0.52/hr and 0.57/hr in the post-hatching phase (week 7 to chick fledging). Mean food delivery rates were also not different between the pre and post-hatching phases; with about 7 items being delivered per hour during both phases. The maximum number of food items seen delivered on a single visit by a Great hornbill male was 80. The delivery of animal matter increased after chick hatching (week 7). There was also a clear pattern in delivery of fruit types. While fig fruit delivery was higher during the pre-hatching phase, non-fig fruit delivery increased after hatching (Fig. 3b).

Fig. 3a. Nest visitation and food delivery by Great hornbills (1997-2000)

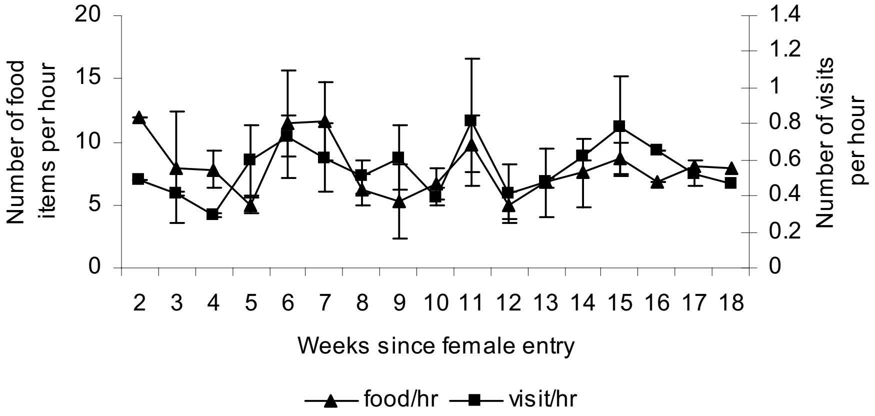
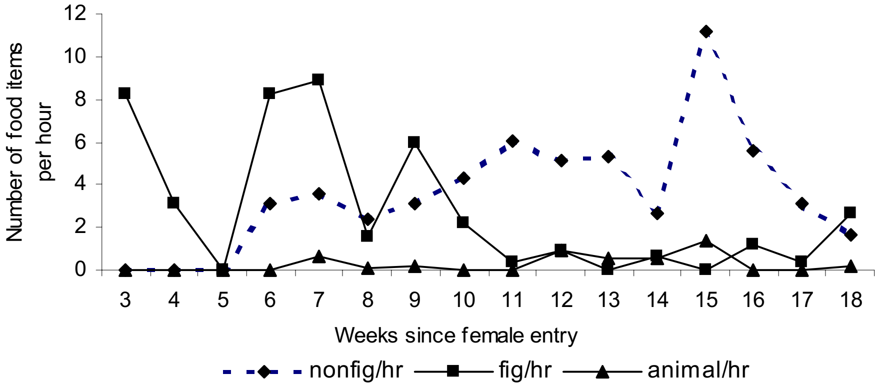


Fig. 3b. Weekly delivery of different food types during the nesting cycle of Great hornbills



5.4.1.2. Nest visitation and food delivery rates at Wreathed hornbill nests (1997-2000)

In 1997, visitation rates were steady throughout the cycle except that it peaked around week 12 and also increased after chick hatching marginally, declining in between. In 1998, visitation rates also increased steadily after week 6 and reached a peak between weeks 14-16. In 1999, nests were not observed in the initial part of the nesting cycle and observations commenced only from the 6th week, but visitation rates again peaked between weeks 12-14. In 2000, a similar trend was seen with visitation rates increasing steadily after week 7 towards the latter part of the nesting cycle and peaking between weeks 13-15.

Patterns in visitation rates were quite similar between years, increasing steadily post-hatching and peaking in weeks 13-16. Thus, overall there is a trend of visitation rates of Wreathed hornbill males increasing steadily after chick hatching, but the peak visitation was in the later part of the nesting cycle and not immediately after hatching. Visitation rates tended to be around 1 visit in 2 hours during most of the nesting cycle to more than 1 visit per hour after chick hatching (Fig. 4a).

Food delivery rates were highest after chick hatching in 1997 and 2000, though frequency of visits was higher later on in the cycle. In 1998 and 1999, food delivery rates closely followed patterns in visitation rates and were highest towards the later part of the cycle. Overall, patterns in food delivery rates were similar between years, though in 1998 and 1999, delivery rates increased later on in the cycle while in 1997 and 2000, the increase was immediately after chick hatching. During peaks in food delivery up to 20-35 items maybe delivered in an hour, while at other times 5 to 10 items maybe delivered per hour (Fig. 4a). But the mean visitation rates were similar in the two phases. In the pre-hatching phase (commencement of nesting to week 6), the visitation rate was 0.52/hr and in the post-hatching phase (week 7 to chick fledging), it was 0.59/hr. Mean food delivery rates were also not different between the pre- and post-hatching phases, with about 10 items being delivered per hour. The maximum number of food items seen delivered on a single visit by a Wreathed hornbill male was 102.

The delivery of animal matter also increased after chick hatching (week 7). There was also a clear pattern in delivery of fruit types. Fig fruit delivery was higher during the pre-hatching phase, while non-fig fruit delivery occurred throughout the cycle, while animal matter in small amounts was delivered in the later part of the cycle (Fig. 4b).

Fig. 4a. Nest visitation and food delivery by Wreathed hornbills (1997-2000)

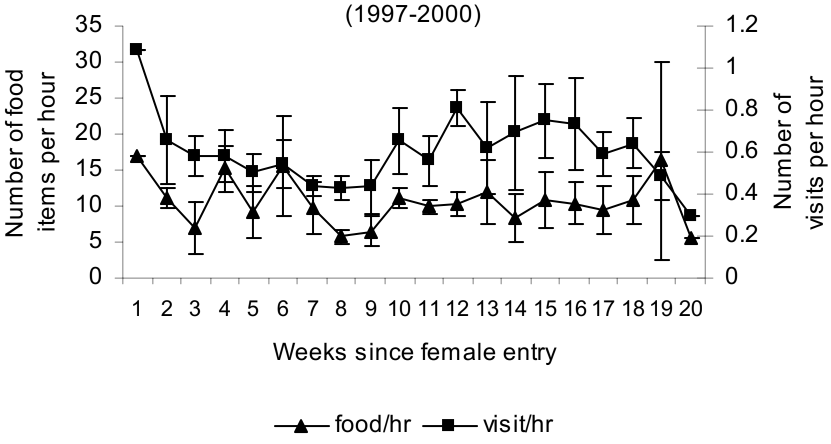
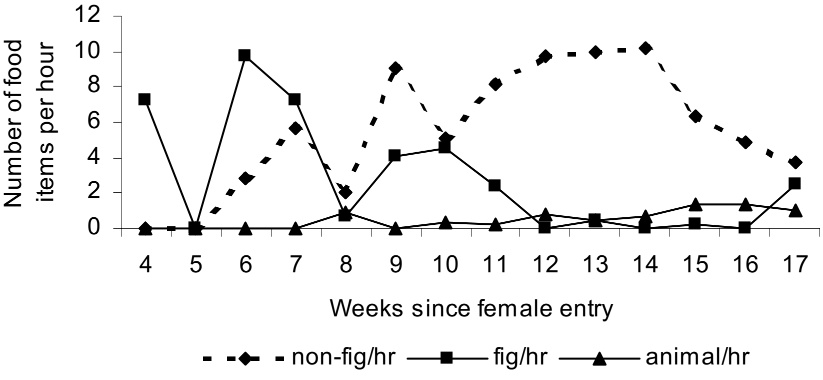


Fig. 4b. Weekly delivery of different food types during the nesting cycle of Wreathed hornbills



5.4.1.3. Nest visitation and food delivery rates of the Oriental Pied hornbill (1999-2000)

Actual dates of nest entry could not be observed for Oriental Pied hornbills, as all nests of this species were discovered only after initiation of nesting. Nesting dates were estimated to be in the 1st week of April, based on literature on nesting durations (Hutchins 1979, Poonswad *et al.* 1987). In addition, dates of fledging were known for 3 nests, and therefore, the approximate dates of nest entry based on the reported duration of nesting of this species from previous studies were ascertained.

Nest visitation rates by Oriental Pied hornbill males were noticeably lower in the pre-hatching phase and increased steadily after the 8th week. Nests of Oriental Pied hornbills were observed only in 1999 and 2000. In 1999, the single nest observed was abandoned around the 14th week, when the remains of a chick were found below the nest. In 2000, three nests of the Oriental Pied hornbill were observed and male visitation rates increased after chick hatching. Thus overall, there was a similar pattern in increased number of visits in the post-hatching period (Fig. 5a). While in the pre-hatching period, visitation rates were around 1 visit or less in 2 hours, in the later part of the nesting cycle, it increased to more than 1 per hour. Food delivery rates followed a similar pattern, with an increase from about 6 food items per hour to about 15 items per hour.

The mean visitation rate in the pre-hatching phase (commencement of nesting to week 5) was 0.41/hr and 0.62/hr in the post-hatching phase (week 6 to chick fledging). Mean food delivery rates were 2.41 per hour in the pre-hatching phase and 6.37 per hour in the post-hatching phases. The maximum number of food items seen delivered on a single visit by an Oriental Pied hornbill male was 52 fig fruits (*Ficus nervosa*).

The delivery of animal matter increased after chick hatching (week 7). There was again a clear pattern in delivery of fruit types, while fig fruit delivery was higher during the pre-hatching phase, and non-fig fruit delivery increased after hatching (Fig. 5b).

Overall there was no significant difference in visitation rates or food delivery rates between the two phases (pooled for all hornbills and all years together, Mann-Whitney U tests, $p > 0.1$, $n = 16$ nests).

The duration of nest visits by the male hornbills and the duration spent in feeding by the three different hornbill species in the different years are shown in Table 3.

Fig. 5a. Nest visitation and food delivery by Oriental pied hornbills (1999-2000)

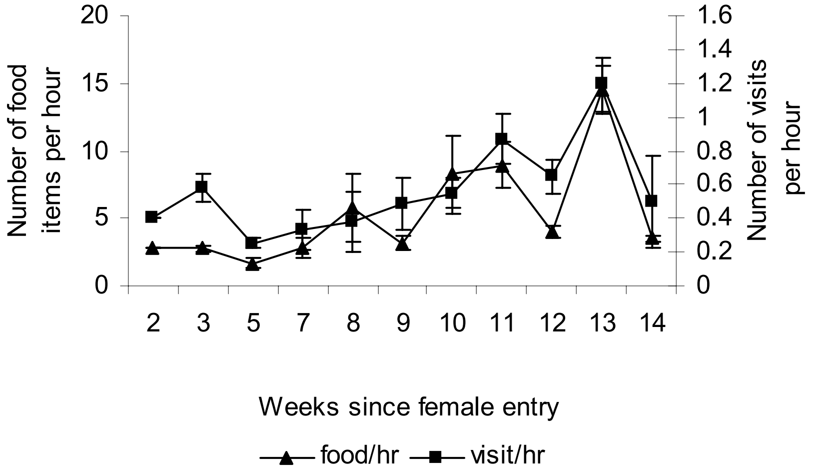


Fig. 5b. Weekly delivery of different food types during the nesting cycle of Oriental pied hornbills

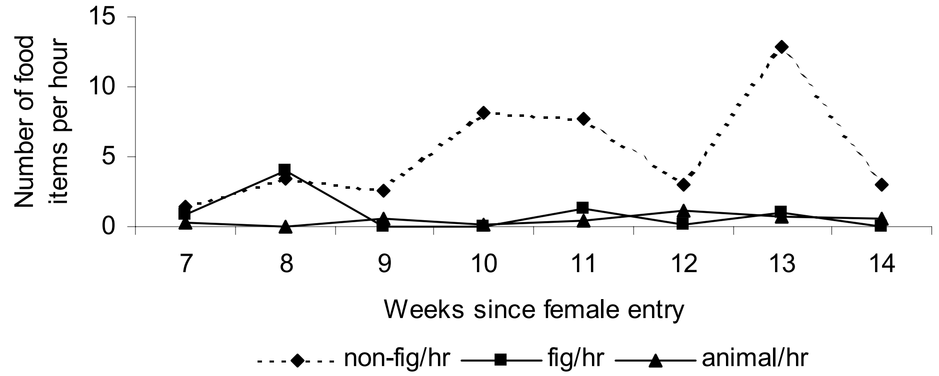


Table 3. Mean nest visitation, food delivery rates, feeding durations and visit durations at nests by males of the three hornbill species in all the four breeding season (1997-2000)

Hornbill species	Year	Visit/hr	Food/hr	Food items/visit	Feeding duration (min)	Visit duration (min)
Wreathed hornbill N = 9	1997	0.39 ± 0.03	10 ± 1.75	18 ± 2.28	4 ± 0.31	28 ± 3.24
	1998	0.70 ± 0.05	10 ± 1.36	14 ± 1.75	4 ± 0.33	15 ± 1.98
	1999	0.72 ± 0.14	15 ± 3.34	18 ± 1.25	3 ± 0.31	14 ± 1.82
	2000	0.70 ± 0.04	12 ± 1.62	17 ± 1.43	2 ± 0.08	6 ± 0.45
Great hornbill N = 8	1998	0.59 ± 0.18	7 ± 1.62	10 ± 1.53	2 ± 0.24	9 ± 1.30
	1999	0.45 ± 0.02	9 ± 0.73	18 ± 1.09	1± 0.16	11 ± 2.43
	2000	0.62 ± 0.05	9 ± 1.06	14 ± 1.45	2 ± 0.11	14 ± 1.44
Oriental Pied hornbill N = 4	1999	0.36 ± 0.03	3 ± 0.91	9 ± 1.84	1 ± 0.17	21 ± 6.5
	2000	0.61 ± 0.06	6 ± 0.89	12 ± 1.64	2 ± 0.09	3 ± 0.21

5.4.1.4. Nesting success

Hatching, fledging and overall nesting success was generally high in all years (Table 4), though there were fewer breeding attempts by Wreathed hornbills in 1999. Hatching success is defined as the proportion of sealed nests that produced a chick and ranged from 86% in 2000 to 100% in other years. It was assumed that chicks had failed to hatch or died, if nests were abandoned very early in the nesting cycle. In 2000, a late nesting Wreathed hornbill female abandoned the nest a few days after entry, while at an Oriental Pied hornbill nest, the nest was abandoned for unknown reasons in early May. Though actual clutch size was not known, only one chick was produced by both Great and Wreathed hornbills. Fledging success, defined as the percentage of nests that successfully fledged young ranged from 88% to 100%. Overall nesting success, defined as the percentage of initiated nests that fledged young was 85% (Table 4).

Table 4. Breeding success at hornbill nests for 4 years in Pakhui NP and adjacent forests

Year	**Hatching success**			**Fledging success**			**Overall nesting success**		
	Nests	*Eggs hatched*	*%*	*Nests*	*Chick fledged*	*%*	*Nests*	*Chick fledged*	*%*
1997	4	4	100	4	3	75	4	3	75
1998	15	15	100	15	13	87	15	13	87
1999	11	11	100	11	9	82	11	9	82
2000	14	12	86	12	12	100	14	12	86
All	44	42	93	42	37	88	44	37	85

Hatching success is defined as the percentage of sealed nests that produced a chick.
Fledging success is defined as the percentage of sealed nests that fledged young.
Overall nesting success is defined as the percentage of initiated nests that fledged young.

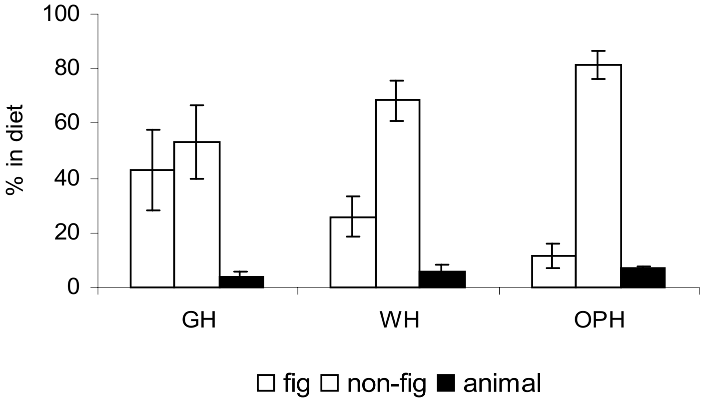
Repeated use of nest trees between years was common (10 nests), though 5 nests that were abandoned in one year were never used again in subsequent years, while at 2 nests, nesting was attempted the following year.

Nests that were successful had significantly higher visitation rates (0.63/hr ± 0.003) and food delivery rates (10/hr ± 1.05) than those that were eventually abandoned (0.36/hr ± 0.003 and 4/hr ± 0.79, n = 20 nests), Mann-Whitney U = 2 (visit/hr), p = 0.002 and Mann-Whitney U = 3 (food/hr), p = 0.003. But if only the pre-hatching visitation rates are compared, the difference was statistically significant only for male visitation rates between successful (0.58/hr ± 0.005) and unsuccessful nests (0.36/hr ± 0.003) (Mann-Whitney U = 5, p = 0.036, n = 14 nests) and not for food delivery (food items per hour (19 ± 2.47) at successful nests, compared to that of unsuccessful ones (16 ± 3.58). Other causes of nesting failure were related to degree of disturbance (see Chapter 7).

5.4.2. Diet of hornbills: composition and variation among hornbill species

Fruits comprised the largest proportion of the hornbill diet for all three species (Fig. 6). Ripe fruits comprised 96% of food items delivered for the Great hornbill, 94% of the Wreathed hornbill and 93 % for the Oriental Pied hornbill. But the contribution of the different food types, figs, non-fig fruits and animal matter, varied between the three species (Fig. 6). A Chi-square test showed that there were significant differences ($X^2 = 143.7$, df = 2, $p < 0.001$) between the Great hornbill and Wreathed hornbill in the contribution of the different food types. Great hornbills consume fig fruits more, while Wreathed hornbills consume mainly non-fig fruits.

Fig. 6. Percent contribution of different food types in the diet of the three hornbill species in the breeding season



On average for three years, figs were recorded at Great hornbill nests on 72% of the days, compared to only 56% days at Wreathed hornbill nests and on 27% days at Oriental Pied hornbill nests. Insect remains were found most frequently at Oriental Pied hornbill nests (36% days) followed by 29% at Wreathed hornbill nests and least at Great hornbill nests 14% days. The proportion of days on which figs were recorded at middens was highest in 1999 for both Great hornbills and Wreathed hornbills (94% and 87% respectively) compared to that recorded for both species in the other 2 years (60% and 41% respectively). Thus fig contribution to the diet varied between species and between years.

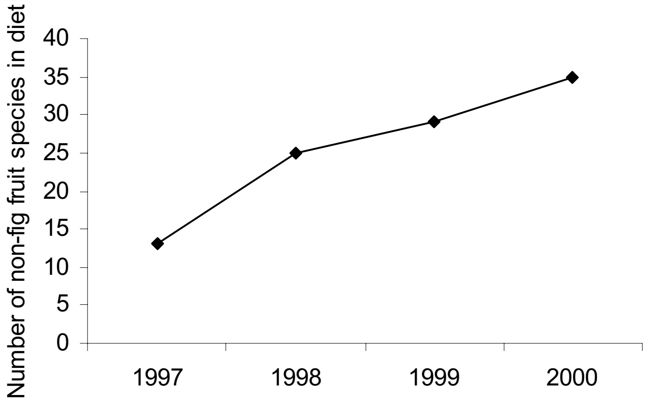
A total of 35 non-fig, 7 fig species and 16 invertebrate and vertebrate species were recorded in the diet (both midden and nest watch data combined) in the breeding season (1997-2000). A few regurgitated seeds of three additional non-fig species were also recorded below non-intensive nests. All fig species recorded in the diet were consumed by all three hornbill species. Animal matter recorded during middens and nest watches included 7 species of beetles, crabs, two unidentified rodent species, flying squirrel (*Belomys* or *Hylopetes*), two small bird species, a snake species, flat-tailed gecko (*Cosymbotus platyurus*), and spotted forest skink (*Sphenomorphus maculatus*) (Appendix 3b). But they formed less than 0.5 %

(numbers) of the total food matter recorded at middens. Seven beetle species were also recorded at middens.

Two lizard species, the flat-tailed gecko (*Cosymbotus platyurus*) and spotted forest skink (*Sphenomorphus maculatus*), were recorded at Wreathed hornbill nests, while crabs and beetles were often recorded but formed a small proportion of the total diet. Great hornbills were recorded delivering vertebrate food matter such as two unidentified rodent species, flying squirrel (*Belomys* or *Hylopetes*), and two bird species, apart from beetles. The Oriental Pied hornbill was recorded feeding on crabs, beetles and a snake was seen delivered once.

Only 11 non-fig species were recorded in the diet from nest watches, while an additional 24 species were recorded from middens, thus indicating the importance of using both methods. The number of non-fig fruit species in the diet cumulatively increased every year from 13 in 1997 to an additional 12 species in 1998, 4 more in 1999 and 6 more in 2000 (Fig. 7). Total food species richness (fig, non-fig and animal species) was highest for Wreathed hornbills (28 species ± 1.52, mean for all years, n = 10 nests), while 20 species each were recorded from both Great hornbill (20. 66 ± 0.95, n = 9) and Oriental Pied hornbill nests (20.25 ± 1.19, n = 4). Species richness ranged from 22 to 35 for Wreathed hornbills, 17 to 25 for Great hornbills, and 18 to 22 for Oriental Pied hornbills. Diet diversity of non-fig species was highest for Wreathed hornbills (14 species ± 1.91), followed by Oriental Pied hornbills (9.5 species ± 1.73) and Great hornbills (8.7 species ± 0.87).

Fig. 7. Cumulative increase of non-fig species in diet of hornbills over four years



Diet breadth (Levins' measure, 1968) for non-fig species based on all species consumed was highest for the Wreathed hornbill (0.061), followed by the Oriental pied hornbill (0.059) and the Great hornbill (0.049) (Fig. 8a). Diet overlap (Pianka's index, 1973) between all pairs of species in non-fig species eaten was very high (0.97) (Fig. 8b). A total of 35 non-fig fruit species were recorded in the middens of 24 nests (over 4 years (1997-2000). The contribution of different species to the non-fig diet and variations between hornbill species and years was determined from seed counts of non-fig fruits (N = 67,412 seeds).

Fig. 8a. Non-fig diet spectrum during the breeding season

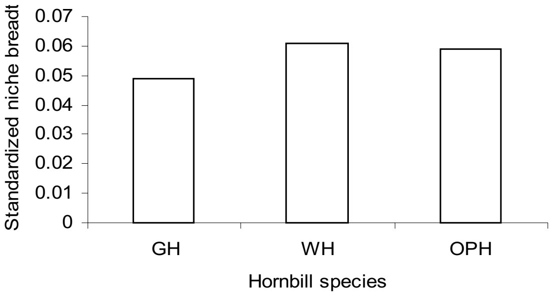
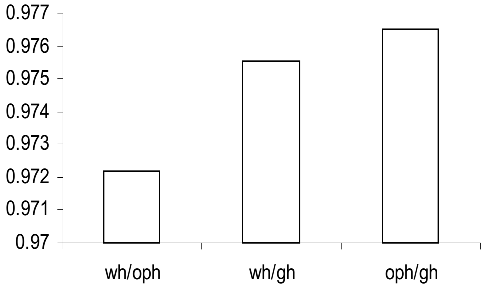


Fig. 8b. Diet overlap in non-fig fruits between pairs of the three hornbill species



Fruits of fifteen non-fig species contributed 97% of the non-fig diet of hornbills in terms of number of fruits delivered, and 99% of the biomass in the non-fig diet, overall for all hornbills. The top 15 non-fig fruit species in terms of number of fruits and biomass is given in Table 5. The first four species contributed 81% of the diet (number of fruits) or 86% in terms of biomass. A single non-fig species, *Polyalthia simiarum* contributed 56% of the non-fig fruits consumed, or 50% of the total non-fig fruit biomass.

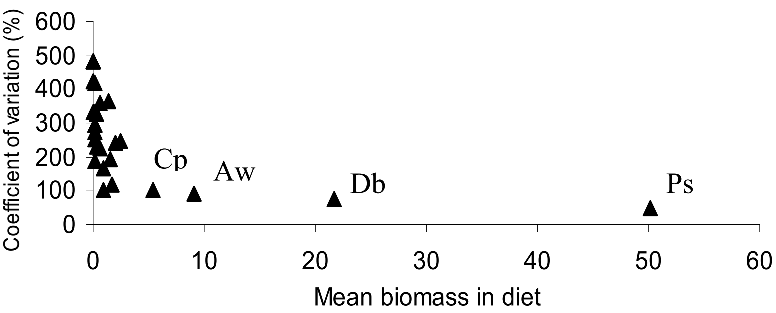
Table 5. The top 15 non-fig food species in the diet in terms of both numbers and biomass contribution to total non-fig fruit diet of hornbills (1997-2000).

Food species	% numbers in diet	Rank	% biomass in diet	Rank
Polyalthia simiarum	56	1	50	1
Dysoxylum binectariferum	12	2	22	2
Amoora wallichi	10	3	9	3
Chisocheton paniculatus	3	4	5	4
Cryptocarya sp.	2	6	2	5
Cryptocarya amygdalina	2	7	2	6
Horsfieldia kingii	1	10	2	7
Phoebe lanceolata	1	9	2	8
Artocarpus chaplasha	1	8	1	9
Litsea panamonja	2	5	1	10
Aglaia sp.	1	13	1	11
Phoebe or *Persea*	1	14	1	12
Cryptocarya sp. 2	1	15	1	13
Litsea umbrosa	1	11	0.36	14
Syzygium sp.	1	12	0.25	15

n = 23 nests, 67, 412 regurgitated seeds of 35 non-fig fruit species

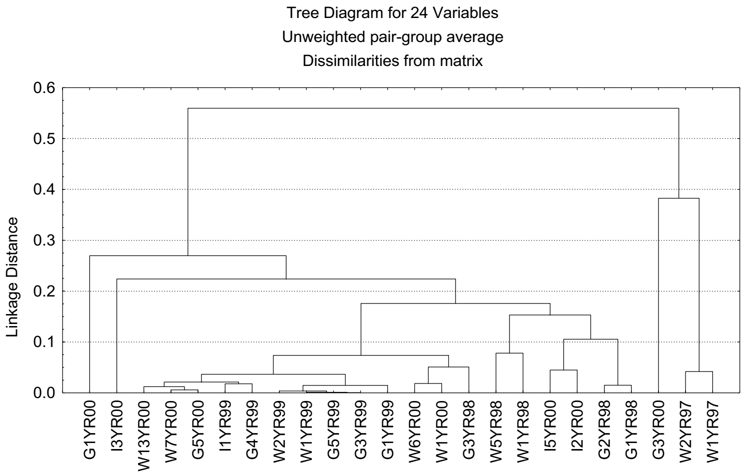
Fig. 9 clearly shows the importance of a few species in the diet. Although a large number of species are consumed overall, there is very high yearly variation in the diet. Most species had very high coefficients of variation, indicating that its contribution to the diet was highly variable, possibly due to yearly variation in fruit availability. The variation was less due to differences between hornbill species in their diet but more because of variation between years in availability of the fruit species.

Fig 9. Non-fig species in diet of hornbills: mean contribution and variation



The dendrogram (Fig. 10) following a cluster analysis also shows that there did not seem to be great differences between the 3 hornbill species in non-fig fruit species in the diet, but that differences between years in diet composition was higher.

Fig. 10. Dendrogram showing the similarity in non-fig diet composition during the breeding season among the three hornbill species in the four years (1997-2000). N = midden counts at 24 nests.



Similarity matrix constructed using Morisita's Index of similarity, which is calculated as:

$$C_\lambda = \frac{2\Sigma^n X_{ij}X_{ik}}{(\lambda_1 + \lambda_2)\, N_j N_k}$$

GH – Great hornbill, WH – Wreathed hornbill, OPH – Oriental Pied hornbill

5.4.2.1. Resource abundance and use

Out of the 35 species recorded in the breeding season diet, 20 species were represented in phenology plots, while the other 15 species that made up only 2% of the contribution (frequency) were not recorded in phenology plots. Seeds of some fruit species (*Pygeum acuminatum*, *Beilshmedia* sp.) that ripen only between November and February were recorded at some middens in early March when hornbills drop fruits on their frequent visits to the nest trees before nest entry takes place. The combined total tree density of these 20 species was about 117 trees/ha.

An index was calculated following (Heithaus *et al.* 1975) which incorporated the relative abundance, dispersion and the length of the fruiting period for each of these species. To test the hypothesis that hornbills forage for non-fig resources that may be rare, the 20 non-fig species that were recorded in phenology plots were used for this analysis. The non-fig food species were assigned a rank from 1 to 9 based on their relative density (rare, common and abundant) and their relative dispersion (dispersed, moderately clumped and highly clumped). The tree density and the degree of dispersion (based on variance to mean ratios) were available for each of these species from the 21 plots of 0.25 ha. Species having less than 1 tree per ha were considered rare, common species were those that had between 1 to 10 trees per ha. Species with tree density > 10/ha were considered abundant. The variance to mean ratio is a simple measure of dispersion and any value greater than 1 is considered clumped (Ludwig & Reynolds 1988). Since all species had a variance to mean ratio greater than 1, all were clumped, but species with variance to mean ratios > 10 were considered as highly clumped. Ranks were given as follows; species that were both rare and dispersed = 1, rare and moderately clumped = 2, rare and highly clumped = 3 ..… , abundant and highly clumped = 9. For eg., *Litsea panamonja* got a rank of 1 because it was rare and dispersed, while *Polyalthia simiarum* got a rank of 9 because it was both abundant and highly clumped (Table 6).

Table 6. Density, dispersion, density/dispersion rank, length of fruiting, and index of abundance of 20 non-fig fruit resources and their contribution to hornbill diet in the breeding season

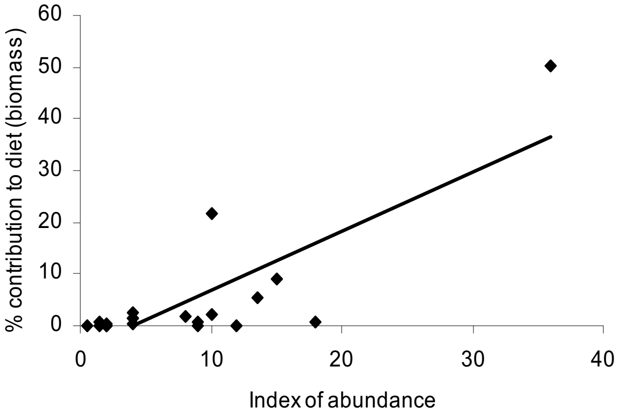
Tree species	**Tree density (ha)**	**Variance to mean ratio**	**Density/ dispersion rank**	**Length of fruiting (months)**	**Index of abundance**	**% in diet (frequency)**	**% in diet (biomass)**
Polyalthia sp.	0.19	4	1	0.5	0.5	0.35	0.15
Sterculia villosa	0.19	4	1	2	2	1.67	0.16
Litsea panamonja	0.19	4	1	1.5	1.5	2.49	0.88
**Beilshmedia* sp.	0.76	10.8	3	0.5	1.5	0.04	0.09
Phoebe lanceolata	0.76	3.8	2	2	4	1.16	1.55
Cryptocarya sp.	0.76	5.5	2	2	4	2.38	2.39
**Syzygium* sp.	0.95	8.24	2	1	2	0.97	0.25
Artocarpus chaplasha	0.95	3.2	2	2	4	1.54	1.34
Horsfieldia kingii	1.14	7.2	5	2	10	1.05	1.65
**Pygeum acuminatum*	1.71	6.13	5	0.5	2.5	0.12	0.17
Litsea umbrosa	1.90	7.24	5	1	5	0.99	0.36
Cryptocarya amygdalina	2.28	3.9	5	2.5	12.5	2.09	2.07
Amoora sp.	2.48	23.57	6	2	12	0.18	0.10
Dysoxylum binectariferum	4.19	9.34	5	2.5	12.5	12.28	21.65
Aglaia sp.	5.14	15.6	6	1.5	9	0.94	0.86
Amoora wallichi	7.43	10.47	6	2.5	15	10.30	9.07
Syzygium syzygioides	16.57	17.5	9	1	9	0.09	0.04
Polyalthia simiarum	20.76	20.35	9	4	36	55.81	50.11
Chisocheton paniculates	21.52	21.22	9	1.5	13.5	2.75	5.34
Phoebe/Persea	27.05	23.24	9	2	18	0.85	0.67

* Species in which fruits fruit ripen mainly in the non-breeding season, but were recorded at hornbill nests either in early March before nest entry,(hornbill pairs dropped fruits/seeds on visits to nest trees) or at the end of the breeding season

An overall index was calculated for each species by multiplying its density/dispersion by length of its fruiting season. The index of abundance was correlated to % contribution in diet to determine whether hornbills search for resources that are. Thus the overall index of abundance for each resource takes into account the density, distribution and period of availability of those resources.

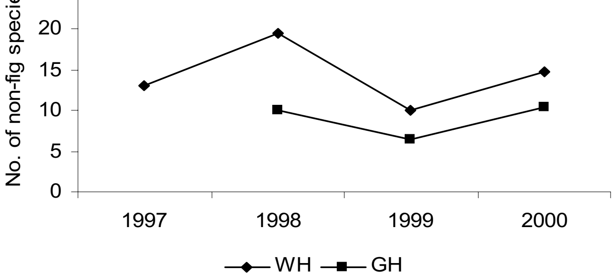
There was a strong positive correlation between the index of resource abundance and % contribution to the diet (biomass) ($r_s = 0.54$, $p < 0.05$, $n = 20$) (Fig. 11), though it was not so strongly correlated with % in diet (frequency) ($r_s = 0.38$, $p = 0.09$, $n = 20$).

Fig.11. Index of resource abundance and non-fig fruit resource use in the breeding season



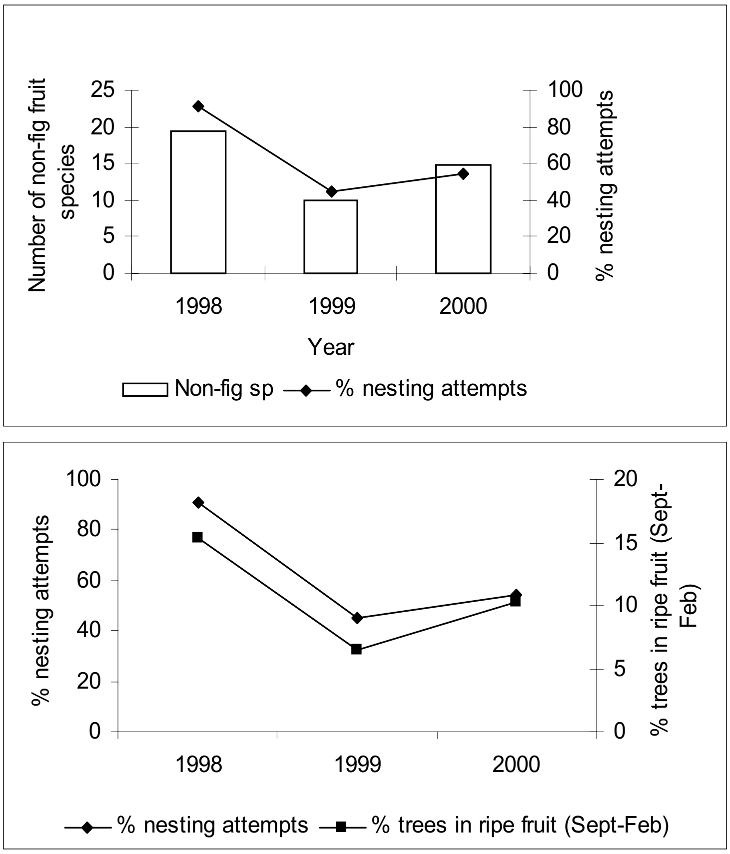
There was a strikingly lower number of species consumed in 1999 when several non-fig species failed to fruit (Fig. 12a). Fruit availability was also lower in the months prior to the breeding season (September to February) and this may have resulted in the fewer nesting attempts by the Wreathed hornbill in that year.

Fig. 12a. Diet diversity of non-fig species (1997-2000)



Nesting attempts are defined as the number of nest trees in which nesting was initiated out of the total known nest trees in that year. There were only 45% nesting attempts by the Wreathed hornbills, 6 out of 11 nests were inactive and no nesting was initiated. In contrast, in 1998, there was 91% nesting attempts and in 2000, nesting attempts were 54 %. Though sample size was too low for a statistical test, there seemed to be a trend of a positive relationship between nesting attempts by Wreathed hornbill and diet species richness in the three years (Fig. 12b) and also with total ripe fruit availability in the months prior to the breeding season (September to February in each year). Rainfall was also lower during the non-breeding season of 1998-1999, than the other years. Nesting attempts of Great hornbill were not similarly affected; it varied from 71% in 1998 and 1999 to 57% in 2000, though diet species richness of non-fig species was also lower in 1999.

Fig. 12b. Nesting attempts by Wreathed hornbills: relationship with non-fig diet species richness and ripe fruit availability prior to the breeding season



5.5. DISCUSSION

5.5.1. Breeding biology

The onset of breeding in African savannah hornbills coincides with the rainy season and has been postulated to be linked to food supply (Kemp 1976a). These species are largely carnivorous/insectivorous and breeding coincided with a period of high animal food abundance (Kemp 1976a). North (1942) had also suggested that the availability of wet mud (in the rainy season) might act as a proximate stimulus to initiate nest-sealing activity. A recent study found that tropical forest birds use long-term cues such as photoperiod to anticipate seasonality and tuned their reproductive activities using short-term cues such as food abundance/rainfall (Wikelski *et al.* 2000).

Among Asian forest hornbills that are primarily frugivorous, the onset of breeding has been found to be in the dry season (peak flowering) (Poonswad *et al.* 1987, Leighton & Leighton 1983). Peak ripe fruit availability in the year coincides with the breeding cycle of most hornbill species that have been studied (Leighton & Leighton 1983, Kannan & James 1999, Kinnaird & O'Brien 1999, Mudappa 2000) (see Table 6). Mud has seldom been found to be used in the sealing plaster in Asian forest hornbills; most studies report the use of faecal material to seal the nest (Poonswad *et al.* 1983, Kannan & James 1999, Kinnaird & O'Brien 1993)

The breeding period of these hornbill species in North-east India were reported to be during April-May (Ali & Ripley 1987). This study established that onset of breeding occurred from early March to early April and ended between July to 1st week of August. Though in the early part of the breeding season (March - May), there is little rainfall and only occasional storms, the heavy monsoonal rains commence from June onwards till mid-September. Thus during a major part of the breeding cycle, there is heavy rainfall. This is unusual in that, breeding cycles of the same hornbill species in Thailand is reported to commence in mid-January and gets over by end-June, before the commencement of the monsoon. Similarly in the Western Ghats, nesting is initiated in February and culminates by end-May for the Great hornbill and the Malabar Grey hornbill (Kannan & James 1997, Mudappa 2000). The differences between these areas in timing of nest initiation and the period of nesting may be related to latitudinal differences between these three areas, with Pakhui NP at the northernmost latitude (27°)(Table 7). The monsoon rains arrives the latest in Pakhui NP, but nevertheless there is heavy rainfall during the nesting period of hornbills in this area, unlike that found in other areas. It has been suggested that hornbills and other cavity-nesting birds would have to finish nesting before the heaviest rains to evade possible disruption due to inclement

Table 7. The breeding season of various Asian hornbill species, climatic conditions, and peak fruiting seasons

GH – Great hornbill, WH – Wreathed hornbill, RNH – Rufous-necked hornbill, HH – Helmeted hornbill, BH – Brown hornbill, PPH – Plain-pouched hornbill, OPH – Oriental Pied hornbill, BCH – Bushy-crested hornbill

Study	**Area**	**Hornbill species**	**Breeding season**	**Latitude**	**Rainfall (mm)**	**Rainy season**	**Fruiting season**
Leighton 1982	Borneo	Wreathed hornbill	January - May	0°	2176	Most of the year, low in Aug-Sept	February-May
Kannan 1994	Western Ghats	Great hornbill	15th Feb - 28th May	10°	1400	Early June - November	February to July
Poonswad *et al.* 1987	Khao Yai NP Thailand	GH, WH, OPH, BH	January -mid-June	14°	3000	June -September	February –May
Poonswad *et al.* 1998	Huai Kha Khaeng NP	GH, RNH, PPH, BH	January - June	15°	1700		
Poonswad	Budo Sungai Padi NP	GH, RH, BCH, HH, WH, WCH	February - September	6°			
Mudappa & Kannan 1997	Western Ghats, southern India	Malabar Grey hornbill	Mid-February - mid-May	10°	1400	Early June - November	February – July
Hussain 1984, Sankaran 1998	Narcondam Island	Narcondam hornbill	February - May	13°	3055	May -October	No data
Kinnaird & O'Brien 1999	Sulawesi Island	Red-knobbed hornbill	June - January	1°	1700	November - May	December – April
O'Brien 1997	Sulawesi Island	Tarictic hornbill	April - July	1°	1700	November - May	December – April
Datta, this study	Pakhui NP, Arunachal Pradesh	GH, WH, OPH	March to July-August	27°	2500	June to early September	April to July

weather and cavity flooding (Kannan & James 1999), but no such case of disruption of nesting or abandonment due to rains was noted during the 4 year study period. The peak ripe fruit availability of non-fig hornbill food species occurred during the rainiest months, suggesting that hornbills time their breeding cycle with fruit availability, even if that period falls in seemingly unsuitable weather conditions. Apart from figs that are available year-round, the fruits of primary forest species belonging to the Meliaceae, Myristicaceae, Lauraceae and Annonaceae have their peak availability during this period (see Chapter 3). In addition, nest cavities are sealed adequately, leaving only a slit for food to be passed by the males; therefore it is unlikely that flooding occurs in the nest cavity due to heavy rainfall. High velocity winds that could potentially affect hornbills that nest high up on tall trees are not a feature of the intermittent monsoon rains that occurs in the rainy season. Aseasonality in breeding of hornbill species is a frequent occurrence in southern Thailand in a much wetter and species-rich rain forest (Pilai Poonswad, *pers. comm.*).

The initiation of breeding varied between years, with earliest initiation occurring in 1999, when there had been a longer dry spell in the preceding months, while in other years, with more even distribution of rainfall, breeding commenced between mid to late March. The Great hornbills always initiated nesting first, followed by Wreathed hornbills and Oriental Pied hornbills as noted in Thailand also (Poonswad *et al.* 1987). The mean durations of nesting by these hornbill species were similar to those found in Thailand (Poonswad *et al.* 1987). The nesting cycle reported for the Oriental Pied hornbills is shorter (Hutchins 1976, Poonswad *et al.* 1987) than what was estimated during this study. The incubation periods and nestling periods were also mostly similar to that reported from Thailand and other studies on captive hornbills (Choy 1980). The nesting duration, incubation period and nestling period of hornbill species is generally positively related to body size, with a few exceptions (Kemp 1979, Poonswad *et al.* 1987). Despite being of a larger body size, the Great hornbills have a shorter nesting cycle than the Wreathed hornbills. This maybe because development of the chick takes longer in the Wreathed hornbills that largely depend on non-fig fruit species in the diet, while Great hornbills eat more figs and larger vertebrate food items. Interestingly, the nesting cycle is longer in the northern populations of the Great hornbills than in the Western Ghats and the reasons for this still remain unclear, though Kannan & James (1990) invoked the necessity of finishing nesting before the early monsoon rains as one possible reason.

Females exit the nest cavity before the chick in Great hornbills and this may be partly because the size of the cavity becomes too small for both the female and the growing chick (the larger cavity sizes that are required by Great hornbills may be more limiting). In Oriental

Pied hornbill nests, when 2 chicks are produced, limited cavity space is reported to cause early emergence of the female (Poonswad *et al.* 1987). Earlier hypotheses on why females emerge early has stressed that the female comes out to help the male in feeding the chick(s) and that possibly, the male is unable to provision both alone. Another hypothesis put forward is that the females are required to remain inside to help in nest sanitation. But if that were the case, it is difficult to explain why female emergence does not occur in all hornbill species. A recent study of the Monteiro's hornbill (*Tockus monteiri*) in Namibia has found that the timing of female departure from the nest is unrelated to chick provisioning or nestling condition and is more related to the female's body condition (Boix-Hinzen *et al.* 2001). In fact, earlier studies on Great hornbills have shown that the female does not greatly augment the food provisioning by the male (Poonswad *et al.* 1983, 1987, Kannan & James 1999) and that she is probably weak after the long confinement (Kannan & James 1999). Thus, the female leaves the nest when her body condition is the poorest. Therefore, factors that affect female body condition, future survival and breeding opportunities may influence the timing of nest departure in some hornbill species. This, of course, does not answer the question why in some hornbills females stay inside the cavity throughout the cycle, such as the Wreathed hornbill. The Wreathed hornbill is a medium-sized hornbill and produces a single chick, possibly cavity space is not a limiting factor for this species. In addition, since the male has a prominent gular pouch and was often seen delivering 80 -100 fruits on a single feeding visit, food provisioning by the male alone may be adequate to feed both the female and chick. The reasons why females stay inside the cavity longer are likely to be related to helping to raise the chick successfully, and growing back her feathers. Several studies (both in the wild and captivity) have reported variable patterns of moulting in hornbill species, and most studies have now reported that there is only a partial moult or no moult (Poonswad *et al.* 1983, Kannan & James 1999). Moulting during the nesting cycle has been postulated to be either related to maintaining body temperature in the hot nesting season or as a way to reduce body size due to lack of space inside the cavity.

Both male and female hornbills make high investments in breeding. The male has to forage for food for himself and supply food to the female and chick(s) throughout the 3-4 month long cycle. The female is also confined to a cavity where there are chances of abandonment by the male and she is totally dependent on the male for food provisioning. In addition, it was noted that conditions inside the cavity might be very hot during the months of April-June, females were observed to stick their beaks out keeping them wide open, as a heat loss mechanism. Only partial moult of feathers seemed to be occurring among hornbills in the area. This seems an insurance against possible nesting failure/abandonment to ensure that the female can exit the nest early if necessary. Indeed, at one Wreathed hornbill nest, where nest entry occurred unusually late (a month after nesting had been initiated), the female emerged out of the nest, a few days after the male stopped provisioning.

The long period of nesting by these hornbill species at the end of which, a single chick is produced, highlights the fact that they could be considered as K-selected species. Nesting failures would be costly for them. The nest-sealing habit and the heights at which they nest are therefore ways in which they ensure successful nesting. Most studies on Asian hornbills, including the present one, have found high nesting success (Poonswad *et al.* 1987, Kannan & James 1999, Kinnaird & O"Brien 1999, Mudappa 2000). The factors that could potentially hamper successful nesting, once breeding is attempted are poor food availability, predation, intra and inter-specific competition, and extraneous factors such as weather and nest tree breakage or cavity damage.

Coupled with these natural constraints are human pressures such as disturbance near the nest cavity, poaching of chicks, and hunting of the adult birds during nesting. Natural predation pressures are generally thought to be minimal for hornbills during nesting, though (Poonswad *et al.* 1987, 1988, 1998) have recorded some instances of predation by viverrid species.

A high degree of overt intra and inter-specific competition among sympatric hornbills, even after nesting had commenced, has been noted by Poonswad *et al.* (1987) in Khao Yai NP, Thailand. This even caused nesting failures or abandonment (Poonswad *et al.* 1987, *pers. obs.*). Such levels of aggression were not seen during this study, though in several instances, Great hornbills chased away Wreathed hornbills from the vicinity of nest trees and nearby fruiting trees. Wreathed hornbills, on the other hand did not chase away Great hornbills, even from their own nest tree. A Great hornbill was also observed inspecting a cavity of a nesting pairs of Wreathed hornbills, even though it was already occupied. Human-related disturbances led to loss of erstwhile nest trees and nest abandonment in a few instances, but generally the impact of disturbances was more related to loss of active nest trees over the years (detailed in Chapter 7), rather than nesting failure once nesting had been initiated. During the breeding season, only two recorded instances of poaching of a Wreathed hornbill chick and female from the nest and hunting of an adult male Wreathed hornbill (commencement of breeding) occurred in the study site. In general, hunting of hornbills is taboo (ban by the *Nishi* tribe) during the breeding season in this area.

5.5.2. Diet of hornbills in the breeding season

Fruits were overwhelmingly important in the diet for all the three hornbill species. Lipid-rich non-fig fruits formed the most important component of the food delivered. The three species partitioned resources broadly in terms of contribution of figs, non-fig fruits and animal matter in the diet. The Great hornbill was found to eat figs relatively more, while the Oriental Pied hornbill and Wreathed hornbill relied more on non-fig fruits. Richness of non-fig fruit species in the diet was also highest for Wreathed hornbills, while vertebrate food matter was more commonly delivered by Great hornbills, though niche breadth of all three species was largely similar. In general, overlap in non-fig fruit species consumed was very high among the species.

Few studies have tried to compare resource use and partitioning among sympatric hornbills in the breeding season (Leighton 1982, Poonswad *et al.* 1983, 1986, 1987). The patterns found largely corroborate the fact that the Wreathed hornbill seems to be non-fig fruit specialist, and that the animal matter it consumes largely consists of crabs and beetles. The Great hornbill relies on figs more and consumes the widest variety of vertebrate food items. The limited information for the Oriental pied hornbills suggests that though it mainly eats non-fig fruits (based on nest watches), both invertebrate and vertebrate food comprises an important part of the diet (middens and nest watches).

Food delivery and nest visitation rates generally increased marginally after the chick hatching for all three species, as has been noted in previous studies (Poonswad *et al.* 1983, 1987, Kannan & James 1999, Kinnaird & O'Brien 1999, Mudappa 2000). In general, studies have found that visitation rates by male hornbills decline just prior to fledging (Poonswad *et al.* 1983, Kannan & James 1999, Kinnaird & O'Brien 1999, Mudappa 2000) but this was not the case during the present study. All the three hornbill species are multiple prey loaders and therefore can deliver many food items at one feeding visit. The hornbills only delivered some larger animal prey, singly. The time spent at the nest and duration of visits was generally lowest for Oriental Pied hornbills, since they are smaller species and deliver fewer fruits per feeding visit. The Wreathed hornbill often spent greater time around the nest cavity when they would preen, in a few instances; disturbance from observers or local people moving in the area resulted in the birds not leaving the nest area. This may have been the possible cause of nest abandonment at a Wreathed hornbill nest in1997 when the male did not feed the female on some visits, and spent a longer time perching either on the nest tree or nearby and also did not make any feeding visits for more than a week.

Such high percentages of fruits in the diet are true for several Asian forest hornbills (Kemp 1995, Kannan & James 1999, Kinnaird & O'Brien 1999), but fruits are low in protein. Growing chicks require more protein than provided primarily by a fruit diet. Animal matter, in the diet thus increases after chick hatching, but only marginally so. The long nesting period of hornbills in general, is probably due to their primary dependence on fruits. In addition, a more frugivorous species such as the Wreathed hornbill has a longer nesting cycle than the Great hornbill, despite being of a smaller body size. Carbohydrates and water are obtained from sugar-rich fruits such as figs and, protein from animal matter, which supplements the lipid-rich diet of the nesting hornbills. Figs have also been found to have high calcium content (3 times higher than non-fig fruits) (O'Brien *et al*. 1998b) that is necessary for egg formation, bone growth and feather development. It has also been found that hornbills are efficient at assimilating dietary protein. Interestingly, it was found that while fig fruit delivery was higher before chick hatching, the delivery of lipid-rich non-fig fruits and animal matter increased after chick hatching. This pattern was similar for all species. Thus, hornbills seemed to be selecting and changing the types of food delivered based on the nesting phase and the necessary requirements of growing chicks. Recent nutrient analysis of fruits and animal matter consumed by Great hornbills, Wreathed hornbills and Oriental pied hornbills have found that overall, there was an increase of protein, carbohydrate, lipids and calcium intakes during the nestling period (Poonswad *et al.* 2001).

It is striking that in spite of the high diversity of food species taken, especially of non-fig fruit species, hornbills relied on only ten non-fig fruit species for 90% of the non-fig diet. *Ceratogymna* hornbills have also been found to consume over 100 species, though the top ten species contributed over 60% of the diet (French *et al.* 2001). Studies have found high variation in the nutrient content of fleshy fruits (Herrera 1982, Martinez del Rio & Restrepo 1992, Corlett 1996) and therefore consumption of a diverse array of fruits maybe essential to meet nutritional requirements. However, recently, French *et al.* (2001) found practically no differences in the nutrient contents of the most preferred fruit species of *Ceratogyma* hornbills and those that were consumed less.

The most important non-fig species in the diet were lipid-rich large-seeded fruits of the families Meliaceae, Myristicaceae, Lauraceae, and Annonaceae. The importance of a few plant families (Meliaceae, Myristicaceae, Lauraceae, Annonaceae) and even similar genera (*Dysoxylum, Amoora, Aglaia, Polyalthia, Beilshmedia, Alseodaphne, Litsea, Cryptocarya*) across tropical forests in Asia (from India to Sulawesi) in the diet of many different hornbill species and the important role they play as seed dispersers points to both an ecological as well as a co-evolutionary link in the distribution, diversity, and abundance of hornbills and that of these plant species. The survival of both hornbills and some of these primary forest species may be largely mutually dependent.

The most important species in the diet were relatively common tree species in the area barring one or two species. Thus, hornbills choose to forage on fruit resources that are common. It was also found that there were greater differences in diet composition between years than between hornbill species, suggesting that there was high annual variability in fruit availability of different food species. Many species are known to fruit supra-annually in tropical rainforests (Medway 1972, Leighton & Leighton 1983) and do not produce fruit every year. The most important species in the diet were recorded in the middens in all years and fruits were also available in all years, barring a few species of the Meliaceae and Myristicaceae during the fruiting failure in 1999, and two species of *Cryptocarya* that was recorded in the diet only in I year. But many other rare species in the diet were recorded only in 1 year or even at only one or two nests. Defense of food trees around the vicinity of nest trees especially in the case of Great hornbills and Oriental Pied hornbills might also result in some species being recorded only at those nests. Some of these species were not recorded in the phenology plots or were rare and are also probably not preferred food species and are possibly consumed by hornbills as supplementary resources. Another pattern is that nests that were spatially closer together had greater diet similarity suggesting the patchy location of fruit resources. In 1999, breeding attempts by Wreathed hornbills (that is more of a non-fig fruit specialist than the Great hornbill) may have been fewer because of a lower fruit availability in the preceding period (non-breeding season) (that may have been tied to poor rainfall). Subsequently, there was lower fruit availability even during the breeding season (reflected in lower non-fig fruit species richness in the diet) and though there was not much impact on nesting success (one nest each of the Great and Oriental pied hornbill were abandoned), the lengths of the nesting cycle was longer in both the large hornbill species in that year compared to other years, suggesting that longer time was required for development because of lack of diverse high-quality food items. The fig contribution to the diet was also higher in that year compared to the other three years. This year was also unusual in that breeding was initiated 15-20 days earlier than other years, possibly because there was a longer dry spell.

Breeding by hornbills has been found to occur in alternate years in Borneo, Indonesia (Leighton 1986, Laman 2001) and it has been speculated that it could be related to fluctuating fruit availability patterns. In the present study area, breeding occurred every year, and in general, there were no pronounced fluctuations in ripe fruit availability of hornbill food species.

5.6. CONCLUSIONS

Breeding biology and breeding season diets of three sympatric hornbills were studied in a lowland semi-evergreen forest of western Arunachal Pradesh. The breeding season for all species started during the dry hot period (peak flowering) preceding the rainy season. Contrary to what most existing studies have reported, the breeding season did not end before the onset of heavy rains, but, instead, continued through the rainy season, with both the chick and female remaining incarcerated in the nest cavity through heavy rains. The incubation period for the Great hornbill was estimated to be 45 to 55 days, and 40-45 days for the Wreathed hornbill. The total nesting cycle of the Great hornbill was 110-129 days (n = 8), and 120-140 days (n = 9) for the Wreathed hornbill. The nesting cycle for Oriental Pied hornbill was estimated to be 93-97 days (n=2), though exact dates of nest entry and sealing was not observed.

Females sealed themselves in the nest cavity using wood chips, seed fragments, and faecal remains containing fig seeds, pulp, and insect chitin. Great hornbill females emerged out of the nest after 88-109 days, while in Wreathed and Oriental Pied hornbill, they emerged together with the chicks, having remained incarcerated throughout the duration of the nesting cycle.

Observations on diets were made through 1467 hours of nest watches (Great hornbill 416 hours, Wreathed hornbill 917 hours, and Oriental Pied hornbill 134 hours) during which time the number, type, and species of food items delivered by the male were recorded. Additionally, information on non-fig fruits and animal matter in the diet was collected by counting regurgitated items below 23 nests; a total of 67,412 seeds of non-fig species, and 44 animal food items were counted. Fruit predominated in the diet of all three species, though animal matter marginally increased in the post-hatching period. In all, a total of 42 plant species and 16 vertebrate species (7 beetle species, two species each of lizard, bird, and rodents, one species of snake, crab, and flying squirrel). Over 90% of the diet of all three hornbill species was comprised of fruits. Lipid-rich fruits of the Meliaceae, Myristicaceae, Lauraceae, and Annonaceae were especially important in the hornbills' diet. Though a wide variety of non-fig fruit species were taken, the top ten species contributed over 90% of the non-fig fruit diet. There were differences in the overall contribution of figs, non-fig fruits and animal matter in the diets of the three hornbill species, but there was a great deal of overlap in both the fig species and the non-fig fruit species consumed. There was greater similarity between hornbill species in food species consumption than between the different years. This was due to the differences in availability of fruit species between the 4 years.

Peak ripe fruit availability occurs in the middle of the breeding season and hornbills relied on a wide array of diverse food items, especially of fruits of more than 30 primary forest species in the breeding season, although only a few species contributed consistently to the diet of most hornbills in all years. Resource overlap is also generally high among the three sympatric species, which may result in interference competition. Indeed, the territorial Great hornbills defend fruit resources from the smaller, more wide-ranging Wreathed hornbills. Breeding opportunities and breeding success can be aggravated by human-induced disturbances such as hunting or the more insidious process of habitat loss and modification. Even though hornbills do occur and nest in logged and secondary forest areas (Johns 1989, Datta 1998, Whitney and Smith 1998), the diverse diet of rare and patchily distributed forest tree species necessitates the presence of large forest tracts or at the least, proximity to mature forest patches. For example, the food species delivered at some nests that were located in degraded secondary forest in Reserve Forests and in a tea estate were all primary forest species that were being brought from nearby forest areas.

Therefore, future management and conservation of hornbills needs to take into consideration that the seasonal variations in fruit production and the spatial differences in food species abundance result in hornbills requiring large areas of forest. Hence reserve forests, secondary forests, and logged forests also need to be considered in conservation plans.

Chapter 6. Foraging of sympatric hornbills in the non-breeding season

6.1. INTRODUCTION

There have been relatively few attempts to determine hornbill diet in the non-breeding season (Poonswad *et. al.* 1998). Some studies have yielded information on the movement and foraging patterns during the non-breeding season (Poonswad & Tsuji 1994, Suryadi *et al.* 1994, 1996, 1998, Kinnaird *et al.* 1996). The main reason for the lack of studies has been the difficulty in tracking birds in the forest to obtain quantitative estimates of diet composition during the non-breeding season. On the other hand, diet composition during the breeding season is relatively easy to assess, once nest trees of the focal species are located. The unique facets of hornbill breeding have resulted in a fascination with this aspect of hornbill biology and a plethora of studies have concentrated on describing the breeding biology and breeding season diet of hornbills (Poonswad *et al.* 1983, 1986, 1987, 1988, Kannan & James 1997, Kinnaird & O'Brien 1993, 1999, Mudappa 2000).

For a full understanding of hornbill biology and life-history, studies documenting the diet composition, foraging behaviour and patterns in fruit availability during the non-breeding season are needed, especially since it has been found to be a relatively lean period for food availability (Leighton 1982, Leighton & Leighton 1983, Kannan & James 1999). Though, most studies have found that immediately after fledging, fruit availability is high (Poonswad *et al.* 1987, Kannan & James 1999, Kinnaird & O'Brien 1999), in subsequent months there is a lean season in fruiting. During this study, peak fruit availability occurred in the middle of the nesting cycle and fell immediately after fledging. In fact, this period of resource crunch may be more crucial in the life-history and decide whether animals are able to breed in the next year. Body condition of female hornbills has been found to be poor after the prolonged confinement inside the nest (Kannan & James 1999, Boix-Hinzen *et al.* 2001), and fledglings require adequate nutrition during this period as they begin to forage independently. Starvation risk is likely because of the inexperience of juvenile birds in tracking resources and energetic demands increase as hornbills range more widely in the non-breeding season (Kinnaird & O'Brien 1999). Observations of post-fledging parental care such as feeding of the chicks by the male and female were noted during the study and juveniles were seen to accompany adult pairs up to October (3-4 months after fledging), but after this, the juvenile birds were not noted with adult pairs and possibly disperse and form juvenile flocks. In any case, resource availability during this period is crucial even if they disperse.

The nesting cycle of the three hornbill species that were the focus of this study lasted from March to early August. Chick fledging occurs between July and August with some annual variations and differences between species. Thus, the non-breeding season falls between August and February (late wet season to relatively drier cold season in the area). The patterns of fruit availability of hornbill food plants (detailed in Chapter 3) show that this is a time of relative scarcity of non-fig fruits.

Sympatric species might have to partition resource use in different ways in order to co-exist if resources are limiting. They could select different food items, forage in different strata or have different temporal use of resources to avoid interference competition (Schoener 1974, Cody 1985, Rosenzweig 1995). The more number of sympatric species there are, one would expect a greater degree of specialization and niche partitioning (Rosenzweig 1995).

In this chapter, the diet composition of hornbills during the non-breeding season (mainly with data from the non-breeding season of 1998-99) is described. An attempt is also made to understand how food characteristics vary among these co-existing species and the extent of overlap in their diets.

6.2. OBJECTIVES

1. To characterize the diet composition of sympatric hornbill species during the non-breeding season
2. To examine how the three sympatric hornbills share resources and how food characteristics vary among co-existing species

6.3. METHODS

6.3.1. Diet composition from below hornbill perch and roost trees

There are two generally accepted ways of studying diet – watches at fruiting trees and transect surveys for feeding records. In this study, a combination of both these methods was used. Additionally, a more quantitative way of describing diet was also devised, which allows detection of many more species (rare species) in the diet, that could be missed from a reliance on only transect walks or fruit tree watches. The method involved a count of the numbers of seeds of fruits eaten by hornbills below perch and roost trees (detailed in Chapter 4).

Difficulties were also faced in observing hornbills at fruiting trees; birds were shy and often flew away due to observer presence. Hornbills are hunted in the area, especially in the non-breeding season and are therefore extremely wary making it difficult to observe them for long periods.

Seed counts at perch and roost trees are easy, but require that roost sites are known, and seed counts below perch trees are reliable only if one has first seen hornbills perching on the tree for sometime, or if it is being regularly used by hornbills near fruiting trees. For instance, during the period when a fig was in fruit, and was being used daily by hornbills, counts were made below the fig tree of seeds of several non-fig fruit species that had been consumed before and are regurgitated and dropped below. The freshly regurgitated seeds dropped by hornbills retain a pink colour, and are smooth since the pulp is removed very cleanly.

Based on 478 records at perch trees during the non-breeding (winter) season of September 1998-March 1999 (7 months), a quantitative estimate of the non-fig species consumed by hornbills was obtained. Seed counts below roost trees used between August and January were also carried out to obtain additional quantitative information on diet species in the non-breeding season.

6.3.2. Feeding records (from trail walks and opportunistic sightings)

Ad-libitum sampling on 6 main trails (totalling *ca.* 16 km) were used to collect data on hornbill diet and foraging characteristics. Opportunistic observations of feeding hornbills were also recorded during other times along longer walks to augment feeding records. These data were collected over three and a half years (February 1997 to May 2000). On sighting hornbills, the following parameters were recorded: i) hornbill species, ii) number of individuals, iii) if feeding, fruit species and type of fruit, iv) position of hornbill in the canopy (lower, middle, or upper canopy and the emergent layer).

6.3.3. Fruit tree watches

A total of *ca.* 40 hours (between August to February during 1997-1999) was spent watching fruiting trees of 5 species of figs and 2 other non-breeding season diet species (*Pygeum acuminatum* and *Actinodaphne obovata*), n = 12 trees. The effort was largely concentrated at fig trees (ca. 37 hours). Birds were often disturbed by observer presence and flew away on approach or when presence was detected, therefore, opportunistic feeding records and seed counts under perch and roost trees to describe hornbill diet in the non-breeding season were used. These data were used to augment feeding observations of figs in the diet and to record interactions among hornbill species.

6.3.4. Fruit characteristics

All fruit species consumed during the non- breeding season were collected for identification. Fruits and seeds were weighed wet, and measured (longest length and width and depth). Fruits > 2 cm in length were defined as being large, while fruits between 0.5 – 2 cm were defined as medium-sized fruits, small fruits were those that were < 0.5 cm in length. Here, fruits are defined as the part that is selected and swallowed by hornbills (along with seed) and not necessarily, the whole fruit. Fruits were also classified by morphology – such as drupes (both single-seeded fleshy fruits with or without an outer skin), dehiscent arillate single or multi-seeded capsules, berry, and figs and the characteristics of the pulp (oily, watery, fleshy). Berries are defined here as either single-seeded or multi-seeded, with a watery pulp. Figs are classified as sugar-rich watery fruits with thousands of tiny seeds embedded in the pulp. During this study, hornbills voided out the seeds (unharmed) of figs only in the faeces and sometimes the seeds of *Sterculia villosa*, while all other seeds were regurgitated out intact. The differences among the 3 hornbill species in fruit types and fruit sizes consumed were determined. Sample sizes were too low to determine degree of overlap between the species in terms of individual non-fig fruit species.

6.3.5. Data analysis

Chi-square tests were used to test for differences in the distributions of feeding strata, food items (fig, non-fig, animal) and fruit types eaten using the data from feeding records.
The spatio-temporal variation in resource availability was determined in a semi-quantitative manner following a method suggested by Heithaus *et al.* (1975) and the relationship between resource use (non-fig fruits) and availability were examined using Spearman's rank correlation.

6.4. RESULTS

6.4.1. Overall diet composition in the non-breeding season

A total of 49 species was recorded in the non-breeding season diet of hornbills using a combination of all three methods. This included 41 non-fig fruit species (including 3 liana species), 7 fig species and the flowers of a single species (Table 1). Three other species were not actually recorded in the diet *(Litsea monopetala, Litsea chinensis, Cinnamommum cecicodaphne*), but are believed to be eaten by hornbills based on fruit characteristics, literature and local tribal information.

Twenty-one species were recorded from below perches, fifteen species below roost trees and 22 from feeding records and observations. Similarity in the diet composition recorded from the three methods was very low, 7.3% (only 3 species were recorded by all three methods). Similarity between any two methods also was low and ranged from 9.75% similarity to 27%. Fig species in the diet were recorded only from feeding records, since it is not possible to determine either the species of fig or number of fruits eaten from the deposited faeces below perch and roost trees. The presence of animal matter in the diet (beetles and crabs) was ascertained below roost trees and from a few feeding records (Plate 5). Thus a combination of the three methods provided the diet profile in the non-breeding season.

The major non-fig species in the diet were thirteen species of Lauraceae, Meliaceae (3 species, two of which actually have peak fruit ripening times in the breeding season), 2 species of Annonaceae (both species partly available in the breeding season), and Rosaceae (2). The rest included one species each of Burseraceae, Rubiaceae, Elaeocarpaceae, Urticaceae, Euphorbiaceae, and Myristicaceae (the latter ripens between February and April and so is available in the early part of the breeding season). As mentioned earlier, hornbills consumed at least 7 fig species in the non-breeding season. Nine food species were recorded only once. Table 1 details the fruit species, their fruit characteristics and the hornbill species that was recorded feeding on them.

6.4.2. Diet composition and resource partitioning: data from feeding records

Fruits comprised the highest proportion in the diet of all species. Only Great hornbills were recorded foraging for insects. Consumption of animal matter is difficult to observe and has probably been underestimated.

Seventy-three percent (n = 70) of all feeding records of Great hornbills were on figs (7 species), 24% were on 7 non-fig species, and 3% on insects. Thirty-five percent (n = 78) of all feeding records of Wreathed hornbills were on figs (6 species), while 65% were on 13 non-fig species. Forty-seven percent (n = 17) of all feeding records of Oriental Pied hornbill were on figs,

Table 1. Food species, family and characteristics of fruits consumed by the three sympatric hornbills during the non-breeding season (late July to early March). Feeding records, n = 165 sightings, seed counts, n = 2977 seeds (perch trees), 2230 seeds (roost trees). GH = Great hornbill, WH = Wreathed hornbill, OPH = Oriental Pied hornbill

Species	**Family**	**Fruiting time**	**Fruit type and size**	**Color of ripe fruit or edible part**	**GH**	**WH**	**OPH**	**Method**
Actinodaphne obovata	Lauraceae	July –September	Fleshy drupe, medium	Black		X		All three
***A. angustifolia*	Lauraceae	September-October?	Fleshy drupe, medium	Black		X		Perch
Alseodaphne peduncularis	Lauraceae	December-January	Fleshy drupe, large	Black	X	X		Perch
Amoora wallichi	Meliaceae	May-July	Arillate, oily capsule, large	Dark red	X	X	X	Roost/feeding records
Aphanamixis polystachya	Meliaceae	November-January	Arillate, oily capsule, medium	Red	X	X		Perch
Beilshmedia assamica	Lauraceae	September-January	Fleshy drupe, large	Black	X	X		Perch/feeding records
Beilshmedia gammieana	Lauraceae	September-January	Fleshy drupe, large	Black		X		Perch/feeding records
Beilshmedia sp.	Lauraceae	September-January	Fleshy drupe, large	Black		X		Perch/feeding records
**Bridelia retusa*	Euphorbiaceae	October	Berry, small	Red-orange			X	Feeding records
Canarium resiniferum	Burseraceae	October-February	Fleshy drupe, large	Black		X		All three
Chisocheton paniculatus	Meliaceae	February-April	Arillate, oily capsule, large	Black	X	X	X	Perch/feeding records
Cinnamommum cecicodaphne	Lauraceae	November-December?	Fleshy drupe, medium	Black				Potential food species
Cryptocarya amygdalina	Lauraceae	June-August	Fleshy drupe, large	Black		X		Roost
Cryptocarya sp.	Lauraceae	June-August	Fleshy drupe, large	Black		X		Perch
***Elaeocarpus ganitrus*	Elaeocarpaceae	November-January	Fleshy drupe, large	Iridescent blue		X		Roost
Ficus altissima	Moraceae	Year-round	Fig, medium-sized	Red	X	X		Feeding records
F. elastica	Moraceae	Year-round	Fig, small	Brown-red	X			Feeding records
F.hookeri	Moraceae	Year-round	Fig, large	Dark red-black	X	X	X	Feeding records
F. macclellandi	Moraceae	Year-round	Fig, small	Yellow	X			Feeding records
F. nervosa	Moraceae	Year-round	Fig, small	Orange-red	X	X		Feeding records

Species	**Family**	**Fruiting time**	**Fruit type and size**	**Color of ripe fruit or edible part**	**GH**	**WH**	**OPH**	**Method**
Ficus sp.	Moraceae	Year-round	Fig		X			Feeding records
Ficus sp.	Moraceae	Year-round	Fig		X			Feeding records
Gnetum ula	Gnetaceae	October-December	Fleshy drupe, small	Pale blue		X		Perch
Horsfieldia kingii	Myristicaceae	February-April	Arillate, oily capsule, large	Yellow	X	X	X	Perch/feeding records
Hyptianthera sp.	Rubiaceae	October-December	Medium-sized berry	Yellow		X		Feeding records
**Laportea crenulata*	Urticaceae	December-January	Small berry	Greenish			X	Feeding records
Litsea chinensis	Lauraceae	August-October	Fleshy drupe, small	Black				Potential food species
Lisea monopetala	Lauraceae		Fleshy drupe,small	Black				Potential food species
Litsea sp.	Lauraceae		Fleshy drupe, small	Blue-black		X		Perch
Livistona jenkinsiana	Palmae	October-December	Fleshy drupe, medium-sized	Blue-black		X		Perch
Derris sp.	Leguminosae		Dehiscent pods with arillate seed	Orange-red			X	Perch, stomach content
**Ostodes paniculata*	Euphorbiaceae	August	Small berry			X		Feeding records
Phoebe lanceolata	Lauraceae	June-August	Fleshy drupe, medium	Black		X		Roost
Platea latifolia	Icacinaceae	September-November	Fleshy drupe, large	Black		X		Perch/roost
Polyalthia simiarum	Annonaceae	May-August, November to March	Fleshy drupe, medium-sized	Black	X	X	X	All three
Polyalthia sp.	Annonaceae		Fleshy drupe	Black		X		Perch/roost
Pygeum acuminatum	Rosaceae	November-January	Fleshy drupe, medium-sized	Black	X	X	X	Perch/feeding records
Pygeum sp.?	Rosaceae	October-November?	Fleshy drupe, medium		X			Perch
**Spondias axillaris*	Anacardiaceae	November-December	Pulpy, fleshy drupe	White		X		Feeding records
Styrax serrulatum	Styraceae	August to October	Small drupe	Black		X		Feeding records
**Vitex pentaphylla*	Verbenaceae	October-December	Small drupe	Black			X	Feeding records

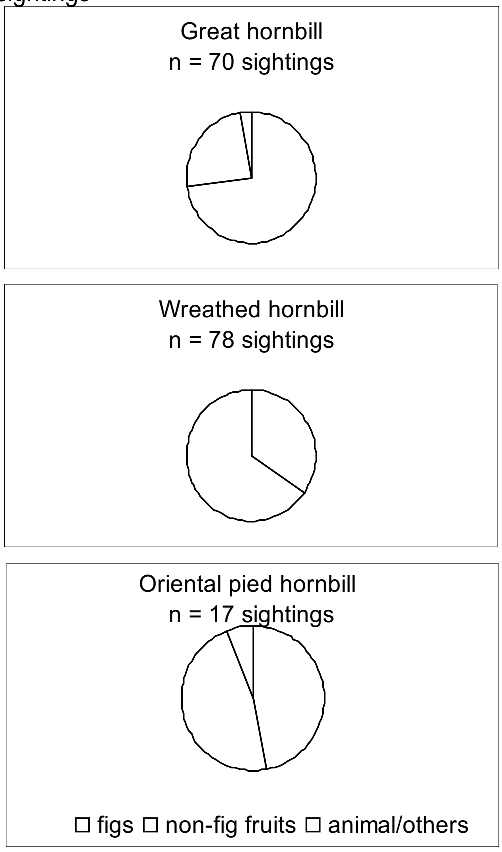
Species	**Family**	**Fruiting time**	**Fruit type and size**	**Color of ripe fruit or edible part**	**GH**	**WH**	**OPH**	**Method**
**Zanthoxylum rhetsa*	Rutaceae	September-November	Small berry	Red	X			Feeding records
**Zizyphus*	Rutaceae	October	Small berry	Dull red-orange			X	Feeding records
Liana species		November-January	Medium-sized drupe, fleshy	Pale blue			X	Perch/feeding records
Syzygium sp.?	Myrtaceae?		Small drupe					???, perch or roost
4 unknown species						X		Roost
1 unknown species					X			Feeding records
**Oroxylum indicum*	Euphorbiaceae	November	Flowers				X	Feeding records

* Recorded only once

[a] Recorded only 1 seed

while 47% were on non-fig species (7 species). One sighting comprised of a pair feeding on flowers of *Oroxylum indicum* (Fig. 1). A Chi-square test was used to determine if there were any differences between Great hornbills and Wreathed hornbills in contribution of fig vs. non-fig matter. Sample sizes for Oriental Pied hornbill were small and therefore not included in the analysis. There was a significant difference between the two larger species in the percentage of fig, non-fig fruits and animal matter in the diet ($X^2 = 33.22$, df = 2, $p < 0.001$).

Fig. 1. Percentage contribution of figs, non-fig fruits and animal matter in the non-breeding season diet of the three hornbill species, n = 165 sightings



There was only 9.5% similarity in non-fig fruit species consumed by all three species. There was greater overlap between Great hornbill and Wreathed hornbill in terms of the number of common species taken (33%) than between Wreathed Hornbill and Oriental Pied hornbill (11%) or between Great hornbill and Oriental Pied hornbill (17%). Non-fig fruit species richness was highest for the Wreathed hornbills (13 species), while Great hornbill and Oriental Pied hornbills were recorded feeding on fruits of 7 species each. Great hornbills were recorded feeding on 6 fig species, Wreathed hornbills on 5 species and Oriental Pied hornbills on 2 species from feeding record observations. Dietary overlap in fig species taken was high, but fruit resource partitioning occurred in terms of the relative contribution of figs and non-figs as well as the kinds of non-fig species taken.

There were differences among the three species in the types of non-fig fruits consumed. The Oriental Pied hornbill fed more on berries (37% of all records). Nearly 42% of all feeding records of the Wreathed hornbill were on lipid-rich drupaceous fruits of the Lauraceae and Annonaceae, while arillate capsular fruits formed 21% of the diet. About 19% of feeding records of Great hornbill were on drupes and 6% on arillate capsular fruits. Berries were less important in the diet of the larger two hornbill species.

All the eight food species that had small-sized fruits were berries. Of these, 5 species were recorded in the diet of the Oriental Pied hornbill. The medium-sized fruits belonged to 4 species (2 species of Lauraceae, 1 species each of Annonaceae and Rosaceae). The large-sized fruits were all the arillate capsular fruits (2 in the Meliaceae and one in the Myristicaceae). These species are mainly consumed and available in the breeding season, but fruits of one species *Amoora wallichi* are available during the early part of August-September and fruits of *Horsfieldia kingii* and *Chisocheton paniculatus* are available in February-March just before the breeding season. Apart from this, 5 species of the Lauraceae also had large-sized single seeded fruits. The drupaceous fruits of Lauraceae, Annonaceae, and Rosaceae are fleshy, black in colour when ripe with a single stony seed, with no outer covering. The arillate capsular fruits of the Myristicaceae have a lipid-rich oily aril (edible part) covering the single seed, and have an outer covering (perianth) that dehisces or spilts when ripe. The edible aril is yellow or red-orange in colour. Hornbills do not swallow the outer part, just picking out the ripe edible aril-covered seed. The fruits of the Meliaceae are also dehiscent arillate capsules, but are multi-seeded, usually 4, the outer covering is hard and splits open on ripening exposing the edible aril-covered seed. The edible arils are black, dark red, or orange in colour. Though, these fruits are multi-seeded, every single seed within a fruit is surrounded by an edible aril and hornbills swallow each individually, therefore in terms of consumption, these are considered as single fruits.

There were differences in the frequency of canopy levels used by the three species (all sighting records), with the Great hornbill mostly sighted in the upper canopy (51%, n = 337), Wreathed hornbill mostly in the emergent layers (69%, n = 567) and the Oriental Pied hornbill in the mid- and lower canopy levels (52%, n = 59). A Chi-square test, showed a significant difference in canopy levels used, ($X^2 = 199.37$, df = 4, $p < 0.01$). However, if only the foraging height records were considered (n = 197), the differences in canopy levels used were less pronounced ($X^2 = 9.3$, df = 4, $p < 0.10 > 0.05$). Sixty-seven percent of Great hornbill foraging was in the upper canopy, 17% in the mid and lower canopy, and 16% in the emergent layer (n = 88). Fifty-five percent of Wreathed hornbill foraging records were in the upper canopy, while

33% was in the mid-canopy, 13% in the emergent layer (n = 95). Sample size for Oriental Pied hornbill is small, however, 43% was in the lower canopy.

In general, foraging flock sizes were small, 83% of Great hornbill sightings were of single birds, pairs or threes, while the rest were of flock sizes ranging from 4 to 35. Seventy percent of sightings of Wreathed hornbills were of birds in flocks ranging from 1 to 3 birds, while the rest were in larger flocks ranging from 4 to 30. Of all sightings in small flocks, 52% were of Great hornbills, while 48% were of Wreathed hornbills. A higher percentage of sightings of Wreathed hornbills were in large flocks (66%) compared to that of Great hornbills (34%).

Differences in flock sizes when hornbills were foraging for figs vs. non-fig fruits were also examined. Presumably, flock sizes at fruiting fig trees should be larger than at non-fig fruiting trees, because fig trees are large and have larger crop sizes with synchronous ripe fruit availability. On the other hand, most non-fig trees are middle-storey, relatively smaller fruits with small ripe fruit crops ripening over a longer time, and flock sizes at these resources should be smaller. This relationship has been suggested and demonstrated by Leighton & Leighton (1983) and Leighton (1986).

Overall, when both species are combined together, there were no differences in the percentage of sightings in small flocks at figs and non-fig species (52% and 47% respectively). A 2X2 Chi-square contingency analysis also showed no significant differences in small and large flocks at non-figs and figs for Wreathed hornbills or for Great hornbills (X^2 = 0.186, df = 1). Mean foraging flock sizes of both species was 4, while overall mean foraging flock sizes at figs was 5 and at non-figs was 3. Mean flock sizes of Wreathed hornbills was 5 at figs and 4 at non-figs and mean flock sizes of Great hornbills was 5 at figs and 2 at non-figs.

6.4.3. Consumption and availability of non-fig diet species: data from perch and roost trees

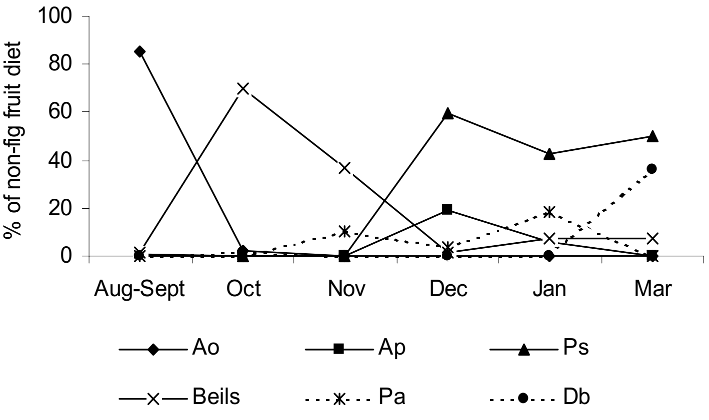
A total of 2977 seeds of 21 non-fig species were counted between September and March below 92 perch trees used by Great hornbills and Wreathed hornbills. A total of 2230 seeds were counted below 7 roost trees in September 1999. Fifteen non-fig species, some insect matter (beetles) and crabs were recorded below roost trees. The data from roost and perch trees were combined (n = 5207 seeds) to obtain an overall estimate of the importance of the various non-fig species eaten during the non-breeding season.

On combining the data, a total of 29 species were recorded in the diet (n = 5207 seeds). Eighteen species that were recorded, formed just 3% of the non-fig diet. The rest of the diet was made up of fruits of 11 species. Sixty percent of the diet was of two species only (*Actinodaphne obovata* and *Polyalthia simiarum*). The next 5 important species formed 27% of the diet (*Pygeum acuminatum*, three species of *Beilshmedia* and *Alseodaphne peduncularis*). Thus, 87% of the non-fig diet in the non-breeding season came from 7 species. Nine fruit tree species recorded in the non-breeding season diet were not represented in the phenology plots, though fruiting individuals of three species were seen. Three liana species were also consumed during the non-breeding season.

6.4.4. Monthly food consumption and availability

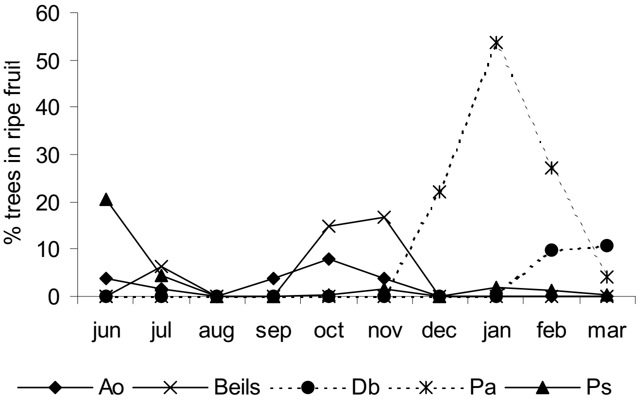
Fifteen species were represented in the phenology plots out of the total of 29 species recorded in the diet from seed counts. But even of those species, in most cases, though a species was recorded in the diet, they were not recorded fruiting in that month in the phenology plots. Therefore, it was not possible to determine monthly or overall preferences for each species. But monthly consumption showed that the contribution of each species varied, while in August-September, *Actinodaphne obovata* was the most consumed, in October, *Canarium strictum* was recorded in the diet more. In November, *Beilshmedia* was the foremost and *Polyalthia simiarum* was the most consumed species in December,January, and March. This is also borne out by the % occurrence of each species in the diet of hornbills, there was asynchrony or a staggered consumption of fruits of these species, showing that in any given month, 1-2 different species were the most important (Fig. 2) also borne out by monthly phenology data (Fig. 3). Most species were recorded in the diet for a mean of 2.6 months; *Polyalthia* was recorded in the diet in 6 months during the non-breeding season. These fruit species were also staggered in their ripe fruit availability.

Fig. 2. Monthly variation in non-fig fruit species consumed during non-breeding season.



Ao – *Actinodaphne obovata*, Ap – *Alseodaphne peduncularis*, Beils – *Beilshmedia* sp., Db – *Dysoxylum binectariferum*, Pa – *Pygeum acuminatum*, Ps – *Polyalthia simiarum*

Fig.3 Fruiting patterns of non-fig species in the non-breeding season.



6.4.5. Do hornbills preferentially consume rare species?

Of the 29 species that were recorded below perch and roost trees, only fifteen species were represented in phenology plots. Of the remaining 14 species, 11 species were of non-fig trees and 3 were liana species. The abundance of lianas in the habitat is unknown and was not quantified at all. The 11 non-fig species were presumably rare in the habitat and were therefore unrepresented. Of the 26 non-fig tree species consumed, overall, 2 non-fig tree species (*Actinodaphne obovata* and *Polyalthia simiarum*) contributed 63% to the diet in the non-breeding season diet, while 7 species formed 34% of the diet. Three of these species were very rare and unrecorded in the phenology plots. Seventeen species formed only 3% of the diet. Given that 11 species were unrecorded, 8 species had densities < 2 tree per ha and four species were < 5 trees/ha, it seemed that hornbills foraged on many non-fig tree species that were rare in the habitat. Of the top 9 species in the diet (in terms of % in diet), three were unrecorded and very rare.

To test the hypothesis that hornbills forage for non-fig resources that may be rare, the fifteen non-fig species that were recorded in phenology plots were used for this analysis. The non-fig food species were assigned a rank from 1 to 9 based on their relative density and their relative dispersion (detailed in Chapter 5). Ranks were given as follows; species that were both rare and dispersed = 1, rare and moderately clumped = 2, rare and highly clumped = 3 ..... , abundant and highly clumped = 9. For example, *Cryptocarya* sp. got a rank of 2 because it was rare and moderately clumped, while *Polyalthia simiarum* got a rank of 9 because it was both abundant and highly clumped (Table 2). An overall index was calculated for each species by multiplying its density/dispersion by length of its fruiting season. For some of the species that mainly fruit in the breeding season, the length of time they were available only during the non-breeding season was considered (August to February). The index of abundance was correlated to percent contribution to the non-fig diet to evaluate whether hornbills show any preference for rare fruit resources.

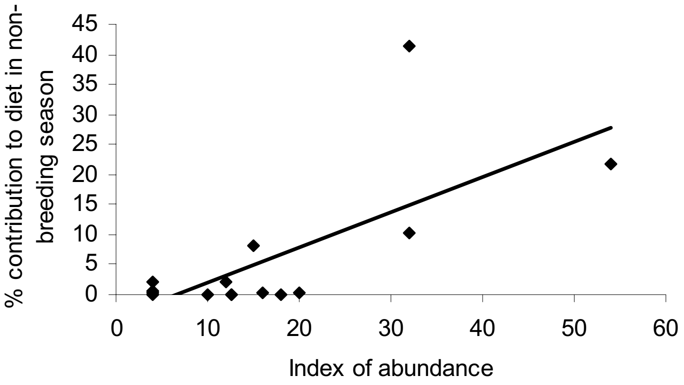
Table 2. Density, dispersion, density/dispersion rank, length of fruiting, and index of abundance of 15 non-fig fruit resources and their contribution to hornbill diet in the non-breeding season

Tree species	**Tree density (ha)**	**Variance to mean ratio**	**Density/dispersion rank**	**Length of fruiting (months)**	**Index of abundance**	**% in diet**
Polyalthia sp.	0.19	4	2	2	4	0.18
*Cryptocarya sp.	0.76	5.5	2	2	4	0.02
Phoebe lanceolata	0.76	3.8	2	2	4	0.52
Syzygium sp.	0.95	8.24	2	2	4	2.12
**Horsfieldia kingii*	1.14	7.2	5	2	10	0.02
Pygeum acuminatum	1.71	6.13	5	3	15	8.04
Elaeocarpus ganitrus	1.9	8.92	5	2.5	12.5	0.02
Beilshmedia sp.	0.76	10.8	8	4	32	10.16
**Cryptocarya amygdalina*	2.28	3.9	5	2.5	12.5	0.12
Actinodaphne obovata	3.24	30.94	8	4	32	41.35
**Dysoxylum binectariferum*	4.19	9.34	5	4	20	0.26
Canarium resiniferum	4.19	4.17	5	3	15	2.14
Livistona jenkinsiana	6.09	61.06	8	3	24	0.04
**Amoora wallichi*	7.43	10.07	8	2	16	0.36
**Polyalthia simiarum*	20.76	20.35	9	6	54	21.79

* Species that largely fruit and are available in the breeding season

The hypothesis that hornbills use resources as they are encountered in the habitat was tested. If this occurred there should have been a positive correlation between resource abundance and resource use. The other alternative is that hornbills search for specific resources that may not necessarily be abundant. When the indices of resource abundance for each of the 15 species were compared to their percentage use, the correlation coefficient was $r_s = 0.51$, $p < 0.05$, $n = 15$. This indicates that hornbills consumed resources as they were encountered and species that were common were the most important in the diet. A scatter plot revealed that there was a clear positive correlation between the index of resource abundance and its percent contribution to the non-fig diet (Fig. 4). The top three species in the diet were also the most common species in terms of abundance. However, a large number of rare species were recorded in the diet suggesting that hornbills do range widely in search of fruits of rare species, though overall contribution of these are low.

Fig. 4. Index of abundance and non-fig fruit resource use by hornbills.



6.4.7. Fruit availability of species consumed in the non-breeding season

The total number of food species consumed in the non-breeding season was 49 species. This includes 41 non-fig fruit species, 7 *Ficus* species and the flowers of *Oroxylum indicum* that were recorded once in the diet of the Oriental Pied hornbill. Three other non-fig fruit species are believed to be hornbill food species based on fruit characters and local tribal information. Thirty-one species are available only in the non-breeding season, excluding the species that fruit mainly in the breeding season, but also have some ripe fruits in part of the non-breeding season. Though the number of species that are available and ripen during this season is higher (31) than the number that are available in the breeding season (30), the combined tree density of tree species that are eaten during the breeding season is much higher than that eaten during the non-breeding season (Fig. 5). Of the 31 species exclusively consumed in the non-breeding season, 20 were not recorded in the phenology plots. Individuals of some food species were not even seen in the area. Fruiting individuals of some species were seen otherwise. Densities of 4 species that were recorded in the plots were less than 1/ha and eight species were less than 5 trees per ha. The most common species in the non-breeding season was *Polyalthia simiarum* (21 trees/ha). Most of the fleshy drupes of the Lauraceae (7 species) fruited in the non-breeding season, as well as 2 species each of the

Rosaceae, Euphorbiaceae, and Rutaceae. One species each of the Meliaceae, Myrtaceae, Palmae, Icacinaceae, Gnetaceae, Burseraceae, Leguminosae, Anacardiaceae, Elaeocarpaceae, Styracaceae, Vitaceae, Rubiaceae, and Annonaceae were the other species that fruited only in the non-breeding season. Seven species remained unidentified.

Most species that were available and consumed in the non-breeding season were medium-sized and small fruits. Unlike the preponderance of a small range of high quality lipid-rich fruits in the diet (belonging mainly to four families) in the breeding season, the non-breeding season diet includes small sugar-rich watery fruits of many other families. Fruit availability of hornbill-food plants was lowest during the non-breeding season of 1998-1999 compared to the other years (Fig. 6).

Fig. 5. Availability of non-fig species: differences in food species density of species consumed in the two seasons.

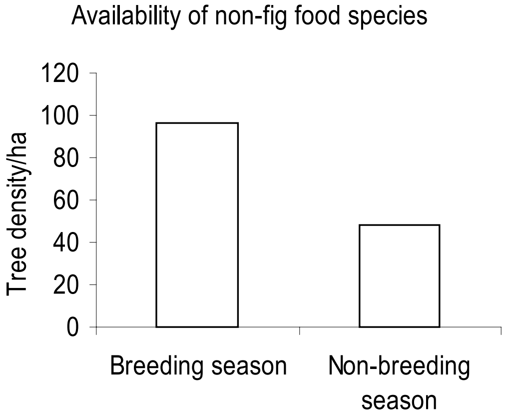
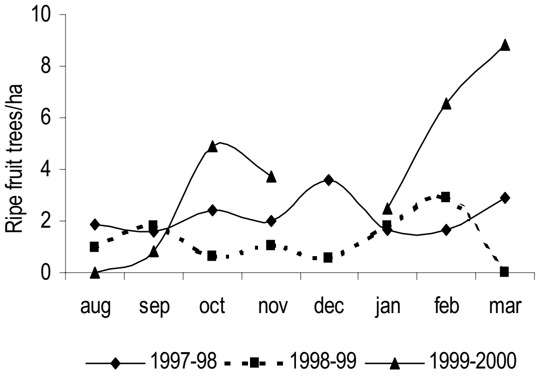


Fig. 6. Ripe fruit availability of hornbill food plants during the 3 non-breeding seasons (1997-2000).



6.5. Discussion

Hornbills consume more species of food items in the non-breeding season than that recorded in the breeding season, but the abundance of these species is low and they are rare at least in the sampled lowland habitat. Hornbills seem to rely heavily on a few relatively common species during the non-breeding season, though a large variety of species are taken. Hornbills tracked the availability of resources with consumption being positively related to its availability. Diet composition changed temporally in accordance with availability of ripe fruits of different non-fig species.

The importance of fruits of several Lauraceae in the later part of the breeding season and in the non-breeding season diet is striking, nearly all the arillate capsular fruits on the other hand ripen earlier during the breeding season. Fruit availability of non-fig species in the winter of 1998-1999 was lower compared to other years, and may have resulted in the lack of nesting by Wreathed hornbills in the subsequent breeding season (March 1999 to August 1999) (see Chapter 5).

Partitioning of food resources among the three species occurred in terms of the relative contributions of figs, non-figs and animal matter in the diet and also at other levels such as the kinds or species of non-fig fruit types, fruit sizes and foraging strata used. Non-fig diet diversity is also greater for the Wreathed hornbill, which is a non-fig fruit specialist, non-territorial and highly mobile. The Great hornbill, a monogamous territorial species with the largest body size fed more on figs than the other two species. There was some indirect evidence that Wreathed hornbills moved over larger areas in that they consumed many non-fig fruit species that are either absent or rare in the lowland habitat, and also from observations of tribal people who suggested that these hornbills move to higher elevation forests seasonally in search of food. Figs fruit asynchronously, occur at relatively high densities in the lowland forest (about 3 trees per ha) and are available throughout the year. The territorial Great hornbills rely on these resources and often exclude the smaller hornbills from these resources (Datta, A. *unpubl. data* from fig tree watches). Generally, most studies have also documented a greater reliance by all *Buceros* species on fig fruits (Leighton 1982, 1986, Poonswad *et al.* 1983, 1986, 1987, 1988 Hadiprakarsa & Kinnaird 2001), while the Wreathed hornbill and other *Aceros* species in most areas, have been seen to rely more on non-fig fruits, though relative importance of figs in the diet varies in different studies (Leighton 1986, Poonswad *et al.* 1983, Kinnaird *et al.* 1996, Hadiprakarsa & Kinnaird 2001).

The importance of figs in the diet of hornbills has been more than adequately stressed in almost all studies on hornbills, and a recent study has suggested that figs offer more nutritional value than previously presumed (O'Brien *et al.* 1998b). It has been suggested that a reliance on figs might require long-distance movements and inhibit territoriality (Hadiprakarsa & Kinnaird 2001). However, where fig densities are relatively high and fruiting is asynchronous, long-distance movements in search of fig crops are less likely, than movements for rare and patchily distributed non-fig fruit species. Home ranges of *Buceros* are smaller than *Aceros* and large-scale movements of *Buceros* are not reported but are much more commonly noted in many *Aceros* species (Leighton 1986, Poonswad & Tsuji 1994, Suryadi *et al.* 1998). Hierarchy based on body size may help to defend fruit resources in smaller territories (Leighton 1982) and during this study, Great hornbills always chased away Wreathed hornbills from fruiting trees. The idea that Great hornbills eat figs, while Wreathed hornbills move greater distances to access spatially patchy high-quality non-fig resources seems to be supported. Communal roosting in larger flocks is also more notable during the non-breeding season and could be related to food finding of patchily distributed non-fig resources (see Chapter 8). Data for the smaller Oriental Pied hornbill are limited, but suggest that they are more generalist feeders, and feed on several small-fruited species, and lianas and forage lower in the canopy. They also occur in low-statured disturbed secondary riverine forests and edges more than in interior primary forest (Datta 1998a).

To conclude, the three hornbill species in the area seem to be partitioning food resources in the non-breeding season. In South-east Asian forests such as in (Borneo, Thailand and Sumatra) where comparative studies of sympatric hornbill assemblages have been carried out, many more hornbill species (though the number of species varies) can co-exist. This is possibly due to greater diversity of hornbill food plant species. However even in these areas, co-existence is made possible by diverse ways of resource partitioning among species (Leighton 1982, Leighton 1986, Hadiprakarsa & Kinnaird 2001).

6.6. CONCLUSIONS

The three hornbill species partitioned food resources by differing in the contribution of figs, non-fig fruits and animal matter in the diet. They also differed in the use of foraging strata and the non-fig fruit types that they consumed. Consumption of different non-fig fruit species closely tracked the peak ripe fruit availability of those species. The availability and density of non-fig fruit species that are consumed in the non-breeding season is much lower compared to that available in the breeding season. Nevertheless, hornbills consumed a similar number of non-fig species in the non-breeding season and diet species richness was high. This contradiction lies in the fact that many species recorded in the diet in the non-breeding season, were either rare or not represented in phenology plots. It is also possible that some of these species are rare in the lowland habitat, (where sampling was carried out) and occurs more commonly at higher elevations. Therefore, this lean period of fruit availability is just a spatial difference in availability for hornbills. This implies that hornbills range widely in search of food resources in the non-breeding season, despite the fact that they rely heavily on a few relatively common non-fig fruit species for the bulk of their diet. Evidence suggests that the Wreathed hornbills especially range far more widely in the non-breeding season for fruit resources. Great hornbills on the other hand are more sedentary and territorial and rely more on figs that are available in both seasons.

Chapter 7. Nest site selection and nesting success of sympatric hornbills

7.1. INTRODUCTION

Hornbills are secondary cavity-nesters, a habit that constrains their ability to breed, and constitutes a potentially important limiting factor. Selection of suitable nest sites is critical in the life history of hornbills, especially because of their peculiar breeding biology, wherein the female is incarcerated in a tree cavity for up to 4 months. They are unable to excavate holes, and therefore must select from those available. Besides the suitability of available cavities for nesting, competition for nest cavities among sympatric hole-nesting birds, other vertebrates, and even bees and wasps, is an important consideration. Nest trees and cavities are also lost due to natural factors such as sinking of the cavity floor, shrinkage of cavity entrance, and tree and branch breakage due to storms. In addition, loss can occur due to felling of nest trees, severe degradation and opening up of the habitat due to human activity, repeated nesting failure either due to disturbance, hunting or removal of chicks leading to subsequent abandonment of nest sites. Thus, apart from food resources, a lack of nesting opportunities may also constrain breeding and population recruitment among hornbills.

While earlier insights into hornbill nesting biology comes from anectodal information (Baker 1927, Madge 1969, Hussain 1984 and Ali & Ripley 1987), lately, more rigorous studies (Poonswad *et al*. 1987, Kannan 1994, Poonwad 1995, Mudappa & Kannan 1997, Kinnaird & O'Brien 1999) have been done on many Asian hornbill species. In India, nest site selection and breeding biology of the Great Hornbill and the Malabar Grey Hornbill have been studied in detail in the Western Ghats, southern India by Kannan (1994) and Mudappa & Kannan (1997) respectively.

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

The focus of this study was to determine the nest site characteristics of three sympatric hornbills, the Great hornbill, Wreathed hornbill, and the Oriental Pied hornbill, factors that are important in nest site selection by these species, and the degree of overlap in nest site characteristics among these three species. These species occur mainly in the lowland foothill forest habitat that is limited in extent in Arunachal Pradesh. This habitat is also easily accessible, and therefore faces the most severe pressures due to past logging, clearing of forest for agriculture, settlements, and hunting. It becomes important, therefore, to identify nest sites and suitable nesting habitats, and assess nesting success and rates of nest tree loss.

Using both univariate and multivariate analyses, an attempt was made to identify important variables that determine nest site selection, and identify those that contribute most to the differences in nest sites chosen by the three sympatric hornbill species. Nesting success and nest tree loss over the 4-year period of study are also discussed in the light of natural and man-induced causes of nesting failure and abandonment. Data on the availability of potential nest tree species, and cavities, and nesting densities, are presented to evaluate whether nest site availability is a limiting factor for hornbill populations in the area. The identification of nest sites, tree species used for nesting, as well as structural characteristics of nest trees selected by hornbills may help in better protection and conservation of these species.

7.2. OBJECTIVES

1. To determine the nest site characteristics of three sympatric hornbill species.
2. To identify the factors that are important in nest site selection by each of these species, and the degree of overlap in nest site characteristics among the three species.

7.3. METHODS

7.3.1. Nest searches and nesting habitat

The study was carried out between March 1997 and July 2000, and observations on nest trees and nesting success were made during the four breeding seasons. The breeding season (from nest entry to chick emergence) of hornbills was from March to early August, with some annual and species variations in starting dates. A total of thirty-six nests were observed over the study period, of which 19 were located on intensive nest searches carried out between February and May of each year, while the remaining 17 were located by offering monetary rewards to local tribals. Most of the nest trees were located either by following lone males, intensive searches in the area by inspecting potential nest trees with cavities for middens (piles of regurgitated seeds and faecal matter) indicating active nests. The presence of seedlings of hornbill food plants and old feathers also provided indirect evidence of use as a nest tree. Two nests were located on the basis of frequent calls heard during nest watches at other nearby nest trees.

The quantification of nesting habitat followed methods suggested by James and Shugart (1970), and subsequently by Kannan (1994) and Mudappa & Kannan (1997).

Vegetation and nest tree parameters (detailed below) were quantified in circular plots of 15-m (0.07 ha), with the nest tree as the centre. The nest tree species was noted. All trees (GBH ≥ 25 cm) were enumerated and GBH (girth at breast height) measured. Canopy cover was quantified by taking readings at 10 points each (every 5 steps) in the four cardinal directions from the nest tree using a canopy densiometer. The altitude of the nest site (using an altimeter), distances to nearest road, habitation, and river were also noted.

The nest tree parameters measured or estimated were height of nest tree, height of nest cavity from the ground, location (main trunk, primary, secondary or tertiary branch) and position of nest cavity (emergent, upper, middle or lower canopy), cavity width and cavity length, girth of nest tree (above buttress), girth at nest cavity, emergence of nest tree, height of first branch of nest tree, tallest tree in plot, distance of tallest tree to nest tree, and nest cavity orientation. If the nest tree was the tallest tree in the plot, then the height of the next tallest tree and its distance to the nest tree were also measured.

The probable mode of cavity formation was also recorded, i.e. formed by a branch breaking off, by woodpecker or barbet activity or by heart rot. This was ascertained by whether the cavity was on a protrusion of an old broken branch or directly on the main trunk or other branches. The shape of the hole also gave an indication whether it was formed by the excavating activity of birds such as woodpeckers.

Parameters such as tree density, and canopy cover were also quantified in similar sized plots located 100 m in a random direction from the nest tree, where the nearest tree of GBH ≥ 80 cm was chosen as the centre tree. Parameters of the centre tree such as tree height, GBH, emergence, height of first branch, and distance from tallest tree were measured. Comparisons of random (non-nest) plots with nest tree plots were made to determine parameters likely to affect choice of nesting habitat by hornbills.

7.3.2. Nest tree species and nest cavity availability

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

7.3.3. Nesting status, attempts and success

Nests were checked at regular intervals for nesting status. Twenty-three nests were monitored intensively, while 14 were observed at 1 to 2-week intervals (data pooled for all 4 years). A few nests (6) were checked only twice, once initially to see if it was active and once at the end of the breeding season. Nesting success was determined by direct observations of chick fledging, or presumed to be successful by indirect evidence such as presence of sealing plaster below the nest, or if the nest had remained active till the end of the breeding season, even if actual chick emergence was not observed. The presence of the family group (male, female and newly fledged chick) either on the nest tree or in the vicinity also often provided indirect evidence of successful nesting. Nest tree reuse by species and turnover in use in different years was also recorded. The presence of competitors and predators at nest trees was also noted.

7.3.4. Data analysis

Non-parametric Mann-Whitney U tests were used to determine differences in 15 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 thirteen nesting habitat and nest tree parameters were ascertained using Kruskal-Wallis 1-Way ANOVA. The Rayleigh test was used to determine if nest cavity orientation differs significantly from random or whether there was statistical evidence of directionality. A circular test statistic was used since this is a circular variable (Zar 1974, Batschelet 1981).

Descriptive statistics and univariate tests of significance provide basic information about the distribution of variables in the groups, and help identify differences among the groups. However, in multivariate procedures, simultaneous consideration allows identification of important relationships.

A simple ordination technique (Principal Component Analysis) was used to illustrate nest site selection by hornbills. Principal Component Analysis (PCA) was performed using SPSS/PC + software using Varimax rotation of factors (Norusis 1990). A Pearson's correlation matrix initially depicts the correlation between the input variables. The PCA was carried out to collapse the twelve nest site variables into a new set of factors or principal components that incorporate the relationships between these variables. Thus, factors that are important in explaining the variation in nest site selection are generated, and subsequently species relationships with these factors can be evaluated graphically. The factor scores that are generated 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 were the most important variables that contributed most to the differences between species. DFA has two main purposes: i) to identify variables that are important for discriminating among groups, and ii) for predicting group membership for new cases whose membership is undetermined. The assumptions of DFA: are i) each group must be a sample from a multivariate normal population, and ii) the population covariance matrices must all be equal. Violations of these assumptions are not considered fatal, although two other less mentioned assumptions, are correlation between means and variances, and redundancy of variables (ill-conditioned matrix), both of which may be more important to guard against. More details on both PCA and DFA are given in Pielou (1984).

Kolmogorov-Smirnov One-sample tests along with histograms of frequency distributions were used to determine normality of variables. All variables were normally distributed. Twelve variables were used in the analysis of 21 nests. Sample size is small and there was multicollinearity, but it was felt that the explanatory power of the analysis would be compromised if some of the variables were dropped, even though they were auto-correlated. DFA was used primarily as an exploratory technique to discern differences between hornbill species in nest site selection, and determine which variables were important in discrimination.

7.4. RESULTS

7.4.1. Nest trees

A total of 36 nest trees of hornbills were located. These included 11 Great hornbill nests (one of these was cut down), 6 Oriental Pied hornbill nests (one cut down), 17 Wreathed Hornbill nests (one nest tree uprooted during a storm and two cut down), and 2 Rufous-necked Hornbill nests. Twenty-one of these nests were located in Arunachal Pradesh and 15 were in the border areas in Assam. Only twelve nests were in dense forest, ten were in open forest, and 14 in edge forest (highly degraded). Searches for nest trees of Rufous-necked hornbill and the Brown hornbill were made in Namdapha TR. Hornbill nests were also located during surveys in Doimara RF, West Kameng district and in unclassed state forests in the Pakke Ka Sangh area in East Kameng district. One nest was also located near Kaziranga NP, Assam in a tea estate. Several nests were located in Nameri NP, Assam adjacent to the south-eastern boundary of Pakhui NP (Fig. 2 in Chapter 2).

7.4.2. Nest site characteristics

Nest trees differed significantly from centre trees of non-nest plots, in terms of size. The height of the tree, emergence, girth, height of the first branch were all significantly greater in nest trees than non-nest centre trees (Table 1). But there was no significant difference in canopy cover, distance to tallest tree and overall tree density between nest plots and non-nest plots, differences were only associated with the structural characteristics of the nest tree and the centre tree of the non-nest plot. However, there was a significant difference in large tree density (GBH ≥325 cm) between nest and non-nest plots. All nest trees (except one Great hornbill nest tree in a tea estate) were emergents. Most nest holes were located in emergent or upper canopy (91%), the remaining were in mid-canopy. Nearly all (30) nest trees were the tallest trees in the nest plots.

Cavity orientation of nest trees selected by hornbills did not differ significantly from random (Rayleigh test, r = 0.3437, p > 0.05, n = 22 nests). The location of the nest hole was usually on the main trunk (56%) or on a broken branch offshoot of the main trunk (19%). The rest of the nests were located on primary branches (12.5%), secondary branches (9%) and tertiary (3%). The shape of the nest cavity varied from elongated (11 nests) to oval (14) to round (7).

Table 1. Parameters of nest-site plots and non-nest plots.

Parameters	**Nest plots** **N = 31**	**Non-nest plots** **N = 21**	**Test statistic U**	**P**
Canopy cover (%)	88.59 ± 4.23 n = 14	88.82 ± 3.59 n = 10	66	0.815
Emergence (m)	16.81 ± 0.87 n = 27	4.31 ± 0.93 n = 19	6	**0.00**
*Nest/centre tree GBH (cm)	425.07 ± 19.83 n = 29	177.57 ± 18.80 n = 21	25	**0.00**
*Nest/centre tree height (m)	35.03 ± 1.05 n = 29	20.75 ± 1.08 n = 20	9.5	**0.00**
*Tallest tree (m)	34.89 ± 1.15 n = 29	27.15 ± 1.44 n = 20	109.5	**0.00**
*Height of first branch (m)	17.21 ± 0.73 n = 28	10.97 ± 1.24 n = 20	111	**0.00**
Distance to tallest tree (m)	9.55 ± 0.82 n = 22	9.15 ± 0.85 n = 20	220	1.00
Tree density (per ha)	n = 31 plots	n = 21 plots		
≥ 25 cm	414.66 ± 49.69	317.17 ± 39.13	262.5	0.24
26-75 cm	287.85 ± 41.64	216.83 ± 34.51	277	0.36
76-125 cm	68.43 ± 9.21	54.54 ± 8.79	282	0.41
126-175 cm	28.28 ± 4.19	26.94 ± 4.57	319.5	0.91
176-225 cm	9.58 ± 2.31	6.06 ± 1.56	295.5	0.53
226-275 cm	4.10 ± 1.88	4.71 ± 1.78	292	0.38
276-325 cm	2.74 ± 1.02	4.04 ± 1.43	295.5	0.44
*≥ 325 cm	13.23 ± 0.63	3.37 ± 1.35	98.5	**0.00**

**Parameters that were significantly different between nest and non-nest plots*

7.4.3. Nest site characteristics of three hornbill species

7.4.3.1. Univariate tests

There was a great deal of overlap in the tree species used for nesting, with *T. nudiflora* being the most important species for all three hornbills (30 of 36 nest trees) (Plate 6). Three trees *Ailanthus grandis*, were also used, one each by the 3 hornbill species. One nest each of the Rufous-necked hornbill was on *Terminalia myriocarpa* and *Altingia excelsa.* All these species are large emergent trees. Structural characteristics of nest trees also did not show much difference among the three hornbill species (Table 2), except in cavity length (Kruskal-Wallis 1 Way ANOVA, $\chi^2 = 9.43$, df = 2, p = 0.009) and girth at nest cavity ($\chi^2 = 4.83$, df = 2, p = 0.08).

There was a significant difference in cavity length between Great hornbill nest holes and both the Wreathed hornbills (Mann-Whitney U tests, M-W U = 13, p = 0.033) and Oriental Pied hornbills (M-W U = 0, p = 0.006). Wreathed hornbill nests and Oriental Pied hornbill nests differed in girth at nest cavity (M-W U = 12.5, p = 0.034). Oriental Pied hornbill nest trees and nest cavity heights were highest, but not significantly different from the others. Wreathed hornbill nests were generally in more dense forests and farther from disturbance, though the difference was not significant. Great hornbill nest holes tended to be more elongated (64%), while Wreathed hornbill nest holes tended to be oval (53%).

Table 2. Nest site characteristics of four hornbill species.

Parameters	**Great hornbill N = 11**	**Wreathed hornbill N = 13**	**Oriental Pied hornbill N = 5**	**Rufous-necked hornbill N = 2**
1. Tree density (per ha) (trees ≥ 25 cm GBH)	434.34± 144.30	519 ± 81.84	431.31± 121.85	410.10 ± 56.56
2. Nest tree height (m)	34.6 ± 1.80	34.64 ± 0.85	37 ± 4.72	34 ± 6
3. Nest tree GBH (cm)	455 ± 41.79	413.71 ± 23.51	397 ± 48.31	708.5 ± 27.5
4. Emergence (m)	17 ± 2.66	17.07 ± 0.66	15.8 ± 1.49	22.5 ± 7.5
5. Height of cavity from ground (m)	19.40 ± 1.30	20.31 ± 1.09	25.80 ± 5.06	19 ± 3
6. Height of first branch (m)	16.3 ± 0.89	18.07 ± 1.31	16.8 ± 1.53	18 ± 8
7. Girth at cavity (cm)	178.27 ± 6.46	185.80 ± 12.69	136 ± 18.6	-
8. Cavity length (cm)	30.42 ± 3.86	22 ± 3.87	15 ± 0.71	-
9. Cavity width (cm)	25.42 ± 6.77	17.1 ± 1.07	14.25 ± 2.28	-
10. Distance to habitation (m)	1213 ± 429.17	1453.57 ± 348.01	1132 ± 589.69	1500 ± 0.0
11. Distance to road (m)	1925 ± 500.73	2092.86 ± 383.51	1840 ± 552.81	6000 ± 4000
12. Distance to river (m)	1905 ± 479.72	1374.28 ± 387.73	846 ± 440.81	2500 ± 500
13. Altitude (m)	360.55 ± 41.12	359.28 ± 28.49	318 ± 18	1100 ± 300

7.4.3.2. Principal component analysis

The PCA was carried out using data from a subset of all nests observed, since 7 of the nest trees had been cut before measurements could be taken. Of the remaining 29 nests, measurements of some variables were not taken at a few nests. Therefore, the analysis could be carried out with only 21 nests (7 Great hornbill, 10 Wreathed hornbill and 4 Oriental Pied hornbill) for which all 12 input variables (excluding altitude) were recorded. Table 3 shows the Pearson's correlation matrix between the 12 variables.

PCA extracted four principal components, which explained 73.09% of the total variance (Table 4). The first component explained 32.33% of the total variance. Nest tree variables such as nest tree height, emergence, girth and height of cavity from ground were positively correlated to the first component. High values on the first component corresponded to tallness of trees, high emergence, large girth trees and nest cavities that are high above the ground. Thus the first component represents, with increasing values, the size of the nest tree. The second component explained an additional 18.19%of the total variance. This component was correlated with tree density, distance to road, habitation and river (Table 4). High values on the second component corresponded to a high tree density and greater distance from human habitation, road and also the river. The second component thus represents, with increasing values, denser forest, greater distance from habitation and hence a lower degree of disturbance. The third component explained 12.6% of the total variance, and was positively correlated to cavity width and cavity length. Thus the third component represents, with increasing values, nest trees with larger cavity size. The fourth factor explained 9.97% of the total variance and was related to height of the first branch and girth at cavity (Table 4).

Table 3. Pearson's correlation coefficient matrix between nest tree variables

	Tree density	**Tree height**	**Height of first branch**	**Nest cavity 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 cavity height				1.000	-0.341	0.393*	-0.189	-0.135	0.389*	-0.118	0.262	0.321
Girth 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 habitation												1.000

**significant at* $p \leq 0.05$

Table 4. Summary statistics of the Principal Component Analysis

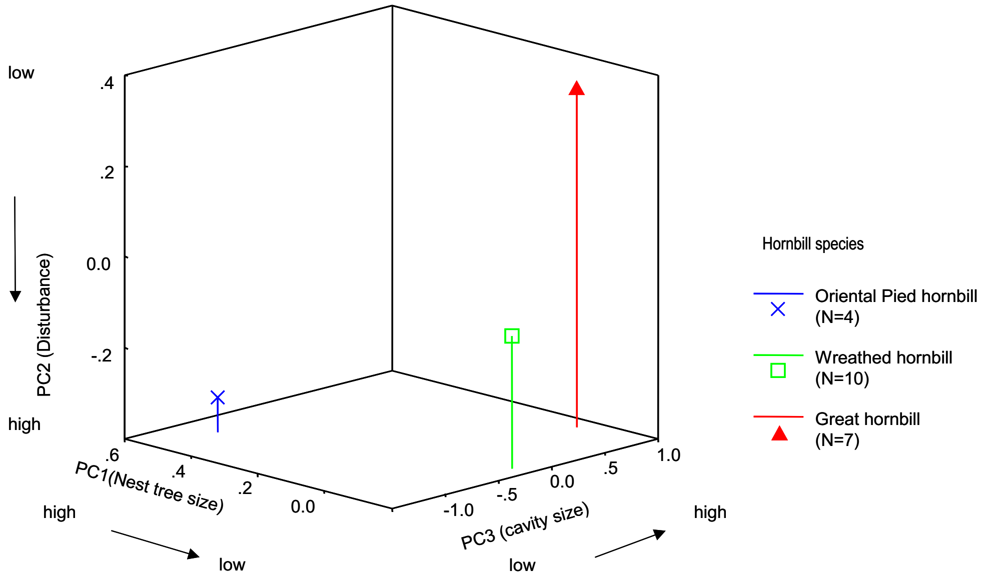
Nest tree variable	Communality	PC1		PC2		PC3		PC4	
		r	*C*	*r*	*C*	*r*	*C*	*r*	*C*
Tree density	0.668	0.113	-0.035	0.657*	0.200	-0.290	-0.105	0.373	0.130
Tree height	0.870	0.903*	0.345	0.053	-0.114	-0.171	-0.046	0.151	0.105
Height of first branch	0.735	0.213	0.089	0.102	-0.129	0.020	0.084	0.824*	0.581
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
Eigen value		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;

**Correlation significant at* $p < 0.05$

Nest site relationships among the 3 species of hornbills can be observed with mean values (mean factor scores) for each species plotted on the components (Fig. 1). As can be seen on the first component axis, the Oriental Pied hornbill nested in taller trees with larger GBH and higher above the ground than the other two species. On the second component, Great hornbill nests were in dense and less disturbed forest, while Wreathed hornbill nests were intermediate between the two other species. Oriental Pied hornbill nests were in more open and disturbed habitats. On the third component, as the size of the hornbill increased, so did the cavity size. Thus, there was increasing values of cavity size selected from Oriental Pied hornbill to Wreathed hornbill to Great hornbill (Fig. 1).

Fig.1 Three dimensional ordination of nest site relationships among the 3 hornbill species on the first 3 principal components using mean factor scores for each species. The first component (PC1), left to right represents a change from larger-sized nest trees to smaller. The second component (PC2), top to bottom represents a change from mature undisturbed forest to more open disturbed forest. The third component (PC3), front to back represents a change from smaller cavities to larger cavities. The total variance explained by the PCA was 73.1%.



To visually interpret the overall nest tree selection patterns among the three hornbill species, all nest trees of the three species were plotted on a scatter plot of their principal component scores. The ordination of the nest trees on two-factor axes revealed few differences among the species.

Fig. 2a shows the relationship of Factor 1 with Factor 2 and there is no clear pattern among species. As can be seen on the first component axis, while Wreathed hornbills used nest trees intermediate in size, there was a wide variation in size of nest trees used by Great hornbills. The dataset for the Oriental Pied hornbill is limited, but despite being considerably smaller in size, it also used large trees. On the second component, again there was high variation in Great hornbill and Oriental Pied hornbill nesting habitat with nests located both in open, disturbed forests as well as in dense undisturbed forest. Wreathed hornbill nests were located in intermediate levels of disturbance. Fig. 2b shows the relationship of Factor 2 with Factor 3 where there seems to be some separation among the three species in Factor 3 indicating that Great hornbill nest cavities were much larger compared to Wreathed and Oriental Pied hornbill cavities. Fig. 2c shows the relationship of Factor 2 (degree of disturbance) with Factor 3 and here again Factor 3 results in some degree of separation among the species. Fig. 2d shows the relationship between the three species in three-factor space.

The relationships among the 3 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 only 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, the Wreathed hornbill (p = 0.031) and the Oriental Pied hornbill (p = 0.005).

Fig. 2a. Hornbill nests in two-factor space showing overlap among 3 hornbill species on the first two principal components

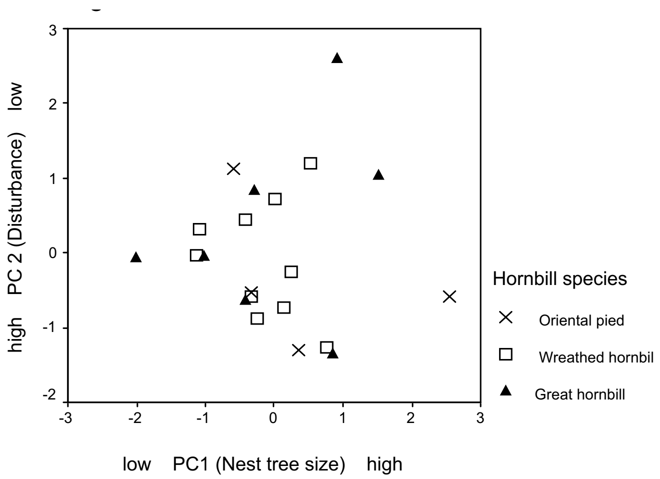


Fig. 2b. Hornbill nests in two-factor space showing overlap among 3 hornbill species on the first and third components

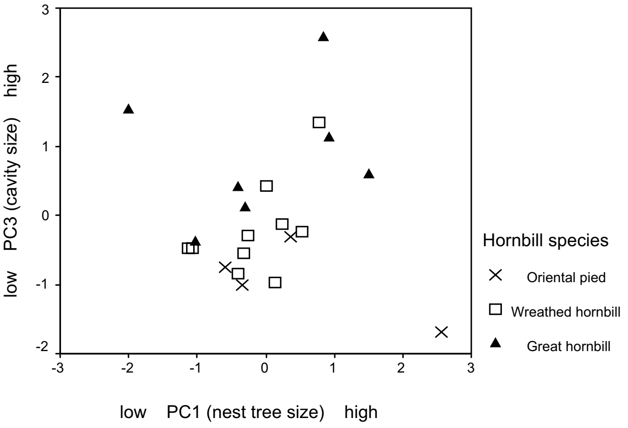


Fig. 2c. Hornbill nests in two-factor space showing overlap among 3 hornbill species on the second and third components.

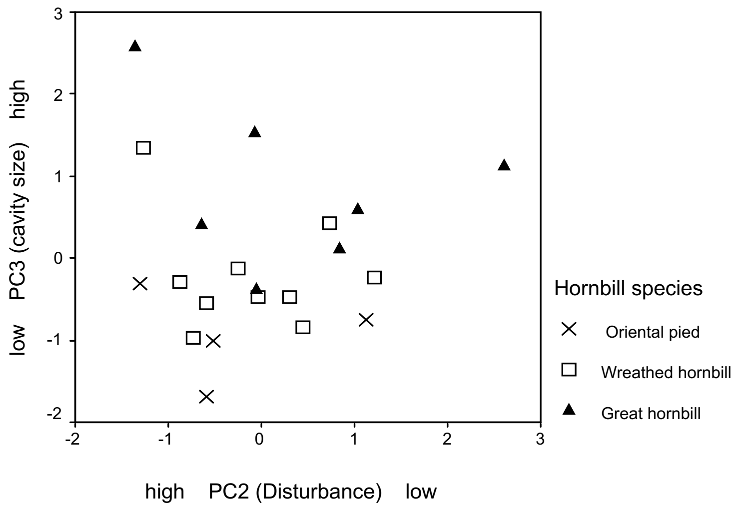
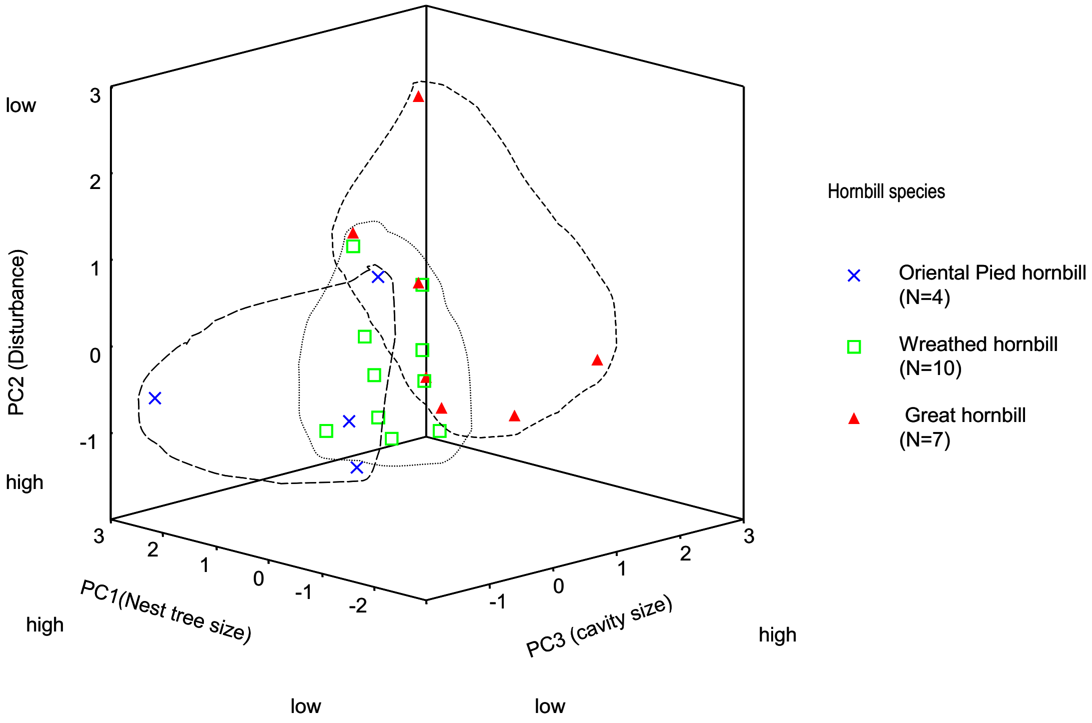


Fig. 2d. Hornbill nests in three-factor space showing overlap among the 3 hornbill species on the first three principal components



7.4.3.3. Discriminant function analysis

A DFA was carried out to determine variables that are important in differentiating among the three hornbill species in nest tree use. The first discriminant function explained 77.9% of the variance (eigen value 2.68), while the second one explained the remaining 22.1% (eigen value 0.76). The canonical correlation with the first function was 0.853, while the canonical correlation with the second function was 0.657.

The factor structure coefficients are the correlations between the variables and the discriminant functions (analogous to factor analysis) and are used to interpret the functions meaningfully.

Two canonical discriminant functions were formed, function 1 was most highly related to cavity size and distance to river, while function 2 was related to nest tree size (Fig. 3). Distance to river, cavity length, and cavity width were the three most important variables in discriminating among the 3 species.

To determine between which groups the functions discriminate, the group centroids and individual scores of groups for the discriminant functions were plotted (Fig. 3). The discriminant scores for each function were also plotted on boxplots to graphically highlight the degree of overlap and separation among the three species along the functions (Fig. 4a, 4b).

The difference between group means was not statistically significant (Wilk's Lambda) for either of the functions. While proceeding with interpretation of non-significant functions may be inappropriate, a clear separation among the three species was achieved when discriminant factor scores and the group centroids of each species were plotted graphically (Fig. 3) and these functions could be meaningfully interpreted and corresponded with the findings of the PCA. In fact in this analysis, the differences between the three species are more clearly highlighted by DFA (Fig. 3) than the PCA (Fig. 2d). The advantage of DFA is that it maximizes differences so separation can be clearly seen (Pielou 1984). Independent of objective statistical tests, a DFA allows visual interpretation of differences among groups.

7.4.4. Potential nest tree species availability

A list of 25 potential nest tree species that occurred in the study area was compiled based on other studies on hornbills in Asian tropical forests with similar tree genera or species (Poonswad 1995, Chimchome *et al.* 1998) and those that generally attain a large tree size.

Fig. 3. Canonical Discriminant Functions for hornbill nests that distinguishes between the three species. Function 1 was related to cavity size and distance to 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.

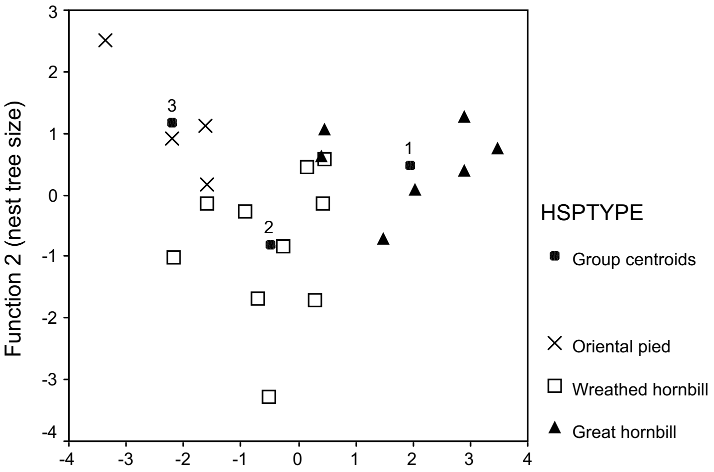


Fig. 4a. Nests of three hornbill species (Discriminant Function 1) showing the variation around the mean values for each species.

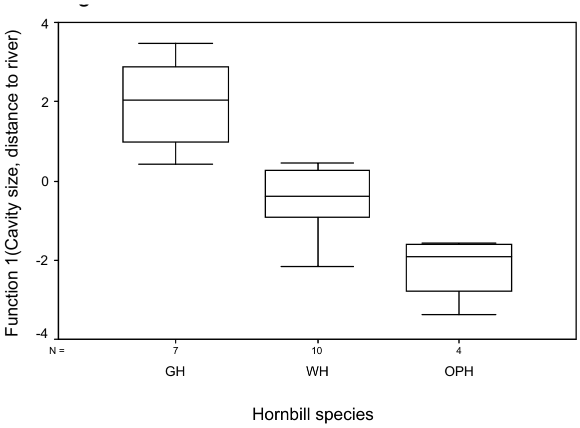
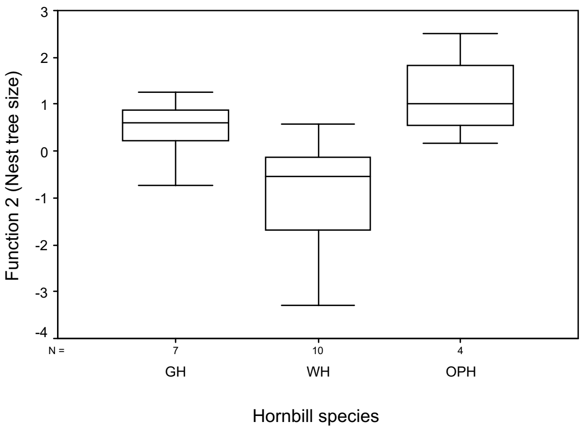


Fig. 4b. Nests of three hornbill species (Discriminant Function 2) showing the variation around the mean values for each species.



Of these, only 2 species (*T. nudiflora* and *Ailanthus grandis*) were used for nesting in the study area. Both these species were softwoods, emergent, large girth trees, relatively more common than other species; in fact *T. nudiflora* was the most common tree species among these. The eleven other softwood species were *Alstonia scholaris*, *Canarium resiniferum*, *Cinnamomum cecicodaphne*, *Duabanga grandiflora*, *Garuga gamblei*, *Gmelina arborea*, *Michelia champaca*, *Michelia* sp., *Sapium baccatum*, *Sterculia alata* and *Toona* sp. (Table 5). No large trees (GBH ≥ 250 cm) of seven of these species were recorded in the twenty-one 0.25 ha plots, thus they were very uncommon, while the combined large tree density of the remaining four softwood species was only 1.14 per ha. Of 25 potential nest species, the availability of large trees of 16 species was 5.89 trees per ha, of which the two recorded nest species (*T.nudiflora* and *A. grandis*) comprised 1.33 trees per ha. No large trees of the other 9 species were recorded in the plots (Table 5).

Apart from wood type, tree size and overall availability of the species must be important factors in nest tree selection. *Terminalia myriocarpa*, *Mesua ferrea*, *M. champaca* and *Garuga gamblei* are also potential nest species but were very rare in the study area and not represented in the study plots. One tree, each of *T. myriocarpa* and *Altingia excelsa* (both durable hardwoods and important timber species) were also recorded as nest tree species used by rufous-necked hornbill in other areas. Both these species also occurred in the main study area, but were not used by the three other sympatric hornbills. *T. myriocarpa* was very uncommon, while *A. excelsa* was as abundant as *T. nudiflora*, however, it may be that suitable trees with cavities were less common on *A. excelsa*, a hardwood. One nest was recorded on *Albizzia* sp. that was planted in a tea estate, but this tree species did not occur in forest habitats.

In the study plots covering 5.25 ha, the overall availability of trees GBH ≥ 250 cm was 7.62 per ha (40 trees) and included 22 species. The overall availability of trees GBH ≥ 300 cm was 4.76 trees per ha (25 trees) and included 14 species.

T. nudiflora is the commonest emergent softwood species occurring in the lowland forests, but the abundance of this species is not uniform. Density of *T. nudiflora* in the Seijusa lowland area (intensive study site) was 2.9 per ha, while in the moister Khari area it was 0.8 per ha. This species is restricted to lowland forest closer to riverine areas on relatively flat terrain, and is not present in higher areas of the park. *T. nudiflora* was not observed in the Mehao WLS (Dibang Valley district) or in Namdapha TR even in relatively lowland foothill forests (Datta, A. unpubl. data). In Namdapha TR, *A. excelsa*, *T. myriocarpa*, and two dipterocarp species, *Shorea assamica* and *Dipterocarpus assamicus* are common emergent species and may be more important nest tree species.

Table 5. Potential nest tree species, tree characteristics and availability.

Tree species	**Tree height**	**Wood type[1]**	**Foliage type**	**Overall tree density/ha**	**Tree density/ha (GBH ≥ 250 cm)**
1. *Ailanthus grandis**	Up to 120 feet	Softwood	Deciduous	1.52	0.19
2. *Altingia excelsa**	50-60 feet	Hardwood, but rots easily	Deciduous	2.28	1.14
3. *Alstonia scholaris*	Large	Softwood	Evergreen	0.38	0
4. *Amoora wallichi*	Middle-sized	Hardwood	Evergreen	7.42	0.57
5.*Artocarpus chaplasha*	Large	Moderately hard	Deciduous	0.95	0.19
6.*Canarium resiniferum*	Large	Softwood	Evergreen	4.19	0.38
7.*Cinnamommum cecicodaphne*	Large	Soft to moderately hard	Evergreen	0.76	0.19
8.*Duabanga grandiflora*	Tall	Softwood	Deciduous	0.76	0
9. *Dysoxylum hamiltonii*	Large	Moderately hard	Evergreen	0.19	0.19
10. *Garuga pinnata*	Large	Moderately hard	Deciduous	2.66	0.19
11. *Garuga gamblei*+	Large	Softwood	Deciduous	0	0
12. *Gmelina arborea*	Large	Softwood	Deciduous	0.57	0.38
13. *Litsea chinensis*	Middle-sized	Moderately hard	Evergreen	1.33	0.19
14. *Mesua ferrea*+	Large	Hardwood	Evergreen	0	0
15.*Michelia champaca*+	Large, tall	Softwood	Evergreen	0	0
16. *Michelia* sp.	Large	Softwood	Evergreen	0.57	0
17. *Phobe cooperiana*	Middle-sized	Moderately hard	Evergreen	1.33	0.19
18. *Sapium baccatum*	Up to 150 feet	Softwood	Deciduous	0.19	0
19. *Schima wallichi*	Large	Moderately hard	Evergreen	1.71	0.38
20. *Sterculia alata*	Large	Softwood	Deciduous	11.62	0.19
21.*Stereospermum chelonoides*	Large	Hardwood, no heartwood	Deciduous	4.57	0.19
22.*Terminalia myriocarpa**+	Very large	Hardwood	Evergreen	0	0
23.*Tetrameles nudiflora**	Up to 150 feet	Softwood	Deciduous	1.9	1.14
24. *Toona* sp.	Large	Softwood	Deciduous	0.19	0
25. *Vitex pentaphylla*	Large	Hardwood	Deciduous	2.47	0.19

[1] Gamble 1985

** actually recorded nest tree species, a planted Albizzia sp. was also used as nest tree in a tea estate*

+ not recorded in plots, but present in area

7.4.5. Potential nest cavity availability

In the 0.44 ha area sampled (180 trees), availability of potential nest tree species was high (72.72 trees per ha). But availability of large-sized (GBH ≥ 300 cm) potential nest tree species was 11.36 trees per ha. Availability of *T. nudiflora* was 2.27 per ha.

Eleven cavities on ten species were recorded, giving a cavity density of 25 per ha, but of these, only 3 cavities were on large-sized potential nest trees (6.8 per ha). Of the 11 cavities recorded in 180 trees sampled, the mean height of cavity from the ground was 4.21m ± 1.64 (n = 7) and ranged from 0.5 m to 11 m. No cavity was at a height suitable for use by hornbills. The lowest height of cavity recorded for hornbills during this study was 12 m, though Oriental Pied hornbills are known to use lower heights (Poonswad 1995). Of the 11 cavities, one was small and used by hill mynas (*Gracula religiosa*), monitor lizards (*Varanus benghalensis*) occupied another, and another was badly broken and too big. Potential nest cavity availability is estimated to be 2.27 per ha.

7.4.5.1. Mode of cavity formation

Eight nest cavities which were located on broken branch offshoots were formed by the breaking of a branch and subsequent heart rot, while 12 were formed possibly by enlargement after initial excavation by primary cavity nesters such as barbets (*Megalaima* spp.) and woodpeckers. Woodpecker and barbet activity seems to facilitate formation of suitable cavities for hornbills. At least eight species of woodpeckers and four species of barbets occur in the area. Holes formed by woodpeckers are commonly seen on *T. nudiflora*, a softwood species (*pers. obs.*), often a row of several, and one below another. Woodpeckers are known to select softwood trees for excavation (Ali & Ripley 1987).

7.4.6. Nest competitors and predators

A yellow-throated marten (*Martes flavigula*) was seen below the nest tree of a Wreathed hornbill nest during the 1997-breeding season. A marten was also sighted in the vicinity of a Great hornbill nest in 2000, though this nest was not in use since 1997. Other reported natural predators are the binturong (*Arctictis binturing*) (Chimchome *et al.* 1998, Poonswad *et al.* 1998) and possibly the smaller arboreal cats. Two monitor lizards were occupying the cavity of a Wreathed hornbill nest on an *A. grandis* tree in 2000, and hornbills did not nest here that year. Monitor lizards were commonly seen in the study area, four other sightings of the species were just outside cavities in trees of *T. nudiflora*, *Pterospermum acerifolium*, *A. grandis* and *G. arborea*. A monitor lizard was also seen occupying a hole in a potential *A. grandis* nest tree. Wasps, bees, snakes and flying squirrels are other species known to occupy hornbill nest cavities (Poonswad *et al.* 1987). Other hole-nesting birds seen using cavities in *T. nudiflora* were Hill myna (4 trees), Red-breasted parakeet (*Psittacula alexandri fasciata*) (3 trees), Broad-billed roller (*Eurystomus orientalis*) (1 tree) and the Great Slaty woodpecker (*Mulleripicus pulverulentus*) (2 trees). Hill mynas were also seen inspecting cavities of nesting hornbills.

7.4.7. Nesting attempts and nesting success

Nineteen (51%) of nests were inactive, while the rest were still active by the end of the study. While some of the inactive nests were totally unusable, some were considered inactive because there was no nesting on these trees for consecutive years. Nests that were being used in terms of at least one nesting attempt, even if unsuccessful due either to abandonment or failure to produce chicks, were considered active nests. Table 6a. shows the incidence of nest tree loss due to natural and human-induced causes during the study period.

Out of a total of 72 nest trees (if the data are pooled for all trees over the 4 years, excluding the broken and cut trees), overall, there was 64% nesting attempts (46 cases), while in 22 cases (31%) there were no nesting attempts. In 4 cases it was not known whether nesting attempts were made. 37 of 46 nesting attempts were successful (80%), while 7 nests were unsuccessful and the fate of 1 was unknown. Table 6b. lists some of the reasons for unsuccessful nesting in the three hornbill species.

The details of the number of total known nests in each year for each hornbill species and number of nesting attempts and successful nests are given in Table 6c. In the first year, few nests were known, nesting attempts were made in 67% of these nests, while successful nesting occurred in 75% of those in which nesting attempts were made. In 1998, the number of nesting attempts in nests was higher (84%), while success at those nests was also high (81%).

Nesting attempts were much lower in 1999 (only 52% of nests), especially in the Wreathed hornbill (33%). But success was high at nests, once nesting was attempted (82%). In 2000, nesting attempts were made in 56% of known nests, while success was 86%. Many of the nests had become inactive by 2000. Nesting attempts showed variation among the 4 years, but once nesting was attempted; success was usually high and similar between the 4 years.

To determine whether nesting attempts were affected by disturbance, differences in tree density and distance to human habitation and road (indicators of degree of disturbance) between active and inactive nests were tested. Active nests are defined as those in which nesting attempts were made irrespective of whether nesting was successful or not. Inactive nests were those nests in which no nesting attempt was made that year. There was a significant difference in tree density (Mann-Whitney U test, U = 522, p = 0.044) and distance to habitation (Mann-Whitney U test, U = 531.5, p = 0.055) between active and inactive nests.

Table 6a. Nest tree loss due to natural causes and human activities (1997-2000).

	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]			
Unkown (nest floor sinking?)	1	2		1 (very old)
Total nest trees lost	5	10	2	2

[a]*One GH nest was possibly affected by disturbance and cavity flooding.*

[b] *These two WH nests became inactive initially possibly due to disturbance, but in following years, nest cavity also shrunk, through disuse.*

Table 6b. Causes of unsuccessful nesting attempts in three hornbill species (1996-2000).

Year	**Hornbill species**	**No. of known nests unsuccessful**	**Cause**	**Remarks**
1996*	WH	1	Female killed	Chick removed from nest
1997	WH	1	Male abandoned nest	Disturbance?
1998	GH	1	Nest tree cut	Hunted
1998	GH	1	Abandoned, chick died	Disturbance, cavity flooding
1998	WH	1	Nest tree cut	Hunted?
1998	WH	1	Nest tree cut	Hunted?
1998	WH	1	Nest tree cut	Hunted?
1999	GH	1	Abandoned	Unknown
1999	OPH	1	Chick found dead below nest	
1999	WH	1	Abandoned	Unknown
2000	WH	1	Abandoned	Late nest entry, male stopped feeding and female came out,
2000	OPH	1	Abandoned	Unknown

** Secondary information*

Table 6c. 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

7.4.8. Nesting density

Thirteen active nests (all 3 species together) were found in 12 km^2 of forest in part of the intensive study area, which yield minimum nesting densities of 1.08 pairs per km^2. Wreathed hornbill nesting density was 0.5/km^2, that of Great hornbill 0.33/km^2 and that of Oriental Pied hornbill 0.25/km^2. Observations suggest that the nesting habitat of hornbills is likely to be restricted mainly to the lowland foothill forests, between 150 m and 600 m in the area. Higher elevation areas in the park may have fewer suitable nest tree species for nesting. Therefore, nesting densities are unlikely to be uniform across the park.

7.5. DISCUSSION

7.5.1. Selection for nest sites

The overwhelming importance of a single species as a nest tree for hornbills has not been reported in other studies, though the importance of *T. nudiflora* as a nest tree for hornbills has been reported from some South-east Asian forests (Mardiastuti *et al.* 1996, Marsden & Jones 1997, Chimchome *et al.* 1998). Marsden & Jones (1997) found that *T. nudiflora* and another *Tetrameles* species were the most commonly used nest species in Sumba by 5 parrot species and the Sumba Wreathed hornbill. Mardiastuti *et al.* (1996) also found that Wreathed hornbills in Java preferred *T. nudiflora* and *Pangium edule* as nest tree species and that preference was presumably related to large size, thin canopy and softness of wood. *Tetrameles* is also an important nest tree for the Narcondam hornbill (Ravi Sankaran, *pers. comm.*). Chimchome *et al.* (1998) found that 83% of Rufous-necked hornbill nests were on

Syzygium spp. in evergreen hill forest, while 67% of Plain-pouched hornbill nest trees were on *T. nudiflora* in lowland mixed deciduous forest. Kinnaird and O'Brien (1999) found that Sulawesi red-knobbed hornbills used 15 species for nesting, though 43% were on a single species, *Palaquium amboinense*. This preferred species is a hardwood, but is susceptible to heart rot that enhances cavity formation. Red-knobbed hornbills showed little preference for nest site characteristics other than tree species.

Poonswad (1995) found that 13 tree genera were used for nesting by the Great hornbill, Wreathed hornbill, Oriental Pied hornbill and Brown hornbill, though 60% of nest trees were of two genera, *Dipterocarpus* and *Eugenia*. Some of the other genera (*viz*. *Altingia*, *Cinnamomum*, *Tetrameles*, *Pterospermum* and *Ficus* sp.) used in Thailand also occur in Arunachal Pradesh, though some of these species were not recorded as nest trees during thi study. Height and size of trees, as well as commonness in the habitat, were important factors in nest tree selection. The two most important nest tree genera were durable hardwoods and Poonswad (1995) contends that this is probably because such trees last longer, and once cavities are formed, they can be used by nesting hornbills for a long time, given their durability.

On the other hand, Kemp (1976b) found no selectivity in nest tree species among *Tockus* hornbills that used common trees. Mudappa & Kannan (1997) found that for the Malabar Grey hornbill structural characteristics such as large DBH and greater height of lowest limb were important parameters in nest site selection, though they chose smaller trees than the sympatric Great hornbill in the Western Ghats, south India. Nest trees were in tall live trees and formed mainly by heart rot where a branch had broken off. Seventeen species were used, of which 30% were on *Alseodaphne semecarpifolia*. Kannan (1994) found that structural characteristics such as large size and maturity of forest around the nest trees were important in nest site selection by the Great hornbill in the Western Ghats, where thirteen tree species were used for nesting.

Though, tree species was the most important criterion during this study, hornbills chose large emergent trees, with cavities higher up on the tree compared to randomly located trees. The structural characteristics (tallness, emergence, softwood, easy cavity formation due to woodpecker/barbet activity, or breakage of branch) and commonness of some tree species determine whether they are used or not. Of 25 potential nest species, the 3 sympatric hornbills in the main study area used only 2 species, while the Rufous-necked hornbill used 2 other species in other areas and a planted *Albizzia* sp. was used in a tea estate. The availability of such large girth emergent softwood species is important, since two of the nest species were softwood species. *T. nudiflora* was the most common emergent tree, attaining heights between

30 and 55 m, and though 24 other species also attain large sizes, few are emergent species, while many are uncommon.

The habitat around the nest tree did not seem to be as important as the characteristics of the nest tree itself, therefore any suitable tree with a cavity is likely to be chosen. The multivariate analysis showed that most of the variation in nest site characteristics can be explained by nest tree size, then by degree of disturbance and thirdly by cavity size. Though the sample size was small, overlap among hornbill species in nest tree species and most structural characteristics were overwhelmingly high: the only difference was in selection for cavity size, which was according to body size. Surprisingly, differences among species in nesting habitat or altitude were minimal, though Oriental Pied hornbill nests were at slightly lower elevations. There was a much larger variation in nesting habitat quality chosen by the Great and Oriental Pied hornbill than the Wreathed hornbill that used less disturbed areas more. The discriminant function analysis showed that species differences in nest use were at a finer level, where there were no gross differences in nest species and nest tree structure. Cavity size and distance to river were the most important variables in differentiating between the species. Oriental Pied hornbill nest trees were closer to rivers, and had cavity entrances significantly smaller than the Great hornbill, though there was no significant difference with the Wreathed hornbill. The Wreathed hornbill also used cavities smaller than the Great hornbill. Although, Oriental Pied hornbill nest trees were often taller than Great hornbill and Wreathed hornbill nests, and the height of the cavity was greater, the difference was not substantial. The only other detailed study of nest site selection by sympatric species is of Poonswad (1995), in which she found that hornbill species selected nest cavities according to body size. Wreathed hornbills used the highest nest cavities, while Brown hornbill nest cavities were nearest to the ground. Interestingly, Oriental Pied hornbill nests in her study, showed great variation in nest cavity height from 2 m to 45 m, while in this study (with a much smaller sample size) the cavities they used were the highest heights from the ground. The Oriental Pied hornbill may indeed be less selective and use a wide range of cavities, given that its habits are more catholic. But in the present study area, the presence of suitable cavities may be restricted to a few potential nest species such as *Tetrameles*, where the higher secondary and tertiary branches have smaller cavities that can be used by this species and not by the larger two species. The shape of the cavity may also be an important criterion for selection, because Great hornbill nest entrances tended to be more elongated, vertical slits (also noted by Poonswad 1995), Wreathed hornbill nest entrances tended to be oval, while Oriental Pied hornbill entrances were round or oval (though sample size for this species is small).

Overlap in nesting habitat between the Rufous-necked hornbill and the other three species is largely precluded, since it occurs in higher elevation forests, from 800 m to above 1500 m, though in Namdapha TR, they are also sighted at similar elevations as Great and Wreathed hornbills. Great hornbills are reported up to 1200 m and Wreathed hornbills do occur up to 1500 m, but are more common at lower elevations and are often infrequent seasonal visitors at higher altitudes of Namdapha TR, Tale Valley WLS and other Reserve Forest areas in Lower Subansiri district and East Kameng district (Datta, A. *unpubl. data*). No information on Brown hornbill nesting requirements could be gathered during this study.

7.5.2. Nest cavity availability and nesting density

The availability estimate of cavities was 2.27 per ha, but sampling was inadequate. Mudappa & Kannan (1997) reported a relatively high density of 10 cavities per ha for the Malabar Grey hornbill, though no estimates of nesting densities are given. The availability of the two most important nest tree species was 1.33 per ha, but actual nesting density was only 1 pair per km^2. Given the high degree of overlap between hornbill species and the importance of a single species as nest tree, it seems likely that availability of suitable nest sites may be a limiting factor. In addition, monitor lizards, flying squirrels, wasps, bees, snakes and several other hole-nesting birds, may also occupy suitable cavities. This may seem counter-intuitive and contrary to the finding that compared to the low nesting density, cavity and nest species availability was seemingly high. So, it may be argued that nests are not limiting because many more cavities are seemingly available than are being used by hornbills. But this estimate of cavity availability is from a very small sample size and may not be reliable.

Broad-billed rollers are known to appropriate holes formed by woodpecker or barbet activity on *Salmalia* or *Tetrameles* (Ali & Ripley 1987). The Northern Hill myna (*Gracula religiosa intermedia*) also uses holes made from borings of woodpeckers. Sometimes several nests of different pairs occur one below another on a straight bole. The Red-breasted parakeet also nests in a natural hole enlarged and excavated by birds, sometimes several nests occur in neighbouring trees in a loose colony, and nest holes of barbets and woodpeckers are frequently used (Ali & Ripley 1987). The size of cavities used by these much smaller-bodied bird species probably precludes competition with the larger hornbill species, but data on distribution of available cavity sizes, sizes of cavity used by different species, and occupancy, are needed to determine whether there is any overlap and possible competition.

Despite the high degree of overlap, there was no evidence of interference competition among the three species, though a few interactions were recorded between the Great hornbill and Wreathed hornbill, where the Great hornbill displaced Wreathed hornbills visiting its nest tree, prior to female entry. Overt intra-specific competition was also rare, though non-breeding pairs were seen perching on active nest trees. No nest take-overs or competitive interactions between species after commencement of nesting were recorded, unlike the high frequency of such interactions, which led to nest abandonment in Thailand (Poonswad *et al.* 1988). No sequential use of nest trees by different species in successive years was recorded, unlike that reported in Thailand. Competition is likely to affect the Wreathed hornbill more, as it nests later than the Great hornbill, and is also intermediate in size and overlaps with both species in nest tree requirements. The Wreathed hornbill is also non-territorial and superseded from food and roost trees generally, by the Great hornbill. The Oriental Pied hornbill, being smaller-bodied, uses much smaller cavities, and may potentially compete with other hole-nesting birds. But given the fact that sequential use of nests by species differing in body size is so common in Thailand, despite the significant differences in mean cavity size, the three sympatric species could potentially use each other's nest cavities.

The estimate of nesting density of three sympatric species in the present study is comparable to that of less than 1 pair per km^2 for four sympatric species in Thailand (Poonswad *et al.* 1987). Kalina (1988) reported maximum densities of 5.6 cavities per km^2 for black-and-white casqued hornbills in Uganda. Kinnaird *et al.* (1996) found the highest nesting densities reported for any hornbill species of 10 pairs per km^2 for the Sulawesi red-knobbed hornbill. A minimum estimate of nesting densities of the Narcondam hornbill on the Narcondam Island is around 2.8 pairs per km^2 (Ravi Sankaran, *pers. comm.*).

The lack of direct competition despite high degree of overlap may argue against any limitation of nest sites. The major divergence seems to be in cavity size. Past selection favoring divergence in size of cavities selected by sympatric species may have resulted in reducing competition, if any. More detailed information on availability of cavities of different sizes, selection of cavities and occupancy rates by other competitors, ratio of breeding pairs vs. non-breeding adult pairs, and a larger sample of nest trees is required to determine limitation of nesting opportunities or occurrence of competition.

7.5.3. Nest tree loss and threats to hornbills and their nesting habitat

There was loss of nest trees due to natural causes such as nest cavity shrinkage, occupation by other cavity-dwelling animals and breakage. Chuailua *et al.* (1998) contend that the vulnerable status of nest trees could be due to discontinuous use of nest cavity, decomposition processes, aging and scarcity of large trees. They found that the most serious reason for nest tree loss was breakage of nest trees and cavities mostly became unsuitable due to the collapse of the nest floor. Though collapse of nest floor is known to be an important reason for loss of a nest cavity, this could not be ascertained during this study, since nest trees were not climbed.

In addition to the natural turnover of nest trees, loss can occur due to felling of the nest tree itself, severe degradation and opening up of the habitat due to human activity, repeated nesting failure either due to disturbance, hunting or removal of chicks leading to subsequent abandonment of nest sites.

More than half of the nest trees monitored was inactive by the end of the study. Five nest trees were lost due to cutting of the nest tree, 8 became inactive mainly because of human disturbances such as proximity to road, habitation, degraded open habitat, human predation, and/or movement of people during the nesting period at nest trees. Two of these nests may have also become inactive due to shrinkage of cavity entrance through disuse. At some nests, repeated unsuccessful nesting attempts, resulted in subsequent abandonment of the nest site.

An important finding of this study is that hornbills do nest in logged forests, unclassed state forests or even degraded forest (Plate 7), though these nesting attempts are usually unsuccessful, usually if the vicinity of the nest tree is subject to human disturbance during the nesting period. This suggests that hornbills would nest successfully even in such marginal habitats, if further degradation of or disturbance at the nest site is halted. Steps could be taken to protect such nest trees (especially in the breeding season), to ensure successful nesting by hornbills. Given the possible limited availability of suitable nesting trees and the fact that hornbills nest in such marginal habitats, it is necessary to widen the scope of conservation plans to include forests outside the existing protected area network (national parks and sanctuaries), which make up more than 70% of the forest area of Arunachal Pradesh. Special measures for protection of reserve forest areas from habitat loss and degradation will go a long way in ensuring the long-term conservation of hornbills. Forest cover in north-east India has declined over a period of 5 years, though the estimated loss is comparatively lower in Arunachal Pradesh (59 km^2), there has been estimated loss of 684 km^2 in Assam from 1993-1997 (F.S.I. 1995, 1997). The latest report (F.S.I 1999) states that forest cover in Arunachal has increased by 245 km^2, due possibly to regeneration of previously logged forest and the ban on logging**.** What is alarming is the accelerated loss of 1031 km^2 in Assam mainly due to tree felling and encroachment. In Naduar and Diplonga reserve forest in adjoining Assam near the study area, an estimated 90 km^2 was lost due to clearing of land for cultivation and illegal settlements by tribal settlers over a period of 5-6 years (1995 to 2001) (Plate 7). Most of

Arunachal Pradesh is hilly, with inaccessible terrain and low human population density. The extent of lowland forest is limited, and being the most accessible, is severely under threat. The foothill lowland habitat, where most nesting by hornbills occur is threatened by habitat loss and degradation due to logging and land clearing for settlements and agriculture. Habitat loss is often insidious, transforming a dense forest into degraded open forest over a period of years, by which time it is too late to halt the process. Though Pakhui NP covers 862 km^2, the lowland foothill forests that form the prime nesting habitat are restricted mainly to the southern part of the park. Lowland forests are the most vulnerable, due to the relative ease of accessibility and nearness to existing human settlements, and suitablility for agricultural lands. In the adjoining reserve forests of Doimara and Papum, selective logging and existing plantations have already caused habitat loss and modification. Logging also has led to the creation of roads and greater accessibility, followed by the creation of settlements, and greater incidence of human activities such as hunting and collection of fuelwood and forest products, creating additional disturbance (Datta & Goyal 1997, Datta 1998a). Logging has been banned since 1996, though logging restarted for 6 months in 1999 to allow mills to clear logs felled in 1996. Though the primary nest tree species (*T.nudiflora*) is not an important timber tree, it used to be felled sometimes, for making matchboxes and boxes; all the other nest tree species and several of the potential nest tree species are important timber species.

Hunting of hornbills at nests is taboo in the Seijusa area during the breeding season, but is carried out during the winter from November to February (non-breeding season). In other areas of Arunachal, hornbills are much more rare (Datta, *unpubl. data, pers. obs.*) and there is no seasonal ban on hunting, thus hornbills have become virtually extinct or very rare in many areas in eastern and central Arunachal (Datta 1998a). Apart from the Rufous-necked hornbill, that frequents forests above 800 m, all the other species are largely restricted to lowland forests, the extent of which is fast declining.

7.6. CONCLUSIONS

The three hornbill species in the lowland forests of Arunachal Pradesh showed a remarkable selection for a single species, *T. nudiflora* as nest tree, which may be used because of its relative commonness, emergent size, and softwood that makes formation of cavities easy either through natural rot after branch breakage or by woodpecker and barbet activity. Several other hole-nesting bird species also nest in this species.

There was a high degree of overlap among the three hornbill species in nest tree species used, nesting habitat selected as well as structural characteristics of nest trees. Cavity size was the major variable that resulted in separation of nest tree characteristics selected by the three species according to body size. Nest trees of the Oriental Pied hornbill also tended to be closer to rivers. Nesting density of all three species together was about 1 pair per km^2. The density of large trees of 25 potential nest species was 7.62 per ha, while that of the two most important nest tree species was 1.33 per ha. Despite the high degree of overlap, there was no evidence for interference competition between the three species, though a few interactions were recorded between the Great hornbill and Wreathed hornbill, where the Great hornbill displaced the Wreathed hornbill. Overt intra-specific competition was also rare. There was no sequential use of nest trees by different species in successive years. Hornbills nested in poor quality degraded habitat in logged forests, and plantations and three nests were even found in relatively clear-cut areas near agricultural fields and tea estates. But most of these nesting attempts were unsuccessful, and the nests were eventually abandoned and became inactive. Several nest trees were irrevocably lost due to cutting. Nest tree loss was high due to both human-induced and natural causes. About half of the known nest trees were inactive by the end of the study. Nesting habitat of these three species seems to be largely restricted to lowland foothill forest, which is more easily accessible and therefore facing the most severe pressures due to past logging, clearing of forest for agriculture, settlements, and hunting. Lowland foothill forest areas in Arunachal Pradesh are already limited in extent, and in many districts are already degraded and lost. Conservation efforts need to focus on prevention of loss and degradation of forests in the border areas between Assam and Arunachal Pradesh, where loss has accelerated in recent years due to illegal settlers clearing land. Pakhui NP and some areas of adjoining Doimara and Papum RFs along with forests in Nameri NP, comprise a large extent of forest that support a good population of hornbills compared to foothill forests in other districts of Arunachal Pradesh, where hunting and habitat loss has been greater. The reserve forests of Khellong Forest Division are a good area for hornbills, and a proposal to declare a part of it a sanctuary, or at least inclusion of these areas in protection measures should be considered. There is already a proposal to conserve and manage the whole area of Pakhui NP, Nameri NP, and adjoining reserve forests as a single conservation unit, with reference to tiger and elephant conservation.

Chapter 8. Roost sites and communal roosting by hornbills

8.1. INTRODUCTION

Avian use of communal roost sites is quite extensively documented in the literature (eg. Crook 1965, Lack 1968, Horn 1968, Zahavi 1971a, 1971b, Ward & Zahavi 1973). Communal roosts are hypothesized as being beneficial for a number of reasons – they might serve as i) information centres to determine the location of food sources, ii) an anti-predatory strategy where there is safety in numbers, and/or iii) a thermoregulatory mechanism to conserve heat. The most widely cited advantage of communal roosting is the information-centre hypothesis, which suggests that roosts function as information centres, sites where unsuccessful foragers can learn the location of food sources by following successful roost mates to food patches (Ward & Zahavi 1973). Many bird species have been reported to roost communally, using a site year after year, and variation in the number of birds was influenced by food abundance. Zahavi (1971a) states that when food supply becomes uneven and declines, birds form larger communal roosts. Flock sizes of many birds show great flexibility depending on food distribution and availability (Heinrich 1988, Heinrich and Marzluff 1991, Brown 1986, 1988, Brown *et al.* 1991).

It has also been suggested that all birds in a roost do not have equal food-finding capabilities, and while subordinate birds parasitise on the dominant birds' superior food-finding capabilities, the dominant birds tolerate this, because their status gives them access to central or higher perches in the roost that buffer them from predation (Weatherhead 1983). According to Crook (1965), it is not necessary that communal roosting have one single advantage, while Horn (1968) suggested that additional advantages could have come into play later, even if communal roosting evolved initially for one primary reason. Another suggested non-foraging benefit of communal roosting is kin-selection benefits. For instance, vultures sharing roosts are often closely related and aggressive interactions between vultures seem to be negatively correlated with relatedness (Rabenold 1986).

Hornbill species that are known to form communal roosts include the Wreathed hornbill and *Ceratogymna* species in Africa, which use the same roost for several months returning daily over long distances in the evening (Leighton 1986, Tsuji *et al.* 1987, Poonswad & Kemp 1993, Kemp 1995). In recent years, communal roosting has been recorded for the Plain-pouched hornbill, where spectacular aggregations and flocks of more than 2000 birds have been recorded (Ho & Sutari 1997, 2000, Pilai Poonswad, *pers. comm.*). Tsuji *et al.* (1987) and

Poonswad & Kemp (1993) mention that though the territorial Great hornbills and Oriental Pied hornbills were seen to roost communally, it was in much smaller numbers than the Wreathed hornbills.

The literature on roosting by hornbills is restricted to counts of birds at roost sites primarily in the non-breeding season and a general description of roosting sites (Kemp 1995, Tsuji *et al.* 1987). In addition, all reports of communal roosting have been during the non-breeding season, and it has been assumed that communal roosting is much less prevalent in the breeding season especially for territorial species such as the Great hornbills. Roosting behaviour of various hornbill species has been rarely described in detail, other than by Reddy (1988) and Kemp (1995) and is usually reported as incidental observations. He speculates that the selection of a roost site is probably determined primarily to avoid predators, while seasonal changes in roost use occur either due to predators, disturbance and/or other less visible reasons such as food-finding. Birds leave the roost at dawn following the first birds to leave for fruiting trees. However, even at the largest communal flocks, most hornbills remain closely associated within their own pairs or family groups (Kemp 1995). Previous information on roosting by hornbills in India exists only from one study on the Malabar Pied hornbill by Reddy (1988) and anecdotal observations by Ali & Ripley (1987).

In this chapter, the characteristics of roost sites and roosting behaviour of three hornbill species, the Great hornbill, Wreathed hornbill and the Oriental Pied hornbill are described. An attempt is also made to understand the use of roosts in the light of hypothesized benefits of communal roosting, and to identify important ecological correlates of communal roosting.

8.2. OBJECTIVES

1. To describe the characteristics of roost sites used by hornbills, and the roosting behaviour of three sympatric hornbill species.
2. To understand the use of roosts, in the light of hypothesized benefits of communal roosting and to identify important ecological correlates of communal roosting.

8.3. METHODS

8.3.1. Roost site characteristics

At the roost sites, structural characteristics of roost trees such as girth at breast height (GBH), tree height, height of the first branch, distance to river, road, and habitation were noted. Circular plots of 15 m radius (0.07 ha) were laid around individual roost trees (taking the roost tree as the centre tree) to determine tree density and species composition around roost trees. All trees above 10 cm GBH were enumerated and measured. The tree densities at roost sites were compared with tree densities at nest sites (n = 31 circular plots of 15 m radius) and foraging areas in the forest (n = 21 plots of 0.25 ha each).

8.3.2. Roost counts

Roost sites were located initially by following hornbills in the direction in which they flew in the evenings or looking for signs of use under potential roost trees. There would be piles of regurgitated seeds below trees used by roosting hornbills. Local people also provided information on traditional roosting areas. After some roosting areas were located, searches in areas with similar habitat characteristics were also carried out.

At roost sites, three observers counted arriving hornbills. The species, group size and composition (age and sex, whenever possible), time of arrival and direction from which they came were noted. Age and sex composition could be determined only for a small subset of the total birds arriving at roosts, partly because birds (especially Great hornbills) often arrive at, or after sunset all together or from several directions simultaneously. Classification could be carried out mainly for the Wreathed hornbill, that is more sexually dichromatic; sexes can be easily distinguished even in flight, and juvenile birds can be classified as well (by the lack of prominent wreaths, smaller body size and often weaker flight, accompanying an adult pair). The adult male has a yellow gular pouch, white neck and throat, rufous head, the rest of the body being black, while females have a blue gular pouch and the entire body is black, besides being smaller than the male. Females resemble males till 1-2 years before attaining sexual maturity, but change in plumage colouration is gradual, enabling classification of subadults at times. Though there are differences between the sexes in Great hornbills in eye colour, casque colouration, and body size, these are difficult to distinguish in flight after dark. Counts at roosts were made usually from 1600 hours till 1800 hours (dusk). Anecdotal observations on the behaviour and movement of the birds were also made. The number of birds using a particular roost site at any given time was monitored for 2 to 10 days in a month. Counts at communal roosts were made in 1997,1998, and 1999 during the non-breeding season (August to January). Breeding season (March to July) counts were made in May-June 2000, though use of the roost sites in the breeding season in previous years was ascertained indirectly by the presence of seedlings/saplings of hornbill food plant species below roost trees. These hornbill food plant species produce fruit only in the breeding season and are thus consumed only during the breeding season, therefore their presence below the roost trees suggested use in that season.

8.3.3. Evening flights to roosts

Counts at roost sites and changes in roost site use could not be tracked throughout the year, therefore additional information on roosting by hornbills was gathered from opportunistic sightings of hornbills on their evening flights to roosts. Records were kept of all birds seen flying in the direction of known roost sites from 1530 hours to 1800 hours. The time of sighting, hornbill species, flock size, age and sex composition, and location were recorded. These data were used to obtain an insight into differences in flocking patterns between species, season, and with diurnal foraging flock sizes.

8.3.4. Diurnal foraging flock sizes

All sightings of hornbills were recorded opportunistically throughout the four years. The time of sighting, hornbill species, flock size, age and sex composition, location, activity when sighted (feeding, perching, flying, calling), tree species used (if feeding or perching), canopy level and location were recorded. These data were used to determine seasonal differences in diurnal foraging flock sizes and compare with roosting flock sizes.

8.3.5. Roost arrival times

The times of arrival at roost sites were noted for all hornbills during roost counts in the breeding and non-breeding season. Data on the sunrise and sunset times for 1997-2000 for the area were obtained from the U.S. Naval Observatory, Astronomical Applications Department (http://aa.usno.navy.mil/data). The arrival times were represented with reference to hours before or after sunset, since the area is far from the equator (27°N).

8.3.6. Communal roosting in hornbills – testing hypotheses

If food-finding and information exchange is the primary reason for communal roosting, frugivorous species dependent on a patchy, unpredictable food supply would be more likely to join communal roosts. Non-territorial, wide-ranging species are also more likely to join communal roosts than species that defend territories. In an attempt to understand if frugivory, non-territoriality and body size could explain the occurrence of communal roosting in hornbill species, information on diurnal flock size, main diet type, breeding and spacing patterns, presence of communal roosting, and the maximum size of roosts for species for which such information is available were tabulated. The source of the information was largely from Kemp (1995 and other studies therein). Chi-square tests of association were used to determine if occurrence of communal roosting was associated with degree of frugivory, territoriality, and body size.

8.4. RESULTS

8.4.1. Roost sites

Four main communal roosting sites were located in Pakhui NP and adjoining reserve forests. One site was located 11 km away from Seijusa near a place called Khari on trees of *Castanopsis indica*, *Endospermum chinensis, Albizzia* sp. and *Macaranga peltata* on a steep cliff face adjacent to Khari *nala*, a perennial stream. Along the Khari *nala*, 1.5 km away from this main roost, birds were also seen to roost on tall emergent trees of *Tetrameles nudiflora*. The other three sites were on isolated deciduous trees in different parts of the successional grassland habitat adjoining the Pakke River, 500m to 1 km away from habitation at different points. The vegetation at the forest edge near the Pakke River consisted mainly of *Dillenia indica,* patches of clumped *Sterculia villosa*, occasional *Tetrameles nudiflora* and *Bombax ceiba*. Dense stands of *Alpinia allughas* were present in the swampy marshy patches as well as in the grasslands between the forest edge and the main river. The river course was dynamic with numerous channels and dry beds forming islands interspersed with grasses and isolated scattered trees of *Bombax ceiba*, two *Albizzia* species, *Acacia catechu*. and a few other pioneer tree species of open habitats. The levels of flooding and inundation changed seasonally. Dense weedy growth of *Eupatorium odoratum*, *Lantana camara* and *Mikania scandens* also covered parts of this grassland area. On the other side of this grassland, were the *Nishi* villages and settlements of Lower Seijusa, Darlong, Upper Seijusa, Bali Basti, A2, A3, and Galoso all along the 16-km stretch of road parallel to the Pakke River, (Fig. 2 in Chapter 2, Plate 8) while the roosting sites were along the park boundary. The width of this grassland along Pakke River is around 500 m. Different parts of this habitat were used by hornbills at different times, or different groups roosted in different parts at the same time. The total extent and area of this roost site is estimated to be 25 km^2. Hornbills also roost at points along the river further downstream in Assam (where the Pakke river is known as the Bordikrai river) in the Nameri NP and in adjacent reserve forests. Apart from this, pairs or family groups were seen to roost separately, either in the same kind of habitat or on emergent trees of *Tetrameles nudiflora* at the forest edge or on steep hillsides.

8.4.2. Roost site characteristics

The structural characteristics of hornbill roost trees are given in Table 1. Only twenty-three percent of roost trees were ≥ 250 cm GBH; indicating that hornbills used relatively small girth trees for roosting. Fifty-eight percent of roost trees were ≥ 22 m in tree height; therefore indicating that hornbills generally used relatively shorter trees for roosting compared to that used for nesting (see Chapter 7). Roost sites were also located between 200 to 420 m altitudes in lowland foothill areas and were close to rivers or perennial streams. Ninety-five percent of the roost trees (n = 22) were within 150 m from a river or a perennial stream; with the exception of one roost tree that was 1 km from the river, but nevertheless, adjacent to a seasonally dry streambed. Seventy-eight percent of the roost trees (n = 22) were less than a km from the main roads; only 2 sites near Khari *nala* were 10-11 km away. Nearly all roost trees were located within 1 km of habitation. Tree density at roost sites was much lower than in hornbill foraging and nesting sites in the forest (Fig. 1).

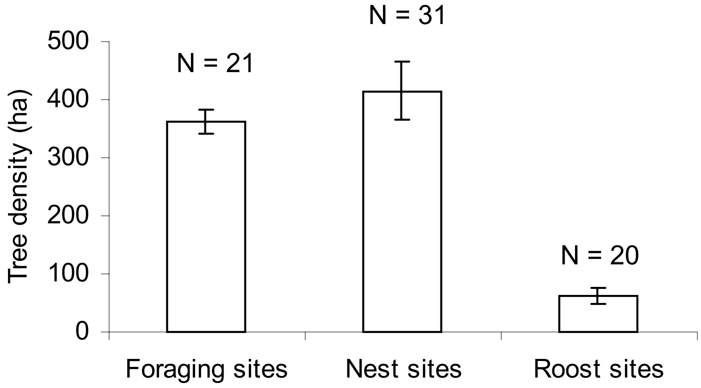
Twenty-eight tree species were found in the successional habitat used for roosting. Some of these were *Albizzia* (3 species), *Alstonia scholaris*, *Bombax ceiba*, *Callicarpa arborea*, *Flacourtia indica*, *Acacia catechu*, *Macaranga peltata*, *Oroxylum indicum*, *Wrightia coccinea*, *Bridelia retusa, Sterculia villosa, Syzygium*, 3 shrubby treelet species and 3-4 unknown species. The ground layer in the three roost sites near the Pakke River was covered with weeds of *Mikania scandens, Eupatorium odoratum* and *Lantana camara*. There were also grasses such as *Saccharum* spp. and other monocots such as *Alpinia allughas*.

The specific tree species used for roosting were *Bombax ceiba* (6), two *Albizzia* spp. (19), an unknown riverine shrubby tree locally called goidari (1), *Tetrameles nudiflora* (2) and individual trees of *Castanopsis indica*, *Endospermum chinensis*, *Macaranga peltata* on the cliff face at Khari *nala*. More trees of *Tetrameles nudiflora*, one tree each of *Ailanthus grandis*, *Duabanga grandiflora* and of *Ficus hookeri* near the forest edge were also used for roosting by pairs or small groups.

Table 1. Roost site characteristics

Roost site characteristics	Mean ± SE
GBH of roost trees	212 cm ± 17.3, n = 27
Roost tree height	24 m ± 1.6, n = 19
Height of lowest limb of roost tree	7 m ± 1.0, n = 19
Distance to human habitation	604 m ± 85.9, n = 22
Distance to road	1436 m ± 628.7, n = 22
Distance to river	90 m ± 44.2, n = 22
Altitude	303 m ± 10.6, n = 22
Tree density (GBH ≥ 9 cm)	102 trees ± 29.4, n = 20 plots
Tree density (GBH ≥ 25 cm)	63 trees ± 13.8, n = 20 plots
Mean GBH of trees in roost plot	67 cm ± 6.2, n = 144 trees

Fig. 1. Tree density at foraging areas and nest sites in the forest and roost sites in more open habitats.



8.4.3. Counts of hornbills at roost sites (1997-2000)

A total of 1739 hornbills were counted at roosts in 331 sightings between 1997-2000. Of this, 226 sightings were of Wreathed hornbills, 96 sightings of Great hornbill and 9 sightings of the Oriental Pied hornbill. A total of 1044 Wreathed hornbills, 631 Great hornbills and 64 Oriental Pied hornbills was counted.

A description of the roost counts in each year, daily numbers, chronology and behaviour at roost sites is given in Appendix 6. Table 2 provides details of the months and days in which roost counts were made, and the maximum number of birds counted at roosts for all the three hornbill species during 1997-2000.

Roost counts were made only in a few months in the 4 years (Table 2), but observation on hornbills flying in the late afternoon and evening to roosts were made throughout the year. In 1997, hornbills were seen flying to roost in the evenings in April, June, October, November and December, apart from the roost counts in August. In 1998-1999, hornbills were observed flying to roost throughout the year. In 2000, hornbills were seen flying to roost from January to April, apart from the roost counts in May-June.

Table 2. Roost counts of the three hornbill species during 1997-2000

Great hornbill *Buceros bicornis*

Year	Season	No. of days	Month	No. of sightings	Mean flock size on roost arrival	Range of roosting flock	Max. nos. seen at roost in a day
1997	Non-breeding	7	August	36	7.7 ± 1.9	19-62	62
1998	Non-breeding	5	January, August, October	15	6.7 ± 1.9	16-47	47
1999	Non-breeding	9	August-September	34	6.7 ± 1.1	14-87	87
2000	Breeding	11	May-June	10	2.1 ± 1.3	2-9	9

Wreathed hornbill *Aceros undulatus*

Year	Season	No. of days	Month	No. of sightings	Mean flock size roost arrival	Range of roosting flock	Max. nos. seen at roost in a day
1997	Non-breeding	7	August	61	3.5 ± 0.4	5-28	28
1998	Non-breeding	5	January, August, October	13	17.7 ± 9.4	25-103	103
1999	Non-breeding	9	August-September	92	4.3 ± 1.1	57-92	92
2000	Breeding	11	May-June	96	3.4 ± 1.3	23-63	63

Oriental pied hornbill *Anthacoceros albirostris*

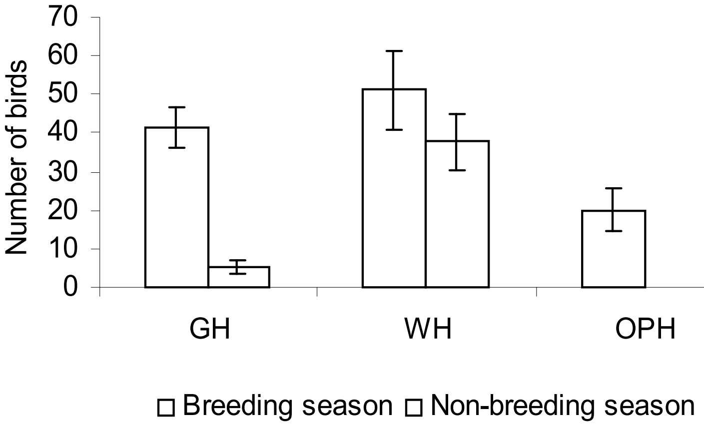
Year	Season	No. of days	Month	No. of sightings	Mean flock size roost arrival	Range of roosting flock	Max. nos. seen at roost in a day
1998	Non-breeding	5	January	5	10.2 ± 2.2	23-28	28
1999	Non-breeding	9	August-September	4	3.3 ± 0.9	2-9	9

8.4.4. Communal roosts: differences between seasons and hornbill species

The mean number of birds at communal roost sites was higher in the non-breeding season (67 ± 11.48) compared to that in the breeding season (40 ± 8.21), but there was no significant difference (Mann-Whitney U test, p = 0.33). The total size of the roosting flock ranged from 7 to 72 birds in the breeding season (only in 2000), while the size of the roosting flock ranged from 9 to 179 in the non-breeding season (1997-1999).

The total number of Wreathed hornbills at roosts ranged from 5 to 103 in the non-breeding season, while it ranged from 6 to 63 in the breeding season. The mean number of Wreathed hornbills at roosts was higher in the non-breeding season (51 ± 10.26, n = 13 days) than in the breeding season (38 ± 7.33) but the difference was not statistically significant (Mann-Whitney U test, p = 0.365). The total number of Great hornbills at a roost ranged from 14 to 87 in the non-breeding season, while it ranged from 2 to 9 in the breeding season. The mean number of Great hornbills (41± 5.43) was significantly higher at roost sites in the non-breeding season than in the breeding season (5 ± 1.65) (Mann-Whitney U test, p = 0.003). The total number of Oriental Pied hornbills at a roost ranged from 9 to 28 in the non-breeding season (20 ± 5.68). No Oriental Pied hornbill roosts were encountered during the breeding season (Fig. 2).

Fig. 2. Mean number of birds at roost sites in the breeding and non-breeding season for the three hornbill species.



8.4.5. Diurnal foraging flock size vs. roosting flock size

The size of a communal roost can be >100 birds, while foraging group sizes in the daytime are much smaller. The mean roosting flock size overall for all species over the study period was 60 birds. Roosting flock size ranged from 5 to 179. The overall mean diurnal foraging flock size over all years and species was 3.34 ± 0.3 (out of a total of 219 sightings of 732 hornbills in foraging groups during the daytime). The median and modal diurnal flock size was 2 and ranged from 1 to 35.

There was a difference in mean diurnal foraging flock size for both the Great hornbill and Wreathed hornbill between the two seasons, with flock sizes being much lower in the breeding season for both species (Fig. 3a). But there was no difference in mean foraging flock size between the two species. The distribution of diurnal foraging flock sizes of all the three species in the 2 seasons is shown in Fig 3b. There was no difference in diurnal foraging flock size and evening flock sizes on flights to roosts, though evening flock sizes were marginally higher, suggesting that possibly hornbills start grouping together prior to leaving for roost sites (Fig 3c).

Fig 3a. Mean diurnal foraging flock size of the three hornbill species in the breeding and non-breeding season

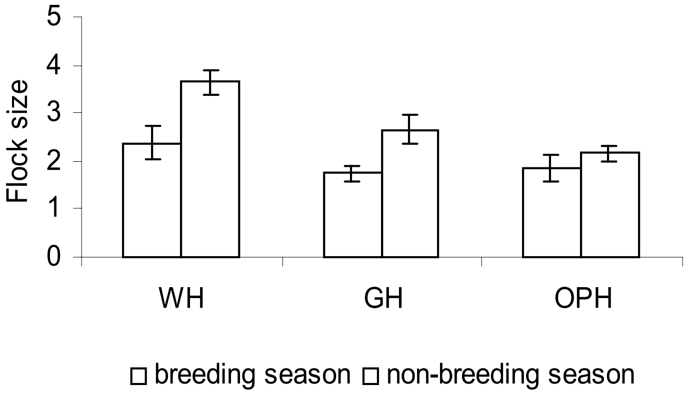


Fig. 3b. Distribution of diurnal foraging flock sizes of hornbills in the breeding and non-breeding season.

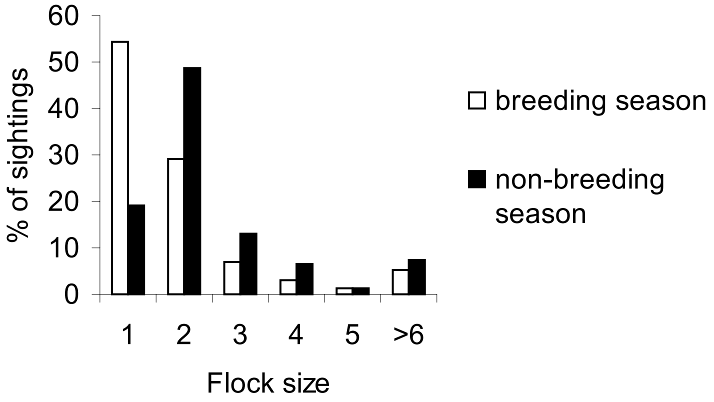
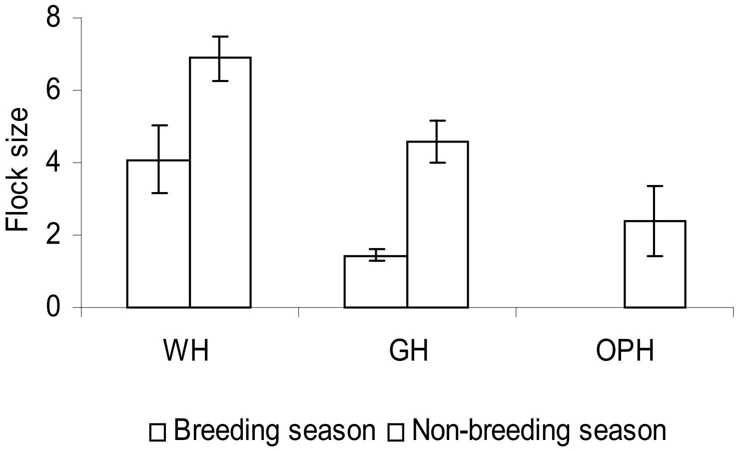
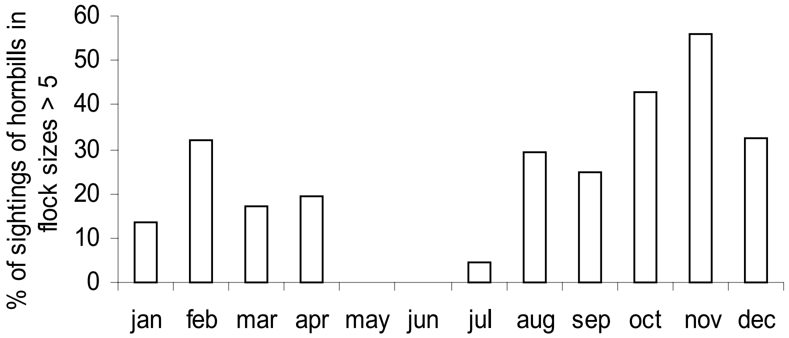


Fig. 3c. Mean flock size of the three hornbill species in the evenings when flying to roosts in the breeding and non-breeding season.



A higher percentage of hornbill sightings were of birds in flock sizes > 5 in the non-breeding season (especially between August and December) than during the breeding season (Fig. 4).

Fig. 4. Percentage of sightings of hornbills in flock sizes > 5 throughout the year (data for all sightings from 1997-2000). No data for June.



8.4.6. Roost arrival times

Roost arrival times were earlier during the non-breeding season (winter, shorter day length) than in the breeding season (summer, longer day length). In the winter months, sunset timings ranged from as early as 16:29 hours in November-December to 17:22 hours in February, while in the summer and monsoon months, the sunset timings ranged from 17:23 hrs in March to 18:18 in June-July. Thus, there was nearly 2 hours difference in sunset timings depending on the time of the year. Sunrise timings ranged from as early as 04:29 hrs in June to 05:45 hrs in March (summer months) to 05:14 hrs in October to 06:11 hrs in January (winter months), with more than one and a half hours difference in time of sunrise in the two seasons.

Most often (82% of sightings), Wreathed hornbills arrived about 25 minutes before sunset (± 1.2) and only in 12% of sightings Wreathed hornbills arrived just 5 minutes (± 1) after sunset in the non-breeding season. In 6% of sightings, Wreathed hornbills arrived exactly at sunset.

The Great hornbills, on the other hand, most often (54% of sightings) arrived either exactly at sunset or up to 9 minutes (± 0.7) after sunset and in 46% of sightings; they arrived about 14 minutes (± 2.5) before sunset in the non-breeding season. The Oriental Pied hornbills were generally seen to arrive at roosts an hour before sunset (± 5.2).

In the breeding season (2000), Wreathed hornbills arrived at roosts about 35 minutes (± 2.6) before sunset while Great hornbills arrived later either 17 minutes before sunset or just after sunset. Oriental Pied hornbills were not seen at roosts in the breeding season.

8.4.7. Seasonal differences in roosting flock composition

An assumption was made that solitary adult males represented breeding males (with the female incarcerated inside the nest). Out of all sightings of solitary adult males of both Great and Wreathed hornbills (n = 157) over the 4 years, there was a much higher proportion of solitary males sighted in the breeding season (85%) than in the non-breeding season (15%) lending validity to the assumption.

In the breeding season roost counts, a total of 328 Wreathed hornbills was counted on 10 days. Out of this, 115 birds (56 sightings) could be classified into adult males (47%), adult females (22%), and subadult birds (31.3%). Fifty percent of sightings were of solitary adult males that arrived at the roost site alone and it is assumed that these birds were breeding males. Thirty-two percent were of non-breeding adult pairs (male and female), and 7% were of subadults that arrived together in separate groups ranging from 2 to 8 birds. Eleven percent of adult birds (both male and female) arrived with subadult flocks, and their breeding status remained uncertain (Fig. 5a). Fifty-two percent of all the adult males seen were single males arriving at the roost. A total of 21 Great hornbills were counted on 4 days at these roosts and roosting flock size ranged from only 1 bird to a maximum of 5 birds on one day.

Out of the total of 1390 birds counted during the non-breeding season roost counts in 1997 and 1999 (August-September), 171 birds (71 sightings) could be classified into adult males, females and subadults/juveniles. Of these 171 birds, 158 were Wreathed hornbills and the rest were Great hornbills. Of the 158 Wreathed hornbills (66 sightings), 44% were adult males, 39% adult females and 16% juveniles or subadults. Thirty-three percent of sightings were of an adult pair with accompanying juvenile. Forty-seven percent of sightings were of adult pairs without any accompanying juvenile (Fig. 5b). Ten sightings (15%) were of solitary birds, an equal number of males (6) and females (6), and 4.5% were of birds (adults and subadults) in flocks ranging from 2 to 10. The fact that breeding males join the roost is supported by the great difference in the proportions of solitary adult males (50%) in the roosting flock in the breeding season when compared to the non-breeding season (only 9%) (Fig. 5a & 5b).

While there were nearly a similar proportion of adult males in both seasons in the roosting flocks, the proportion of adult females was lower in the breeding season as expected (some proportion of females were inside the nest), and there were a higher percentage of subadults in the non-breeding season (Fig. 5c).

Fig. 5a. Composition of roosting flocks of Wreathed hornbills in the breeding season.

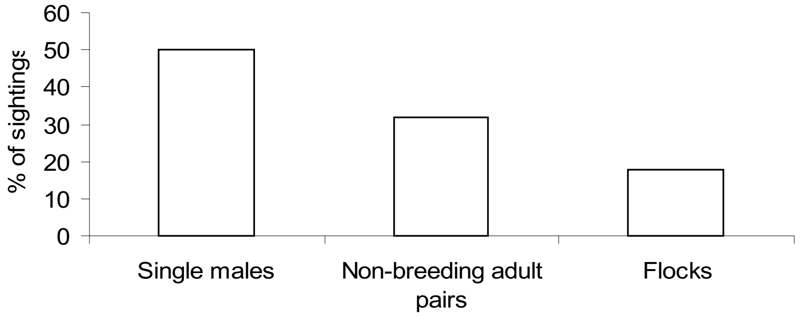


Fig. 5b. Composition of roosting flocks of Wreathed hornbills in the non-breeding season.

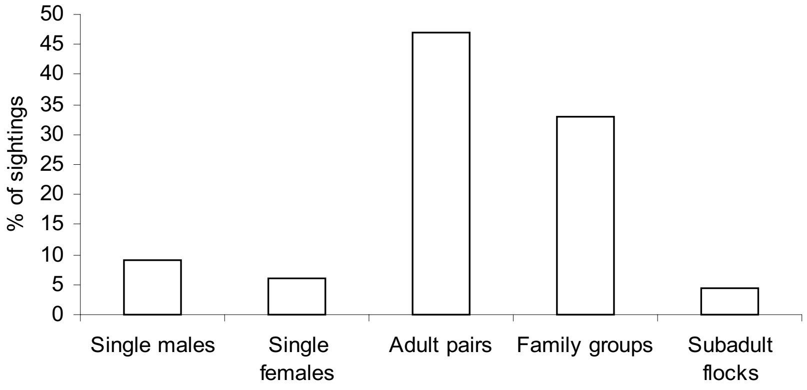
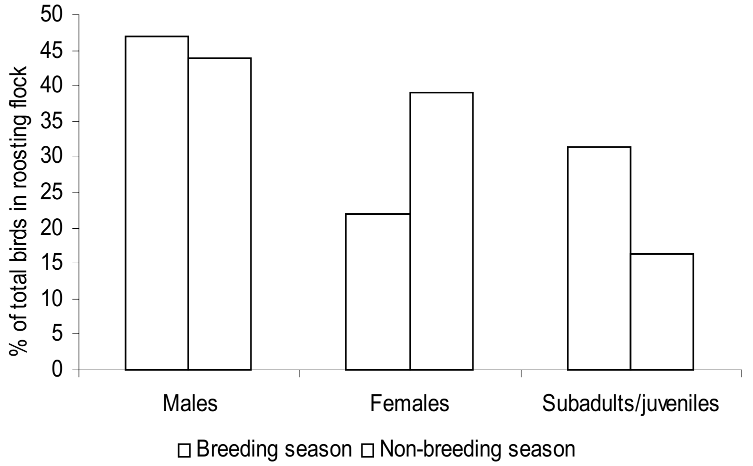


Fig. 5c. Seasonal variation in the percentage of birds in different age/sex classes in the roosting flocks of Wreathed hornbills, n = 115 birds in the breeding season and n = 158 birds in the non-breeding season.



8.4.8. Communal roosting in hornbills – towards an explanation

Information on diurnal flock size, main diet type, breeding and spacing patterns, presence/absence of communal roosting, the maximum size of roosts for 45 hornbill species is presented in Tables 3a, 3b. Out of 54 hornbill species worldwide, 21 species are less than 500 g, while 9 species are between 501 –1000 g, 14 species are between 1001 – 2000 g, 6 species are between 2001- 3000 g and only 4 species are > 3001 g. Out of 41 hornbill species, 15 are non-territorial and 26 are territorial. Out of 47 hornbill species, 16 are primarily carnivorous, 6 had a mixed diet, and 25 species are primarily frugivorous.

Out of 45 hornbill species for which adequate information existed, 21 species have not been reported to roost communally, 19 species are reported to form small communal roosts and 5 to form large communal roosts. Out of 31 Asian species, 16 species were mainland (some of them also occur on islands) species, while 15 were only island species. All African species occur on the mainland.

All Asian and African species (n = 45) for which adequate information exists were incorporated into the analysis. Chi-square tests (2X2 contingency table) were carried out to determine if frugivory or non-territoriality and communal roosting were associated together significantly more than expected by chance. There was no significant difference in the observed associations from expected associations ($\chi^2 = 1.12$, df = 1, $p > 0.05$) for communal roosting and frugivory, similarly there was no significant association between non-territoriality and communal roosting ($\chi^2 = 0.59$, df = 1, $p > 0.05$). There was also no significant association between degree of frugivory and non-territoriality ($\chi^2 = 2.28$, df = 1, $p > 0.05$). But out of 23 frugivorous hornbills, 19 were communal roosting (83%). On the other hand, out of 15 carnivorous species, 9 (64%) species are not reported to form communal roots, while 6 species form small roosts. Out of 6 with mixed diets, only 1 species forms communal roosts.

Also, 76% of all communal roosting species were frugivorous, while only 23% of communally roosting species were carnivorous. Out of 14 non-territorial species, 11 are communal roosting (78%), while only 11 out of 26 territorial species (42%) are communal roosting. Out of 21 frugivorous species, 67% (14) are non-territorial, while only 33% (7) are territorial. Out of 14 carnivorous species, all are territorial. Therefore despite the lack of statistical significance, frugivory and non-territoriality does seem to be associated with each other and partially seem to account for the phenomenon of communal roosting.

Table 3a. Hornbill species, flock sizes, diet, ranging/spacing patterns, roosting behaviour and numbers at roosts (excluding 5 Asian species for which there is practically no information)

Hornbill species	Flock sizes	Diet	Ranging, movement and spacing	Roosting behaviour	Maximum numbers seen at roost site	Source
1. *Ocyceros griseus* Malabar Grey Hornbill	5-20	Largely frugivorous	Monogamous, possibly territorial at nest	None reported	None reported Breeding male roosting close to nest	Divya Mudappa, *pers.comm* Not studied in detail
2. *Ocyceros gingalensis* Sri Lankan Grey Hornbill	2-15?	Largely frugivorous?	Monogamous, possibly with helpers	None reported	None reported	Not studied in detail
3. *Ocyceros birostris* Indian Grey Hornbill	2-8 30 at fruiting trees	Mixed	Monogamous, possibly with helpers, territorial at nest	None reported	None reported	Not studied in detail
4. *Anthracoceros coronatus* Malabar Pied Hornbill	4-58 74	Largely frugivorous	Monogamous, otherwise undescribed	Communal roosting throughout the year, in dense riverine foliage, in inner branches over water or bamboo patch. Roost used for 20 years. In breeding season only subads and non-breeders come to roost. Breeding males roost near nests	Up to 44 in April Only 3-12 in June-September (breeding season)	Reddy 1988
4. *Anthracoceros albirostris* Oriental Pied Hornbill	2-6 50 at fruiting trees	Largely frugivorous	Monogamous	Communal roosting	Up to 130 in Thailand in non-breeding season 23-28 in NE India in non-breeding season	Tsuji *et al.* 1987 Datta, this study
5. *Anthracoceros marchei* Palawan Hornbill	Solitary, pairs to small groups	Largely frugivorous	Undescribed	None reported	None reported	Not studied in detail
6. *Anthracoceros malayanus* Malay Black Hornbill	2-6 up to 33 at fruiting trees	Largely frugivorous	Monogamous and year–round territorial	None reported	None reported	Leighton 1982, 1986 Becker & Wong 1985
7. *Buceros bicornis* Great Hornbill	2-40	Largely frugivorous	Monogamous and year-round territorial Breeding season range – 3.7 km2 Non-breeding season range – 14.7 km2	Regular communal roosting, using same routes, on topmost branches of thinly foliaged trees, spaced out over neighbouring trees. Noisy at dawn and moves out in smaller parties than when coming in at dusk	Up to 70 in Thailand Up to 87 in NE India Up to 200	Tsuji *et al.* 1987 Datta, this study Baker 1927, Ali & Ripley 1987
8. *Buceros rhinoceros* Great Rhinoceros Hornbill	2-25	Largely frugivorous	Monogamous, resident and territorial, possibly with helpers at times?	None reported	None reported	Leighton 1982, 1986
9. *Buceros hydrocorax* Great Phillipine Hornbill	2-7 up to 12	Largely frugivorous	Monogamous and territorial, breeding in co-operative groups with helpers	Regular calling from roosts, joins larger flocks of Mindanao Wrinkled Hornbill	Up to 20 or more	McGregor 1909* Rand & Rabor 1960* Witmer 1989– breeding only
10. *Buceros vigil* Great Helmeted Hornbill	2-8	Mixed	Monogamous, resident and territorial	None reported	None reported	Leighton 1982, 1986
11. *Penelopides exarhatus* Sulawesi Tarictic Hornbill	2-10	Mixed	Group-territorial, co-operative breeder	None reported	None reported	Tim O'Brien & Margaret Kinnaird, *pers.comm.*

Hornbill species	Flock sizes	Diet	Ranging, movement and spacing	Roosting behaviour	Maximum numbers seen at roost site	Source
12. *Penelopides panini* Visayan Tarictic Hornbill	Small groups up to 12	Mixed	Unknown	None reported	None reported	Not studied in detail
13. *Penelopides manillae* Luzon Tarictic Hornbill	Groups of up to 14	Mixed	Group-territorial, co-operative breeder?	None reported	None reported	Not studied in detail
14. *Aceros comatus* White-crowned Hornbill	2-8 Up to 20	Mainly carnivorous	Monogamous, resident and territorial, co-operative breeding	Appears to return to fixed roost sites among isolated trees on tips of twigs	None reported	Leighton 1982, 1986
15. *Aceros nipalensis* Rufous-necked Hornbill	2-8	Frugivorous	Monogamous, not territorial?	None reported	None reported	Not studied in detail
16. *Aceros cassidix* Sulawesi Wrinkled Hornbill	2- Up to 50 at fruiting trees	Frugivorous	Monogamous, non-territorial, wide-ranging, mobile Non-breeding season range – 39.8 to 55.8 km2	None reported, Explicitly mentions not finding permanent roosting sites or large roosting flocks in 3 year study.	None reported	Suryadi *et al.* 1998 Margaret Kinnaird, *pers.comm.*
17. *Aceros corrugatus* Sunda Wrinkled Hornbill	2-30	Frugivorous	Monogamous, non-territorial, wide-ranging, mobile	Uses roosts, flying up to 10 km	None reported	Leighton 1982, 1986
18. *Aceros leucocephalus* Mindanao Wrinkled Hornbill	2-6 up to 37, 20-40	Largely frugivorous	Monogamous, non-territorial	Roosting reported	None reported	Stott 1947
19. *Aceros plicatus* Papuan Wreathed Hornbill	2-small flocks	Largely frugivorous	Monogamous	Hundreds roost together, as many as 45 leave together at dawn	Up to hundreds	Gillard & LeCroy 1967* LeCroy and Peckover 1983*
20. *Aceros narcondami* Narcondam Hornbill	Up to 50 at fruiting trees	Largely frugivorous	Monogmous, non-territorial	None reported Studies only in breeding season	None reported	Hussain 1984 Ravi Sankaran *pers.comm.*
21. *Aceros subruficollis* Plain-pouched Hornbill	6-20 Over 50 at fruiting trees	Frugivorous	Monogamous, non-territorial	Shared roosts with *A. undulatus*. Recent reports of hundreds flying to roosts, mixed roosts in Thailand	2421 in Temengor 1227 in Temengor 764 in Tasek Kenering 1665 in Tasek Temengor	Davison 1995*, Yaacob 1994* Ho & Sutari 1997, 2000 Pilai Poonswad, *pers.comm.*
22. *Aceros undulatus* Wreathed Hornbill	2-20 Up to 40 at fruiting trees	Frugivorous	Monogamous, wide-ranging, non-territorial, nomadic	As many as 264 on one tree, 400 at roost. 40 on single tree in NE India	700 in Khao Yai 1000 in Khao Yai 103 in NE India	Tsuji *et al.* 1987 Tsuji *et al.* 1987 Datta, this study
23. *Aceros everetti* Sumba Wreathed Hornbill	2-5 Up to 15	Largely frugivorous	Monogamous, defence of fruiting trees reported during breeding season	Long flights above canopy when returning to roosts	Up to 70 birds may gather at roost site But other observers have not noted communal roosting	Juhaeni 1993 Tim O'Brien & Margaret Kinnaird, *pers. comm.*
24. *Anorrhinus austeni* Austen's Brown Hornbill	5-30	More carnivorous	Monogamous co-operative breeder, group-territorial Breeding range – 4.3 km2	Up to 50-60 roosting together in non-breeding season reported, but breeding flocks roosted separately close to individual nests	Up to 50-60	Tsuji *et al.* 1987 Tsuji 1996
25. *Anorrhinus tickelli* Tickell's Brown Hornbill	Unrecorded	Unrecorded	Probably monogamous co-operative breeder	None reported	None reported	Not studied in detail
26. *Anorrhinus galeritus* Bushy-crested Hornbill	2-20 Median - 7	Largely frugivorous	Monogamous co-operative breeder, group-territorial	Fixed roost sites on isolated trees near a stream, where they perch on tips of twigs	Roost size not mentioned	Kemp & Kemp 1974 Leighton 1982, 1986

Table 3b. African hornbills

Hornbill species	Flock size	Diet	Ranging, spacing and movement patterns	Roosting behaviour	Maxmimum numbers at roost site	Source
1. *Bucorvus leadbateri* Southern Ground Hornbill	2-11 mean – 3.5	Carnivorous	Group-territorial, co-operative breeding	No regular roost sites	No communal roosting	Kemp 1995
2. *Bucorvus abyssinicus* Northern Ground Hornbill	2-6 mean - 2.2	Carnivorous	Monogamous, not co-operative breeder	No regular roost sites	No communal roosting	Kemp 1995
3. *Tockus alboterminatus* African Crowned Hornbill	2-7 Up to 80	Mixed	Monogamous, territorial	Roosts on long thin branches or vines usually in a valley near a stream, in open areas, up to 6 regular roost sites per territory	Numbers not reported	Kemp 1995
4. *Tockus bradfieldi* Bradfield's Hornbill	2 – to small groups Up to 62 birds at food concentrations, wanders in large flocks	Carnivorous	Monogamous, territorial during breeding season	None reported		Kemp 1995
5. *Tockus fasciatus* African Pied Hornbill	3-5 Up to 70 in non-breeding season	Largely frugivorous	Monogamous, probably territorial	Communal roosting reported?		Kemp 1995
6. *Tockus hemprichii* Hemprich's hornbill	2-14	Largely carnivorous	Probably monogamous and territorial	None reported		Kemp 1995
7. *Tockus pallidirostris* Pale-billed Hornbill	2-8	Little known	Monogamous, but little known	None reported		Kemp 1995
8. *Tockus nasutus* African Grey Hornbill	2 up to 100 in congregations, wanders in large flocks	Carnivorous	Monogamous and territorial when breeding, wide-ranging movements in non-breeding season	Roosts on thin branches, often at regular site	No details of numbers	Kemp 1995
9. *Tockus monteiri* Monteiro's Hornbill	2 Up to 47 in dry season	Largely carnivorous	Monogamous and territorial during breeding season	Roosts in trees, often on rock faces or even on rock ledges	No details of numbers	Kemp 1995
10. *Tockus erythrorhynchus* African Red-billed Hornbill	2 to small groups Several hundred in dry season, wanders in large flocks	Carnivorous	Monogamous and territorial during breeding season	Returns to regular roost site in territory, roosts in tree close to trunk or main limb.	No details of numbers	Kemp 1995
11. *Tockus leucomelas* Southern Yellow-billed Hornbill	2-family groups	Carnivorous	Monogamous and territorial	Returns to regular roost site in territory, often against main limb of tree	No details of numbers	Kemp 1995
12. *Tockus flavirostris* Eastern yellow-billed Hornbill	Pairs	Carnivorous	Monogamous and territorial	None reported		Kemp 1995
13. *Tockus deckeni* Von der Decken's Hornbill	Pairs	Carnivorous	Monogamous and territorial	None reported		Kemp 1995
14. *Tockus hartlaubi* Dwarf Black Hornbill	2-8	Carnivorous	Apparently resident and territorial, monogamous	None reported		Kemp 1995
15. *Tockus camurus* Dwarf Red-billed Hornbill	2-12	Carnivorous	Probably territorial, co-operative breeder	None reported		Kemp 1995

Hornbill species	**Flock size**	**Diet**	**Ranging, spacing and movement patterns**	**Roosting behaviour**	**Maxmimum numbers at roost site**	**Source**
16. *Tockus albocristatus* Long-tailed Hornbill	2-5	Carnivorous	Monogamous, probably territorial	None reported		Kemp 1995
17. *Ceratogymna fistulator* Piping Hornbill	2-20 rarely 40-50	Largely frugivorous	Monogamous, little known	Usually roosts communally, sometimes at tree on hillside	No details of numbers	Kemp 1995
18. *Ceratogymna bucinator* Trumpeter Hornbill	2-48 Up to 100 at fruiting trees	Largely frugivorous	Monogamous, non-territorial, except for area around nest, but co-operative breeding recently reported	Pairs and families roost together, but also communally, travelling up to 15 km. Roosts in remote stands of large trees along watercourses, in hills near rivers or in dry savannah. Sites used for many years, numbers drop in breeding season. Changed roost sites 5 km apart within a week	Up to 200 may roost in same area	
19. *Ceratogymna cylindricus c.* Brown-cheeked Hornbill Subspecies – White-thighed Hornbill *C.c. albotibialis*	2-6 Up to 90 at fruiting trees	Largely frugivorous	Monogamous, non-territorial, except around nest tree	Roosts after preliminary moving around near sunset on end of hanging dead limb or high on dead tree	No details of numbers	Good 1952*
20. *C. subcylindricus* Grey-cheeked Hornbill	2, 20-50	Largely frugivorous	Monogamous with no obvious territoriality, but defends nest tree	Roosts in pairs on outer branches of trees, using same site regularly, congregating in large loose flocks (seen in West Kenya)	Communal roosting reported, but no numbers given	Kalina 1988
21. *C. brevis* Silvery-cheeked Hornbill	2 to small flocks up to 100 at fruiting trees	Largely frugivorous	Monogamous with no territoriality, defends nest area	Often roosts communally in adjacent large trees. Disperses from roosts, singly, in pairs or small flocks before sunrise, returning around sunset. Also roosts singly or in pairs and breeding male roosts alone away from nest tree. Roost site may be regular or vary from night to night	Up to 200 birds together	Trump 1982*
22. *Ceratogymna atrata* Black-casqued Wattled Hornbill	2-5 Up to 40 at fruiting trees	Largely frugivorous	Possibly group territorial and co-operative breeding, defends the area around the nest which includes the regular roost sites	Pairs appear to maintain a core area where they also roost, roosts on large branches, high in forest trees.	No details of numbers	Kemp 1995
23. *C. elata* Yellow-casqued Wattled Hornbill	2-12	Largely frugivorous	Monogamous, little known	Communal roosts perched low on a swamp	Up to 50 recorded	Buttikofer in Bates 1930 (Kemp 1995)

** References in Kemp (1995), not seen in original*

8.5. DISCUSSION

8.5.1. Roost site characteristics and why hornbills roost in open habitats?

From the description of roost sites, it is evident that hornbills generally roost in relatively open habitats, away from the forests where they forage and nest. Roosting sites have a much lower tree density, and the trees are often comparatively short-statured isolated deciduous (often leafless) trees. In the few cases, where they roost near the forest edge, they use tall emergent *Tetrameles nudiflora* trees, perching on the topmost thinner branches. These areas possibly afford greater visibility either for birds to see predators or for advertisement of their presence to conspecifics. Their behaviour at roosts seems contradictory - they seem to advertise their presence for the purpose of assembling a larger number of birds by displaying and calling, but they first settle at a pre-roost site for a while, before flying into the final roost trees after sunset. This behaviour was especially seen in the Great hornbill. They also settle on the topmost thinner branches of roost trees rather than on stronger lower branches. If hornbills choose a site that is safe from terrestrial predators then they do not have to bother to be secretive. Being out in the open away from forests, and choosing leafless trees such as *Albizzia* and *Bombax ceiba,* may all serve to reduce the incidence of predator visitations. If the site is known to be safe in itself, then there is no need to suppress what may be other reasons for communal gathering, such as social stimulus through calling and display. Kemp (1995) observed that ground hornbills and the African Crowned hornbill *Tockus alboterminatus* also indulge in mock-roosting or gather in pre-roosts, flying off to the final roost site only at dusk. This has also been observed in Malabar Pied hornbills by Reddy (1988). Such behaviour seems like an anti-predatory strategy.

These sites may be chosen as ideal centres for information exchange between foraging birds, but it is difficult to determine the primary reason for selection of such habitats, since these areas also possibly afford greater visibility and better protection from heavier, arboreal and nocturnal predators. The known reported predators of hornbills are binturong (*Arctictis binturong*) and yellow-throated marten (*Martes flavigula*), but most instances of predation have been of chicks and rarely of females at nest trees (Poonswad *et al.* 1987, 1988, 1998). Other predators could be the small cats such as leopard cat (*Felis bengalensis*), marbled cat (*Pardofelis marmorata*), golden cat (*Catopuma temmincki*), and clouded leopard (*Neofelis nebulosa*). But all these nocturnal predators actively hunt inside the forest and are not known to actively hunt in the habitat chosen for roosting. The fact that hornbills fly away from the forest up to 6 km in the evenings to gather in such open areas suggests some anti-predatory benefits. On the other hand, all hornbills in a given population may not roost communally; therefore it is hard to figure out why only some individuals in the population roost communally, while others do not. This would occur if the primary reason for gathering in roosts was related to food-finding, where some individuals may not need to join the roost because of their superior knowledge about the location of food sources. Zahavi (1971a) suggested that vulnerability to predators may be secondarily important and therefore constrains birds that are gathering in such large numbers for other reasons (*viz.* food-finding) to adopt certain anti-predatory strategies. While trying to maximise foraging benefits, they would have to minimise predation risks.

8.5.2. Communal roosting and roosting behaviour

The Great hornbills and Wreathed hornbills roosted communally in mixed species roosts most of the time in similar locations but on separate trees. Roosting hornbills are usually spread out over a length of 200 - 300 m on different trees in a linear fashion. Both the Great hornbills and Wreathed hornbills use communal roosts throughout the year, but the size of the roost varies throughout the year. Roost sites are used regularly year after year but they shift their roosting areas periodically probably in relation to location of food sources. At any given time, a roost site is used for up to 1- 2 months or for a few days. Birds were seen arriving to roost sites from several different directions such as from the north, east, north-west and south-west and it was estimated that they travelled as much as 6-10 km to reach the roost sites. The mixed roost of Great hornbills and Wreathed hornbills near Khari *nala* in January 1998 was probably used because of the locally abundant ripe fruits of *Livistona jenkinsiana* in that year in the area during that time. The data on presence of saplings of hornbill food plants under roost trees shows evidence of use of these roost sites for up to 4-5 years, though survival of food plants after the first year is low (Chapter 4).

The Wreathed hornbills start arriving earlier at the roosts, but the Great hornbills on arrival often displace the Wreathed hornbills from individual roost trees. After arriving, Wreathed hornbills perch for a while, but often hop from branch to branch, circle or fly to neighbouring trees till they finally settle down. They also often approach the roost site by assembling initially in one tree, and moving on subsequently, often flying back and returning, calling repeatedly. In the breeding season, especially they were seen to gather in pre-roost areas as described by Zahavi (1971a) and Ward & Zahavi (1973). Great hornbills come at dusk after sunset, nearly half an hour after the first Wreathed hornbills arrive. The Great hornbills arrive all together,usually, since they gather in pre-roost areas before they finally come into the main roost after dark (a possible anti-predatory strategy because of the higher hunting pressures by local tribals on this species). Therefore, birds arrive initially, in normal diurnal flock sizes, but towards dusk, when they all fly in together, there is less obvious pair or group cohesion.

The Wreathed hornbill relies more on patchy non-fig fruit resources than the Great hornbill. They are also non-territorial with home range sizes of around 10 km^2 in the breeding season and 28 km^2 in the non-breeding season. It was also estimated that birds travel as far as 10 km to reach roost sites (Tsuji *et al.* 1987, Poonwad & Tsuji 1994) and nomadic flocks travel widely in the non-breeding season (Leighton 1986). The Great hornbill despite being larger in body size is estimated to have smaller home range sizes of 3.7 km^2 in the breeding season and 14.7 km^2 in the non-breeding season, is resident and maintains year-round territories (Poonswad & Tsuji 1994). Wreathed hornbills roost in larger flocks than the Great hornbill in Thailand, though the maximum number seen during this study is much smaller than that reported in Thailand where > 1000 birds roosted together. In Thailand, they also found that both species roosted and fed in the same area and that the Great hornbills did not join or roost in flocks as regularly as the Wreathed hornbills (Tsuji *et al.* 1987). The Great hornbill is also competitively superior to the Wreathed hornbill, often displacing the latter from fruiting and roosting trees. Since they maintain territories, the need to join large communal roosts is less important for this species and therefore, it possibly does so, only in the relatively fruit-poor non-breeding season.

8.5.3. Foraging flock sizes and roosting flock sizes

The disparity in size of foraging groups and the number of birds found in roosts shows that many more birds aggregate at roosts than is necessary to form foraging groups (Buckley 1996). This may argue against the idea of foraging benefits from communal roosting. But large numbers may be found because of some advantage in associating with larger number of birds *per se*. Joining a large flock may increase the chances that there will be other foragers willing to depart with an individual when it is ready to go foraging. As a result of a series of optimal individual decisions, roosts grow to contain more birds than necessary to form foraging groups. In addition, the aggregations of birds at roost sites may be tied to keeping track of changing resource distribution which might be more difficult to do if birds chose to roost alone. Indeed, roost sites shifted periodically over months probably in response to location of fruit-rich patches.

8.5.4. Seasonal differences in flock sizes

There was no difference in flock size between species, though Wreathed hornbills generally had larger flock sizes than the Great hornbill or the Oriental Pied hornbill. The territorial Great hornbill showed differences in degree of communal roosting between the seasons while the non-territorial Wreathed hornbill did not show significant changes in roost sizes. But both species had smaller roost sizes in the breeding season, when food supplies are greatest. Daily movements and ranges are also shorter because of the necessity of foraging in the vicinity of nest trees. This provides indirect evidence that the primary reason for flocking is unlikely to be related to predation pressure, since it seems implausible that predation pressures would vary seasonally and that too differentially for the two species.

Diurnal foraging flock sizes, evening roost flight flock sizes and roosting flock sizes were consistently higher during the non-breeding season than in the breeding season. Though a part of the reason lies in the fact that flock size distribution in the breeding season was skewed towards single males, still the degree of flocking was greater in the non-breeding season when there was a lean season in fruiting. Increased foraging efficiency by flocking has been proposed by Moynihan (1962) and Cody (1971). Flocking tends to occur when food availability is low (Cody 1971, Morse 1970). However, individual birds in flocks spend more time feeding and less time watching, suggesting that protection from predators is the primary reason for flocking and improved feeding is a secondary consequence (Lazarus 1979). Leighton (1986) suggests that diet and foraging strategy influences flock sizes in hornbills. Leighton (1986) rules out predation as a factor influencing flock size and postulates that though hornbills may be susceptible to nocturnal predators while roosting (small felids, civets), the relative advantages of forming small or large flocks to elude predators should not limit diurnal group size, since birds could regroup in the mornings.

Another possible non-foraging advantage of communal roosting is thermoregulation. Although up to 40 - 50 Wreathed hornbills roosted together on the same tree, sometimes up to 6 birds on a single branch, roosting birds rarely huddled together. In addition, nightime temperatures in these lowland foothill forests are not lower than 10°C and hornbills also roost in the warm summer months.

8.5.5. Why do hornbills roost communally?

The argument that the primary explanation for communal roosting in hornbills might lie in food finding comes from several lines of evidence. Firstly, there are seasonal changes in size of communal roosts corresponding to variation in food abundance and distribution. It is unlikely that these seasonal changes are due to seasonally varying predation risks. Secondly, the non-territorial, wide-ranging, and more frugivorous Wreathed hornbills form communal roosts more regularly than the Great hornbills that maintain territories, are less dependent on non-fig fruits and are also competitively superior. The Wreathed hornbills roost communally throughout the year, albeit in smaller numbers during the resource-rich nesting period.

It might be argued that smaller-sized species are more vulnerable to predation and thus more likely to form larger roosting flocks. This was not the case, since the Oriental Pied hornbill that is much smaller, forms smaller roosting flocks than the Wreathed hornbill and the Great hornbill and also did not join roosts communally with the 2 larger species.

Communal roosting is reported in a wide range of avian species (eg. parrots, wagtails, waders, geese, finches, crows, ravens, falcons/kestrels, vultures) and has usually been related to food finding (Ward & Zahavi 1973 and references cited therein). It has also been shown that species that rely on patchy and localised food sources are often more likely to roost communally. All these species have been shown to join larger flocks during the resource-poor period. More recent quantitative studies have also demonstrated that communal roosting is related to food-finding (Loman & Tamm 1980, Caccamise 1993, Caccamise & Morrison 1986, 1986, Chapman *et al.* 1989, Rabenold 1987, Buckley 1996, Caccamise *et al.* 1983, Caccamise *et al.* 1997,Morrison & Caccamise 1985, 1990).

All hornbills roost, but do all hornbills roost communally and/or join roosting flocks of other sympatric hornbill species? The phenomenon of communal roosting seems to be more common among the more frugivorous species and also those that are non-territorial, wide-ranging and highly mobile. Of the 31 Asian species, some degree of communal roosting has been reported in 13 species. Of these 13, 7 belong to the *Aceros*. There are 11 *Aceros* species, and out of the four in which communal roosting has not been reported, one is the Visayan Wrinkled hornbill *Aceros waldeni* which has not been studied at all and is restricted to three islands of the Philippines and probably faces imminent extinction (Kemp 1995). Two other species, *viz.* the Rufous-necked hornbill and the Narcondam hornbill have mainly been studied in the breeding season and communal roosting may have been overlooked. While the former species is threatened and rare, the latter occurs only on a tiny island with the total population size estimated at 300-400 birds. The Sulawesi Red-knobbed hornbill has not been seen to use permanent roost sites and no large flocks flying to roosts were ever recorded during a comprehensive study on the species (Kinnaird *et al*. 1996, Suryadi *et al.* 1998). Fig densities and both fig and non-fig fruit biomass were exceptionally high in the area and this species may not have the need to roost communally given the high food abundance and low seasonality (Kinnaird *et al.* 1996). It is also doubtful whether the Sumba Wreathed hornbill roosts communally, because, though Juhaeni (1993) reports roosts of up to 70 birds, Margaret Kinnaird and Tim O'Brien (*pers. comm.*) have not seen them using communal roosts in extensive population surveys of the species. Island species belonging to the

Aceros such as the Sulawesi Wrinkled hornbill, Sulawesi red-knobbed hornbill, and Sumba Wreathed hornbill are not known to roost communally. Many island species also have small population sizes that may restrict the formation of large roosts. But it may also be argued that the reasons for the lack of large communal roosts in island species may be the absence of natural predators on many of these islands.

The 6 other species in which roosting is reported includes two of the *Anthracoceros* genus, one, possibly two of the *Anorrhinus* genus and two of the *Buceros* genus, though the size of communal roosts is much smaller in these species than that reported for species of the *Aceros* genus. In addition, the Brown hornbill and Great hornbill did not join or form communal roosts in the breeding season (*Tsuji et al.* 1987, Datta, this study). The largest reported single roost size of Oriental Pied hornbill was 130 and roosting has not been reported yet in the breeding season. The Bushy-crested hornbill, a group-territorial co-operative breeder is reported to use fixed roost sites, but no other information on communal roosts or numbers is available.

Of all the 13 Asian species in which some degree of communal roosting is reported, only five are territorial (*Buceros, Anorrhinus* and *Aceros comatus*), all the others in the *Aceros* genus are non-territorial, wide-ranging, highly mobile, while the two *Anthracoceros* species are non-territorial, though not as wide-ranging as *Aceros* species. Some territorial species may not be territorial throughout the year, when food supplies drop either seasonally or erratically as during droughts (such as some of the *Buceros* spp. and *Tockus* spp.). Nomadic flocks are then formed during the day. Some of these may roost as flocks, when the flock movements take them far from the normal territory or breeding areas. In these species, communal roosting may be more a consequence than a plan of the change in food availability.

Of the 23 African species, use of regular roost sites has been reported in 12 species, but communal roosting has been explicitly reported only in 5 of the *Ceratogymna* species that are largely frugivorous forest hornbills. But roost sizes ranged from 50 to 200 birds, unlike the spectacular aggregations reported for Wreathed hornbills and Plain-pouched hornbills (Tsuji *et al.* 1987, Ho & Sutari 1997, 2000). All these *Ceratogymna* species are largely frugivorous and also appear to be mainly non-territorial, some defending the area around the nest tree during the breeding season. Of the other 7 species, in which use of regular roost sites is reported, one is *Ceratogymna atrata*, which is possibly group territorial and a co-operative breeder, roosting in pairs or family groups. The other is *Ceratogymna cylindricus* (a relatively uncommon species), which is known to use certain roost sites, but communal roosting has not been reported. The other 5 species are all savannah-dwelling, largely carnivorous *Tockus* species that are known to use regular roost sites in certain kinds of habitats, but communal roosting has not been reported. This pattern seems to underline the importance of the information-centre hypothesis in explaining communal roosting. Additional support comes from that fact many of the smaller species (that are likely to be more vulnerable to predation) do not roost communally, while more of the larger-bodied species are reported to roost communally. In addition, the size of communal roosts changes seasonally even for the species that form large roosts and is related to the availability of fruit resources. Predation pressure is unlikely to vary seasonally and result in changes in roosting patterns and flock sizes. Frugivorous and non-territorial species seem more likely to roost communally than the more carnivorous and territorial species, though there are exceptions. The occurrence of communal roosting in hornbill species across the world, in general, seems to be associated with frugivory and non-territoriality, and partly with body size.

8.6. CONCLUSIONS

Communal roosting by hornbills is a year-round phenomenon, unlike what most previous literature suggested: that hornbills roost communally only in the non-breeding season. Communal roosting also occurred at the same sites even in the breeding season (March to July) though the congregations were much smaller during this period. A high proportion of the roosting flocks in the breeding season were comprised of breeding males, an observation that has not been reported earlier. The phenomenon of communal roosting is most likely related to enhanced food-finding, since hornbills roost in larger numbers in the non-breeding season and the wide-ranging, often nomadic Wreathed hornbills that forage more on patchy non-fig fruits roost in larger numbers than the territorial Great hornbill that forages more on figs. An important finding of the study is that hornbills regularly used roost sites that were located in areas close to habitation, in habitats that are subjected to disturbance from cattle grazing and occasional fires. The communal roost sites were located either on isolated deciduous trees in successional grassland habitats adjoining rivers, or on trees on steep cliff faces and mud banks near small perennial streams. These areas were away from the forests used by hornbills for foraging and nesting. The selection of an open habitat may be related to safety from nocturnal arboreal forest predators, though generally predation of adult hornbills by natural predators is rare. Given the hunting pressures on hornbills, in these areas, it is surprising that hornbills still choose to roost in these areas. For some reason, hunting of hornbills at these roost sites does not seem to occur frequently. But the vulnerability of both roosting hornbills and these habitats requires that these identified roost sites are adequately protected and monitored to ensure the continued use of these sites. The adjoining roosting sites in Assam also require monitoring and protection, given the degree of human disturbance and habitat loss in the last five years in the area. These roost sites can also be used to gather important demographic information on hornbill populations. Continued monitoring over several years and identification of other roosting sites would help in assessing the population status and identifying any decline in numbers.

Literature cited

ALI, S. AND S. D. RIPLEY. 1987. Compact Handbook of the Birds of India and Pakistan. 2nd edition. Oxford University Press, 737 pp.

ANDRESEN, E. 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. *Biotropica* 31(1): 145-158.

ANON. 1994. The Indian Wildlife Protection Act, 1972 (as amended upto 1993). 2nd edition. Natraj Publishers, Dehra Dun. 158 pp.

ASHTON, P. S., T. J. GIVNISH, AND S. APPANAH. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* 132(1): 44-66.

ASQUITH, N. M., J. TERBORGH, A. E. ARNOLD, AND C. MAILEN RIVEROS. 1999. The fruits the agouti ate: *Hymenaea courbaril* seed fate when its disperser is absent. *J. Trop. Ecol.* 15: 229-235.

ATHREYA, R. A. AND S. KARTHIKEYAN. 1995. A report on a visit to the wildlife sanctuaries of the Dafla hills of Arunachal Pradesh. Unpublished report submitted to Arunachal Pradesh Forest Department.

ATHREYA, R. A., A. S. CAPTAIN AND V. R. ATHREYA. 1997. A faunal survey of Namdapha Tiger Reserve, Arunachal Pradesh, India. Unpublished report submitted to Arunachal Pradesh Forest Department. 50 pp.

ATHREYA, V. R. AND A. J. T. JOHNSINGH. 1995. Survey of the clouded leopard (*Neofelis nebulosa*) in North-east India. Unpublished report, Wildlife Institute of India, Dehradun. 40 pp.

AUGSPURGER, C. K. 1982. A cue for synchronous flowering. *In* E. G. Leigh Jr., A. S. Rand, D. M. Windsor (Eds.), The ecology of a Neotropical Forest: seasonal rhythms and long-term Changes, pp. 133-150. Smithsonian Institution Press, Washington D.C. 469 pp.

AUGSPURGER, C. K. AND C. K. KELLY. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* (Berlin) 61: 211-217.

BAKER , E. C. S.1927. Fauna of British India. Birds. 2nd edn. Vol. 4. London: Taylor and Francis. 471 pp.

BALASUBRAMANIAM, P. AND SARAVANAN, R. 2001. Fruiting seasonality and food selection by Indian Pied Hornbill in a riverine forest in Western Ghats, India. Paper presented at the Third International Hornbill Workshop, 9-12 May, Phuket, Thailand.

BARIK, S. K., R. S TRIPATHI, H. N. PANDEY AND P. RAO. 1996. Tree regeneration in a subtropical humid forest: effect of cultural disturbance on seed production, dispersal and germination. *J. Appl. Ecol.* 33: 1551-1560.

BATSCHELET, E. 1981. Circular Statistics in Biology - (Mathematics in Biology Series). Academic Press Inc., London. 371 pp.

BECKER, P. AND M. WONG. 1985. Seed dispersal, seed predation and juvenile mortality of *Aglaia* sp. (Meliaceae) in lowland dipterocarp forest. *Biotropica* 17:230-237.

BEEHLER, B. 1983. Frugivory and polygamy in birds of paradise. *Auk* 100: 1-12.

BENNETT, E. L., A. J. NYAOI, AND J. SOMPUD. 1997. Hornbills *Buceros* spp. and culture in Northern Borneo: can they continue to co-exist? *Biol. Conserv.* 82: 41-46.

BLATE, G. M., D. R. PEART AND M. LEIGHTON. 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. *Oikos* 82: 522-538.

BOIX-HINZEN, C., M. S. L. MILLS AND M. A. DU PLESSIS. 2001. Determinants of timing of female nest departure in Monteiro's Hornbill *Tockus monteiri*. Paper presented at the Third International Hornbill Workshop, Phuket, Thailand, 9-12 May, 2001.

BORCHERT, R. 1983. Phenology and control of flowering in tropical trees. *Biotropica* 15(2): 81-89.

BORGES, R. M. 1993 . Figs, Malabar giant squirrels and fruit shortages within two Indian tropical forests. *Biotropica* 25(2): 183-190.

BRANDEIS, D. 1906. Indian trees. Archibald Constable and Co. Ltd., London. Reprinted in 1990 by Bishen Singh Mahendra Pal Singh, Dehradun. 767 pp.

BROWN, C. R. 1986. Cliff swallow colonies as information centers. *Science* 234: 83-85.

BROWN, C. R. 1988. Social foraging in Cliff Swallows: Local enhancement, risk sensitivity, competition and the avoidance of predators. *Anim. Behav*. 36: 780-792.

BROWN, C. R., M. BOMBERGER BROWN, AND M. L. SHAFFER. 1991. Food-sharing signals among socially foraging Cliff Swallows. *Anim. Behav.* 42: 551-564.

BUCKLEY, N. J. 1996. Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures. *Auk* 113(2): 473-488.

BUSTAMANTE, R. O. AND M. CANALS. 1995. Dispersal quality in plants: how to measure efficency and effectiveness of a seed disperser. *Oikos* 73(1): 133-135.

BYERS, C. R., R. STEINHORST, AND P. R. KRAUSMAN. 1984. Clarification of a technique of analysis of utilization-availability data. *J. Wildl. Manage.* 48(3): 1050-1053.

CACCAMISE, D. F. 1993. The 'patch-sitting hypothesis': A parsimonious view of communal roosting behaviour. *Wilson Bull.* 105: 372-377.

CACCAMISE, D. F. AND D. W. MORRISON. 1986. Avian communal roosting: Implications of diurnal activity centers. *Am. Nat.* 128(2): 191-198.

CACCAMISE, D. F. AND D. W. MORRISON. 1988. Avian communal roosting: A test of the patch-sitting hypothesis. *Condor* 90: 453-458.

CACCAMISE, D. F., L. A. LYON AND J. FISCHL. 1983. Seasonal patterns in roosting flocks of starlings and common grackles. *Condor* 85: 474-481.

CACCAMISE, D. F., L. M. REED, J. ROMANOWSKI AND P. C. STOUFFER. 1997. Roosting behaviour and group territoriality in American Crows. *Auk* 114(4): 628-637.

CAPTAIN, A. AND B. B. BHATT. 1997. Some snakes of the Itanagar area of Papumpare District, Arunachal Pradesh. *Arunachal Forest News* 15: 12-14.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York. 234 pp.

CHAMPION, H. G. AND S. K. SETH. 1968. A revised survey of the forest types of India. Manager of Publications. Government of India. New Delhi. 404 pp.

CHAPMAN, C. A., L. J. CHAPMAN, & L. LEFEBVRE. 1989. Variability in parrot flock size: possible functions of communal roosts. *Condor* 91: 842-847.

CHAPMAN, C. A., R. WRANGHAM, AND L. J. CHAPMAN. 1994. Indices of habitat-wide fruit abundance in tropical forests. *Biotropica* 26: 160-171.

CHAPMAN, C. A., R. WRANGHAM, L. J. CHAPMAN, D. K. KENNARD, AND A. E. ZANNE. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *J. Trop. Ecol.* 15: 189-211.

CHARLES-DOMINIQUE, P. 1993. Speciation and evolution: an interpretation of frugivory phenomena. *Vegetatio* 107/108: 75-84.

CHIMCHOME, V., A. VIDHIDHARM, S. SIMCHAREON, S. BUMRUNGSRI, AND P. POONSWAD. 1998. Comparative study of the breeding biology and ecology of two endangered hornbill species in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *In* P.Poonswad (Ed.), The Asian Hornbills: Ecology and Conservation, pp. 111-136. Thai Studies in Biodiversity No.2: 1-336, Biodiversity Research and Training Program, Bangkok, 325 pp.

CHOWDHURY, H. J. 1998. Orchids of Arunachal Pradesh. Bishen Singh Mahendra Pal Singh, Dehra Dun, India. 824 pp.

CHOWDHURY, H. J., G. S. GIRI, G. D. PAL, A. PRAMANIK, AND S. K. DAS. 1996. Materials for the flora of Arunachal Pradesh. Botanical Survey of India, Howrah, India.

CHOY, P. K. 1980. Breeding the Great Indian Hornbill (*Buceros bicornis*) at Jurong Bird Park. *Int. Zoo Yr. Bk.* 20: 204-206.

CHUAILUA, P., K. PLONGMAI, AND P. POONSWAD. 1998. Status of nest cavities of hornbills in Khao Yai National Park, Thailand. *In* P. Poonswad (Ed.) The Asian Hornbills: Ecology and

Conservation, pp. 219-226. Thai Studies in Biodiversity No.2: 1-336, Biodiversity Research and Training Program, Bangkok, 325 pp.

CLARK, D. A. AND D. B. CLARK 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *Am .Nat.* 124: 769-788.

CLUTTON-BROCK, T. H. AND P. H. HARVEY. 1984. Comparative approaches in investigating adaptation. *In* J. R. Krebs and N. B. Davies (Eds.), Behavioural Ecology: an evolutionary approach, pp. 7-29. 2nd edition, Blackwell Science Publications, Oxford.

COATES-ESTRADA, R. AND A. ESTRADA. 1988. Frugivory and seed dispersal in *Cymbopetalum baillonii* (Annonaceae) at Los Tuxtlas, Mexico. *J. Trop. Ecol.* 4: 157-172.

*CODY, M. L. 1971. Finch flocks in the Mojave Desert. *Theor. Pop. Biol.* 2:142-58.

CODY, M. L. 1985. Habitat selection in birds: Academic Press. 558 pp.

COLE, B. J. 1981. Overlap, regularity, and flowering phonologies. *Am. Nat.* 117-993-997.

COLLAR, N., M. J. CROSBY, AND A. J. STATTERSFIELD. 1994. Birds to watch 2: the world list of threatened birds. Birdlife International, Cambridge, United Kingdom. 408 pp.

CONDIT, R., P. S. ASHTON, P. BAKER, S. BUNYAVEJCHEWIN, S. GUNATILLEKE, N. GUNATILLEKE, S.P. HUBBELL, R. B. FOSTER, A. ITOH, J. V. LAFRANKIE, H. S. LEE, E. LOSOS, N. MANOKARAN, R. SUKUMAR, AND T. YAMAKURA. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288(5470): 1414-1418.

*CONNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *In* P.J. den Boer and G. R. Randwell (Eds.) Dynamics of populations, pp. 298-312. Pudoc, Wageninigen.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

CONNER, R. N. AND C. S. ADKISSON. 1976. Discriminant Function Analysis: A possible aid in determining the impact of forest management on woodpecker nesting habitat. *Forest Science* 22(2): 122-127.

CONNER, R. N. AND C. S. ADKISSON. 1977. Principal Component Analysis of woodpecker nesting habitat. *Wilson Bulletin* 89(1): 122-129.

CORLETT, R.T. 1996. Characteristics of vertebrate-dispersed fruits in Hong Kong. *J. Trop. Ecol.* 12: 819-833.

CORLETT, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) region. *Biological Review* 73: 413-448.

*CROOK, J. H. 1965. The adaptive significance of avian social organization. *Symp. Zool. Soc. Lond.* 14: 181-218.

DATTA, A. 1998a. Hornbill abundance in unlogged forest, selectively logged forest and a plantation in western Arunachal Pradesh. *Oryx* 32 (4): 285-294.

DATTA, A. 1998b. Records of turtles from Pakhui Wildlife Sanctuary, Arunachal Pradesh, northeast India. *J. Bombay nat. Hist. Soc.* 95(1): 121-123.

DATTA, A. 1998c. Evidence of clouded leopard *Neofelis nebulosa* in Pakhui Wildife Sanctuary, Arunachal Pradesh. *J. Bombay nat. Hist. Soc.* 95(3): 498-499.

DATTA, A. 1999a. Small carnivores in two protected areas of western Arunachal Pradesh, north-east India. *J. Bombay nat. Hist. Soc.* 96(3): 399-404.

DATTA, A. 1999b. Pangolin sightings in western Arunachal Pradesh. *J. Bombay nat. Hist. Soc.* 96(2): 310.

DATTA, A. 2001. Pheasant abundance in selectively logged and unlogged forests of western Arunachal Pradesh, north-east India. *J. Bombay nat. Hist. Soc.* 97(2): 177-183.

DATTA, A. AND S. P. GOYAL. 1997. Responses of arboreal mammals to selective logging in western Arunachal Pradesh. Unpublished report. Wildlife Institute of India, Dehradun. 73 pp.

DATTA, A., P. SINGH, R. M. ATHREYA, AND S. KARTHIKEYAN. 1998. Birds of Pakhui Wildlife Sanctuary in western Arunachal Pradesh. *Newsletter for Birdwatchers* 38(6): 91-96.

DATTA, A., G.S. RAWAT AND P. SINGH. *In press*. The effect of post-dispersal factors on regeneration success of hornbill food plants: some preliminary evidence. Paper presented at the Proceedings of the National Wildlife Seminar, August 26-28, 1998, Wildlife Institute of India, Dehradun.

DAVIDAR, P. 1983. Birds and neotropical mistletoes: effects on seedling recruitment. *Oecologia* (Berlin) 60: 271-273.

DIAZ, I., C. PAPIC, AND J. J. ARMESTO. 1999. An assessment of post-dispersal seed predation in temperate rain forest fragments in Chiloe Island, Chile. *Oikos* 87: 228-238.

*DINGLE, R. V. AND J. ROGERS. 1972. Pleistocene palaeogeography of the Agulhas Bank. Transactions of the Royal Society of South Africa 40: 155-165.

*DINGLE, R. V., W. G. SIESSER AND A. R. NEWTON. 1983. Mesozoic and Tertiary Geology of Southern Africa. Balkema, Rotterdam, The Netherlands.

DUARAH, D. K. 1995. A Handbook of Arunachal Pradesh. M/s Frontier Publisher and Distributors.

ELWIN, V. 1959. A Philosophy for NEFA. Shillong, India, 310 pp.

ELWIN, V. 1999. Myths of the North-east Frontier of India. Reprint. 448 pp.

F.S.I. 1995. State of the Forest Report, India, 1995. Forest Survey of India, Dehradun.

F.S.I. 1997. State of the Forest Report, India, 1997. Forest Survey of India, Dehradun.

F.S.I. 1999. State of the Forest Report, India, 1999. Forest Survey of India, Dehradun.

*FIGUEROA, J., J.J., ARMESTO, AND J. F. HERNANDEZ. 1996. Estrategias de germinacion y latencia de semillas en especies del bosque templado de Chiloe. *Rev. Chil. Hist. Nat.* 69: 243-251.

FLEMING, T. H. AND B. L. PARTRIDGE. 1984. On the analysis of phenological overlap. *Oecologia* (Berlin) 62: 344-350.

FLEMING, T. H. 1991. Fruiting plant-frugivore mutualism: The Evolutionary Theatre and the Ecological Play. *In* P. W. Price, T. M. Lewinsohn, G. W. Fernandes and W. W. Benson (Eds.), Plant-Animal Interactions: Evolutionary ecology in Tropical and Temperate Regions, pp. 119-143. John Wiley & Sons, Inc.

FORGET, P-M. 1990. Seed dispersal of *Vouacapoua americana* (Caesalpiniaceae) by cavimorph rodents in French Guiana. *J. Trop. Ecol.* 6: 459-468.

FORGET, P-M. 1993. Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia* (Berlin): 94: 255-261.

FORGET, P-M. 1996. Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. *J. Trop. Ecol.* 12: 751-761.

FORGET, P-M., E. MUNOZ, AND E. G. LEIGH. 1994. Predation by rodents and bruchid beetles on seeds of *Scheelea* palms on Barro Colorado Island, Panama. *Biotropica* 26(4): 420-426.

FORGET, P-M. AND T. MILLERON. 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oeclogia* (Berlin) 87: 596-599.

FORGET, P-M., T. MILLERON, AND F. FEER. 1998. Patterns of post-dispersal seed removal by Neotropical rodents and seed fate in relation to seed size. *In* D.M. Newberry, H.H.T. Prins and N. Brown (Eds.), Dynamics of Tropical communities, pp. 25-49. 37th Symposium of the British Ecological Society, Blackwell Science, Oxford. 635 pp.

FORGET, P-M., K. KITAJIMA, AND R. B. FOSTER. 1999. Pre- and post-dispersal seed predation in *Tachigali versicolor* (Caesalpiniaceae): effects of timing of fruiting and variation among trees. *J. Trop. Ecol.* 15: 61-81.

FOSTER, R. B. 1982a. The seasonal rhythm of fruitfall on Barro Colorado Island. *In* E. G. Leigh, A. S. Rand, D. M. Windsor (Eds.), The ecology of a Neotropical forest: seasonal rhythms and long-term changes, pp.151-172. Smithsonian Institution Press, Washington D.C. 469 pp.

FOSTER, R. B. 1982b. Famine on Barro Colorado Island..*In* E. G. Leigh, A. S. Rand, D. M. Windsor (Eds.), The ecology of a Neotropical forest: seasonal rhythms and long-term changes, pp. 201-212. Smithsonian Institution Press, Washington D.C. 469 pp.

*FOURNIER, L. AND C. CHARPANTIER. 1975. El tamaño de la muestra y la frecuencia de las observaciones en el estudio de características fenológicas de los árboles tropicales. *Turrialba* 25: 45-48.

FRANKIE, G. W., H. G. BAKER, AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62: 1049-1057.

FRENCH, A. R., A. LAMPERTI, E. S. DIERENFIELD AND T. B. SMITH. 2001. Nutrient analysis of fleshy fruits in the diet of African *Ceratogymna* hornbills. Paper presented at the Third International Hornbill Workshop, Phuket, Thailand, 9-12 May, 2001.

FÜRER-HAIMENDORF, C. VON. 1962. The Apa Tanis and their neighbours, a primitive society of the Eastern Himalayas. RKP. 166 pp.

FÜRER-HAIMENDORF, C. VON. 1982. Highlanders of Arunachal Pradesh. Delhi 1982.

FÜRER-HAIMENDORF, C. VON. 1983. Himalayan adventure, early travels in North-east India. Sterling Publishers, New Delhi. 243 pp.

GAMBLE, J. S. 1985. A Manual of Indian timbers. International Book Distributors, 2nd edition, Reprint 1985, 868 pp.

GANESH, T. AND P. DAVIDAR. 1999. Fruit biomass and relative abundance of frugivores in a rain forest of southern Western Ghats, India. *J. Trop. Ecol.* 15: 399-413.

GANESH, T. AND P. DAVIDAR. 2001. Dispersal modes of tree species in the wet forests of southern Western Ghats. *Current Science* 80(3): 394-399.

GAUTIER-HION, A. 1990. Interactions among fruit and vertebrate fruit-eaters in an African tropical rain forest. *In* K. S. Bawa and M. Hadley (Eds.), Reproductive ecology of tropical forest plants, pp. 219-230. Man and the Biosphere Series (Vol. 7). UNESCO, Paris and The Parthenon Publishing Group. 421 pp.

GAUTIER-HION, A. AND G. MICHALOUD. 1989. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology* 70: 1826-1833.

GAUTIER-HION, A., J.-M. DUPLANTIER, R. QURIS, F. FEER, C. SOURD, J.-P. DECOUX, G. DUBOST, L. EMMONS, C. ERARD, P. HECKETSWEILER, A. MOUNGAZI, C. ROUSSILHON, AND J.-M. THIOLLAY. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* (Berlin) 65: 324-337.

GILBERT, L. E. 1980.Food web organization and the conservation of neotropical diversity. *In* M. E. Soule and B. A. Wilcox (Eds.), Conservation Biology: the science of scarcity and diversity, pp. 11-33. Sinauer Associates, Inc., Sunderland, Massachusetts. 584 pp.

GLEASON, S. K. 1981 Character displacement in flowering phenologies. *Oecologia* (Berlin) 51: 294-295.

GOLDING, R. R. AND M. G. WILLIAMS. 1986. Breeding the Great Indian hornbill *Buceros bicornis* at the Cotswold Wild Life Park. *Int. Zoo Yr. Bk.* 24/25: 248-252.

GONZALEZ, L. A., R. MURUA, AND C. JOFRE. 1989. The effect of seed availability on population density of *Oryzomys* in southern Chile. *J. Mamm.* 70: 401-405.

GOTELLI, N. J. AND G. L. ENTSMINGER. 2000. ECOSIM: Null models software for ecology. Version 6.14 Acquired Intelligence Inc. & Kesey-Bear. Burlington, VT 05465

GOVERNMENT OF ARUNACHAL PRADESH. 1998. Arunachal Pradesh at a glance. Directorate of Economics and Statistics, Arunachal Govt. Press, Itanagar.

GRAHAM, C .H., T. C. MOERMOND, K. A. KRISTENSEN, AND J. MVUKIYUMWAMI. 1995. Seed dispersal effectiveness by two bulbuls on *Maesa lanceolata*, an African Montane forest tree. *Biotropica* 27(4): 479-486.

GRIERSON, A. J. C. AND D. G. LONG. 1984. Flora of Bhutan, including a record of plants from Sikkim. Vol. 1 - Vol. 3. Royal Botanic Gardens, Edinburgh. 834 pp.

HADIPRAKARSA, Y. AND M. F. KINNAIRD. 2001. Foraging characteristics of an assemblage of four Sumatran hornbill species. Paper presented at the Third International Hornbill Symposium and Workshop, 9-12 May, Phuket, Thailand.

HEINRICH, B. 1988. Winter foraging at carcasses by three sympatric corvids with emphasis on recruitment by the raven, *Corvus corax*. *Behav. Ecol. Sociobiol.* 23: 141-156.

HEINRICH, B. AND J. M. MARZLUFF. 1991. Common ravens yell because they want to attract others? *Behav. Ecol. Sociobiol.* 28: 13-21.

HEITHAUS, E. R., T. H. FLEMING AND P. A. OPLER. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology* 56: 841-854.

HERRERA, C. M. 1981. Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos* 36: 51-58.

HERRERA, C. M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* 63: 773-785.

HERRERA, C. M. 1985. Determinants of plant-animal coevolution: the case of mutualistic vertebrate seed dispersal systems. *Oikos* 44: 132-141.

HILTY, S. L. 1980. Flowering and fruiting periodicity in a premontane forest in Pacific Columbia. *Biotropica* 12(4): 292-306.

HO, H. C. AND S. SUTARI. 1997. Spectacular movements of hornbills, possibly plain-pouched hornbills *Aceros subruficollis*, in Peninsular Malaysia. *Oriental Bird Club Bull.* 25: 59-61.

HO, H. C. AND S. SUTARI. 2000. Observations of Plain-pouched hornbills *Aceros subruficollis* in Tasek Temengor, Peninsular Malaysia. *Forktail* 16: 65-67.

HOLBROOK, K. M. AND T. B. SMITH. 2000. Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia* (Berlin) 125: 249-257.

*HORN, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's blackbird (*Euphagus cyanocephalus*). *Ecology* 49: 682-694.

HOWE, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58: 539-550.

HOWE, H. F. 1980. Monkey dispersal and waste of a Neotropical fruit. *Ecology* 61(4): 945-959.

HOWE, H. F. 1981. Dispersal of a neotropical nutmeg (*Virola sebifera*) by birds. *Auk* 98: 88-98.

HOWE, H.F. 1984a. Implications of seed dispersal by animals for the management of tropical reserves. *Biol. Conserv.* 30: 261-281.

HOWE, H.F. 1984b. Constraints on the evolution of mutualisms. *Am. Nat.* 123: 764-777.

HOWE, H. F. 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* (Berlin) 79: 417-426.

HOWE, H. F. 1990. Seed dispersal by birds and mammals: implications for seedling demography. *In* K. S. Bawa and M. Hadley (Eds.), Reproductive ecology of tropical forest plants, pp. 191-218. Man and Biosphere Series, (Vol. 7). UNESCO, Paris and the Parthenon Publishing Group. 421 pp.

HOWE, H. F. 1993. Aspects of variation in a Neotropical seed dispersal system. *Vegetatio* 107/108: 149-162.

HOWE, H. F. AND D. DE STEVEN. 1979. Fruit production, migrant bird visitation, and seed dispersal of *Guarea glabra* in Panama. *Oecologia* (Berlin) 39: 185-196.

HOWE, H. F. AND G. A. VANDE KERCKHOVE. 1979. Fecundity and seed dispersal of a tropical tree. *Ecology* 60: 180-189.

HOWE, H.F. AND G. A. VANDE KERCKHOVE. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology* 62: 1093-1106.

HOWE, H. F. AND L.C. WESTLEY. 1988. Ecological relationships of plants and animals. Oxford Univ. Press, New York, Oxford. 273 pp.

HOWE, H. F., E. W. SCHUPP, AND L. C. WESTLEY. 1985. Early consequences of seed dispersal for a Neotropical tree (*Virola surinamensis*). *Ecology* 66(3): 781-791.

HOWE H. F. AND J. SMALLWOOD. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201-228.

HUBBELL S. P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. *Science* 203: 1299-1309.

HUBBELL, S. P. AND R.B. FOSTER. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. *In* S.L. Sutton, T.C. Whitmore and A.C. Chadwick (Eds.), Tropical rain forest: Ecology and Management, pp. 25-42. Blackwell Science Publications, Oxford. 498 pp.

HURLBERT, S. H. 1978. The measurement of niche overlap and some relatives. *Ecology* 59: 67-77.

HUSSAIN S. A. 1984. Some aspects of the biology and ecology of Narcondam Hornbill (*Rhyticeros narcondami*). *J. Bombay nat. Hist. Soc.* 81(1): 1-18.

HUTCHINS, M. 1976. Breeding biology and behaviour of the Indian pied hornbill *Anthracoceros m.* malabarcus. *Int. Zoo Yr. Bk.* 16: 99-104.

IUCN. 1990. 1990 IUCN Red List of Threatened Animals. IUCN, Gland, Switzerland & Cambridge, UK. 192 pp.

IZHAKI, I. AND U. N. SAFRIEL. 1990. The effect of some Mediterranean scrubland frugivores upon germination patterns. *J. Ecol.* 78: 56-65.

IZHAKI I., C. KORINE, AND Z. ARAD. 1995. The effect of bat (*Rousettus aegypticus*) dispersal on seed germination in eastern Mediterranean habitats. *Oecologia* (Berlin) 101: 335-342.

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

JANSON, C. H. 1983. Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science* 219: 187-189.

JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* 23: 620-637.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104: 501-528.

JANZEN, D. H. 1971. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2: 465-492

JANZEN, D. H. 1983. Dispersal of seeds by vertebrate guts. *In* D. J. Futuyama and M. Slatkin (Eds.), Coevolution, pp. 232-262. Sinauer, Sunderland, Massachusetts. 555 pp.

JANZEN, D. H. 1986. Mice, big mammals, and seeds: It matters who defecates what where. *In* A. Estrada and T.H. Fleming (Eds.), Frugivores and Seed Dispersal, pp. 251-271. Dordrecht: W.Junk.

JANZEN, D. H. AND P. S. MARTIN. 1982. Neotropical anachronisms: the fruit the gomphotheres ate. *Science* 215: 19-27.

JARMAN, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48: 215-267.

JOHNS, A.D. 1987. The use of primary and selectively logged rainforest by Malaysian hornbills (Bucerotidae) and implications for their conservation. *Biol. Conserv.* 40: 179-190.

JOHNS, A. D. 1989. Recovery of a Peninsular Malaysian rainforest avifauna following selective timber logging: the first twelve years. *Forktail* 4: 89-106.

JORDANO, P. 1983. Fig seed predation and dispersal by birds. *Biotropica* 15(1): 38-41.

JORDANO, P. 1995. Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *Am. Nat.* 145: 163-191.

JUHAENI, D. 1993. Little known bird. Sumba Hornbill *Aceros everetti*. *Oriental Bird Club Bulletin* 18: 19-20.

JUSTINIANO, M. J. AND T. S. FREDERICKSEN. 2000. Phenology of tree species in Bolivian Dry forests. *Biotropica* 32(2): 276-281.

KALINA, J. 1988. Nest intruders, nest defence and foraging behaviour in the Black-and-white Casqued Hornbill *Bycanistes subcylindricus*. *Ibis* 131:567-571.

KANJILAL, U. N., P. C. KANJILAL AND A. DAS. 1934. Flora of Assam, Vol. I to IV. A Von Book Company. Reprinted in 1982. 1750 pp.

KANNAN, R. 1994. Ecology and conservation of the Great pied hornbill (Buceros bicornis) in the Western Ghats of Southern India. Unpublished Ph.D. Dissertation, University of Arkansas, Fayetteville. 157 pp.

KANNAN, R. AND D. A. JAMES. 1997. Breeding biology of the Great Pied Hornbill (*Buceros bicornis*) in the Anaimalai Hills of southern India. *J. Bombay nat. Hist. Soc.* 86(3):448-449.

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.

KAUL, R. AND A. AHMED. 1993. Pheasant surveys in Arunachal Pradesh, India. *In* D. Jenkins (Ed.), Pheasants in Asia 1992, pp. 50-54. World Pheasant Association, Reading.

KAUL, R. AND K. HARIDASAN. 1987. Forest types of Arunachal Pradesh – a preliminary study. *J. Econ. Tax. Bot.* 9: 379-389.

KATTI, M. V., N. MANJREKAR, S. MUKHERJEE AND D. SHARMA. 1990. Wildlife survey in Arunachal Pradesh with special reference to takin. Unpublished report, Wildlife Institute of India, Dehradun.

KATTI, M. V., SINGH, P., MANJREKAR, N., MUKHERJEE, S. AND SHARMA, D. 1992. An ornithological survey in eastern Arunachal Pradesh, India. *Forktail* 7: 75-89.

KEMP, A. C. 1970. Some observations on the sealed-in nesting method of hornbills (Family: Bucerotidae). *Ostrich* (Suppl.) 8: 149-155.

KEMP, A. C. 1976a. Factors affecting the onset of breeding in African hornbills. *In* Proceedings of the 16th International Ornithological Congress, pp. 248-257. August 1974. Australian Academy of Science, Canberra, August, 1976.

KEMP, A. C. 1976b. A study of the ecology, behaviour and systematics of *Tockus* hornbills (Aves: Bucerotidae). Pretoria: Transvaal Museum. 125 pp.

KEMP, A. C. 1979. A review of the hornbills: biology and radiation. *Living Bird* 17: 105-36.

KEMP, A. C. 1988a. The behavioural ecology of the Southern Ground Hornbill: are competitive offspring at a premium? *In* Proc. Int. 100. DO-G Meeting, Current Topics Avian Biol. pp. 267-271. Bonn, 1988.

KEMP, A.C. 1988b. The systematics and zoogeography of Oriental and Australasian hornbills (Aves: Bucerotidae). *Bonner Zoologische Beiträge*: 39: 315-45.

KEMP, A. C. 1995. The Hornbills. Oxford University Press. Oxford, U.K. 302 pp.

KEMP, A. C. AND M. I. KEMP. 1972. A study of the biology of the Monteiro's Hornbill. *Annals of the Transvaal Museum* 27(13): 255-268.

KEMP, A. C. AND M. I. KEMP. 1974. Report on a study of hornbills in Sarawak, with comments on their conservation. World Wildlife Fund Project Report 2/74. Unpublished manuscript.

KEMP, A. C. AND M. I. KEMP. 1980. The biology of the Southern Ground Hornbill *Bucorvus leadbateri* (Vigors) (Aves: Bucerotidae). *Annals of the Transvaal Museum* 32(4): 65-100.

KEMP, A. C. AND T. M. CROWE. 1985. The systematics and zoogeography of Afrotropical hornbills (Aves: Bucerotidae). *In* K. L. Schuchmann (Ed.), Proc. International Symposium African Vertebrates, pp. 279-324. Bonn, 1985.

KINNAIRD, M. F. 1992. Phenology of flowering and fruiting of an East African riverine forest ecosystem. *Biotropica* 24(2a): 187-194.

KINNAIRD, M. F. 1998. Evidence for effective seed dispersal by the Sulawesi Red-knobbed hornbill *Aceros cassidix*. *Biotropica* 30 (1): 50-55.

KINNAIRD, M. F. AND T. G. O'BRIEN. 1993. Preliminary observation on the breeding biology of the endemic Sulawesi Red-knobbed Hornbill (*Rhyticeros cassidix*). *Tropical Biodiversity* 1(2): 107-112.

KINNAIRD, M. F. AND T. G. O'BRIEN. 1999. Breeding ecology of the Sulawesi Red-knobbed Hornbill *Aceros cassidix*. *Ibis* 141: 60-69.

KINNAIRD, M. F., T. G. O'BRIEN, AND S. SURYADI. 1996. Population fluctuation in Sulawesi Red-knobbed hornbills: tracking figs in space and time. *Auk* 113(2): 431-440.

KITAMURA, S. 2000. Seed dispersal by hornbills in a tropical rain forest in Khao Yai National Park, Thailand. M.Sc. thesis, Kyoto University, Japan. 185 pp.

KREBS, C. J. 1989. Ecological Methodology. Harper & Row Publishers, New York. 654 pp.

KREBS, J. R. AND N. B. DAVIES, EDITORS. 1991. Behavioural Ecology: an evolutionary approach. Blackwell Science Publications, Oxford. 512 pp.

KRIJGER, C. L., M. OPDAM, M. THERY, AND F. BONGERS. 1997. Courtship behaviour of manakins and seed bank composition in a French Guianan rain forest. *J. Trop. Ecol.* 13: 631-636.

KUMAR, R. S. AND P. SINGH. 1999. A study on pheasant distributions in Arunachal Pradesh, Eastern Himalayas, India. Unpublished report, Wildlife Institute of India, 52 pp.

LACEY, E. P. 1980. The influence of hygroscopic movement on seed dispersal in *Daucus carota* (Apiaceae). *Oecologia* (Berlin) 47: 100-114.

LACK, D. 1968. Ecological adaptations for breeding in birds. Chapman & Hall, London.

LAMAN, T.G. 2001. Hornbills of Gunung Palung National Park, Borneo, Indonesia: Observations on habitat use, reproduction and conservation issues. Paper presented at the Third International Hornbill Workshop, Phuket, Thailand, 9-12 May, 2001.

LAMBERT, F. 1989a. Fig-eating by birds in a Malaysian lowland rain forest. *J. Trop. Ecol.* 5: 401-412.

LAMBERT, F. 1989b. Pigeons as seed predators and dispersers of figs in a Malaysian lowland rain forest. *Ibis* 131: 521-527.

LAMBERT, F. AND A. G. MARSHALL. 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *J. Ecol.* 79: 793-809.

*LAZARUS, J. 1979. Flock size and behaviour in captive red-billed weaver birds (*Quelea quelea*): Implications for social facilitation and the functions of flocking. *Behaviour* 71:127-145.

LEIGH, E. G. AND D.S. WINDSOR. 1982. Forest production and regulation of primary consumers on Barro Colorado Island. *In* E. G. Leigh, A. S. Rand and D. S. Windsor (Eds.), The ecology of a Neotropical forest: seasonal rhythms and long-term changes, pp. 111-122. Smithsonian Institution Press, Washington, D.C. 469 pp.

LEIGHTON, M. 1982. Fruit resources and patterns of feeding, spacing and grouping among sympatric Bornean hornbills (Bucerotidae). Unpublished Ph.D. thesis. University of California, Davis.

LEIGHTON, M. 1986. Hornbill social dispersion: variations on a monogamous theme. *In* D. I. Rubenstein and R. W. Wrangham (Eds.), Ecological aspects of social evolution, pp. 108-130. Princeton University Press. 551 pp.

LEIGHTON, M. AND D. R. LEIGHTON. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. *In* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (Eds.), Tropical Rain Forest: Ecology and Management, pp. 181-196. Blackwell Science Publications, Oxford. 498 pp.

LEVEY, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* 129: 471-485.

LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecol. Monogr.* 58(4): 251-266.

LEVINS, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, N.J.

LIEBERMAN, D. 1982. Seasonality and phenology in a dry forest in Ghana. *J. Ecol.* 70: 791-806.

LOMAN, J. AND S. TAMM. 1980. Do roosts serve as "information centres" for crows and ravens? *Am. Nat.* 115(2): 285-305.

LUDWIG, J. A. AND J. F. REYNOLDS. 1988. Statistical ecology. John Wiley & Sons, New York. 337 pp.

MACARTHUR, R. H. AND LEVINS, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101: 377-385.

MADGE, S. G. 1969. Notes on the breeding of the bushy-crested hornbill. *Malay Nat. J.* 23: 1-6.

MADHUSUDAN, M.D. AND A. J. T. JOHNSINGH.1998. Analysis of habitat-use using ordination: The Nilgiri tahr in southern India. *Current Science* 74(11): 1000-1003.

MAGURRAN, A. E. 1988. Ecological diversity and its measurement. Croom Helm, London. 179 pp.

MALO, J. E. AND F. SUAREZ. 1995. Herbivorous mammals as seed dispersers in a Mediterranean *dehesa*. *Oecologia* (Berlin) 104: 246-255.

MANI, M. S., EDITOR. 1974. Ecology and Biogeography of India. Dr. W. Junk Publishers, The Hague. 773 pp.

MANLY, B. F. J. 1994. Multivariate Statistical Methods: A Primer. 2nd Edition. Chapman and Hall, London. 215 pp.

MARDIASTUTI, A., Y. A. MULYANI, D. RINALDI, AND PURYANTO. 1996. Nest site characteristics of Wreathed hornbill *Aceros undulatus* in Meru Betiri National Park, East Java, Indonesia. Paper presented at the Second International Asian Hornbill Workshop, Bangkok, Thailand, April 1996.

MARSDEN, S. J. AND M. J. JONES. 1997. The nesting requirements of the parrots and hornbill of Sumba, Indonesia. *Biol. Conserv.* 82:279-287.

MARTINEZ DEL RIO, C. AND RESTREPO, C. 1992. Ecological and behavioural consequences of digestion in frugivorous animals. *Vegetatio* 107/108: 205-216.

MCCONKEY, K. AND M. GALETTI. 1999. Seed dispersal by sun bear *Helarctos malayanus* in central Borneo. *J. Trop. Ecol.* 15: 237-241.

MCKEY, D. 1975. The ecology of coevolved seed dispersal systems. *In* L. E. Gilbert and P. H. Raven (Eds.), Coevolution of Animals and Plants, pp. 159-191. Austin, Tx: Univ. Tex. Press. 263 pp.

MEDELLIN, R. A. 1994. Seed dispersal of *Cecropia obtusifolia* by two species of oppossums in the Selva Lacandona, Chiapas, Mexico. *Biotropica* 26(4): 400-407.

MEDWAY, L. 1972. Phenology of a tropical rainforest in Malaya. *Biol. J. Linn. Soc.* 4:117-46.

*MESERVE, P.L., B. K. LANG, R. MURUA, A. MUNOZ-PEDEROS, AND L. GONZALEZ. 1991. Terrestrial small mammal characteristics in a primary growth Chilean temperate rainforest. *Rev. Chil. Hist. Nat.* 64: 157-169.

*MILLER, K. G. AND R. G. FAIRBANKS. 1985. Caenozoic record of climate and sea level. *South African Journal of Science* 81: 248-249.

MITTERMEIER, R. A., N. MYERS, J. B. THOMSEN, G. A. B. DA FONSECA, AND S. OLIVIERI. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Cons. Biol.* 12: 516-520.

MOREAU, R. E. 1966. The bird faunas of Africa and its islands. Academic Press, London.

MORRISON, D. W. AND D. F. CACCAMISE. 1985. Ephemeral roosts and stable patches? A radio-telemetry study of communally roosting starlings. *Auk* 102: 793-804.

MORRISON, D. W. AND D. F. CACCAMISE. 1990. Comparison of roost use by three species of communal roostmates. *Condor* 92: 405-412.

MORSE, D. H. 1970. Ecological aspects of some mixed species foraging flocks of birds. *Ecol. Monogr.* 40: 119-68.

*MOYNIHAN, M. H. 1962. The organization and probable evolution of some mixed species flocks on Neotropical birds. *Smithson. Misc. Coll.* 143(7).

MUDAPPA, D. 2000. Breeding biology of the Malabar Grey Hornbill (*Ocyceros griseus*) in southern Western Ghats. *J. Bombay nat. Hist. Soc.* 97(1): 15-24.

MUDAPPA, D. 2001. Ecology of the Brown palm civet (*Paradoxurus jerdoni*) in the tropical rainforests of the Western Ghats, India. Ph.D. thesis submitted to Bharathiar University, Coimbatore. 162 pp.

MUDAPPA, D. AND R. KANNAN. 1997. Nest-site characteristics and nesting success of the Malabar Gray Hornbill in the Southern Western Ghats, India. *Wilson Bull.* 109(1): 102-111.

MURALI, K.S. AND R. SUKUMAR. 1994. Reproductive phenology of a dry tropical forest in Mudumalai, southern India. *J. Ecol.* 82: 759-767.

*MURUA, R. AND L. GONZALEZ. 1986. Regulation of numbers in two rodent species. *Rev. Chil. Hist. Nat.* 59: 193-200.

MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. DA FONSECA, AND J. KENT. 2000. Biodiversity hotpots for conservation priorities. *Nature* 403: 853-858.

NANDA, A. R. 1992. Census of India 1991, Final Population totals, Paper 1 of 1992 (Vol.1), Ministry of Home Affairs, Govt. of India.

NAKANISHI, H. 1996. Fruit color and fruit size of bird-disseminated plants in Japan. *Vegetatio* 123: 207-218.

NEU, W.C., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38: 541-545.

NORTH, M. E. W. 1942. The nesting of some Kenya colony hornbills. *Ibis* (14)6: 499-508.

NORUSIS, M. J. 1990. SPSS/PC+ Advanced Statistics 4.0. SPSS Inc., Chicago. 481 pp.

NOTMAN, E., D. L. GORCHOV, AND F. CORNEJO. 1996. Effect of distance, aggregation, and habitat on levels of seed predation for two mammal-dispersed Neotropical rain forest tree species. *Oecologia* (Berlin): 106: 221-227.

O'BRIEN, T.G. 1997. Behavioural ecology of the North Sulawesi Tarictic Hornbill *Penelopides exarhatus exarhatus* during the breeding season. *Ibis* 139: 97-101.

O'BRIEN, T. G., M. F. KINNAIRD, E. S. DIERENDFELD, N. L. CONKLIN, R. W. WRANGHAM, AND S. C. SILVER. 1998b. What's so special about figs? *Nature* 392: 668.

O'BRIEN, T. G., KINNAIRD, M. F., JEPSON, P. & SETIWAN, I. 1998. Effect of forest size and structure on the distribution of Sumba Wreathed Hornbills *Aceros everetti*. *In* P. Poonswad (Ed.), The Asian Hornbills: ecology and conservation, pp. 209-218. Thai studies in Biodiversity No. 2, Biodiversity Research and Training Program, Bangkok.

OLSON, S. L. 1985. The fossil record of birds. *In* D. S. Farner, J. R. King, and K. C. Parkes (Eds.), Avian Biology, Vol. 8, pp. 136-138. Academic Press, London.

OLSON, D. M. AND E. DINERSTEIN. 1998. The global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. *Cons. Biol.* 12: 502-515.

OPLER, P. A., G. W. FRANKIE, AND H. G. BAKER. 1980. Comparative phonological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 68: 167-188.

OSTFELD, R. S., C. G. JONES, AND J. O. WOLFF. 1996. Of mice and mast. *BioScience* 46: 232-329.

PACKER, A. AND K. CLAY. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404: 278-281.

PADMAWATHE, R. 2001. Patterns in species composition and distribution of vascular epiphytes in low-lying semi-evergreen forests of Arunachal Pradesh, India. M. Sc. Dissertation submitted to Saurashtra University, Rajkot, Gujarat.

PAWAR, S. AND A. BIRAND 2001. A survey of amphibians, reptiles and birds in Northeast India. CERC Technical Report #6, Centre for Ecological Research and Conservation, Mysore.

PERES, C. A. 2000. Identifying keystone plant resources in tropical forests: the case of gums from *Parkia* pods. *J. Trop. Ecol.* 16(2): 287-317.

PIANKA, E. R. 1973. The structure of lizard communities. *Ann. Rev. Ecol. Syst.* 4: 53-74.

PIELOU, E. C. 1984. Interpretation of Ecological Data: A primer on Classification and Ordination. John Wiley, New York. 263 pp.

PLEASANTS, J. M. 1980. Competition for bumblebee pollinators in Rocky Mountain plant communities. *Ecology* 61(6): 1446-1459.

PLEASANTS, J. M. 1990. Null-model tests for competitive displacement: the fallacy of not focussing on the whole community. *Ecology* 71(3): 1078-1084.

POOLE, R. W. AND B. J. RATHCKE. 1979. Regularity, randomness, and aggregation in flowering phonologies. *Science* 203: 470-471.

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

POONSWAD, P. AND A. C. KEMP. 1993. Manual to the Conservation of Asian Hornbills. Hornbill Project, Thailand, Faculty of Science, Mahidol University, Bangkok. 511pp.

POONSWAD, P. AND A. TSUJI. 1994. Ranges of males of the Great hornbill *Buceros bicornis*, Brown Hornbill *Ptilolaemus tickelli* and Wreathed hornbill *Rhyticeros undulatus* in Khao Yai National Park, Thailand. *Ibis* 136: 79-86.

POONSWAD, P., A. TSUJI, AND C. NGARMPONSAI. 1983. A study of the breeding biology of hornbills (Bucerotidae) in Thailand. *Proceedings of the Jean Delacour/ICFB Symposium on Breeding Birds in Captivity.* February 24-27, 1983, Los Angeles, California, USA.

POONSWAD, P., A. TSUJI, AND C. NGARMPONGSAI. 1986. A comparative ecological study of four sympatric hornbills (Family Bucerotidae) in Thailand. *In* H. Ouellet (Ed.), Acta XIX

Congressus Internationalis Ornithologici, pp. 2781-2791. Ottawa, Canada, 22-29 June, 1986. University of Ottawa Press.

POONSWAD, P., A. TSUJI, AND C. NGAMPONGSAI. 1987. A comparative study on breeding biology of four sympatric hornbill species (Family Bucerotidae) in Thailand with implications for breeding in captivity. Proceedings of the Jean Delacour/IFCB Symposium on Breeding Birds in Captivity: 250-315. February 11-15, 1987, North Hollywood, California, USA: International Foundation for the Conservation of Birds.

POONSWAD, P., A. TSUJI, R. LIEWVIRIYAKIT, AND N. JIRAWATKAVI. 1988. Effects of external factors on hornbill breeding and population. Proceedings of the 5th World Conference on Breeding Endangered Species in Captivity. October 9-12, 1988, Cincinnati, Ohio.

POONSWAD, P., A. TSUJI, N. JIRAWATKAVI, AND V. CHIMCHOME. 1998. Some aspects of the food and feeding ecology of sympatric hornbills in Khao Yai national Park, Thailand. In P. Poonswad (Ed.), The Asian hornbills: Ecology and conservation, pp. 137-157. Thai Studies in Biodiversity No. 2., Biodiversity Research and Training Program, Bangkok, 325 pp.

POONSWAD, P., A. TSUJI AND N. JIRAWATKAVI. 2001. The nutrition of hornbills during the breeding season in Khao Yai National Park, Thailand. Paper presented at the Third International Hornbill Workshop, Phuket, Thailand, 9-12 May 2001.

POULIN, B., S. J. WRIGHT, G. LEFEBVRE, AND O. CALDERON. 1999. Interspecific synchrony and asynchrony in the fruiting phenologies of bird-dispersed plants in Panama. *J. Trop Ecol.* 15: 213-227.

POULSEN, J., C. J. CLARK, E. F. CONNER, AND T. B. SMITH. *in press*. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology.*

PRASAD, S.N. AND M. HEGDE. 1986. Phenology and seasonality in the tropical deciduous forest of Bandipur, South India. *Proc. Indian Acad. Sci. (*Plant Sciences). 96: 121-123.

*PUTZ, F. E. 1979. Aseasonality in Malaysian tree phenology. Malay. For. 42: 1-24.

RABENOLD, P. P. 1986. Family associations in communally roosting Black vultures. *Auk* 103: 32-41.

RABENOLD, P. P. 1987. Recruitment to food in Black vultures: evidence for following from communal roosts*. Anim. Behav.* 35: 1775-1785.

RAMAN, T. R. S. 2001. Effect of Slash-and-Burn Shifting cultivation on rainforest birds in Mizoram, Northeast India. *Cons. Biol.* 15(3): 685-698.

RAMAN, T. R. S., G. S. RAWAT, AND A. J. T. JOHNSINGH. 1998. Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *J. Appl. Ecol.* 35: 214-231.

RAMAN, T. R. S. AND MUDAPPA, D. 2001. Correlates of hornbill distribution and abundance in rainforest fragments in the Southern Western Ghats, India. Paper presented at the Third International Hornbill Workshop, 9-12 May, Phuket, Thailand.

RAO, R. AND P. K. HAJRA. 1986. Floristic diversity of the eastern Himalaya: in a conservation perspective. *Proc. Indian Acad. Sci. (*Animal Sciences/Plant Sciences) Supplement November: 103-125.

RASMUSSEN, P. C. 2000. A review of the taxonomy and status of the Plain-pouched Hornbill *Aceros subruficollis*. *Forktail* 16: 83-91.

RATHCKE, B. AND E. P. LACEY. 1985. Phenological patterns of terrestrial plants*. Ann. Rev. Ecol. Syst.* 16: 179-214.

REDDY, M. S. 1988. Some aspects of tecology and behaviour of hornbills with special reference to *Anthracoceros coronatus* (Boddaert) from North Kanara District of Western Ghats. Unpublished Ph.D. Thesis, Karanatak University, Dharwad.

REDDY, M. S. AND S. BASALINGAPPA. 1995. The Food of Malabar Pied Hornbill. *Journal of Ecological Society* 8: 23-28.

REDDY, M. S., K. S. MURALIDHAR, M. GANDHI, AND S. BASALINGAPPA. 1990. Distribution and variation in number of Malabar Pied hornbills *Anthracoceros coronatus* (Boddaert) in selected areas of North Kanara forest of Western Ghats in Karnataka, India. *The Indian Zoologist* 14: 63-73.

REID, N. 1989. Dispersal of mistletoes by honey eaters and flowerpeckers: components of seed dispersal quality. *Ecology* 70: 137-145.

REILLY, S. E. 1988. Breeding the rhinoceros hornbill *Buceros rhinoceros* at the Audubon Park & Zoological Garden. *Int. Zoo Yr. Bk.* 27: 263- 269.

RIDLEY, H. N.1930. The dispersal of plants throughout the world. L. Reeve & Co., Ashford. 744 pp.

RIPLEY, S. D. AND B. M. BEEHLER. 1990. Patterns of speciation in Indian birds. *J. Biogeogr.*17: 639-648.

RIPLEY, S. D. AND B. M. BEEHLER. 1989. Ornithogeographic affinities of the Andaman and Nicobar Islands. *J. Biogeogr.* 16: 323-332.

RODGERS, W. A. AND H. S. PANWAR. 1988. Planning a protected area network in India. Wildlife Institute of India, Dehradun. 267 pp.

ROSENZWEIG, M. L. 1995. Species diversity in space and time. Cambridge: Cambridge University Press.

SAKAI, S., K. MOMOSE, T. YUMOTO, T. NAGAMITSU, T. NAGAMASU, A. A. HAMID, AND T. NAKASHIZUKA. 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *Am. J. Botany* 86: 1414-1436.

SANCHEZ-CORDERO, V. AND R. MARTINEZ-GALLARDO. 1998. Postdispersal fruit and seed removal by forest-dwelling rodents in a lowland rainforest in Mexico. *J. Trop. Ecol.* 14: 139-151.

*SANFT, K. 1960. Bucerotidae (Aves/Upupae). Das Tierreich 76: 1-176.

SCHUPP, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108: 15-29.

SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185: 27-39.

SEN, P. K. 1978. Working plan of Khellong Forest Division for 10 years. Forest Department of Arunachal Pradesh.

SHUKLA, B. K. 1959. The Daflas of the Subansiri Region. Shillong.

SHUKLA, R. P. AND P. S. RAMAKRISHNAN 1982. Phenology of trees in a sub-tropical humid forest in north-eastern India. *Vegetatio* 49: 103-109.

SIBLEY, C. G. AND J. E. AHLQUIST. 1991. Phylogeny and classification of birds: a study in molecular evolution. Yale University Press, New Haven.

SIEGEL, S. AND CASTELLAN, N. J. JR. 1988. Non-parametric statistics for the behavioural sciences. 2nd edition, McGraw-Hill, New York. 312 pp.

*SIESSER, W. G. AND R.V. DINGLE. 1981. Tertiary sea-level movements around southern Africa. *J. Geology* 89: 523-526.

SINGH, P. 1991. Avian and mammalian evidences in Pakhui Wildlife Sanctuary in East Kameng district, Arunachal Pradesh. *Arunachal Forest News* 9(2): 1-10.

SINGH, P. 1995. Recent bird records from Arunachal Pradesh, India. *Forktail* 10: 65-104.

SINGH, P. 1999. Bird survey in selected localities of Arunachal Pradesh, India. Unpublished report, Wildlife Institute of India, Dehradun.

SMYTHE, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *Am. Nat.* 104: 25-35.

SMYTHIES, B. E. 1986. The birds of Burma (revised edn). Nimrod Press, Liss. 432 pp.

*SNOW, D. W. 1962. The natural history of the oilbird, *Steatornis caripensis*, in Trinidad, WI, Part 2. Population, breeding ecology and food. *Zoologica* 47: 199-221.

SNOW, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. *Oikos* 15: 274-281.

SNOW, D. W. 1981. Tropical frugivorous birds and their food plants: a World Survey. *Biotropica* 13(1): 1-14.

STAPANIAN, M. A. 1982. Evolution of fruiting stratgeies among fleshy-fruited plant species of eastern Kansas. *Ecology* 63: 1422-1431.

STATTERSFIELD, A. J., M. J. CROSBY, A. J. LONG, AND D. C. WEGE. 1998. Endemic bird areas of the world: priorities for biodiversity conservation. Birdlife International, Cambridge, United Kingdom. 846 pp.

STILES, E. W. 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science* 198: 1177-1178.

STILES, E. W. 1979. Reply to Poole and Rathcke. *Science* 203: 471.

STILES, F. G. AND L. ROSSELI. 1993. Consumption of the fruits of the Melastomataceae by birds: how diffuse is coevolution? *Vegetatio* 107/108: 57-73.

*STOTT, K. 1951. A nesting record of hornbills in captivity. *Avicultural Magazine* 57: 113-118.

STRUHSAKER, T. T. 1997. Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Gainesville, Florida.

SUN, C., A. R. IVES, H. J. KRAEUTER AND T. C. MOERMOND. 1997. Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia* (Berlin) 112: 94-103.

SURYADI, S., M. F. KINNAIRD, AND T. G. O'BRIEN. 1998. Home ranges and daily movements of the Sulawesi Red-knobbed hornbill *Aceros cassidix* during the non-breeding season. *In* P. Poonswad (Ed.), The Asian hornbills: ecology and conservation, pp. 159-170. Thai Studies in Biodiversity No. 2. 325 pp.

SURYADI, S., M. F. KINNAIRD, T. G. O'BRIEN, J. SUPRIATNA, AND S. SOMADIKARTA. 1994. Food preference of the Sulawesi Red-knobbed hornbill during the non-breeding season. *Tropical Biodiversity* 2: 377-384.

SURYADI, S., M. F. KINNAIRD, T. G. O'BRIEN, AND J. SUPRIATNA. 1996. Time budget of the Sulawesi Red-knobbed hornbill, *Rhyticeros cassidix*, during the non-breeding season at Tangkoko-Duasaudara Nature Reserve, North Sulawesi. *In* D. J. Kitchener and A. Suyanto (Eds.), Proceedings of the First International Conference on eastern Indonesian-Australian vertebrate fauna, pp. 123-126. Manado, Indonesia, November 22-26, 1994.

TEMPLE, S. A. 1977. Plant-animal mutualism: co-evolution with dodo leads to near extinction of plant. *Science* 203: 1364.

TERBORGH, J. 1983. Five New World Primates: a study in comparative ecology. Princeton Univ. Press, Princeton, New Jersey.

TERBORGH, J. 1986. Keystone plant resources in the tropical rainforest. *In* M. E. Soule (Ed.), Conservation Biology: the science of scarcity and diversity, pp. 330-344. Sinauer Associates, Inc. Sunderland, Massachusetts. 584 pp.

TERBORGH, J. 1990. Seed and fruit dispersal - commentary. *In* K. S. Bawa and M. Hadley (Eds.), Reproductive ecology of Tropical forest plants, pp. 181-190. Man and the Biosphere Series (Vol. 7). UNESCO, Paris and The Parthenon Publishing Group. 421 pp.

TRAVESET, A. AND M. F. WILLSON. 1997. Effect of birds and bears on seed germination of fleshy-fruited plants in temperate rainforests of southeast Alaska. *Oikos* 80: 89-95.

TSUJI, A. 1996. Hornbills – Masters of Tropical Forests. Sarakdee Press, Bangkok, Thailand. 93 pp.

TSUJI, A., P. POONSWAD, AND N. JIRAWATKAVI. 1987. Application of radio-tracking to study ranging patterns of hornnbills (Bucerotidae) in Thailand. Proc. Jean Delacour/IFCB Symp. Breeding birds in Captivity: 316-351. North Hollywood, Calif.: International Foundation for the Conservation of Birds.

TUTIN, C. E. G. AND M. FERNANDEZ. 1993. Relationship between minimum temperature and fruit production in some tropical forest trees in Gabon. *J. Trop. Ecol.* 9: 241-248.

VAN DER PIJL, L. 1972. Principles of Dispersal in Higher Plants. Berlin: Springer. 2nd edition, 162 pp.

VAN SCHAIK, C. P. 1986. Phenological changes in a Sumatran rain forest. *J. Trop. Ecol.* 2: 327-347.

VAN SCHAIK, C. P., J. TERBORGH, AND S. J. WRIGHT. 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Ann. Rev. Ecol. Syst.* 24: 353-377.

VOYSEY, B. C., K. E. MCDONALD, E. M. ROGERS, C. E. G. TUTIN, AND R. J. PARNELL.1999. Gorillas and seed dispersal in the Lope Reserve, Gabon. I: Gorilla acquisition by trees. *J. Trop. Ecol.* 15: 23-38.

VOYSEY, B. C., K. E. MCDONALD, E. M. ROGERS, C. E. G. TUTIN, AND R. J. PARNELL. 1999. Gorillas and seed dispersal in the Lope Reserve, Gabon. II: Survival and growth of seedlings. *J. Trop. Ecol.* 15: 39-60.

WALSH, A. L. AND S. HARRIS. 1996. Foraging habitat preferences of vespertilionid bats in Britain. *J. Appl. Ecol.* 33: 508-518.

WARD, K. 1941. Assam Adventure. London.

WARD, P. AND A. ZAHAVI. 1973. The importance of certain assemblages of birds as 'information-centres' for food-finding. *Ibis* 115: 517-534.

WEATHERHEAD, P. J. 1983. Two principal strategies in avian communal roosts. *Am. Nat.* 121(2): 237-243.

WENNY, D. G. 1999. Two-stage dispersal of *Guarea glabra* and *G. kunthiana* (Meliaceae) in Monteverde, Costa Rica. *J. Trop. Ecol.* 15: 481-496.

WENNY, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3: 51-74.

WENNY, D. G. AND D. J. LEVEY. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proc. Natl. Acad. Sci.* 95: 6204-6207.

WHEELWRIGHT, N. T. 1985a. Competition for dispersers and the timing of flowering and fruiting in a guild of tropical trees. *Oikos* 44: 465-477.

WHEELWRIGHT, N. T. 1985b. Fruit size, gape width and the diets of fruit-eating birds. *Ecology* 66(3): 808-818.

WHEELWRIGHT, N. T. 1991a. Frugivory and seed dispersal: “La Coevolucion ha Muerto –Viva la Coevolucion!” *TREE* 6(10): 312-313.

WHEELWRIGHT, N. T. 1991b. How long do fruit-eating birds stay in the plants where they feed? *Biotropica* 23(1): 29-40.

WHEELWRIGHT, N. T. AND G. ORIANS. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology and constraints on coevolution. *Am. Nat.* 119: 402-413.

WHITE, L. J. T. 1994. Patterns of fruit-fall phenology in the Lope Reserve, Gabon. *J. Trop. Ecol.* 10: 289-312.

WHITMORE, T.C. 1998. An Introduction to tropical rain forests. 2nd edition. Oxford University Press, Oxford. 226 pp.

WHITNEY, K. D. AND T. B. SMITH. 1998. Habitat use and resource tracking by African *Ceratogymna* hornbills: implications for seed dispersal and forest conservation. *Animal Conservation* 1: 107-117.

WHITNEY, K. D., M. K. FOGIEL, A. M. LAMPERTI, K. M. HOLBROOK, D. M. STAUFFER, B. D. HARDESTY, V. T. PARKER AND T. B. SMITH. 1998. Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve Cameroon. *J. Trop. Ecol.* 14: 351-371.

WHITTAKER, R.J. AND S.H. JONES. 1994. The role of frugivorous birds and bats in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *J. Biogeogr.* 21: 245-258.

WIKELSKI, M., M. HAU, J. C. WINGFIELD. 2000. Seasonality of reproduction in a Neotropical rain forest bird. *Ecology* 81(9): 2458-2472.

WITMER, M. 1993. Cooperative breeding by Rufous Hornbills on Mindanao Island, Philippines. *Auk* 110(4): 933-936.

WITMER, M. C. AND A.S. CHEKE. 1991. The dodo and the tambalacoque tree: an obligate mutualism reconsidered. *Oecologia* (Berlin) 61(1): 133-135.

WRIGHT, S. J., C. CARRASCO, O. CALDERÓN AND S. PATON. 1999. The El Niño Southern Oscillation, variable fruit production and famine in a tropical forest. *Ecology* 80: 1632-1647.

YASUDA, M., S. MIURA AND N. A. HUSSEIN. 2000. Evidence for food hoarding behaviour in terrestrial rodents in Pasoh Forest Reserve, a Malaysian lowland rainforest. *J. Tropical Forest Science* 12(1): 164-173.

ZAHAVI, A. 1971a. The function of pre-roost gatherings and communal roosts. *Ibis* 113: 106-109.

ZAHAVI, A. 1971b. The social behaviour of the White Wagtail *Motacilla alba alba* wintering in Israel. *Ibis* 113: 203-211.

ZAR, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Engelwood Cliffs, N.J., USA. 718 pp.

* Not seen in original

APPENDIX 1. Study species in Arunachal Pradesh

Three sympatric hornbill species, the Great hornbill (*Buceros bicornis*), Wreathed hornbill (*Aceros undulatus*) and the Oriental Pied hornbill (*Anthracoceros albirostris*) were the focus of this study in western Arunachal Pradesh. Anecdotal information on the other two species, the Rufous-necked hornbill (*Aceros nipalensis*) and the Brown hornbill (*Anorrhinus austeni*) was also collected.

1. Austen's Brown hornbill or Brown hornbill (*Anorrhinus austeni*) (also known as the White-throated brown hornbill, formerly *Ptilolaemus tickelli*)

Distribution: Range countries – India, Myanmar, Thailand, Laos, Vietnam and south China. In India, restricted to eastern Arunachal Pradesh and Assam. Reported recently from Namdapha Tiger Reserve (TR), evidence seen in Jairampur Forest Division in Changlang district, and possibly occurs in lower areas near Deomali in Tirap district. Also sighted from areas in Upper Assam in Joypur Reserve Forest (RF), Tinsukia district and in Cachar Hills (K. Kakati, A. Birand, *pers.comm.*). Distribution in other areas of north-east India inadequately known, though it may occur or have occurred in Nagaland and Manipur (Ali & Ripley 1987).
Body mass: male: 933 g, female: 755 g (Kemp 1995)
Habitat: Dense evergreen forest from plains to 900 m.
Major diet: Mixed diet, but largely carnivorous. Arthropods, molluscs and small vertebrates, berries, drupes, capsular fruits of primary forest species belonging to Lauraceae, Meliaceae, Annonaceae and figs (Moraceae).
Breeding habits and breeding season in Arunachal Pradesh: Monogamous, territorial, co-operative breeder, April to July/August.
Global conservation status: Lower risk/near threatened (IUCN 1990).
Threats in Arunachal Pradesh and Assam: Extensive habitat loss/modification (especially in Upper Assam and Tirap district) with a naturally restricted and localised range in India, hunting occurs (by *Tangsas*) but much less than other hornbill species. Probably the most threatened of the species in north-east India, in terms of total population in India, since it has a restricted distribution and most of its lowland habitat in Assam has been destroyed. Most commonly sighted in Namdapha TR in lowland evergreen forest in the Haldibari-Bulbulia area.

2. Oriental Pied hornbill (*Anthracoceros albirostris*) (also known as Indian Pied hornbill, earlier wrongly named as *Anthracoceros malabaricus*) – two subspecies, the subspecies in India is *A.a. albirostris.*

Distribution: South Nepal, south Bhutan, north Bangladesh, northern and north-eastern India, Myanmar, Mergui Archipelago, south China, Vietnam, Laos, Cambodia, and parts of Thailand, north-east peninsular Malaysia. Possibly overlaps with Malabar Pied hornbill (*A. coronatus*) in south Bihar, and hill forests of Orissa and West Bengal, no known hybrids.
Body mass: male: 738 g, female: 624 g (Kemp 1995)
Habitat: Forest edge, open moist deciduous and evergreen forests, riverine forest, secondary, logged forests and even gardens and agricultural fields.
Major diet: Mixed diet but largely frugivorous. Fruits of secondary forest species, lianas, and of Lauraceae, Meliaceae and Annonaceae and figs (Moraceae) as well as insects, crabs, small vertebrates.
Breeding habits and breeding season in Arunachal Pradesh: Monogamous, sometimes territorial, March/April to July.
Global conservation status: Not threatened, generally common and widespread distribution, not mentioned in the IUCN Red Data Book
Threats in Arunachal Pradesh: Can survive in somewhat degraded forest, but loss of forest cover especially in lowland foothill forests can cause declines, hunted less than the other three larger species.

Common near riverine forests especially in Khari area of Pakhui National Park (NP).

3. Rufous-necked hornbill (*Aceros nipalenis*)

Distribution: Nepal (believed extinct), north-east India, Bhutan, east Myanmar, north & west Thailand, south China, north Laos and north Vietnam. Unconfirmed in Cambodia.
Body mass: male: 2500 g, female: 2270 g (Kemp 1995)
Major diet: Frugivorous, mainly berries, drupes, capsular fruits of primary forest species belonging to Lauraceae, Meliaceae, Annonaceae and figs (Moraceae), also some animal matter.
Habitat: Hill evergreen forest from 500 m up to 2100 m
Breeding habits and breeding season in Arunachal Pradesh: Monogamous, non-territorial (?), April to July/August. Mostly sighted in pairs.
Global conservation status: Vulnerable, not critically endangered, but faces high risk of extinction in the wild in the medium-term future (IUCN 1990). The species is rare in most parts of its range, though in Bhutan it is more common. In India, status is better only in some protected areas of Arunachal Pradesh such as Namdapha TR (Changlang district), Eagle's nest and Sessa Wildlife Sanctuary (WLS), higher areas in Papum, Doimara RF, East & West Kameng districts, also occurs in Mehao WLS (Dibang Valley district) and Tale Valley WLS (Lower Subansiri district).
Threats in Arunachal Pradesh: Habitat loss/conversion/modification due to logging, shifting cultivation, settlements. Rare in most parts of Arunachal Pradesh due to both habitat loss and hunting. In eastern AP, status better in Namdapha TR and in forests above 800 m elevation in western AP in East & West Kameng district around Eagle's Nest WLS and in Khellong Forest Division. In Namdapha TR, commonly sighted even in lower elevation areas near Deban, Haldibari, Hornbill camp and Bulbulia. Heavily hunted and prized by several local tribal groups, especially in higher elevation areas, where the Great and Wreathed hornbills are less commonly seen. Hunted by *Nishis*, *Wanchos*, *Tangsas*, *Mishmis*, *Adis* and *Apatanis* in the subtropical evergreen forests. Forest loss is possibly a lesser threat for this species, because the condition and extent of forests at higher elevations in some areas are better than the foothill forests, but hunting is a more serious proximate threat to this species.

4. Wreathed hornbill (*Aceros undulatus*) (also known as Bar-pouched Wreathed Hornbill)

Distribution: North-east India, south Bhutan, Myanmar, Thailand, Cambodia, Vietnam, Laos, peninsular Malaysia, Indonesia on Sumatra and adjacent islands, Java, Bali, Kalimantan, Sarawak, Sabah, Brunei and other smaller islands.
Body mass: male: 2515 g, female: 1950 g (Kemp 1995)
Major diet: Frugivorous, mainly berries, drupes, capsular fruits of primary forest species belonging to Lauraceae, Meliaceae, Annonaceae and figs (Moraceae). Also beetles and crabs.
Habitat: Lowland foothill semi-evergreen and evergreen forest, but also up to 1800 m.
Breeding habits and breeding season in Arunachal Pradesh: Monogamous, non-territorial, March to early August.
Global conservation status: Not threatened, not mentioned in the IUCN Red Data Book.
Threats in Arunachal Pradesh: Habitat loss/conversion/modification due to logging, shifting cultivation, settlements, more common than the Great hornbill in parts of central and eastern Arunachal Pradesh, but still rare due to both habitat loss and hunting. Status is better in Namdapha TR and in foothill forests of western Arunachal, in East & West Kameng district around Pakhui NP and in Khellong Forest Division, but recent extensive habitat loss in adjacent areas in Assam has reduced the range. Lowland foothill forests are most important for the species, but flocks of this species move seasonally to higher areas. It can occur in logged forests and plantations near larger intact forests, provided not heavily hunted and if the habitat is not subjected to further degradation. It is less hunted than the other two large hornbills and relatively more common. Local taboos on hunting during the breeding season (March to July/August) by *Nishis* in the

Seijusa area have probably resulted in reduced hunting pressures for some time in the year in this small area.

5. Great Hornbill (*Buceros bicornis*) (also known earlier as Great Pied or the Great Indian hornbill)

Distribution: Disjunct distributions in India – in Western Ghats, and from Himalayan foothills in Uttaranchal, to south Nepal, Bhutan and north-east India. Myanmar, some islands in the Mergui archipelago, south China, Vietnam, Laos, Cambodia, Thailand, peninsular Malaysia and several adjacent islands, an isolated population in Indonesia on Sumatra.
Body mass: male: 3007 g, female: 2211 g (Kemp 1995)
Major diet: Largely frugivorous, but also a predator especially during the breeding season, taking birds, reptiles, and small mammals such as rats and flying squirrels. Figs form the major diet, followed by berries, drupes and capsular fruits of Lauraceae, Meliaceae and Annonaceae.
Habitat: Primary evergreen forest and moist deciduous forest, mainly on lowland plains but can extend up to 2000 m. Also seen in selectively logged forests and plantations close to larger forested tracts.
Breeding habits and breeding season in Arunachal Pradesh: Monogamous, territorial, March to July.
Global conservation status: Lower risk/near threatened (IUCN 1990).
Threats in Arunachal Pradesh: Habitat loss/conversion/modification (due to logging, shifting cultivation, settlements), rare to locally extinct in parts of central and eastern Arunachal Pradesh, due to both habitat loss and hunting. Status better in Namdapha TR and especially in foothill forests of western Arunachal Pradesh in East & West Kameng district around Pakhui NP and in Khellong Forest Division, but recent extensive habitat loss in adjacent areas in Assam has reduced the range. Lowland foothill forests are most important for the species. Can occur in logged forests and plantations near to larger intact forests, provided not heavily hunted and if the habitat is not subjected to further degradation. This species is the most heavily hunted and prized hornbill species by several local tribal groups. Local taboos on hunting during the breeding season (March to July/August) by *Nishis* in the Seijusa area have probably resulted in reduced hunting pressures for some time in the year in this small area.

Appendix 2. List of identified tree species in phenology plots, their dispersal mode and major consumers

Tree species	Family	Dispersal mode	Dispersers/consumers
Drimycarpus racemosus	Anacardiaceae	Animal	Mammals
Mangifera sylvatica	Anacardiaceae	Animal	Mammals
Spondias axillaris	Anacardiaceae	Animal	Deer, wild pig, Malayan giant squirrel
Spondias sp.	Anacardiaceae	Animal	Deer, wild pig
Miliusa roxburghiana	Annonaceae	Animal	Birds
Polyalthia simiarum	Annonaceae	Animal	Hornbills, also bats?
Polyalthia sp.	Annonaceae	Animal	Hornbills
Alstonia scholaris	Apocynaceae	Wind	
Wrightia tomentosa	Apocynaceae	Animal?	
Oroxylum indicum	Bignoniaceae	Wind	
Radermachera sp.	Bignoniaceae	Animal	Bar-tailed cuckoo dove
Stereospermum chelonoides	Bignoniaceae	Wind	
Ehretia acuminata	Boraginaceae	Animal?	
Ehretia laevis	Boraginaceae	Animal?	
Canarium resiniferum	Burseraceae	Animal	Hornbills, deer, wild pig
Garuga pinnata	Burseraceae	Animal	Macaques, parakeets
Bauhinia purpurea	Caesalpiniaceae	Wind	
Crataeva religiosa	Capparidaceae	Animal	Mammals?
Calophyllum sp.	Clusiaceae	Animal	Birds
Garcinia sp.	Clusiaceae	Animal	Primates
Kayea assamica	Clusiaceae	Unknown	
Terminalia bellerica	Combretaceae	Animal	Squirrels
Tetrameles nudiflora	Datiscaceae	Wind	
Dillenia indica	Dilleniaceae	Animal/water	Elephants, water
Diospyros toposia	Ebenaceae	Animal	Deer
Elaeocarpus aristatus	Elaeocarpaceae	Animal	
Elaeocarpus ganitrus	Elaeocarpaceae	Animal	Civets, birds
Aporusa dioica	Euphorbiaceae	Animal	Mammals
Baccaurea ramiflora	Euphorbiaceae	Animal	Deer, wild pig
Croton roxburghii	Euphorbiaceae	Animal	Deer, wild pig
Croton sp.1	Euphorbiaceae	Animal?	
Croton sp.2	Euphorbiaceae	Animal?	
Endospermum chinense	Euphorbiaceae	Animal?	
Glochidion assamicum	Euphorbiaceae	Animal	Birds
Macaranga denticulata	Euphorbiaceae	Animal	Bulbuls
Mallotus philippensis	Euphorbiaceae	Animal	Birds?, gravity-dispersed
Ostodes paniculata	Euphorbiaceae	Animal	Birds
Sapium baccatum	Euphorbiaceae	Animal	Birds
S. eugeniaefolium	Euphorbiaceae	Animal	Birds
Castanopsis indica	Fagaceae	Wind	
C. hystrix	Fagaceae	Wind	
Lithocarpus macrophylla	Fagaceae	Wind	

Tree species	Family	Dispersal mode	Dispersers/consumers
Flacourtia indica	Flacourtiaceae	Animal?	
Gynocardia odorata	Flacourtiaceae	Animal	Civets
Altingia excelsa	Hamamelidaceae	Wind	
Engelhardtia spicata	Juglandaceae	Wind	
Actinodaphne obovata	Lauraceae	Animal	Hornbills
Beilshmedia sp.	Lauraceae	Animal	Hornbills
Cryptocarya amygdalina	Lauraceae	Animal	Hornbills
Cinnamommum cecicodaphne	Lauraceae	Animal	Birds
C. tamala	Lauraceae	Animal	Birds
Cryptocarya sp.	Lauraceae	Animal	Hornbills, hill myna, pigeons
Dodecadaenia	Lauraceae	Animal?	
Persea/Phoebe	Lauraceae	Animal	Hornbills
Litsea chinensis	Lauraceae	Animal	Hornbills
L. monopetala	Lauraceae	Animal	Hornbills
L. panamonja	Lauraceae	Animal	Hornbills
L. umbrosa	Lauraceae	Animal	Hornbills
Phoebe attenuata	Lauraceae	Animal	Hornbills
P. cooperiana	Lauraceae	Animal	Birds
P. lanceolata	Lauraceae	Animal	Hornbills
Leea indica	Leeaceae	Animal	Birds
Duabanga grandiflora	Lythraceae	Animal	Birds, squirrels
Lagerstroemia parviflora	Lythraceae	Animal?	
L. speciosa	Lythraceae	Animal?	
Michelia sp.	Magnoliaceae	Animal	Birds
Talauma hodgsonii	Magnoliaceae	Animal	Squirrels
Talauma sp.	Magnoliaceae	Animal	Squirrels
Kydia calycina	Malvaceae	Wind	
Aglaia sp.	Meliaceae	Animal	Hornbills
Aglaia sp.	Meliaceae	Animal	Mammals
Amoora sp.	Meliaceae	Animal	Hornbills
Amoora wallichi	Meliaceae	Animal	Hornbills
Chisocheton paniculatus	Meliaceae	Animal	Hornbills
Chukrasia tabularis	Meliaceae	Wind	
Dysoxylum binectariferum	Meliaceae	Animal	Hornbills
D. hamiltonii	Meliaceae	Animal	
Toona febrifuga	Meliaceae	Wind	
Albizzia lucida	Mimosaceae	Wind	
Artocarpus chaplasha	Moraceae	Animal	Hornbills, squirrels
Ficus hookeri	Moraceae	Animal	Birds, mammals
F. lamponga	Moraceae	Animal	Civets, bats
F. macclellandi	Moraceae	Animal	Birds, mammals
F. mysorensis	Moraceae	Animal	Birds, mammals
F. nervosa	Moraceae	Animal	Birds, mammals
F. pomifera	Moraceae	Animal	Civets, bats
F. scandens	Moraceae	Animal	Birds
F. elastica	Moraceae	Animal	Birds/mammals

Tree species	Family	Dispersal mode	Dispersers/consumers
Ficus sp.	Moraceae	Animal	Birds
Morus laevigata	Moraceae	Animal	Birds
Horsfieldia kingii	Myristicaceae	Animal	Hornbills, MI pigeon
Knema angustifolia	Myristicaceae	Animal	Hornbills, pigeons
Syzygium formosum	Myrtaceae	Animal	Birds, mammals?
Syzygium sp.	Myrtaceae	Animal	Birds
S. syzygioides	Myrtaceae	Animal	Hornbills, other birds
Linoceira denticulata	Oleaceae	Unknown	
Livistona jenkinsiana	Palmae	Animal	Hornbills
Dalbergia paniculata	Papilionaceae	Wind	
Helicia nilagirica	Proteaceae	Animal	Squirrels?
Carallia brachiata	Rhizophoraceae	Animal	Birds
Pygeum acuminatum	Rosaceae	Animal	Hornbills, hill myna, barbets
Hyptianthera sp.	Rubiaceae	Animal	Hornbills
Tricalycia sp.	Rubiaceae	Animal?	
Evodia roxburghiana	Rutaceae	Animal	Birds
Micromelum integerrimum	Rutaceae	Animal	Bulbuls
Zanthoxylum rhetsa	Rutaceae	Animal	Birds
Z. oxyphyllum	Rutaceae	Animal	Birds
Meliosma simplicifolia	Sabiaceae	Animal?	
Meliosma sp.	Sabiaceae	Animal?	
Casearia graveolens	Samydaceae	Animal	Birds?
Aesculus assamicus	Sapindaceae	Wind?	
Xerospermum glabratum	Sapindaceae	Animal	Squirrels
Ailanthus grandis	Simaroubaceae	Wind	
Turpinia pomifera	Staphylaceae	Animal	Deer, wild pig
Pterospermum lancifolium	Sterculiaceae	Wind	
P. acerifolium	Sterculiaceae	Wind	
Sterculia alata	Sterculiaceae	Wind	
S. hamiltoniana	Sterculiaceae	Animal	
S. villosa	Sterculiaceae	Animal	Birds
Stryrax serrulatum	Styracaceae	Animal	Hornbills
Schima khasiana	Theaceae	Wind	
S. wallichi	Theaceae	Wind	
Saurauia nepalensis	Theaceae	Animal	
Grewia microcos	Tiliaceae	Animal?	
Trema orientalis	Ulmaceae	Animal	Birds
Callicarpa macrophylla	Verbenaceae	Animal	Birds
Gmelina arborea	Verbenaceae	Animal	Deer, wild pig
Premna benghalensis	Verbenaceae	Animal	Ruminants
Vitex pentaphylla	Verbenaceae	Animal	Civets, birds
V.peduncularis	Verbenaceae	Animal	Civets, birds

APPENDIX 3a. Recorded hornbill food plant species (including 5 possible food species), tree densities/dispersion, and fruit types

Plant species (ripe fruits)	Tree density (Mean ± S.E.)	Tree dispersion (V/M ratio)	Family	Fruit type	Season
1.*Actinodapnhe obovata*	3.24 ± 2.18	30.94	Lauraceae	Fleshy succulent drupe	Non-breeding
2. *A. angustifolia*	Not recorded in plots	-	Lauraceae	Fleshy succulent drupe	Non-breeding
3.*Alseodaphne peduncularis*	Not recorded in plots	-	Lauraceae	Fleshy succulent drupe	Non-breeding
4. *Aphanamixis polystachya*	Not recorded in plots	-	Meliaceae	Arillate dehiscent capsules	Non-breeding
5. *Aglaia* sp.	5.14 ± 1.95	15.6	Meliaceae	Arillate dehiscent capsules	Breeding
6. *Amoora wallichi*	7.8 ± 2.02	10.47	Meliaceae	Arillate dehiscent capsules	Breeding
7. *Amoora* sp.	2.48 ± 1.67	23.57	Meliaceae	Arillate dehiscent capsules	Breeding
8. *Artocarpus chaplasha*	0.95 ± 0.38	3.2	Moraceae	Succulent achenes in fleshy perianth	Breeding
9. *Beilshmedia1*	1.71 ± 0.94	10.8	Lauraceae	Fleshy succulent drupe	Non-breeding
10. *Beilshmedia2*	Not recorded in plots	-	Lauraceae	Fleshy succulent drupe	Non-breeding
11. *Beilshmedia3*	Not recorded in plots	-	Lauraceae	Fleshy succulent drupe	Non-breeding
12. *Bhesa robusta*	Not recorded in plots	-	Celastraceae	Arillate dehiscent	Breeding
13. *Bridelia retusa*	Not recorded in plots	-	Euphorbiaceae	Berry	Non-breeding
14. *Canarium strictum*	4.4 ± 0.96	4.17	Burseraceae	Fleshy succulent drupe	Non-breeding
15.*Cinnamomum cecicodaphne*	0.76 ± 0.45	5.5	Lauraceae	Fleshy succulent drupe	Non-breeding
16. *Cryptocarya amygdalina*	2.28 ± 0.65	3.9	Lauraceae	Fleshy succulent drupe	Breeding
17. *Cryptocarya* sp2	0.76 ± 0.45	5.5	Lauraceae	Fleshy succulent drupe	Breeding
18. *Chisocheton paniculatus*	21.52 ± 1.36	21.22	Meliaceae	Arillate dehiscent capsules	Breeding
19. *Dysoxylum binectariferum*	4.19 ± 1.36+	9.34	Meliaceae	Arillate dehiscent capsules	Breeding
20. *Elaeocarpus ganitrus*	1.90 ± 0.9	8.92	Elaeocarpaceae	Fleshy drupe	Non-breeding
21. *Gnetum ula*	Not enumerated	-	Gnetaceae, liana	Drupe?	Non-breeding
22. *Horsfieldia kingii*	1.14 ± 0.62	7.2	Myristicaceae	Arillate dehiscent	Breeding
23. *Knema angustifolia*	6.66 ± 4.41	61.28	Myristicaceae	Arillate dehiscent	Breeding
24. *Laportea crenulata*	0.19 ± 0.19	4	Euphorbiaceae	Berry	Non-breeding
25. *Litsea panamonja*	0.19 ± 0.19	4	Lauraceae	Fleshy succulent drupe	Breeding
26. *Litsea* sp.	Not recorded in plots	-	Lauraceae	Fleshy succulent drupe	Non-breeding
27. *Litsea chinensis*	1.33 ± 0.50	4	Lauraceae	Fleshy succulent drupe	Non-breeding
28. *Litsea monopetala*	0.19 ± 0.19	4	Lauraceae	Fleshy succulent drupe	Non-breeding
29. *Litsea umbrosa*	2 ± 0.85	7.24	Lauraceae	Fleshy succulent drupe	Breeding
30. *Livistona jenkinsiana*	6.09 ± 4.21	61.06	Lauraceae	Fleshy succulent drupe	Non-breeding
31. *Pygeum acuminatum*	1.71 ± 0.71	6.13	Rosaceae	Fleshy succulent drupe	Non-breeding
32. *Phoebe lanceolata*	0.76 ± 0.45	3.8	Lauraceae	Fleshy succulent drupe	Breeding

Plant species (ripe fruits)	**Tree density (Mean ± S.E.)**	**Tree dispersion (V/M ratio)**	**Family**	**Fruit type**	**Season**
33. Phoebe sp.	22.48 ± 4.99	23.24	Lauraceae	Fleshy succulent drupe	Breeding
34. Phoebe cooperiana	1.33 ± 0.75	8.8	Lauraceae	Fleshy succulent drupe	Non-breeding
35. Phoebe attenuata	4.38 ± 2.02	19.69	Lauraceae	Fleshy succulent drupe	Breeding
36. Persea or *Phoebe* sp.	5.14 ± 2.52	25.87	Lauraceae	Fleshy succulent drupe	Breeding
37. Polyalthia simiarum	21.8 ± 4.71	20.35	Annonaceae	Fleshy succulent drupe	Both
38. Polyalthia sp.2	0.19 ± 0.19	4	Annonaceae	Fleshy succulent drupe	Both
39. Sterculia villosa	0.19 ± 0.19	4	Sterculiaceae		Breeding
40. Syzygium syzygioides	18.31 ± 3.89	17.50	Myrtaceae	Fleshy succulent drupe	Breeding
41. Syzygium sp 2.	0.95 ± 0.61	8.24	Myrtaceae	Fleshy succulent drupe	Non-breeding
42. Styrax serrulatum	4.38 ± 1.10	5.81	Styracaceae	Drupe?	Non-breeding
43. Platea latifolia	Not recorded in plots	-	Icacinaceae	Fleshy succulent drupe	Non-breeding
44. Vitex pentaphylla	3.62 ± 1.14	7.16	Verbenaceae	Drupe	Non-breeding
45. Zizyphus sp.	Not recorded in plots	-	Rutaceae	Berry	Non-breeding
46. Zanthoxylum rhetsa	2.67 ± 1.08	9.2	Rutaceae	Berry	Non-breeding
47. Ficus hookeri	0.57 ± 0.31	0.004	Moraceae	Fig syconia	Both
48. Ficus altissima	Not recorded in plots	-	Moraceae	Fig syconia	Both
49. Ficus nervosa	1.33 ± 0.97	14.8	Moraceae	Fig syconia	Both
50. Ficus cyrtophylla/clavata	Not recorded in plots	-	Moraceae	Fig syconia	Both
51. Ficus macclellandi	Not recorded in plots	-	Moraceae	Fig syconia	Both
52. Ficus elastica	0.38 ± 0.26	3.8	Moraceae	Fig syconia	Both
53. Ficus sp. 1 (small pink)	Not recorded in plots	-	Moraceae	Fig syconia	Both
54. Ficus sp. 2 (small maroon)	0.19 ± 0.19	4	Moraceae	Fig syconia	Both
55. Ficus mysorensis	0.19 ± 0.19	4	Moraceae	Fig syconia	Both
56. Hyptianthera sp.	0.95 ± 0.54	6.56	Rubiaceae	Berry	Non-breeding
57. Derris sp.	Not enumerated	-	Leguminosae, liana	Dehiscent pods with edible aril	Non-breeding
58. Ostodes paniculata	Not recorded in plots	-	Euphorbiaceae	Small berry	Non-breeding
59. Spondias sp.	0.19 ± 0.19	4	Anacardiaceae	Drupe	??
60. Syzygium sp.?	0.19 ± 0.19	4	Myrtaceae?	Drupe	Non-breeding
61. Pygeum sp.	Not recorded in plots	-	Rosaceae	Fleshy succulent drupe	Non-breeding
62. Bluefruit liana	Not enumerated	-	Liana	Drupe	Non-breeding
63. Oroxylum indicum	0.19 ± 0.19	4	Bignoniaceae	Flower	
18 other unknown species	Not recorded in plots	-			

Appendix 3b. List of invertebrate and vertebrate species recorded in hornbill diet

1. *Anomala viridis* Family Scarabaeidae, Order Coleoptera
2. *Diastocera wallichi* Family Cerambycidae, Order Coleoptera
3. *Monochamus versteegi* Family Cerambycidae, Order Coleoptera
4. *Aeloesthes holosericea* Family Cerambycidae, Order Coleoptera
5. *Tanymecus* sp. Family Curculionidae, Order Coleoptera
6. Unidentified beetle species (2)
7. Crab
8. Spotted forest skink *Sphenomorhus maculatus*
9. Flat-tailed gecko *Cosymbotus platyurus*
10. Snake
11. Flying squirrel *Belomys* or *Hylopetes*
12. Unidentified rodent species (2)
13. Unidentified bird species (2)

Appendix 4. Fig species, their life forms, fruit characteristics and consumers

Fig species	Life-form and size	Fruit characteristics	Consumers
Ficus nervosa	Free-standing, large trees	Small, reddish orange, globose with peduncle	Hornbills, pigeons, barbets, other frugivorous birds, squirrels
Ficus lamponga	Free-standing, medium-sized trees	Cauliflorous, large, reddish with peduncle	Civets, bats, deer
Ficus pomifera	Free-standing, large trees	Cauliflorous, globose with peduncle on short leafless branches	Civets, bats, deer
Ficus heterophylla	Free-standing, creeping, straggling shrub	Medium, yellow with peduncle	
Ficus scandens	Free-standing, small shrubby climber		Birds?
Ficus hirta	Free-standing, erect small shrubby trees	Large, densely hairy, pink-red	
Ficus hispida	Free-standing, small tree	Obovoid, clustered on long leafless panicles hanging on trunk or branches	Sambar, barking deer, wild pigs
Ficus cyrtophylla	Epiphytic, shrub or medium-sized tree	Small, yellow-orange, tomentose with peduncle	Hornbills, green pigeons, barbets, frugivorous birds
Ficus cunia	Small tree	Small, globose with peduncle	Birds?

Fig species	**Life-form and size**	**Fruit characteristics**	**Consumers**
Ficus elastica	Strangler, large	Small, sessile	Hornbills, pigeons, barbets, other frugivorous birds, squirrels
Ficus altissima	Strangler, large	Medium, ovoid, red, sessile	Hornbills, pigeons, barbets, other frugivorous birds, squirrels
Ficus mysorensis	Strangler, large	Medium, red-black, ovoid, sessile	Hornbills, pigeons, barbets, other frugivorous birds, squirrels
Ficus hookeri	Strangler, large	Large, black-red, dark purple	Hornbills, pigeons, barbets, other frugivorous birds, squirrels, civets
Ficus rumphii	Strangler, large	Small, sessile, black	Hornbills and other frugivorous birds
Ficus macclellandi var. *rhododendrifolia*	Strangler, large	Medium, yellow, sessile	Hornbills, pigeons, barbets, other frugivorous birds, squirrels, civets
Ficus sp. 1	Strangler	Small, pink	Hornbills and other frugivorous birds
Ficus sp. 2	Strangler	Small, maroon	Hornbills and other frugivorous birds
F15	Strangler		
F5a	Strangler		
F12	Strangler		
F20	Strangler		
Fig	Epiphytic climber		Birds?
Fig	Epiphytic climber		Birds?
Fig	Epiphytic climber		Birds?
Unknown	Strangler	Male fruits only?	Not eaten
F1sp	Strangler		

Appendix 5. A description of fruiting patterns and fruit characteristics of selected hornbill food plant species

1. Amoora wallichi (Meliaceae) – This species usually bears 4-seeded capsular fruits that dehisce on ripening. In the study area, ripe fruits of this species were available from May to August with a fruiting peak in June-July and the pattern did not vary between years, though the intensity of fruiting was lowest in 1999. This species fruited in all years. The trees are large, up to 20 m in height. The fruit is capsular and broadly pyriform (3-4 celled, 2-3 seeded) with an orange-red fleshy edible aril, the seeds are maroon to dark brown and kidney-shaped. The main fruiting peak is reported from August to September (Kanjilal *et al*. 1934, Grierson & Long 1984).

2. Pygeum acuminatum (Rosaceae) – The fruits are single-seeded drupes and ripe fruits are black in color (Kanjilal e*t al.* 1934). Ripe fruits were available between November and February with a fruiting peak in December-January and there was not much variation between years. This species fruited in all years. Fruiting intensity was relatively lower during November 1999-February 2000.

3. Polyalthia simiarum (Annonaceae) – The fruits are single-seeded berries borne in bunches and ripe fruits are black in color. The species had two fruiting periods in a year, the main one from May to July and again later from December to February. Consequently ripe fruits of this species were available for a large part of the year. Although ripe fruiting trees were not recorded in the phenology plots during the winter of 1997-1998 and very few in winter of 1998-99, but fruiting trees were seen in the study area. They were also recorded in the diet of hornbills in winters. They are evergreen trees, generally 15-20 m in height, with a straight bole and thin horizontal branches. The fruit is an ellipsoid berry/drupe, turning from green to orange-red to blue-black on ripening gradually narrowed to a stalk 3-4cm long, the seeds are ovoid, grooved and transversely ribbed. The species is fairly common in foothill forests of Arunachal Pradesh and other NE hill states. The fruiting period is reported to be from May-June. In the study area, apart from the main fruiting peak from May to July, individuals with ripe fruits were noted from December to February.

4. Dysoxylum binectariferum (Meliaceae) – This species usually bears 4-seeded capsular fruits, which dehisce on ripening. The greenish-yellow heart-shaped seed are completely covered by a shiny black edible aril. This species fruits from February to May with the peak in March-April. This species did not fruit in 1999 in the phenology plots, although a few trees must have been fruiting, because it was consumed in small amounts by hornbills. It is a medium-sized evergreen species, generally 12-15 m in height. The capsules are globose, orange-yellow, 4-5 celled, seeds are green to yellow in color, heart-shaped, covered by an edible shiny black aril. The main fruiting peak is from April to June. Fruits take a long time to ripen and the capsules dehisce on ripening.

5. Chisocheton paniculatus (Meliaceae) – The fruits are 3-4 seeded dehiscent capsules, the dark red-brown seeds are surrounded partly by an edible orange-white aril. The species fruits from April to July, with the peak in May-June. Ripe fruit availability of this species was relatively lower in 1998 and 1999. These are evergreen trees about 12 m in height. The fruit is a 2-5 celled globose capsule, pinkish-red. The glossy dark black/chestnut-colored seed is partly surrounded on top by orange-white arillode. The main fruiting is from mid-May to June.

6. Horsfieldia kingii (Myristicaceae) – The fruits are solitary supported by a persistent perianth, the cream-colored ovoid seed is enclosed by a bright yellow entire edible aril. The species fruits from February to May with peak fruiting in February to March. Ripe fruits of this species were only recorded in 1997 and 1998, while in 1999, there was a failure of fruiting. Only one individual was monitored in 2000, which did not fruit, but trees with ripe fruits were seen in the study area and also recorded in hornbill diet. It is an evergreen tree, generally 10-12 m in height. The branches are usually crowded on top of the trunk and somewhat horizontal. Fruiting has been earlier reported to be in June. The fruits dehisce on ripening. The fruit and seed are edible and used as a substitute for betel nut.

7. Actinodaphne obovata (Lauraceae) – The fruits are single-seeded drupes with fleshy pulp and black on ripening. The species fruits from June to November with a peak in September-October, but ripe fruit availability patterns varied between years. A few trees with ripe fruits were recorded in May in1998, while in 2000, one tree with ripe fruits was recorded as early as March.

8. Canarium resiniferum (Burseraceae) – The fruits are single-seeded drupes, black in color when ripe. The species fruits from July to March, but peak ripe fruit availability was between November to December. There was some variability in peak ripe fruiting times recorded for this species that may have been due in part to sometimes recording semi-ripe fruits incorrectly as ripe. The species fruited every year.

9. Livistona jenkinsiana (Palmae) – The fruit is a round single-seeded drupe, the ripe fruit color is a leaden dark blue. The species does not fruit every year and seems to show supra-annual fruiting. There was no fruiting in the winter of 1995-96 and fruiting occurred in 1996-1997. Fruiting was recorded in 1997-98 from October 1997 to February 1998, with the peak in October. No fruiting occurred in 1998-99.

10. Styrax serrulatum **(**Styracaceae) – This species bears small berries that are supported by a persistent calyx tube and the flesh is dry and ripe fruits are black. The species shows some annual variations in fruiting schedules from May to December, but the peak ripe fruit availability is usually between July and early October. The species did not bear fruit in 1999. In 1997, fruiting occurred between July and December, while in 1998, fruiting occurred between May and September. In 2000, ripe fruits were recorded even in April.

11. Cryptocarya amygdalina (Lauraceae) – This species bears single-seeded drupes with ovoid elongated seeds and a ripe fleshy pulp that is black in color. Fruiting of the species seems to be supra-annual in that they fruited in the first 2 years while no fruiting was recorded in 1999 and 2000. Ripe fruits become available during June-July.

Appendix 6. Description of roost counts, daily numbers at roost, chronology and behaviour of hornbills on arrival at roosts (1997-2000).

1997

Counts at a roost site (next to the Pakke River near the Irrigation Bridge on the Assam-Arunachal Pradesh border) were made on 7 consecutive days from August 25 to 31 in 1997 (non-breeding season). Great hornbill flock size on arrival at roost sites ranged from 1 to 56. The median and modal flock size was 2. Wreathed hornbill flock size on arrival ranged from 1 to11. The median and the modal flock size were 2. The total number of hornbills arriving at the roost fluctuated over the 7-day period with roost size ranging from only 19 great hornbills on the 5th day to 70 hornbills on the 2nd and 3rd day. Oriental Pied hornbills were not seen to roost along with the larger two species. The Wreathed hornbills (8-12) roosted on *Bombax ceiba* and *Albizzia* trees on the east bank of Pakke River, a few roosted on the west bank on two days, while most Great hornbills (19-62) roosted on two *Albizzia* trees on the west bank, while some roosted on a few *Albizzia f*urther downstream. The Wreathed hornbills generally arrived earlier than the Great hornbills, most of the Great hornbills arrived *en masse* after sunset. The Great hornbill followed each other in singles, twos and threes, gliding in silently. On one occasion, a pair of Wreathed hornbills also roosted with 19 Great hornbills on the west bank, while the rest of the Wreathed hornbills roosted on the east bank. On another day, five Wreathed hornbills roosted on the west bank, 3 of which were displaced from the *Albizzia* tree on the arrival of Great hornbills. Eleven Wreathed hornbills were also seen flying to roost upstream near Sukan *nala*.

1998

Counts at a roost site on a cliff face adjacent to Khari *nala* were made on 23rd and 24th January 1998. A count was also made on 28/9/98 near the Irrigation Bridge and on 24/10/98 near a *nala* on a steep hillside on a *Tetrameles nudiflora* tree, near A2 village. A total of 388 hornbills were counted in 34 sightings. Great hornbill flock size on arrival at roost sites ranged from 1 to 25. The median flock size was 3.5 and the modal flock size was 2. Wreathed hornbill flock size ranged from 1 to 100. The median and modal flock size was 2. Oriental Pied hornbill flock size ranged from 6 to 17. The median and modal flock size was 7.

On 23rd January, 44 Great hornbills and 100 Wreathed hornbills came to the roost. The Wreathed hornbills kept flying around perching on different trees, with more than 50 birds perched on a single *Albizzia* tree. On the 2nd day, 47 Great hornbills and 99 Wreathed hornbills visited the main roost. The bulk of the Wreathed hornbills flew in from west and north-west, while the Great hornbills came in from the east and north-east. Wreathed hornbills arrived earlier than the Great hornbill. The Great hornbills initially settled about 100-300 m apart from the main roosting flock of Wreathed hornbills on trees on top of the cliff ridge, then later flew towards the area where some of the Wreathed hornbills had settled, causing the Wreathed hornbills to fly off to settle in other trees. The 50 or more Wreathed hornbills that had initially started gathering on one tree which was situated lower down on the sides of the cliff face, eventually flew in to roost trees on top of the cliff face or higher on the cliff slopes. A troop of Assamese macaques also was seen to use these cliff faces as sleeping sites near dusk.

Twenty-eight Oriental pied hornbills were seen roosting 500 m away from the mixed communal roost of Great hornbills and Wreathed hornbills on the 1st day on a single emergent *Tetrameles nudiflora* on the edge of Khari nala. The Oriental pied hornbills also gathered at the roost tree between 3:30 to 4:30 pm. On the 2nd day, 23 Oriental Pied hornbills were seen on the same tree.

A few pairs and small groups of Great and Wreathed hornbills were also seen roosting solitarily on emergent *Tetrameles nudiflora* at different points along Khari *nala* close to the forest camp. A few flying birds may have later joined the main roosting flock about 1.5 km away. It is estimated that about 3-10% of hornbills were roosting in pairs or smaller flocks in January 1998.

In August-September 1998, Great hornbills and Wreathed hornbills were not seen to use the roost site in the Irrigation bridge, but roosted further upstream in Arunachal Pradesh along the river margins close to the forest edge. On 27 and 28 September, *ca.* 20 or more Wreathed hornbills roosted on a fig and nearby *Tetrameles nudiflora* near an old failed plantation, while 5 Wreathed hornbills roosted on a nearby *Ailanthus grandis* tree. There were several ripe fruiting trees of *Beilshmedia* spp. in the vicinity, on which Wreathed hornbills were foraging on in the daytime during this period. In late October 1998, 16-20 Great hornbills roosted on an emergent *Tetrameles nudiflora* near a dry *nala* bed adjacent to a vertical cliff face. A pair of Wreathed hornbills were also seen roosting solitarily on a small riverside tree 3-4 km downstream along Pakke River on the west bank in Assam. In late September, 25 Wreathed hornbills were sighted roosting on *Albizzia* trees along the Pakke River near the Irrigation Bridge.

1999

Counts at a roost site along the Pakke River near the mouth of the Sukan *nala* were made on 11th, 12th, 15th, 26th September. Six hundred and thirty-nine hornbills were seen in 130 sightings. Great hornbill flock size ranged from 1 to 31. The median flock size was 5 and the modal was 2. Wreathed hornbill flock size ranged from 1 to 70. The median flock size was 3 and the modal flock size was 2. Oriental Pied hornbill flock size ranged from 2 to 6. The median flock size was 2.5 and the modal flock size was 2.

On 26th August 1999, 2 pairs of Oriental Pied hornbills were seen roosting solitarily on two separate *Albizzia* trees on the east bank of Pakke River, while a pair of wreathed roosted on an *Albizzia* tree on the West Bank. A flock of 4 were also sighted flying further downstream into Assam. A flock of 70 Wreathed hornbills roosted in the grove of *Bombax ceiba* and *Albizzia* trees on the east bank about 100 m away from the riverside. But on the next day, they were seen using an area further downstream. Though, no Great hornbills were counted in the area, they were heard and seen flying further downstream in Assam. They may have shifted their roost sites due to disturbance.

During August-September 1999, *ca.* 7 Oriental Pied hornbills were reported to be roosting in a village bamboo grove in Assam. On 28th August, 2 Wreathed hornbills were seen flying near the bridge and the main flock roosted much further downstream in the reserve forests of Assam. The main communal roost shifted upstream in September 1999 near the junction of Sukan *nala* with Pakke River. The roost size varied from 88 to 179. Wreathed hornbill numbers ranged from 57 to 92, while Great hornbill numbers ranged from 14 to 87. The maximum size of roost was seen on 26th September when 87 Great hornbills and 92 Wreathed hornbills roosted together. On 17th September, no counts were made at the roost sites but 12 wreathed hornbills were seen flying towards the roost site. Nine Oriental Pied hornbills were seen roosting on forest edge near the Khari *nala* in September. A pair of Great hornbills also roosted alone throughout September on an isolated *Albizzia* tree in the middle of a river island near the Irrigation Bridge. About 4% of hornbills roosted in pairs or smaller flocks during August-September 1999. Apart from this, during a short visit to Doimara R.F. west of Pakhui NP, 5 Wreathed hornbills were seen roosting on an isolated *Bombax ceiba* in a field near the Belsiri *nala* in Foothills on 18th September. A pair of Great hornbills was seen roosting on *Polyalthia simiarum* on a steep hillside in Doimara and 2 Wreathed hornbills were seen flying to roost in Doimara on 19th September.

2000

Counts were made at the roost site used between August-September 1999 along the Pakke River near the mouth of the Sukan *nala* on 3rd, 8th, 12th, 14th, 17th 22nd and 25th May and 16th June (breeding season). On 15th May, a count was made about 2 km away at the roost site near the Irrigation Bridge. A total of 349 hornbills were seen in 106 sightings. The flock size of Great hornbills on arrival at roosts ranged from 1 to 5. The median flock size was 2, while the modal was 1. Wreathed hornbill flock size ranged from 1 to 31. The median and modal flock size was 2.

Wreathed hornbills and very few Great hornbills were seen to use the same roost site but slightly further downstream on a line of 4-5 *Albizzia* trees. But they first gathered at a pre-roost site on the opposite bank in a grove of *Sterculia villosa* trees, the birds following each other from tree to tree, often some perching on a particular tree for sometime, while a few would fly ahead. The birds were noisy, calling to each other, selfpreening and allopreening, playing and mock fighting during this time. Only at dusk, after most birds had gathered at the pre-roost trees, did the hornbills all start flying into the final roost trees.

The total number of hornbills arriving at the roost fluctuated over the month with roost size ranging from only 22 hornbills on the 4th day to 72 hornbills on the 9th day. On day 1 (3rd May), 23 Wreathed hornbills were seen at the roost site. Wreathed hornbill numbers varied from 20 to 63, while Great hornbill numbers varied from 2 to 9. Great hornbills did not visit the roost on all days. On the first 3 days, no Great hornbills were seen; two lone Great hornbill males were seen roosting along with the Wreathed hornbills on the 4th day. A group of 3 were seen on day 7 and 7 Great hornbills were seen on day 8, and 9 birds were seen on day 9. On 15th May, 7 Wreathed hornbills were seen at a different location near the Irrigation Bridge. In early June, the flock had moved upstream towards Upper Seijusa. But on 16th June, 23 Wreathed hornbills were seen again at the Sukan *nala* roost site.