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Foraging Patterns of Sympatric Hornbills during the Nonbreeding Season in Arunachal Pradesh, Northeast India[1]

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ABSTRACT

The diet and food resource partitioning of three sympatric hornbills (Great Hornbill *Buceros bicornis*, Wreathed Hornbill *Aceros undulatus*, and Oriental Pied Hornbill *Anthracoceros albirostris*) during the nonbreeding season were studied relative to fruit availability in a foothill semievergreen forest of Arunachal Pradesh, northeast India. Hornbills fed on fruits of 49 plant species that comprised over 95 percent of their diet. Hornbill species partitioned food resources by varying the relative contribution of figs and non-fig fruits in the diet. Similarity in non-fig fruit diet was low. Ten species contributed to over 90 percent of the non-fig diet. The availability of non-fig fruits was much lower in the nonbreeding season than in the breeding season; however, despite lower fruit availability during the nonbreeding season, hornbills had a wide diet breadth and indirect evidence suggests that Wreathed Hornbills foraged widely in this season for fruit. Great Hornbills relied more on figs that were available year-round. The diverse diet breadth that included rare and patchy fruit resources underscores the importance of conserving large forest tracts for hornbills.

Key words: Aceros undulatus; Anthracoceros albirostris; *Arunachal Pradesh;* Buceros bicornis; *foraging; frugivory; fruit availability; hornbills; nonbreeding season; northeast India; resource partitioning; sympatry.*

The unique facets of hornbill breeding have resulted in a plethora of studies on the breeding biology and breeding season diet of hornbills (Poonswad *et al.* 1983, 1986, 1987; Kannan & James 1997; Kinnaird & O'Brien 1999; Mudappa 2000); however, there have been relatively few studies of hornbill diet in the nonbreeding season, possibly due to the difficulty of tracking birds in tropical forests to quantify diet composition during this season (Poonswad *et al.* 1998). A few studies have yielded information on hornbill movement and foraging patterns during the nonbreeding season (Poonswad & Tsuji 1994, Kinnaird *et al.* 1996, Suryadi *et al.* 1998).

For a full understanding of hornbill biology and life history, however, studies determining the diet, foraging behavior, and fruit availability during the nonbreeding season are needed (Leighton 1982, Leighton & Leighton 1983, Kannan & James 1999). Although most studies have found that immediately after fledging, fruit availability is high (Poonswad *et al.* 1987, Kannan & James 1999, Kinnaird & O'Brien 1999), there is a lean season in fruiting during subsequent months (Leighton & Leighton 1983, Kannan & James 1999, Kinnaird & O'Brien 1999). Body condition of female hornbills has been found to be poor after the prolonged confinement inside the nest (Kemp 1995, Kannan & James 1999, Boix-Hinzen *et al.* 2001), and fledglings require adequate nutrition during this period as they grow and begin to forage independently. Starvation of juvenile birds is likely to be a major mortality factor (Kinnaird & O'Brien 1999), especially because of their inexperience in tracking resources and increased energetic demands as they range more widely in the nonbreeding season (Poonswad & Tsuji 1994, Kinnaird & O'Brien 1999).

Earlier studies on hornbills in India have focused on the breeding biology of single species and were restricted to southern India (Kannan & James 1997, Mudappa 2000). Our study determined the diet of three sympatric hornbill species (Great Hornbill *Buceros bicornis*, Wreathed Hornbill *Aceros undulatus*, and Oriental Pied Hornbill *Anthracoceros albirostris*) in relation to fruit availability. Sympatric species may partition resources in order to

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coexist if resources are limiting. They may select different food items, forage in different strata, or differ temporally in use of resources to avoid competition (Schoener 1974, Cody 1985, Rosenzweig 1995). In this paper, the diet of hornbills during the nonbreeding season is described in relation to fruit availability to understand how resource use varies among three coexisting species. Such studies are valuable for conservation of hornbills, many of which are threatened and vulnerable due to habitat loss and hunting (Datta 1998, Raman 2001).

STUDY SITE

The study was conducted in the foothill forests of Arunachal Pradesh (AP), eastern Himalaya. AP has the world's northernmost tropical rain forests (Whitmore 1998). The state has diverse habitat types spanning a wide elevational range from 100 to over 6000 m and is recognized as one of the global biodiversity hotspots (Mittermeier *et al.* 1998, Olson & Dinerstein 1998, Myers *et al.* 2000).

The study was conducted in Pakke Tiger Reserve (TR, 862 km^2, 26°54′–27°16′N, 92°36′–93°09′E) in East Kameng district of western AP. The park is surrounded by contiguous forests on most sides and bounded by rivers in the east, west, and north. Numerous small rivers and perennial streams drain the area. The terrain is undulating and hilly, with elevation ranging from 150 to over 2000 m. The central and northern part of the sanctuary is relatively inaccessible due to dense vegetation and hilly terrain, whereas hunting, fishing, and collection of cane and other minor forest products occur along the southern boundary.

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

The vegetation of the reserve is classified as Assam Valley tropical semievergreen forest 2B/C1 (Champion & Seth 1968). The forests are multistoried and rich in epiphytic flora, woody lianas, and climbers. A total of 343 woody species of flowering plants have been recorded from the foothills of the park, with a high representation of Euphorbiaceae and Lauraceae (Datta & Goyal 1997, Datta 2001). Major emergent species include *Tetrameles nudiflora*, *Ailanthus grandis*, and *Altingia excelsa* (Singh 1991). The forests along the lower plains and foothills are dominated by *Polyalthia simiarum*, *Pterospermum acerifolium*, *Sterculia alata*, *Stereospermum chelonioides*, *A. grandis*, and *Duabanga grandiflora* (Singh 1991, Datta 2001). Evergreen species include *A. excelsa*, *Mesua ferrea*, *Dysoxylum binectariferum*, *Beilschmedia* sp., and other middle-story trees in the Lauraceae and Myrtaceae. Subtropical broadleaf forests of the Fagaceae and Lauraceae dominate the hilltops and higher reaches. Slopes are dominated by *M. ferrea* and *Castanopsis* spp. Moist areas near streams have a profuse growth of bamboo, cane, and palms. Along the larger perennial streams, there are shingle beds with patches of tall grassland, which give way to lowland moist forests with *Dillenia indica* and *Talauma hodgsonii*. The study site (*ca* 12 km^2) was located in the drier southeastern part of the park at 150 to 600 m near the AP–Assam border.

METHODS

Diet composition determined below hornbill perches and roost trees.—We used a combination of methods to determine diet: recording feeding observations along trails, seed counts below perches and seed counts below roost trees. Observations at fruiting trees could not be carried out because hornbills are hunted in the area and therefore extremely wary. Instead, we counted the numbers of seeds of non-fig fruits eaten and subsequently regurgitated by hornbills below their perches and roost trees. The freshly regurgitated seeds dropped by hornbills retain a pink color, and are smooth because the pulp is cleanly removed.

Feeding records.—Sampling on six main trails (totaling *ca* 16 km) was also used to determine hornbill diet and foraging characteristics (February 1997–May 2000). Opportunistic observations of feeding hornbills were also recorded to augment feeding records. Upon sighting hornbills, the following were recorded: (1) hornbill species; (2) number of individuals; (3) whether feeding and fruit species; and (4) position of hornbill in the canopy (*i.e.*, lower: <5 m, middle: 5–15 m, upper canopy: at or near the highest level of the general tree canopy, or the emergent layer). Fig species in the diet were recorded only from feeding records, since it is not possible to determine the species or number of figs from feces. The presence of animal matter in the diet (beetles and crabs) was ascertained below roost trees and were based on few feeding records.

FRUIT CHARACTERISTICS.—All fruit species consumed were collected for identification. Fruits and seeds were weighed wet and measured (length, width, and depth). Fruits more than 2 cm in length were defined as large, while fruits 1–2 cm were defined as medium-sized fruits and small fruits were those below 1 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: drupes (both single-seeded fleshy fruits with or without an outer skin); dehiscent arillate single; or multi-seeded capsules, berry, and figs; as well as by characteristics of the pulp (oily, watery, and fleshy). Berries were defined as either single-seeded or multi-seeded with a watery pulp. Figs were classified as sugar-rich watery fruits with thousands of tiny seeds embedded in the pulp. Hornbills voided the seeds (unharmed) of figs in the feces and sometimes the seeds of *Sterculia villosa*, while all other seeds were regurgitated intact.

FRUIT AVAILABILITY.—We sampled 0.4 percent of the intensive study area by randomly placing 21 phenology plots of 0.25 ha each (5.25 ha) to monitor fruiting patterns. Plants with girth at breast height (GBH) of 30 cm or greater were included in the sample (1899 trees) and their GBH measured. We tagged each tree with aluminum tags indicating tree species and number in the plot. We recorded the phenology of all tree species (165 spp.) within the plots monthly. We collected all plants not identified in the field and assigned a temporary code. Phenological data on lianas and shrubs were not collected. Since figs were not adequately represented in the plots (only 16 individuals in 21 plots), we counted and tagged all adult fig trees within 30 m of both sides on three trails (total area covered was 48 ha) and estimated their density; however, we could not monitor the phenology of these individuals systematically every month. Two to three people monitored the study plots every month from February 1997 to July 2000, omitting the months of July and December in 1999. The phenophases recorded were the presence/absence of 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 the total number of trees for each species in fruit during every month in each plot.

To test the hypothesis that hornbills forage for rare non-fig fruits, the non-fig species in the diet recorded in phenology plots 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). An index of abundance 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. 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/ha were considered rare and common species were those that had between 1 and 10 trees/ha. Species with tree density greater than 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 greater than 10 were regarded 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; common and dispersed = 4, etc. For example, *Cryptocarya* sp. was given a rank of 2 because it was rare and moderately clumped, while *P. simiarum* was given 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 duration of availability during only the nonbreeding season (August–February) was considered. This index of resource abundance was correlated with percent contribution to the non-fig diet to evaluate if hornbills preferred rare fruit resources.

DATA ANALYSES.—All statistical analyses were carried out using EXCEL and SPSS/PC (Norusis 1990). The nonparametric Spearman's rank correlation and chi-square contingency tests (Zar 1974, Siegel & Castellan 1988) and the Sørenson's similarity index were used (Magurran 1988).

RESULTS

OVERALL DIET COMPOSITION IN THE NONBREEDING SEASON.—We recorded 49 fruit species in the nonbreeding season diet of hornbills (Table 1). This included 41 non-fig species (including 3 liana species), 7 fig species, and the flowers of a single species (Table 1). Three species were not actually recorded in the diet (*Litsea monopetala*, *Litsea chinensis*, and *Cinnamommum cecicodaphne*), but are probably eaten by hornbills based on fruit characteristics and local tribal information. The major non-fig species in the diet were 13 species of Lauraceae, 3 of Meliaceae and 2 species each of Annonaceae and Rosaceae (Table 1). Similarity in the diet composition recorded from the three methods was very low (7.3%), with only 3 species recorded by all three methods.

CONSUMPTION AND AVAILABILITY OF NON-FIG DIET SPECIES: DATA FROM PERCHES AND ROOST TREES.—A total of 2977 seeds from 21 non-fig species was counted between September and March 1999 below 92 perch trees used by Great Hornbills and Wreathed Hornbills. A total of 2230 seeds from 15 non-fig species was counted below 7 roost trees in September 1999. Some insect matter (beetles) and crabs were recorded below roost trees. An overall estimate of the importance of the various non-fig species eaten during the nonbreeding season was obtained by combining the data from perches and roost trees. On combining the data, a total of 29 non-fig species was recorded in the diet ($N = 5207$ seeds). Sixty-three percent of the diet was of two species only (*Actinodaphne obovata* and *P. simiarum*). The next 5 important species formed 27 percent of the diet (*Pygeum acuminatum*, 3 species of *Beilshmedia*, and *Alseodaphne peduncularis*). Thus, 87 percent of the non-fig diet during the nonbreeding season came from 7 species.

DO HORNBILLS PREFERENTIALLY CONSUME RARE SPECIES?—Of the seeds of 29 plant species that we recorded below perches and roost trees, only 15 species were represented in phenology plots (Table 2). Of the remaining 14 species, 11 were non-fig trees and 3 were liana species. The abundance of lianas in the habitat is unknown. The 11 non-fig species were presumably rare and therefore unrepresented in the plots. Given that 11 diet species were unrecorded, 8 had densities of less than 2 trees/ha and 4 were less than 5 trees/ha, it appeared that hornbills foraged on many rare non-fig tree species. There was a positive correlation between the index of resource abundance for a given tree species and its percent contribution to the non-fig diet ($r_s = 0.51$, $P < 0.05$, $N = 15$).

FRUIT AVAILABILITY PATTERNS.—The lean fruiting season for hornbills was in the nonbreeding season from August to February (Fig. 1), while a pronounced fruiting peak of hornbill food plant species occurred during the breeding season (April–June, wet season). There was annual variation in fruit availability, and fruiting was especially low during the nonbreeding season of 1998–1999 compared to the other three years (Fig. 1).

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 (Fig. 2). Of the nine fig species in the diet, four were not recorded in plots. The density of the other fig species was 2.7/ha. Figs fruited asynchronously and were available in both seasons (Fig. 2).

Eleven non-fig tree species that fruited and were consumed in the breeding season had a combined tree density of 106 trees/ha. Although the number of species that fruited and were consumed during the nonbreeding season was higher (33) than that available in the breeding season (11 spp.), their combined tree density was only 32 trees/ha. Of these 33 species exclusively consumed in the non-breeding season, 16 were not recorded in the phenology plots. Densities of 5 species that were recorded in the plots were less than 1 tree/ha, 8 species were less than 5 trees/ha, and only one species (*Livistona jenkinsiana*) had a density of 6 trees/ha (Table 2). The most common non-fig species was *P. simiarum* (21 trees/ha), which fruited 9 months of the year (May–August and November–March) and was thus available during both seasons.

DIET COMPOSITION AND RESOURCE PARTITIONING: DATA FROM FEEDING RECORDS.—Fruits comprised the highest proportion (>95%) in the diet of all hornbill species. Only Great Hornbills were recorded foraging for insects. Consumption of animal matter is difficult to observe and was probably underestimated.

Seventy-three percent ($N = 70$) of all feeding records for Great Hornbills (Fig. 3) was on figs (7 spp.). Thirty-five percent ($N = 78$) of all feeding records for Wreathed Hornbills was on figs (6 spp.); the rest were on 13 non-fig species. Great hornbills ate significantly more figs than Wreathed Hornbills ($\chi^2 = 33.22$, df = 2, $P < 0.001$). Forty-seven percent ($N = 17$) of all feeding records for Oriental Pied Hornbills (Fig. 3) was on figs, while 47 percent was on non-fig species (7 spp.).

Significant differences ($\chi^2 = 24.56$, df = 2, $P < 0.001$) occurred among the three hornbill species in the size of fruit consumed (both fig and non-fig). The Oriental Pied Hornbill ate more

TABLE 1. *Species, family, and characteristics of fruits consumed by the three sympatric hornbills in Pakke Tiger Reserve, Arunachal Pradesh, India, during the nonbreeding season (late July–early March) based on 165 sightings (feeding records), 2977 seeds under perch trees, and 2230 seeds under roosts. Method refers to feeding records = F, seed counts below perch = P, and roost trees = R. Fruit type and size: Fl. = fleshy; Pul. = pulpy; oil. = oily; Aril. cap. = arillate capsule; med. = medium; sm. = small; and lrg. = large. GH = Great Hornbill; WH = Wreathed Hornbill; and OPH = Oriental Pied Hornbill.*

Species	Family	Fruiting time	Fruit type & size	Color	GH	WH	OPH	Method
Actinodaphne obovata	Lauraceae	July–Sept.	Fl. drupe, med.	Black		X		P, R, F
[a]*A. angustifolia*	Lauraceae	Sept.–Oct.?	Fl. drupe, med.	Black		X		P
Alseodaphne peduncularis	Lauraceae	Dec.–Jan.	Fl. drupe, lrg.	Black	X	X		P
Amoora wallichi	Meliaceae	May–July	Aril. cap., oil., lrg.	Maroon	X	X	X	R, F
Aphanamixis polystachya	Meliaceae	Nov.–Jan.	Aril. cap., oil., med.	Red	X	X		P
Beilshmedia assamica	Lauraceae	Sept.–Jan.	Fl. drupe, lrg.	Black	X	X		P, F
B. gammieana	Lauraceae	Sept.–Jan.	Fl. drupe, lrg.	Black		X		P, F
Beilshmedia sp.	Lauraceae	Sept.–Jan.	Fl. drupe, lrg.	Black		X		P, F
[a]*Bridelia retusa*	Euphorbiaceae	Oct.	Berry, sm.	Red–orange			X	F
Canarium resiniferum	Burseraceae	Oct.–Feb.	Fl. drupe, lrg.	Black		X		P, R, F
Chisocheton paniculatus	Meliaceae	Feb.–Apr.	Aril. cap., oil. lrg.	Black	X	X	X	P, F
Cinnamommum cecicodaphne	Lauraceae	Nov.–Dec.	Fl. drupe, med.	Black				Potential fds
Cryptocarya amygdalina	Lauraceae	June–Aug.	Fl. drupe, lrg.	Black		X		R
Cryptocarya sp.	Lauraceae	June–Aug.	Fl. drupe, lrg.	Black		X		P
[a]*Elaeocarpus ganitrus*	Elaeocarpaceae	Nov.–Jan.	Fl. drupe, lrg.	Bright blue		X		R
Ficus altissima	Moraceae	Year-round	Fig, med.	Red	X	X		F
F. elastica	Moraceae	Year-round	Fig, sm.	Brown–red	X			F
F. hookeri	Moraceae	Year-round	Fig, lrg.	Dark red–black	X	X	X	F
F. macclellandi	Moraceae	Year-round	Fig, sm.	Yellow	X			F
F. nervosa	Moraceae	Year-round	Fig, sm.	Orange–red	X	X		F
Ficus sp.	Moraceae	Year-round	Fig		X			F
Ficus sp.	Moraceae	Year-round	Fig		X			F
Gnetum ula	Gnetaceae	Oct.–Dec.	Fl. drupe, med.	Pale blue		X		P
Horsfieldia kingii	Myristicaceae	Feb.–Apr.	Aril. cap. oil. lrg.	Yellow	X	X	X	P, F
Hyptianthera sp.	Rubiaceae	Oct.–Dec.	Berry, med.	Yellow		X		F
[a]*Laportea crenulata*	Urticaceae	Dec.–Jan.	Berry sm.	Greenish			X	F
Litsea chinensis	Lauraceae	Aug.–Oct.	Fl. drupe, sm.	Black				Potential fds
L. monopetala	Lauraceae		Fl. drupe, sm.	Black				Potential fds
Litsea sp.	Lauraceae		Fl. drupe, sm.	Blue–black		X		P
Livistona jenkinsiana	Palmae	Oct.–Dec.	Fl. drupe, med.	Blue–black		X		P
Derris sp.	Leguminosae		Dehiscent pods, aril, med.	Orange–red			X	P, stomach content
[a]*Ostodes paniculata*	Euphorbiaceae	Aug.	Berry, sm.			X		F
Phoebe lanceolata	Lauraceae	June–Aug.	Fl. drupe, med.	Black		X		R
Platea latifolia	Icacinaceae	Sept.–Nov.	Fl. drupe, lrg.	Black		X		P, R
Polyalthia simiarum	Annonaceae	May–Aug. Nov.–Mar.	Fl. drupe, med.	Black	X	X	X	P, R, F

TABLE 1. *Continued.*

Species	Family	Fruiting time	Fruit type & size	Color	GH	WH	OPH	Method
Polyalthia sp.	Annonaceae		Fl. drupe, med.	Black		X		P, R
Pygeum acuminatum	Rosaceae	Nov.–Jan.	Fl. drupe, med.	Black	X	X	X	P, F
Pygeum sp.	Rosaceae	Oct.–Nov.?	Fl. drupe, med.		X			P
[a]*Spondias axillaris*	Anacardiaceae	Nov.–Dec.	Pul., Fl. drupe, lrg.	White		X		F
Styrax serrulatum	Styracaceae	Aug.–Oct.	Drupe, sm.	Black		X		F
[a]*Vitex pentaphylla*	Verbenaceae	Oct.–Dec.	Drupe, sm.	Black			X	F
[a]*Zanthoxylum rhetsa*	Rutaceae	Sept.–Nov.	Berry, sm.	Red	X			F
[a]*Zizyphus* sp.	Rutaceae	Oct.	Berry, sm.	Red–orange			X	F
Liana species		Nov.–Jan.	Fl. drupe, med.	Pale blue			X	P, F
Syzgium sp.	Myrtaceae		Drupe, sm.		?	?		R
4 unknown species						X		R
1 unknown species					X			F
[a]*Oroxylum indicum*	Euphorbiaceae	Nov.	Flowers				X	F

[a] Recorded only once.

small fruits (75%) than the Great hornbill (19%) or the Wreathed hornbill (6%). In addition, the larger two hornbills ate significantly (χ^2 = 34.16, df = 1, $P < 0.001$) more capsules and drupes (96% of non-fig fruits) than the Oriental Pied Hornbill, which fed mostly on berries (75% of non-fig fruits). All non-fig food species that had small-sized fruits were berries or drupes. The medium and large fruits were either arillate dehiscent capsules or fleshy single-seeded drupes.

There was 9.5 percent similarity (Sørenson) in non-fig fruit species consumed by all three species. In general, similarity in non-fig diet was low between hornbill species pairs. There was greater similarity between the Great Hornbill and Oriental Pied Hornbill in terms of the number of non-fig species consumed (0.45) than between the Wreathed Hornbill and Oriental Pied Hornbill (0.24) or between the Great Hornbill and Wreathed Hornbill (0.39). Non-fig fruit species richness was highest in the diet of Wreathed Hornbills (30 spp., enumerated from all methods), while the Great Hornbill and Oriental Pied Hornbill were recorded feeding on fruits of 11 species each. Dietary overlap in fig species taken was high.

There were significant (χ^2 = 199.37, df = 4, $P < 0.01$) differences in the use of canopy levels by the three species (Fig. 4a; all sight 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); however, if only the foraging height records were considered (N = 197), the differences in canopy levels used were less pronounced (χ^2 = 9.3, df = 4, $0.05 < P < 0.10$). Sample size for the Oriental Pied Hornbill was small; however, 43 percent of the sightings was in the lower canopy (Fig. 4b).

Eighty-three percent of Great Hornbill sightings (N = 71) was of single birds, pairs, or threes; the rest were of flocks ranging from 4 to 35. Seventy percent of Wreathed Hornbill sightings (N = 77) was of 1 to 3 birds; the rest were in flocks ranging from 4 to 30. A significantly (χ^2 = 4.49, df = 1, $P < 0.05$) higher percentage of Wreathed Hornbill foraging flocks was in numbers greater than 3 (40%) compared to that of the Great Hornbill (24%). There were no significant differences in small and large flocks at non-figs and figs for the Wreathed Hornbill or the Great Hornbill (χ^2 = 0.186, df = 1).

TABLE 2. *Density, dispersion (variance to mean ratio), density/dispersion rank, length of fruiting season and index of abundance for 15 non-fig fruit resources and their contribution to hornbill diet during the nonbreeding season in Pakke Tiger Reserve, Arunachal Pradesh, India.*

Tree species	Tree density (ha)	Variance/ mean ratio	Rank	Length of fruiting (mo)	Index of abundance	% in diet
Polyalthia sp.	0.19	4	2	2	4	0.18
[a]*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
[a]*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
[a]*Cryptocarya amygdalina*	2.28	3.9	5	2.5	12.5	0.12
Actinodaphne obovata	3.24	30.94	8	4	32	41.35
[a]*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
[a]*Amoora wallichi*	7.43	10.07	8	2	16	0.36
[a]*Polyalthia simiarum*	20.76	20.35	9	6	54	21.79

[a] Species that fruit mainly in the breeding season.

DISCUSSION

Although the availability of non-fig fruit species that were consumed during the nonbreeding season was much less than in the breeding season, hornbills consumed a greater number of non-fig species during the nonbreeding season. This contradiction lies in the fact that many species recorded in the diet during the nonbreeding season were either rare or not represented in phenology plots. It is also possible that some of these species occur more commonly outside the sampling area. The large number of rare species recorded in the diet suggests that hornbills range widely in search of fruits of rare species, although overall contributions of these were low. This implies that hornbills range widely in search of food resources in the nonbreeding season. Observations by tribal people also indicated that Wreathed Hornbills move seasonally to higher elevation forests in search of rare and patchily distributed resources.

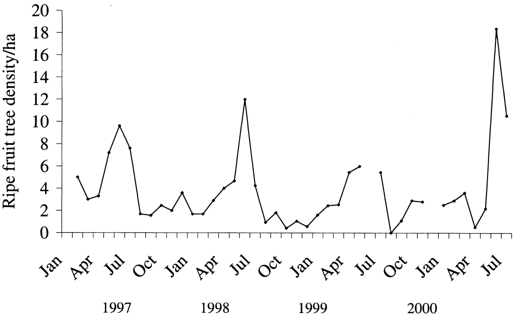

FIGURE 1. Patterns in ripe fruit availability of hornbill food plants (1997–2000) in Pakke Tiger Reserve, Arunachal Pradesh, India.

Despite the wide diet breadth, hornbill foraging patterns were selective in that they relied on a few common species for the bulk of their diet; however, the positive relation between resource abundance and percent contribution to diet indicates that hornbills consumed fruit resources as they were encountered and common species were most important in their diet. Aaron French (personal communication) also found that although African forest hornbills (*Ceratogymna* spp.) consumed fruits of over 100 species, the top 10 diet species contributed over 60 percent of the diet and that there were no pronounced nutritional differences between the most consumed and least consumed fruit species. Nevertheless, consumption of a diverse array of fruits may be essential to meet nutritional requirements since there is usually high variation in the nutrient content of fleshy fruits (Herrera 1982, Martinez del Rio & Restrepo 1992, Corlett 1996). Most fruits that were available and consumed in the nonbreeding season were small and medium in size. While hornbills consumed a small range of high quality lipid-rich fruits (belonging mainly to four families) during the breeding season (Datta 2001), the nonbreeding season diet included small sugar-rich watery fruits from many other families.

The Great Hornbill and Wreathed Hornbill

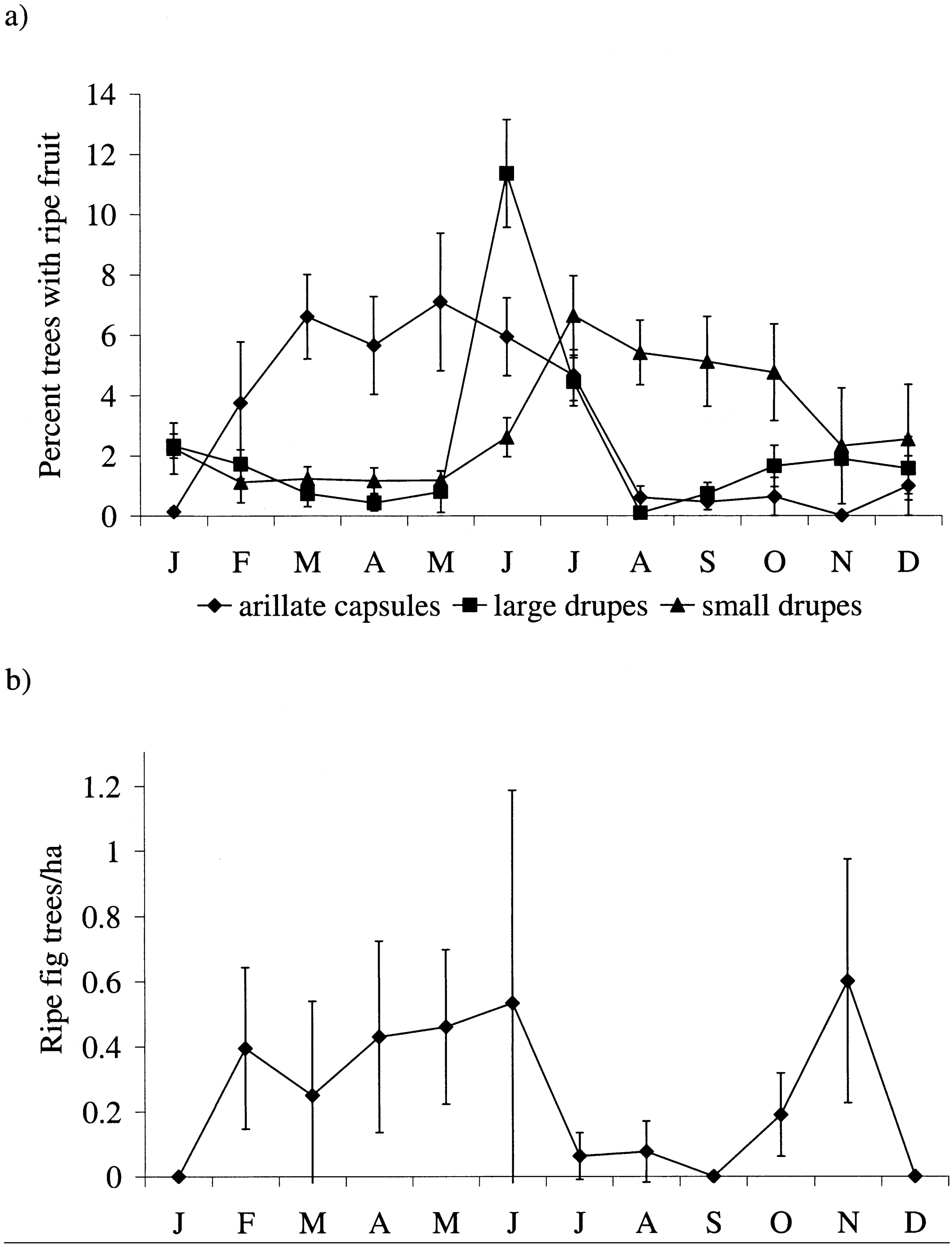

FIGURE 2. a. Ripe fruit availability of non-fig fruit types (1997–2000) in Pakke Tiger Reserve, Arunachal Pradesh, India. Error bars are standard errors of the mean for percentage of trees with ripe fruit for each fruit type category over four years. b. Ripe fruit availability of figs (1997–2000) in Pakke Tiger Reserve, Arunachal Pradesh, India. Error bars are standard errors of the mean for fig fruit tree density over four years.

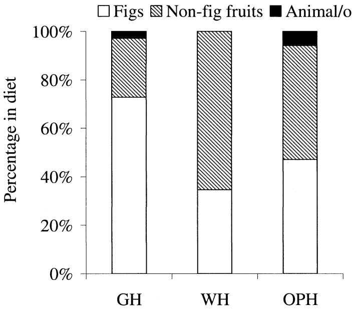

FIGURE 3. Percentage contribution of figs, non-figs, and animal matter in the nonbreeding season diet of three hornbill species in Pakke Tiger Reserve, Arunachal Pradesh, India. $N = 165$ sightings, GH = Great Hornbill, WH = Wreathed Hornbill, OPH = Oriental Pied Hornbill.

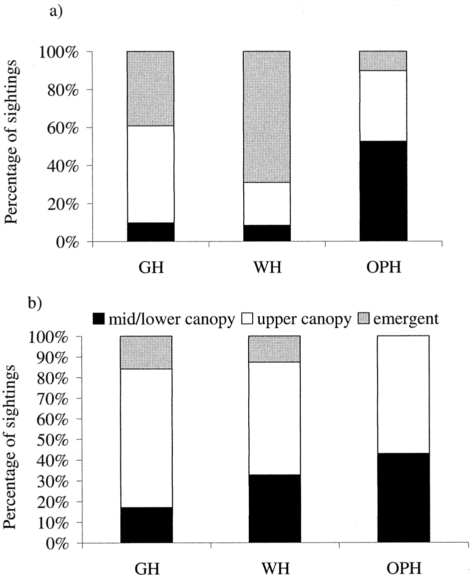

FIGURE 4. a. Use of canopy levels by the three hornbill species in Pakka Tiger Reserve, Arunachal Pradesh, India. $N = 963$ sightings, GH = Great Hornbill, WH = Wreathed Hornbill, OPH = Oriental Pied Hornbill. b. Foraging levels used by the three hornbill species in Pakke Tiger Reserve, Arunachal Pradesh, India. $N = 197$ sightings, GH = Great Hornbill, WH = Wreathed Hornbill, OPH = Oriental Pied Hornbill.

seemed to be partitioning resources broadly in terms of the relative contributions of figs and non-figs in the diet. In addition, the Oriental Pied Hornbill differed from the two larger hornbill species by consuming smaller-sized berries more than arillate capsules and drupes. Also, there were some differences in foraging strata used by the three species. Non-fig diet diversity was also greater for the Wreathed Hornbill. The greater flocking behavior and nomadic tendencies of *Aceros* have been attributable to their specialized diet of lipid-rich fruits, which are patchy in space and time (Leighton & Leighton 1983, Tsuji *et al.* 1987, Poonswad & Tsuji 1994). Therefore, during periods of fruit shortage they track fruit resources over larger areas (Leighton & Leighton 1983).

The Great Hornbill, a monogamous territorial species with the largest body size, consumed more figs than the other two species. Figs fruit asynchronously, occur at relatively high densities in the lowland forest, and are available throughout the year (Datta 2001). Hierarchy based on body size may help this species to defend fruit resources in smaller territories (Leighton 1982), and during this study, Great Hornbills always chased away Wreathed Hornbills from fruiting fig trees (Datta, pers. obs.). The Great Hornbill in southern India and in Thailand is also territorial and largely a fig fruit specialist (Poonswad & Tsuji 1994, Kannan & James 1999). Previous studies have also documented a greater reliance by all *Buceros* species on fig fruits (Leighton 1982, 1986; Poonswad *et al.* 1983, 1986, 1987; Hadiprakarsa & Kinnaird 2001), and the Wreathed Hornbill and other *Aceros* species in most areas rely more on non-fig fruits although relative importance of figs in the diet varies (Poonswad *et al.* 1983, Leighton 1986, Kinnaird *et al.* 1996, Hadiprakarsa & Kinnaird 2001).

It has been suggested that a reliance on figs may 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 are much more commonly noted in many *Aceros* species (Leighton 1986, Poonswad & Tsuji 1994, Suryadi *et al.* 1998), which are even considered nomadic at times. The idea that Great Hornbills eat figs while Wreathed Hornbills move greater distances to access patches of high-quality non-fig resources seems to be supported. Communal roosting by Wreathed Hornbills in larger flocks is also more notable during the nonbreeding season and could be related to foraging on patchily distributed non-fig fruits (Datta 2001). Great Hornbills also roost communally in the nonbreeding season, while few join roosts during the breeding season (Datta 2001).

Data for the smaller Oriental Pied Hornbill are limited, but suggest that they are more generalist feeders, feeding on several small-fruited trees and lianas and foraging lower in the canopy. They also occur more often in disturbed, secondary riverine forests of low stature and edges than in interior primary forest (Datta 1998).

To conclude, the three hornbill species in the area seem to be partitioning food resources in the nonbreeding season. In Southeast Asian forests such as in Borneo, Thailand, and Sumatra, where comparative studies of sympatric hornbill assemblages have been conducted, coexistence is also made possible by diverse ways of resource partitioning among species (Leighton 1982, 1986; Hadiprakarsa & Kinnaird 2001). The differing use of resources and the wide diet breadth of hornbills during the nonbreeding season despite low fruit availability in the foothill forest imply that hornbills (mainly the Wreathed Hornbill) range more widely, possibly in higher elevation forests during the nonbreeding season. Conservationists must consider the importance of including the large, surrounding reserve forest patches that lie outside designated protected areas to effectively protect hornbills, especially when fruit resources are rare and patchy in distribution.

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LITERATURE CITED

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, 9–12 May 2001, Phuket, Thailand.

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, India.

Cody, M. L. 1985. Habitat selection in birds. Academic Press, Orlando, Florida.

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

Datta, A. 1998. Hornbill abundance in unlogged forest, selectively logged forest and a plantation in western Arunachal Pradesh. Oryx 32: 285–294.

———. 2001. An ecological study of sympatric hornbills and fruiting patterns in a tropical forest in Arunachal Pradesh. Ph.D. dissertation. Saurashtra University, Rajkot, India.

———, and S. P. Goyal. 1997. Responses of arboreal mammals to selective logging in western Arunachal Pradesh. Unpublished report. Wildlife Institute of India, Dehradun, India.

French, A. R., A. Lamperti, E. S. Dierenfield, and T. B. Smith. 2001. Nutrient analysis of fleshy fruit in the diet of African Ceratogymna hornbills. Paper presented at the Third International Hornbill Workshop, 9–12 May 2001, Phuket, Thailand.

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 2001, Phuket, Thailand.

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. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. Ecology 63: 773–785.

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: 448–449.

———, and, ———. 1999. Fruiting phenology and the conservation of the Great Pied Hornbill (*Buceros bicornis*) in the Western Ghats of Southern India. Biotropica 31: 167–177.

Kemp, A. C. 1995. The hornbills. Oxford University Press, Oxford, England.

Kinnaird, M. F., and T. G. O'Brien. 1999. Breeding ecology of the Sulawesi Red-knobbed Hornbill *Aceros cassidix*. Ibis 141: 60–69.

———, ———, and S. Suryadi. 1996. Population fluctuation in Sulawesi Red-knobbed Hornbills: tracking figs in space and time. Auk 113: 431–440.

Leighton, M. 1982. Fruit resources and patterns of feeding, spacing and grouping among sympatric Bornean hornbills (Bucerotidae). Ph.D. dissertation. University of California, Davis, California.

———. 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, Princeton, New Jersey.

———, 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, Oxford, England.

Ludwig, J. A., and J. F. Reynolds. 1988. Statistical ecology. John Wiley and Sons, New York, New York.

Magurran, A. E. 1988. Ecological diversity and its measurement. Croom Helm, London, England.

Martinez del Rio, C., and C. Restrepo. 1992. Ecological and behavioural consequences of digestion in frugivorous animals. Vegetatio 107/108: 205–216.

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. Conserv. Biol. 12: 516–520.

Mudappa, D. 2000. Breeding biology of the Malabar Grey Hornbill (*Ocyceros griseus*) in southern Western Ghats. J. Bombay Nat. Hist. Soc. 97: 15–24.

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.

Norusis, M. J. 1990. SPSS/PC+. SPSS, Inc., Chicago, Illinois.

Olson, D. M., and E. Dinerstein. 1998. The global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. Conserv. Biol. 12: 502–515.

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.

———, ———, 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, Thailand.

———, ———, 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, 24–27 February 1983, Los Angeles, California.

———, ———, and ———. 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. 22–29 June 1986. University of Ottawa Press, Ottawa, Ontario, Canada.

———, ———, and ———. 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, pp. 250–315. 11–15 February 1987, International Foundation for the Conservation of Birds. North Hollywood, California.

Raman, T. R. S. 2001. Effect of slash-and-burn shifting cultivation on rainforest birds in Mizoram, northeast India. Conserv. Biol. 15: 685–698.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, England.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185: 27–39.

Siegel, S., and N. J. Castellan Jr. 1988. Non-parametric statistics for the behavioural sciences, 2nd edition. McGraw-Hill, New York, New York.

Singh, P. 1991. Avian and mammalian evidences in Pakhui Wildlife Sanctuary in East Kameng district, Arunachal Pradesh. Arunachal For. News 9: 1–10.

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. Biodiversity Research and Training Program, Bangkok, Thailand.

Tsuji, A., P. Poonswad, and N. Jirawatkavi. 1987. Application of radio-tracking to study ranging patterns of hornnbills (Bucerotidae) in Thailand. Proceedings of the Jean Delacour/IFCB Symposium on Breeding Birds in Captivity, pp. 316–351. International Foundation for the Conservation of Birds. North Hollywood, California.

Whitmore, T. C. 1998. An introduction to tropical rain forests, 2nd edition. Oxford University Press, Oxford, England.

Zar, J. H. 1974. Biostatistical analysis. Prentice–Hall, Engelwood Cliffs, New Jersey.