SOME ASPECTS OF FOOD AND FEEDING ECOLOGY OF SYMPATRIC HORNBILL SPECIES IN KHAO YAI NATIONAL PARK, THAILAND

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ABSTRACT

Hornbills are known to be omnivorous. The food of four hornbill species studied at Khao Yai National Park could be divided into animals and fruits (further divided into figs and non-fig fruits). The proportions of different foods consumed by hornbills varied from species to species. The fruits eaten by the hornbills were categorised into one of 4 groups: fleshy pulp and fine seeds (figs), split-husked when ripening, dry flesh with a single stone-seed, and soft or juicy flesh with a single stone-seed.

The four hornbill species that were studied consumed relatively similar types of food. The male and female Great Hornbills *Buceros bicornis*, while sharing duty in feeding the nestling, and the breeding male Brown Hornbills *Anorrhinus (Ptilolaemus) tickelli* and nest helpers, showed high similarity of food brought to broods.

Food preference was determined and it was found that hornbills feed more on fruits which are abundant rather than on fruits with a high nutritional value. Aside from figs, among the first 12 ranks, *Polyalthia viridis*, *Strombosia* spp., and *Horsfieldia glabra* were the most preferred by all four hornbill species. Among animal foods, centipedes and cicadas were most preferred.

INTRODUCTION

Feeding is one of the essential activities of all animals, so there is no doubt that most animals are dominated by their never-ending demand for food. The structure and behaviour of most animals are affected by the nature of their required foods and the way in which they are obtained (McFarland, 1981).

Many birds feed on a mixed diet with a more or less marked preference for certain kinds of food (Dorst, 1974). In frugivorous vertebrate species which have fixed ranges or year-round territories, the diet may change from more preferred fruit species to less preferred ones when the former become scarce. Birds with high energetic demand per unit body mass supplement their frugivory by hunting animal prey (Leighton & Leighton, 1983).

Asian hornbills are generally frugivorous, but they sometimes become omnivorous, particularly in the breeding season. Proportions of animal food in the diet may vary by species and perhaps by season (Poonswad et al., 1986).

In this paper, results of investigations on food and feeding are presented with an emphasis on feeding biology, types of food and their nature, food consumption, food similarity and food preference of four sympatric hornbill species during the breeding season at Khao Yai National Park.

STUDY AREA AND METHODS

The study area was an area of approximately 70 km^2 in Khao Yai National Park, central Thailand (approximately 14°15'–30'N and 101°20'–24'E), with an altitudinal range of 400–1,060 m a.s.l. The habitat consists of seasonally wet evergreen forest (62 km^2) and grassland (8 km^2) (Fig. 1).

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The average temperature ranges from 17° C in December and January to 28° C in April and May. The average annual rainfall was 2,270 mm (NATIONAL PARKS DIVISION, 1987). During the dry season (December to April) most of the small streams become dry.

Fruit and animal food were collected and recorded on regular visits to nests whilst studying breeding behaviour during the breeding seasons from 1982–1985. Food samples were also collected at fruit trees.

Observations at the nests were carried out from 14 January–28 June at 2–10 day intervals. Food items and the amount of food which males and nest helpers brought to broods were recorded at one hour intervals from 0600–1700 hours.

Food items were identified using binoculars (8 × 30), spotting scopes (×20 and ×40) and/or photographs taken with 400, 500 and 800 mm telephoto lenses, depending on the distance from the observation blind to the nest. Regurgitated seeds and dropped food, as well as faeces, were collected to help ascertain the identification of some food items. Food plant specimens were prepared for identification if a fruiting food-tree was found. Plant samples were then sent to the Forest Herbarium, Royal Forest Department, for further identification. Efforts were made to identify the food items at least with regard to family.

The four hornbill species studied are Great *Buceros bicornis*, Wreathed *Rhyticeros undulatus*, Oriental Pied *Anthracoceros albirostris* and Brown Hornbills *Anorrhinus* (*Ptilolaemus*) *tickelli*.

Foraging Methods

Direct and indirect observations were made to investigate foraging methods used by hornbills, such as cracking, probing, hawking, plucking, snatching, etc. These methods were defined in the following manner:

Cracking tree bark: The bird inserted its bill in the cracked bark of either a living or dead branch.

Probing: The bird put its bill into a tree cavity and searched.

Hawking: The bird took prey in the air.

Plucking: The bird used its bill to pluck food (usually fruit) without much effort, from a perch.

Snatching: The bird picked up food, such as a fruit or an insect on a leaf, with speed.

The types of food brought by the males can be an indicator of his foraging method. For example, fish were probably caught by snatching.

Food Consumption

Observations were made every other week at each nest, recording from the first to the last feeding of the day. Frequency and total amount of food brought per hour by males were recorded. The wet weight of each food item was assessed based on the average wet weight of the same food item (which was obtained when males dropped it while feeding or when it was collected elsewhere later). For animal food, fresh specimens of the animal used for weighing may not always have been the same species as those actually eaten by hornbills, but they were in the same groups and similar in size and were obtained within the study site (this presumption was necessary because of the difficulty of collecting and identifying the species in this tropical environment). There was no attempt to study how many kinds of plant species produced fruit food during the breeding season, but duration of various fruit species brought to broods was recorded.

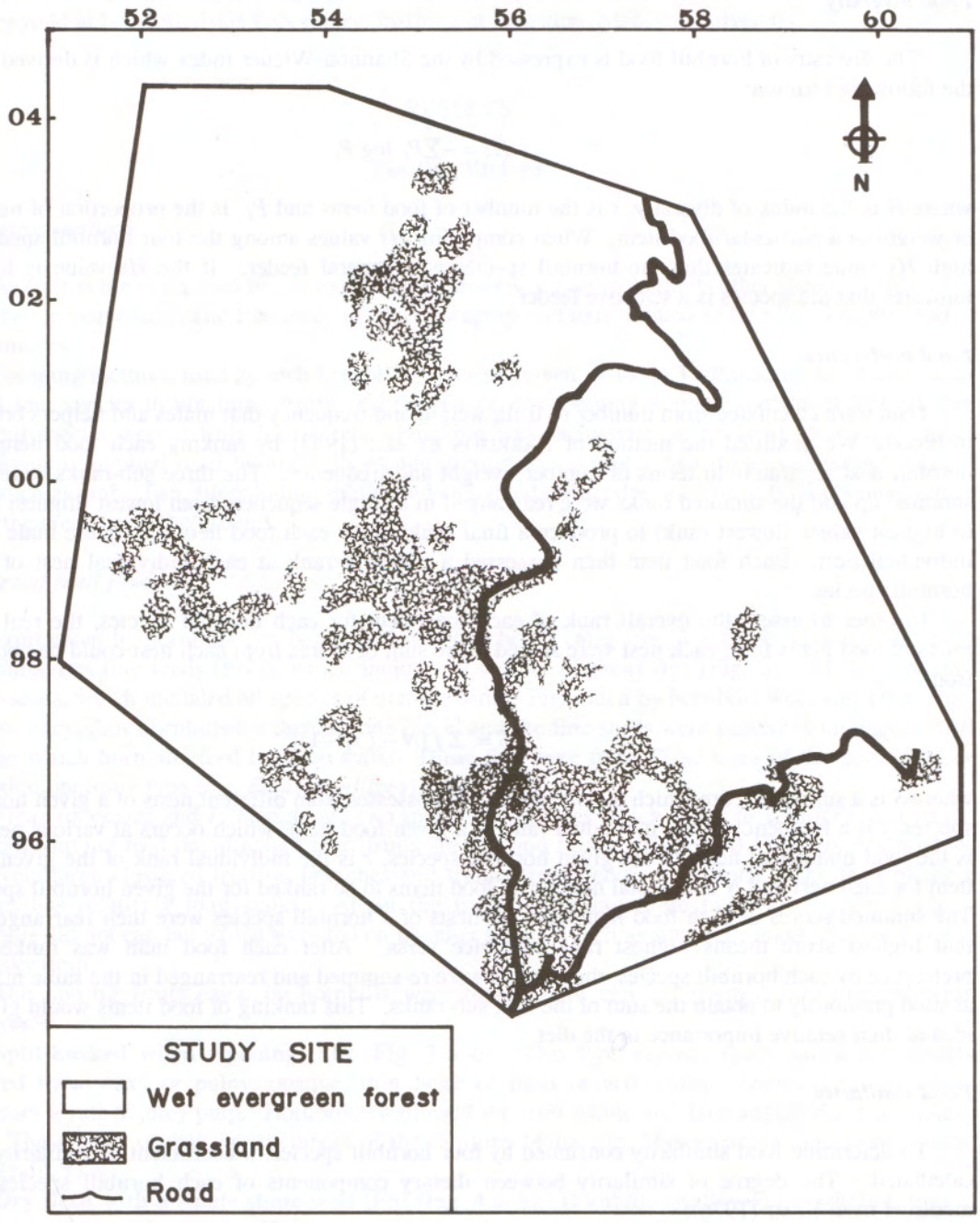

Figure 1. A map of Khao Yai National Park showing the study area, from 1:50,000 sheet 52371.

Data Analysis

Food diversity

The diversity of hornbill food is expressed by the Shannon-Wiener index which is derived from the following formula:

$$Hs = -\sum_{i=1}^{s} P_i \log P_i$$

where H is the index of diversity, s is the number of food items and P_i is the proportion of number or weight of a particular food item. When comparing Hs values among the four hornbill species, a high Hs value indicates that the hornbill species is a general feeder. If the Hs value is low, it indicates that the species is a selective feeder.

Food preference

Data were calculated from number of fruit, weight and frequency that males and helpers brought to broods. We modified the method of HARRISON ET AL., (1983) by ranking each food item in a hornbill nest separately in terms of number, weight and frequency. The three sub-ranks were then summed up and the summed ranks were rearranged in a single sequence, from lowest (highest rank) to highest values (lowest rank) to produce a final ranking for each food item fed by the male at an individual nest. Each food item then possessed a different rank at each individual nest of each hornbill species.

In order to assess the overall rank of each food item for each hornbill species, the real final ranks of food items from each nest were scored. The sum of scores from each nest could be obtained from

$$S = \sum_{i=1}^{p} f[N - (r_i - 1)]$$

where S is a summed score which a given food item possesses from different nests of a given hornbill species, f is a frequency of the individual rank of a given food item, which occurs at various nests, p is the total number of nests of the given hornbill species, r is the individual rank of the given food item for each nest and N is the total number of food items to be ranked for the given hornbill species. The summed scores of each food item from all nests of a hornbill species were then rearranged, so that highest score means highest rank and vice versa. After each food item was ranked for preference by each hornbill species, these ranks were re-summed and rearranged in the same manner as used previously to obtain the sum of the first sub-ranks. This ranking of food items would give an idea of their relative importance in the diet.

Food similarity

To determine food similarity consumed by four hornbill species, a coefficient of similarity was calculated. The degree of similarity between dietary components of each hornbill species was modified from KEMP (1976):

$$C = 2W / (a+b)$$

where C is the similarity coefficient, W is the sum of all food items in the diet which four species share in common, a is the sum of all food items in the diet of one species, and b is the sum of all food items in the diet of the other species.

Nutritional value

Fruits which were major components of the diet were sent for analysis of nutritional value and energy yield at Food Analysis Laboratory, Institute of Nutrition, Mahidol University.

RESULTS

Feeding Biology

Foraging methods

As fruit is the main food for all four hornbill species, foraging methods other than plucking were observed infrequently. The frequency of other foraging methods seemed to be related to the degree of carnivory.

Foraging methods used by each hornbill species are given in Table 1. Plucking was mostly used by all four species in obtaining fruits, and the use of this foraging method confirmed that all four hornbill species were mainly fruit eaters. Plucking was exclusively an arboreal foraging method. The foraging method used by hornbills on the ground was not observed directly, although animal food such as crabs, fish, filopaludina snails, and elongated millipedes, may have been obtained either from the creek or on the ground.

Nature of fruit food

Fruit eaten by hornbills can be divided into two broad categories, i.e. those having a soft pulp and numerous fine seeds (FNS), which include all species of *Ficus* figs (Fig. 2), and those having stone-seeds, which included all species of non-fig fruits. Figs eaten by hornbills were soft when ripe, but not juicy, thus hornbills ate them as one piece, and the fine seeds were passed in the faeces. All figs on which hornbills feed have no stalk. These figs were from *Ficus* trees of the strangling or smooth monotrunk type (e.g. *Ficus capillipes*).

Ficus racemosa and *F. hispida* are two species of fig trees which occur in Khao Yai but which hornbills did not feed on, although their fruits are soft and fleshy. These two *Ficus* species produce relatively large clustered fruit on branches and trunks from February to April. The fruit of these species has relatively long stalks. All of the fruits (including these two *Ficus* species) which hornbills did not eat, but which were fed on by other animals such as squirrels, had either long stalks or husky flesh.

The non-fig fruits eaten by hornbills were diverse and can be grouped into the following categories:

Split-husked when ripening (SF) (Fig. 3 a–b): This type exposes seeds which are usually covered by a waxy or pulpy, opaque, thin layer of flesh or aril, except *Knema laurina,* which possesses a rather juicy pulp. Hornbills swallowed the fruit whole and later regurgitated the stone-seed. These types of fruit are members of the families Meliaceae, Myristicaceae, and Connaraceae (Appendix 1).

Dry flesh with a single stone-seed (FS) (Fig. 4 a–b): Hornbills swallowed the whole fruit and regurgitated the stone-seed. These fruits are members of the families Burseraceae, Annonaceae, Olacaceae, Elaeocarpaceae and Symplocaceae (Appendix 1).

Soft or juicy flesh with a single stone-seed (FJ) (Fig. 5): Hornbills swallowed the whole fruit and regurgitated the stone-seed. All of these fruits possess a pulp which is relatively easily separated from the seed. Fruits of this type are members of the families Myrtaceae, Podocarpaceae, Urticaceae, Elaeagnaceae, and Lauraceae (Appendix 1).

Table 1. Frequency and percentage of different foraging methods used by the four hornbill species observed during the breeding and non-breeding seasons. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Foraging method	Frequency of use by species									
	GH		WH		PH		BH		All species	
	No.	%	No.	%	No.	%	No.	%	No.	%
Cracking tree bark	23	11.8	5	1.8	9	4.4	0	0	37	4.4
Probing	7	3.6	0	0	3	1.5	0	0	10	1.2
Hawking	0	0	0	0	12	6	21	13.6	33	4
Plucking	165	84.6	276	98.2	170	84.6	122	78.7	733	88.1
Snatching	0	0	0	0	7	3.5	12	7.7	19	2.3
Total	**195**	**100**	**281**	**100**	**201**	**100**	**155**	**100**	**832**	**100**

No hornbills were observed to feed on fruits with thick pericarps which require peeling, such as those of *Nephelium*. The pulp of such fruits, which are common in the study site, is relatively difficult to separate from the seed, as compared with the previously mentioned non-fig fruits.

Food availability

Various *Ficus* species were present throughout the period of study, although no attempt was made to specifically document this. The availability of ripe crops of some non-fig fruit is shown in Table 2. During the 4 years of data collection, there were 5 species, *Horsfieldia glabra*, *Knema laurina*, *Strombosia* spp., *Polyalthia viridis* and *Dysoxylum* sp., which supplied ripe crops throughout. *Polyalthia viridis* was the most remarkable long-period fruit supplier, particularly in 1985. Another interesting species was *Dysoxylum* sp., which was a good supplier except in 1984. Unfortunately, no study was made on the productivities of these non-fig trees.

Food consumption

Food consumed by the four hornbill species can be classified as figs, non-fig fruit, and animals. The feeding rate for fruit foods varied significantly according to the size of hornbill. The two larger species, the Great Hornbill and the Wreathed Hornbill, consumed fruit at a higher rate (g/h) than the two smaller species, Oriental Pied Hornbill and Brown Hornbill (Table 3). However, the feeding rate of animal food did not vary according to bird size. There were significant differences between the four hornbill species in consuming animal food, except between Great and Oriental Pied Hornbills, and Great and Brown Hornbills (Table 3). Brown Hornbills fed on animal food at the highest rate, whereas the Wreathed Hornbills fed at the lowest rate.

It was found that there was no significant correlation between the feeding rate and the length of breeding cycle in any of the hornbill species ($r_s = 0.433$, $n = 9$, $P > 0.05$; $r_s = -0.40$, $n = 4$, $P > 0.05$; $r_s = -0.342$, $n = 12$, $P > 0.05$; $r_s = -0.257$, $n = 6$, $P > 0.05$).

The results clearly showed that broods of the two larger hornbill species ate more fruit than did those of the smaller ones (Table 3). Considering the two categories of fruits, fig and non-fig, it was found that broods of the two larger species consumed significantly more fig than those of the two smaller species (Table 3), but there was no significant difference in the consumption rate of non-fig fruit by these four hornbill species (Table 3). Hence, the two larger species preferred figs more than the smaller species. In contrast, no hornbill species had any special favour for non-fig fruits.

Figure 2. An example of the fruit and seeds of a fig species, *Ficus altissima*.

a) Ripe fruit

(b) Seeds.

Figure 3. An example of a SF (split-husked when ripening) fruit species, of the genus *Dysoxylum*.

a) Unripe fruit.

b) Ripe fruit and seeds.

Figure 4. An example of a FS (dry flesh with a single stone-seed) fruit species, *Polylthia viridis.*

Figure 5. An example of a FJ (soft or juicy with a single stone-seed) fruit of the genus *Elaegnus.* Unripe fruit (green), ripe fruit (orange) and seeds are pictured.

Food diversity and similarity

The food eaten by the four hornbill species was very diverse. There were approximately 125 species recorded as food items. They comprised 36 identified fruits (Appendix 1), 26 unidentified fruits and at least 9 groups of animals (Appendix 2). The diversity of food eaten by the hornbills did not vary according to the size of the hornbill. Of the four hornbill species, Oriental Pied Hornbills fed on the greatest variety of food items (fruit and animals), whereas Wreathed Hornbills fed on the least variety (Table 4). The results of the calculation of Shannon-Wiener indices of diversity in Table 4 show the degree of specialisation among these four hornbill species. Wreathed and Brown Hornbills are considered as specialists in taking fruit (*Hs* = 1.557) and animal (*Hs* = 1.083) respectively, when compared with the other two species (Table 4). As shown in Appendix 2, Great Hornbills were more specialised in hunting large prey than Oriental Pied and Brown Hornbills. It appeared that the diversity of food eaten by each species was proportional to its average breeding success (Table 4).

Since these four hornbill species live sympatrically, they were expected to use the same food resources. Food items recorded eaten by the hornbills showed relatively high similarities (Appendices 1 & 2). Of 36 identified species of fruits, 21 (58%) were eaten by all four species. Only four fruit species were eaten only by one of the hornbill species. These were *Jasminum* sp., *Trichosanthes tricuspidata* and *Sloanea sigun* eaten by the Oriental Pied Hornbills, and *Podocarpus polystachya* eaten by the Brown Hornbills. It is interesting to note that, besides figs, fruits of trees in the family Meliaceae, which yield high energy, were eaten by all four hornbill species (Table 6).

The degree of food similarity between hornbill species, as shown in Table 5, indicates that all four species of hornbills ate similar food. Hence, they obtained food from the same sources. When considering the rate of taking animal food within the same species, Wreathed Hornbill showed the lowest degree of similarity between individuals, whereas the Brown Hornbill showed the highest degree of similarity. This suggests that individual male Wreathed Hornbills hunted from different sources. In contrast, it is indicated that Brown Hornbills hunted for animal food together.

In the case of Great Hornbills, females of which share feeding duty with males after their emergence, the males and the females brought similar food items to broods ($C = 0.83$, $n = 16$). In Brown Hornbills, a co-operative breeding species, almost exactly the same food items were brought to the broods by both the breeding male and the helpers ($C = 0.93$, $n = 14$). Hence, the breeding male and the helpers were foraging together.

Food preference

It is very difficult to investigate the food preference of these four hornbill species under natural conditions. However, data collected during the breeding seasons of 1982–1985 revealed variations in feeding of food items. These variations were found within and between the species of hornbills, thus permitting ranking preference (Tables 6 and 7). Among 12 non-fig fruits, *Polyalthia viridis*, *Strombosia* sp., and *Horsfieldia glabra* were most preferred by all four species. In animal foods, centipedes and cicadas were most preferred.

When considering total food by weight alone, the percentage of the 12 most-preferred non-fig fruits (Table 6) that contributed to the total food are presented in Figure 6. It was apparent that *Polyalthia viridis* contributed most (26.9%) in the total food of Wreathed Hornbills by weight, whereas the rest of the fruit species were in similar proportion. Brown Hornbills had *Polyalthia viridis*, *Strombosia* sp., *Dysoxylum* sp. and *Cinnamomum subavenium* in similar percentages (9.1%, 8.3%, 8.7%, 9.7% respectively) of their total diet. Except for *Polyalthia viridis*, the Brown Hornbill chose to feed more on high energy yielding fruits (Table 6).

The nutritional values of some fruit food recorded in the breeding season indicated that hornbills did not always select those fruits of highest nutritional value (Table 6). Rather, the data suggested

that hornbills would select fruit by availability or abundance, in combination with other characteristics such as the ease of eating or of removing the seed, the attractiveness of the fruit by colour, and so forth.

DISCUSSION

Diet Composition and Preferences

Details of diet composition and food preferences observed in this study differ from those found for seven species of Bornean hornbills (LEIGHTON, 1986). All hornbills at Khao Yai National Park fed on figs, non-fig fruits, and animals in decreasing order of consumption. Brown Hornbills consumed animals most, followed by figs and non-fig fruits. Except for the Helmeted Hornbill *Buceros (Rhinoplax) vigil* which feeds mostly on figs followed by animals, Bornean hornbills fed on non-fig fruits, figs, and animals in decreasing order of consumption (LEIGHTON, 1986). LEIGHTON (1986) also observed that non-territorial *Rhyticeros* hornbills hunted less for animal prey and consumed more lipid-rich, drupaceous fruits of the families Lauraceae and Burseraceae, fruits which are equivalent to non-fig fruits in this study. This is similar to the diet of Wreathed Hornbills in this study, but during the breeding season they were found to consume a great quantity of fruit of *Polyalthia viridis*, despite the fact that this fruit was relatively low energy or low lipid. This species consumed less lipid-rich fruit in the breeding season. Thus, richness in lipids is less important in food selection than abundance, availability or the other characteristics discussed below.

Bushy-crested Hornbills *Anorrhinus galeritus* have a breeding strategy similar to Brown Hornbills (co-operative breeding system), but the composition of the diet is different, with non-fig fruits taken most, followed by figs and then animals (LEIGHTON, 1986). The differences in diet composition between the two species may be due to the differences in the availability and abundance of food types within the area and/or competition with other species which live sympatrically.

Hornbills at Khao Yai also had a completely different diet from African hornbills, *Bucorvus* spp. and *Tockus* spp., which are mainly insectivorous (KEMP, 1976, 1979). It is obvious that the habitat types have strong influence on food and feeding strategies of hornbills. The African hornbills live in savannas where fruit trees may be scarce as compared with the forest habitat of the species studied.

LEIGHTON (1986) stated that hornbills prefer lipid-rich fruits. From this study, it is suggested that the preference for such fruits may be limited to the non-breeding season, when hornbills could spend more time searching out more favourite fruits. In the breeding season, breeding males may have to spend the minimum amount of time to gather as much food as possible for females and broods. Moreover, competition pressure should be higher in the breeding season than in the non-breeding season. For these reasons, hornbills would feed on less favoured, but more abundant fruits in the breeding season.

It is hypothesised that hornbill preference for fruits is chiefly determined by abundance of the food fruits. SORENSEN (1981) and FOSTER (1990) have shown that birds become less concerned with the quality of food when a large quantity of the food is available, and they also become less selective. Indeed, birds may not be able to determine the pulp composition and nutritional richness. *Ficus* was obviously the most important dietary component in the hornbill's diet, although it yielded relatively low energy (POONSWAD ET AL., 1988). Figs are available monthly or even weekly (POONSWAD ET AL., *in press*). Among the non-fig fruits, *Polyalthia viridis* was the most common. Our observations in this study strongly indicate that all four hornbill species fed on fruits which were abundant, regardless of nutritional value. The large amount of any food item consumed by hornbills should reflect the abundance of such food. This confirms that abundance is an important factor for food preference.

Table 2. Duration of fruiting of some species of non-fig fruits which were brought to the broods of all four hornbill species during the breeding seasons of 1982–1985 at Khao Yai National Park.

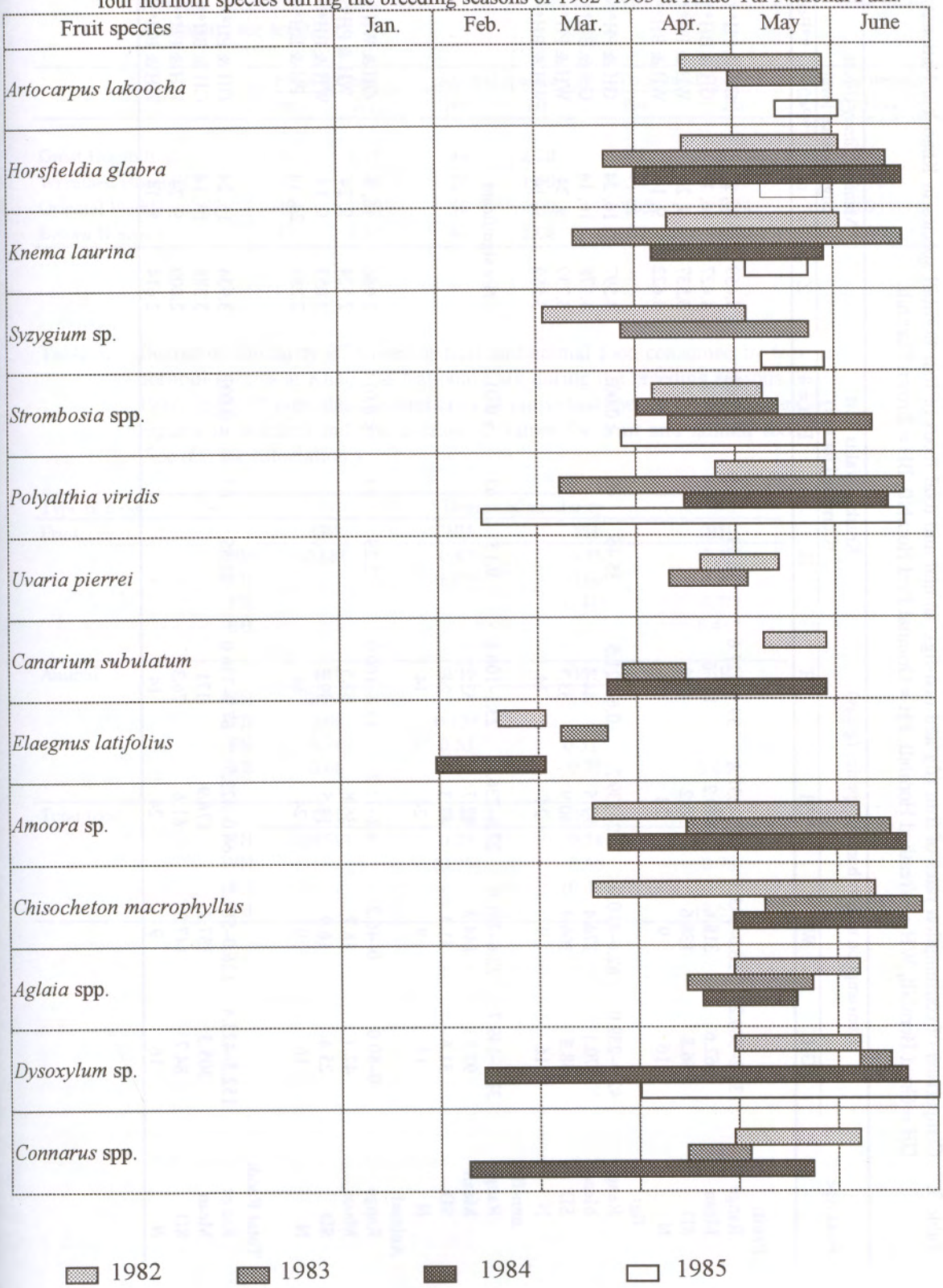

Table 3. Comparison of consumption rates of fruit (fig and non-fig), animal and total foods of four hornbill species in Khao Yai National Park. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Food type	Consumption rate by hornbill species (g/day)				Kruskal-Wallis Test (Corrected for ties)			Mann-Whitney U-test Significance level		
	GH	WH	PH	BH	H	*n*	P(df = 3)	Z	n1, n2	*P<0.05, **P<0.01
Fruit:										
Range	135.2–360.2	126.0–545.3	61.8–237.6	39.9–227.6	36.09	63	< 0.001	4.459	16, 24	GH & PH**
Mean	262.6	318.6	140.2	107.6				4.427	16, 14	GH & BH**
SD	66.8	138.6	50.2	44.8				3.537	9, 24	WH & PH**
N	16	9	24	14				3.622	9, 14	WH & BH**
fig:										
Range	42.9–239.0	62.6–410.0	5.2–139.2	0.6–121.5	35.46	63	< 0.001	4.597	16, 24	GH & PH**
Mean	170.1	174.4	57.5	44.4				4.178	16, 14	GH & BH**
SD	58.8	106.4	30.9	33.5				3.739	9, 24	WH & PH**
N	16	9	24	14				3.559	9, 14	WH & BH**
non-fig:										
Range	31.6–149.7	22.6–231.0	27.6–236.1	23.1–106.1	9.13	63	> 0.01	Not significant		
Mean	92.5	144.2	82.7	63.2						
SD	31.6	81.3	44.3	24						
N	16	9	24	14						
Animal:										
Range	0–80.0	0–46.2	4.2–71.2	13.2–160.0	12.29	63	< 0.01	2.066	16, 9	GH & WH*
Mean	42.7	18.7	36.8	63.5				2.324	9, 24	WH & PH*
SD	25.4	16.9	18.5	39.2				3.055	9, 14	WH & BH**
N	16	9	24	14				2.285	24, 14	PH & BH*
Total Food:										
Range	152.3–423.4	126.0–587.2	66.0–323.5	67.9–336.0	22.55	63	< 0.001	3.934	16, 24	GH & PH**
Mean	305.3	337.3	176.9	171				3.388	16, 14	GH & BH**
SD	84.7	147.3	61.6	76.3				2.809	9, 24	WH & PH**
N	16	9	24	14				2.614	9, 14	WH & BH**

Table 4. Diversity of food eaten by four hornbill species during the breeding season and their average breeding success (1982–1985). *Hs* = Shannon-Weiner index (calculated separately, see text).

	Fruit species		Animal species		Total food species		Average breeding
	No.	*Hs*	No.	*Hs*	No.	*Hs*	success
Great Hornbill	37	1.70	44	2.20	81	1.95	0.87
Wreathed Hornbill	30	1.56	20	1.50	50	1.53	0.78
Oriental Pied Hornbill	49	1.89	56	2.00	105	1.94	0.91
Brown Hornbill	41	1.90	41	1.08	82	1.50	0.89

Table 5. Degree of similarity (*C* value) of fruit and animal food consumed by four hornbill species at Khao Yai National Park during the breeding seasons of 1982–1985. * indicates the similarity of individual species between years. Figures in brackets indicate average *C* values for fruit and animal food. (See text for calculation.)

Type of food		Degree of similarity			
Fruit		GH	WH	PH	BH
	GH	0.68*	0.83	0.75	0.82
	WH		0.37*	0.69	0.84
	PH			0.44*	0.70
	BH				0.44*
Animal		GH	WH	PH	BH
	GH	0.49*			
	WH	0.68	0.13*		
	PH	0.74	0.63	0.51*	
	BH	0.66	0.73	0.75	0.66*
Total food		GH	WH	PH	BH
	GH	(0.59)	0.75	0.74	0.73
	WH		(0.25)	0.66	0.78
	PH			(0.48)	0.72
	BH				(0.55)

Table 6. Ranks of 12 important non-fig fruits consumed by all four hornbill species in Khao Yai National Park during the breeding seasons of 1982–1985. GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill, ND = no data.

Family	Species name	Energy (kcal) per 100g fruit net weight	Rank of fruit by hornbill species				Summed Rank	Fruit Rank
			GH	WH	PH	BH		
Annonaceae	*Polyalthia viridis*	90.97	2	2	2	2	8	1
Connaraceae	*Connarus* sp.	ND	20	11	16	5	52	10
Lauraceae	*Cinnamomum subavenium*	261.00	4	24	8	10	46	9
Meliaceae	*Amoora cucullata*	275.00	3	8	6	8	25	5
	Dysoxylum sp.	250.90	5	7	5	7	24	4
	Chisocheton macrophyllus	323.47	9	5	14	17	45	8
Moraceae	*Artocarpus lakoocha*	98.35	18	19	10	24	71	12
Myristicaceae	*Horsfieldia glabra*	57.60	7	4	3	4	18	3
	Knema laurina	66.92	10	16	12	14	52	10
Myrtaceae	*Syzygium cumini*	87.57	8	10	7	6	31	6
Oleaceae	*Strombosia* sp.	221.20	6	3	4	3	15	2
Palmae	*Livistona speciosa*	199.00	12	13	16	9	40	7

Table 7. Ranks of 17 identified animal foods consumed by four species of hornbills during the breeding seasons of 1982–1985 in Khao Yai National Park.

	Rank of animal food by hornbill species				Summed rank	Animal rank
	GH	WH	PH	BH		
INSECTS						
Locust	12	10	2	1	33	7
Beetle	11	1	5	11	28	6
Cricket	18	17	21	7	63	15
Wasp's nest	6	17	18	8	69	16
Caterpillar	3	15	5	9	30	8
Cicada	9	8	1	2	18	2
OTHER ARTHROPODS						
Centipede	4	2	7	3	16	1
Millipede	8	3	8	4	23	5
Crab	21	4	8	18	51	11
REPTILES						
Snake	4	17	17	22	60	14
Lizard	2	7	6	5	20	3
AVES						
Bird	16	8	23	24	71	17
Bird's chick	7	8	15	19	49	10
Bird's egg	1	10	4	6	21	4
MISCELLANEOUS						
Snail + shell	14	13	11	10	48	9
Earthworm	9	12	13	20	54	12
Rat	4	14	14	24	56	13

CONCLUSIONS

The nature of the fruit food eaten by these four hornbill species was grouped into fleshy pulp with fine seeds, split-husked when ripe, dry flesh with a single stone-seed and soft or juicy flesh with a single stone-seed.

The broods of the larger species consumed more fruit than those of the smaller species. But the four hornbill species did not consume animal food according to their sizes. The Brown Hornbill consumed the highest amount of animal food, whereas the Wreathed Hornbill consumed the least.

These four sympatric hornbill species consumed relatively similar foods, indicating that they were foraging from the same food sources. Both the male and female Great Hornbills and the male and helper Brown Hornbills showed very high similarities in the food items fed to their broods.

Food preference was influenced by abundance rather than nutritional value. Among the first 12 ranks of the non-fig fruits, *Polyalthia viridis* and *Strombosia* sp. were the most preferred fruit species. Among animal food, centipede and cicada were most preferred.

Hornbills are omnivorous, feeding on a great diversity of fruits and animals. The Great and Oriental Pied Hornbills consumed the greatest diversity of food, showing that they are generalists when compared with the Wreathed and Brown Hornbills.

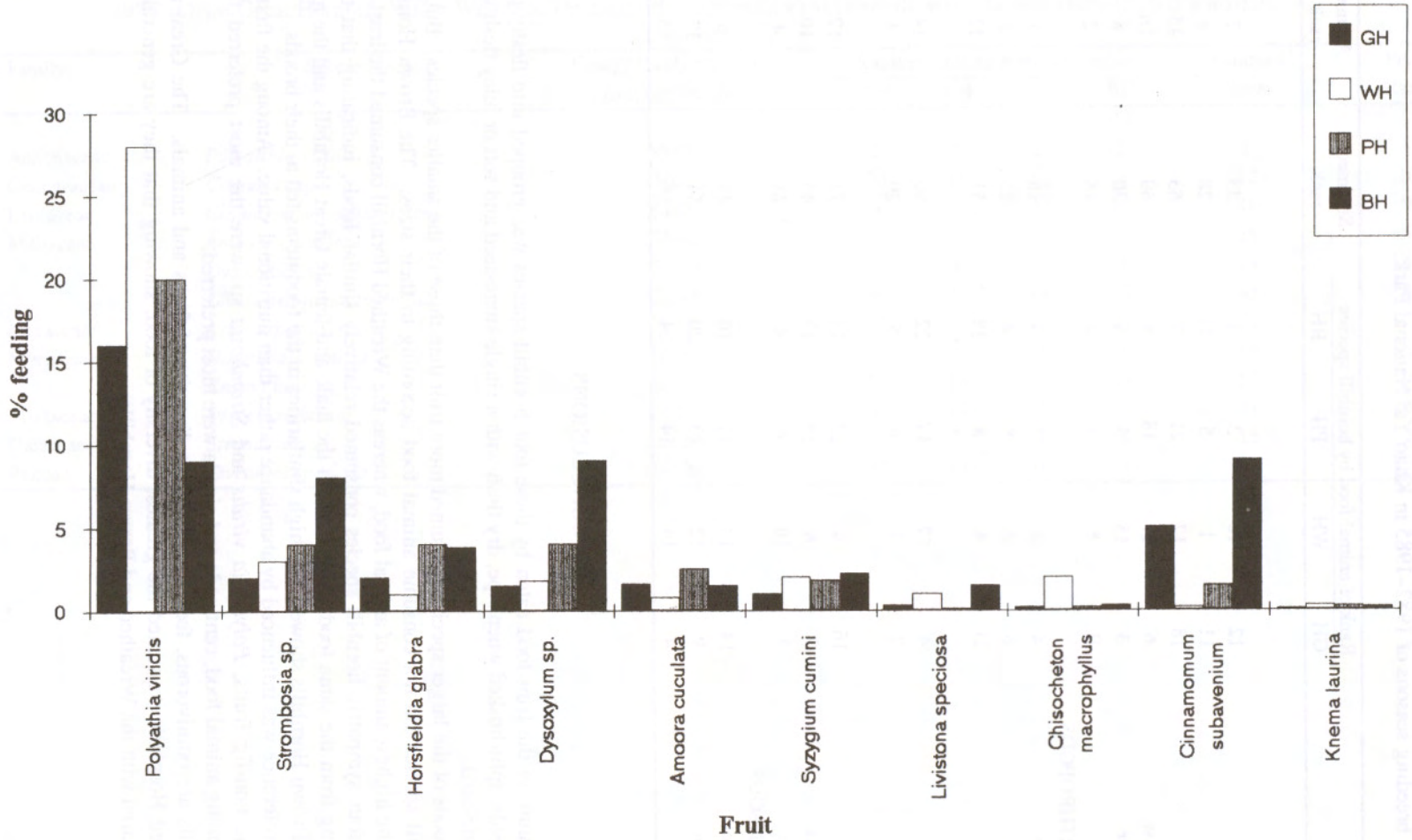

Figure 6. Percentage of various non-fig fruits consumed by four hornbill species at Khao Yai National Park during 1981-1985

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Appendix 1. List of the identified fruit eaten during the breeding season by the four hornbill species at Khao Yai National Park (1981–1985). GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill. FNS = Soft flesh with fine seeds, FS = Dry flesh with a stone-seed, SF = Split-husk with a stone seed, FJ = Fleshy and juicy. + = feeding observed.

Fruit species	Characteristics of fruit	Hornbill species observed feeding on fruit			
		GH	WH	PH	BH
MORACEAE					
Ficus drupacea	FN	+	+	+	+
F. aurantiasia	"	+	+	+	+
F. benjamin	"	+	+	+	+
F. altissima	"	+	+	+	+
Ficus spp.	"	+	+	+	+
URTICACEAE					
Artocarpus lakoocha	FJ		+	+	+
MYRISTICACEAE					
Horsfieldia glabra	SF	+	+	+	+
Knema laurina	"	+	+	+	+
MYRTACEAE					
Syzygium cumini	FJ	+	+	+	+
S. sp. (1)	"	+		+	+
S. sp. (2)	"	+	+	+	+
S. sp. (3)	"	+		+	+
S. sp. (4)	"	+	+	+	+
CONNARACEAE					
Connarus sp. (1)	SF		+	+	+
Connarus sp. (2)	"	+	+	+	+
PIPERACEAE					
Piper ribesoides	Unknown	+		+	+
PODOCARPACEAE					
Podocarpus polystachya	FJ				+
OLEACEAE					
Jasminum sp.	FS	+			+
SAPINDACEAE					
Lepisanthes rubiginosa	FJ	+		+	
SYMPLOCACEAE					
Symplocos laurina	FS	+		+	+
OLACACEAE					
Strombosia sp.	FS	+		+	+

Appen. 1 (cont'd)

ANNONACEAE					
Polyalthia viridis	SF	+	+	+	+
Uvaria pierrei	"		+	+	+
BURSERACEAE					
Canarium subulatum	FS	+	+	+	+
CUCURBITACEAE					
Trichosanthea tricuspidata				+	+
ELAEAGNACEAE					
Elaeagnus latifolia	FJ	+	+	+	+
ELAEOCARPACEAE					
Elaeocarpus grandiflorus	FS	+	+	+	+
Sloanea sigun	SF			+	
LAURACEAE					
Cinnamomum subavenium	FJ	+	+	+	+
Litsaea cubeba	FS	+	+	+	+
MELIACEAE					
Amoora cuculata	SF	+	+	+	+
Dysoxylum sp.	"	+	+	+	+
Chisocheton macrophyllus	"	+	+	+	+
Aglaia sp. (1)	"	+	+	+	+
Aglaia sp. (2)	"			+	+
Aglaia sp. (3)	"	+	+	+	+

Appendix 2. List of animals observed being eaten during the breeding season by the four hornbill species at Khao Yai National Park (1982–1985). GH = Great Hornbill, WH = Wreathed Hornbill, PH = Oriental Pied Hornbill, BH = Brown Hornbill.

Common name	Scientific name	Order or family	Hornbill species seen feeding on item
MAMMALS			
Insect-eating bat	Unidentified sp.	Chiroptera	BH, GH
Common Tree-shrew	*Tupaia glis*	Tupaiidae	GH
Rat	*Rattus* spp.	Muridae	GH, PH
Variable Squirrel	*Callosciurus finlaysoni*	Sciuridae	GH
Flying squirrel	Unidentified sp.	Sciuridae	GH
BIRDS			
Barbets	*Megalaima* spp.	Capitonidae	GH
Nightjars	*Caprimulgus* spp.	Caprimulgidae	GH
Greater Racket-tailed	*Dicrurus paradiseus*	Dicruridae	GH
Collared Scops-owl	*Otus lempiji*	Strigidae	GH
Eggs & chicks	Unidentified sp.	Pycnonotidae & Columbidae	GH, WH, PH, BH
REPTILES			
Blind snake	*Typhlops* spp.	Typhlopidae	GH, PH
Pit viper	Unidentified spp.	Viperidae	GH, BH
Green Pit Viper	*Trimeresurus steinegeri*	"	GH, BH
Lizard	*Acanthosaura* spp.	Agamidae	GH, WH, PH, BH
Flying lizard	*Draco maculatus*	"	GH, BH, PH
Common Hill Skink	*Sphenomorphus* spp.	Scincidae	GH, BH, PH
Common Flat-tailed Gecko	*Coscymbotus platyurus*	Gekkonidae	GH, PH
Gecko	*Cyrtodactylus* spp.	"	GH
MOLLUSCS			
Filopaludina snail	*Filopaludina* spp.	Viviparidae	PH
Land snail	*Cyclophorus* spp.	Cyclophoridae	GH, WH, PH, BH
Sea mussel shell	*Mytilus smaragdinus*	Mytilidae	PH
INSECTS			
Metallic wood borer	*Chrysochroa* spp.	Buprestidae	BH, PH
	Lepidiota stigma	Scarabacidae	BH, PH
	Onitis spp.	"	BH, PH
	Xylotrupes gidean	"	BH, PH
Scarab beetle	Unidentified sp.	"	GH
Round buffalo dung beetle	*Copris* spp. (1)	"	PH
Flat buffalo dung beetle	*Copris* spp. (2)	"	PH
Long-horned beetle	*Apriona* spp.	Cerambycidae	PH, BH
Stag beetle	Unidentified sp.	Lucanidae	GH, WH, PH, BH
Stag beetle	*Acaraius grandis*	Passalidae	GH, WH, PH, BH
	Mouhotia batesi	Carabidae	PH
Cetonid	Unidentified sp.	Cetonidae	GH, WH, PH, BH
Click beetle	" "	Elatiridae	GH, WH, PH, BH
Assassin bug	" "	Reduviidae	PH

Appendix. 2 (cont'd)

Green cicada	" "	Cicadidae	GH, WH, PH, BH
Brown cicada	" "	"	GH, WH, PH, BH
Ant	" "	Formicidae	PH
Digger wasp	" "	Scoliidae	GH
Wasp	*Vespa bicolor*	Vespidae	BH, PH
Wasp nest	" "	"	GH, BH, PH
Butterflies	Unidentified sp.	Lepidoptera	BH, PH
Moths	" "	"	BH, PH
Noctuid moth	" "	Noctuidae	BH
Psychid	" "	Psychidae	WH, BH
Stem borer	" "	Cossidae	BH, PH
Lacewing	" "	Neuroptera	PH
Grasshopper	" "	Orthoptera	GH, PH, BH
Leaf insect	" "	Lepidoptera	GH, WH, PH, BH
Leaf insect	*Pseudophilus tetans*	Tettigoniidae	WH, PH, BH
Long-horned grasshopper	*Holochlara* spp.	"	PH, BH
Mantid egg	Unidentified sp.	Orthoptera	PH
Walking stick	" "	Phasmatidae	GH, PH, BH
Tree-cricket	*Malasumma* spp.	Gryllidae	PH
Crickets	Unidentified sp.	"	GH, PH, BH
Dragonfly	" "	Odonata	PH
Wild cockroach	*Erguala capucina*	Blattidae	GH, WH, PH, BH
Cockroaches	Unidentified sp.	"	GH, WH, PH, BH
Caterpillar	" "	Lepidoptera	GH, WH, PH, BH
OTHER ARTHROPODS			
Crab	Unidentified sp.	Unidentified	GH, WH, PH, BH
Centipede	*Scolopendra* spp.	Scolopendridae	GH, WH, PH, BH
Elongate millipede	Unidentified sp.	Julidae	GH, WH, PH, BH
Broad-rounded millipede	" "	Sphaerotheridae	GH, WH, PH, BH
Flat Millipede	" "	Poloydesmidae	GH, WH, PH, BH
Common scorpion	" "	Scorpionidae	PH
Giant scorpion	*Heterometrus* sp.	"	GH, PH
Spider	Unidentified sp.	Araneida	PH
MISCELLANEOUS			
Earthworm	*Pheretima* spp.		GH, PH, BH
Small green frog	Unidentified sp.	Ranidae	GH, PH
Frogs	" "	"	GH, PH
Fish	" "	Pisces	PH